5.3.4 Temporal variation of benthic communities within individual estuaries

Before examining the temporal community patterns in each estuary in detail, a brief overview is presented. Within each estuary, a very high degree of temporal variability was evident between years and seasons, with significant differences at the upper, middle and lower sites (Table 5.3.4). This was true for all estuaries, except in the upper site of Woolgoolga Lake, where there was no significant difference ($p = 0.056$) between years. In addition, the relationship between

Table 5.3.4 PERMANOVA results testing for temporal differences at the scales of year ($df = 1$) and season ($df = 3$). *P*-value given is permutational *(p_perm)* as results produced a high number of unique values compared to the number of permutations. Bold font indicates a significant result.

		Upper		Middle		Lower	
		F	*p*	**F**	*p*	**F**	*p*
Station	Year	**2.680**	**0.020**	**8.322**	**0.001**	**7.129**	**0.001**
	Season	**8.538**	**0.001**	**4.296**	**0.001**	**4.986**	**0.001**
	Year x Season	**4.623**	**0.001**	**10.630**	**0.001**	**6.202**	**0.001**
Corindi	Year	**4.024**	**0.001**	**3.331**	**0.002**	**6.500**	**0.001**
	Season	**3.374**	**0.001**	**3.308**	**0.001**	**6.856**	**0.001**
	Year x Season	**2.557**	**0.001**	**2.592**	**0.001**	**4.899**	**0.001**
Arrawarra	Year	**8.704**	**0.001**	**11.408**	**0.001**	**9.739**	**0.001**
	Season	**7.671**	**0.001**	**12.253**	**0.001**	**5.705**	**0.001**
	Year x Season	**4.115**	**0.001**	**9.676**	**0.001**	**4.984**	**0.001**
Darkum	Year	**12.394**	**0.001**	**7.761**	**0.001**	**15.144**	**0.001**
	Season	**8.728**	**0.001**	**5.513**	**0.001**	**4.558**	**0.001**
	Year x Season	**6.937**	**0.001**	**3.556**	**0.001**	**4.631**	**0.001**
Woolgoolga	Year	1.819	0.056	**25.549**	**0.001**	**18.337**	**0.001**
	Season	**3.615**	**0.001**	**17.107**	**0.001**	**7.113**	**0.001**
	Year x Season	**3.571**	**0.001**	**11.084**	**0.001**	**9.666**	**0.001**
Willis	Year	**12.453**	**0.001**	**8.892**	**0.001**	**7.073**	**0.001**
	Season	**6.213**	**0.001**	**14.874**	**0.001**	**5.661**	**0.001**
	Year x Season	**9.176**	**0.001**	**9.939**	**0.001**	**5.069**	**0.001**
Hearns	Year	**6.873**	**0.001**	**8.996**	**0.001**	**2.803**	**0.011**
	Season	**13.486**	**0.001**	**10.509**	**0.001**	**5.073**	**0.001**
	Year x Season	**3.300**	**0.001**	**5.513**	**0.001**	**5.173**	**0.001**
Moonee	Year	**20.651**	**0.001**	**8.234**	**0.001**	**3.862**	**0.002**
	Season	**11.361**	**0.001**	**7.417**	**0.001**	**6.815**	**0.001**
	Year x Season	**9.803**	**0.001**	**7.160**	**0.001**	**3.207**	**0.001**
Coffs	Year	**5.788**	**0.001**	**5.501**	**0.001**	**4.816**	**0.001**
	Season	**2.566**	**0.001**	**6.243**	**0.001**	**8.623**	**0.001**
	Year x Season	**6.896**	**0.001**	**6.870**	**0.001**	**6.445**	**0.001**

seasons and years was not consistent, with highly significant interactions between years and seasons present at all sites in all estuaries.

5.3.4.1 Station Creek

The entrance of Station Creek was only closed for the first sampling time (January 2003). The benthic fauna here generally presented discrete communities between sampling times within each year at all sites (Fig. 5.3.4.1.1). However, the nMDS ordinations did reveal some overlap at the upper site from July to October 2003 and, at the lower site, between all 2003 sampling times except January. Pairwise *a posteriori* comparisons (Table 5.3.4.1) confirmed that all sampling times in each year, except for April and July 2003 at the middle site (p_mc = 0.119), were significantly different (p_mc < 0.05).

Plots where data are combined for 2003 and 2004 (Fig. 5.3.4.1.1 g, h, i) demonstrate that seasonal patterns are not repeated from 2003 to 2004, which is further supported by the pairwise comparisons for each season from 2003 to 2004, where only the April samples in the upper sites were not significantly different between years. The faunal community at the time when the entrance of this estuary was closed (January 2003) is completely separated from all other sampling times in the upper site and is similar to the community present in July 2004 for the middle and lower sites.

In the upper site the differences between sampling times in 2003 were primarily due to higher abundances of *Armandia intermedia* and *Spisula trigonella* in January and low abundances of all species in July. In the middle site a very high abundance of *A. intermedia* during October distinguished sampling times during 2003, as did the presence of *S. trigonella* in January, which was absent at other times. Differences between sampling times in the lower site during 2003 were mainly attributable to high abundances of Leptocheliidae sp. in January and the presence of *Scoloplos normalis* in October.

Sampling times in 2004 were differentiated by high abundances of *A. intermedia* during July in the upper site and, in the middle site, to high abundances of *Soletellina alba* during January and the presence of both *A. intermedia* and *Victoriopisa australiensis* during July. In the lower site,
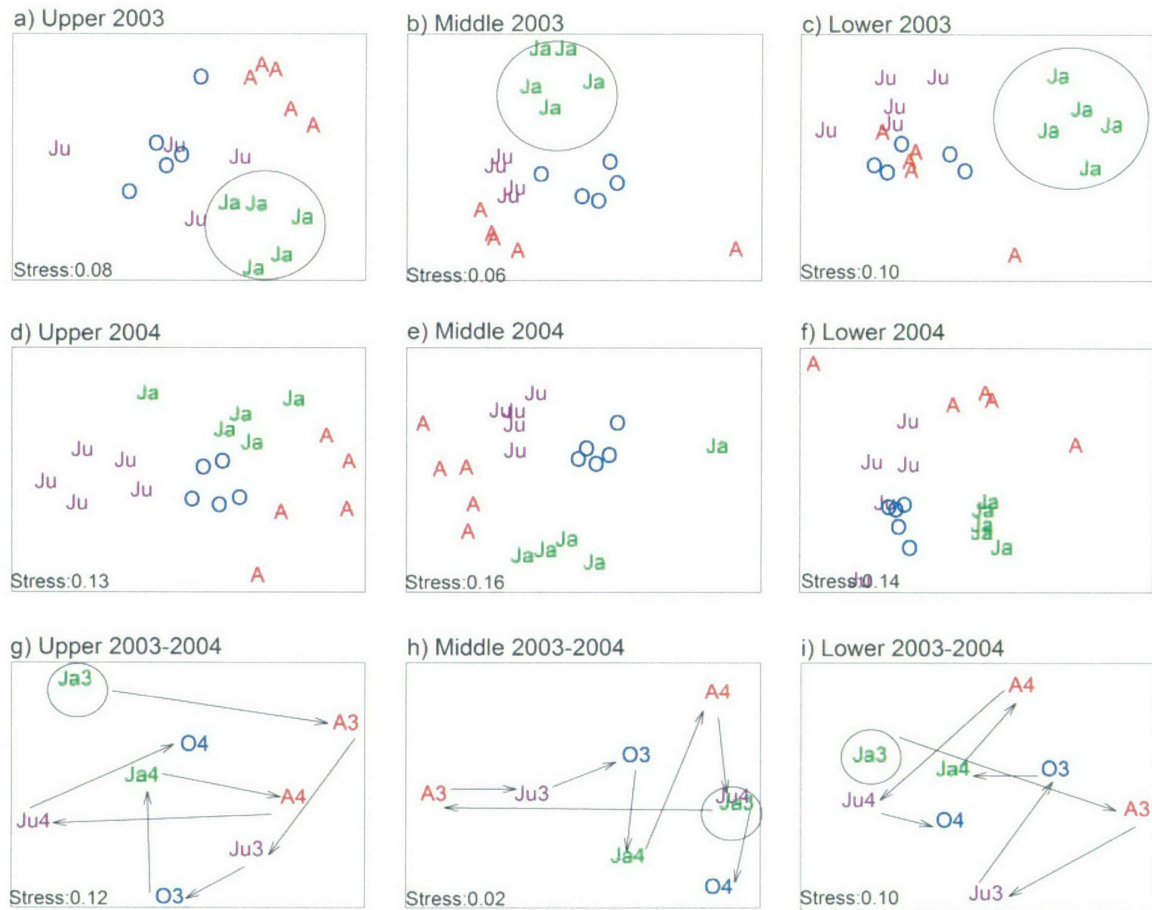
Fig. 5.3.4.1.1 Two-dimensional nMDS plots of benthic community structure in the upper, middle and lower sites of Station Creek in 2003 (a-c) and 2004 (d, e, f). For each year data points represent samples collected in January (Ja), April (A), July (Ju) and October (O). Also shown (g, h, i) are sample data averaged for each season and plotted in relation to one another. After each seasonal symbol '3' denotes data from 2003 and '4' data from 2004. Circles or polygons around data points indicate sampling times when the estuary entrance was closed. Kruskal-Wallis stress values are given for all plots.

differences between 2004 sampling times were due to higher abundances of *S. normalis* and *A. intermedia* in January and relatively low abundances of all fauna in April.

When comparing the sampling times from year to year, January 2003 was differentiated from January 2004 by higher abundances of *A. intermedia* at the upper site in 2003, an increase in *S. alba* at the middle site in 2004 and, at the lower site, greater abundances of Leptocheliidae sp. in 2003 and *S. normalis* in 2004. Differences between April sampling times were due to higher

abundances of *N. estuarius* at both the upper and middle sites in 2003, as well as a higher abundance in 2003 of *S. normalis* at the lower site. The two July sampling times were distinguished by an increase in the abundance of *A. intermedia* at all sites during 2004 and differences between October sampling times were due to greater abundances of *S. normalis* at the middle and lower sites.

Table 5.3.4.1 Station Creek pairwise comparisons between the seasons of each year and between the corresponding seasons from 2003 to 2004. Results given are the *t*-statistic and Monte Carlo *p*-value (*p_mc*). Bold font indicates a significant result.

	Upper		Middle		Lower	
Comparison groups	*t*	*p_mc*	*t*	*p_mc*	*t*	*p_mc*
2003						
January – April	**3.990**	**0.002**	**2.844**	**0.002**	**2.705**	**0.003**
January – July	**2.175**	**0.016**	**3.481**	**0.001**	**2.731**	**0.002**
January – October	**2.928**	**0.003**	**2.535**	**0.003**	**2.963**	**0.003**
April – July	**2.432**	**0.016**	1.542	0.119	1.524	0.083
April – October	**3.060**	**0.001**	**2.544**	**0.001**	1.006	0.364
July – October	0.651	0.667	**3.588**	**0.003**	**1.916**	**0.013**
2004						
January – April	**2.040**	**0.026**	**2.326**	**0.003**	**2.340**	**0.004**
January – July	**3.007**	**0.001**	**2.733**	**0.004**	**2.874**	**0.002**
January – October	**2.189**	**0.014**	**2.868**	**0.003**	**4.355**	**0.001**
April – July	**3.169**	**0.001**	**2.358**	**0.003**	**1.849**	**0.021**
April – October	**2.234**	**0.013**	**2.998**	**0.001**	**2.474**	**0.003**
July – October	**3.225**	**0.001**	**3.669**	**0.001**	**2.249**	**0.003**
January 2003 – January 2004	**2.277**	**0.009**	**2.509**	**0.004**	**2.534**	**0.003**
April 2003 – April 2004	1.705	0.086	**2.822**	**0.002**	**2.154**	**0.009**
July 2003 – July 2004	**1.931**	**0.026**	**4.572**	**0.002**	**2.384**	**0.003**
October 2003 – October 2004	**2.319**	**0.018**	**3.770**	**0.002**	**3.692**	**0.002**

When mean data are combined for all sampling times at all sites (Fig. 5.3.4.1.2) a general diagonal gradient is apparent from the upper sites in the lower-left side of the nMDS plot to the lower sites in the upper-right. This gradient still remained during entrance closure (January 2003), however, at this time the communities of each site tended towards the right-hand extremity of the ordination. July 2004 samples, which were taken following a period of low rainfall when most other intermittent estuaries were closed, also tended towards this end of the plot.
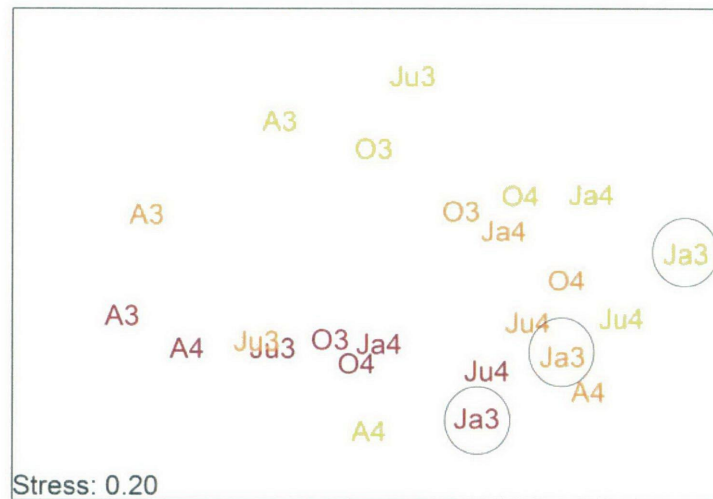
Fig. 5.2.4.2.1 Two-dimensional nMDS plot of benthic community structure at Station Creek in 2003 and 2004. Seasonal samples in each year have been averaged and data points are colour-coded by site: upper (red); middle (orange); lower (yellow). Circles indicate sampling times when the estuary entrance was closed. Kruskal-Wallis stress value also given.

5.3.4.2 Corindi River

In the permanently open Corindi River, there was considerable overlap between 2003 sampling times in the upper and middle sites (Fig 5.3.4.2.1. a, b), with only the October community being significantly different to that of January and April in the upper site (p_mc = 0.007; 0.032, respectively) and the January community being significantly different to that of July and October in the middle site (p_mc = 0.004; 0.014, respectively) (Table 5.3.4.2). In 2004, these two sites displayed slightly less overlap (Fig. 5.3.4.2.1 d, e) with additional significant pairwise comparisons among sampling times, specifically between July and both April and October (p_mc = 0.025; 0.010, respectively) in the upper site, as well as when comparing October to April and July (p_mc = 0.004; 0.003, respectively) in the middle site (Table 5.3.4.2). In contrast, sample times were quite discrete in the lower site of Corindi River during both 2003 and 2004, with significant differences for all pairwise comparisons, except between July and October in 2003 (p_mc = 0.073) and between July and January in 2004 (p_mc = 0.198).

Differences between sampling times in the upper site during 2003 were mainly attributable to the presence of *Nozeba topaziaca* in January and *Nephtys gravieri* in April, which were absent at other times, and high abundances of *V. australiensis*, *S. normalis*, and *Tellina imbellis* in
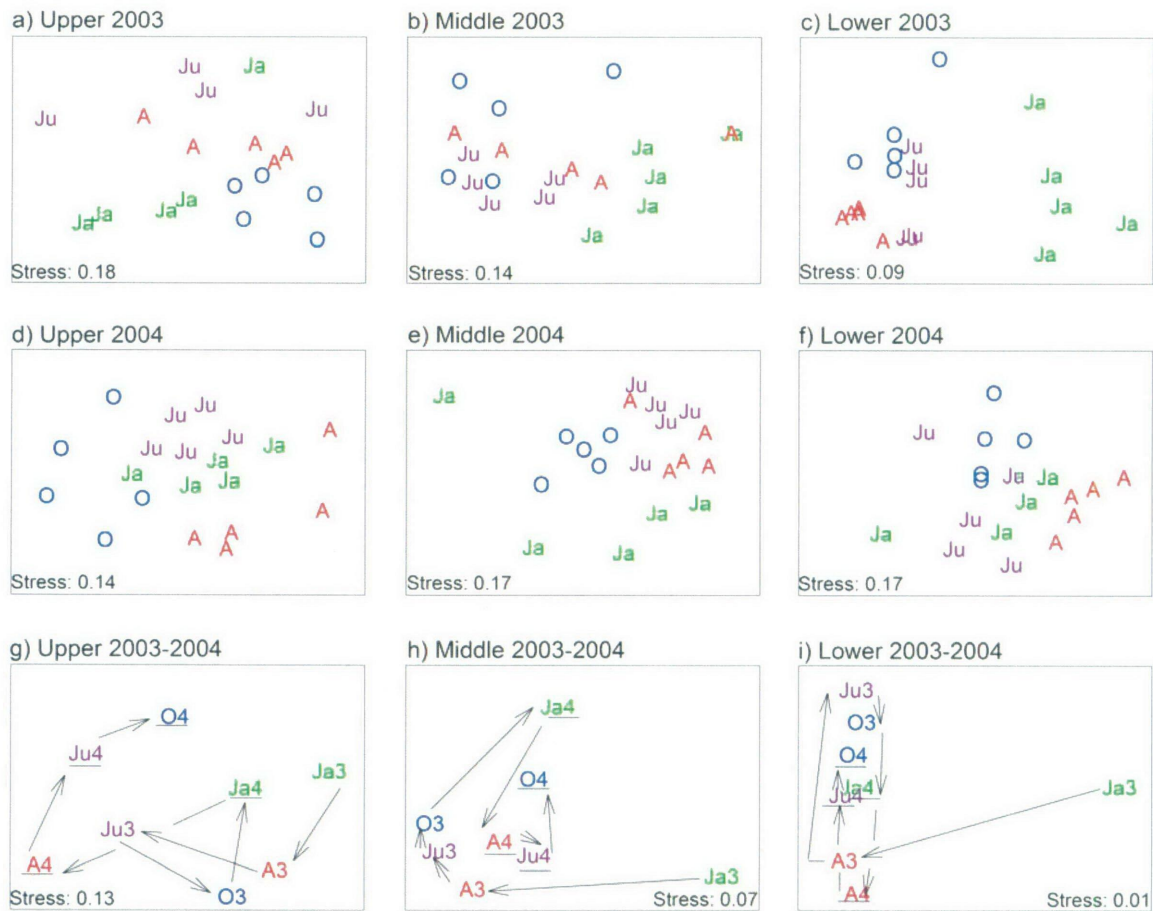

Fig. 5.3.4.2 Two-dimensional nMDS plots of benthic community structure in the upper, middle and lower sites of Corindi River in 2003 (a – c) and 2004 (d – f). For each year data points represent samples collected in January (Ja), April (A), July (Ju) and October (O). Also shown (g, h, i) are sample data averaged for each season and plotted in relation to one another. After each seasonal symbol '3' denotes data from 2003 and '4' data from 2004. Kruskal-Wallis stress values are given for all plots.

October. In the same year sampling times at the middle sites were differentiated by the presence of *Australonereis ehlersi* in January, *N. gravieri* and *Trypaea australiensis* in July, and also higher abundances of *T. australiensis* in October. Differences between sampling times at the lower site in 2003 were due to high abundances of *Urohaustorius metungi* in April and its low abundance in January, as well as the presence of *Mictyris longicarpus* in July.

Table 5.3.4.2 Corindi River pairwise comparisons between the seasons of each year and between the corresponding seasons from 2003 to 2004. Results given are the *t*-statistic and Monte Carlo *p*-value (*p_mc*). Bold font indicates a significant result.

Comparison groups	Upper		Middle		Lower	
	t	*p_mc*	*t*	*p_mc*	*t*	*p_mc*
2003						
January – April	1.655	0.064	1.383	0.125	**3.512**	**0.002**
January – July	1.528	0.051	**2.285**	**0.004**	**2.910**	**0.002**
January – October	**2.061**	**0.007**	**1.944**	**0.014**	**2.742**	**0.003**
April – July	1.427	0.121	1.382	0.161	**2.471**	**0.006**
April – October	**1.663**	**0.032**	1.372	0.116	**2.431**	**0.001**
July – October	1.567	0.054	1.463	0.075	1.556	0.073
2004						
January – April	1.659	0.052	1.452	0.086	**1.748**	**0.038**
January – July	1.609	0.056	**1.708**	**0.031**	1.282	0.198
January – October	**1.977**	**0.018**	1.581	0.061	**1.839**	**0.038**
April – July	**1.805**	**0.022**	1.554	0.068	**2.073**	**0.006**
April – October	**1.693**	**0.025**	**2.362**	**0.004**	**2.895**	**0.001**
July – October	**1.997**	**0.010**	**2.370**	**0.003**	**2.093**	**0.009**
January 2003 – January 2004	1.489	0.101	1.368	0.111	**2.869**	**0.002**
April 2003 – April 2004	**1.736**	**0.025**	1.450	0.082	**1.550**	**0.046**
July 2003 – July 2004	1.398	0.109	**2.017**	**0.013**	**1.931**	**0.012**
October 2003 – October 2004	**2.178**	**0.008**	**2.024**	**0.012**	**2.126**	**0.020**

In 2004 the differences between sampling times at the upper site were primarily due to the low abundances, or absence, of many species in April. At the middle site a high abundance of *S. alba* in January and *T. australiensis* in both July and October were largely responsible for the differences between sampling times. Again, in 2004, varying abundances of *U. metungi*, higher in April and lower in July, differentiate between sampling times at the lower site. The presence of *Mysella vitrea* in October was also important.

On occasion, there was a tendency for community structure to cluster by season over the two sampling years (Fig. 5.3.4.2.1 g-i), especially the January sampling times at the upper site, April sampling times at both the middle and lower sites, and October sampling times at the lower site. Significant differences, however, were found for comparisons of most sampling times from year to year, excepting January in both the upper and middle sites, April in the middle site and July in the upper site (Table 5.3.4.2). From 2003 to 2004 differences between the January sampling

times at the lower site were due to an increase in *U. metungi* in 2004. For April sampling times *U. metungi* was actually greater in abundance at the lower site in 2003, as was *N. gravieri* at the upper site.
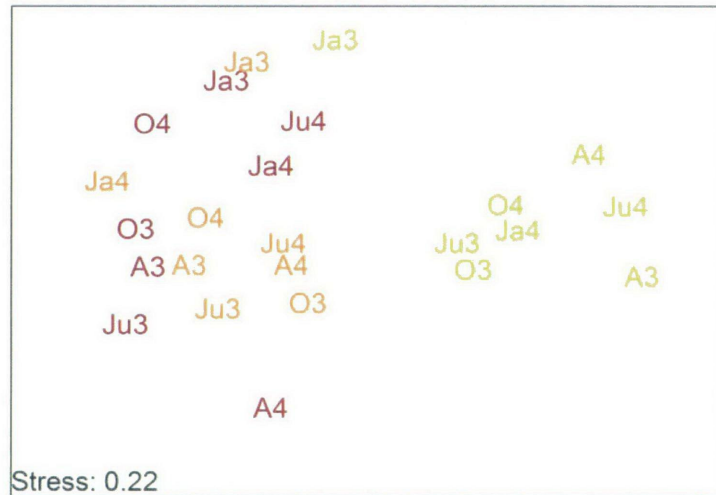

Fig. 5.3.4.2.2 Two-dimensional nMDS plot of benthic community structure at Corindi River in 2003 and 2004. Seasonal samples in each year have been averaged and data points are colour-coded by site: upper (red); middle (orange); lower (yellow). Kruskal-Wallis stress value is given.

In comparison to 2004, July 2003 was characterised by an increase in *M. longicarpus* at the lower site and lower abundances of *A. ehlersi* and *N. gravieri* at the middle site. October sampling times were mainly differentiated by the occurrence of *V.* at the upper site in 2003 and an increase in *U. metungi* at the lower site during 2004.

When comparing all sampling times for all sites (Fig. 5.3.4.2.2), the lower site for all times, excluding January 2003, were completely separated from the upper and middle sites. Sites could not be distinguished further in this summary nMDS plot as, throughout time, there was great overlap between the upper and middle sites. Although there was a high stress value for this plot, exploration of patterns using a three-dimensional ordination confirmed this overlap between the upper and middle sites.

5.3.4.3 Arrawarra Creek

Arrawarra Creek had four entrance closures and was closed for 21.7 % of the study duration. nMDS plots for Arrawarra Creek in 2003 (Fig. 5.3.4.3.1 a-c) suggest a considerable degree of separation between sampling times, especially at the middle site. These differences between sampling times were significant for all pairwise comparisons (Table 5.3.4.3) and mainly due to the absence of both *A. intermedia* and *Simplisetia aequisetis* at the upper site in April and very high abundances of *A. intermedia* across all sites in July, with up to 170 per sample at the upper site. Both *A. intermedia* and *Orthoprionospio cirriformia* were also absent from the lower site in October 2003. In 2004 all sampling times appeared discrete in the upper and middle sites (Fig. 5.3.4.3.1 d, e), whereas there was overlap between all sampling times, excluding January, in the lower site. All pairwise comparisons for 2004 were significantly different, except for those between April and both July and October at the lower site. SIMPER analysis of the 2004 sampling times revealed that the species primarily responsible for these differences were *A. intermedia*, which was more abundant at the upper and middle sites in July, and *Simplisetia aequisetis*, which was more abundant at the upper and lower sites in October. *Arthritica helmsi* was also more abundant at the upper site in July when compared to all other sampling times and *Notomastus estuarius* was absent for both the January and October sampling times in 2004.

Over the two-year period, January sampling times for both years were grouped closely together at all sites but were significantly different at both the middle and lower sites (Table 5.3.4.3). With this exception, there were no repeatable seasonal, as supported by significant Year x Season interactions (Table 5.3.4), or entrance-related patterns. From 2003 to 2004, January samples were differentiated by an increase in the abundance of *S. normalis* at the upper and lower site in 2004, as well as an increase in the abundance of *Arthitica helmsi* at the middle site. The April 2003 community was very different to that for all other sampling times due to low abundance of some species and the absence of many others. In comparison to July 2003, July 2004 was characterised by an increase in *A. helmsi* and a decrease in *S. aequisetis* at the upper site, a decrease in *A. intermedia* at the middle site, and decreases in both *S. normalis* and *Mysella vitrea* at the lower site. October 2004 had higher abundances of *A. helmsi* at the upper site and *S. aequisetis* at the lower site, when compared to October 2003. October 2004 also featured comparatively lower abundances of all species at the middle site. For all sites, October 2003 had higher abundances of *S. normalis* than October 2004.
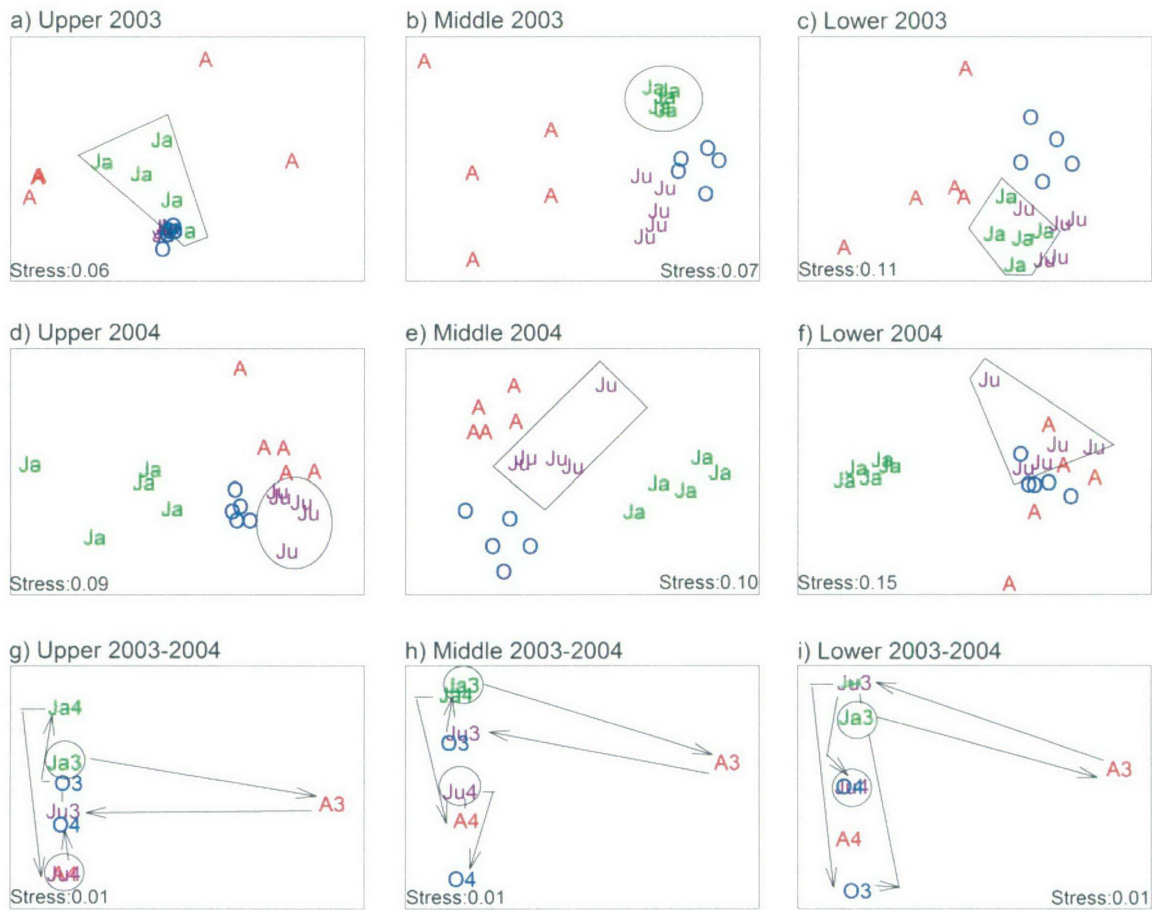
Fig. 5.3.4.3.1 Two-dimensional nMDS plots of benthic community structure in the upper, middle and lower sites of Arrawarra Creek in 2003 (a – c) and (d – f) 2004. For each year data points represent samples collected in January (Ja), April (A), July (Ju) and October (O). Also shown (g, h, i) are sample data averaged for each season and plotted in relation to one another. After each seasonal symbol '3' denotes data from 2003 and '4' data from 2004. Circles or polygons around data points indicate sampling times when the estuary entrance was closed. Kruskal-Wallis stress values are given for all plots.

The summary nMDS plot of all sampling time averages (Fig. 5.3.4.3.2) shows that the community at the lower site completely separated from the other two sites over time. The communities of the upper and middle sites, however, overlapped considerably over time. None of these changes appeared to be related to the status of the entrance at the time of sampling.

Table 5.3.4.3 Arrawarra Creek pairwise comparisons between the seasons of each year and between the corresponding seasons from 2003 to 2004. Results given are the *t*-statistic and Monte Carlo *p*-value (*p_mc*). Bold font indicates a significant result.

| Comparison groups	Upper		Middle		Lower	
	t	*p_mc*	*t*	*p_mc*	*t*	*p_mc*
2003						
January – April	**1.787**	**0.034**	**3.438**	**0.002**	**2.190**	**0.008**
January – July	**2.341**	**0.006**	**2.189**	**0.001**	**1.787**	**0.031**
January – October	**2.115**	**0.022**	**2.928**	**0.003**	**2.569**	**0.003**
April – July	**2.681**	**0.005**	**3.138**	**0.002**	**2.502**	**0.006**
April – October	**2.573**	**0.001**	**3.513**	**0.001**	**2.420**	**0.001**
July – October	**2.464**	**0.003**	**2.597**	**0.003**	**2.661**	**0.003**
2004						
January – April	**2.697**	**0.001**	**4.894**	**0.001**	**2.775**	**0.001**
January – July	**3.096**	**0.001**	**2.943**	**0.001**	**3.268**	**0.001**
January – October	**2.813**	**0.002**	**4.328**	**0.001**	**3.461**	**0.002**
April – July	**2.066**	**0.011**	**2.126**	**0.010**	1.287	0.165
April – October	**2.592**	**0.004**	**3.789**	**0.001**	1.103	0.292
July – October	**2.686**	**0.002**	**2.462**	**0.003**	**1.723**	**0.024**
January 2003 – January 2004	1.343	0.143	**3.606**	**0.002**	**2.462**	**0.006**
April 2003 – April 2004	**2.370**	**0.003**	**3.353**	**0.001**	**2.369**	**0.002**
July 2003 – July 2004	**3.519**	**0.002**	**2.299**	**0.006**	**2.504**	**0.005**
October 2003 – October 2004	**3.402**	**0.003**	**3.330**	**0.002**	**2.735**	**0.004**
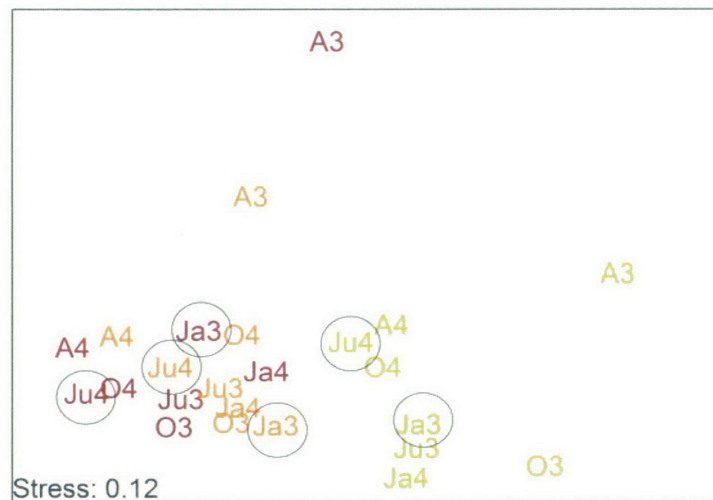
Fig. 5.3.4.3.2 Two-dimensional nMDS plot of benthic community structure at Arrawarra Creek in 2003 and 2004. Seasonal samples in each year have been averaged and data points are colour-coded by site: upper (red); middle (orange); lower (yellow). Circles indicate sampling times when the estuary entrance was closed. Kruskal-Wallis stress value also given.

5.3.4.4 Darkum Creek

Of all the estuaries studied, Darkum Creek was closed for the greatest proportion of time (76.3 %). At the upper site of Darkum Creek, all sampling times were completely separated from one another in the nMDS plots (Fig. 5.3.4.4.1 a, d), as were the 2004 sampling times at the middle site (Fig. 5.3.4.4.1 e). A substantial degree of overlap between sampling times was present at the lower site for both years and at the middle site in 2003. All pairwise comparisons between sampling times were significantly different for the upper in 2003 and 2004, and for the middle site in 2004 (Table 5.3.4.4). Most of the remaining pairwise comparisons were also significantly different, except those between April and both January and July at the lower site in 2003, January and July at the middle site in 2003, and between July and October at the lower site in 2004. Overall, the main differences between sampling times at the upper site during 2003 were due to high abundances *A. helmsi*, *S. aequitsetis* and *O. cirriformia* in October, and low abundances or absences of most species in January and July. The middle site was defined by higher abundances of *A. helmsi* in October and absences of both this species in January and *S. normalis* in April. Likewise, the lower site had very low abundances of most species in January and April of 2003. Sampling times in 2004 mostly differed due to higher abundances of *A. helmsi* and *S. normalis* at both the upper and middle sites in October, low abundances of all species at the upper and middle sites in April, and high abundances of *Soletellina alba* at the lower site in July and October.

There were no repeatable seasonal patterns in the benthic community of Darkum Creek from 2003 to 2004 (Fig. 5.3.4.4.1 g-i), as supported by the significant Year x Season interactions (Table 5.3.4). The observed patterns also did not appear to relate to the entrance status, which was open for only two of the sampling occasions (April and October 2004). Pairwise comparisons of sampling times from 2003 to 2004 were significantly different for all except April at the middle site ($p = 0.063$) (Table 5.3.4.4). An increase in the abundance of *A. helmsi* across each of the upper, middle and lower sites was primarily responsible for the differences between January 2003 and January 2004. An increase in the abundance of this species in 2004 also differentiated between July sampling times at the upper and middle sites. In contrast, at these sites, the differences between both the April and October sampling times from 2003 to 2004 were mainly due to higher abundances of *S. aequisetis* in 2003. Increases in the abundance
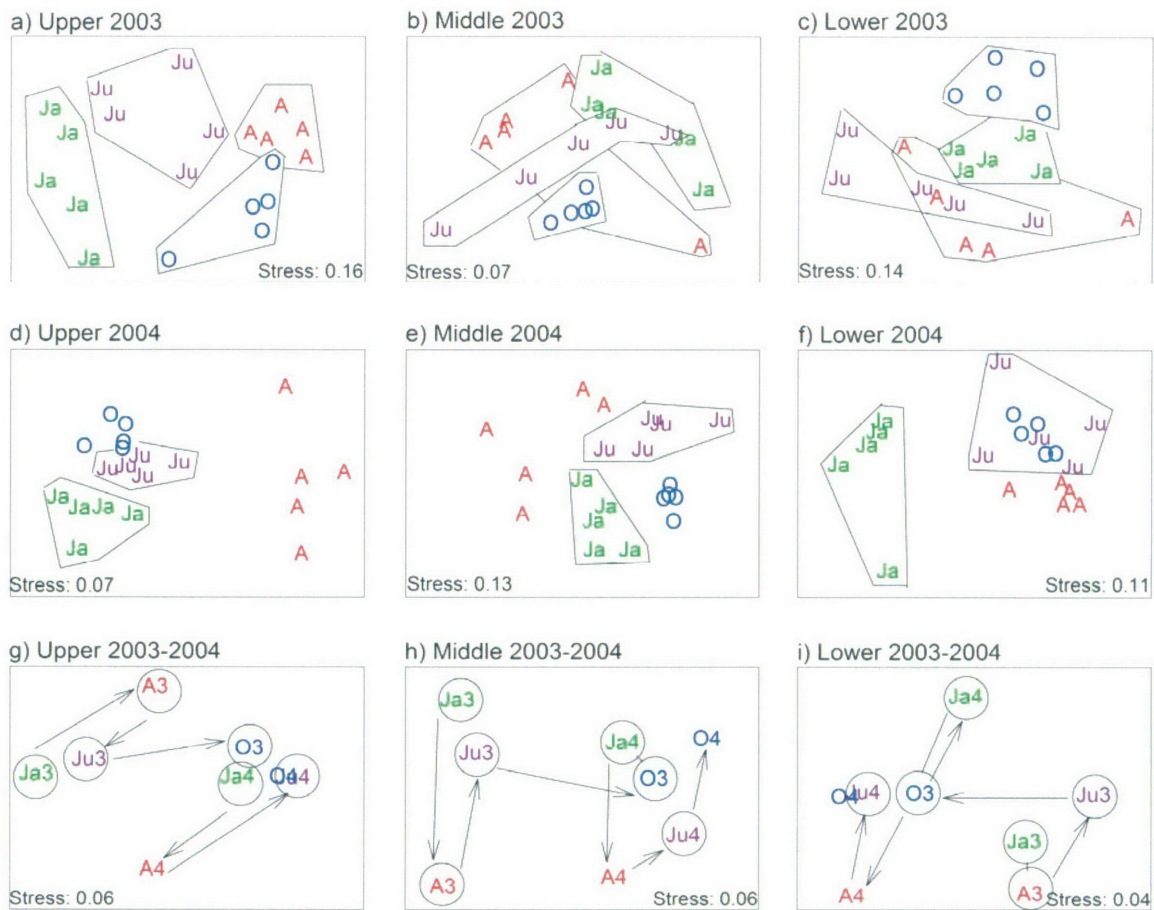
Fig. 5.3.4.4 Two-dimensional nMDS plots of benthic community structure in the (a) upper, (b) middle and (c) lower sites of Darkum Creek in 2003 and (d, e, f) 2004. For each year data points represent samples collected in January (Ja), April (A), July (Ju) and October (O). Also shown (g, h, i) are sample data averaged for each season and plotted in relation to one another. After each seasonal symbol '3' denotes data from 2003 and '4' data from 2004. Circles or polygons around data points indicate sampling times when the estuary entrance was closed. Kruskal-Wallis stress values are given for all plots.

of the bivalve *S. alba* at the lower site in 2004 differentiated between the April, July and October sampling times of each year.

The summary nMDS plot with the average sampling times shown for each site presents a persistent gradient between the upper, middle and lower sites over time. This gradient is not strongly defined due to its condensed nature on the left-hand side of the graph. All sampling times that were conducted when the entrance of this estuary was open tended towards this condensed end of the gradient, where differences between the communities of each site were reduced. However, the other times when community structure similarly converged between sites, October 2003 and July 2004, were times during lengthy closures.

Table 5.3.4.4 Darkum Creek pairwise comparisons between the seasons of each year and between the corresponding seasons from 2003 to 2004. Results given are the *t*-statistic and Monte Carlo *p*-value (*p_mc*). Bold font indicates a significant result.

| Comparison groups	Upper		Middle		Lower	
	t	*p_mc*	*t*	*p_mc*	*t*	*p_mc*
2003						
January – April	**2.939**	**0.002**	1.780	0.053	1.295	0.190
January – July	**1.844**	**0.020**	1.222	0.233	**1.980**	**0.022**
January – October	**2.451**	**0.003**	**2.932**	**0.003**	**2.271**	**0.008**
April – July	**2.615**	**0.007**	1.596	0.086	1.159	0.293
April – October	**2.858**	**0.001**	**2.623**	**0.001**	**2.019**	**0.008**
July – October	**2.254**	**0.005**	**2.274**	**0.009**	**2.542**	**0.003**
2004						
January – April	**4.010**	**0.001**	**1.909**	**0.019**	**3.250**	**0.001**
January – July	**2.566**	**0.007**	**2.340**	**0.008**	**2.564**	**0.005**
January – October	**3.226**	**0.002**	**2.724**	**0.003**	**3.130**	**0.002**
April – July	**3.243**	**0.002**	**2.083**	**0.010**	**2.016**	**0.014**
April – October	**3.873**	**0.001**	**3.073**	**0.001**	**2.881**	**0.002**
July – October	**1.847**	**0.018**	**2.145**	**0.003**	1.629	0.051
January 2003 – January 2004	**2.693**	**0.002**	**2.590**	**0.004**	**2.677**	**0.003**
April 2003 – April 2004	**3.832**	**0.001**	1.592	0.063	**2.614**	**0.002**
July 2003 – July 2004	**2.773**	**0.003**	**2.182**	**0.009**	**2.850**	**0.003**
October 2003 – October 2004	**1.780**	**0.043**	**2.563**	**0.006**	**2.576**	**0.007**
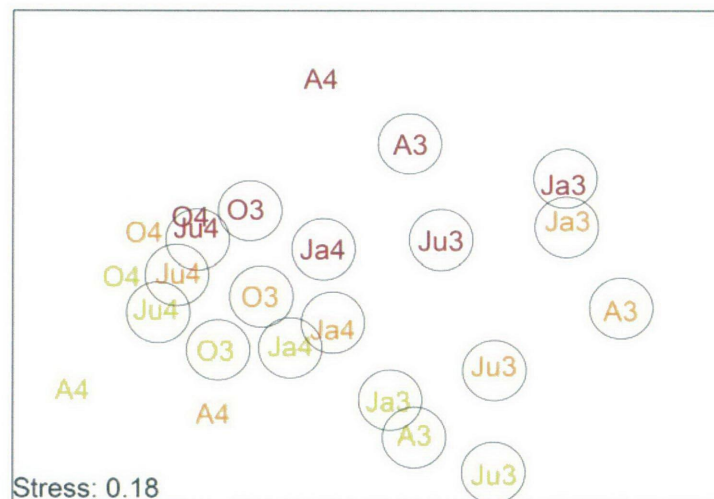
Fig. 5.3.4.4.2 Two-dimensional nMDS plot of benthic community structure at Darkum Creek in 2003 and 2004. Seasonal samples in each year have been averaged and data points are colour-coded by site: upper (red); middle (orange); lower (yellow). Circles indicate sampling times when the estuary entrance was closed. Kruskal-Wallis stress value also given.

5.3.4.5 Woolgoolga Lake

The entrance of Woolgoolga Lake closed four times and the estuary was without marine input for approximately half of the study duration (51.7 %). A high degree of overlap between sampling times was evident at the upper site of Woolgoolga Lake during both 2003 and 2004 (Fig. 5.3.4.5.1 a, d). There were no significant differences between October and both January and July in 2003, or between April and both January and October in 2004 (2004) (Table 5.3.4.5). In contrast, the sampling times within each year comprised highly discrete communities at the middle and lower site (Fig. 5.3.4.5.1 b, c, e, f), where significant differences were revealed for all pairwise comparisons, other than between April and July at the lower site in 2004. The differences between sampling times at both the upper an middle sites in 2003 were primarily a result of higher abundances of *Batillaria australis* in January and *Cerithium corallium* in July. At the lower site in 2003, greater abundances of *M. vitrea* in January, *U. metungi* in April and *S. normalis* in July differentiated the sampling times. In contrast, differences between sampling times at the lower site in 2004 were due to the absence of *U. metungi* for all times other than January and an increase in the abundance of *S. alba* in October. In 2004, sampling times at the upper site were primarily distinguished by greater abundances of *A. intermedia* in January, *O. cirriformia* in July and *V. australiensis* in October. Higher abundances of *V. australiensis* at the middle site in April were also responsible for differences between sampling times in this year, as were higher abundances of both *B. australis* and *C. corallium* in January.

There was a high degree of variation when comparing the 2003 to 2004 sampling times (Fig. 5.3.4.5.1 g-i), with significant differences for all pairwise comparisons at all sites, except between the January sampling times of each year at the upper site (Table 5.3.4.5). At the middle site the January and April samples in 2003 were considerable outliers in comparison to all other sampling times, due to low abundances or absences of all species at these times. January sampling times were primarily differentiated by higher abundances of *C. corallium* at the middle site in 2004 and *M. vitrea* at the lower site in 2003. In 2004 a greater abundance of both *B. australis* and *C. corallium* was responsible for the differences between April sampling times at the middle site. Again, at the middle site, the same two species also differentiated July samples; however, they were more abundant in 2003. October sampling times were mainly separated by higher abundances of *V. australiensis* at the upper site in 2004 and *N. estuarius* at

the middle site in 2003. At the lower site, all differences between sampling times over the two years were due to greater abundances of *U. metungi* in 2003 and an increase in the abundance of *S. alba* in 2004.
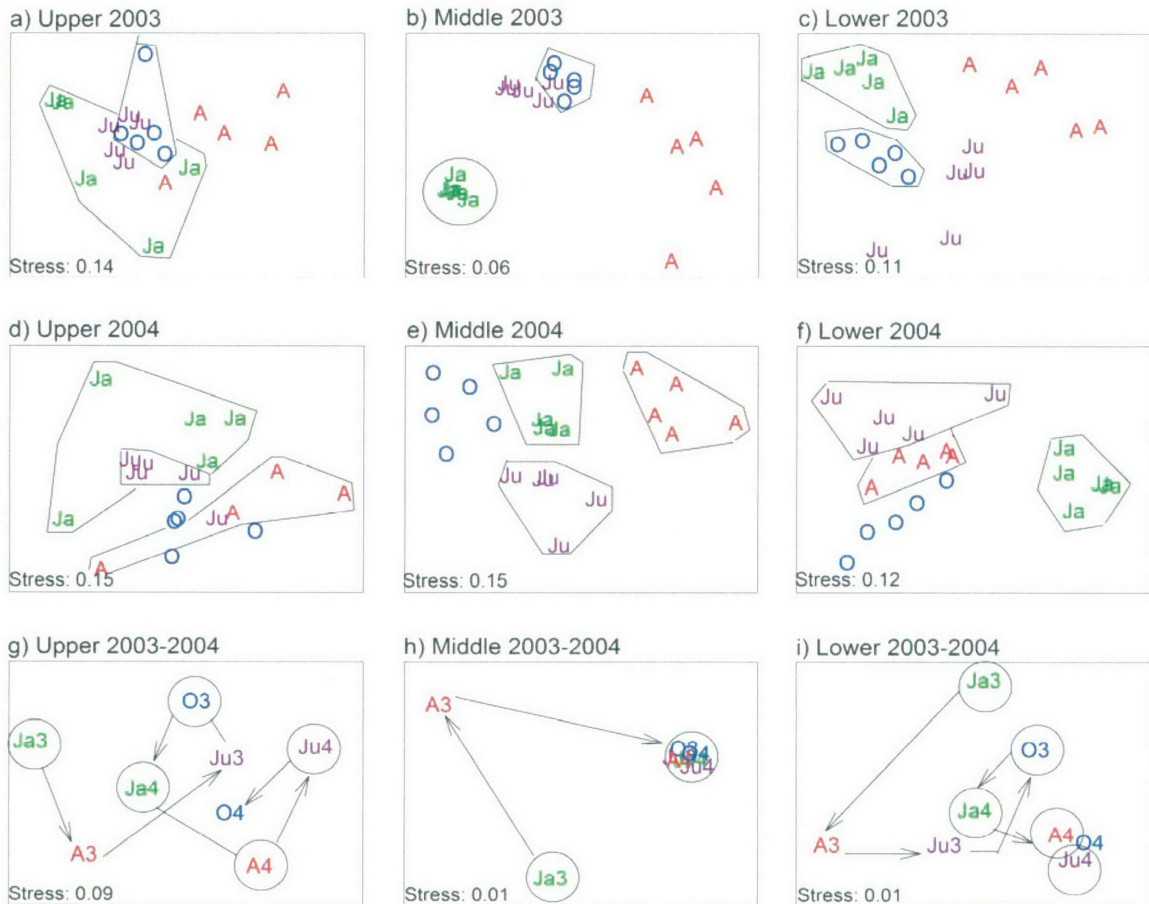

Fig. 5.3.4.5.1 Two-dimensional nMDS plots of benthic community structure in the (a) upper, (b) middle and (c) lower sites of Woolgoolga Lake in 2003 and (d, e, f) 2004. For each year data points represent samples collected in January (Ja), April (A), July (Ju) and October (O). Also shown (g, h, i) are sample data averaged for each season and plotted in relation to one another. After each seasonal symbol '3' denotes data from 2003 and '4' data from 2004. Circles or polygons around data points indicate sampling times when the estuary entrance was closed. Kruskal-Wallis stress values are given for all plots.

Examination of the summary nMDS plot of all sites over time suggests that a persistent gradient was evident between the upper, middle and lower sites of Woolgoolga Lake (Fig. 5.3.4.5.2). However, a small degree overlap was evident between the upper and middle sites during several periods of entrance closure, including April and July 2004 and, to a lesser extent, October 2003.

Table 5.3.4.5 Woolgoolga Lake pairwise comparisons between the seasons of each year and between the corresponding seasons from 2003 to 2004. Results given are the *t*-statistic and Monte Carlo *p*-value (*p_mc*). Bold font indicates a significant result.

| Comparison groups	Upper		Middle		Lower	
	t	*p_mc*	*t*	*p_mc*	*t*	*p_mc*
2003						
January – April	**1.793**	**0.028**	**4.834**	**0.002**	**3.711**	**0.002**
January – July	**2.011**	**0.012**	**5.559**	**0.001**	**3.099**	**0.002**
January – October	1.457	0.089	**5.532**	**0.001**	**2.316**	**0.008**
April – July	**2.870**	**0.005**	**3.866**	**0.002**	**2.491**	**0.007**
April – October	**1.997**	**0.010**	**3.174**	**0.001**	**3.276**	**0.001**
July – October	1.550	0.073	**2.801**	**0.003**	**2.186**	**0.006**
2004						
January – April	1.449	0.107	**3.187**	**0.001**	**3.702**	**0.001**
January – July	**2.068**	**0.019**	**2.322**	**0.009**	**3.527**	**0.001**
January – October	**1.971**	**0.022**	**2.035**	**0.018**	**4.317**	**0.001**
April – July	**1.980**	**0.014**	**3.630**	**0.001**	1.313	0.165
April – October	1.585	0.062	**3.644**	**0.001**	**1.812**	**0.037**
July – October	**2.402**	**0.004**	**2.693**	**0.001**	**2.254**	**0.004**
January 2003 – January 2004	1.355	0.147	**4.837**	**0.002**	**3.828**	**0.002**
April 2003 – April 2004	**1.663**	**0.038**	**4.143**	**0.001**	**4.320**	**0.001**
July 2003 – July 2004	**3.110**	**0.003**	**3.581**	**0.002**	**2.508**	**0.005**
October 2003 – October 2004	**1.789**	**0.035**	**2.457**	**0.006**	**2.997**	**0.004**
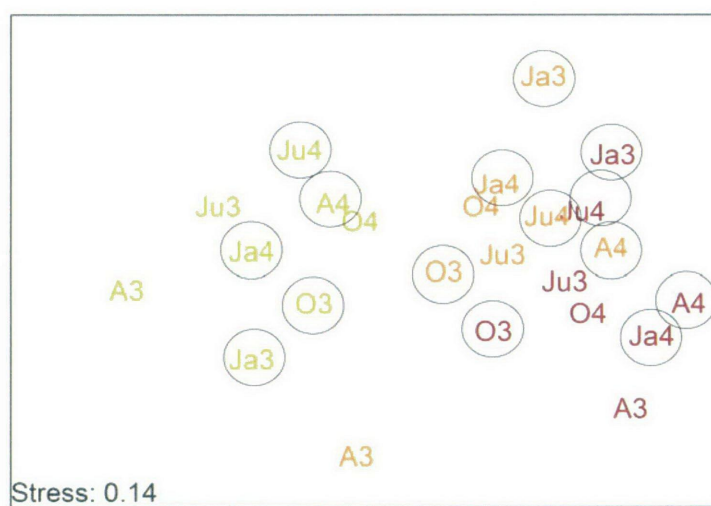
Fig. 5.3.4.5 Two-dimensional nMDS plot of benthic community structure at Woolgoolga Lake in 2003 and 2004. Seasonal samples in each year have been averaged and data points are colour-coded by site: upper (red); middle (orange); lower (yellow). Circles indicate sampling times when the estuary entrance was closed. Kruskal-Wallis stress value also given.

5.3.4.6 Willis Creek

The entrance of Willis Creek was the most dynamic, closing a total of eight times. Samples collected in January 2003, when the estuary entrance was closed, were significantly different to all other samples at each of the upper, middle and lower sites (Table 5.3.4.6). The other time of entrance closure in this year, October, was also significantly different to all other sampling times but only at the upper and middle sites. There was considerable overlap (Fig. 5.3.4.6.1 a, c), and fewer significant differences, between the remaining sampling times at the upper and lower sites; all pairwise comparisons for the middle site were significantly different. Changes in community structure during this year were mainly due to higher abundances of Chironomidae sp. in January and *Fluviolanatus subtortus* in October at the upper site, greater abundances in April of *Scyphoproctus towraiensis* and of *N. estuarius* in January at the middle site, and the absence of *S. normalis* at the lower site for all times except October.

A high degree of variation was also evident in 2004 (Fig. 5.3.4.6.1 d-f) with significant differences between all sampling times at the upper and middle sites (Table 5.3.4.6). At the lower site there was no significant difference between January and April ($p = 0.520$). In 2004, the only sampling time that coincided with entrance closure was July and the samples collected at this time remained separate to all others. This pattern was consistent across all sites. Assemblage differences were due to greater abundances of Chironomidae sp. at the upper site and *S. towraiensis* at the middle site in April, a July increase in *O. cirriformia* at the upper and middle sites and, at the lower site, higher abundances of *F. subtortus* in January.

When comparing sampling times from 2003 to 2004 (Fig. 5.3.4.6.1 g-i) seasonal patterns were not consistent between the two years, with significant Year x Season interactions for all sites (Table 5.3.4). Overall, however, some patterns were evident in relation to entrance status, particularly at the middle site, where sampling times that occurred when the entrance was closed all grouped towards then left-hand side of the plot. All pairwise comparisons between sampling times from 2003 to 2004 were significantly different, except between April 2003 and 2004 at the lower site. These differences were primarily a result of higher abundances of *S. towraiensis* in April 2003 at both the upper and middle site, as well as at the upper site in July 2003. July sampling times were also differentiated by an increase in the abundance of *O. cirriformia* at the upper and middle site. Comparisons between January sampling times showed that both *Ascorhis*
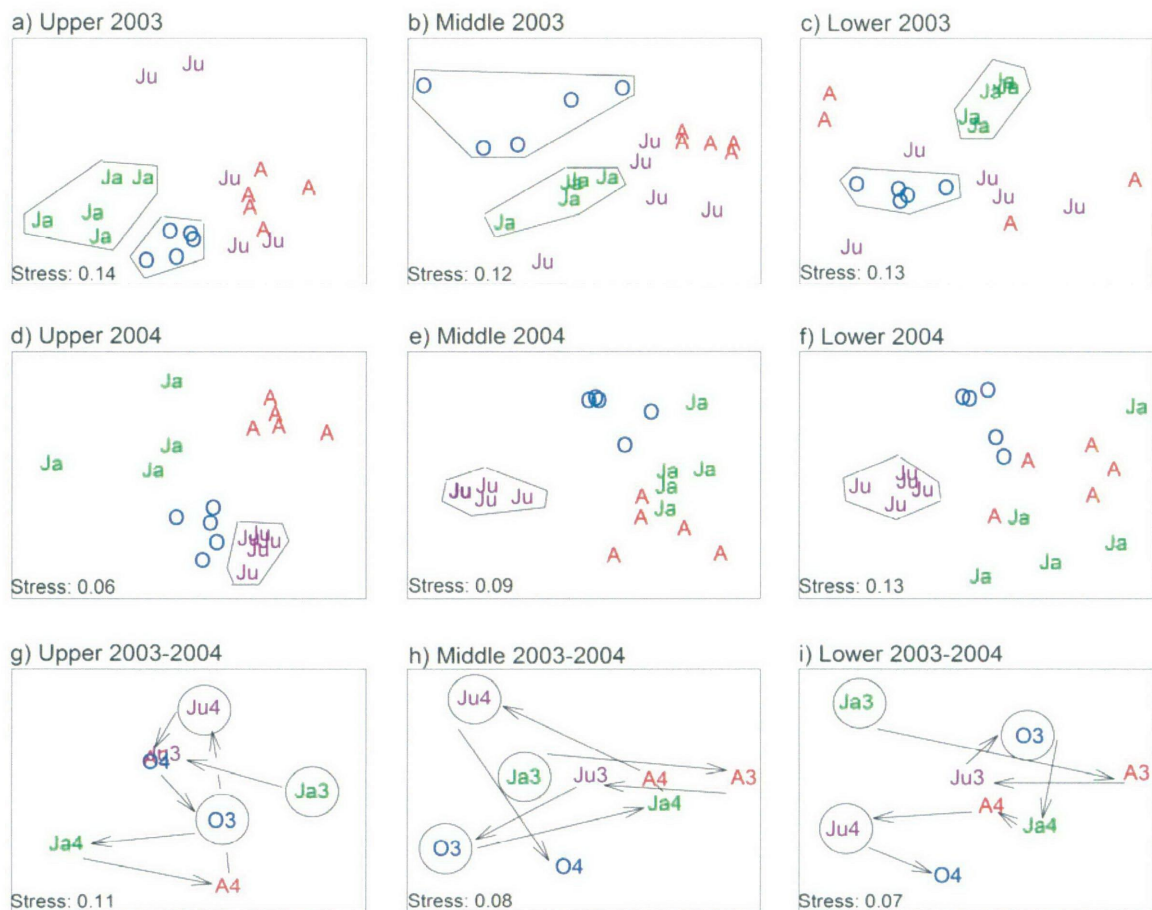
Fig. 5.3.4.6.1 Two-dimensional nMDS plots of benthic community structure in the (a) upper, (b) middle and (c) lower sites of Willis Creek in 2003 and (d, e, f) 2004. For each year data points represent samples collected in January (Ja), April (A), July (Ju) and October (O). Also shown (g, h, i) are sample data averaged for each season and plotted in relation to one another. After each seasonal symbol '3' denotes data from 2003 and '4' data from 2004. Circles or polygons around data points indicate sampling times when the estuary entrance was closed. Kruskal-Wallis stress values are given for all plots.

tasmanica and Chironomidae sp. were absent from the upper site in January 2004, *N. estuarius* was more abundant at the middle site in 2003 and *O. cirriformia* was more abundant at the lower site in 2003. October sampling times were mainly differentiated by higher abundances in 2003 of Chironomidae sp. and *O. cirriformia* at the middle site, and an increase during 2004 of *A. tasmanica* at the lower site.

The summary nMDS plot of all sampling times at all sites (Fig. 5.3.4.6.2) revealed no clear gradient between the upper, middle and lower sites. However, a strong demarcation relating to entrance status was evident, whereby all sampling times that occurred when the estuary's

Table 5.3.4.6 Willis Creek pairwise comparisons between the seasons of each year and between the corresponding seasons from 2003 to 2004. Results given are the *t*-statistic and Monte Carlo *p*-value (*p_mc*). Bold font indicates a significant result.

| Comparison groups	Upper		Middle		Lower	
	t	*p_mc*	*t*	*p_mc*	*t*	*p_mc*
2003						
January – April	**3.637**	**0.002**	**6.140**	**0.002**	**2.183**	**0.008**
January – July	**2.488**	**0.002**	**2.291**	**0.009**	**2.221**	**0.007**
January – October	**3.129**	**0.003**	**2.455**	**0.007**	**5.041**	**0.002**
April – July	1.353	0.192	**2.119**	**0.037**	1.188	0.276
April – October	**3.223**	**0.001**	**3.785**	**0.001**	**1.990**	**0.016**
July – October	**1.996**	**0.030**	**2.046**	**0.024**	1.866	0.052
2004						
January – April	**2.414**	**0.003**	**2.298**	**0.013**	0.898	0.520
January – July	**2.691**	**0.004**	**6.117**	**0.001**	**2.692**	**0.006**
January – October	**2.097**	**0.019**	**3.067**	**0.004**	**2.291**	**0.016**
April – July	**4.827**	**0.001**	**6.474**	**0.001**	**3.977**	**0.001**
April – October	**5.223**	**0.001**	**4.349**	**0.001**	**3.041**	**0.002**
July – October	**4.580**	**0.001**	**6.929**	**0.001**	**6.764**	**0.001**
January 2003 – January 2004	**2.392**	**0.006**	**3.664**	**0.002**	**2.540**	**0.005**
April 2003 – April 2004	**4.341**	**0.001**	**3.049**	**0.004**	1.180	0.267
July 2003 – July 2004	**2.471**	**0.009**	**3.028**	**0.006**	**2.322**	**0.007**
October 2003 – October 2004	**5.871**	**0.001**	**2.887**	**0.004**	**5.946**	**0.001**
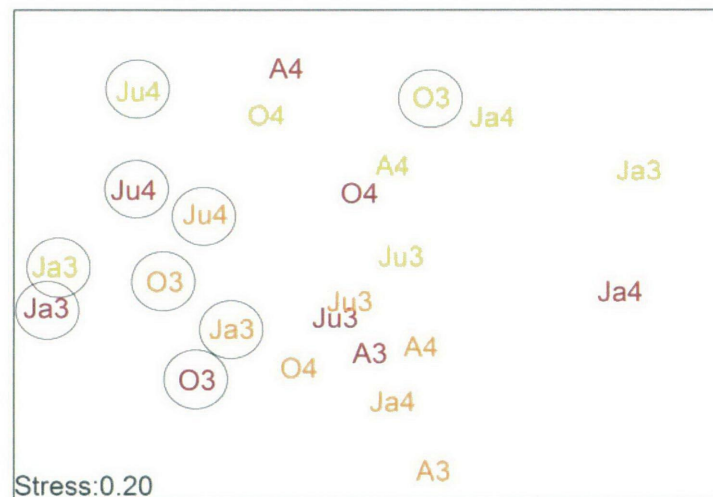
Fig. 5.3.4.6.2 Two-dimensional nMDS plot of benthic community structure at Willis Creek in 2003 and 2004. Seasonal samples in each year have been averaged and data points are colour-coded by site: upper (red); middle (orange); lower (yellow). Circles indicate sampling times when the estuary entrance was closed. Kruskal-Wallis stress value also given.

entrance was closed clearly grouped to the left-hand side of the plot, with the only exception being samples from the lower site in October 2003.

5.3.4.7 Hearns Lake

Hearns Lake generally experienced long entrance closures and was closed for 71.3 % of the study duration. At the upper site of Hearns Lake in 2003 only the October sampling time was significantly different to all other times (Table 5.3.4.7), with considerable overlap between the January, April and July assemblages (Fig. 5.3.4.7.1 a). All sampling times at the middle site in this year supported discrete communities (Fig. 5.3.4.7.1 b) with significant differences between all pairwise comparisons. At the lower site in 2003 only the July sample, when the estuary entrance was open, was significantly different to all other times. During this July sample the lower site contained high abundances of *Australonereis ehlersi*. Differences between sampling times at the upper and middle sites in this year were mainly due to very high abundances of *A. helmsi* during October (av. 154 per sample) and greater abundances of *O. cirriformia* in January. *S. normalis* was also more abundant at the middle site during April.

Temporal changes throughout 2004 were varied, with substantial overlap between the assemblages of April and July at the upper site, April and January at the middle site, as well as between January and October at the lower site (Fig. 5.3.4.7.1 d-f). All other pairwise comparisons between sampling times in this year were significantly different (Table 5.3.4.7). As seen in 2003, assemblage variation in 2004 was mostly due to high abundances of *A. helmsi* in October at both the upper and middle sites. Sampling times in this year were also differentiated by greater abundances of two other species in April, specifically, *N. estuarius* at the upper and middle sites, and *S. normalis* at the lower site.

All comparisons of sampling times from 2003 to 2004 were significantly different (Table 5.3.4.7) and the lack of any apparent seasonal patterns in the nMDS ordination for each site (Fig. 5.3.4.7.1 g-i) is supported by the significant Year x Season interactions (Table 5.3.4). Temporal variation in these plots did not appear to be related to the estuary's entrance status at the time of sampling. Over time, both the January and October sampling times were differentiated by greater abundances of *O. cirriformia*, *S. normalis* and *S. aequisetis* across all sites in 2003. April sampling times were differentiated by higher abundances of *S. normalis* in
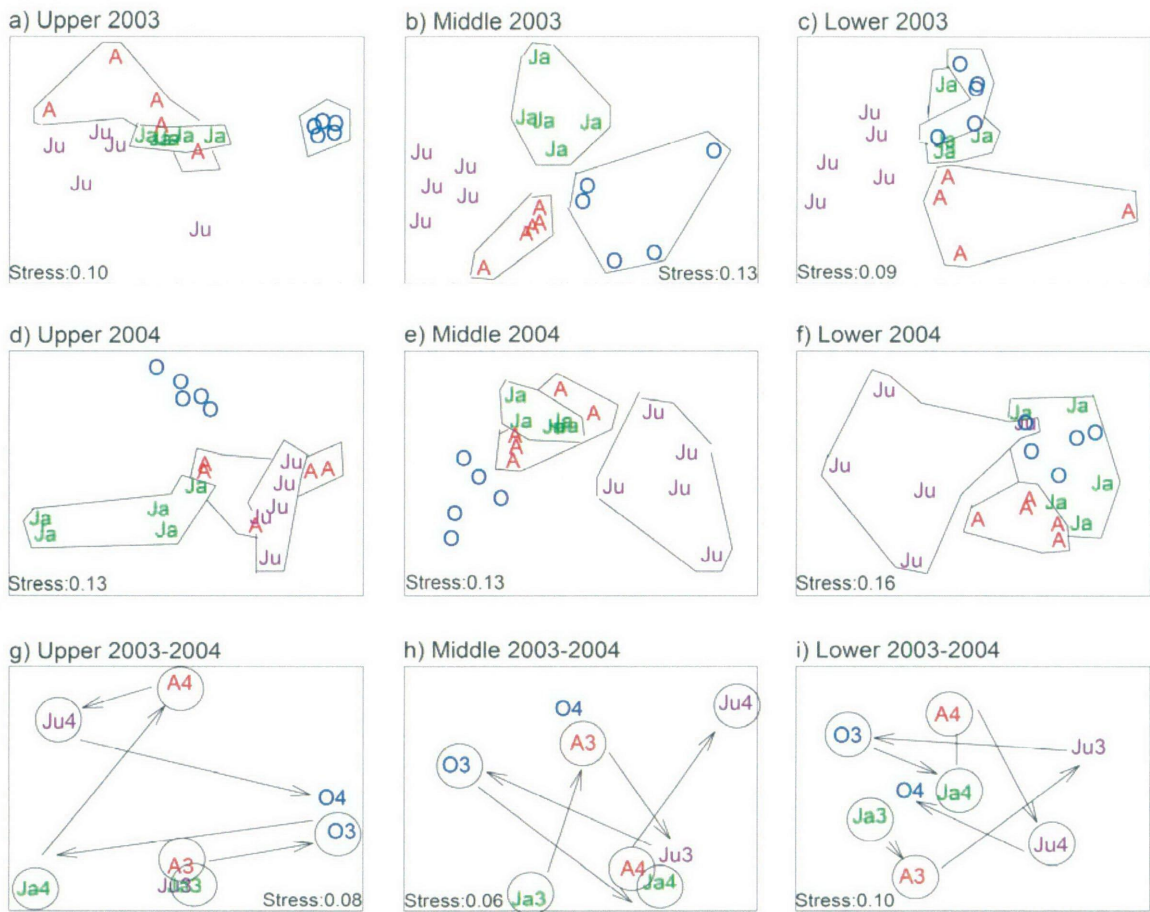
Fig. 5.3.4.7 Two-dimensional nMDS plots of benthic community structure in the (a) upper, (b) middle and (c) lower sites of Hearns Lake in 2003 and (d, e, f) 2004. For each year data points represent samples collected in January (Ja), April (A), July (Ju) and October (O). Also shown (g, h, i) samples data averaged for each season and plotted in relation to one another. After each seasonal symbol '3' denotes data from 2003 and '4' data from 2004. Circles or polygons around data points indicate sampling times when the estuary entrance was closed. Kruskal-Wallis stress values are given for all plots.

2003 and of *N. estuarius* in 2004 at both the upper and middle sites. In contrast, *S. normalis* was more abundant in April 2004 at the lower site. In comparison to July 2003, July 2004 was characterised by an increase in *N. estuarius* abundance the upper site, the absence of *A. ehlersi* at both the middle and lower sites, and the absence of *S. aequisetis* at the middle site only.

The summary nMDS plot including all sampling times across all sites (Fig. 5.3.4.7.2), reveals that the benthic community of the lower site was continually very different to those of the other sites. Over time, a high degree of overlap was evident between the upper and middle sites, particularly during times of entrance closure.

Table 5.3.4.7 Hearns Lake pairwise comparisons between the seasons of each year and between the corresponding seasons from 2003 to 2004. Results given are the *t*-statistic and Monte Carlo *p*-value (*p_mc*). Bold font indicates a significant result.

| Comparison groups	Upper		Middle		Lower	
	t	*p_mc*	*t*	*p_mc*	*t*	*p_mc*
2003						
January – April	1.544	0.096	**2.766**	**0.002**	1.289	0.212
January – July	1.566	0.075	**3.075**	**0.002**	**3.364**	**0.001**
January – October	**5.291**	**0.001**	**2.122**	**0.011**	1.508	0.106
April – July	1.675	0.064	**3.472**	**0.002**	**2.189**	**0.013**
April – October	**3.430**	**0.001**	**2.460**	**0.001**	**1.862**	**0.028**
July – October	**3.400**	**0.001**	**3.282**	**0.002**	**3.414**	**0.001**
2004						
January – April	**2.490**	**0.007**	1.548	0.092	**2.399**	**0.007**
January – July	**3.017**	**0.006**	**2.807**	**0.004**	**2.013**	**0.029**
January – October	**4.004**	**0.001**	**4.224**	**0.001**	1.858	0.072
April – July	1.597	0.073	**2.489**	**0.004**	**2.343**	**0.006**
April – October	**3.581**	**0.001**	**2.565**	**0.007**	**2.295**	**0.009**
July – October	**4.167**	**0.001**	**3.181**	**0.001**	**2.497**	**0.004**
January 2003 – January 2004	**2.546**	**0.015**	**3.010**	**0.002**	**2.038**	**0.031**
April 2003 – April 2004	**1.792**	**0.023**	**2.554**	**0.002**	**2.163**	**0.010**
July 2003 – July 2004	1.340	0.164	**2.447**	**0.007**	**2.266**	**0.008**
October 2003 – October 2004	**3.663**	**0.002**	**2.249**	**0.019**	1.881	0.039
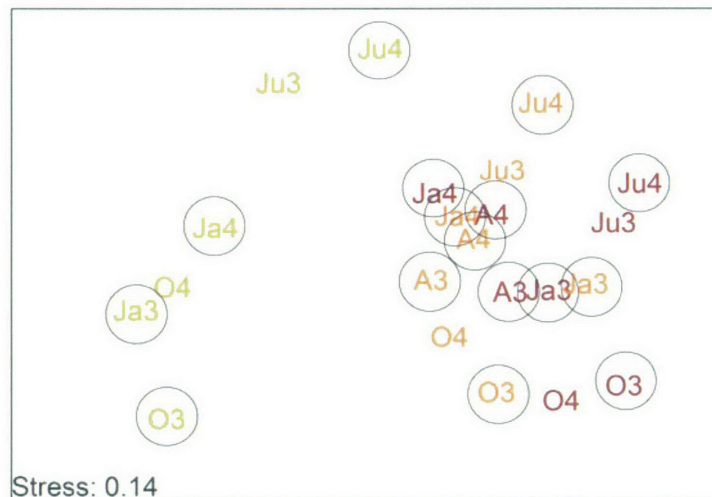
Fig. 5.3.4.7.2 Two-dimensional nMDS plot of benthic community structure at Hearns Lake in 2003 and 2004. Seasonal samples in each year have been averaged and data points are colour-coded by site: upper (red); middle (orange); lower (yellow). Circles indicate sampling times when the estuary entrance was closed. Kruskal-Wallis stress value also given.

5.3.4.8 Moonee Creek

Community structure at the upper and middle sites of the permanently open Moonee Creek were discrete between sampling times in 2003 (Fig. 5.3.4.8.1 a, b), with significant differences for all pairwise comparisons, except between January and July at the upper site ($p = 0.051$) and between April and October at the middle site ($p = 0.433$) (Table 5.3.4.8). At the lower site, however, there was a high degree of overlap between the 2003 sampling times, except for January, which was significantly different to all other times due to a greater abundance of *U. metungi*. At the upper site these assemblage differences were primarily due to higher
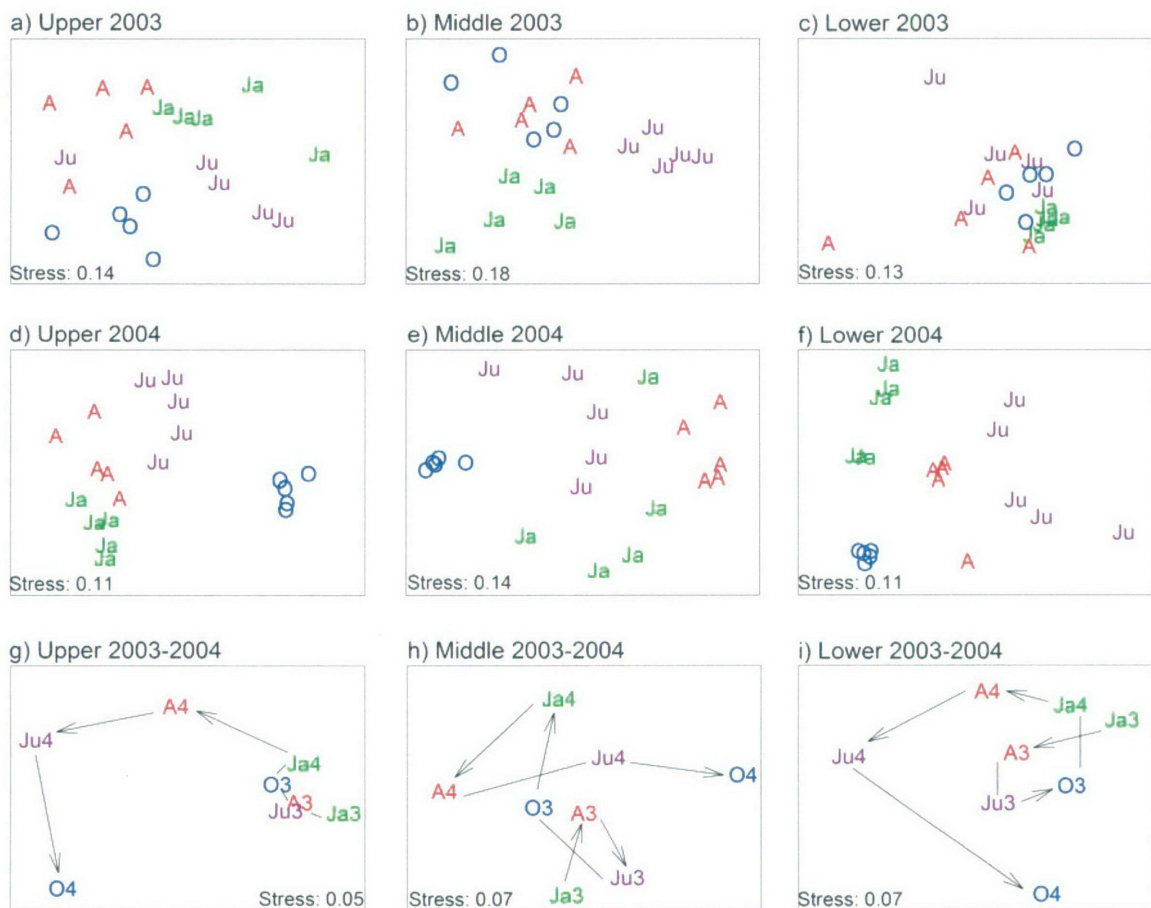
Fig. 5.3.4.8.1 Two-dimensional nMDS plots of benthic community structure in the (a) upper, (b) middle and (c) lower sites of Moonee Creek in 2003 and (d, e, f) 2004. For each year data points represent samples collected in January (Ja), April (A), July (Ju) and October (O). Also shown (g, h, i) are sample data averaged for each season plotted in relation to one another. After each seasonal symbol '3' denotes data from 2003 and '4' data from 2004. Kruskal-Wallis stress values are given for all plots.

abundances of *M. vitrea* in January and July, and of *A. helmsi* in April. Sampling times at the middle site were differentiated by the presence of *Nozeba topaziaca* in January and a greater abundance of *Trypaea australiensis* in July.

In 2004 sampling times were also discrete (Fig. 5.3.4.8.1 d-f), especially at the upper and lower sites, where all pairwise comparisons between sampling times were significantly different (Table 5.3.4.8). At the middle site there was no significant difference between January and July ($p = 0.191$). As in 2003, differences between sampling sites at the upper site were due to higher abundances of *M. vitrea* in January and July, and of *A. helmsi* in April. At the middle site sampling times were differentiated by high abundances of most species in October and either low abundances or absences of most species in April. At the lower site *U. metungi* was most abundant in January.

When comparing all samples over time there was no consistent seasonal pattern (Fig. 5.3.4.8.1 g-i), except at the lower site where there was no significant difference between years for April ($p = 0.065$) and January ($p = 0.235$) sampling times (Table 5.3.4.8). The main differences between the two years at the upper site were due to higher abundances of *M. vitrea* and *A. helmsi* for all times in 2003. At the middle site, the variation between sampling times from year to year was primarily a result of lower abundances of all species during January, April and July 2004. In contrast, October sampling times were differentiated by the absence of *S. aequisetis* and *A. intermedia* during 2003 at both the middle and lower sites. Temporal variation at the lower site was also marked by an increase in *U. metungi* in July 2003 and the presence of Anthuridae sp. in July 2004.

Over time, there was a strong separation between sites, with the upper site remaining clearly different to the middle and lower sites. There was, however, some temporal overlap between the middle and lower sites but only for July 2004 (Fig. 5.3.4.8.2)

Table 5.3.4.8 Moonee Creek pairwise comparisons between the seasons of each year and between the corresponding seasons from 2003 to 2004. Results given are the *t*-statistic and Monte Carlo *p*-value (*p_mc*). Bold font indicates a significant result.

| Comparison groups	Upper		Middle		Lower	
	t	*p_mc*	*t*	*p_mc*	*t*	*p_mc*
2003						
January – April	**1.832**	**0.027**	**2.006**	**0.018**	**1.888**	**0.045**
January – July	1.649	0.051	**3.423**	**0.001**	**1.898**	**0.016**
January – October	**2.809**	**0.003**	**2.109**	**0.009**	**2.115**	**0.017**
April – July	**2.290**	**0.016**	**3.122**	**0.002**	1.045	0.392
April – October	**2.455**	**0.001**	0.980	0.433	1.562	0.070
July – October	**2.473**	**0.004**	**3.087**	**0.002**	1.190	0.236
2004						
January – April	**2.377**	**0.006**	**1.994**	**0.015**	**2.626**	**0.002**
January – July	**3.285**	**0.001**	1.296	0.191	**2.847**	**0.002**
January – October	**5.439**	**0.001**	**3.144**	**0.002**	**3.979**	**0.001**
April – July	**2.524**	**0.002**	**2.885**	**0.002**	**2.055**	**0.011**
April – October	**4.827**	**0.001**	**5.873**	**0.001**	**4.287**	**0.001**
July – October	**4.355**	**0.001**	**3.486**	**0.001**	**3.616**	**0.001**
January 2003 – January 2004	**2.232**	**0.009**	**1.773**	**0.026**	1.227	0.235
April 2003 – April 2004	**2.834**	**0.003**	**3.111**	**0.002**	1.549	0.065
July 2003 – July 2004	**3.190**	**0.003**	**2.472**	**0.008**	**1.798**	**0.028**
October 2003 – October 2004	**7.108**	**0.001**	**4.173**	**0.001**	**2.845**	**0.005**
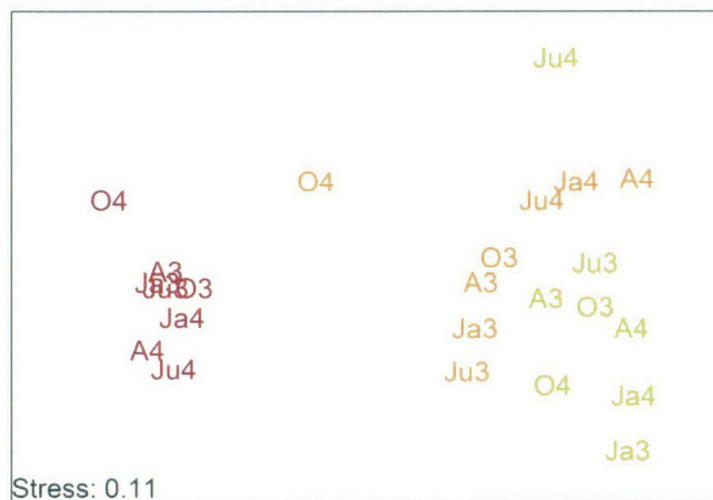
Fig. 5.3.4.8.2 Two-dimensional nMDS plot of benthic community structure at Moonee Creek in 2003 and 2004. Seasonal samples in each year have been averaged and data points are colour-coded by site: upper (red); middle (orange); lower (yellow). Kruskal-Wallis stress value also given.

5.3.4.9 Coffs Creek

The permanently open Coffs Creek displayed considerable temporal variation (Fig. 5.3.4.9.1), particularly at the middle site where all sampling times were significantly different to one another in both 2003 and 2004. For the other sites, there were non-significant pairwise comparisons between April and July at the upper ($p = 0.083$) and lower ($p = 0.074$) sites in 2003, January and July at the upper site in 2004 ($p = 0.059$) and between January and April at the lower site in 2004 ($p = 0.077$) (Table 5.3.4.9). These temporal changes were mainly due to higher abundances of *A. helmsi* and *V. australiensis* at the upper site in January 2003 and October 2004. *Tellina imbellis* was also more abundant at the upper site in October 2004 and at the middle site in January 2003.
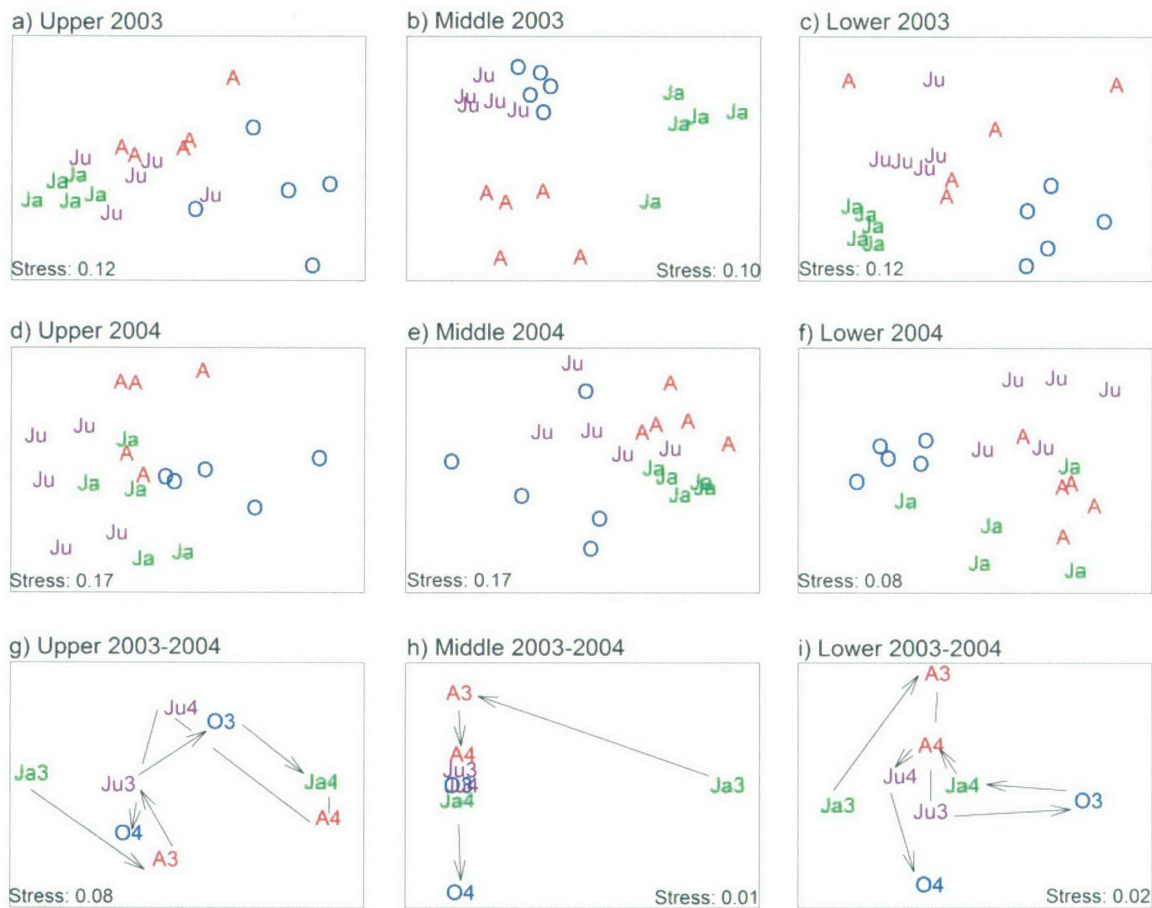
Fig. 5.3.4.9.1 Two-dimensional nMDS plots of benthic community structure in the (a) upper, (b) middle and (c) lower sites of Coffs Creek in 2003 and (d, e, f) 2004. For each year data points represent samples collected in January (Ja), April (A), July (Ju) and October (O). Also shown (g, h, i) are sample data averaged for each season and plotted in relation to one another. After each seasonal symbol '3' denotes data from 2003 and '4' data from 2004. Kruskal-Wallis stress values are given for all plots.

Differences at the middle site were also a result of low abundances or absences of many other species in April 2003 and in October 2004, as well as increased abundances of *S. alba* in October 2003 and January 2004. At the lower site of Coffs Creek, sampling times were differentiated by higher abundances of *U. metungi* in January 2003 and July 2004, as well as increased abundances of *Nassarius jonasii* in October 2003 and *M. vitrea* in October 2004.

All comparisons of each sampling time from 2003 to 2004 (Fig. 5.3.4.9.1 g-i) were significantly different at the upper and middle sites. At the lower site, however, there was no significant difference between April 2003 and April 2004 ($p = 0.289$) or between July 2003 and July 2004 ($p = 0.090$), suggesting some repeated temporal patterns at these times of year (autumn, winter). Variation between sampling times from 2003 to 2004 at the upper site were due to higher abundances of *A. helmsi*, *S. normalis* and *V. australiensis* across all times in 2003. Assemblage changes at the middle site involved higher abundances of most species, especially *M. vitrea*, *S. alba* and *N. jonasii*, in July and October 2003, as well as in January and April 2004. Changes in the abundance of *U. metungi*, which was greater in January 2003 and absent in October 2003,

Table 5.3.4.9 Coffs Creek pairwise comparisons between the seasons of each year and between the corresponding seasons from 2003 to 2004. Results given are the *t*-statistic and Monte Carlo *p*-value (*p_mc*). Bold font indicates a significant result.

Comparison groups	Upper		Middle		Lower	
	t	*p_mc*	*t*	*p_mc*	*t*	*p_mc*
2003						
January – April	**2.640**	**0.004**	**2.548**	**0.004**	**2.511**	**0.006**
January – July	**1.916**	**0.018**	**3.646**	**0.001**	**3.035**	**0.002**
January – October	**3.090**	**0.003**	**3.080**	**0.002**	**4.608**	**0.002**
April – July	1.516	0.083	**2.680**	**0.005**	1.621	0.074
April – October	**1.908**	**0.012**	**2.550**	**0.001**	**1.993**	**0.009**
July – October	**2.094**	**0.009**	**2.631**	**0.003**	**3.202**	**0.001**
2004						
January – April	**1.823**	**0.040**	**3.233**	**0.001**	1.592	0.077
January – July	1.570	0.059	**2.649**	**0.007**	**2.606**	**0.009**
January – October	**2.321**	**0.012**	**2.405**	**0.006**	**2.610**	**0.009**
April – July	**1.965**	**0.019**	**2.173**	**0.005**	**2.590**	**0.009**
April – October	**2.605**	**0.008**	**2.111**	**0.012**	**4.364**	**0.001**
July – October	**2.386**	**0.004**	1.558	**0.049**	**4.097**	**0.001**
January 2003 – January 2004	**3.524**	**0.002**	**3.912**	**0.002**	**3.579**	**0.002**
April 2003 – April 2004	**2.121**	**0.013**	**2.337**	**0.002**	1.141	0.289
July 2003 – July 2004	**1.950**	**0.017**	**1.647**	**0.046**	1.595	0.090
October 2003 – October 2004	**2.653**	**0.009**	**2.126**	**0.010**	**3.666**	**0.002**

Ja3   A3
          Ja4
      JUJ94
       O3   A4

Ja3
   Ju3O3Ju4   O4   O4

                                A3
O4 A4
   A3 Ja4   JyЭ4 Ja3
                    Ja4
                        Ju4
            O3

Stress: 0.10

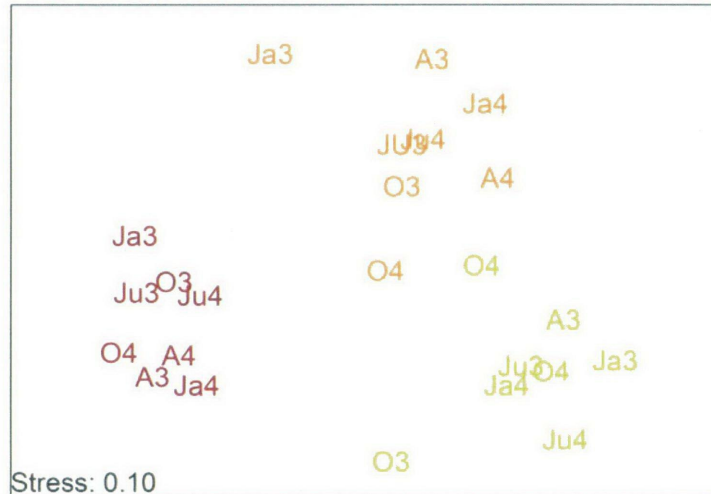**Fig. 5.3.4.9.2** Two-dimensional nMDS plot of benthic community structure at Coffs Creek in 2003 and 2004. Seasonal samples in each year have been averaged and data points are colour-coded by site: upper (red); middle (orange); lower (yellow). Kruskal-Wallis stress value also given.

mostly differentiated between sampling times from 2003 to 2004 at the lower site. Over time there was a persistent separation between each of the upper, middle and lower sites, with no overlap between any of the sites in the summary nMDS plot of all sampling times at all sites (Fig. 5.3.4.9.2).

5.3.5 Temporal variation of univariate community variables within individual estuaries

Species Richness (S)

Willis Creek consistently had low species richness across all sites with the maximum average of 6 species occurring at the upper site in January 2003 (Fig. 5.3.5.1). In contrast, the maximum average species richness values, 15 and 16 species, occurred in the middle site of Coffs Creek at the same time and at the middle site of Moonee Creek in October 2004, respectively. Similarly, most other estuaries, including Corindi River, Arrawarra Creek, Woolgoolga Lake and Hearns Lake, also had their highest average mean species richness at their middle site. In comparison to

the species richness patterns in the other estuaries, Hearns Lake was unique in that its lower site always had a lower species richness than both the upper and middle sites.

Species richness showed significant differences for all temporal factors across most sites and complex changes as demonstrated by the Year x Season interaction term (Table 5.3.5). in which there were six estuaries that were not significantly different between years for at least one of their sites. These were the upper site for Corindi River and Darkum Creek, the middle site for Woolgoolga Lake and the lower site for Corindi River, Willis Creek, Hearns Lake and Coffs Creek. Species richness in Woolgoolga Lake was also not significantly different between seasons at the middle site, and the Year x Season interaction term was not significantly different at the upper sites of Darkum Creek and Woolgoolga Lake, or at the middle site of Corindi River.

Fig. 5.3.5.1 Seasonal species richness measurements (mean ± S.E.) for 2003 and 2004 in the upper, middle and lower sites of each estuary. Horizontal lines above a season indicate that the estuary entrance was closed at the time of sampling.
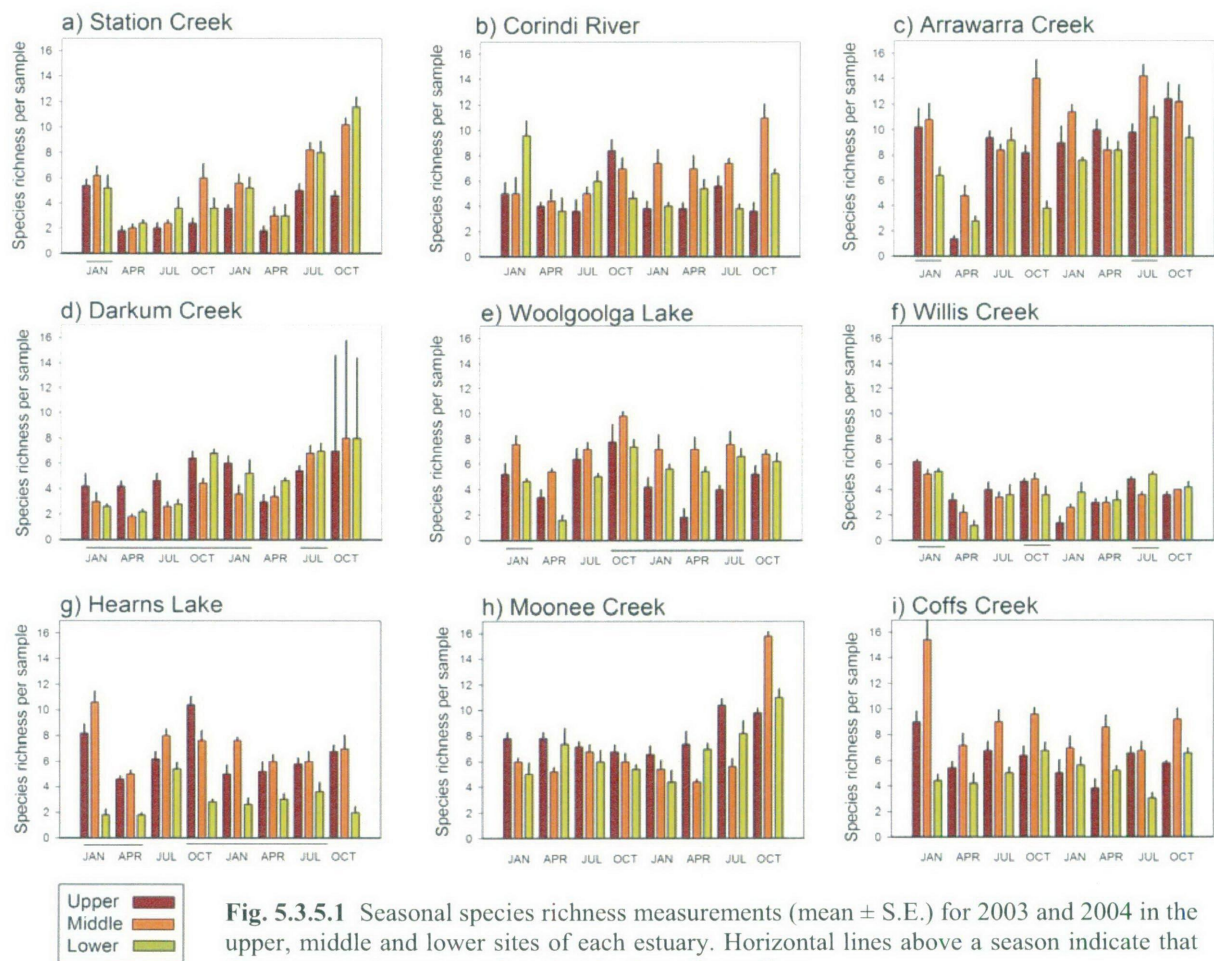
Total Number of Individuals (N)

The total number of individuals per sample had a much greater range (Fig. 5.3.5.2) with Arrawarra Creek, Hearns Lake and Moonee Creek supporting more than 300 individuals per sample in their upper sites at the same time. Whilst Arrawarra Creek quite consistently had a very high average number of individuals in its upper and middle sites, as did Moonee Creek in its upper site, most other sites generally supported a much lower number of individuals, averaging anywhere between 5 and 80.
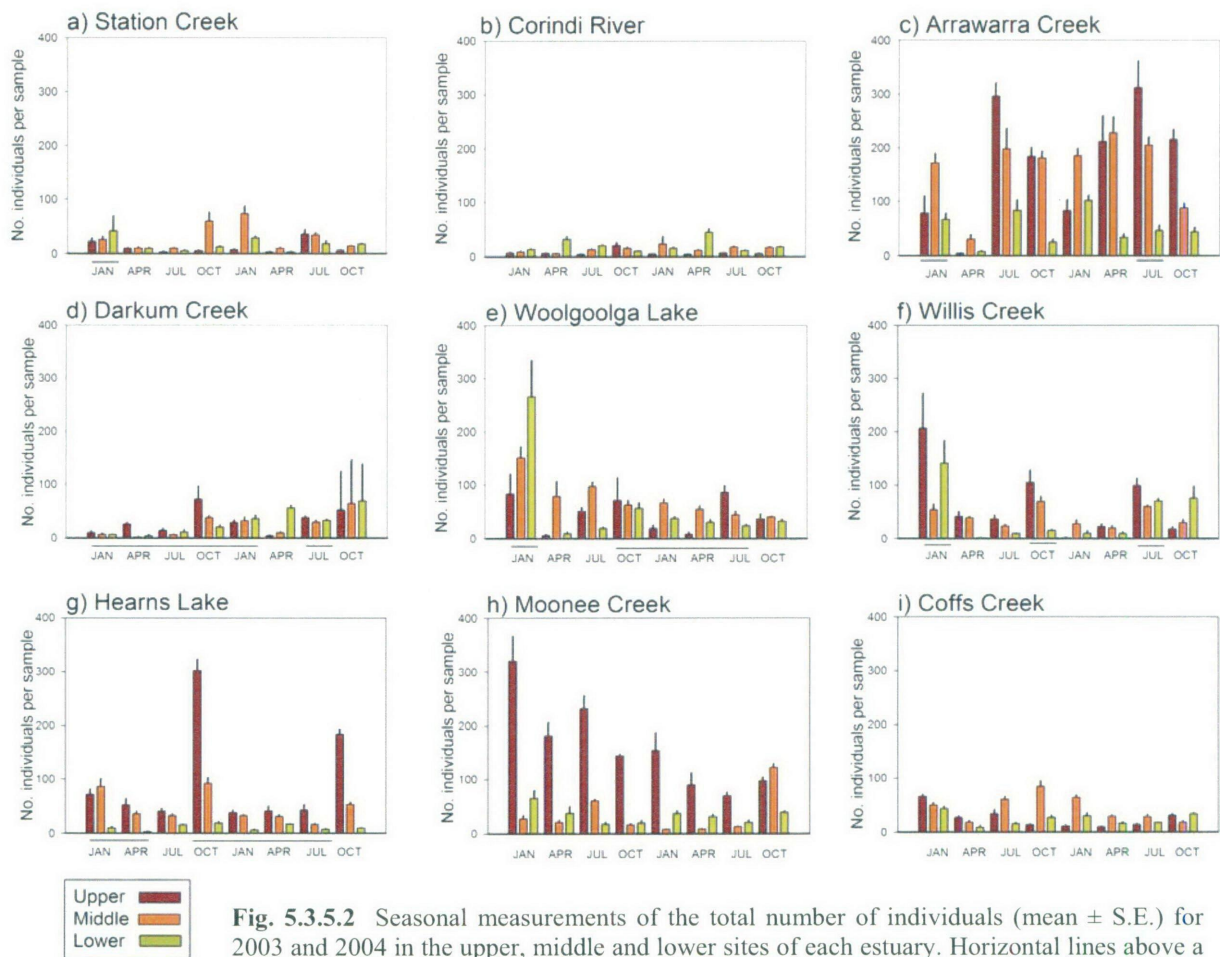
Fig. 5.3.5.2 Seasonal measurements of the total number of individuals (mean ± S.E.) for 2003 and 2004 in the upper, middle and lower sites of each estuary. Horizontal lines above a season indicate that the estuary entrance was closed at the time of sampling.

Although there was still generally a high degree of temporal variability in the number of individuals across some factors, there were quite a few exceptions to this. Few estuaries showed significant differences between years at their lower sites and the total number of individuals in Station Creek was not significantly different between years at any site (Table 5.3.5). There was

no significant differences across any factor at the middle site of Corindi River and, at their upper sites, Darkum Creek and Woolgoolga Lake were only significantly different between seasons for the total number of individuals. As for species richness, the temporal changes in the total number of individuals were complex and seasonal changes were generally not consistent due to significant Year x Season interactions (Table 5.3.5).

Table 5.3.5 Summary of results of two-way ANOVAs for species richness and the total number of individuals per sample at each of the upper, middle and lower sites of all estuaries. $d.f. = 1,16$ for comparisons between years and $d.f. = 3,16$ for comparisons between seasons. '-' indicates a non-significant results ($p > 0.05$), significant results are shown by '*' ($p < 0.05$) and '**' ($p < 0.001$).

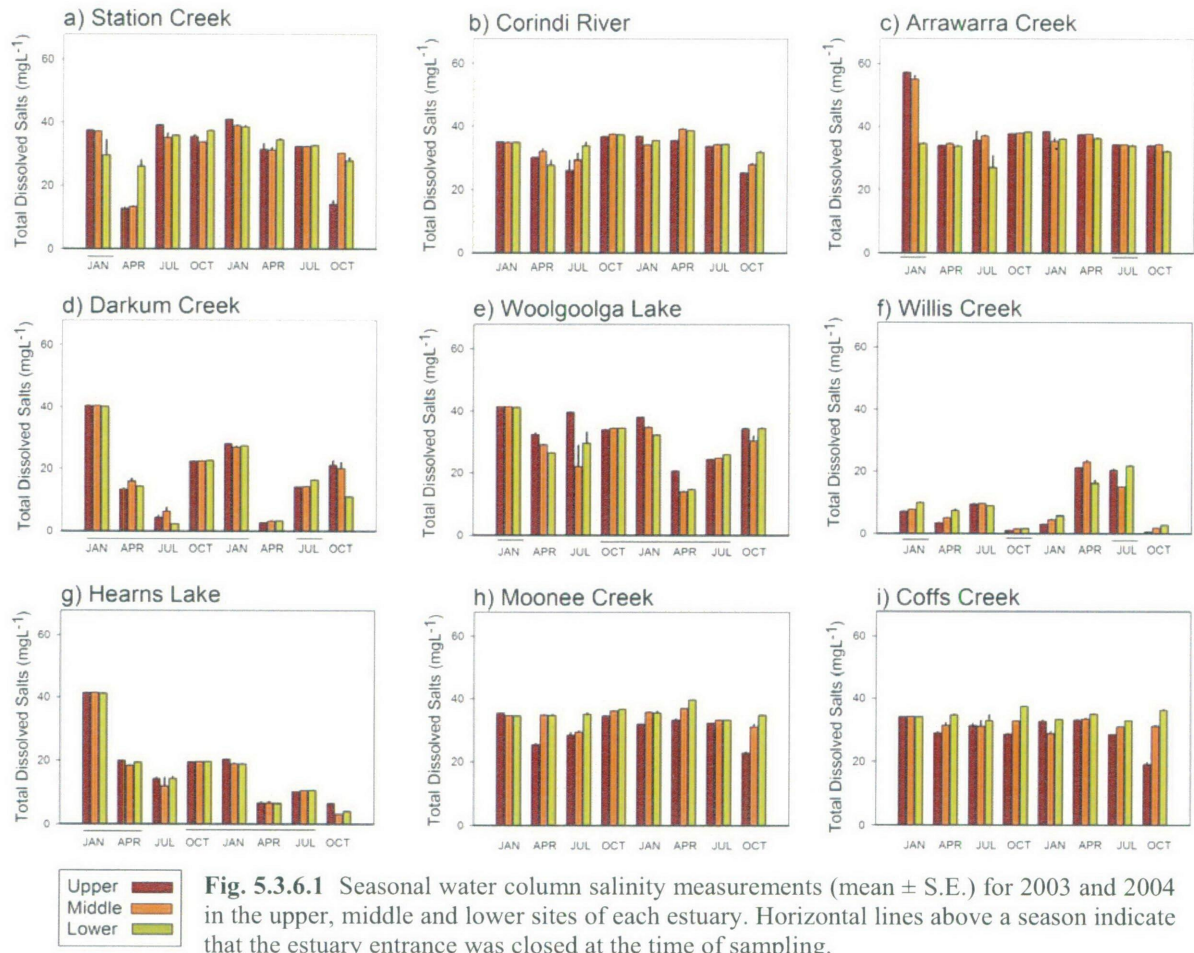|			STA	COR	ARR	DAR	WOO	WIL	HEA	MOO	COF
S	Upper	Year	*	-	**	-	*	**	**	*	*
		Season	**	*	**	**	**	*	**	*	*
		Year x Season	**	**	**	-	-	**	*	**	*
	Middle	Year	**	**	*	**	-	*	*	**	*
		Season	**	*	**	**	-	**	**	**	*
		Year x Season	**	-	*	*	*	**	*	**	**
	Lower	Year	**	-	**	**	**	-	-	*	-
		Season	**	*	**	**	**	**	**	*	**
		Year x Season	**	**	*	*	**	*	*	*	*
N	Upper	Year	-	*	*	-	-	*	**	**	**
		Season	*	*	**	**	*	-	**	**	**
		Year x Season	**	**	*	-	-	**	**	-	**
	Middle	Year	-	-	*	**	**	*	**	*	**
		Season	**	-	*	**	*	*	**	**	**
		Year x Season	**	-	**	*	-	**	*	**	**
	Lower	Year	-	-	-	**	*	-	-	-	-
		Season	*	**	**	**	**	*	*	*	**
		Year x Season	-	*	*	*	**	**	**	*	*

5.3.6 Temporal variation of physico-chemical variables within individual estuaries

All water column variables were highly variable over time with significant differences between years and seasons for all variables at all estuaries (Table 5.3.6.1). There was also significant Year x Season interactions for nearly all water column variables at all estuaries, showing a lack of consistent seasonal patterns from 2003 to 2004 (Table 6.3.6.1). Salinity was significantly different at the scales of Year and Season, as well as for the Year x Season interaction across all sites in the intermittent estuaries, except for the lower sites of Station and Arrawarra creeks. The permanently open estuaries, Corindi River, Moonee Creek and Coffs Creek, were slightly less

variable, particularly at the scale of Year. Salinity was most stable in these estuaries, remaining in the range of 25 – 35 mgL^{-1} across all sites (Fig. 5.3.6.1 b, h, i). For the intermittently closed estuaries, salinity was most variable overtime in Darkum Creek, Willis Creek and Hearns Lake, with the lowest salinities for each of the upper, middle and lower sites always being in one of

Table 5.3.6.1 Summary of results of two-way ANOVAs for the physico-chemical water column variables (TDS = total dissolved salts, DO = dissolved oxygen, Temp. = temperature) in the upper, middle and lower sites of each estuary. *d.f.* = 1,16 for comparisons between years and *d.f.* = 3,16 for comparisons between seasons. '-' indicates a non-significant results ($p > 0.05$), significant results are shown by '*' ($p < 0.05$) and '**' ($p < 0.001$).

			COR	MOO	COF	STA	ARR	DAR	WOO	WIL	HEA
TDS	Upper	Year	-	*	**	*	**	**	**	**	**
		Season	**	**	**	**	**	**	**	**	**
		Year x Season	**	**	**	**	**	**	**	**	**
	Middle	Year	-	-	*	**	**	**	*	**	**
		Season	**	**	-	**	**	**	**	**	**
		Year x Season	**	**	**	**	**	**	*	**	**
	Lower	Year	**	*	-	-	-	**	**	**	**
		Season	*	**	**	-	**	**	**	**	**
		Year x Season	**	**	-	**	**	**	**	**	**
DO	Upper	Year	-	**	**	**	-	**	*	**	**
		Season	**	**	**	**	**	**	**	**	**
		Year x Season	**	**	**	**	**	**	**	**	**
	Middle	Year	-	**	**	**	-	**	**	**	**
		Season	**	**	**	**	**	**	**	**	**
		Year x Season	**	**	**	**	**	**	**	**	**
	Lower	Year	**	**	**	-	**	**	**	*	**
		Season	**	**	**	**	**	**	**	**	**
		Year x Season	**	**	**	**	**	**	**	**	**
pH	Upper	Year	**	**	*	-	**	**	-	-	*
		Season	**	**	**	**	**	**	**	-	**
		Year x Season	**	**	**	**	**	**	-	**	**
	Middle	Year	-	-	**	**	**	**	*	**	**
		Season	**	**	**	**	**	**	*	**	**
		Year x Season	**	**	**	**	**	**	**	**	**
	Lower	Year	**	**	**	-	**	**	**	**	**
		Season	**	**	**	-	**	**	**	**	**
		Year x Season	**	**	**	-	**	**	**	**	**
Temp.	Upper	Year	**	**	**	**	-	-	**	**	**
		Season	**	**	**	**	**	**	**	**	**
		Year x Season	**	**	**	**	**	**	**	**	**
	Middle	Year	**	**	**	**	**	-	**	**	**
		Season	**	**	**	**	**	**	**	**	**
		Year x Season	**	**	**	**	**	**	**	**	**
	Lower	Year	**	**	-	**	**	-	**	**	**
		Season	**	**	**	**	**	**	**	**	**
		Year x Season	**	**	**	**	**	**	**	**	**

Fig. 5.3.6.1 Seasonal water column salinity measurements (mean ± S.E.) for 2003 and 2004 in the upper, middle and lower sites of each estuary. Horizontal lines above a season indicate that the estuary entrance was closed at the time of sampling.
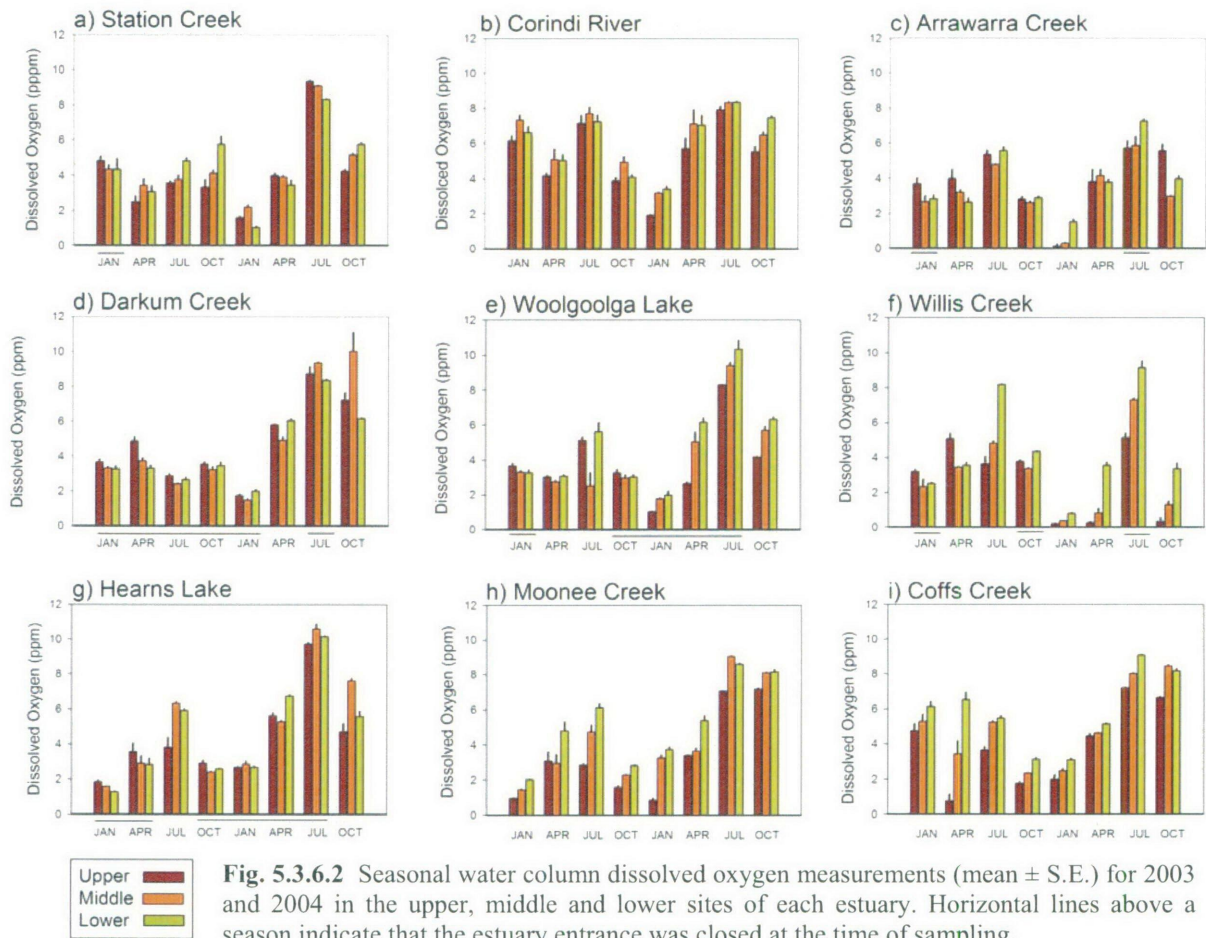
these three estuaries. Occasionally, some of the intermittent estuaries clearly presented salinity gradients not typically representative of those in estuaries. These specifically included Station and Arrawarra creeks in January 2003, Darkum Creek in October 2004 and Woolgoolga Lake in January 2004. At these times these estuaries had an inverse salinity gradient, whereby salinity was greatest at their upper sites and lowest at their lower sites.

Dissolved oxygen was also highly variable in each estuary over time (Fig. 5.3.6.1), with non-significant results only present at the annual scale in the upper and middle sites of Corindi River and Arrawarra Creek, and at the lower site of Station Creek (Table 5.3.6.1). The temporal trends in dissolved oxygen were similar across estuaries, with each reaching their maximum (8 - 11 ppm) in July 2004 and remaining relatively high for the following sample in October. Similarly,

most estuaries had their lowest dissolved oxygen levels (< 2 ppm) in January 2004. Significant Year x Season interactions were present across all sites in all estuaries.

On visual inspection (Fig. 5.3.6.3), pH appeared relatively stable over time with most estuaries maintaining a pH of approximately 8 throughout the two year period. The main deviations to this were a slightly greater range in Woolgoolga Lake and Willis Creek, with pH oscillating between 7 and 9. Some reductions in pH were also evident in January 2004, primarily at

Fig. 5.3.6.2 Seasonal water column dissolved oxygen measurements (mean ± S.E.) for 2003 and 2004 in the upper, middle and lower sites of each estuary. Horizontal lines above a season indicate that the estuary entrance was closed at the time of sampling.

Arrawarra Creek. Overall, however, significant differences between Year, Season, and a significant interaction between these factors, dominated pH results across the upper, middle and lower sites in all estuaries (Table 5.3.6.1). A few tests were not significantly different for Year, including those for the upper sites of Station Creek, Woolgoolga Lake and Willis Creek, and the middle sites of Corindi River and Moonee Creek. There was no significant annual or seasonal temporal variation at the lower site of Station Creek or at the upper site of Willis Creek.

Temperature was temporally variable and was mostly highly significantly different for all factors at each site of the nine estuaries. There was no significant annual variation at any of the sites in Darkum Creek, the lower site of Coffs Creek, or at the upper site of Arrawarra Creek (Table 5.3.6.1). Despite across-the-board significance of Year x Season interactions, all estuaries displayed typical seasonal trends for both years, whereby temperature was greater in summer (January) and at a minimums in winter (July) (Fig. 5.3.6.4).

Fig. 5.3.6.3 Seasonal water column pH measurements (mean ± S.E.) for 2003 and 2004 in the upper, middle and lower sites of each estuary. Horizontal lines above a season indicate that the estuary entrance was closed at the time of sampling.
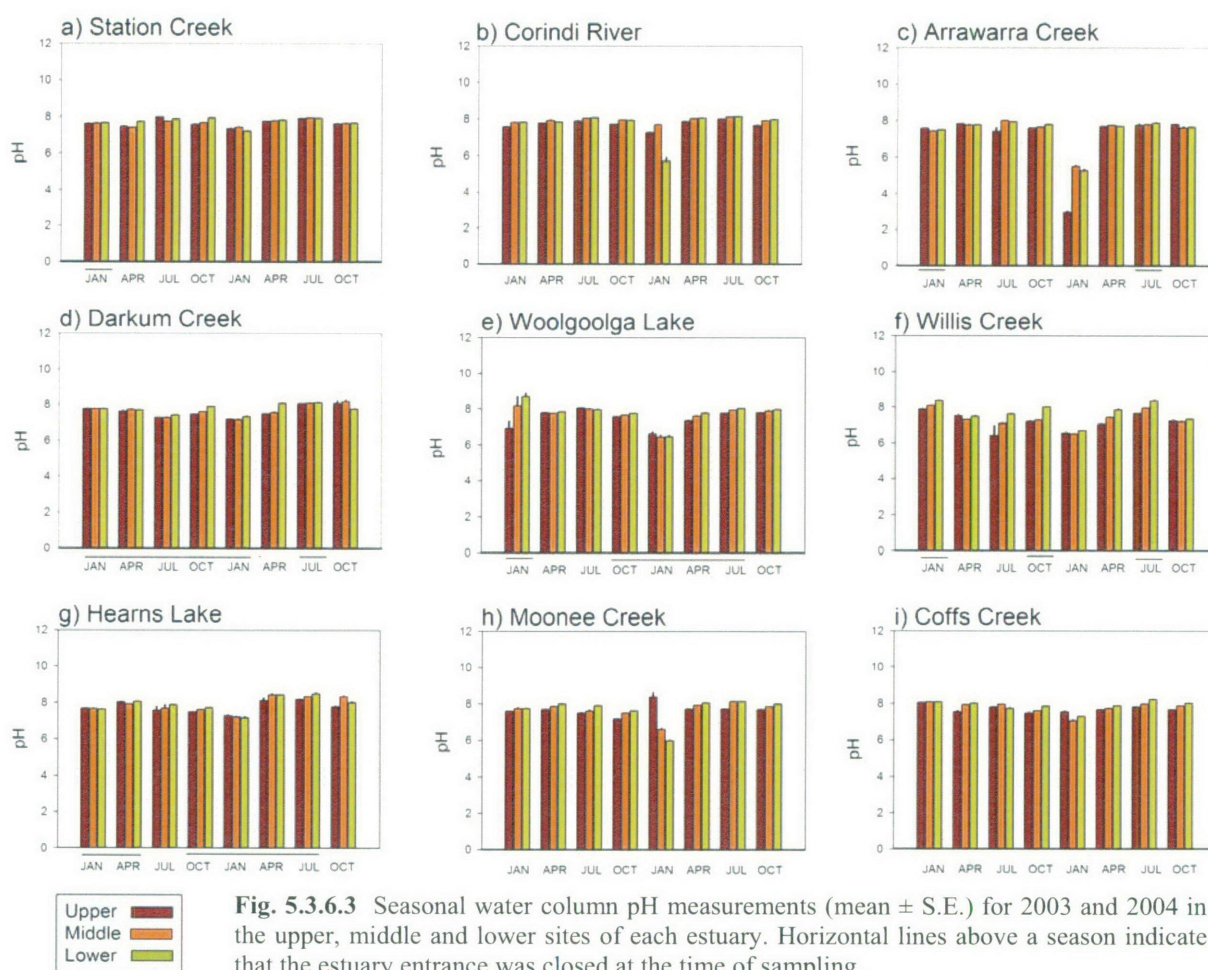
In contrast to the water column variables, sediment parameters showed much less variation over time, with fewer significant differences between years and seasons at all estuaries, especially for grain size and homogeneity (Table 5.3.6.2). Sediment homogeneity, in particular, was relatively consistent over time for all sites in each estuary (Figs. 5.3.6.6). The main temporal fluctuations in grain size were at the middle sites of Woolgoolga Lake and Arrawarra Creek, the lower site

of Station Creek and the upper site of Corindi River (Fig. 5.3.6.5). Apart from Station Creek, each of these sites had a larger grain size than that of the respective sites in other estuaries. Whilst relatively consistent overall, the greatest temporal variation in sediment homogeneity was at the upper sites for the majority of estuaries and at the middle site for Corindi River, Arrawarra and Willis creeks, as well as at the lower site of Station Creek.

Figure 5.3.6.4 Seasonal water column temperature measurements (mean ± S.E.) for 2003 and 2004 in the upper, middle and lower sites of each estuary. Horizontal lines above a season indicate that the estuary entrance was closed at the time of sampling.
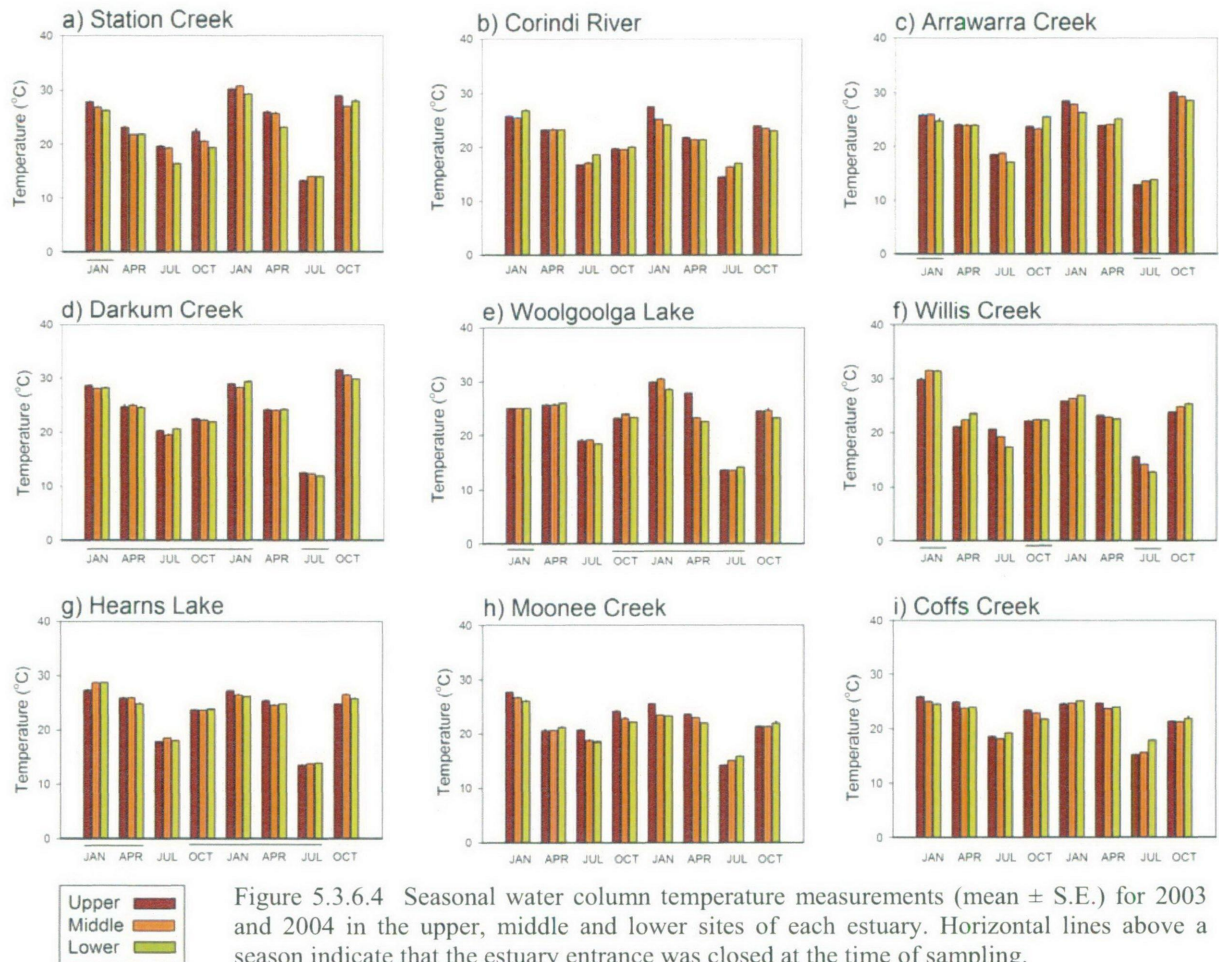
Of all the sediment variables, organic content showed the highest variability over time with significant differences seasonally and for the Year x Season interaction term at all sites of most estuaries (Table 5.3.6.2). Organic content was particularly variable at the upper sites of Willis Creek, as well as at Hearns and Woolgoolga lakes. It also showed considerable peaks (> 15 %) at the upper site of Willis and Coffs creeks in October 2004 (Fig. 5.3.6.7).

Fig. 5.3.6.5 Seasonal sediment graphic mean grain size measurements (mean ± S.E.) for 2003 and 2004 in the upper, middle and lower sites of each estuary. Horizontal lines above a season indicate that the estuary entrance was closed at the time of sampling.
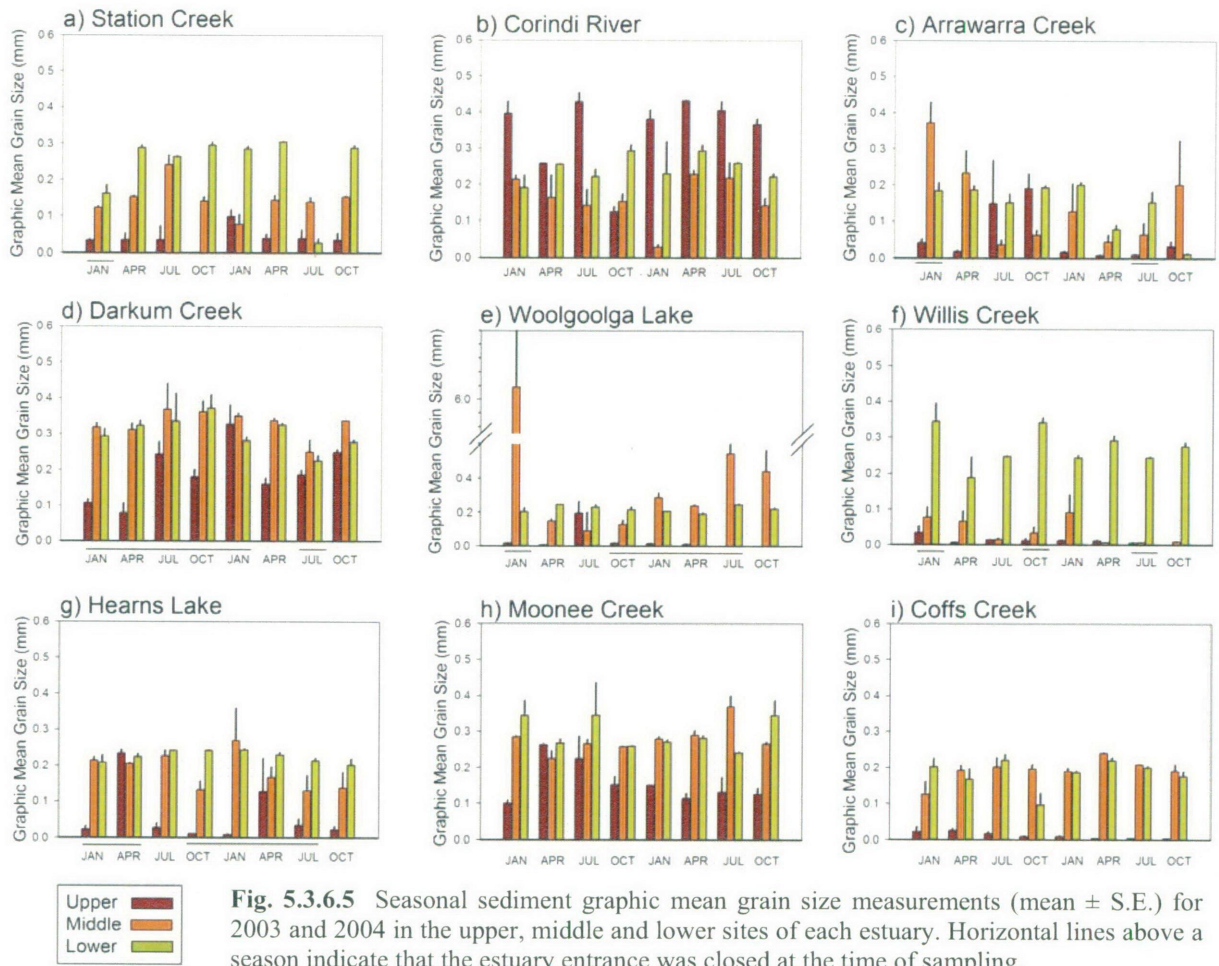
Correlations with Community Patterns

In six estuaries, Corindi River, Moonee Creek, Coffs Creek, Hearns Lake, Station Creek and Arrawarra Creek, the individual physico-chemical variable that returned the strongest correlation with the faunal community over the full two-year period was sediment organic content, closely followed by sediment homogeneity (Table 5.3.6.3). This relationship was strongest for both organic content and sediment homogeneity in Coffs Creek (ρ = 0.718; 0.571, respectively).

Whilst organic content continued to correlate strongly with the benthic communities in Willis Creek, Darkum Creek and Woolgoolga Lake, the strongest relationship with an individual physico-chemical variable for these estuaries was in fact with sediment homogeneity for

Woolgoolga Lake and Willis Creek (ρ = 0.474; 0.207, respectively) and with salinity in Darkum Creek (ρ = 0.294). The best correlations with combinations of physico-chemical variables for most estuaries were usually with the three sediment variables, grain size, homogeneity and organic content, together with salinity (Table 5.3.6.3). Dissolved oxygen and the estuary entrance status at the time of sampling also featured strongly in the BIOENV analysis for Willis Creek.

Table 5.3.6.2 Summary of results of two-way ANOVAs for the physico-chemical sediment variables (GGS = graphic mean grain size, GSD = graphic standard deviation, OC = organic content) in the upper, middle and lower sites of each estuary. *d.f.* = 1,16 for comparisons between years and *d.f.* = 3,16 for comparisons between seasons. '- ' indicates a non-significant results ($p > 0.05$), significant results are shown by '*' ($p < 0.05$) and '**' ($p < 0.001$).

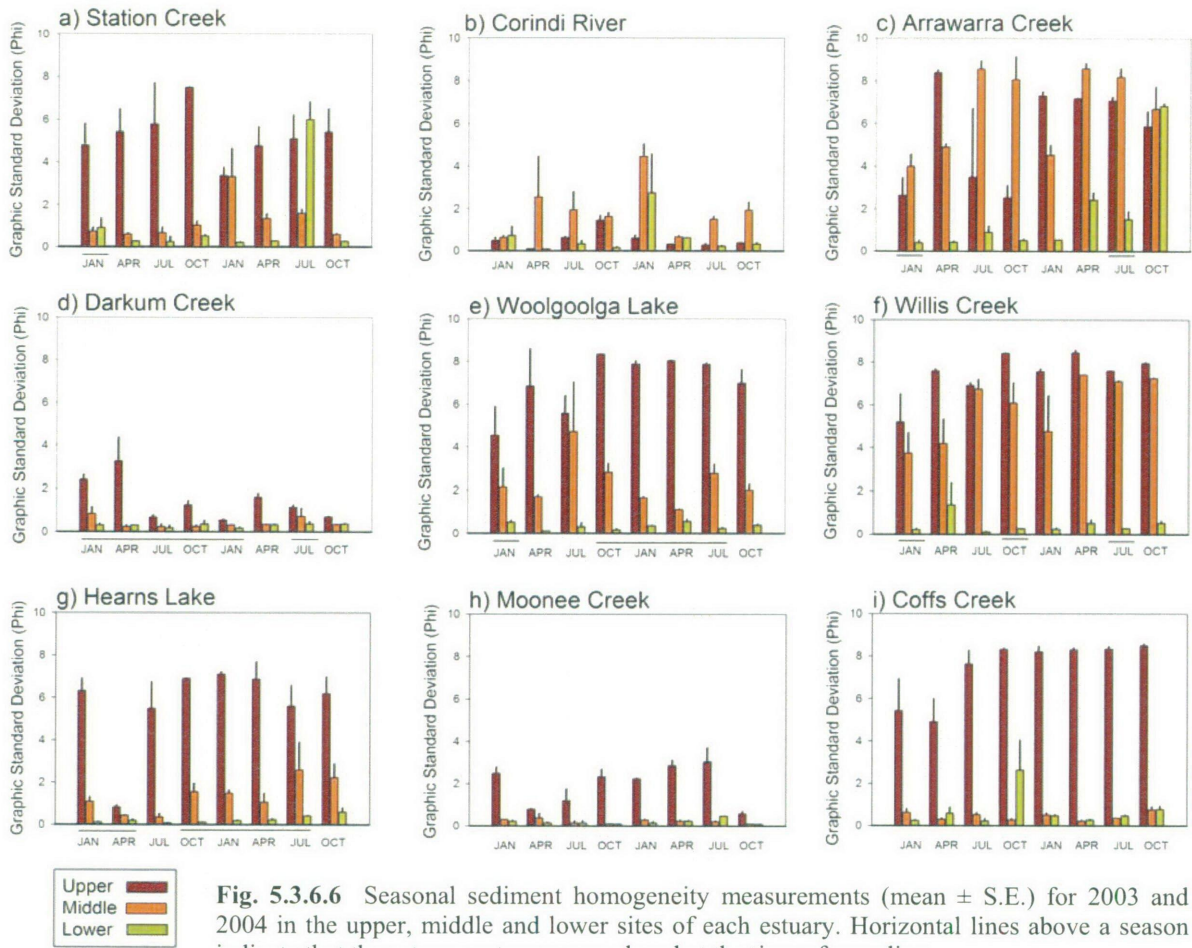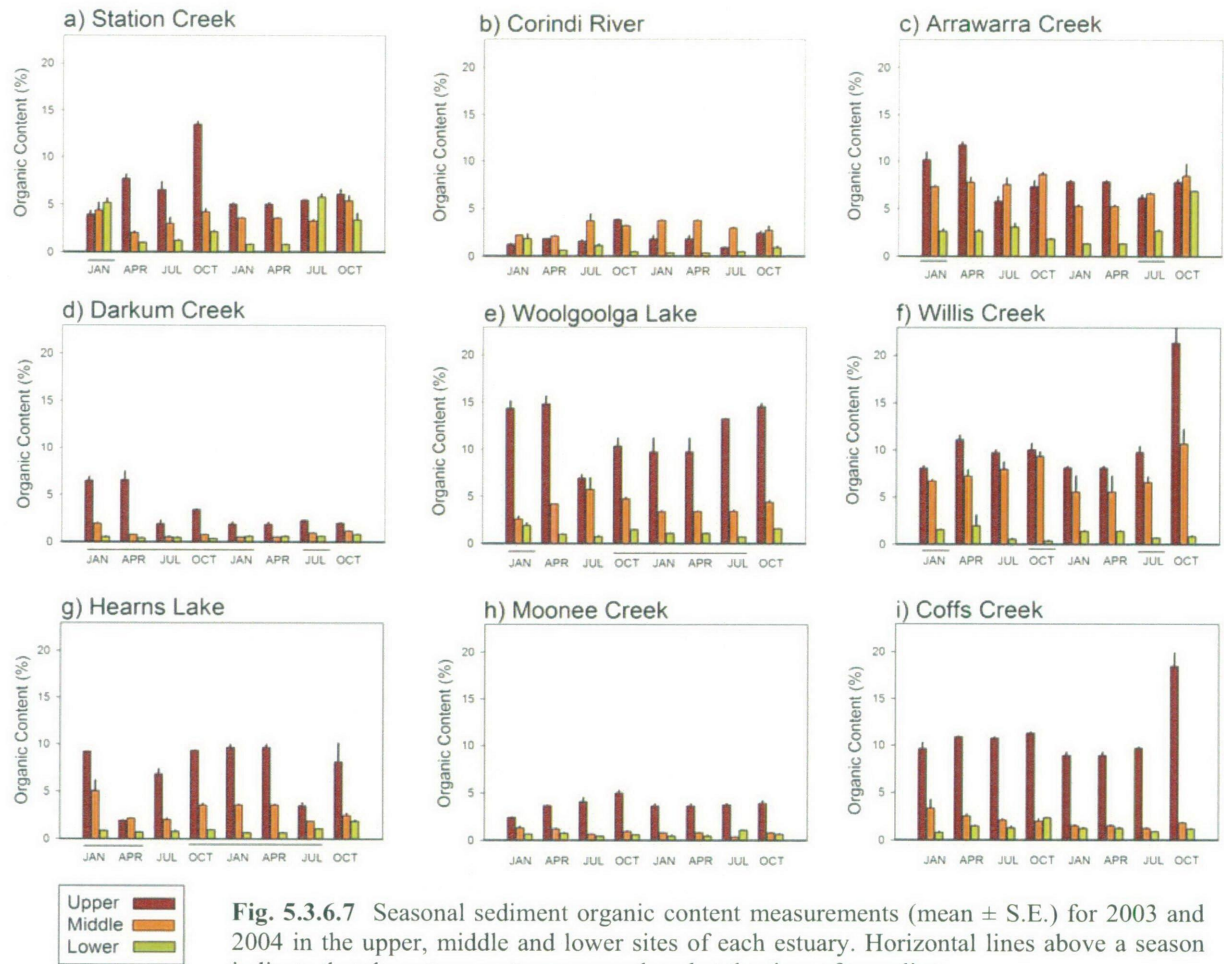|			COR	MOO	COF	STA	ARR	DAR	WOO	WIL	HEA
GGS	Upper	Year	**	*	*	-	*	*	**	-	-
		Season	**	-	-	-	*	*	**	-	*
		Year x Season	**	*	-	-	-	*	**	-	-
	Middle	Year	-	*	-	*	-	*	-	-	-
		Season	-	*	-	**	-	*	-	-	-
		Year x Season	*	*	-	*	-	*	-	-	-
	Lower	Year	-	-	-	*	**	*	-	-	-
		Season	-	-	*	**	*	-	-	-	-
		Year x Season	-	*	-	**	**	-	-	-	-
GSD	Upper	Year	*	-	*	-	*	*	-	-	*
		Season	**	-	-	-	*	*	-	*	*
		Year x Season	**	**	-	-	*	-	-	-	*
	Middle	Year	-	-	-	-	-	-	-	-	-
		Season	-	-	-	-	**	-	*	-	-
		Year x Season	-	-	-	-	*	-	-	-	-
	Lower	Year	-	-	-	*	**	-	-	-	*
		Season	-	*	-	**	**	-	-	-	-
		Year x Season	-	*	-	**	**	-	*	-	-
OC	Upper	Year	**	-	-	**	*	**	-	*	-
		Season	**	**	**	**	**	**	-	**	**
		Year x Season	*	**	*	**	*	**	**	**	*
	Middle	Year	-	**	*	-	*	*	*	-	-
		Season	**	**	-	**	*	**	**	*	**
		Year x Season	*	-	-	-	-	**	*	-	-
	Lower	Year	-	-	**	-	**	**	-	-	**
		Season	-	-	**	**	**	*	**	-	**
		Year x Season	*	**	**	**	**	**	*	-	**

Fig. 5.3.6.6 Seasonal sediment homogeneity measurements (mean ± S.E.) for 2003 and 2004 in the upper, middle and lower sites of each estuary. Horizontal lines above a season indicate that the estuary entrance was closed at the time of sampling.

Table 5.3.6.3 Results of BIOENV showing the Spearman rank correlation coefficient (ρ) for correlations between individual physico-chemical variables (and the best combinations of these variables) and the full community data for all sampling times within each estuary. The best individual variable for each estuary is shown in bold.

	Variable	ρ								
		STA	COR	ARR	DAR	WOO	WIL	HEA	MOO	COF
1	Total dissolved salts	0.140	0.069	0.021	**0.294**	0.033	0.043	-0.003	0.218	0.103
2	Dissolved oxygen	0.042	-0.004	-0.073	0.003	0.014	0.067	0.100	0.114	0.060
3	pH	0.071	0.044	-0.142	-0.016	0.031	0.180	0.041	0.179	0.128
4	Temperature	0.112	0.086	-0.103	-0.067	0.005	0.091	0.202	0.094	0.007
5	Sediment grain size	0.039	0.179	0.096	0.197	0.296	0.054	0.112	0.225	0.522
6	Sediment homogeneity	0.204	0.065	0.312	0.168	**0.474**	**0.207**	0.391	0.418	0.571
7	Organic content	**0.225**	**0.239**	**0.422**	0.227	0.473	0.191	**0.448**	**0.666**	**0.718**
8	Entrance status at time of sampling	0.013	n/a	-0.054	0.039	0.040	0.149	0.041	n/a	n/a
	Best combination	0.247	0.314	0.422	0.369	0.519	0.227	0.459	0.666	0.718
		1,6,7	*1,5,7*	*7*	*1,5-7*	*5-7*	*2,6-8*	*6,7*	*7*	*7*

Fig. 5.3.6.7 Seasonal sediment organic content measurements (mean ± S.E.) for 2003 and 2004 in the upper, middle and lower sites of each estuary. Horizontal lines above a season indicate that the estuary entrance was closed at the time of sampling.

5.4 Discussion

5.4.1 Frequency and duration of entrance openings and closures in the intermittently closed estuaries of the Solitary Islands Marine Park

The intermittently closed estuaries of the Solitary Islands Marine Park were each unique in their entrance dynamics and experienced a broad range of frequencies and durations of entrance closure. This was despite these estuaries all being situated within a 30 km stretch of coast and, therefore, also being largely exposed to very similar climatic conditions. The number of entrance closures within the timeframe of the study ranged from one at Station Creek to eight at Willis Creek. Station Creek was also closed for the least time overall (7.5 %), whilst the entrance of Darkum Creek was closed for more than three quarters of the duration of the study

(76.2 %). There was also a vast difference in the duration of entrance closures. The shortest closure lasted only 7 days at Arrawarra Creek; Darkum Creek, again, represented the other extreme with the longest recorded closure of 260 days. This range of variability in entrance dynamics between the estuaries of a region is not unusual. A two-year study of five intermittent estuaries within the Eurobodalla Shire on the NSW south coast (MacKenzie et al. 2002) likewise found entrance dynamics to be highly variable between estuaries. For instance, in those estuaries, the range in the number of closures (3 – 14) was greater and the range in individual closure durations (2 – 258 days) was almost identical to the present study. While the range in the percentage time closed was not as large (58 – 98), all the estuaries in this south coast study were closed for greater than 50 % of the study duration. In comparison, only half of the estuaries in the current study (Darkum, Woolgoolga and Hearns) were closed for a comparable proportion of time. The Western Victorian Estuaries Classification Project (Mondon et al. 2003) also identified major differences in entrance dynamics among the intermittent estuaries of that region and these differences were again very similar to those presented here. Over a maximum of 304 observation days, the Victorian project reported 12 estuaries that experienced entrance closure with the number of closures for each estuary ranging from 1 to 8. The proportion of time that estuaries were closed throughout the study also varied greatly from 1 – 86 %, though only three of the estuaries were closed for greater than 50 % of the study.

5.4.2 *Temporal variation in the relationship between and within the intermittently closed and permanently open estuary types*

The extensive differences initially observed between the benthic communities of intermittently closed and permanently open estuary types in January 2003 (Chapter 4; Hastie & Smith 2006) remained consistent throughout the two years of this temporal study, with highly significant differences separating the two estuary types at each of the upper, middle and lower sites, on all sampling occasions. Even when the data were pooled across all sites, the benthic assemblages of each estuary type remained significantly different. These persistent differences in community structure, even when all estuary entrances are open, strongly support the idea that the two estuary types are different from an ecological point of view, which is likely due to the long-term effects of repeated closures on either environmental and/or biological factors.

However, the relationship between the two estuary types is not as stable as these results may first suggest. The analyses used to examine the community differences between estuary types are very powerful tests and, on closer inspection of the results, considerable ranges in the test statistic, Global *R*, were observed over the two-year sampling period. This variation peaked with Global *R* covering 57 and 40 % of its usual range for the tests conducted on the lower sites and all sites combined, respectively. Used here as a measure of the similarity between the two estuary types, this variation in Global *R* indicates that, although the two estuary types remained significantly different, there were times when the estuary types were in fact much more similar than at other times. This temporal variation in the relationship between the intermittently closed and permanently open estuary types did not display regular seasonal or annual variation. Instead, it correlated well with the number of intermittent estuaries that were closed at each sampling time. Whilst this was initially examined for the pooled data, once divided into the component sites, it was clear that this pattern was primarily evident at the lower sites of the estuaries. Further, the strength of the relationship between the similarity of the estuary types and the number of closed estuaries was surprising, considering that the measure of the "number of closed estuaries" is based on instantaneous observations and does not take into account the duration that individual estuaries had been either open or closed prior to sampling.

Most of the changes in the relationship between the intermittently closed and permanently open estuaries were largely due to changes in the abundance of only eight of the 135 species collected during this study. All eight species, comprising four polychaetes, three bivalves and an amphipod, were very common throughout the duration of the study and, at times, highly abundant. Although most of the univariate analyses on the abundances of these species individually showed no significant differences between types, their combined effects continued to contribute to the to assemblage differences between estuary types. Thus, it was still important to examine their average abundance trends for each estuary type. Apart for the amphipod *U. metungi,* the average abundances of each were relatively low and stable in the lower sites of the permanently open estuaries. In contrast, in the lower sites of the intermittently closed estuaries, the average abundances of the same species, especially *S. normalis*, *N. estuarius* and *O. cirriformia*, were variable and often much higher than those in the permanently open estuaries, particularly during times when a number of the intermittent estuaries were closed. Most of the eight species were usually associated with the middle and upper sites of all estuaries but tended

to be either common or highly abundant in the lower sites of the intermittent estuaries at these times.

Likely mechanisms driving the irregular, increased abundances of these species at the lower sites of the intermittent estuaries include: (1) entrance closures affecting environmental conditions in a way that temporarily favoured an extended downstream distribution (e.g. increased organic content, reduced water movement and changes in water column salinity, dissolved oxygen and temperature); and (2) entrance dynamics affecting the occurrence of marine-dependent species at the lower sites, either by a physical barrier during recruitment periods, or by physico-chemical conditions becoming intolerable to some fauna, so that interspecific competition is reduced and the remaining fauna are able to thrive. As the timing of their irregular fluxes at the lower sites of the intermittent closed estuaries were not always consistent between species, it is probable that the assemblage patterns observed were a result of a combination of these mechanisms. Further support for these mechanisms is found when circumstances are reversed (i.e. opening events). For example, at the lower sites among the intermittent closed estuaries, the previously high abundances of *M. vitrea* and *O. cirriformia* were often dramatically reduced following entrance opening events.

A high degree of variation was consistently present within both the intermittently closed and permanently open estuary types for all sampling occasions. Even at sampling times that followed periods when all of the intermittent estuaries had been open (e.g. July 2003, April 2004), highly significant differences remained. Only a few similarities were revealed between estuaries and these were mainly in the lower sites of the intermittent estuaries in 2003, occurring when samples were quite depauperate, particularly those from the lower site of Hearns Lake and Darkum Creek.

The continued high degree of variation between the estuaries nested within each type can be partly attributed to the equally variable physico-chemical conditions, which revealed significant differences at this scale for all water column variables at all sites and, excepting sediment homogeneity at the lower sites, for all sediment variables at most sites. Physico-chemical variables, therefore, were also unique between individual estuaries throughout the duration of the study. In contrast, there were only a few instances when physico-chemical variables differed between the two estuary types. These patterns were mainly due to the high levels of variation

within each estuary type. Reduced dissolved oxygen levels coincided with increased temperatures in the intermittently closed estuaries during January and October 2004. There was also a temperature difference between estuary types in July 2004, at which time overall water temperatures were considerably colder in the intermittent closed estuaries. The temperature differences were associated with a lack of tidal exchange with warmer marine waters as most intermittent estuaries were closed at these times.

The persistent assemblage differences between estuary types could not as readily be related to physico-chemical factors as each of the water column and sediment variables: (1) generally failed to reveal significant differences between estuary types; and (2) were highly variable through time. However, the range in physico-chemical conditions was, in turn, likely due to the variation in estuary catchment size and its effect on entrance dynamics. Catchment size was the one environmental factor that remained constant and its influence was emphasized by it continuing to be the environmental variable that had the strongest correlation with the full community data for each sampling time on all occasions except April 2003. Organic content and salinity also repeatedly featured strongly when correlating the community data for all estuaries with environmental factors. Interestingly, April 2003 was one of the three samples that took place when all entrances were open. It was also the time when the similarity between estuary types was at its greatest at the lower sites and for all sites pooled. Although this continues to raise the question of whether the entrance status or catchment size were most important in structuring communities, there were another two sampling times when all estuaries were open and on both occasions catchment size correlated best with community data. Thus, of the factors considered in this study, it appears that catchment size was most important in determining the differences in community structure between these estuaries.

5.4.3   *Temporal variation within individual estuaries*

Benthic patterns in each estuary were highly variable, both seasonally and annually, at all sites. However, patterns of seasonal variation were not consistent for each sampling year. Overall, this resulted in significant community differences between all sampling times for most estuaries. Equally variable temporal trends in estuarine benthic communities have likewise been observed in other Australian and South African intermittent and permanently open estuaries (Jones 1987; Morrisey et al. 1992b; Platell & Potter 1996; Konandjembo et al. 2001; Mackay & Cyrus 2001;

Teske & Wooldridge 2001; Teske & Wooldridge 2003). In regard to the temporal variation in the intermittently closed estuaries, the findings of Teske and Wooldridge (2001) contrast completely with the current study in that they detected no seasonal changes in benthic communities. They attributed these results to high rates of water extraction, which had reduced the intensity of seasonal floods and associated physico-chemical processes. The results also contrast to those of Platell and Potter (1996) who found that seasonal variation in benthic communities was cyclical, repeating in consecutive years. In the current study, the most notable temporal overlap between sampling times for an individual site occurred in lower Hearns Lake, where there were considerable assemblage similarities between sample times when the entrance was closed. In the intermittently closed estuaries, there were also, always, differences in community structure between times of entrance closure and times when the estuary was open, except at the upper site of Woolgoolga Lake and the lower site of both Arrawarra and Darkum creeks.

Both the seasonal and annual community differences in each estuary were due to changes in the abundance, or even simply the presence/absence, of the species that typically characterised each estuary. These comprised a core of nine species that each contributed greatly to the temporal variation in four or more estuaries and included: *A. intermedia*; *S. normalis*; *S. alba*; *V. australiensis*; *N. estuarius*; *U. metungi*; *S. aequisetis*; *A. helmsi* and *O. cirriformia*. Note that most of these were also the species that consistently contributed to the persistent spatial differences between estuary types and are, therefore, key indicators of community variation in these systems. The remaining species that were important contributors to temporal community variation tended to be estuary-specific and included: *B. australis* and *C. coralium* at Woolgoolga Lake; *F. subtortus* and *A. tasmanica* at Willis Creek; *A. ehlersi* at Hearns Lake; *T. imbellis* and *N. jonasii* at Coffs Creek; *T. australis* at Moonee Creek; *T. australis*, *N. gravieri* and *M. longicarpus* at Corindi River. Similar studies have, likewise, found species compositions among estuaries to differ between seasons and between the corresponding seasons of different years (Konandjembo et al. 2001), and that these variations may display little synchrony between species, even at the same site (Rainer 1981). Such changes reflect not only the varying responses of species to environmental conditions but also differences among species in the timing of key reproductive, recruitment and mortality events.

When comparing the relationship over time between the assemblages of the upper, middle and lower sites in each estuary some interesting, though varied, patterns emerged. A persistent gradient, or separation between sites was present in Coffs, Moonee, Station and Darkum creeks, although, in Darkum Creek, this gradient was very condensed. At Corindi River and Arrawarra Creek, there was a persistent separation of the lower site in comparison to the other two sites but considerable temporal overlap between the upper and middle sites. Community structure in Woolgoolga and Hearns lakes also displayed some temporal overlap between the upper and middle sites, which primarily occurred during times of entrance closure. Closure effects were also evident in Station Creek; however, they did not disrupt the gradient between sites, rather, the assemblages during entrance closure tended towards one extremity of the range of community structure. Similarly, in Willis Creek there was also a clear demarcation between assemblages when the entrance was closed and open. There was, however, no persistent gradient over time between any of the sites at Willis Creek, which is likely due to the high freshwater input from the sewerage outfall there.

Physico-chemical variables were also temporally highly variable within each estuary and, like community structure, the seasonal variation was not consistent between years. This high degree of variability was especially true for all water column parameters, particularly at Darkum Creek, Willis Creek and Hearns Lake. In regard to notable variations in dissolved oxygen, hypoxic conditions occurred throughout all sites of both Arrawarra and Willis creeks in January 2004. These conditions were due to the decomposition of large amounts of marcoalgae, though the source of algae was different for each estuary. For Arrawarra Creek algae was washed in from nearby marine habitats, whilst in Willis Creek the algae originated internally from a large algal bloom that persisted, as did the hypoxic conditions, for the following three months. Salinity was relatively stable in the estuaries that the greatest marine input, but varied greatly in those with limited marine input, especially Darkum Creek, Woolgoolga Lake, Willis Creek and Hearns Lake. These estuaries experienced both their highest and lowest salinities while entrances were closed. As such, the relationship between salinity and entrance state in intermittent estuaries is not a simple one. Rather, an intermittently closed entrance, particularly one that is closed more often than not, can result in highly variable salinities with an extreme range over time and it may, in fact, be this range in salinity that determines community structure in the intermittently closed estuaries. The high degree of variability in both dissolved oxygen and salinity would have undoubtedly contributed to the temporal changes in community structure seen here and

these factors have, elsewhere, been found to determine benthic community structure and govern distributions over time in both intermittently closed and permanently open estuaries (Nordby & Zedler 1991; Dauer & Ranasinghe 1992; Konandjembo et al. 2001; Mackay & Cyrus 2001).

Sediment grain size and homogeneity were not as variable as the water column parameters, with many similarities at both temporal scales. In contrast, sediment organic content was highly variable, both seasonally and annually, in all estuaries. More importantly, organic content was also the individual environmental variable that correlated best with the community patterns over time for most estuaries. The main exception to this was Darkum Creek, where salinity showed the strongest correlation with the benthic community over time. Whilst sediment grain size continues to be repeatedly highlighted in the literature as one of the most important factors determining the distribution of estuarine benthic fauna, particularly in intermittently closed estuaries where fauna are more accustomed to changes in salinity (Schlacher & Wooldridge 1996a; Constable 1999; Constable & Fairweather 1999; MacFarlane & Booth 2001; Teske & Wooldridge 2003) the current findings support organic content as a more likely causal factor in determining faunal distributions over time. Organic content is an indicator of the availability of food for benthic fauna as particulate organic matter is the dominant food-source for deposit feeders and can also be utilised by suspension feeders following resuspension (Snelgrove & Butman 1994). Alternatively, Snelgrove and Butman (1994) have suggested that correlations between fauna and sediment variables may not be caused by those aspects of the sediment itself, but by the physical processes that created that particular sedimentary environment (e.g. hydrodynamic regime). Leonard et al. (1998) and Hernandez-Arana et al. (2003) also support the influence of water stability and flow-driven variation in structuring estuarine benthic communities. However, for all of the intermittently closed estuaries, the status of their entrance at the time of sampling and, hence, changes in their hydrodynamic regime, ranked poorly when comparing environmental and community patterns.

While this lack of a relationship between entrance status and the temporal community trends in each estuary appears to contradict the earlier findings reported here, where spatial differences between the intermittently closed and permanently open estuaries became less distinct when more of the intermittent estuaries were open, it supports those of Edgar and Barrett (2002). They found seasonal and interannual variation in Tasmanian estuaries to be much lower than the spatial variation between estuaries. So, in summary, whilst each estuary was highly variable

over time, this temporal variation did not detract from the persistent and long-term spatial individuality of estuaries, both biologically and physico-chemically, even among those of the same estuary type. Ultimately, this is a reflection of the range of intrinsic features represented by the estuaries within a region, including variations in factors such as their catchment size and entrance dynamics, as well as other factors that were not assessed here, including catchment uses, the degrees of both urbanisation and land clearance, and entrance and other modifications. It also further stresses the need to consider the implications of high levels of ecological heterogeneity between estuaries when considering effective estuarine classification and management (Edgar et al. 2000; HRCNSW 2002; Hirst 2004; Hastie & Smith 2006).