CHAPTER 5

TEMPORAL VARIATION IN THE BENTHIC COMMUNITIES OF INTERMITTENTLY CLOSED AND PERMANENTLY OPEN ESTUARIES

5.1 Introduction

Estuaries are non-equilibrium environments that regularly experience change on a number of temporal scales, from those due to daily tidal patterns to larger-scale, monthly, seasonal and annual changes. For example, salinity is one of the most important physico-chemical variables in estuaries and can fluctuate daily with the tides, as well as at larger scales with seasonal changes in climatic variables, including rainfall and temperature. Similarly, seasonal variation in benthic communities can be brought about changes in other factors such as freshwater inflow (Jones 1987; Stephens & Imberger 1996; Teske & Wooldridge 2001). Benthic communities are accustomed to this natural temporal variation and some authors have even suggested that small-scale changes in factors such as freshwater inflow and salinity are necessary for maintaining the integrity of estuarine habitats (Schlacher & Wooldridge 1996a). Estuaries, therefore, tend to be more sensitive to rare, large-scale or high-intensity events (Harris 2005). These less frequent, but generally more stressful, disturbances may include changes such as long-term alteration of benthic habitat and episodic events such as floods and drought-induced hypersaline periods (Owen & Forbes 1997). Consequently, it is usually the frequency or extent of such events that is important in structuring estuarine benthic communities.

In southeast Australian permanently open estuaries, estuarine benthic communities have similarly been shown to fluctuate on a periodic, irregular or unpredictable basis, especially in response to non-seasonal climatic events such as droughts and floods (Poore & Rainer 1979;

Rainer 1981; Jones 1987). In addition, regular temporal variation in benthic communities is also of significant importance in many Australian estuaries, with this variation being present at scales from days to years (Rainer 1981; Moverley et al. 1986; Jones 1987; Morrisey et al. 1992b; Moverley & Hirst 1999; Edgar & Barrett 2002). Such variation is usually due to changes in sediments, migration, recruitment, or to a range of disturbances (Morrisey et al. 1992b).

Likewise, the ecological patterns of temporal variation in intermittently closed estuaries can be due to both seasonal influences and irregular climatic events (Owen & Forbes 1997; Cowley & Whitfield 2001; Mackay & Cyrus 2001; Teske & Wooldridge 2001; Malcolm et al. 2004). However, in comparison to permanently open estuaries, both seasonal and irregular changes are more likely to be related to changes in freshwater inflow (Teske & Wooldridge 2001). This is because the amount of freshwater inflow directly affects the status of an estuary's entrance, which has flow-on effects to many other biotic and abiotic factors. For example, flooding and extreme storm events in intermittently closed estuaries can cause the abundances of benthic populations to plummet (Nordby & Zedler 1991), especially in channel areas that experience massive losses of benthic habitat. Reductions in the diversity of fish communities have also been observed following opening events as, presumably, the fauna use such opportunities to migrate to oceanic waters (Malcolm et al. 2004). Further, for most intermittently closed estuaries it is likely that temporal changes in benthic communities may be more pronounced than in permanently open estuaries. For example, intermittent estuaries are generally smaller than permanently open estuaries (Mondon et al. 2003; Hastie & Smith 2006). Therefore, it would be expected that the effects of anthropogenic disturbances such as pollution would be magnified in these estuaries, particularly if the disturbance occurs at times when they have been closed for an extended period.

Although intermittently closed estuaries are, therefore, likely to exhibit greater temporal fluctuations, such changes have only just begun to be assessed, particularly in Australia. Without a thorough understanding of the natural patterns of temporal variation in intermittent estuaries we cannot begin to assess the effects of anthropogenic disturbances on these systems. The environmental impacts of artificial opening and the ongoing development of areas adjacent to these estuaries are increasingly raising concern for this vulnerable estuary type. Such issues should be a priority in estuarine management as intermittently closed estuaries are the most abundant estuary type in NSW. In addition, according to Turner et al. (2004), less than 12 % of the estuaries in NSW have avoided degradation and remain in a near-pristine condition. The increasing awareness of potential anthropogenic effects on these systems is a topical issue, not only in the Solitary Islands Marine Park and the Coffs Harbour City Council area, but throughout coastal NSW.

The work presented here to examine the temporal variation in estuaries is divided into two main components. Firstly, distinct differences between the benthic communities of intermittently closed and permanently open estuary types following the extreme conditions of extended entrance closure have previously been described in the spatial component of this thesis (Chapter 4). This temporal study aimed to investigate how this relationship between estuary types changed over a two-year period, with sampling conducted on a seasonal basis, as well as following major climatic events that changed the entrance status of most of the intermittent estuaries. It was predicted that, as more of the intermittently closing estuaries opened, the differences between the two estuary types would become less distinct due to both the opportunities for recruitment from outside the estuary and changes in water quality to conditions that favour a wider variety of fauna.

Secondly, because Chapter 4 revealed discrete communities among the estuaries nested within each estuary type, additional temporal analyses also focused on the annual and seasonal variation within each individual estuary.

5.2 Methods

5.2.1 Study Location and Design

Within the Solitary Islands Marine Park each of the nine estuaries (six intermittent and three permanently open) that had previously been examined from a spatial variation perspective (Chapter 4) were again investigated here in terms of temporal variation. As a quick reference, their entrance type and catchment size are summarised below (Table 5.2.1). Following the design established for the previous spatial study conducted in January 2003, this study continued to use the same three sites along the length of each estuary, one in each of the lower, middle and upper reaches. Sites measured 10 x 10 m and were situated in the middle of the main estuary channel. Surrounding landmarks and GPS coordinates were used to relocate these sites throughout the study.

Table 5.2.1 Summary of the entrance type and catchment size of each estuary surveyed during the study. Data on catchment size courtesy of Coffs Harbour City Council.

Estuary	Entrance type	Catchment size (km^2)
Station Creek	Intermittently closed	24.0
Corindi River	Permanently open	148.0
Arrawarra Creek	Intermittently closed	20.0
Darkum Creek	Intermittently closed	7.0
Woolgoolga Lake	Intermittently closed	25.0
Willis Creek	Intermittently closed	3.3
Hearns Lake	Intermittently closed	9.0
Moonee Creek	Permanently open	39.5
Coffs Creek	Permanently open	25.0

For all estuaries, each site was sampled towards the latter half of each season, specifically the last week of the second month over the two-year period from January 2003 (Summer) to October 2004 (Spring). The nature of the intermittently closed estuaries means that significant temporal changes may be irregular and unpredictable. Therefore, it was also necessary to incorporate opportunistic, event-based sampling into the study design. As such, in addition to the regular seasonal program, sampling also occurred following any major floods that lead to breakout events across all closed estuaries. To aid this, regular observations were made of the entrance status of all intermittently closed estuaries, particularly during times of high rainfall, when closed estuaries were likely to open.

Throughout the study there were two such breakout events. The first occurred in late February 2003 and sampling took place two weeks later in March, giving time for flood waters to recede and settle. The second major flood event coincided with the October 2004 seasonal sampling, which was consequently postponed until all estuaries were safe and accessible one week later.

5.2.2 Sampling Procedure

Nine sets of samples were taken throughout the two-year period. On each occasion five macrofaunal samples were collected from each site in each estuary. The positions of the samples within each site were haphazard rather than random due to the restrictions imposed by using a remote sampling device and manoeuvring a vessel in a relatively small area. Samples were collected, from non-vegetated substrates, using a 0.068 m^2 van Veen grab and immediately sieved through a 1 mm mesh. Fauna retained were washed into a mesh bag (approx. 0.4 mm mesh size) and relaxed in a magnesium chloride solution. In the laboratory the samples were preserved in 10 % formalin before identification and enumeration.

Water column salinity, dissolved oxygen, temperature and pH were measured each time a fauna sample was collected using a TPS 90-FLT multi-probe. Three replicate 50 ml sediment samples were also collected at each site on each sampling occasion, except for January 2003 when only one sediment sample was collected at each site. Sediment samples were oven-dried at 100 ^{o}C for 24 hr and weighed prior to combustion at 550 ^{o}C for 6 hr to calculate organic content (percentage difference after combustion). To measure grain size, samples were initially wet-sieved through a 63 μm mesh to extract the mud fraction, which was dried and weighed. The remaining sand fraction (> 63 μm) was sieved through a stack of nested sieves to enable calculations of grain size and sediment homogeneity. For all samples collected from March 2003 onwards, sediment calculations were done using the SoilVision software (SoilVision Systems Ltd., 2004).

5.2.3 Statistical Methods

5.2.3.1 Temporal variation in the relationship between the communities of the intermittently closed and permanently open estuary types

For the multivariate analyses of community structure to examine the relationship between the benthic assemblages of the intermittently closed and permanently open estuaries, data were separated for each of the upper, middle and lower sites and presented for each sampling occasion in 2003 and 2004. Data for each site, and with all sites pooled, were analysed to test the hypothesis that there was no difference in community structure between the intermittent and permanently open estuary types for each sampling occasion. In doing so, the temporal consistency of the spatial differences between the estuaries nested within each type were also tested. Using PRIMER (Clarke & Gorley 2001) data were square-root transformed prior to construction of a Bray-Curtis similarity matrix and, for comparisons between estuary types only, two-dimensional ordinations of assemblages were created using non-metric multidimensional scaling (nMDS). Where nMDS ordinations collapsed due to the presence of an outlying sample with zero counts, the offending sample was excluded from the plot (Clarke et al. 2006). The significance of differences in community structure was assessed using a series of one-way analyses of similarity (ANOSIM) following the statistical procedure established previously in Chapter 4. The contribution of individual species to the differences observed was calculated using the similarity percentages (SIMPER) routine.

To more closely examine how the similarity of estuary types changed over time, the *R*-values generated by ANOSIM for each site, as well as those for all sites pooled, were plotted chronologically. Each of these similarity datasets was also correlated with the number of estuaries that were closed at the entrance for each sampling time using a simple linear regression. Similarly, the abundances of the species consistently contributing the most to the differences between estuary types were plotted chronologically for each estuary type using average abundance data extracted directly from the SIMPER results. Two-way nested analysis-of-variance (ANOVA) was used to evaluate differences in the abundances of these species between estuary types and between the estuaries nested within each type.

5.2.3.2 Temporal consistency of spatial variation of environmental variables between and within the intermittently closed and permanently open estuary types

Two-way nested analysis-of-variance (ANOVA) was used to evaluate differences in physico-chemical variables between estuary types and between the estuaries nested within each type. Analyses were conducted separately for each of the upper, middle and lower sites. Where necessary data were transformed prior to analysis to improve homoscedasticity. The BIOENV function was also used to explore correlations between the macrofaunal data from each sampling occasion and environmental variables, including all physico-chemical parameters and catchment size.

5.2.3.3 Temporal variation within individual estuaries

Variation at the seasonal and annual scale was investigated for each estuary. Hence, only the regular seasonal samples, not the March 2003 event-based sample, were included in these analyses. Using PRIMER (Clarke & Gorley 2001), community data were analysed separately for each of the upper, middle and lower sites and square-root transformed prior to construction of a Bray-Curtis similarity matrix. For each year, two-dimensional ordinations of assemblages were created using non-metric multidimensional scaling (nMDS). Additional ordinations combining the two years are also given, with data presented as averages for each sampling time (n = 5). As this was a balanced design, it was possible to use the powerful PERMANOVA procedure for significance testing of community variation between years and between seasons for each estuary (Anderson 2005). Data used in this procedure were also square-root transformed and analyses were based on Bray-Curtis similarities. The contribution of individual species to the differences observed was calculated using the similarity percentages (SIMPER) routine. As a qualitative comparison between the upper, middle and lower sites and how their relationship changed over time, a summary nMDS was produced for each estuary, including all sampling times for all sites.

A two-way orthogonal analysis-of-variance (ANOVA) was used to evaluate differences between both years and seasons for each of the water column and sediment variables, as well as for the univariate community variables, species richness and the total number of individuals. Correlations between the full, temporal set of community data and environmental variables for each estuary were examined using BIOENV. For these correlations, the environmental variables included each of the water column and sediment parameters and, for the intermittently closed estuaries, the estuary entrance status (i.e. open or closed) at the time of sampling.

5.3 Results

5.3.1 Frequency and duration of entrance openings and closures in the intermittently closed estuaries of the Solitary Islands Marine Park throughout 2003 and 2004

Over time, many of the changes in environmental influences, such as the input of marine waters, and particularly the changes to, or loss of, habitat via sediment scouring in the intermittently closed estuaries were clearly noticeable by visual observation. This is especially true for entrance openings as, in comparison to entrance closures, which are relatively gradual, opening events were usually quite dramatic with the rate of water drainage escalating rapidly. This corresponded with an equally rapid reduction in water levels and exposure of benthic areas (Figs. 5.3.1.1). The sediment scouring in many of the larger entrance opening events resulted in 1 – 2 m depths of sediment being washed away from the entrance and lower reaches of some estuaries. Other examples of obvious changes in these estuarine systems included the occurrence of a large algal bloom in Willis Creek (Fig. 5.3.1.2), which persisted for three months from January 2004, and the accumulation of decaying kelp in Arrawarra Creek during February 2004 (Fig. 5.3.1.3).

Over the 24 months that the six intermittent estuaries were observed, Station Creek closed the smallest proportion of time (7.5 %) and the next estuary to be closed least often was Arrawarra Creek (21.7 %) (Fig. 5.3.1.4, Table 5.3.1). In contrast, Darkum Creek closed for the greatest proportion of time (76.3 %), closely followed by Hearns Lake (71.3 %). Both Woolgoolga Lake and Willis Creek displayed intermediate periods of closure, remaining closed for 51.7 % and 39.6 % of the time, respectively. The longest entrance closures were observed at Darkum Creek and Hearns Lake, which closed for 260 and 217 days, respectively. In the case of Darkum Creek, this equates to over eight and a half months, from July 2003 to March 2004, that this estuary was without any marine input. Across the six intermittently closed estuaries, the number of closures during the two-year period ranged from one at Station Creek to eight at Willis Creek. All other intermittent estuaries had either four or five closures. The erratic nature of Willis Creek was further reflected by it having the shortest opening of any of the estuaries, four days before closing again, as well as the second shortest closure (eight days).

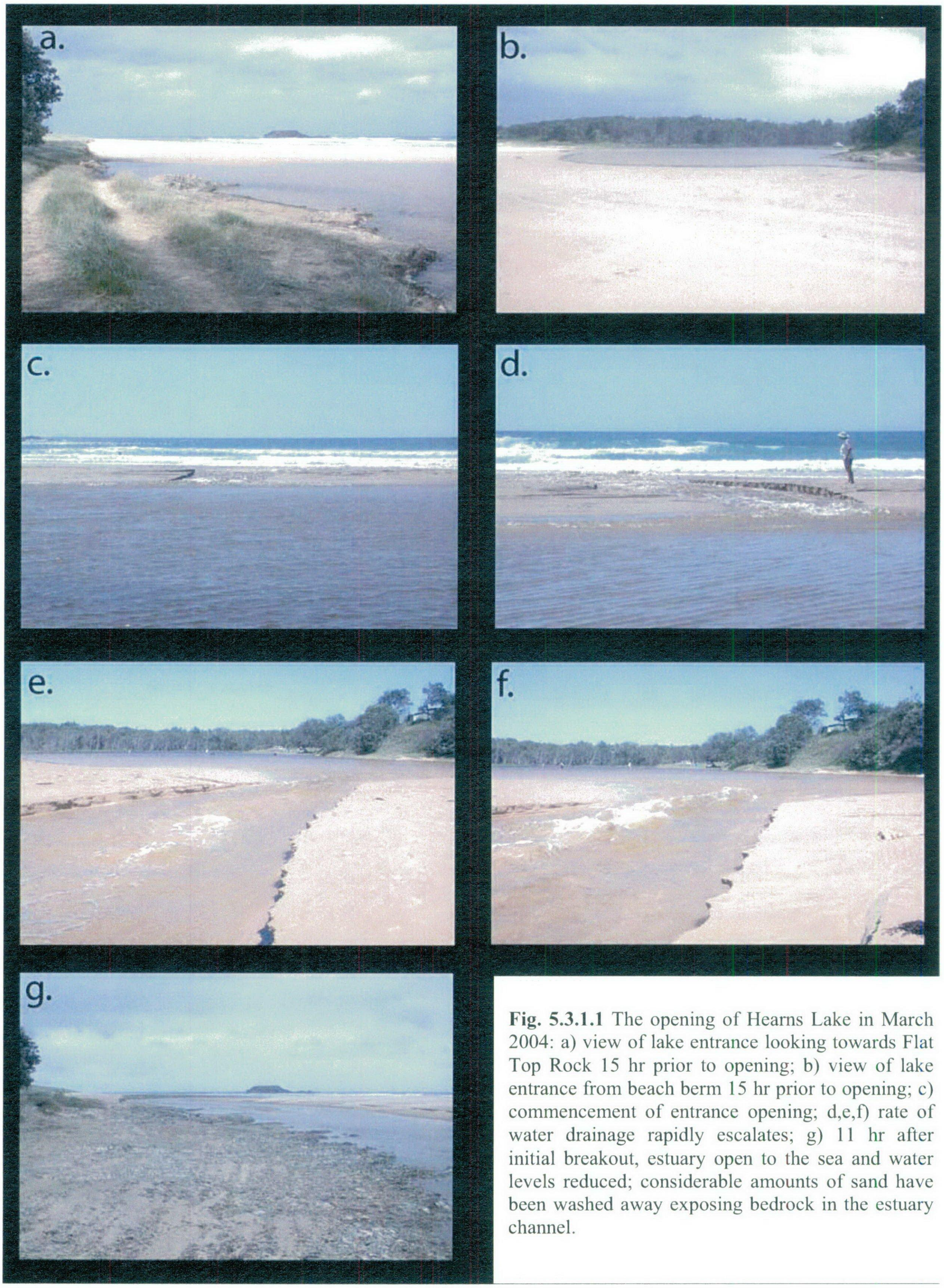

Fig. 5.3.1.1 The opening of Hearns Lake in March 2004: a) view of lake entrance looking towards Flat Top Rock 15 hr prior to opening; b) view of lake entrance from beach berm 15 hr prior to opening; c) commencement of entrance opening; d,e,f) rate of water drainage rapidly escalates; g) 11 hr after initial breakout, estuary open to the sea and water levels reduced; considerable amounts of sand have been washed away exposing bedrock in the estuary channel.

Fig. 5.3.1.2 Algal bloom throughout entire upper reaches of Willis Creek, January 2004.

Fig. 5.3.1.3 Stranded kelp decaying along the shoreline of Arrawarra Creek, February 2004.

Fig. 5.3.1.4 Graphical representation of the status of all estuary entrances throughout the duration of the temporal study. Closed entrances had no connection with the ocean at any time during the tidal cycle.

Table 5.3.1 Summary of frequency and duration of the openings and closures of the six intermittently closed estuaries over the two-year period from January 2003 to December 2004.

	Station	Arrawarra	Darkum	Woolgoolga	Willis	Hearns
Total number of openings	1	4	4	4	7	4
Total number of closures	1	4	5	5	8	5
Total time open	92.5 %	78.3 %	23.7 %	48.3 %	60.4 %	28.7 %
Total time closed	7.5 %	21.7 %	76.3 %	51.7 %	39.6 %	71.3 %
Shortest opening (days)	n/a	36	27	14	4	33
Longest opening (days)	675	420	42	185	156	84
Shortest closure (days)	n/a	7	21	10	8	20
Longest closure (days)	55*	55*	260	154	84	217

* Observations of these particular closures at the beginning of 2003 commenced after these estuaries had already been closed for a number of months, therefore closure periods have realistically been longer than those indicated.

During the January 2004 another three estuaries were also closed but opened earlier than Darkum Creek. However, of the estuaries opening in the first few months in 2004, one was opened artificially. Woolgoolga Lake was opened by Coffs Harbour City Council on the 30th January 2004 (Fig. 5.3.1.5) in accordance with their management plan for the estuary, which states that, to protect council infrastructure, it should be opened if water levels reach 1.8 m above height datum (Coffs Harbour City Council 1992).

5.3.2 Temporal variation in the relationship between the benthic communities of the intermittently closed and permanently open estuary types

Upper Sites

Two-dimensional nMDS plots of samples from the upper estuarine sites in 2003 revealed a high degree of variation between the benthic communities of the intermittently closed and permanently open estuaries, with all but one occasion (April) showing complete separation between the communities of these two estuary types (Fig. 5.3.2.1). Even when some overlap between the communities did occur in April 2003, it remained minimal, involving only two data

Fig. 5.3.1.5 Entrance of Woolgoolga Lake: a) two days before; and b) one day after artificial opening, which occurred on 30th January 2004. The drop in water level and exposure of sand flats is also shown by comparing views of one of the more predominant parts of the estuary taken before (c) and after (d) artificial opening.

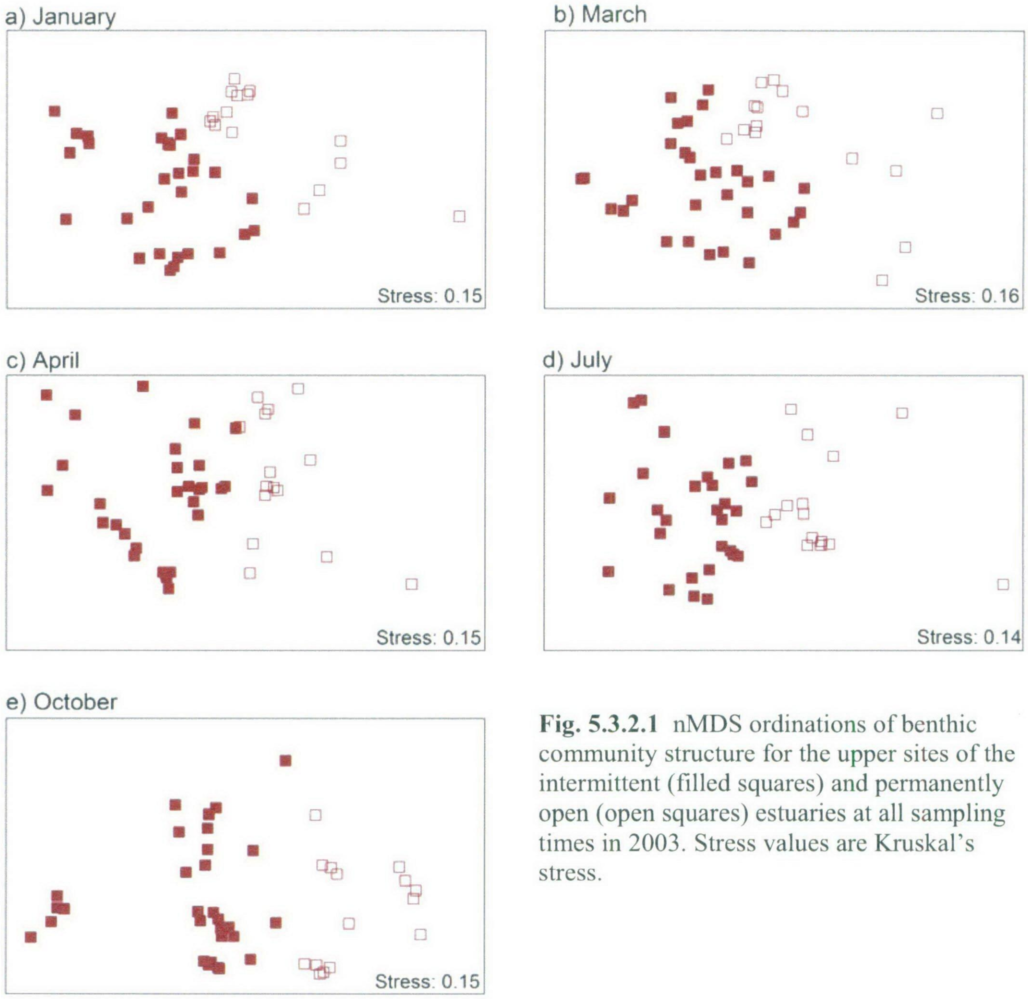

Fig. 5.3.2.1 nMDS ordinations of benthic community structure for the upper sites of the intermittent (filled squares) and permanently open (open squares) estuaries at all sampling times in 2003. Stress values are Kruskal's stress.

points. Analyses-of-similarity for these upper sites indicated that the differences between the permanently open and intermittent estuary types in 2003 were highly significant (Global R = 0.444, 0.335, 0.388, 0.419 and 0.492 for the consecutive sampling times from January to October; p = 0.001 for all tests) (Table 5.3.2.1). SIMPER analyses revealed that the species primarily responsible for these differences were *Mysella vitrea* and *Victoriopisa australiensis,* which had greater average abundances in the permanently open estuaries for all sampling times, and *Notomastus estuarius*, which had greater abundances within the intermittent estuary type (Table 5.3.2.2). The higher average abundances of *Orthoprionospio cirriformia* and *Simplisetia aequisetis* in the intermittent estuaries on a few occasions were also prominent in the SIMPER analyses between estuary types; however, their contributions to the overall dissimilarity were irregular throughout 2003. *Scoloplos normalis* and *Arthitica helmsi* were also always important in differentiating between the benthic communities of the two estuary types but the type that contained the greater abundances of these species varied across sampling times.

In 2004, the upper sites of the two estuary types separated well in the nMDS ordinations for January, April and July (Fig. 5.3.2.2). However, differences were not as distinct in October, with considerable overlap in the nMDS ordination. Despite this, ANOSIM results for the upper sites confirmed highly significant differences between the estuary types for all 2004 samples (Global R = 0.370, 0.358, 0.684, 0.357 for January, April, July and October, respectively; p = 0.001 for all tests) (Table 5.3.2.1).

Dissimilarity between estuary types for the upper sites in this year were partially due to *N. estuarius*, which consistently had greater average abundances in the intermittent estuary type (Table 5.3.2.2). Higher abundances of *O. cirriformia* in the intermittent estuaries also contributed a large proportion to the difference between estuary types on all but one occasion (January) in 2004. *A. helmsi* and *Armandia intermedia* always featured strongly in the SIMPER analyses between estuary types in these upper sites, however, the estuary type in which they dominated was inconsistent during this year.

Table 5.3.2.1 Summary of one-way ANOSIM results testing for differences between the intermittently closed and permanently open estuary types at each of the upper, middle and lower sites, as well as for all sites combined, between January 2003 and October 2004. Bold font indicates a significant test ($p < 0.05$).

	Upper		Middle		Lower		All Sites	
	R	*p*	*R*	*p*	*R*	*p*	*R*	*p*
2003								
January	**0.444**	0.001	**0.595**	0.001	**0.509**	0.001	**0.403**	0.001
March	**0.335**	0.001	**0.534**	0.001	**0.240**	0.004	**0.268**	0.001
April	**0.388**	0.001	**0.378**	0.001	**0.192**	0.001	**0.175**	0.001
July	**0.419**	0.001	**0.527**	0.001	**0.401**	0.001	**0.348**	0.001
October	**0.492**	0.001	**0.525**	0.001	**0.758**	0.001	**0.408**	0.001
2004								
January	**0.370**	0.001	**0.347**	0.001	**0.362**	0.001	**0.292**	0.001
April	**0.358**	0.001	**0.604**	0.001	**0.447**	0.001	**0.382**	0.001
July	**0.684**	0.001	**0.636**	0.001	**0.621**	0.001	**0.571**	0.001
October	**0.357**	0.001	**0.291**	0.001	**0.340**	0.001	**0.282**	0.001

Table 5.3.2.2 SIMPER results for analyses between estuary types at their upper sites in 2003 and 2004. The average dissimilarity between estuary types is given for each sampling time. Information about the species contributing more than 5 % of the average dissimilarity between estuary types is also given, including their percentage contribution and average abundance per sample in the estuary type (**I** = intermittently closed; **P** = permanently open) where they were most abundant. '-' indicates species did not contribute more than 5 % of the average dissimilarity between estuary types at that particular sampling time.

	2003					2004			
	Jan	Mar	Apr	Jul	Oct	Jan	Apr	Jul	Oct
Ave. dissim.	88.0	87.5	88.0	90.2	87.1	88.3	93.4	90.3	83.6
M. vitrea	9.9 % **P**: 53.6	9.6 % **P**: 29.7	7.7 % **P**: 17.3	11.1 % **P**: 50.8	9.2 % **P**: 27.1	11.4 % **P**: 26.0	6.9 % **P**: 8.7	-	-
S. normalis	7.1 % **P**: 8.8	8.4 % **I**: 5.3	11.2 % **P**: 5.1	6.0 % **I**: 4.0	8.4 % **I**: 11.9	9.4% **I**: 4.8	6.5 % **P**: 1.4	-	6.8 % **I**: 5.9
N. estuarius	5.3 % **I**: 6.2	8.7 % **I**: 5.4	10.9 % **I**: 6.2	6.0 % **I**: 3.4	-	5.7 % **I**: 2.4	10.1 % **I**: 6.0	6.9 % **I**: 6.4	6.5 % **I**: 3.5
A. intermedia	5.7 % **I**: 5.1	-	-	8.9 % **I**: 30.9	7.9 % **I**: 10.7	8.5 % **I**: 5.9	5.2 % **I**: 14.0	9.4 % **I**: 27.2	7.6 % **P**: 9.1
A. helmsi	13.0 % **P**: 50.7	12.5 % **P**: 32.8	12.3 % **P**: 34.5	11.1 % **P**: 21.6	11.0 % **I**: 32.1	13.8 % **P**: 22.0	12.9 % **P**: 19.0	9.6 % **I**: 19.8	16.2 % **I**: 43.0
S. towraensis	-	6.0 % **I**: 6.2	7.1 % **I**: 5.7	-	-	7.3 % **I**: 4.5	-	-	-
T. imbellis	-	-	-	-	5.1 % **P**: 2.4	7.3 % **P**: 2.1	-	-	5.7 % **P**: 3.7
O. cirriformia	5.7 % **I**: 7.5	-	-	6.6 % **I**: 5.4	8.3 % **I**: 14.7	-	7.2 % **I**: 7.8	14.5 % **I**: 25.4	6.8 % **I**: 5.9
L. triangularis	-	-	5.4 % **P**: 2.1	-	-	-	5.9 % **P**: 1.2	-	-
N. gravieri	-	-	5.9 % **P**: 1.1	-	-	-	5.7 % **P**: 0.87	-	-
V. australiensis	6.1 % **P**: 6.9	8.7 % **P**: 7.5	9.7 % **P**: 6.3	8.4 % **P**: 8.1	-	-	-	-	7.2 % **P**: 4.9
S. aequisetis	-	6.5 % **I**: 10.9	-	5.7 % **I**: 11.2	7.1 % **I**: 18.1	-	-	-	5.8 % **I**: 10.3
F. subtortus	-	-	-	-	5.9 % **I**: 11.3	-	-	-	6.5 % **I**: 3.8
C. coralium	-	5.6 % **I**: 4.7	-	-	-	-	-	-	-

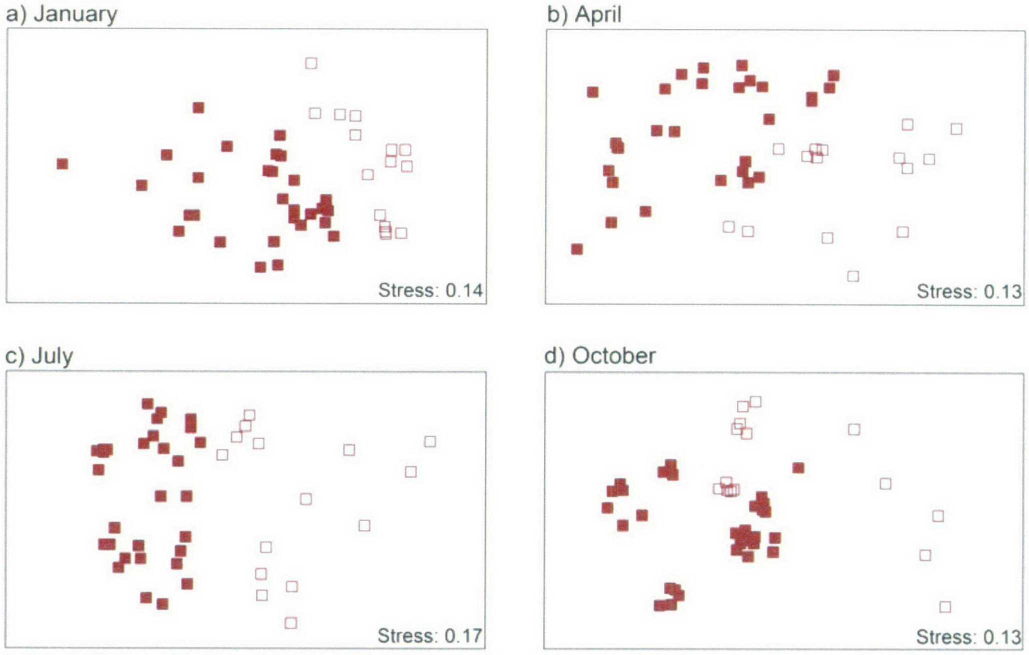

Fig. 5.3.2.2 nMDS ordinations of benthic community structure for the upper sites of the intermittent (filled squares) and permanently open (open squares) estuaries at all sampling times in 2004. Stress values are Kruskal's stress.

Middle Sites

The middle sites showed a clear demarcation between estuary types in the nMDS ordinations for the 2003 samples (Fig. 5.3.2.3). While this trend generally continued into 2004, it was not quite as clear for the January and October 2004, with these two times displaying some overlap (Fig. 5.3.2.4), particularly during October when samples from Station Creek grouped closely with those from the permanently open estuary type in the lower right-hand corner of the plot (Fig. 5.3.2.4 d). Nonetheless, highly significant differences (p = 0.001) resulted for the analyses between estuary types for all 2003 and 2004 sample times (Global R = 0.595, 0.534, 0.378, 0.527, 0.525, 0.347, 0.604, 0.636, 0.291 for consecutive samples from January 2003 to October 2004) (Table 5.3.2.1). The higher average abundances of some species, namely *S. normalis, N. estuarius* and *A. intermedia*, on most occasions in the intermittent estuaries, were largely responsible for the differences between the estuary types (Table 5.3.2.3). *M. vitrea* also consistently contributed to the dissimilarity between types at these sites with greater average abundances in the permanently open estuaries for all samples throughout 2003 and 2004, except for April 2003 when it had a higher abundance in the intermittently closed estuary type.

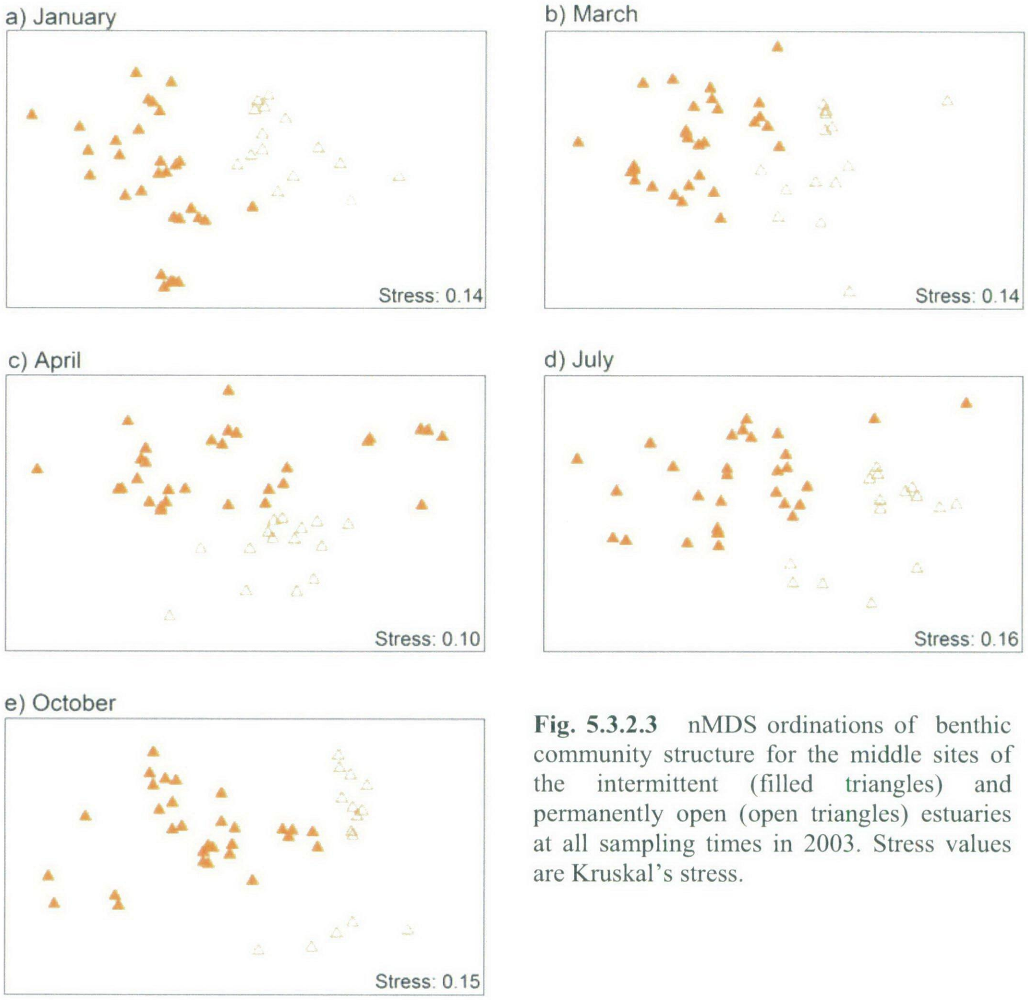

Fig. 5.3.2.3 nMDS ordinations of benthic community structure for the middle sites of the intermittent (filled triangles) and permanently open (open triangles) estuaries at all sampling times in 2003. Stress values are Kruskal's stress.

Table 5.2.3.3 SIMPER results for analyses between estuary types at their middle sites in 2003 and 2004. The average dissimilarity between estuary types is given for each sampling time. Information about the species contributing more than 5 % of the average dissimilarity between estuary types is also given, including their percentage contribution and average abundance per sample in the estuary type (**I** = intermittently closed; **P** = permanently open) where they were most abundant. '-' indicates species did not contribute more than 5 % of the average dissimilarity between estuary types at that particular sampling time.

	2003					2004			
	Jan	Mar	Apr	Jul	Oct	Jan	Apr	Jul	Oct
Ave. dissim.	94.3	93.8	94.3	91.2	89.1	88.6	96.4	90.2	83.8
M. vitrea	5.1 % **P**: 5.2	10.8 % **P**: 8.5	16.4 % **I**: 9.6	12.1 % **P**: 16.2	9.8 % **P**: 16.6	7.4% **P**: 7.4	6.7 % **P**: 3.5	5.4 % **P**: 4.2	7.4 % **P**: 10.4
S. normalis	6.5 % **I**: 12.1	6.6 % **I**: 5.7	6.3 % **I**: 2.6	5.85 % **I**: 4.9	9.6 % **I**: 20.5	7.8 % **I**: 12.2	-	5.6 % **I**: 4.3	6.9 % **I**: 7.6
N. estuarius	5.0 % **I**: 4.9	9.0 % **I**: 6.0	9.2 % **I**: 3.1	6.8 % **I**: 4.2	-	5.1% **I**: 3.3	6.0 % **I**: 3.5	-	-

Table 5.2.3.3 cont.

	Jan	Mar	Apr	Jul	Oct	Jan	Apr	Jul	Oct
A. intermedia	7.1 % **I**: 7.8	5.8 % **I**: 5.1	-	10.3 % **I**: 28.7	6.8 % **I**: 11.6	5.3 % **I**: 9.7	8.7 % **I**: 14.8	8.0 % **I**: 18.8	-
A. helmsi	-	-	-	-	9.3 % **I**: 13.7	7.9 % **I**: 8.7	6.1 % **I**: 3.9	-	7.9 % **I**: 13.9
S.aequisetis	-	-	-	-	-	5.2 % **I**: 6.8	-	-	5.8 % **P**: 10.0
T. australiensis	-	-	5.1 % **P**: 0.8	11.9 % **P**: 12.2	-	-	-	6.1 % **P**: 3.7	-
S. alba	-	-	-	-	5.6 % **P**: 8.9	11.2 % **P**: 12.3	-	-	-
N. jonasii	6.9 % **P**: 5.9	-	-	-	-	6.8 % **P**: 4.7	-	-	-
O. cirriformia	5.0 % **I**: 4.8	-	-	-	-	-	-	11.7 % **I**: 13.8	-
S. towraiensis	-	-	7.7 % **I**: 6.2	-	-	-	-	-	-
N. gravieri	-	-	-	5.8 % **P**: 2.4	-	-	-	-	-
U. metungi	-	8.3 % **P**: 6.7	-	-	-	-	-	-	-

Fig. 5.3.2.4 nMDS ordinations of benthic community structure for the middle sites of the intermittent (filled triangles) and permanently open (open triangles) estuaries at all sampling times in 2004.

Lower Sites

A high degree of overlap between the communities of the two estuary types was evident in the ordinations of the lower sites during March and April of 2003 (Fig. 5.3.2.5 b, c). For all other sample times, however, this was not the case and the communities of each estuary type were clearly distinguishable (Figs. 5.3.2.5, 5.3.2.6). Analysis-of-similarity determined that the communities differed significantly between estuary types on all sampling occasions in 2003 and 2004, including March and April of 2003 (Global R = 0.509, 0.240, 0.192, 0.401, 0.758, 0.362, 0.447, 0.621, 0.340 respectively for consecutive sampling times between January 2003 and October 2004, inclusive; p = 0.004 for March 2003, p = 0.001 for all other tests) (Table 5.3.2.1).

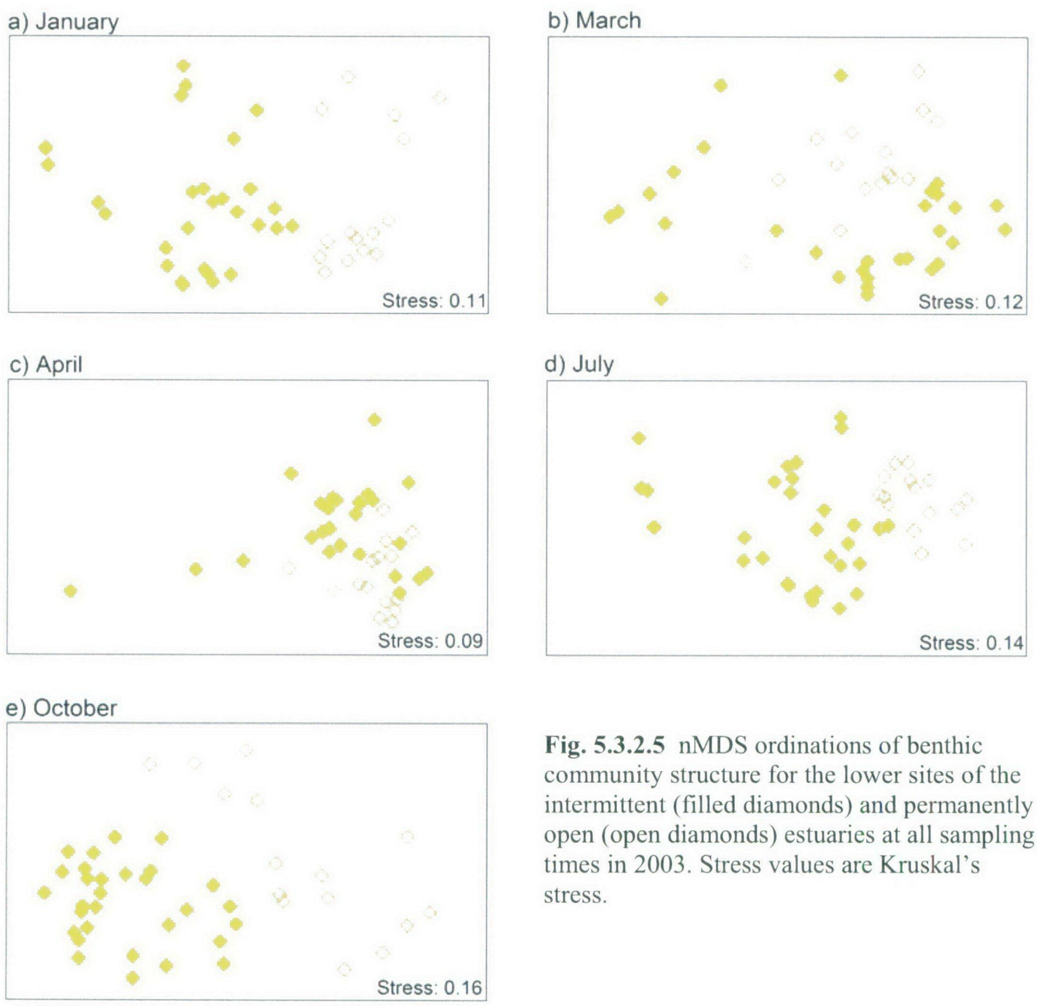

Fig. 5.3.2.5 nMDS ordinations of benthic community structure for the lower sites of the intermittent (filled diamonds) and permanently open (open diamonds) estuaries at all sampling times in 2003. Stress values are Kruskal's stress.

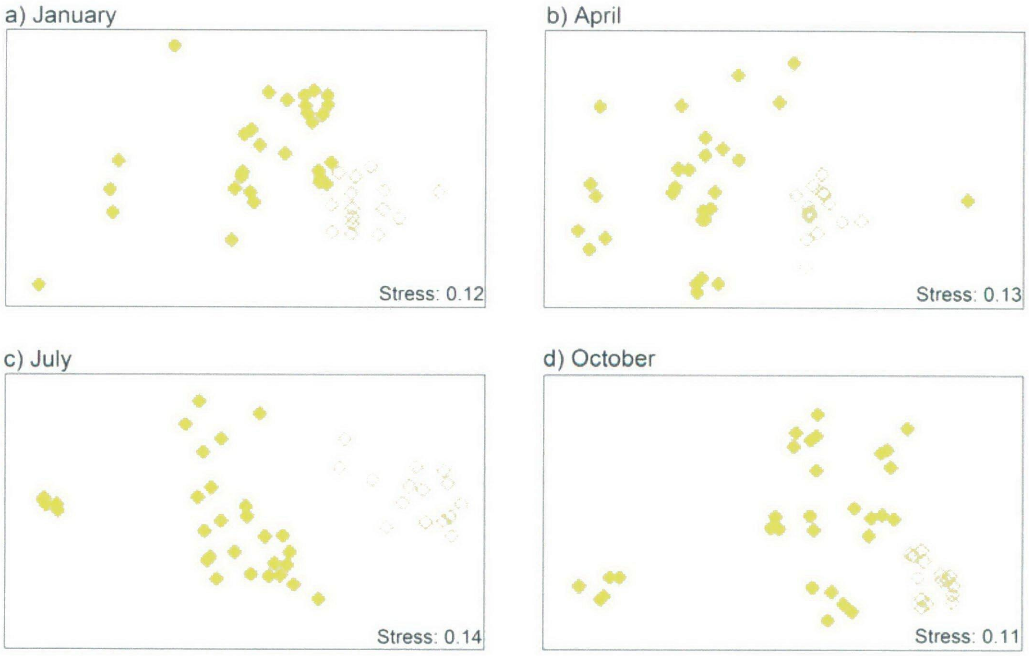

Fig. 5.3.2.6 nMDS ordinations of benthic community structure for the lower sites of the intermittent (filled diamonds) and permanently open (open diamonds) estuaries at all sampling times in 2004. Stress values are Kruskal's stress.

Two species were consistently largely responsible for these differences. These were *S. normalis*, which had greater average abundances in the intermittent estuaries for all sampling times, and *Urohaustorius metungi*, which was always more abundant in the permanently open estuaries (Table 5.3.2.4). Higher average abundances of *M. vitrea* in the intermittent estuary type throughout 2003 and *Soletellina alba* in 2004 also contributed considerably to the average dissimilarity between estuary types during each of these years. Similarly, the increased average abundances of *Nassarius jonasii* in the permanently open estuaries featured strongly in the SIMPER analyses for 2003. In regards to *M. vitrea*, it is interesting to note that its prominence in the lower sites of the intermittent estuaries contrasts to the upper and middle sites, where the SIMPER results show it to have higher abundances in the permanently open estuaries.

Table 5.3.2.4 SIMPER results for analyses between estuary types at their lower sites in 2003 and 2004. The average dissimilarity between estuary types is given for each sampling time. Information about the species contributing to more than 5 % of the average dissimilarity between estuary types is also given, including their percentage contribution and average abundance per sample in the estuary type (I = intermittently closed; P = permanently open) where they were most abundant. '-' indicates species did not contribute to more than 5 % of the average dissimilarity between estuary types at that particular sampling time.

	2003					2004			
	Jan 93.4	Mar 86.5	Apr 88.2	Jul 84.8	Oct 82.2	Jan 82.6	Apr 92.1	Jul 93.6	Oct 78.2
M. vitrea	12.3 % **I**: 46.9	11.3 % **I**: 5.4	8.3 % **I**: 1.0	10.2 % **I**: 4.7	8.0 % **I**: 5.6	8.2 % **I**: 4.3	-	5.1 % **I**: 2.2	10.2 % **P**: 8.3
U. metungi	21.5 % **P**: 31.1	20.2 % **P**: 8.8	30.4 % **P**: 18.2	21.1 % **P**: 10.2	13.4 % **P**: 5.8	23.6 % **P**: 17.2	25.1 % **P**: 21.8	17.0 % **P**: 9.3	16.5 % **P**: 10.9
S. normalis	10.4 % **I**: 7.6	13.2 % **I**: 3.7	10.1 % **I**: 1.9	12.3 % **I**: 11.4	20.0 % **I**: 13.0	15.0 % **I**: 19.2	9.1 % **I**: 5.7	7.5 % **I**: 3.8	8.6 % **I**: 7.5
N. estuarius	-	7.3 % **I**: 2.1	-	-	-	-	-	-	-
A. tasmanica	-	-	-	-	-	-	-	-	6.0 % **I**: 3.6
S. alba	-	-	-	-	5.5 % **I**: 0.9	-	7.0 % **I**: 6.3	5.8 % **I**: 3.6	9.9 % **I**: 9.0
S. aequisetis	-	-	-	-	-	-	-	-	5.2 % **I**: 3.6
N. jonasii	5.05 % **P**: 1.5	5.2 % **P**: 0.6	6.3 % **P**: 1.0	-	9.1 % **P**: 4.9	-	-	-	-
P. undulata	-	-	-	-	-	8.1 % **P**: 4.1	7.7 % **P**: 2.3	-	-
F. subtortus	-	-	-	-	-	-	5.3 % **I**: 3.4	-	-
O. cirriformia	-	-	-	-	-	-	-	6.3% **I**: 3.3	-

<u>All Sites Combined</u>

Analyses combining the data from each of the upper, middle and lower sites give a generalized view of the differences between the communities of the two estuary types. When combining these sites the communities of each estuary type overlap greatly in all of the nMDS ordinations, except for January 2003 and, to a lesser degree, October 2003 and July 2004 (Figs. 5.3.2.7, 5.3.2.8). However, even with the data pooled across sites, ANOSIMs still indicate highly

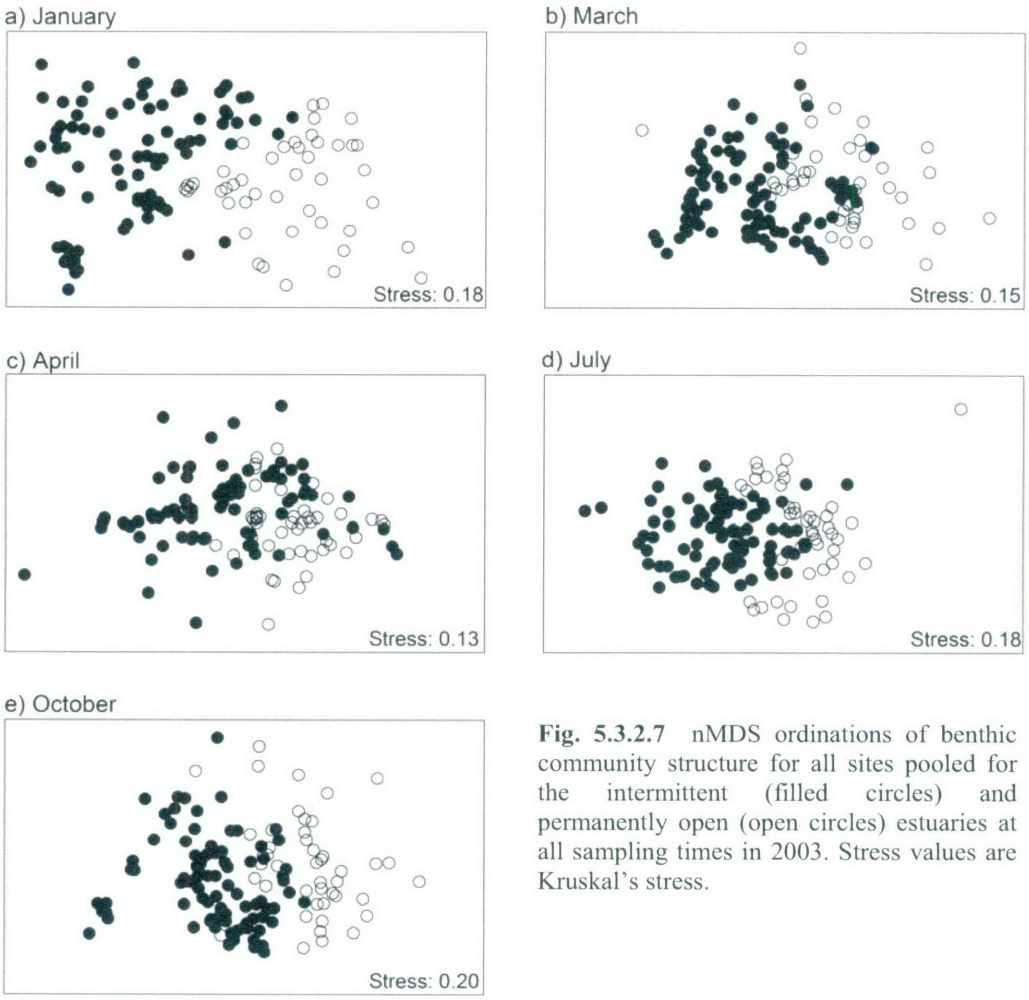

Fig. 5.3.2.7 nMDS ordinations of benthic community structure for all sites pooled for the intermittent (filled circles) and permanently open (open circles) estuaries at all sampling times in 2003. Stress values are Kruskal's stress.

significant differences between the two estuary types for all sampling times (Global R = 0.403, 0.268, 0.175, 0.348, 0.408, 0.292, 0.382, 0.571, 0.282 for consecutive samples from January 2003 to October 3004, inclusive; $p = 0.001$ for all tests) (Table 5.3.2.1). SIMPER analyses show that, when all sites are pooled, the differences between the two estuary types were mostly due to differences in the average abundances of five species. Specifically, *S. normalis* had a greater average abundance in the intermittent estuary type for all sampling times and *A. intermedia* was also more abundant in the intermittent estuaries on all the occasions that it contributed to the dissimilarity between estuary types (Table 5.3.2.5). The three times that *A. intermedia* did not contribute more than 5 % of the dissimilarity between estuary types were the same three times when all of the intermittent estuaries were open. The other species that featured strongly in the SIMPER analyses between estuary types when all sites were pooled were *M. vitrea* and *U.*

metungi, which were more abundant in the permanently open estuary type, and *A. helmsi*, which was inconsistent as to the estuary type in which it was most abundant.

Table 5.3.2.5 SIMPER results for analyses between estuary types for all sites combined during 2003 and 2004. The average dissimilarity between estuary types is given for each sampling time. Information about the species contributing more than 5 % of the average dissimilarity between estuary types is also given, including their percentage contribution and average abundance per sample in the estuary type (**I** = intermittently closed; **P** = permanently open) where they were most abundant. '-' indicates species did not contribute more than 5 % of the average dissimilarity between estuary types at that particular sampling time.

	2003					2004			
	Jan	Mar	Apr	Jul	Oct	Jan	Apr	Jul	Oct
Ave. dissim.	92.1	90.4	92.0	90.7	86.9	87.8	94.3	92.0	84.7
M. vitrea	8.6 % **P**: 19.9	9.6 % **P**: 12.9	11.2 % **P**: 8.8	11.2 % **P**: 23.1	9.4 % **P**: 14.9	8.7 % **P**: 11.7	6.1 % **P**: 4.3	-	6.7 % **P**: 6.3
U. metungi	7.5 % **P**: 10.8	8.8 % **P**: 5.1	9.9 % **P**: 6.2	7.6 % **P**: 4.1	-	8.8 % **P**: 5.8	9.9 % **P**: 7.7	6.0 % **P**: 3.5	-
S. normalis	7.0 % **I**: 7.2	9.2 % **I**: 4.9	8.7 % **I**: 2.6	7.3 % **I**: 6.8	10.9 % **I**: 15.1	10.0 % **I**: 12.2	5.9 % **I**: 2.2	5.9 % **I**: 3.8	7.4 % **I**: 7.0
N. estuarius	-	8.6 % **I**: 4.5	8.1 % **I**: 3.2	-	-	-	6.15 % **I**: 3.3	-	-
A. intermedia	5.8 % **I**: 5.1	-	-	7.2 % **I**: 20.0	5.7 % **I**: 7.52	6.1 % **I**: 6.1	5.2 % **I**: 9.7	6.9 % **I**: 16.0	-
A. helmsi	5.7 % **P**: 16.9	5.6 % **P**: 11.2	5.7 % **P**: 11.5	5.6 % **P**: 7.2	7.8 % **I**: 15.4	8.6 % **P**: 7.4	6.6 % **P**: 6.3	5.7 % **I**: 7.8	9.1 % **I**: 19.2
S. towraensis	-	-	5.4 % **I**: 4.2	-	-	-	-	-	-
T. australiensis	-	-	-	5.8 % **P**: 4.4	-	-	-	-	-
S. alba	-	-	-	-	-	5.8 % **P**: 4.2	-	-	5.6 % **I**: 3.3
S. aequisetis	-	-	-	-	-	-	-	-	5.3 % **I**: 5.4
O. cirriformia	-	-	-	-	5.3 % **I**: 6.1	-	-	11.1 % **I**: 14.2	-

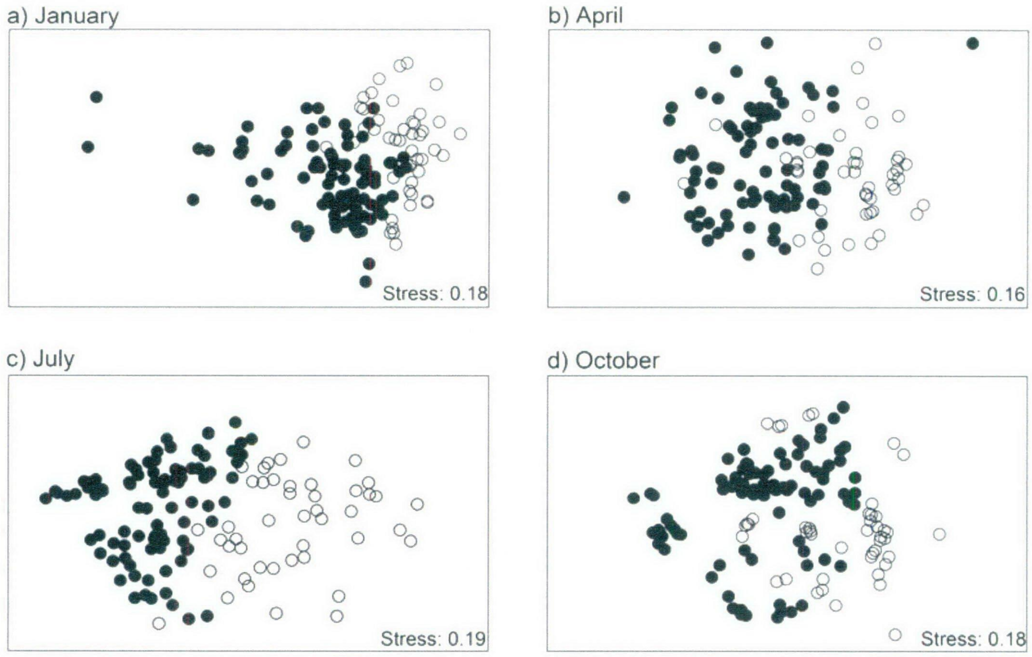

Fig. 5.3.2.8 nMDS ordinations of benthic community structure for all sites pooled for the intermittent (filled circles) and permanently open (open circles) estuaries at all sampling times in 2004. Stress values are Kruskal's stress.

<u>A Closer Examination of the Temporal Trends between Estuary Types</u>

Whilst there were always highly significant differences between the benthic communities of the intermittently closed and permanently open estuary types, there was still great variation in the Global *R* values, which provide a measure of the similarity between the two types. Even when the data from all sites were combined, the Global *R* varied from 0.175 to 0.571 (Table 5.3.2.1), covering 40 % of its usual range (i.e. 0 - 1) (Clarke & Warwick 2001). This variation was greatest in the lower sites alone, where Global *R* varied from 0.192 to 0.758. Therefore, despite the repeated significant differences between the estuary types during this study, there were times when the two estuary types were more similar than at other times. To examine this further, the Global *R* results for all sites combined were plotted in chronological order for the full length of the study. The number of closed estuaries was plotted in the same graph to get a feel for any emergent patterns. The trend in these Global *R* values closely matched the number of intermittent estuaries that had closed entrances at the time of sampling (Fig. 5.3.2.9) and correlating the number of closed estuaries with the Global *R* values for all sites combined produced a significant positive relationship ($r = 0.772$; $p = 0.015$) between these two variables

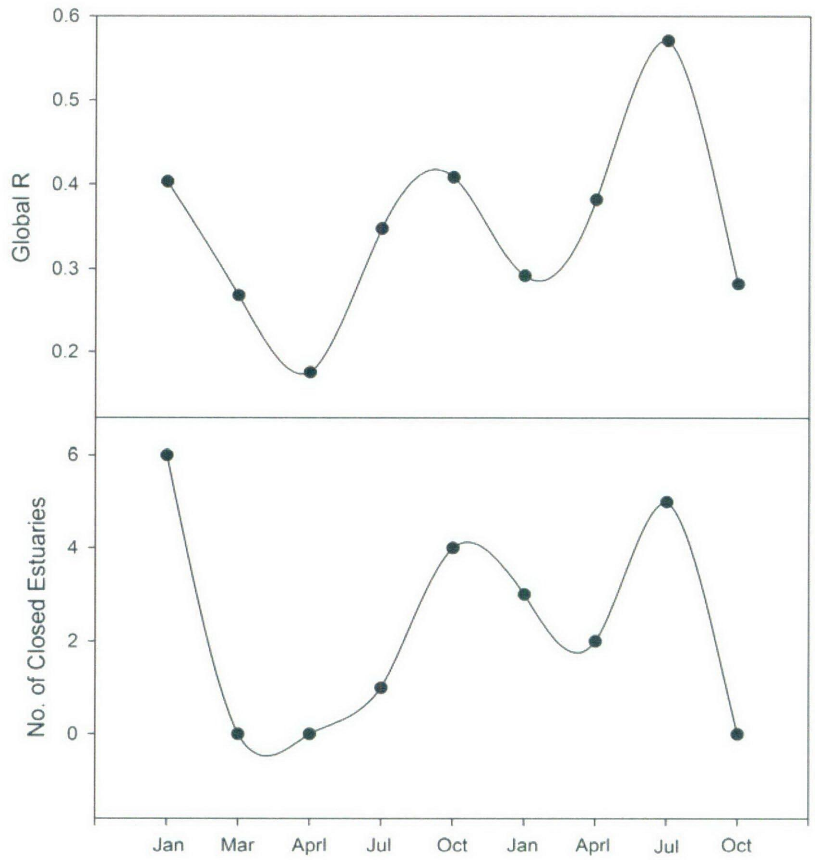

Fig. 5.3.2.9 Trends in Global *R* (differences between permanently open and intermittently closed estuary types) and the number of closed estuaries for data from all sites pooled within each estuary; January 2003 – October 2004.

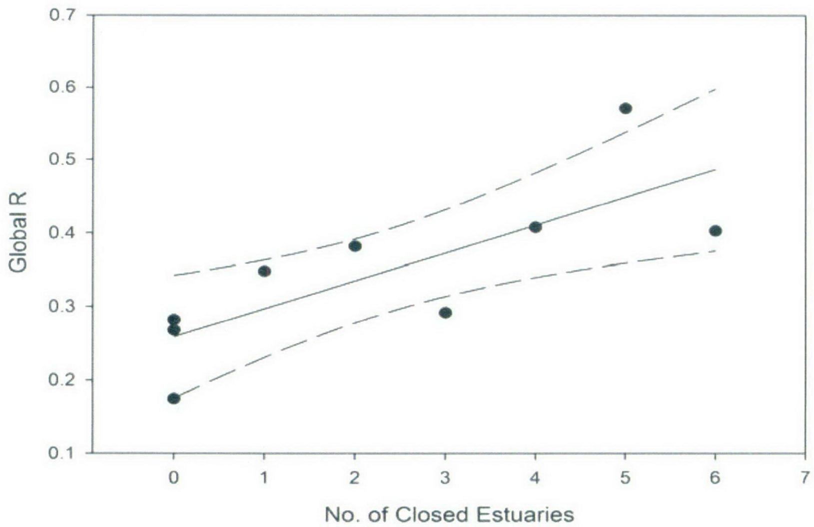

Fig. 5.3.2.10 Plot of Global *R* against the number of closed estuaries for all sites pooled within each estuary. Regression equation: Global $R = 0.259 + 0.038$ (number of closed estuaries); $r = 0.772$.

(Fig. 5.3.2.10, Table 5.3.2.6). Additionally, almost 60 % of the Global *R* variation was accounted for by the variation in the number of closed estuaries ($r^2 = 0.596$).

This relationship between the similarity of the two estuary types and the number of closed estuaries was broken down further for the upper, middle and lower sampling sites. For each of these sites the similarity between the two estuary types (Fig. 5.3.2.11) also appeared to be related to the number of closed estuaries but to varying degrees. This was reflected in the results of regression analysis for the upper and lower sites ($p = 0.050$; $r = 0.666$; $p = 0.014$; $r = 0.774$, respectively); however, there was no significant relationship for the middle site (Table 5.3.2.6). The relatively strong result at the lower sites was nearly identical to that for all sites combined. This suggests that the overall patterns of similarity between estuary types when all sites are pooled, and the relationship between these similarities and the number of closed estuaries, are largely due to effects in the lower sites of the estuaries.

Table 5.3.2.6 Correlation coefficients (r) and coefficients of determination (r^2) resulting from linear regressions of 2003 and 2004 similarity (Global R) results between the intermittently closed and permanently open estuary types at the upper, middle and lower sites, as well as for all sites combined, with the number of estuaries closed at each sampling time.

	r	r^2	p
All Sites	0.772	0.596	0.015
Upper	0.666	0.444	0.050
Middle	0.561	0.315	0.116
Lower	0.774	0.599	0.014

Focusing on the data for the lower sites and all sites combined, which produced the strongest results for this relationship, trends in the abundances of the main species contributing to the differences between estuary types were examined more closely to further detail how these were responding to entrance status. Apart from *U. metungi,* the average abundances of species in the lower sites of the permanently open estuary type were relatively low and stable (Fig. 5.3.2.12). In contrast, in the lower sites of the intermittently closed estuaries, the average abundances of this species were considerably variable and often higher than those in permanently open estuaries. When comparing these average abundances to the similarity between estuary types in the lower sites, *O. cirriformia* most closely resembled the trends observed, with the average

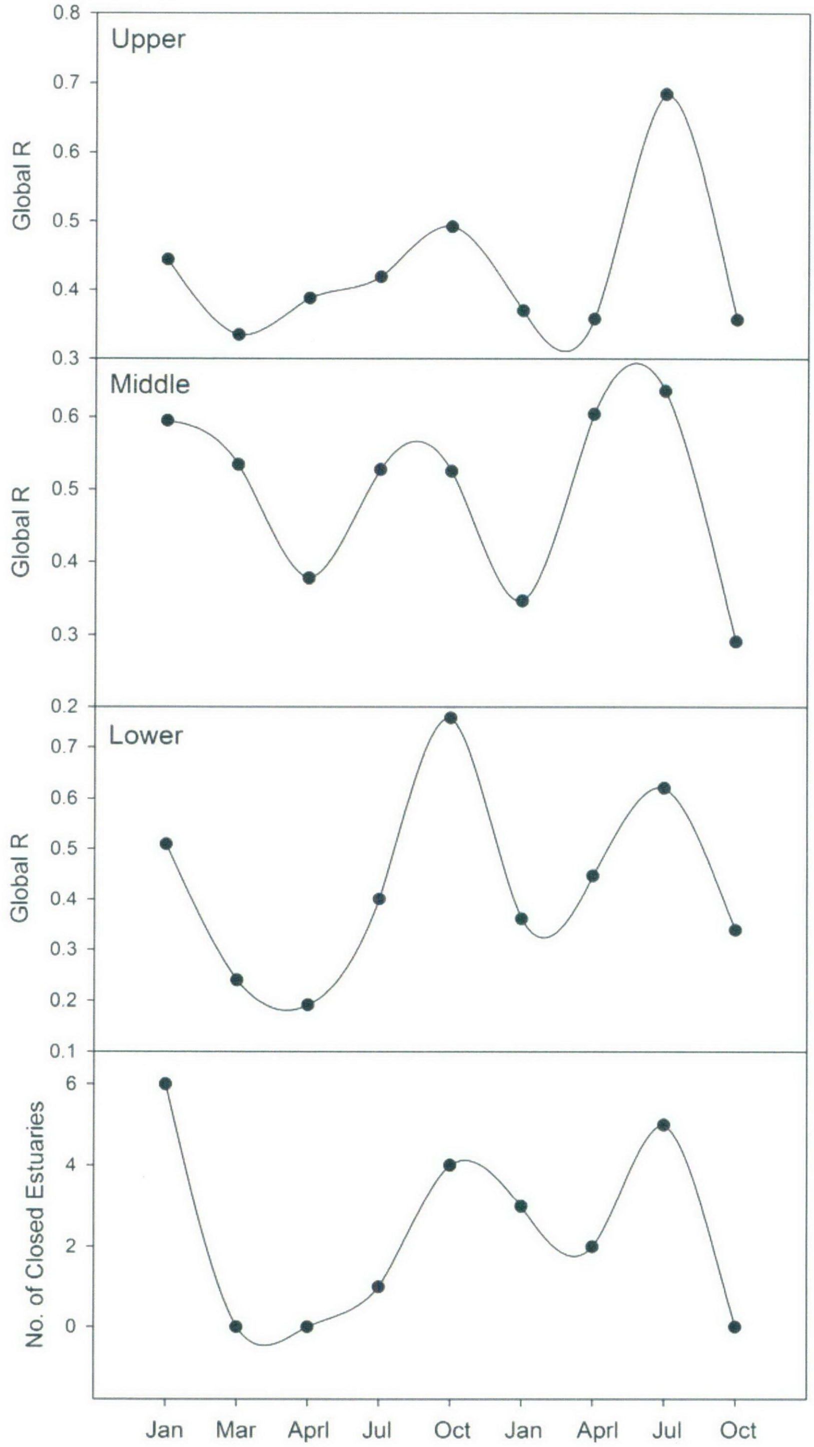

Fig. 5.3.2.11 Trends in Global *R* (differences between permanently open and intermittently closed estuary types) for each of the upper, middle and lower sites; as well as the number of closed estuaries. January 2003 – October 2004.

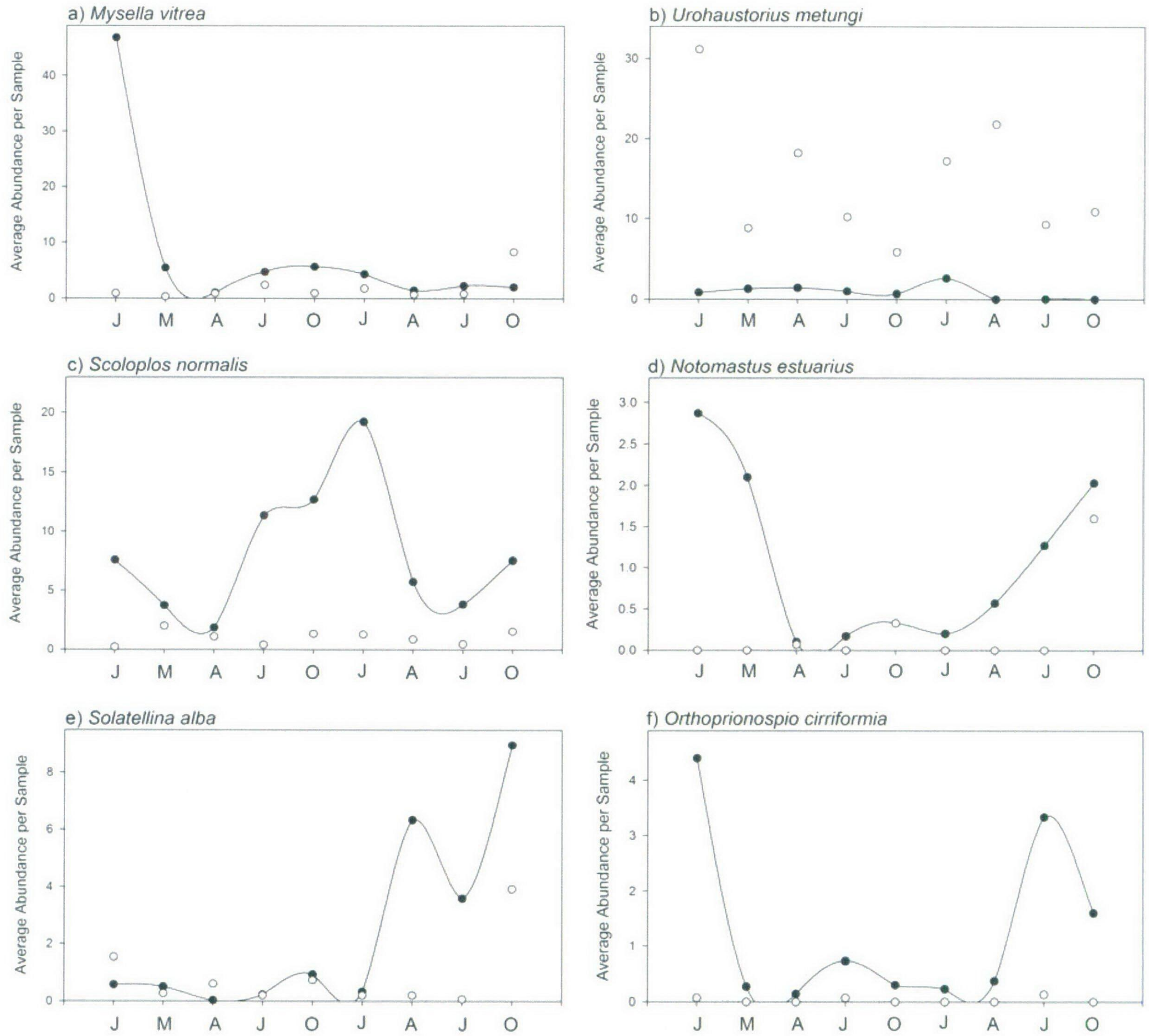

Fig. 5.3.2.12 Trends of averages abundance of the species contributing the most to differences between the intermittently closed and permanently open estuary types at the lower sites. Data extracted directly from SIMPER analysis results. Filled circles represent the intermittent estuary type and open circles represent the permanently open estuary type.

abundances being most dissimilar (i.e. greater in the intermittent estuary type) when sampling occurred near the end of lengthy closures for many of the intermittently closed estuaries (i.e. January 2003, July 2004) (Fig. 5.3.2.12 f). The average abundances of *O. cirriformia* in the intermittent estuaries then declined and tended more towards those in the permanently open estuary type following major opening events (i.e. March - April 2003, October 2004). The average abundances of *M. vitrea* and *S. normalis* in the intermittent estuaries also declined to

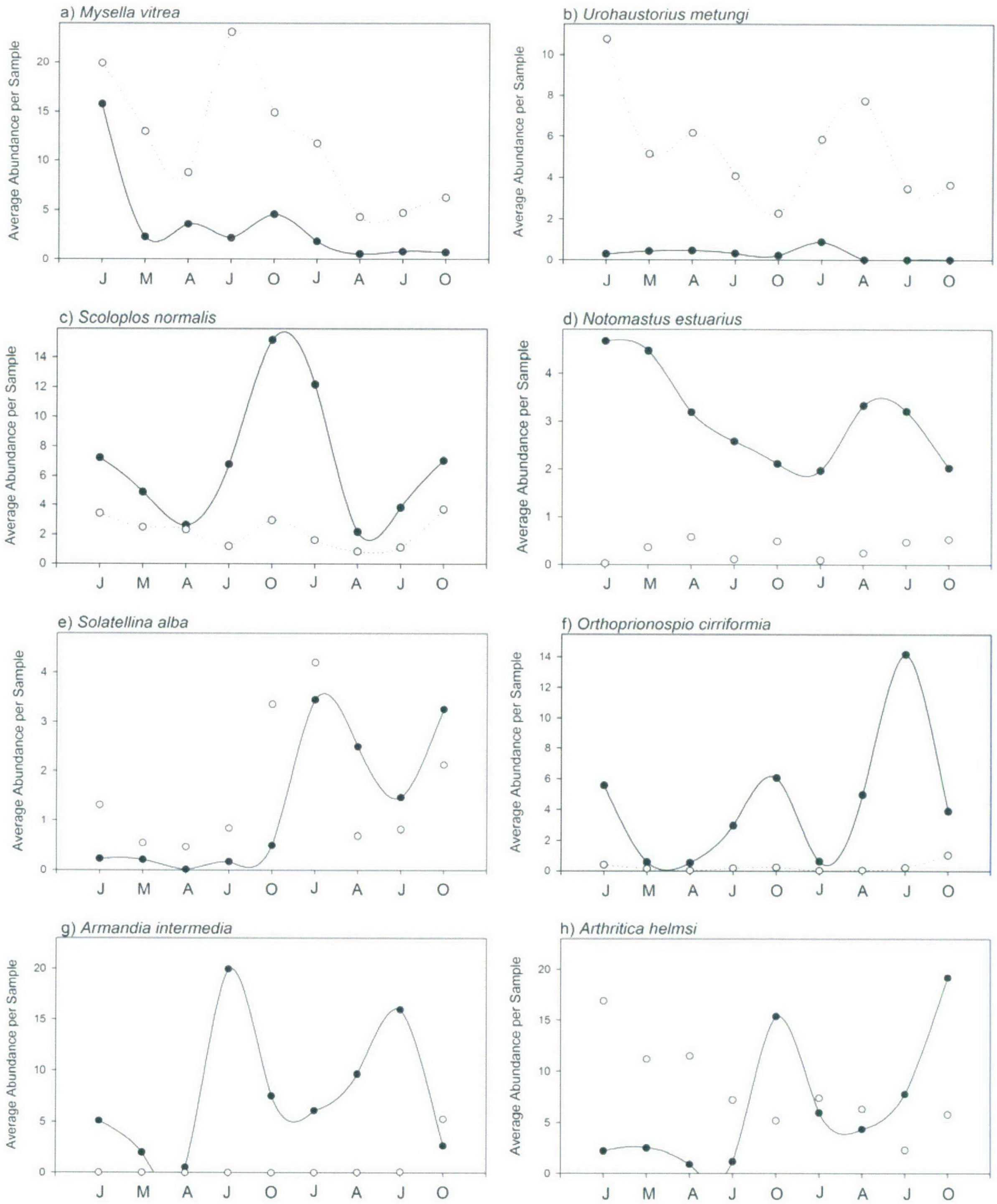

Fig. 5.3.2.13 Trends of averages abundances of the species contributing the most to differences between the intermittently closed and permanently open estuary types when all sites are combined. Data extracted directly from SIMPER analysis results. Filled circles represent the intermittent estuary type and open circles represent the permanently open estuary type.

values similar to those in the permanently open estuaries for the times in 2003 when all estuaries were open; however, neither species repeated this trend for the major event in October 2004. Abundances of *N. estuarius* in the intermittent and permanently open estuary types converged in both April 2003, when both approached zero, and October 2004, when both increased rapidly (Fig. 5.3.2.12 d), which would also have contributed to the greater similarities between the two estuary types at these times. The average abundances of *U. metungi* and *S. alba* revealed no consistent patterns that reflected the trends observed in the relationship between estuary types at the lower sites.

Patterns in the average abundances of the species that contributed the most to the dissimilarities between estuary types when all sites were combined were quite varied and complex (Fig. 5.3.2.13). Again, the average abundance of *O. cirriformia* was greater in the intermittent estuaries and presented a trend resembling that of similarity between estuary types throughout the study (Fig. 5.3.2.13 f), with peaks in January and October 2003, as well as in October 2004; all of these were times when many of then intermittent estuaries were closed. Abundance also declined to values more similar to that in the permanently open estuaries on all of the three occasions when all estuaries were open. Similarly, *A. intermedia* generally had greater average abundances in the intermittent estuaries and reflected the trends in similarity between estuary types in that they were most similar to those in the permanently open estuaries (i.e. approached zero) at times when all of the intermittent estuaries were open (Fig. 5.3.2.13 g). None of the other six species listed as primarily contributing to the overall dissimilarity between estuary types displayed abundance trends that were consistent with the assemblage differences between the two estuary types.

Despite the patterns of species distribution and abundance revealed by the community analyses, univariate analyses of the abundances of each of the major contributors to the dissimilarity between estuary types were generally not significantly different ($p > 0.05$) between estuary types, except for *Urohaustorius metungi*, which usually displayed a significant difference between estuary types (Tables 5.3.2.7, 5.3.2.8). There were seven exceptions to this trend, of which five occurred during either the March 2003, April 2003 or October 2004 sampling times when all of the intermittent entrances were open. These included no significant differences between estuary types in the abundance of *U. metungi* in March 2003 (lower sites: $p = 0.112$; all sites combined: $p = 0.133$), a significant difference between estuary types in the abundance of *Solatellina alba* when all sites were combined April 2003 ($p = 0.012$), and significant differences between estuary types in the abundance of *Mysella vitrea* for both the lower sites and all sites analyses ($p = 0.044$; 0.036, respectively). The remaining two exceptions occurred at the lower sites in October 2003 when there was no difference between estuary types in the abundance of *U. metungi* ($p = 0.067$) and a significant difference between types did occur for *Scoloplos normalis* ($p = 0.010$). The lack of significant differences between estuary types for most species was driven by high levels of variation among the estuaries nested within type (Tables 5.3.2.7, 5.3.2.8).

Table 5.3.2.7 Summary of two-way nested ANOVA results comparing the abundances of important discriminatory species between estuary types ($df = 1, 36$) and among the estuaries nested within each type ($df = 7, 36$) at the lower sites only. Results given are the F-statistic and bold indicates a significant result ('*' $p < 0.05$; '**' $p < 0.001$).

		2003					2004			
		Jan	Mar	Apr	Jul	Oct	Jan	Apr	Jul	Oct
Mysella vitrea	Type	0.58	1.11	0.01	0.30	0.35	0.45	0.21	0.53	**6.02***
	Estuary (Type)	**4.82****	**9.64****	**2.44***	**3.45***	**11.95****	**5.29****	**9.28****	1.46	**10.48****
Urohaustorius metungi	Type	**7.19***	3.09	**8.87***	**37.92****	4.67	**5.65***	**13.03***	**26.19****	**75.52****
	Estuary (Type)	**9.76****	**16.04****	2.23	**2.33***	**4.31***	**14.23****	**8.34****	**16.28****	0.22
Scoloplos normalis	Type	1.67	0.45	0.27	0.72	**12.39***	0.89	1.79	2.27	1.99
	Estuary (Type)	**11.42****	**6.89****	**5.76****	**19.83****	**4.05***	**91.52****	**21.06****	**8.82****	**39.68****
Notomastus estuarius	Type	0.47	0.67	0.09	1.42	0.01	1.17	2.51	1.03	2.01
	Estuary (Type)	**25.28****	**16.94****	1.53	1.46	**2.42***	**5.14****	2.26	**9.54****	1.55
Soletellina alba	Type	1.91	0.16	4.53	0.02	0.05	0.17	0.71	0.73	0.36
	Estuary (Type)	**3.47***	**12.57****	**4.56****	**2.90***	**4.61***	**3.31***	**33.66****	**37.89****	**39.73****
Orthoprionospio cirriformia	Type	0.47	0.63	1.17	1.59	0.61	1.76	1.05	1.21	1.04
	Estuary (Type)	**21.04****	1.44	0.86	**4.34***	**13.24****	2.14	**3.84***	**12.56****	**2.53***

Table 5.3.2.8 Summary of two-way nested ANOVA results comparing the abundances of important discriminatory species between estuary types ($df = 1, 36$) and among the estuaries nested within each type ($df = 7, 36$) when all sites are combined. Results given are the *F*-statistic and bold indicates a significant result ('*' $p < 0.05$; '**' $p < 0.001$).

		2003					2004			
		Jan	Mar	Apr	Jul	Oct	Jan	Apr	Jul	Oct
Mysella vitrea	Type	0.03	2.11	0.64	3.41	1.41	3.56	4.19	4.42	**6.69***
	Estuary (Type)	**4.82****	**6.99****	**4.36****	**5.17****	**5.60****	**3.41***	**3.84***	**2.63***	**6.74****
Urohaustorius metungi	Type	**6.93***	2.89	**8.91***	**25.28***	**5.96***	**5.59***	**15.71***	**51.19****	**69.34****
	Estuary (Type)	**3.03***	**12.16****	1.38	1.44	**2.35***	**2.93***	1.83	0.82	0.03
Scoloplos normalis	Type	0.35	0.36	0.02	0.40	2.23	0.79	0.82	1.39	0.60
	Estuary (Type)	**14.79****	**18.63****	**11.61****	**27.18****	**15.72****	**34.88****	**5.55****	**9.39****	**20.57****
Notomastus estuarius	Type	1.60	2.47	2.75	3.48	1.06	1.00	0.73	1.56	1.41
	Estuary (Type)	**21.13****	**7.86****	**4.02***	**5.65****	**4.82****	**11.31****	**10.97****	**5.67****	**4.19****
Soletellina alba	Type	4.56	1.10	**11.50***	2.03	2.52	0.03	0.53	0.14	0.14
	Estuary (Type)	**4.41****	**2.77***	**2.24***	**2.84***	**3.52***	**4.32****	**5.70****	**8.55****	**6.71****
Orthoprionospio cirriformia	Type	1.70	1.10	1.57	1.46	2.07	1.27	0.58	2.49	1.10
	Estuary (Type)	**9.27****	**5.03****	**3.53***	**11.80****	**6.26****	**4.81****	**19.83****	**11.24****	**11.09****
Armandia intermedia	Type	1.97	1.17	1.59	0.67	1.55	1.12	0.60	0.84	0.32
	Estuary (Type)	**11.37****	**5.28****	1.54	**21.14****	**9.96****	**14.15****	**23.04****	**14.71****	**13.25****
Arthritica helmsi	Type	2.31	1.25	2.01	1.73	0.47	0.04	0.11	0.44	0.83
	Estuary (Type)	**4.70****	**5.59****	**5.04****	**4.32****	**8.82****	**6.96****	**4.37****	**6.94****	**7.72****

5.3.3 Temporal consistency of other spatial patterns within and between the intermittently closed and permanently open estuary types

Assemblage Patterns

The high level of variation previously observed within both the intermittently closed and permanently open estuary types during the January 2003 sampling period (Chapter 4) continued for all of the subsequent sampling occasions. ANOSIMs revealed significant differences ($p < 0.05$) among the intermittently closed estuaries at each of the upper, middle and lower sites for all sampling times in 2003 and 2004 (Tables 5.3.3.1, 5.3.3.2). Pairwise comparisons between the estuaries within this type show that, on nearly all occasions, the estuaries were significantly different from one another. Of the total of 120 comparisons, there were only eight exceptions, all of which occurred in 2003. One was in April and showed that there was no significant difference ($p = 0.571$) between the upper sites of Station and Arrawarra creeks at this time. The remaining exceptions were all for the lower sites; no significant differences were found between Darkum Creek and Hearns Lake ($p = 0.151$) in January, or between Hearns Lake and Station ($p = 0.159$), Darkum ($p = 0.295$) or Willis ($p = 0.095$) creeks in April. Also in April, there was no significant difference between the lower sites of Darkum and Arrawarra creeks ($p = 0.111$). Similarly, October 2003 revealed no significant differences between the lower sites of Hearns Lake and Arrawarra ($p = 0.103$) or Station ($p = 0.063$) creeks.

For the permanently open estuaries, ANOSIMs revealed significant differences ($p < 0.05$) between estuaries at all sites for all sampling times (Tables 5.3.3.1, 5.3.3.2). Pairwise comparisons revealed significant differences between all combinations of estuaries for all sites on all but one occasion. This was July 2003 when there was no significant difference between the lower site of Moonee Creek and Corindi ($p = 0.071$) or Coffs ($p = 0.103$) creeks.

Table 5.3.3.1 Summary of results for all sequential one-way ANOSIMs with the Global R given to test for differences between estuary types and for differences between the estuaries nested within each type at each site for 2003. The R-statistic testing individual pairwise comparisons among the estuaries within each type are given are also given and bold font indicates a non-significant test ($p > 0.05$). ICE = intermittently closed estuary type, POE = permanently open estuary type. Estuary names are abbreviated to their first three letters.

Comparisons	January			March			April			July			October		
	Upper	Middle	Lower	Upper	Middle	Lower	Upper	Middle	Lower	Upper	Middle	Lower	Upper	Middle	Lower
Type															
ICE *vs* POE	0.444	0.595	0.509	0.335	0.534	0.240	0.388	0.378	0.192	0.419	0.527	0.409	0.492	0.525	0.758
Estuaries(Type)															
ICE	0.739	0.907	0.891	0.894	0.738	0.717	0.714	0.762	0.484	0.769	0.858	0.687	0.839	0.906	0.730
POE	0.799	0.876	0.621	0.814	0.700	0.505	0.899	0.680	0.544	0.612	0.969	0.279	0.941	0.841	0.841
Intermittent															
Sta - Arr	0.872	1.000	0.912	0.780	0.944	0.836	**-0.047**	0.672	0.350	0.600	1.000	0.968	0.902	0.796	0.436
Sta - Dar	0.700	0.704	0.972	0.908	**-0.022**	0.722	0.928	0.326	0.264	0.504	0.626	0.596	0.804	1.000	0.840
Sta - Woo	0.576	1.000	0.984	0.868	1.000	0.820	0.872	0.656	0.900	0.580	1.000	0.680	0.490	0.964	0.968
Sta - Wil	1.000	1.000	1.000	0.964	0.763	0.528	0.792	0.792	0.673	0.548	0.976	0.444	0.918	0.972	0.716
Sta - Hea	1.000	1.000	1.000	0.996	1.000	0.820	0.968	0.640	**0.096**	0.616	1.000	0.620	0.900	0.868	**0.234**
Arr - Dar	0.528	0.740	0.976	0.668	0.384	0.336	0.694	0.620	**0.120**	0.952	0.624	0.796	0.476	1.000	0.880
Arr - Woo	0.396	1.000	0.796	0.760	0.936	0.812	0.516	1.000	0.592	1.000	1.000	0.976	0.764	1.000	0.984
Arr - Wil	0.928	1.000	1.000	0.928	1.000	0.984	0.669	1.000	0.909	0.924	1.000	0.636	1.000	0.936	0.896
Arr - Hea	0.432	1.000	0.992	0.820	0.932	0.600	0.628	0.996	0.258	0.864	1.000	1.000	0.992	0.816	**0.180**
Dar - Woo	0.520	0.764	1.000	0.964	0.472	0.368	0.860	0.574	0.748	0.976	0.608	0.542	0.588	1.000	0.776
Dar - Wil	0.964	0.772	1.000	1.000	0.288	0.880	1.000	0.750	0.636	0.872	0.776	0.642	1.000	0.880	0.836
Dar - Hea	0.804	0.724	**0.136**	0.792	0.348	0.512	0.436	0.500	**0.052**	0.464	0.612	0.644	0.620	0.644	0.692
Woo - Wil	0.800	1.000	1.000	1.000	1.000	0.992	0.834	1.000	1.000	0.944	1.000	0.692	0.992	0.988	1.000
Woo - Hea	0.552	1.000	1.000	1.000	1.000	0.996	0.808	0.984	0.800	1.000	1.000	0.604	0.940	1.000	1.000
Wil - Hea	1.000	1.000	1.000	0.916	0.956	0.932	1.000	1.000	**0.509**	0.744	0.996	0.700	1.000	0.820	0.548
Permanently open															
Cor - Moo	0.820	0.916	0.996	0.848	0.666	0.632	0.968	0.820	0.520	0.508	1.000	**0.248**	0.980	0.948	0.660
Cor - Cof	0.816	0.864	0.924	0.880	0.556	0.414	0.888	0.708	0.760	0.540	1.000	0.460	0.780	0.936	0.976
Moo - Cof	1.000	0.992	0.360	1.000	0.948	0.532	0.996	0.656	0.398	1.000	1.000	**0.116**	1.000	0.960	0.952

Table 5.3.3.2 Summary of results for all sequential one-way ANOSIMs with the Global *R* given to test for differences between estuary types and for differences between the estuaries nested within each type at each site for 2004. The *R*-statistic testing individual pairwise comparisons among the estuaries within each type are given are also given and bold font indicates a non-significant test ($p > 0.05$). ICE = intermittently closed estuary type, POE = permanently open estuary type. Estuary names are abbreviated to their first three letters.

Comparison groups	January			April			July			October		
	Upper	Middle	Lower	Upper	Middle	Lower	Upper	Middle	Lower	Upper	Middle	Lower
Type												
Intermittent *vs* Permanent	0.370	0.347	0.362	0.358	0.604	0.447	0.684	0.636	0.621	0.357	0.291	0.340
Estuaries (Type)												
Intermittently closed	0.721	0.909	0.810	0.838	0.971	0.809	0.976	0.974	0.904	0.396	0.974	0.991
Permanently open	0.915	0.492	0.615	0.705	0.986	0.847	0.995	0.848	0.617	0.787	0.909	0.820
Intermittently closed												
Station - Arrawarra	1.000	0.632	0.960	0.832	0.960	0.616	1.000	1.000	0.908	1.000	1.000	1.000
Station - Darkum	0.988	0.774	0.932	0.426	0.856	0.700	1.000	1.000	0.992	1.000	1.000	1.000
Station - Woologoolga	0.654	0.632	1.000	0.725	0.896	0.648	0.600	1.000	0.996	0.800	1.000	1.000
Station - Willis	0.744	0.896	0.820	0.884	1.000	0.658	1.000	1.000	1.000	1.000	1.000	1.000
Station - Hearns	0.972	0.624	0.996	0.804	0.992	0.658	0.992	1.000	0.908	1.000	1.000	1.000
Arrawarra - Darkum	0.500	1.000	0.888	1.000	1.000	1.000	1.000	1.000	0.984	1.000	1.000	0.968
Arrawarra - Woolgoolga	0.448	1.000	1.000	0.769	1.000	0.720	0.972	1.000	0.952	0.852	1.000	0.932
Arrawarra - Willis	0.844	1.000	0.784	1.000	1.000	0.992	1.000	1.000	1.000	1.000	1.000	1.000
Arrawarra - Hearns	0.884	1.000	1.000	1.000	1.000	0.784	1.000	1.000	0.880	1.000	1.000	0.936
Darkum - Woolgoolga	0.524	1.000	0.664	0.819	0.932	1.000	0.976	0.998	0.744	0.876	1.000	0.960
Darkum - Willis	0.838	1.000	0.808	0.920	1.000	0.996	1.000	0.928	1.000	1.000	1.000	1.000
Darkum - Hearns	0.864	1.000	0.868	0.884	0.740	1.000	0.960	0.720	0.816	0.928	0.668	1.000
Woolgoolga - Willis	0.569	1.000	0.820	0.756	1.000	1.000	0.932	1.000	1.000	0.932	1.000	1.000
Woolgoolga - Hearns	0.522	1.000	0.988	0.863	1.000	1.000	1.000	0.996	0.868	0.976	1.000	1.000
Willis - Hearns	0.775	1.000	0.694	1.000	1.000	0.964	1.000	0.792	0.996	1.000	1.000	1.000
Permanently open												
Corindi - Moonee	0.912	0.412	0.276	0.550	1.000	0.828	1.000	0.800	0.728	0.900	0.984	0.916
Corindi - Coffs	0.824	0.432	0.760	0.636	1.000	0.864	1.000	0.992	0.420	0.868	0.952	0.688
Moonee - Coffs	1.000	0.736	0.880	1.000	1.000	0.924	1.000	0.748	0.788	0.980	0.896	0.960

Physico-chemical Patterns

Most of the water column variables displayed considerable variation, either in some or all estuaries, over time. Dissolved oxygen, for example, was below 4.00 ppm in all estuaries in January 2004, with minima for some sites of only 0.02 ppm. In contrast, dissolved oxygen levels in July 2004 were greater than 4.00 ppm in all estuaries, with many exceeding 8.00 ppm (Fig. 5.3.3.1). Salinity varied more between estuaries, with Willis and Darkum creeks, as well as Hearns Lake, often presenting greatly reduced salinity levels (to a minimum of 1.1 mgL^{-1} in Willis Creek) throughout their upper, middle and lower sites (Fig. 5.3.3.2). pH was relatively consistent throughout the study, generally ranging from 7.5 to 8.0 (Fig. 5.3.3.3). The most notable deviations to this occurred in January 2004 when the pH in a number of estuaries, mainly in their lower sites, dropped below 6.0 and reached a minimum of 2.8 in the upper site of

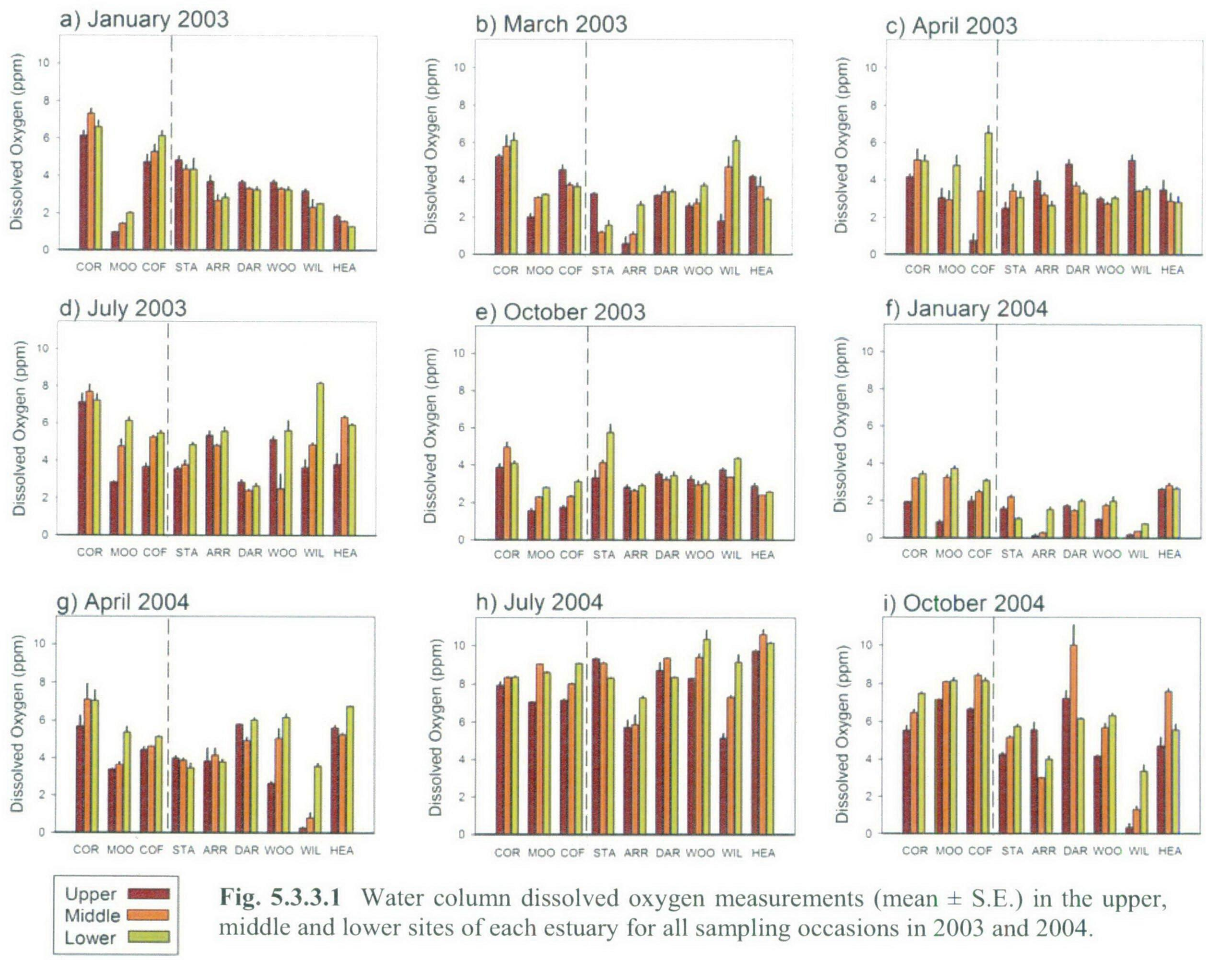

Fig. 5.3.3.1 Water column dissolved oxygen measurements (mean ± S.E.) in the upper, middle and lower sites of each estuary for all sampling occasions in 2003 and 2004.

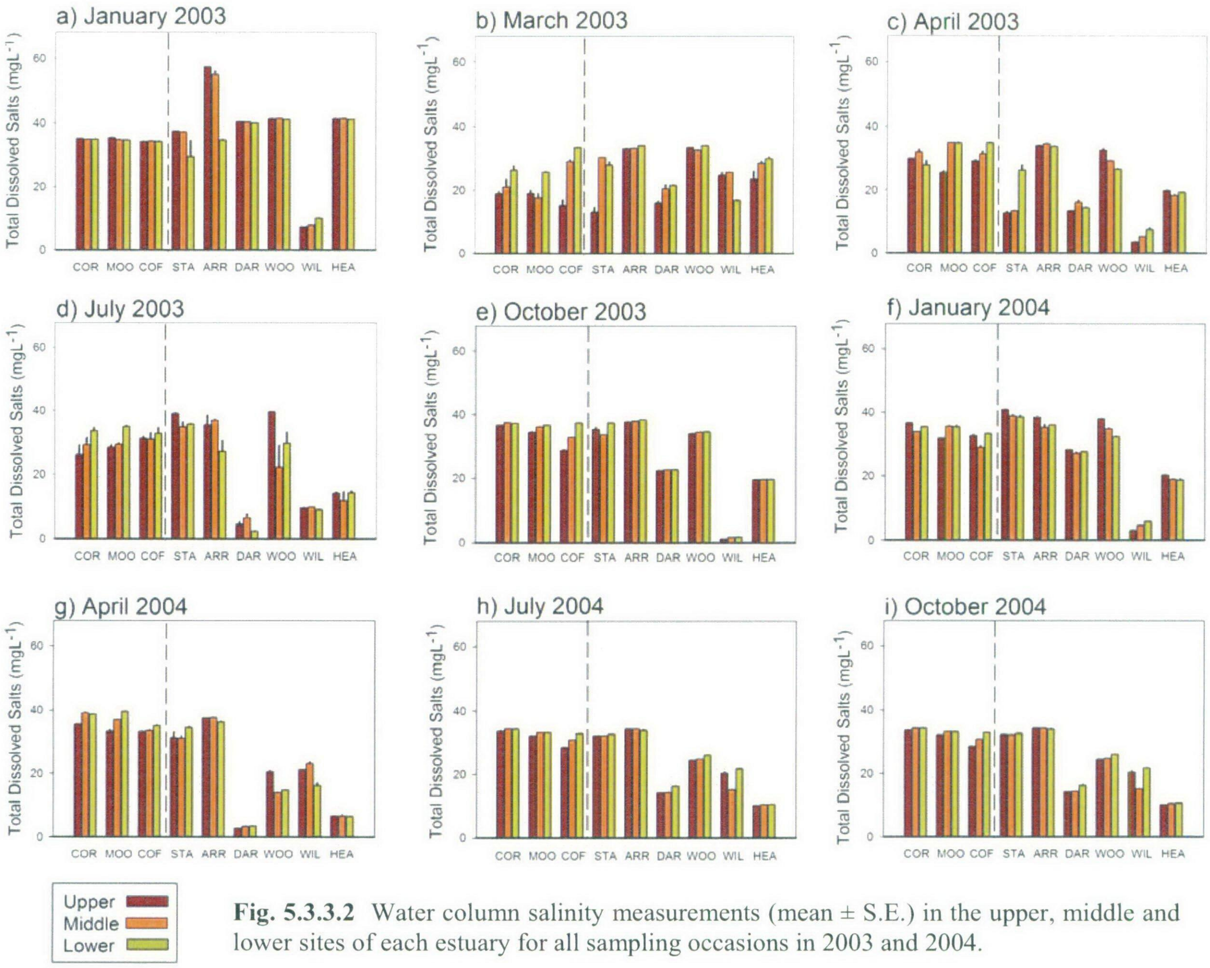

Fig. 5.3.3.2 Water column salinity measurements (mean ± S.E.) in the upper, middle and lower sites of each estuary for all sampling occasions in 2003 and 2004.

Arrawarra Creek during this time. As would be expected, overall water temperatures displayed seasonal variation between the warmer and cooler times of the year, ranging from 11.8 °C at Darkum Creek in July 2004 to 31.8 °C at Willis Creek in January 2003 (Fig. 5.3.3.4).

The January 2003 pattern of no significant differences ($p > 0.05$) between estuary types for all water column variables due to highly significant ($p < 0.001$) within-type variation continued at the upper, middle and lower sites for all sampling times throughout 2003 (Table 5.3.3.3). The only exception during this time was the pH in the lower sites during April, which was significantly different both between estuary types ($p = 0.034$) and between the estuaries nested within each type ($p = 0.011$). Whilst significant, the difference in pH between the estuary types

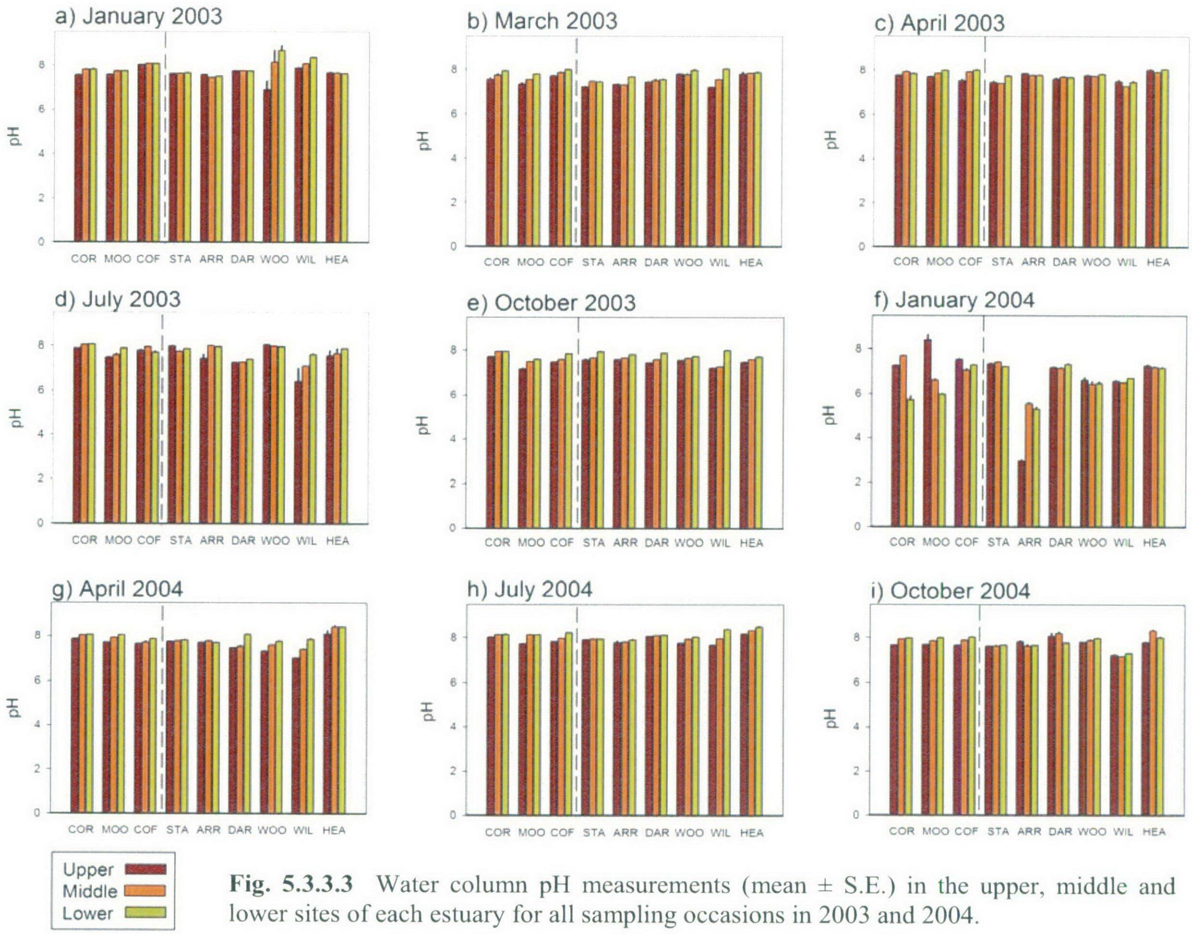

Fig. 5.3.3.3 Water column pH measurements (mean ± S.E.) in the upper, middle and lower sites of each estuary for all sampling occasions in 2003 and 2004.

was small with the permanently open estuaries averaging approximately 7.65 and the intermittent estuaries averaging 7.8.

ANOVA results for salinity and pH in 2004 were similar to those for 2003; that is, no significant differences were evident between the two estuary types, primarily due to highly significant differences between the estuaries nested within each type (Table 5.3.3.5). Both dissolved oxygen and temperature, however, were more variable between estuary types, despite significant within-type variation. In 2004, temperatures in the middle and lower sites were significantly different between estuary types for all sampling times, except April. Specifically, temperatures in the intermittently closed estuary type had a larger range (12 – 32 ^{o}C) when compared to that of the permanently open estuaries (14 – 27 ^{o}C). As such, temperatures in the intermittent estuaries were greater than those in the permanently open estuaries during the warmer sampling months, January and October, and cooler during the winter sample, July.

Temperatures in the upper sites were also significantly different between estuary types in October 2004, reaching a maximum of 32 °C in the intermittent estuaries, compared to a maximum of 24 °C in the permanently open estuaries. Similarly, dissolved oxygen was significantly different between estuary types for the middle and lower sites in January 2004 and for the lower sites only in October 2004 (Table 5.3.3.3). In each of these instances, dissolved oxygen was reduced in the intermittent estuaries when compared to the permanently open estuaries.

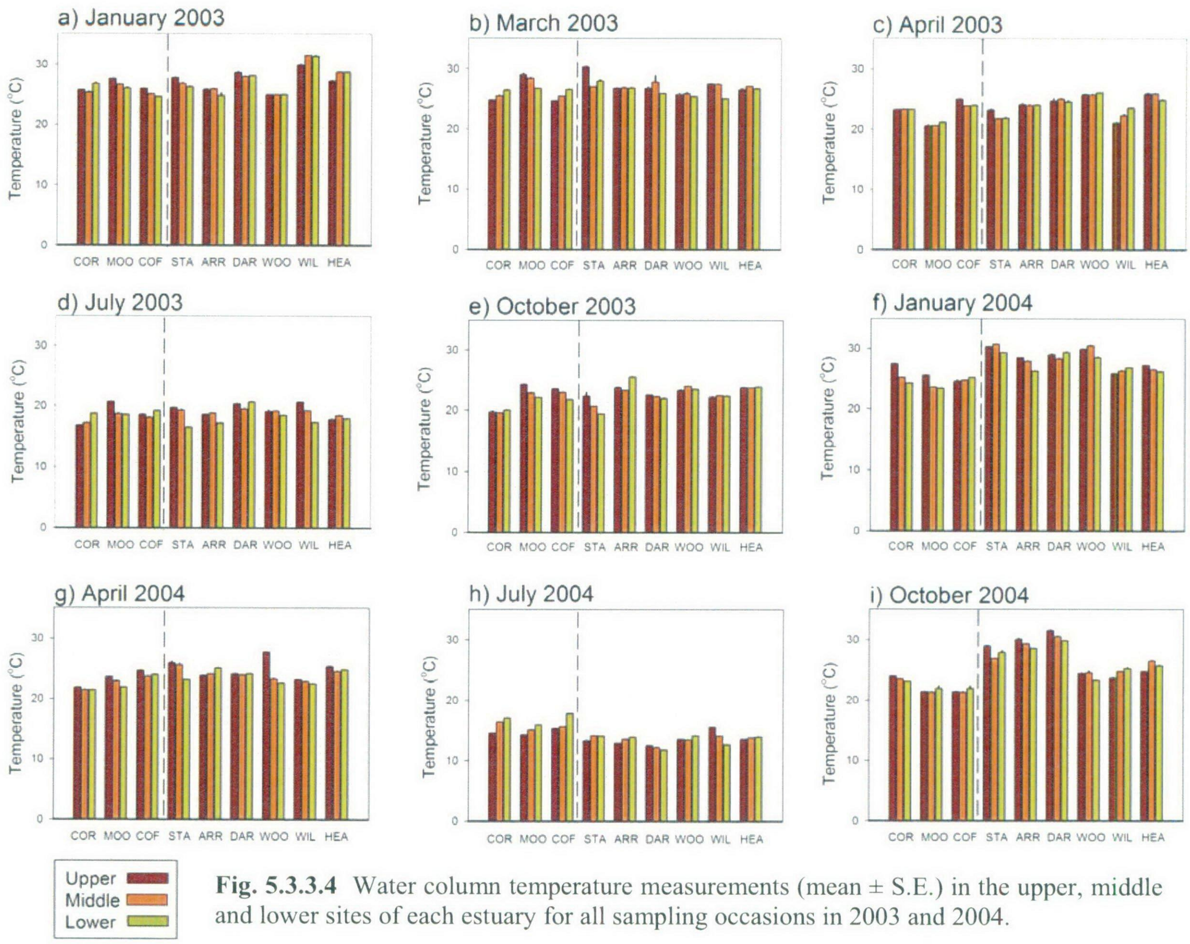

Fig. 5.3.3.4 Water column temperature measurements (mean ± S.E.) in the upper, middle and lower sites of each estuary for all sampling occasions in 2003 and 2004.

Sediment variables were more consistent and showed less variation over time. The graphic mean grain size in all estuaries at all times generally ranged between very fine sand (0.06 mm) and medium sand (0.40 mm) (Fig. 5.3.3.5). At times, the mean grain size was much larger in the middle site of Woolgoolga Lake (January 2003) and in both the upper and middle sites of

Table 5.3.3.5 Summary of results of two-way nested ANOVAs for the physico-chemical water column variables on all sampling occasions between January 2003 and October 2004. *d.f.* = 1,36 for comparisons between estuary type and *d.f.* = 7,36 for comparisons between estuaries nested within type. '-' indicates a non-significant results ($p > 0.05$), significant results are shown by '*' ($p < 0.05$) and '**' ($p <0.001$).

			2003					2004			
			Jan	Mar	Apr	Jul	Oct	Jan	Apr	Jul	Oct
TDS	Upper	Type	-	-	-	-	-	-	-	-	-
		Estuary(Type)	**	**	**	**	**	**	**	**	**
	Middle	Type	-	-	-	-	-	-	-	-	-
		Estuary(Type)	**	**	**	**	**	**	**	**	**
	Lower	Type	-	-	-	-	-	-	-	-	-
		Estuary(Type)	**	**	**	**	**	**	**	**	**
DO	Upper	Type	-	-	-	-	-	-	-	-	-
		Estuary(Type)	**	**	**	**	**	**	**	**	**
	Middle	Type	-	-	-	-	-	*	-	-	-
		Estuary(Type)	**	**	**	**	**	**	**	**	**
	Lower	Type	-	-	-	-	-	*	-	-	*
		Estuary(Type)	**	**	**	**	**	**	**	**	**
pH	Upper	Type	-	-	-	-	-	-	-	-	-
		Estuary(Type)	**	**	**	**	**	**	**	**	**
	Middle	Type	-	-	-	-	-	-	-	-	-
		Estuary(Type)	**	**	**	**	**	**	**	**	**
	Lower	Type	-	-	*	-	-	-	-	-	-
		Estuary(Type)	**	**	*	**	**	**	*	**	**
Temp.	Upper	Type	-	-	-	-	-	-	-	-	*
		Estuary(Type)	**	**	**	**	**	**	**	**	**
	Middle	Type	-	-	-	-	-	*	-	*	*
		Estuary(Type)	**	**	**	**	**	**	**	**	**
	Lower	Type	-	-	-	-	-	*	-	*	*
		Estuary(Type)	**	**	**	**	**	**	**	**	**

Arrawarra Creek (March 2003). At these particular times, the mean grain of these sites was 4.00 - 7.00 mm, which is classified as pebbles. In terms of the graphic standard deviation, or sediment homogeneity, the upper sites of most estuaries remained extremely poorly sorted, with a standard deviation greater than 4.0 Phi (Fig. 5.3.3.6). The middle sites of all estuaries were also, to a lesser extent, poorly sorted and the most homogenous sediments were found in the lower sites. Here sediment homogeneity averaged 1.0 Phi, which is classed as moderately well sorted. Organic content was also consistently highest in the upper sites of most estuaries (Fig. 5.3.3.7), averaging approximately 10 %. In contrast, organic content was nearly always at its lowest in the sediments of the lower estuary sites, with a typical mean of about 2 %. The ANOVAs for all sediment variables in January 2003 detected no significant differences between estuary types for any variable at any of the sites. This pattern continued for all sampling occasions throughout 2003 and 2004, with only one exception (Table 5.3.3.4). This occurred in

January 2004 when a significant difference was found in the sediment homogeneity between the intermittent and permanently open estuary types at the middle sites. At this time the sediments at the middle sites of the intermittent estuary type were, overall, more poorly sorted than those in the middle sites of the permanently open estuary type.

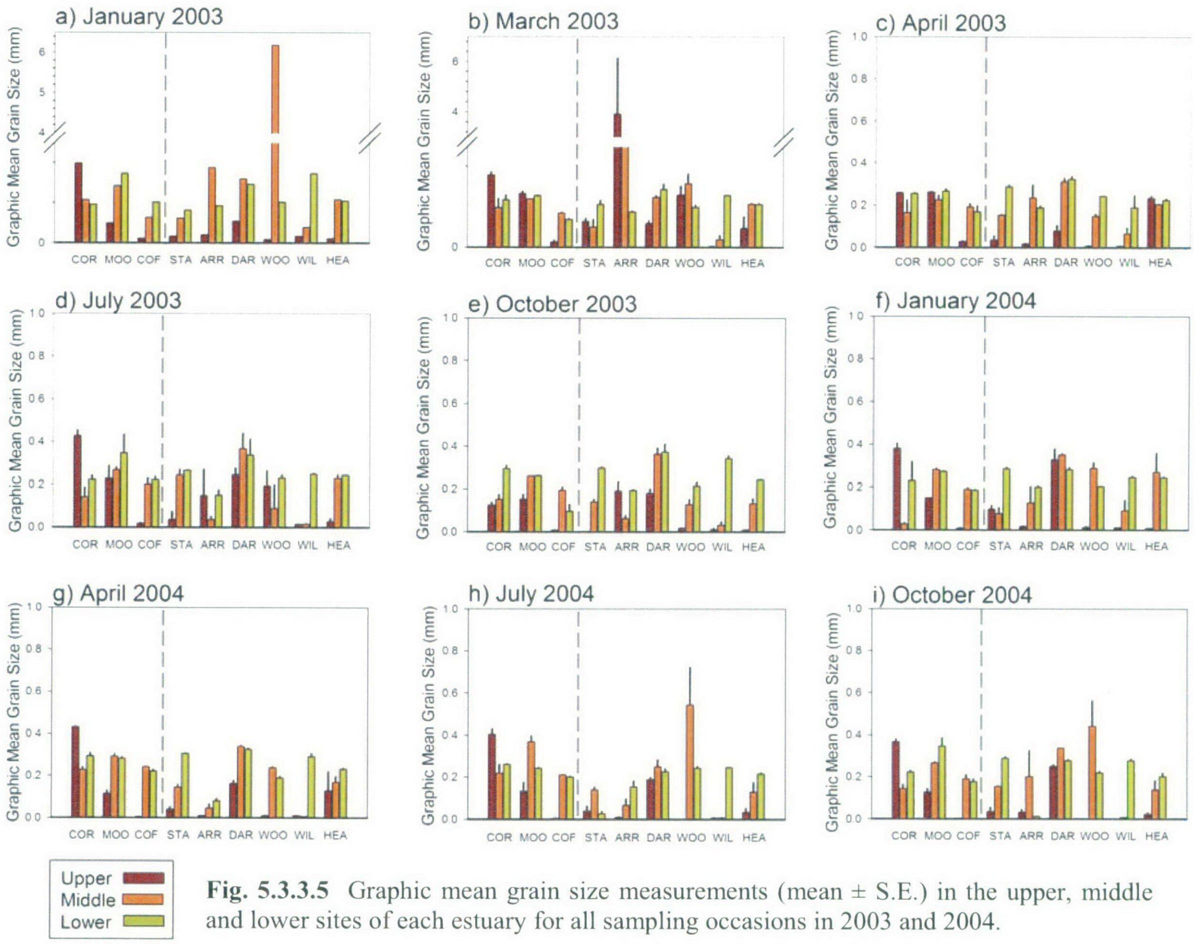

Fig. 5.3.3.5 Graphic mean grain size measurements (mean ± S.E.) in the upper, middle and lower sites of each estuary for all sampling occasions in 2003 and 2004.

Results were more variable when examining sediment differences among the estuaries nested within each type. Grain size was generally significantly different between the estuaries nested within each estuary type, with only one or two exceptions at each site (Table 5.3.3.4). Similarly, organic content was significantly different between the estuaries nested within each type on all but one occasion (April 2003) when there was no significant difference between estuaries at their lower sites. Sediment homogeneity usually produced significant differences among the estuaries of each type in their upper and middle sites. However, this was not the case at the lower sites, where differences in sediment homogeneity were less consistent, resulting in no significant differences between estuaries nested within type for almost half of the sampling times.

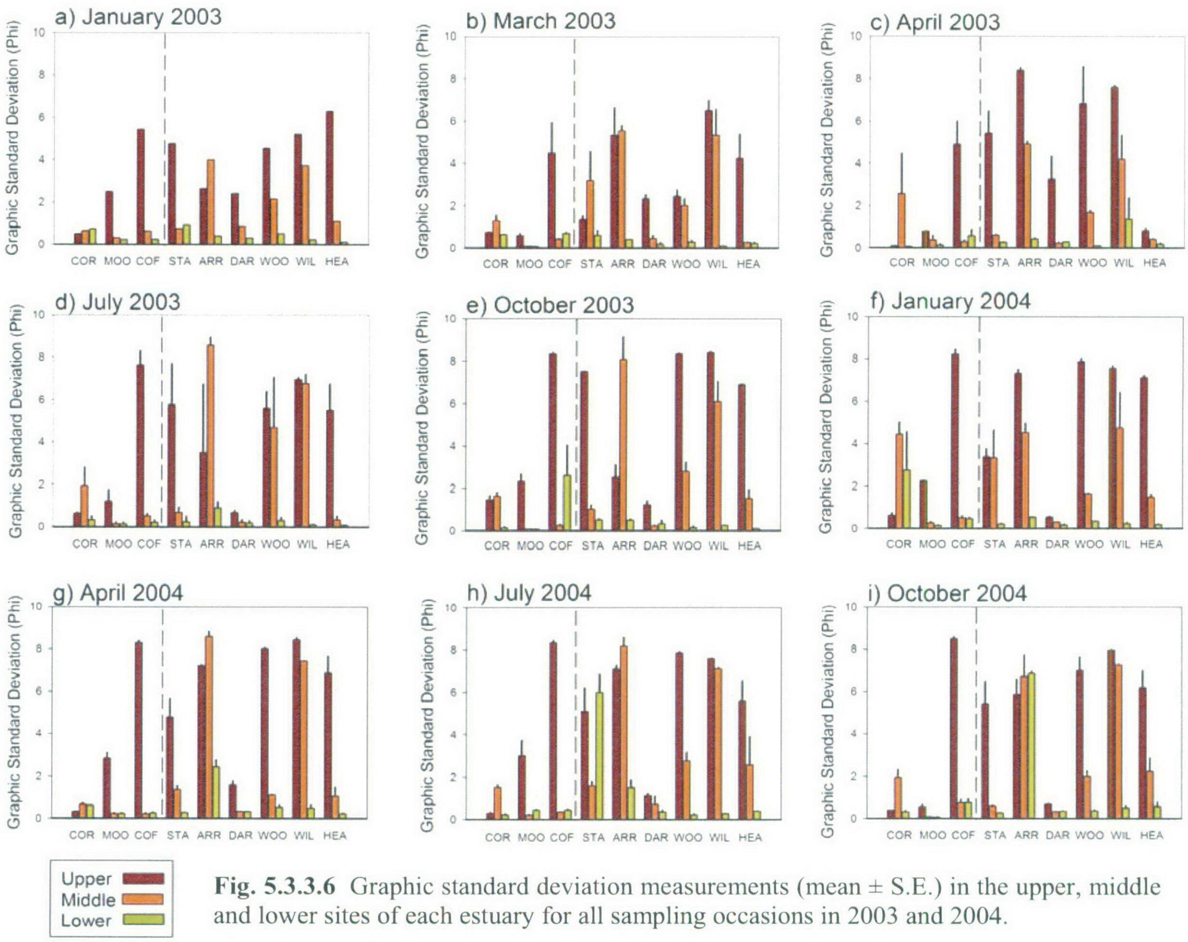

Fig. 5.3.3.6 Graphic standard deviation measurements (mean ± S.E.) in the upper, middle and lower sites of each estuary for all sampling occasions in 2003 and 2004.

Correlations between Community Structure and Environmental Variables

As in January 2003, the individual physico-chemical variable that was most closely correlated with community patterns was catchment size on all but one sampling occasion (Table 5.3.3.5). For the times when catchment size had the strongest relationship, its correlation coefficient (ρ) varied between 0.333 and 0.462. In April 2003, sediment homogeneity had the strongest individual correlation with the community data; however, this relationship was not particularly

strong (ρ = 0.283) and only slightly better than that associated with catchment size (ρ = 0.251). The strongest correlation was always produced when a combination of environmental variables was used. Although the specific combination varied for each sample time, they usually comprised catchment size, sediment homogeneity, organic content, and temperature.

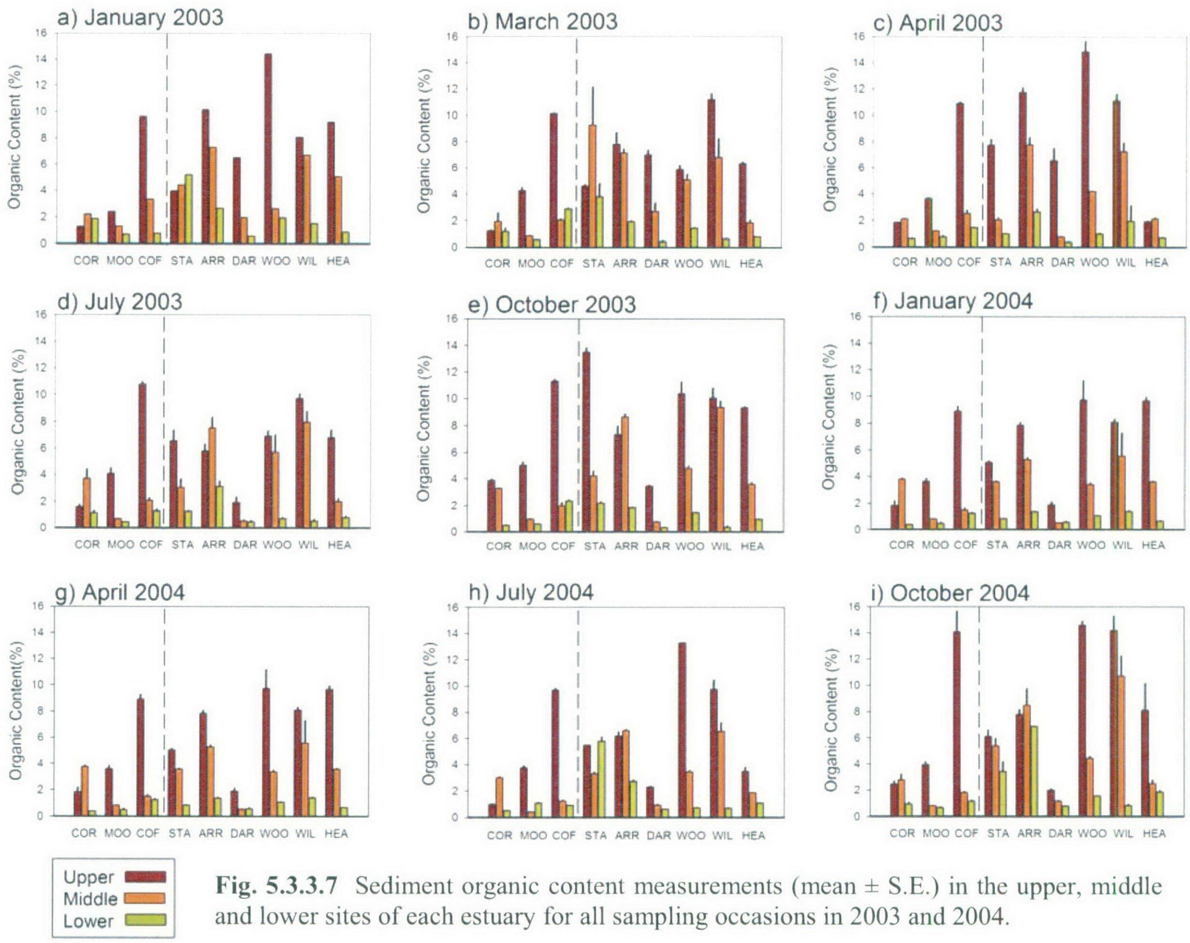

Fig. 5.3.3.7 Sediment organic content measurements (mean ± S.E.) in the upper, middle and lower sites of each estuary for all sampling occasions in 2003 and 2004.

Table 5.3.3.4 Summary of results of two-way nested ANOVAs for the physico-chemical sediment variables, graphic mean grain size (GMGS), graphic standard deviation (GSD) and organic content (OC), on all sampling occasions between January 2003 and October 2004. *d.f.* = 1,18 for comparisons between estuary type and *d.f.* = 7,18 for comparisons between estuaries nested within type. '-' indicates a non-significant results ($p > 0.05$), significant results are shown by '*' ($p < 0.05$) and '**' ($p < 0.001$).

			2003					2004			
			Jan	Mar	Apr	Jul	Oct	Jan	Apr	Jul	Oct
GMGS	Upper	Type	-	-	-	-	-	-	-	-	-
		Estuary(Type)	**	-	**	**	**	**	**	**	**
	Middle	Type	-	-	-	-	-	-	-	-	-
		Estuary(Type)	-	-	*	**	**	*	**	*	*
	Lower	Type	-	-	-	-	-	-	-	-	-
		Estuary(Type)	*	**	*	**	**	-	**	**	**
GSD	Upper	Type	-	-	-	-	-	-	-	-	-
		Estuary(Type)	-	*	*	**	**	**	**	**	**
	Middle	Type	-	-	-	-	-	*	-	-	-
		Estuary(Type)	*	*	*	**	**	*	**	**	**
	Lower	Type	-	-	-	-	-	-	-	-	-
		Estuary(Type)	-	*	-	**	-	-	**	**	**
OC	Upper	Type	-	-	-	-	-	-	-	-	-
		Estuary(Type)	**	**	**	**	**	**	**	**	**
	Middle	Type	-	-	-	-	-	-	-	-	-
		Estuary(Type)	**	*	**	**	**	*	*	**	**
	Lower	Type	-	-	-	-	-	-	-	-	-
		Estuary(Type)	**	**	-	**	**	**	**	**	**

Table 5.3.3.5 BIOENV results showing the Spearman rank correlation coefficient (ρ) for correlations between individual physico-chemical variables, and the best combinations of these variables (in italics), with the full community data for each sampling time between January 2003 and October 2004. The strongest correlation for an individual variable at each time is shown in bold.

	Variable	ρ								
		2003					2004			
		Jan	Mar	Apr	Jul	Oct	Jan	Apr	Jul	Oct
1	Total dissolved salts	0.255	0.039	0.246	0.098	0.243	0.373	0.077	0.084	0.350
2	Dissolved oxygen	0.210	0.154	-0.029	0.147	0.076	0.256	0.173	0.013	0.281
3	pH	0.075	0.124	0.143	0.116	0.246	0.050	0.115	0.170	0.313
4	Temperature	0.196	0.111	-0.023	0.143	0.205	0.220	0.236	0.379	0.046
5	Sediment grain size	0.089	0.080	0.166	0.169	0.296	0.175	0.188	0.144	0.218
6	Sediment homogeneity	0.135	0.172	**0.283**	0.228	0.273	0.140	0.199	0.311	0.177
7	Organic content	0.226	0.233	0.238	0.279	0.278	0.189	0.239	0.314	0.253
8	Catchment size	**0.453**	**0.377**	0.251	**0.377**	**0.462**	**0.403**	**0.333**	**0.426**	**0.448**
	Best combinations	0.497	0.422	0.352	0.437	0.546	0.499	0.376	0.521	0.479
		2,5-8	*2,4,6-8*	*1,3,6-8*	*2,4,6-8*	*3,4,6-8*	*2,4,7-8*	*2,4,6-8*	*3,4,6-8*	*1,3,7-8*