Port Curtis Macrobenthic

Monitoring Programme

Surveys: 1995 – 2001

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U N I V E R S I T Y

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EXECUTIVE SUMMARY

Changes in benthic community structure in Port Curtis were examined from quantitative $(0.1m^2)$ grab samples collected at 30 stations on 12 sampling periods between 1995 and 2001. The total fauna collected included 35421 individuals and 409 species, of which nearly 90% are apparently undescribed. Filter-feeding organisms dominated the bedforms at the survey locations and accounted for more than 50% of the abundance and 30% of the species richness. The small bivalve mollusc *Carditella torresi* was the most common organism collected, and represented more than 14% of the total number of individuals. Most other organisms were rare by comparison, and 98% of species individually accounted for less than 2% of the total abundance.

Temporal and spatial differences in community structure between stations were determined using a combination of Bray-Curtis dissimilarity indices, non-metric multidimensional scaling and analysis of variance techniques. Ordinations of species abundance data revealed strong ecological gradients principally driven by depth and sediment structure. Depth related differences in benthos were most pronounced between the subtidal and intertidal zones, and species abundance and richness were both significantly lower in the intertidal. Species abundance and richness were also found to be significantly lower in sediments that were either too coarse or too fine.

Seasonal and interannual differences in species richness and abundance were significant, and both parameters displayed similar long-term trends. Over the course of this study mean species richness and abundance progressively declined and subsequently recovered by approximately 72%. Similar temporal trends were also evident for all common dietary groups (filter feeders, deposit feeders, scavengers and predators), and it appears that drivers underpinning observed changes have a consistent influence at most trophic levels.

Explanations for long-term trends in abundance and richness were determined through correlation analyses with key environmental variables. Both species richness and abundance were found to be highly correlated with turbidity measurements observed 4 months previously ($r^2 > 0.8$, $p < 0.01$). This remarkable finding suggests that high levels of turbidity promote recruitment and growth of benthic organisms in Port Curtis. Strong correlations between regional rainfall, freshwater inflow, nutrient and chlorophyll *a* concentrations, add further support to the hypothesis that recent changes in benthic productivity within the estuary are principally the result of long-term climatic cycles including El Niño events.

INTRODUCTION

Port Curtis is a shallow, semi-enclosed estuarine system situated on the central coast of Queensland approximately 500 kilometres north of the state capital Brisbane. Bounded by two large offshore islands (Curtis Island and Facing Island), the waters of Port Curtis form a narrow coastal embayment approximately 200 km² in area. Freshwater flows are seasonally significant, and two major rivers (Boyne and Calliope) and numerous creeks discharge into the port. Strong tidal currents and a 5m tidal range also have major influences on the area's marine and intertidal ecosystems. The area supports a wide range of marine habitats including mangroves, seagrass beds, salt-marshes, coral reefs, and extensive mudflats and subtidal soft-sediments.

Many of the regions coastal environments are considered significant in terms of conservation value. The Great Barrier Reef World Heritage Area commences at the low water mark on the mainland side of the Narrows and includes Curtis Island, while the offshore areas east of Curtis Island are included within the Mackay/Capricorn Section of the Great Barrier Reef Marine Park (GBRMPA, 1998). Areas in and around Port Curtis also provide important feeding grounds for the endangered species *Dugong dugon* and have been declared part of the Rodd's Bay Dugong Sanctuary (GBRMPA, 1999).

Industrial growth in the Port Curtis hinterland over the last 40 years has resulted in the development of several foreshore manufacturing, processing and bulk handling facilities. These include major alumina and aluminium processing plants, a coal-fired power station, a cement works, several chemical

refineries, and an extensive network of shipping wharves and storage facilities. The Port of Gladstone is now Queensland's largest multi-cargo port and the fifth largest port in Australia, handling more than 50 million tonnes of cargo each year. Other significant industries within the region include mining, agriculture, fishing and tourism.

As the population and industries of the Port Curtis region continue to grow, so too does the potential for environmental degradation. Considerable visible changes to the coastline of Port Curtis have occurred in recent times, with over 650 hectares of mangroves and 990 hectares of salt-marsh being lost due to reclamation or environmental stress since the 1940's (QDEH, 1994). Concomitant changes to water quality and many subtidal marine habitats are largely undetermined due to a lack of quantitative, historical data.

For several decades now, researchers have used measures of change in benthic marine communities to identify and monitor man-made impacts on the sea (Poore and Kudenov, 1978; Gray and Christie, 1983; Warwick, 1993). The utility of the technique stems largely from the fact that benthic organisms are relatively non-mobile and tend to integrate effects of pollutants over time. Additionally, benthic organisms are comparatively easy to sample and enumerate to species level. In Port Curtis, several studies have also adopted macrobenthic sampling to assess the extent and persistence of man-made impacts. These include applications in the assessments of maintenance dredging at the Clinton Coal wharf, dredge spoil dumping in the outer harbour, land reclamation at Auckland Point and foreshore developments near Fisherman's Landing (WBM, 1991; WBM 1993a; WBM, 1996; SKM, 1999). Unfortunately, all of these surveys have only measured short-term change in macrobenthos (< 18 months duration) over limited geographical areas.

In 1993, the Gladstone Port Authority (GPA) commissioned the consultants WBM Oceanics to design a long-term macrobenthic monitoring programme for Port Curtis. The aims of this study were to quantitatively assess whether current or future anthropogenic activities significantly impact fauna and the Port Curtis ecosystem (WBM, 1993b cited in Small et al., 2001). To achieve these aims GPA established 16 sampling stations within the confines of Port Curtis during 1995. A further 14 stations were established by Southern Pacific Petroleum (SPP) between November 1995 and November 2000. Ten benthic grab samples have been taken from each of the 30 Port Curtis stations on an annual basis (during November) since their establishment. Additional sampling at the 16 GPA stations during April each year has resulted in a total complement of 460 grab samples being collected from Port Curtis in most recent calendar years.

The bedforms of Port Curtis now represent one of the most intensively surveyed areas of soft-sediment in Australian waters. With more than 2600 benthic grab samples processed to date, the benthic sampling effort applied in Port Curtis now far surpasses that level of sampling applied in water bodies adjacent to major metropolitan centres including Port Phillip Bay on Melbourne's foreshore (~1500 grabs: Poore et al., 1975; Poore and Rainer, 1979; Coleman, 1993; Currie and Parry, 1996; Wilson et al., 1998; Currie and Parry, 1999). Despite the wealth of available benthic data for Port Curtis, no attempt has yet been made to examine the environmental significance of any underlying temporal and spatial trends. This paper therefore examines a recent chronology of macrofaunal community structure in Port Curtis, and specifically considers observed differences in relation to physical, climatic and anthropogenic factors.

MATERIALS AND METHODS

Grab sampling
Changes in the distribution and abundance of infauna at 30 stations in Port Curtis (Figure 1) were determined from van Veen grab samples collected on 12 sampling periods between 1995 and 2001. To avoid the possible confounding influence of large rainfall events on benthic species composition, all sampling was conducted over a 2-3 week period in April (post-wet season) and November (pre-wet season) of each year (ie Nov 95, Stations 1-20; Apr 96, Stations 1-20; Nov 97, Stations 1-20; Apr 97, Stations 1-24; Nov 97, Stations 1-24; Apr 98, Stations 1-24; Nov 98, Stations 1-24; Apr 99, Stations 1-24; Nov 99, Stations 1-24; Apr 00, Stations 1-16; Nov 00, Stations 1-30; Apr 01, Stations 1-16). A total of 10 replicate $0.1m^2$ grabs were collected at each station and sampling period, and a 100g sub-sample removed from each for sediment grain size analysis. The remaining sample was sieved on a

1mm mesh, and the fauna retained, sorted, identified and enumerated to the highest taxonomic level (generally species). Due to apparent inconsistencies in the discrimination and counting of live gastropod molluscs, this taxonomic group was omitted from all subsequent analyses.

Sediment structure

Particle size analysis was conducted on sediments from each sampling station to determine the strength of associations between macrobenthic faunal assemblages and the nature of the sediments surrounding them. A 100g sub-sample of sediment from each grab was air-dried and ground with a mortar and pestle to retain discrete particles. The sample was then weighed and sieved through an agitated stack of Endecott test sieves with apertures of 2mm, 1mm, 500µm, 250µm, 125µm and 63µm. After dry sieving the sediment fractions remaining on the sieves were wet with sodium hexa-meta-phosphate dispersing solution, and the resultant slurry hand washed through the sieve stack until the wash water was clear. The residual material was then air-dried at 40°C until a constant mass was reached. The mass of each fraction was subsequently expressed as a percentage of the total sample mass.

Statistical analysis

Spatial and inter-annual differences between benthic communities at the 30 Port Curtis stations were examined using Bray-Curtis (B-C) dissimilarity measures (Bray and Curtis, 1957). The B-C dissimilarity measure is given by the following relationship:

$$\delta_{jk} = \frac{\sum_{i=1}^{s}\left|n_{ij} - n_{ik}\right|}{\sum_{i=1}^{s}\left(n_{ij} - n_{ik}\right)}$$

where n_{ij} = the number of the ith species in the jth sample, n_{ik} = the number of the ith species in the kth sample and δ_{jk} = dissimilarity between the jth and kth samples summed over all s species. This dissimilarity measure was chosen because it is not affected by joint absences, it gives more weighting to abundant than rare species, and it has consistently performed well in preserving 'ecological distance' in a variety of simulations on different types of data (Field et al., 1982; Faith et al., 1987).

The number of individuals of each species at each station and sampling period was summed prior to all community analysis. Double square root ($N^{\frac{1}{4}}$) transformations were also applied to the data before calculating B-C dissimilarity measures. These transformations were made to prevent abundant species from influencing the B-C dissimilarity measures excessively (Clarke and Green, 1988; Clarke, 1993). Multidimensional scaling (MDS) ordination was subsequently used to map spatial and temporal relationships in the B-C dissimilarities for all 30 stations and 12 sampling periods. The computer package PRIMER (Clarke and Gorley, 2001) was employed for all non-metric ordinations in this study. The final configurations presented were the best solutions (ie. exhibited the lowest 'stress' values, or least distortion) from a minimum of 100 random starts. Species which contributed most to differences between groups identified in MDS plots were determined using the SIMPER routine in PRIMER.

The statistical significance of spatial and temporal differences in infaunal species abundance and richness was further examined using two-way fixed factor analysis of variance (ANOVA). Prior to these analyses, homogeneity of variance was examined using Cochran's test and heterogeneity removed where necessary with a double square root transformation. This transformation was used rather than a Log (N+x) transformation as it was consistent with the transformation used in the MDS plots, it avoided the need for an arbitrary selection of x, and because the results of analyses using log (N=x) and double square root transformations are rarely distinguishable (Field et al., 1982; Clarke and Green, 1988).

Power analyses were undertaken to determine the statistical power associated with each tests performed on the macrobenthic dataset. For the purposes of these analyses, the probability of committing a Type I error was set at 10% ($\alpha = 0.1$) to reduce Type II error.

Environmental parameters

While there is increasing evidence that global atmospheric changes have a profound influence on the abundance and distribution of many marine organisms including plankton, pelagic fish and cetaceans (Shane, 1995; Fromentin and Planque, 1996; Grover et al., 2002), the effects of global climatic change

on marine benthic assemblages remain largely unknown. This situation is principally due to a paucity of long-term benthic data sets that span completely, recurrent, atmospheric cycles of known duration (eg El Niño events; 5-8 years). The Port Curtis dataset is arguably the most comprehensive long-term benthic dataset in Australia, and offers an unprecedented opportunity to investigate the direct and indirect effect of climate change on benthic communities. To this end, seasonal changes in the mean abundance and diversity of benthic organisms in Port Curtis were examined in relation to temporal changes in a range of global and local environmental parameters. These included measures of the Southern Oscillation Index (SOI), rainfall and freshwater flows in the Port Curtis catchment, and ambient measures of turbidity, chlorophyll *a* and dissolved reactive phosphate. Pearson correlation coefficients were used to examine the strength of association between the monthly means of all variables, and additionally to determine the presence of any delayed effects (4 months lag) on benthic abundance and diversity.

Environmental data for these analyses were obtained from a variety of state, federal and statutory government sources. Values for the Southern Oscillation Index (SOI), which represent monthly differences in air pressure between Tahiti and Darwin, were provided by the Commonwealth Bureau of Meteorology. Local mean monthly rainfall (mm) and freshwater flows (ML) were determined from daily measures recorded at the Department of Natural Resources and Mines' monitoring station on the Calliope River at Castlehope (approximately 15km upstream from Port Curtis). Monthly mean turbidity measurements (NTU) were derived from continuous logs (10 minute intervals) on a nephelometer unit deployed by the Gladstone Port Authority at Wiggins Island near the mouth of the Calliope River. This location was also proximal to the site for monthly measurements of surface chlorophyll *a* concentration by the Queensland Environmental Protection Agency. Finally, mean monthly phosphate concentrations were obtained from a continuous seawater analyser (Greenspan Aqualab, 6 hour intervals) recently established by the Gladstone Port Authority at Clinton Wharf.

RESULTS

General observations
A total 409 species and 35421 individuals were found in the 2640 grab samples collected between November 1995 and April 2001. Of these species, nearly 90% (366) are apparently undescribed. Polychaetes, molluscs and crustaceans together accounted for more than 86% of the individuals and 83% of all species collected. Other less common taxa encountered included echinoderms, chordates, cnidarians, sipunculids, pycgnogonids, nematodes, nemerteans and platyhelminths (Tables 1A-B).

Filter feeding organisms dominated the infaunal communities in Port Curtis, and accounted for more than 50% of the total abundance and nearly 30% of the total species richness (Tables 1A-B). Deposit feeding organisms were also common, and represented more than 25% of the total abundance. The same group was also the most diverse, and accounted for nearly 35% of the total species compliment. Other trophic groups including predators, scavengers, grazers and parasites, were rarely encountered. Collectively these feeding groups represented less than 20% of the total number of individuals, and less than 35% of the total species diversity.

The bivalve mollusc *Carditella torresi* was the most abundant species found during the study. This small (<5mm), filter feeding organism represented more than 14% of the total infaunal abundance, and was principally found at subtidal sampling stations. Few other species could be considered numerically dominant within the port. The ascidian *Ascidia sydneiensis* was the second most common species overall, but accounted for less than 4% of the combined abundance. A further eight species (including the bivalves *Corbula tunicata, Mimachlamys gloriosa, Leionuculana superba, Mactra abbreviata, Placamen tiara*, the ascidian Ascidiacea sp. 5, the polychaete worm *Eunice vittata* and the caridean shrimp *Alpheus* sp.) were represented in 2-3% of the total. However, the majority of organisms (98% of species) were collected infrequently, and individually contributed less than 2% to the total abundance.

Macrobenthic community analyses
The MDS ordination (Figure 2A) maps spatial and temporal changes in benthic community structure at the 30 stations sampled between November 1995 and April 2001. The stress coefficient of 0.25

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indicates that the ordination is not unduly distorted (Clarke, 1993), and a fair representation of the input dissimilarities in 2 dimensions.

Because each sampling station has been assigned a separate symbol in Figure 2A, the relative locations and scatter of each symbol group represents the degree by which the community structure at each station differs, and furthermore how it has changed between seasons and years. Unfortunately there is considerable overlap in the spread of station symbols in this ordination, and few clear patterns are readily apparent. When station depths are superimposed on the same ordination, a distinct site pattern is evident (Figure 2B). Symbols for stations sampled in the intertidal zone of the port (stations 21, 22, 23, 24) form a discrete and cohesive grouping in this ordination, and plot towards the upper right of the page. In contrast, symbols classifying stations located in 0-5m and 5-10m depth zones largely intergrade and plot though much of the central region of the ordination.

While depth appears to have a profound influence on the community structure of macrobenthic fauna within Port Curtis, sediment structure also plays an important role in modifying ecological gradients in the waterway. This latter observation is readily demonstrated when the percentage of fine mud found at each station and sampling period is superimposed on the MDS ordination of benthic community structure (Figure 2C). In the ordination, stations located in the muddiest environments (76-100% silt) plot towards the lower right of the page, while less muddy stations progressively plot towards the upper left of the page. Remarkably this pattern is preserved in stations situated in both intertidal and subtidal habitats.

Bubble-plots of species richness, abundance and diversity superimposed on the MDS ordination (Figure 3A-D) provide compelling visual explanations for apparent spatial differences in community composition with depth and sediment structure. In these plots the diameter of the circle represents the magnitude of the variable on a monotonic scale, and high concentrations of larger circles infer regional elevations in that variable. By comparing Figure 3B with Figures 2B, 2C, and 3A, it is evident that most species on average are found in subtidal rather than intertidal environments. It is also clear from the same comparisons that species richness within the port is greatest in environments that are neither too silty nor too sandy. Similar distributional patterns are also evident in infaunal abundances (Figure 3C), with most organisms being recorded from moderately silty (26-75% silt), subtidal locations.

While measures of species richness and abundance are highly correlated (r^2=0.61, p<0.01), observed trends for these parameters do not translate to similar patterns in diversity. Measures of Shannon-Wiener diversity (H') (Figure 3D) are broadly similar across most sampling stations/periods (μH'= 2.54 ± 0.03), and there is no tendency for this parameter to either increase or decrease with sampling depth or sediment structure. On closer examination, it is clear that this result is principally due to consistently high evenness values at most sampling stations/periods (μJ' = 0.79 ± 0.01). In other words, there is little species dominance, and individuals are uniformly distributed between species at each sampling station and period.

Species contributions to group differences
Species making major contributions to differences in community structure between the intertidal and subtidal regions were identified by calculating relative contributions to the overall average dissimilarity value (87.64; Appendix I). Remarkably, most organisms principally accounting for observed assemblage differences were bivalve molluscs. *Carditella torresi*, Bivalve #30, *Mactra abbreviata*, *Placamen tiara*, *Azorinus* sp. 2, *Leionuculana superba*, *Corbula tunicate* and *Tellina* sp. 7, collectively accounted for more than 16% of the average dissimilarity. These species were not necessarily abundant, by and large, but exhibited disproportionate population sizes between the intertidal and subtidal zones.

Despite regional differences in abundance, few bivalve species could be regarded as characteristic of either the intertidal or subtidal zone. No one organism, for example, contributed 3% or more to the overall average dissimilarly, and it appears that much of the observed difference between the intertidal and subtidal is due to the presence or absence of suites of generally uncommon species. A total of 402 species were encountered at subtidal locations and 143 species found in the intertidal. Of these species, 136 were found in both the intertidal and subtidal zones, 226 were exclusively found in the subtidal, and further 7 species were restricted to the intertidal.

Temporal trends in community structure

While the ordination plot presented in Figure 2A shows variation in benthos at all stations over the duration of the study, it does not readily demonstrate the level of change in community structure evident at each sampling station with time. To better illustrate temporal shifts in species composition at all 30 stations, the locations of individual stations and sampling periods have been highlighted on a series of individual plots (Figure 4A-B). In these plots the lengths of the lines connecting the larger circles (individual stations) indicate the magnitude of change in infaunal community structure between successive samplings ie short lines indicate little temporal change while longer lines reflect large temporal change. Additionally, the scatter of symbols in these plots provides a measure of the relative variation in community structure at each station, with tighter groupings of circles indicating greater temporal stability in species composition and abundance.

As the lengths of the lines connecting successive samplings vary both at, and between, individual stations, it appears that temporal influences on community structure are inconsistent. Station 10 for example shows 3 equal and moderately-sized shifts in composition during the first 4 samplings (November 95, April 96, November 97 and April 97). Station 14, by comparison, displays 3 progressively smaller changes in composition over the same period, while station 9 displays the opposite. There is also little uniformity in the direction of change between samplings, and no general tendency for the most recent sampling locations in each plot to converge. Indeed the location of the final sampling in several stations (1, 14, 17) is very much removed from the original configuration. At other sampling stations (9, 10, 16, 19, 20, 22, 23) there is a tendency for the most recent sampling location to be proximal to the position of the earliest sampling. In this latter group of stations the composition of organisms very closely resembles that initially described.

In general, most stations display tight and relatively cohesive ordination groupings, indicating that there has been little overall change in the composition of organisms at their locations over the course of this study (Figure 4A-B). Five stations (1, 2, 7, 23, 24) do, however, exhibit considerable temporal scatter and highlight major shifts in community structure at these locations. The large change at station 1 can be readily explained by the relocation of the initial sampling site during April 1998 to a position 400m offshore. This relocation is a unique characteristic of the dataset, and was undertaken to accommodate land reclamation and wharf developments at the original sampling site. In the ordination of station 1 (Figure 4A) the relocation coincides with a marked shift (to the left) in the positions of stations sampled after the 5th successive sampling (November 1997), and underpins community differences associated with a change in sampling from inshore silts to offshore sands and gravel.

Explanations for the large temporal changes in community structure at four other stations identified above are much more ambiguous. Stations 2 and 7 are located on moderately steep-shelving banks with variable sediment structures, and it is plausible that apparent temporal differences for these stations more accurately reflect small-scale spatial heterogeneity in sediment type. Additionally, both of these stations are located directly adjacent to major shipping channels, and may be subject to the direct and indirect effects of shipping traffic as well as the periodic effects of capital and maintenance dredging activities. Stations 23 and 24, by comparison, are located on large intertidal mudflats, several kilometres distant from any shipping channel. Both stations, nevertheless, undergo pronounced and pulsed changes in community structure during the 4th sampling period (November 1998). Because at this time the community structure for these stations more closely resembles that of a subtidal community (plotted on the MDS's towards the foot of the page), it is speculated that grab samples taken for these locations on this date were in fact collected from below the lowest astronomical tide. Shallow, subtidal drainage channels spread over much of intertidal zone at this location, and it is thought that inadvertent and coincidental sampling within such channels represents the most likely explanation for observed changes in community structure at these sites.

A further series of MDS ordinations were constructed to investigate the collective nature of temporal trends in community structure across the port (Figure 5A-C). In these analyses, only data for stations 1-16 could be considered; stations 17-30 were sampled irregularly over time and there inclusion would have resulted in an unbalanced design and biased estimates of both species abundance and diversity. As in the previous ordinations the lengths of the lines joining successive sampling periods provide a measure of dissimilarity. In the base ordination (Figure 5A) these lines become progressively longer during successive sampling periods up to April 1998, and the temporal trajectory tracks to the right hand side of the ordination. At this juncture, the community structure is most removed from its initial composition in November 1995. The high dissimilarity is maintained over the following three

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samplings, but by April 2000 there is evidence that the community structure is moving back to its initial composition. By November 2000, the community composition more closely resembles that originally described, but still remains distinct and plots towards the top of the ordination. The dissimilarity from the initial composition is, however, once again increased over the following sampling period, with April 2001 plotting at the apex of the ordination.

The principal drivers responsible for observed temporal movements in the pooled MDS ordination are readily determined from bubble plots of species richness and abundance (Figures 5B and 5C respectively). As previously described the diameter of the circle in these plots represent the magnitude of the variable, however, for additional clarity the summed counts for each variable are also given. In the plot of species richness there is a distinct trend of declining species numbers along a theoretical axis running between the upper left and lower right-hand corner of the ordination. A similar gradient is also evident in the plot of species abundance. Collectively these plots show that species richness and abundance within the inner harbour declined by more than half during the 2.5 year period to April 1998, but subsequently recovered to similar numbers over the ensuing 2.5 year period. Additionally, they indicate that despite apparent recruitment successes quite different suites of species survive in the port over the longer term. This is best evidenced by the degree of separation on the ordination of the November 1995 and November 2000 samplings. Both of these sampling periods have similar counts of species (and individuals) but share fewer than half of their combined species richness (131/280).

Two-way ANOVAs on temporal and spatial differences
The effects of sampling date and location on benthic species abundance are summarised in Table 2A. As the table shows significant (p<0.001) date, station and interaction terms (date*station), *post-hoc* multiple comparison tests were conducted for each main effect, and a series of marginal mean plots constructed to examine the interaction. The *post-hoc* Student-Newman-Keuls (SNK) test for differences in abundance between stations (Table 2B) shows that abundance was significantly lower during both April 1998 and April 1999, than at all other sampling periods. The table also confirms that more individuals were collected, on average, during November 1995 than at any other period during the study. There is little evidence in this table of any distinct seasonal patterns in species abundance with samples collected in April (post-wet) intergrading with those of November (pre-wet) over the duration of the study. A *post-hoc* SNK test also shows that mean abundances are significantly lower at most intertidal and several shallow subtidal stations (17, 18, 21, 22, 23; Table 2C). Additionally, it indicates that abundances are significantly greater at station 12, 27 and 30, than at all other stations sampled. Despite such station differences, no longshore patterns in abundance are evident within the port, and there is no tendency for the number of individuals to change incrementally towards the northern or southern reaches of the inner harbour. Few patterns are also evident in the direction and magnitude of change in abundance between stations over time (Figures 6A-B). Although species abundances were generally lower midway through the term of the sampling project at most stations, seasonal changes for individual stations were frequently unparalleled, and undoubtedly contributed to the significant interaction term detailed in the ANOVA table (Table 2A).

Results of a two-way ANOVA to assess differences in species richness between sampling dates and stations are presented in Table 3A. This table shows that there were significant differences (p<0.001) in species richness between sampling dates and stations and, additionally, a significant (p<0.001) date*station interaction. Like species abundance, the *post-hoc* SNK test for richness shows that this variable was significantly lower during April 1998 and April 1999, and significantly higher during November 1995 (Table 3B). It is noteworthy that the rank ordering of station dates in this table follows precisely that described for abundance (Table 2B). This relationship further validates the high degree of dependence between the number of species and individuals within the port, but also suggests that external seasonal and/or inter-annual influences elicit broadly similar responses in the population structures of most species. The multiple comparison test for station related differences in richness (Table 3C) also follows closely that for species abundance. It confirms that richness is significantly lower at all intertidal and one shallow subtidal station (17, 21, 22, 23, 24), furthermore it shows that richness is significantly highest at station 27 (in the Narrows). Plots of changes in individual station richness, once again, closely mirror those for abundance and generally display reduced numbers of species around the midpoint of the sampling project (Figures 7A-B). No two stations, however, follow the same seasonal trajectory for species richness, and therein largely explain the presence of a significant station*date interaction term in the ANOVA table (Table 3A).

While differences are apparent between stations in the direction and magnitude of seasonal changes in both species richness and abundance, stations collectively exhibit unequivocal longer-term trends within the port (Figure 8). These are expressed as gradual declines in the number of organisms and species within the harbour from November 1995 to April 1998, and rapid increases in the same parameters from November 1999 to November 2000. These trend lines quite literally display the pulse of the port over a five year period, and indicate that overall species numbers and abundances have declined and subsequently recovered by approximately 72%. Remarkably, these same temporal trends in abundance and richness are maintained in the four most common dietary groups (suspension feeders, deposit feeders, scavengers and predators) (Figures 9A-B). It would therefore appear that the factors underpinning such changes have a consistent influence on most species, regardless of inherent differences in functional ecology.

Environmental influences
SOI values during the course of this study were initially positive, but became strongly negative through most of 1997 and early 1998. The index subsequently returned to a positive value in mid 1998, and remained largely positive through to the end of the study in April 2001 (Figure 10A). Sustained negative values of the SOI are generally indicative of El Niño weather episodes, and are typically expressed by decreases in the strength of Pacific trade winds and reductions in rainfall over north-eastern Australia (Commonwealth Bureau of Meteorology, *pers com.*). Positive values of the SOI, conversely, result in increased trade wind strength, and higher than average levels of precipitation throughout north-eastern Australia. While the SOI was not directly correlated with local monthly rainfall (Table 4A), it appears that general trends for rainfall in the Port Curtis catchment were broadly consistent with predicted changes in rainfall for the continent. This is demonstrated in a plot of monthly rainfall totals at Castlehope (Figure 10B), which shows that rainfall was markedly lower during the strong El Niño episode of 1997/1998, than at any other time during the study.

Because of variations in the intensity and duration of rainfall, and the porosity of catchment soils, freshwater run-off in creeks and rivers is not always directly correlated with the volume of precipitation. There was, however, a highly significant relationship between regional rainfall and the volume of freshwater entering Port Curtis (Table 4A). Flow volumes in the Calliope River peaked during the study in January 1996, just after the first sampling event, and all subsequent monthly discharges were markedly reduced (<60%). Flow volumes did increase towards the end of the study, with two successive monthly flows in September and October 2000 collectively approximating the total volume discharged in January 1996. Between these dates, however, freshwater flow to the port was markedly reduced (Figure 10C).

Soil erosion and the seaward transport of sediments during intense freshwater flow events are a common feature in northern Australian coastal waterways. This mobilisation of sediments in the water column during such events is typically expressed by increased levels of turbidity in the receiving waters. In Port Curtis, levels of turbidity appear to closely follow the amount of freshwater inflow (Figures 10C-D). Despite this, measures of turbidity at Wiggins Island (mouth of the Calliope River), were not strongly correlated with the volume of freshwater flowing through the waterway (Table 4A).

The absence of a statistically significant correlation between flow and turbidity, suggests that other environmental factors may be influencing turbidity in the receiving waters of the port. Tidal re-suspension of fine sediments is probably quite significant in shallower regions of the port (including Wiggins Island, where the turbidity logger was deployed) as the tidal range for the port is relatively high (<5m). It is however unlikely that tidal influences have had a major impact on longer term turbidity measures for the port, given that tidal movements follow short-term and repetitive cycles of known periodicity, and would have been expressed equally over the duration of the study. Other possible confounding influences on turbidity at this location include wind-driven re-suspension of sediments during storm events and mobilisation of sediments during land reclamation works and dredging activities. Unfortunately the extent by which each of these factors may have influenced turbidity at the mouth of the Calliope River is difficult to assess from available data sources.

The role of freshwater flows in the transport of nutrients from terrestrial sources to coastal waterways is widely understood. In Port Curtis, this linkage is effectively demonstrated by the strong correlation between flow through the Calliope River and the concentration of dissolved reactive organic phosphate at Clinton Wharf (approximately two kilometres from the river mouth) (Figure 10F and Table 4A). Likely sources for the influx of phosphate and other nutrients to the port include point source

discharges from a sewerage treatment plant situated on the Calliope River (approximately four kilometres upstream from the Clinton Wharf), and agricultural run-off from heavily grazed native and improved pastures in the upper catchment. Nutrients, including phosphate salts, are essential in maintaining and promoting primary production in aquatic ecosystems. This biological dependence is tentatively confirmed in Port Curtis by the strong correlation in concentrations of phosphate and chlorophyll *a* in the water column (Table 4A). Measures of chlorophyll *a* provide a rudimentary assessment of phytoplankton standing-stock, and fluctuations in this parameter can reflect the bio-availability of food for higher trophic organisms, including many benthic invertebrates. Trends in chlorophyll *a* concentrations at the Calliope River mouth appear to closely follow general trends in benthic abundance and richness within the port (Figures 10F & 8), however no direct correlations were detected between the levels of chlorophyll *a* and either the number or diversity of benthic organisms. The lack of any significant correlations here is not unexpected since benthic recruitment responses to favourable conditions will not be expressed simultaneously. Reproductive maturation, larval duration and juvenile growth rates differ between species and hence delayed responses in population size (as determined from collections of organisms larger than 1mm) are anticipated.

In an effort to investigate possible delayed responses in Port Curtis benthos to variations in available food, correlation analyses were additionally conducted between all aforementioned environmental parameters and time-series measures of species abundance and richness advanced in time by 4 months. In this analysis, chlorophyll *a* was found to be uncorrelated with abundance and richness, as were measures of the SOI, rainfall, flow, and phosphate. Turbidity, however, was found to be highly correlated with both abundance and richness. Indeed more than 80% of the variation in both species abundance and richness could be explained by differences in turbidity. This remarkable finding suggests that high turbidity within Port Curtis indirectly promotes benthic invertebrate recruitment. Furthermore the result appears to challenge a widely held assumption that sustained levels of high turbidity are deleterious to benthic community structure. A plausible explanation for these phenomena is that turbidity measurements for the port more accurately reflect suspended bio-available organic loads. Turbidity measurements in this study were derived colorimetrically and did not differentiate suspended inorganic fractions from suspended organic material.

DISCUSSION

While it is widely accepted that estuarine ecosystems are highly productive and critical to the maintenance of coastal bird-life and fisheries, very little is known about the invertebrate faunas that inhabit them. Invertebrate organisms play important roles in the diets of many shorebird and fish species, and can profoundly influence the abundance and species composition of these tertiary consumers (Bottom and Jones, 1990; Skagen and Oman, 1996; Stillman *et al.*, 2000). Invertebrates also play an integral role in the recycling of nutrients, and conservation of water quality within estuarine systems (Harris, 1999; Peterson and Heck, 1999). Understanding temporal and spatial change in invertebrate community structure, and the factors underpinning them, is therefore essential to the better management of these waterways.

The present study suggests that global climatic phenomena can have a pervasive and significant impact on the benthic fauna of a sub-tropical estuarine system. During the most significant El Niño episode of recent times (1997/1998), invertebrate numbers and diversity in Port Curtis were more than halved. This apparent drought induced change was similar in magnitude over a large geographical range (>15km), and appears to have been conferred equally across most trophic components of the benthos. While the relative importance of each invertebrate species in Port Curtis as a dietary item for demersal fish has yet to be determined, it is likely that certain components feature highly as prey items for a number of demersal fish species. It is reasonable, therefore, to assume that significant changes in the population structures of demersal fish have occurred as a result of the general decline in benthos in Port Curtis. Historical trends in recreational fish catches for Port Curtis largely confirm this. Between 1995/96 and 1998/99 average catch rates (median number of fish/person/trip) progressively declined by 66%, but numbers of fish caught subsequently increased by a similar amount between 1998/99 and 2000/01 (Platten, 2002). Sand whiting *Sillago ciliata* were the most common species caught in this study, and occurred in more than 80% to the total catch. As benthic invertebrates, and crustaceans in particular, represent the principal food source for fish in this genera (Hyndes *et al.*, 1997), it is speculated that changes in sand whiting numbers (at least) represent a direct response to the availability

of invertebrate prey items in the estuary, and an indirect response to the frequency of rainfall events and freshwater inflow.

The importance of freshwater flows in sustaining and promoting the health of estuarine fish populations is becoming increasingly apparent. A number of recent studies have shown that pulses in river inflow play a critical role in altering the composition of larvae and distribution of juvenile fish and adults within estuarine systems (Bottom and Jones, 1990; Strydom *et al.*, 2002). Other longer term research has found that prolonged drought conditions result in reduced species richness and trophic diversity (Livingston, 1997). In the Fitzroy River Estuary, located approximately 40km to the north of current study site in Port Curtis, new research is showing that the incidence of major flood events has a significant effect on the recruitment success and subsequent growth of estuarine fish species including barramundi (Robins *et al.*, 2002). As flows in the Fitzroy River Estuary are regulated by a barrage located 50km upstream from the river mouth, it is increasingly recognised that the natural dynamics and productivity of this estuary are under threat from upstream water allocation processes.

The current rapid industrial expansion of the Port Curtis region is placing increasing demands on a finite supply of freshwater from the immediate catchments. Options are therefore being investigated by local, state and federal agencies for directing flows from the Fitzroy River to supply several newly established and prospective industries in and around the city of Gladstone. Under these circumstances the volume of freshwater entering the lower Fitzroy Estuary would be depleted, quite possibly resulting in reduced fisheries productivity. Such changes might also threaten populations of resident predators such as dolphins and sea eagles, which have considerable conservation and ecotourism values. An alternative solution being considered involves harvesting water from an artificial impoundment, created by damming the Calliope River approximately 15km upstream from Port Curtis. In either scenario the ecological consequences are predictably negative, as the construction of dams, weirs and barrages across otherwise unimpeded rivers invariably cause a wide range of deleterious environmental impacts (O'Neill, 1994).

Cyclical changes and random between-year variation make long-term human change in benthic communities often difficult to detect (Gray and Christie, 1983). Unfortunately data is often inadequate to determine whether any particular ecological change is directional rather than an unusual random fluctuation or part of a cyclical change. Like many estuaries with urbanised catchments, Port Curtis receives pollution from a wide range of sources including urban and industrial developments, commercial and recreational shipping and rural agriculture. While some impacts (eg introductions of exotic marine organisms) are probably contributing to irreversible changes to the ecology of the Port, the relative significance of other man-made impacts (eg fishing pressure and the growth of tourism) is unclear.

Much of the uncertainty particularly over the longer-term significance of human disturbances in Port Curtis stems from limitations in sampling design. All current sampling stations are located within the industrialised inner harbour, and as such may be subject by varying degrees to human disturbances that are widespread in character. Several sampling and analytical solutions to this ubiquitous design problem have been proposed in recent years (Green, 1979; Bernstein and Zalinski, 1983; Stewart-Oaten *et al.*, 1986; Underwood, 1991; Underwood, 1994; Keough and Mapstone, 1995). Central to all of these proposals is the need to establish and monitor control sites (ideally several) as well as putatively impacted sites, both before and after a planned development. This so called BACI design framework relies on the logic that an impact would cause a change in a given response variable (eg mean species abundance) before compared to after the onset of the disturbance that exceeds the average change in the control/s over the same period. In these designs, explicit statements about the presence or absence of an effect can be provided from an assessment of the significance of interactions occurring between control and impacted sites over time.

In principal, it would appear that less ambiguous assessments of anthropogenic change in Port Curtis benthos may be promoted by establishing and sampling additional control stations out-with the geographical influence of any human disturbance. In practice, selecting appropriate control sites that are not spatially correlated by either disturbances or recruitment processes is problematic. Several significant changes to the Australian coastline have occurred since European settlement, and the ongoing contributions of such changes to benthic community structure are difficult to assess. Estuaries that are un-industrialised and situated adjacent to Port Curtis may not necessarily be good controls for gauging human induced change in Port Curtis; particularly, as they themselves may be subject to

progressive impacts from, for example, undocumented agricultural and forestry practices in their upper catchments. Despite such caveats, few other options are presently available. While the use of adjacent estuarine systems as controls may be less than perfect, it currently represents the best possible solution for bench-marking any future human degradation of marine communities in Port Curtis.

In an effort to establish more suitable controls, an extensive pilot sampling project was recently undertaken. This study involved the collection of replicate benthic grab samples from over 180 stations located throughout the Curtis coast, and embraced a comprehensive range of depth and sediment types. Many of the sampling stations were located in nearby estuarine systems to the north and south of Port Curtis (Fitzroy River Estuary and Colosseum Inlet respectively), while others were located in oceanic waters to the east of the port. Spatial analysis of these biological data that expressly consider physical processes (detailed in a recently developed regional hydrodynamic model, Ian Webster, CSIRO, *pers com.*), should facilitate the identification of uncontiguous and relevant controls for Port Curtis. Moreover, the pilot study should significantly enhance our understanding of biodiversity and endemicity of marine benthos within the Port Curtis region.

Hutchings (1999) recently reviewed the knowledge base for macro-invertebrates in Australian estuaries, and confirmed that most of our taxonomic and ecological understanding stems from only a limited geographical region. The paucity of information on sub-tropical estuaries is highlighted in the present study by the fact that nearly 90% of the organisms collected are apparently undescribed. While the lack of an identity for most species collected is probably a reflection of natural range limitations, it is a matter of some concern that several organisms collected in Port Curtis may be introduced.

The establishment of exotic organisms in ports as a result of translocation on hulls and in ballast water of commercial shipping is not a new phenomenon (Byrne *et al.*, 1997). The issue has only received attention in recent years as the impacts caused by biological invasions become apparent. The devastating effects of introductions such as the zebra mussel *Dreissena polymorpha* into the Great Lakes (Griffiths *et al.*, 1991; Strayer 1991), the ctenophore *Mnemiopsis leidyi* into the Black Sea (Vinogradov *et al.*, 1989) and the clam *Potamocorbula amurensis* into San Francisco Bay (Carlton *et al.*, 1990) have all served to highlight the serious nature of this problem.

The Port of Gladstone extends more than 15km along the foreshore of Port Curtis, and is the fifth largest multi-cargo port in Australia. Because of the port's principal role in recent times as an international bulk export facility, the adjacent marine environment is considered vulnerable to introductions mediated by ballast water. Large quantities of water entrained in the hulls of vessels at overseas locations have been discharged into the port in recent years (~10 million tonnes annually since 1995, Lewis *et al.*, 2001), and with it quite possibly large numbers of exotic organisms. Of course, not all organisms introduced to a new environment will establish sustainable populations, and many that do, may not cause serious ecological changes (Clare Eno *et al.*, 1997). New federal legislation prohibiting vessels deemed 'high risk' from discharging ballast water within Australian ports, should limit the incidence of exotic introductions, and in the longer term safeguard indigenous biodiversity. However, until such times as the taxonomic identities of most benthic organisms in Port Curtis are resolved, there will be considerable uncertainty over the estuary's perceived image as a largely unperturbed ecosystem.

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Figure 1. Map of Port Curtis showing the locations of 30 stations sampled for macrobenthos between November 1995 and April 2001.
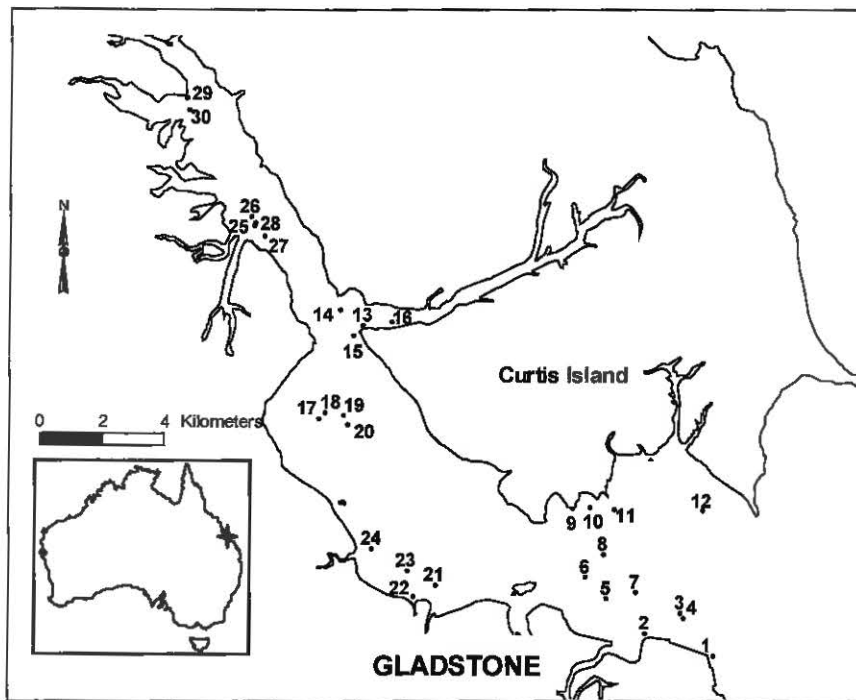
Figure 2. Non-metric MDS plots of A) benthic community structure at 30 stations sampled in Port Curtis between November 1995 and April 2001, B) depth superimposed on community ordination, C) sediment structure superimposed on community ordination.

A
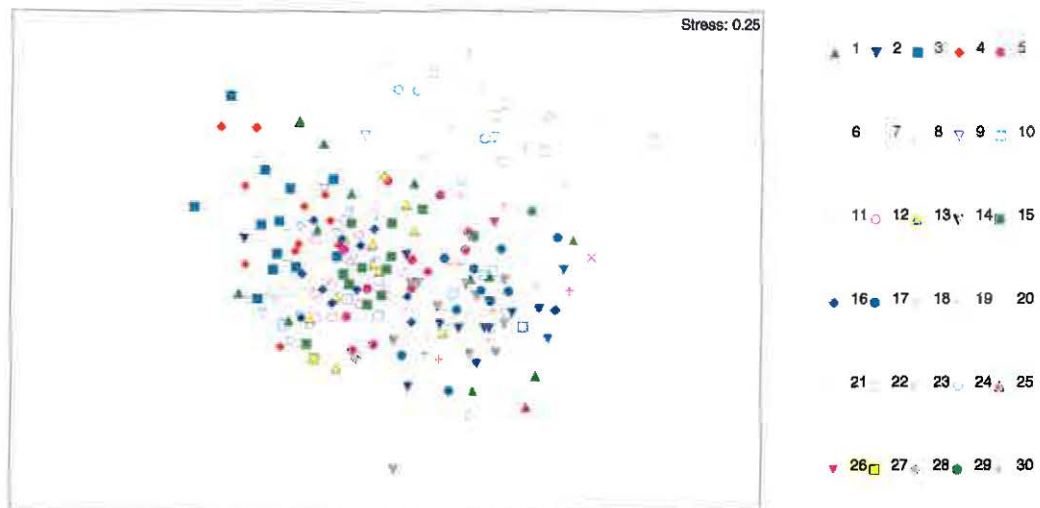
B
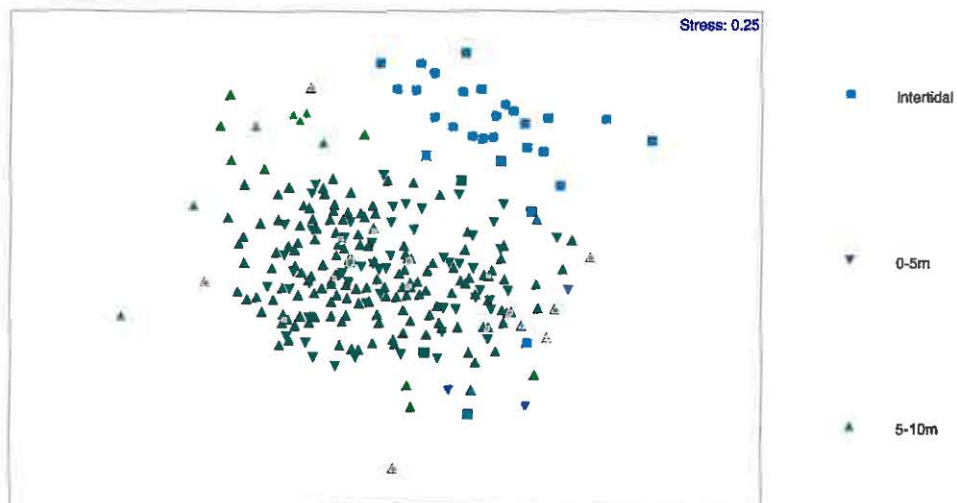
C
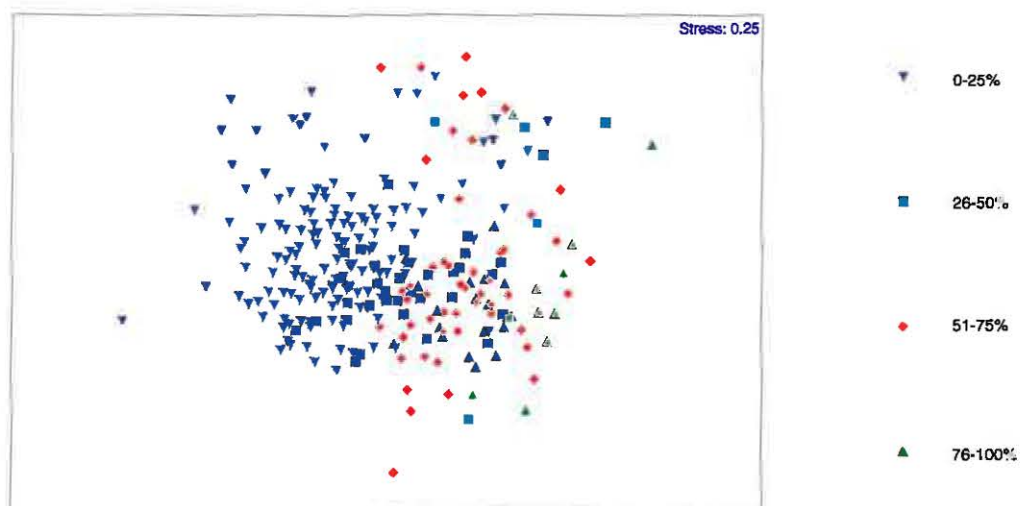
Figure 3. Plots of: A- Sampling stations, B – Species richness, C – Species abundance, and D – Shannon Weiner diversity superimposed on a non-metric MDS ordinations of benthic community structure.
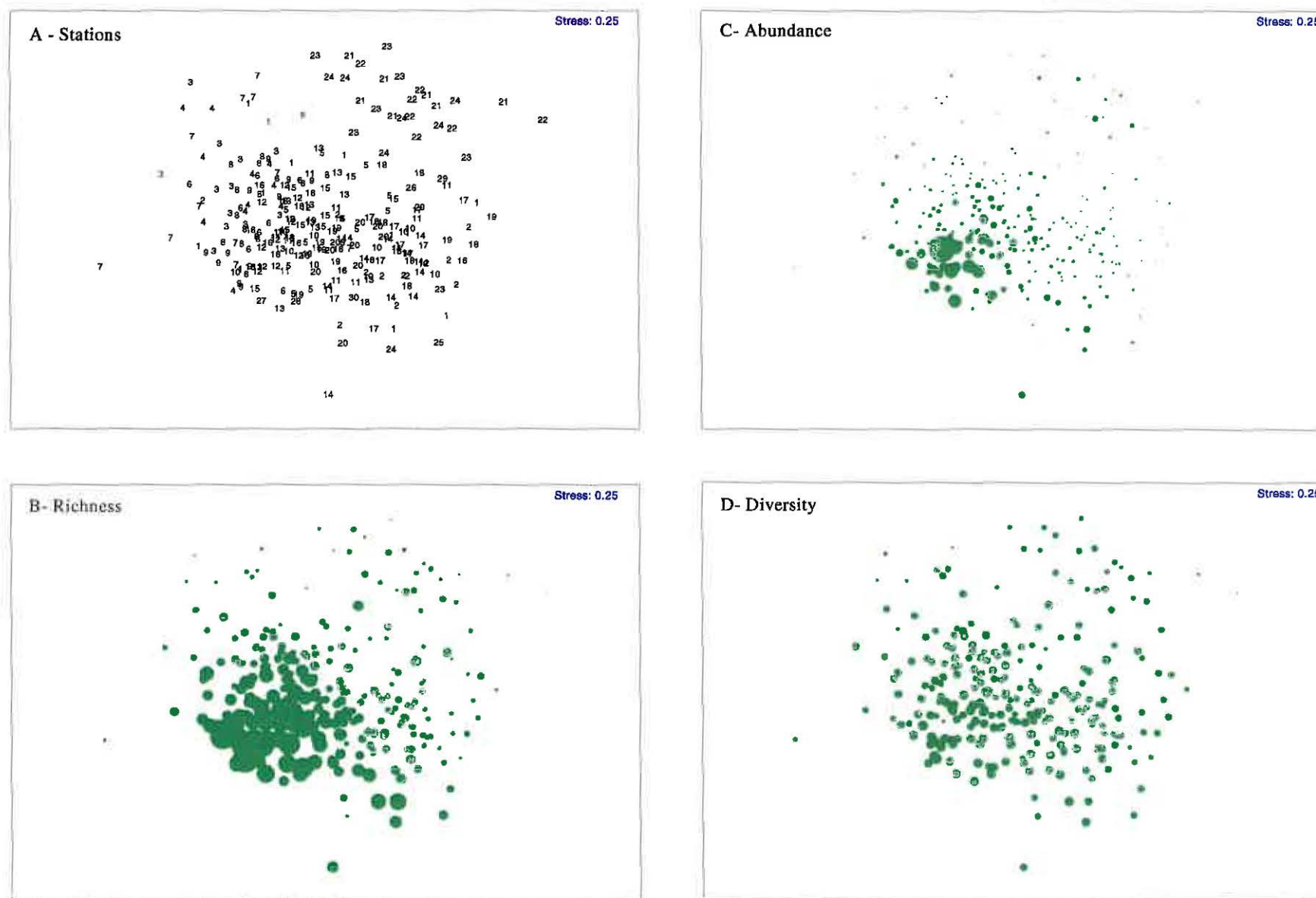
Figure 4A. Non-metric MDS plots of seasonal changes in community structure at each sampling station (large circles) superimposed on an ordination of all sampling stations * sampling periods (small circles) for the period November 1995 – April 2001. Solid lines with arrows indicate the temporal sequence of sampling.
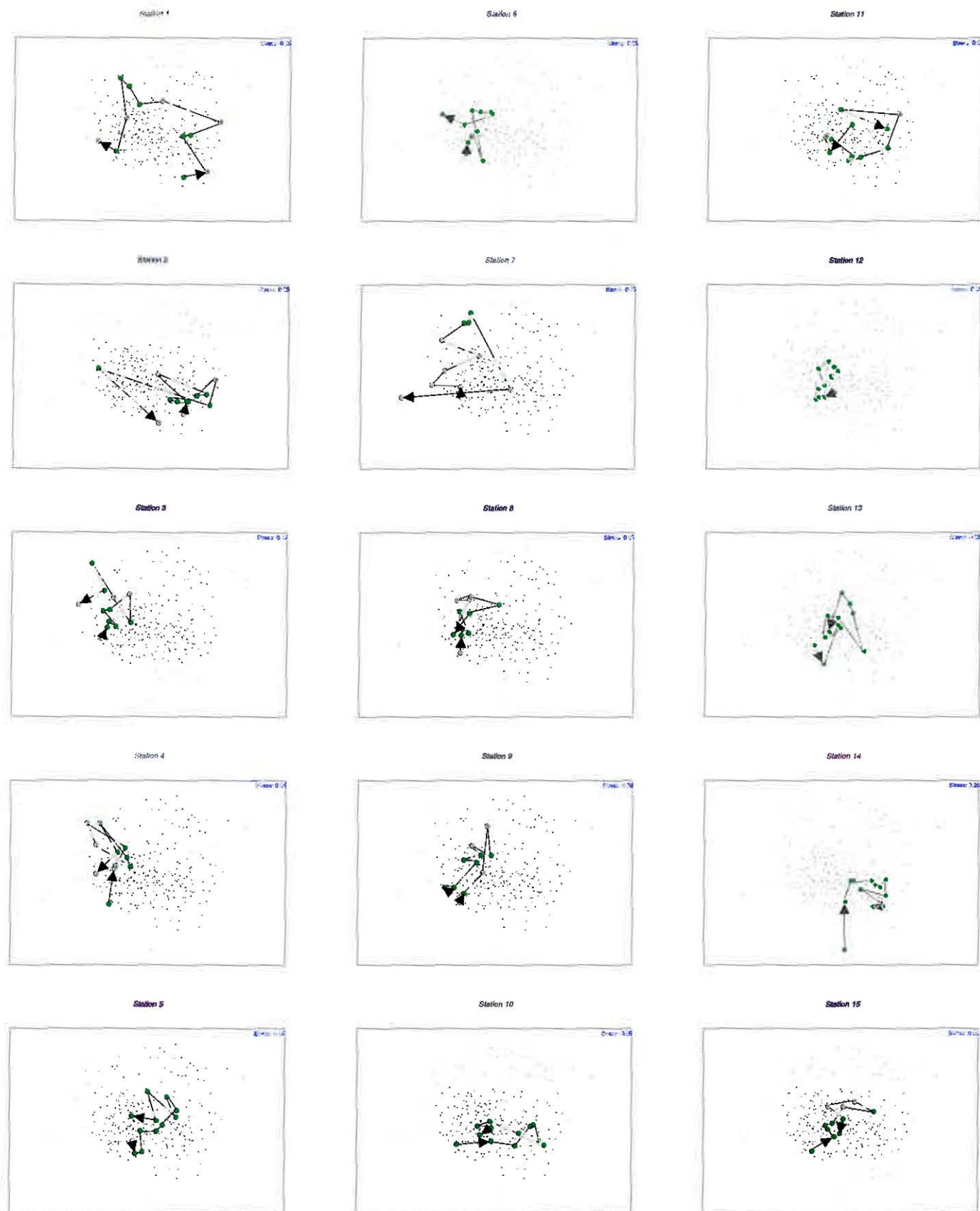
Figure 4B. Non-metric MDS plots of seasonal changes in community structure at each sampling station (large circles) superimposed on an ordination of all sampling stations * sampling periods (small circles) for the period November 1995 – April 2001. Solid lines with arrows indicate the temporal sequence of sampling.
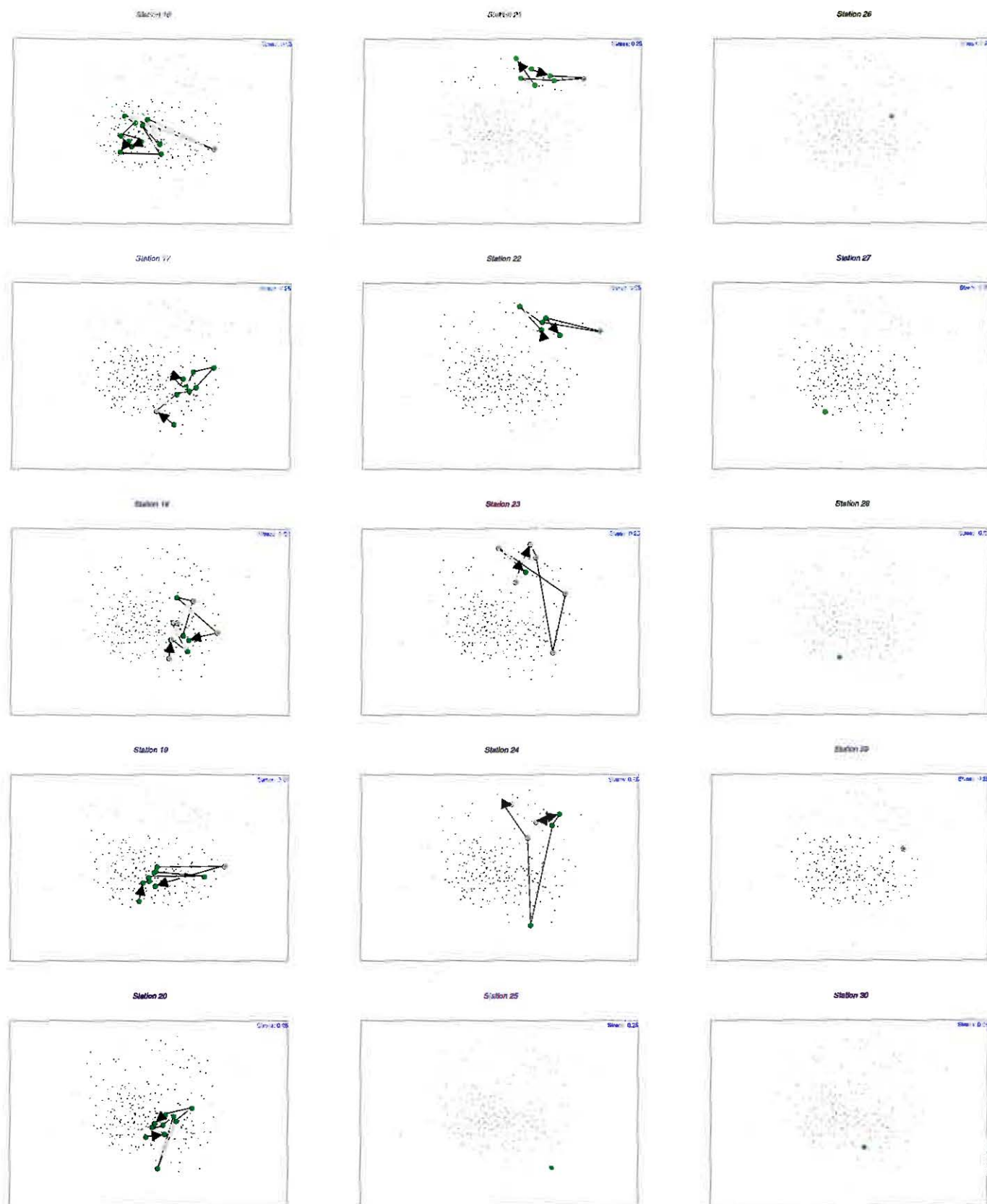
Figure 5. Non-metric MDS plots showing: A) seasonal change in benthic community structure between November 1995 and April 2001 (data pooled from stations 1-16), B) total species richness (16 stations*10 grab samples) superimposed on primary ordination, and C) total species abundances (160 grab samples) superimposed on primary ordination.
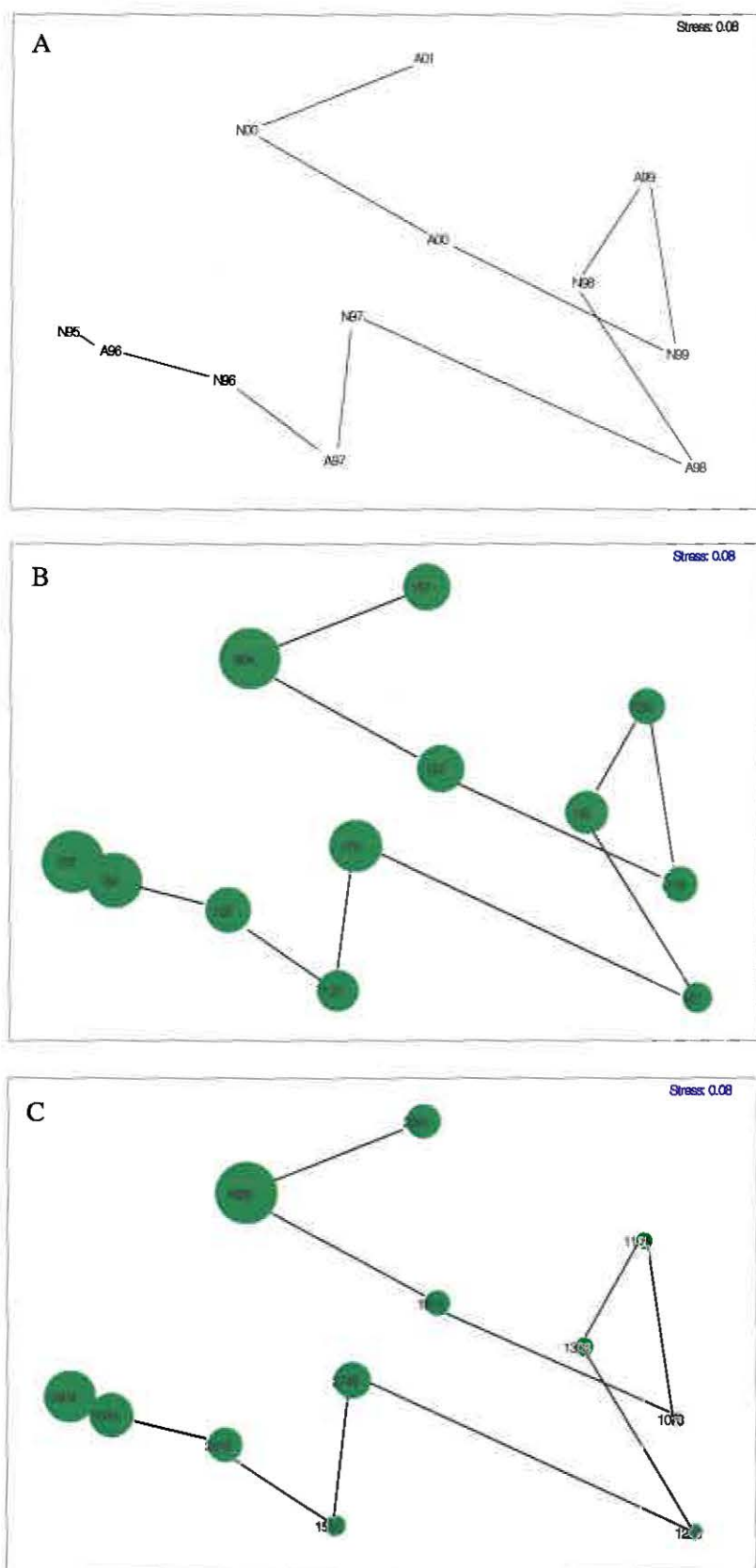
Figure 6A. Plots of changes in mean species abundance at Port Curtis sampling stations surveyed between November 1995 and April 2001. Means and associated standard errors are given for double square-root transformed abundances collected in 10*0.1m² van Veen grabs / sampling date.
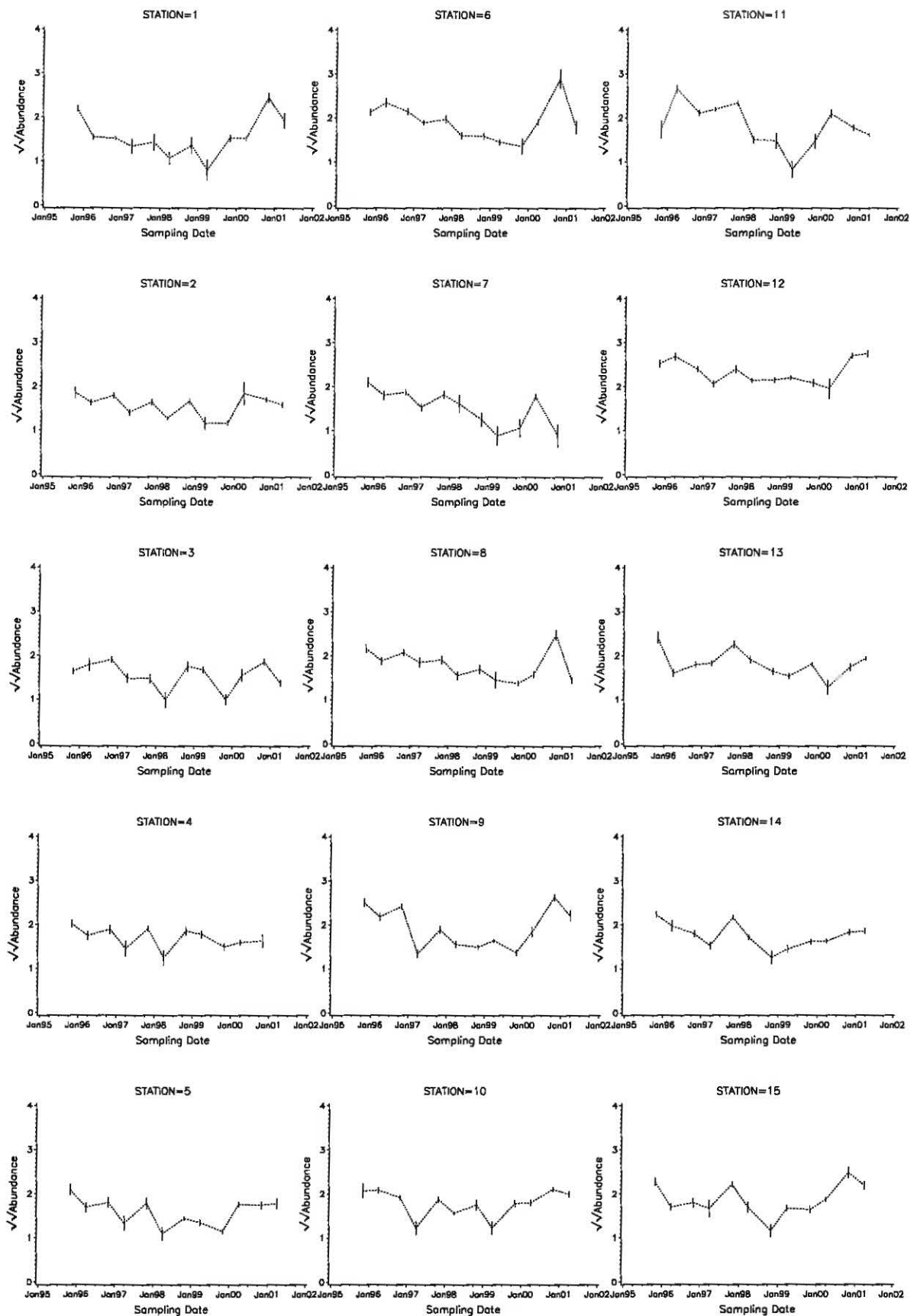
Figure 6B.   Plots of changes in mean species abundance at Port Curtis sampling stations surveyed between November 1995 and April 2001.   Means and associated standard errors are given for double square-root transformed abundances collected in $10*0.1m^2$ van Veen grabs / sampling date.
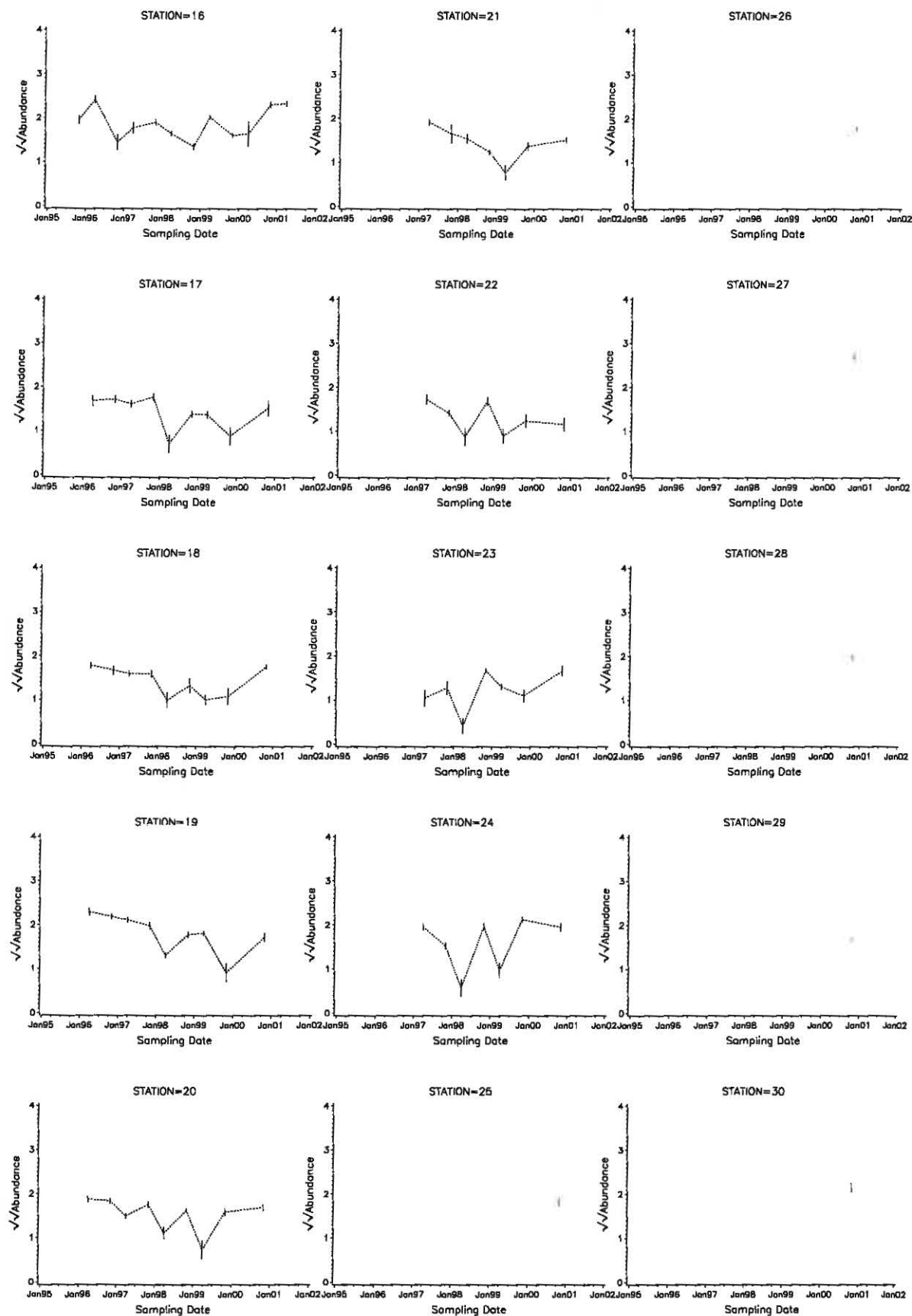
Figure 7A. Plots of changes in mean species richness at Port Curtis sampling stations surveyed between November 1995 and April 2001. Means and associated standard errors are given for double square-root transformed species counts collected from 10*0.1m² van Veen grabs / sampling date.
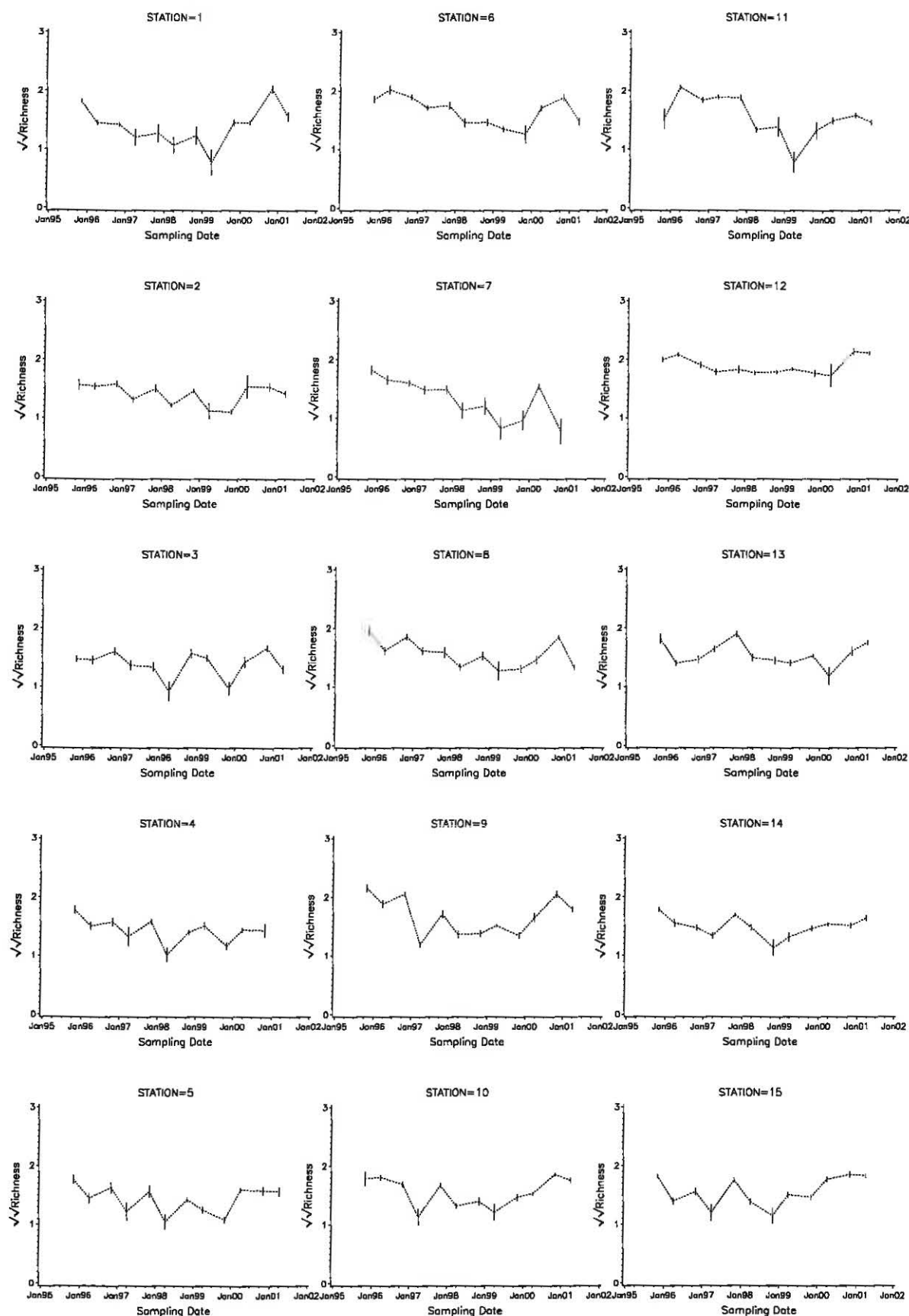
Figure 7B. Plots of changes in mean species richness at Port Curtis sampling stations surveyed between November 1995 and April 2001. Means and associated standard errors are given for double square-root transformed species counts collected from $10*0.1m^2$ van Veen grabs / sampling date.
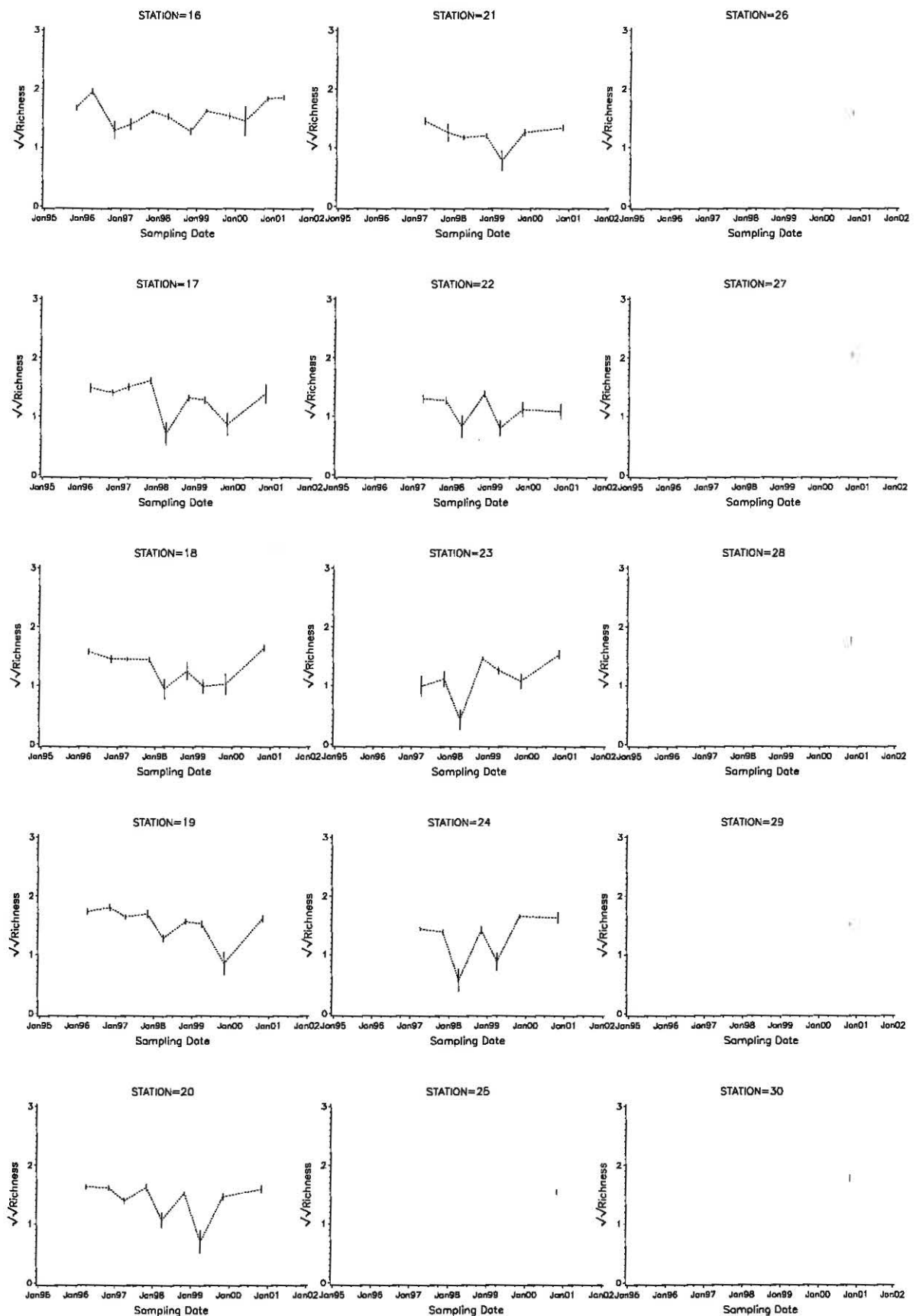
Figure 8. Seasonal changes in infaunal species richness (broken line) and abundance (solid line) in Port Curtis. Mean and associated standard errors are derived from 10 replicate $0.1m^2$ van Veen grabs collected from 16-30 sampling stations on twelve sampling periods between November 1995 and April 2001.

25
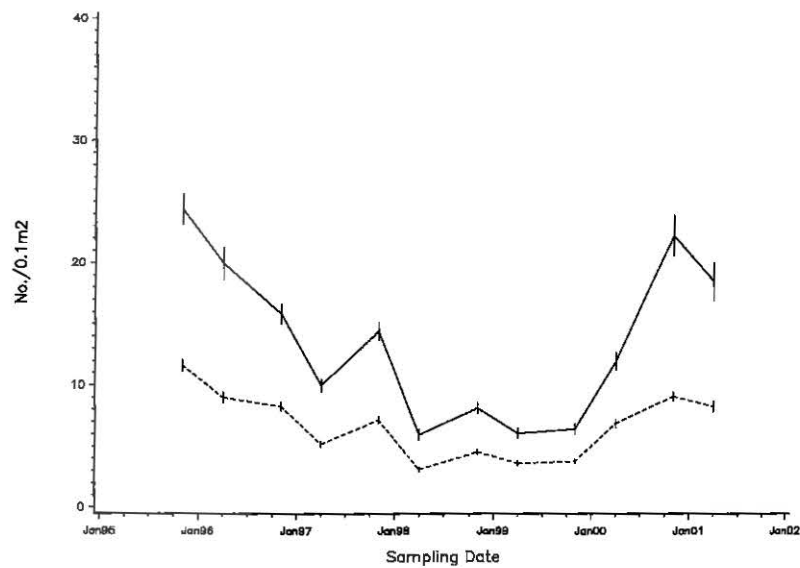
Figure 9. Seasonal changes in the abundances (A) and richness (B) of six infaunal species groupings based on feeding type (deposit feeder, predator, scavenger, grazer and suspension feeder). Mean and associated standard errors are derived from 10 replicate $0.1m^2$ van Veen grabs collected from 16-30 sampling stations on twelve sampling periods between November 1995 and April 2001.

A
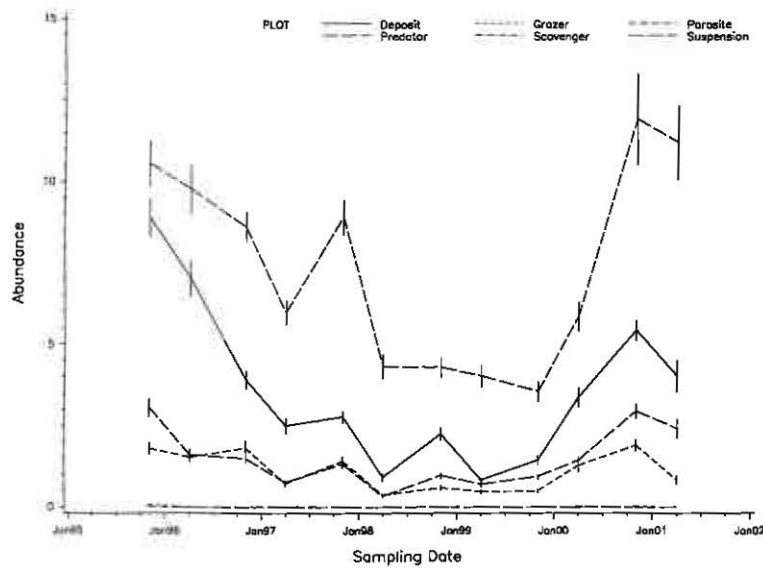
B
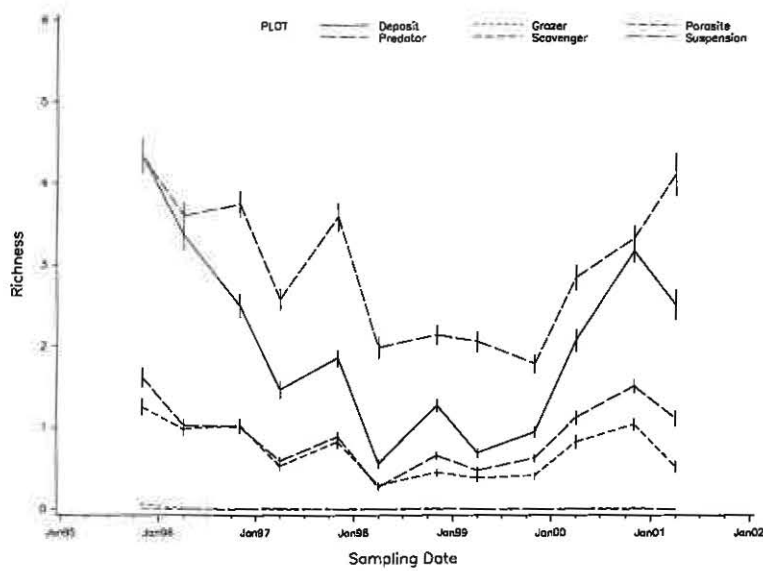
Figure 10. Time series data for Port Curtis showing changes in: A) Southern Oscillation Index, B) total monthly rainfall at Castlehope, C) total monthly freshwater discharge from the Calliope River, D) mean monthly turbidity at Wiggins Island, E) chlorophyll *a* concentration at the mouth of the Calliope River, and F) phosphate concentrations at the Clinton Coal Wharf. Curves for quadratic regressions have been superimposed on all plots to highlight temporal trends.

(A)

(D)

(B)

(E)

(C)

(F)

27
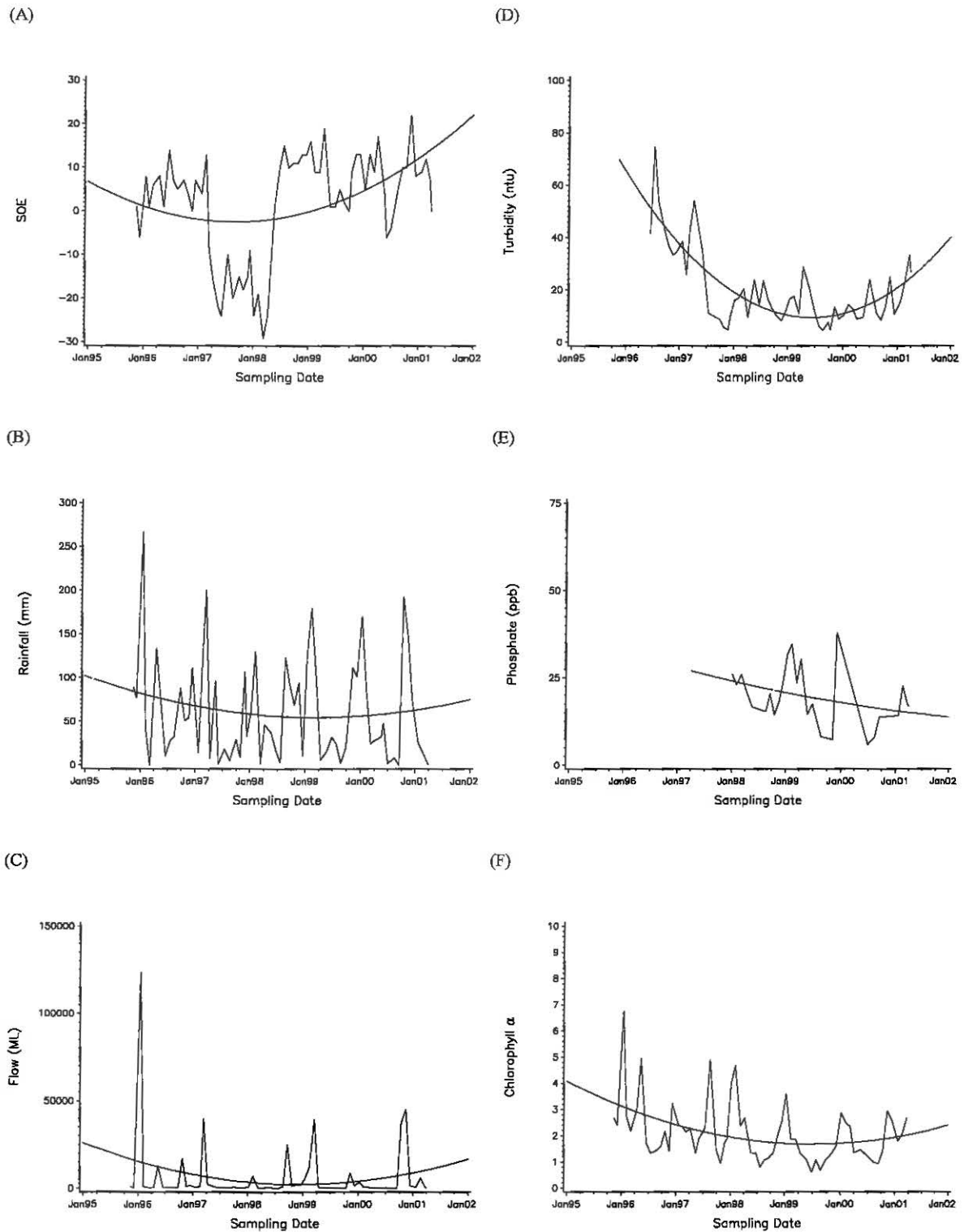
Table 1A. Change in mean abundance (N per $0.1m^2 \pm$ s.e.) of infaunal species groupings (based on taxonomic affinity and feeding type) at 16-30 sampling stations surveyed on 12 sampling dates between November 1995 and April 2001.

	Nov-95	Apr-96	Nov-96	Apr-97	Nov-97	Apr-98	Nov-98	Apr-99	Nov-99	Apr-00	Nov-00	Apr-01	Abundance
Taxonomic affinity													
Molluscs	10.33 ± 0.71	8.99 ± 0.69	8.28 ± 0.41	6.64 ± 0.40	8.89 ± 0.50	4.51 ± 0.37	5.60 ± 0.34	4.08 ± 0.32	4.26 ± 0.34	6.01 ± 0.48	7.38 ± 0.54	9.06 ± 1.04	18099
Polychaetes	8.05 ± 0.59	6.29 ± 0.58	3.55 ± 0.27	1.85 ± 0.17	2.52 ± 0.20	0.53 ± 0.06	1.56 ± 0.15	1.03 ± 0.09	1.28 ± 0.10	2.67 ± 0.19	5.46 ± 0.32	3.59 ± 0.36	8258
Crustaceans	2.73 ± 0.28	1.91 ± 0.21	2.60 ± 0.33	0.86 ± 0.10	2.03 ± 0.21	0.78 ± 0.15	0.72 ± 0.09	0.66 ± 0.11	0.65 ± 0.09	1.77 ± 0.25	2.47 ± 0.21	1.17 ± 0.18	4017
Chordates	1.68 ± 0.21	1.21 ± 0.27	0.73 ± 0.12	0.13 ± 0.04	0.43 ± 0.07	0.05 ± 0.01	0.08 ± 0.02	0.12 ± 0.03	0.05 ± 0.02	0.25 ± 0.06	5.41 ± 1.29	2.42 ± 0.45	2923
Echinoderms	1.34 ± 0.18	1.30 ± 0.17	0.47 ± 0.07	0.43 ± 0.15	0.27 ± 0.05	0.05 ± 0.01	0.14 ± 0.03	0.16 ± 0.04	0.20 ± 0.04	1.19 ± 0.21	1.34 ± 0.22	2.16 ± 0.45	1774
Cnidarians	0.14 ± 0.04	0.22 ± 0.07	0.17 ± 0.05	0.09 ± 0.03	0.28 ± 0.08	0.03 ± 0.01	0.01 ± 0.01	0.02 ± 0.01		0.03 ± 0.02	0.09 ± 0.02	0.09 ± 0.05	246
Sipunculids	0.02 ± 0.01	0.01 ± 0.01	0.01 ± 0.01			0.01 ± 0.01				0.04 ± 0.02	0.07 ± 0.02		43
Pycnogonids	0.06 ± 0.02	0.04 ± 0.02	0.06 ± 0.03	0.01 ± 0.01							0.01 ± 0.01	0.01 ± 0.01	36
Nemerteans	0.04 ± 0.02	0.02 ± <.01	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.01						0.01 ± 0.01	0.01 ± <.01	21
Platyhelminthes	0.01 ± 0.01	0.01 ± 0.01											3
Nematodes							0.01 ± <.01						1
Feeding type													
suspension	10.56 ± 0.71	9.78 ± 0.75	8.61 ± 0.46	6.00 ± 0.38	8.93 ± 0.54	4.33 ± 0.37	4.30 ± 0.31	4.03 ± 0.35	3.55 ± 0.31	5.86 ± 0.46	11.93 ± 1.40	11.21 ± 1.14	19274
deposit	8.90 ± 0.59	7.03 ± 0.57	3.94 ± 0.29	2.50 ± 0.24	2.78 ± 0.18	0.92 ± 0.12	2.24 ± 0.19	0.83 ± 0.07	1.44 ± 0.14	3.38 ± 0.29	5.44 ± 0.31	4.01 ± 0.50	9276
predator	3.06 ± 0.28	1.61 ± 0.18	1.50 ± 0.13	0.77 ± 0.07	1.33 ± 0.13	0.34 ± 0.04	0.98 ± 0.09	0.70 ± 0.08	0.94 ± 0.09	1.44 ± 0.12	2.95 ± 0.23	2.42 ± 0.29	3918
scavenger	1.81 ± 0.18	1.53 ± 0.16	1.82 ± 0.25	0.73 ± 0.09	1.41 ± 0.16	0.38 ± 0.05	0.59 ± 0.08	0.48 ± 0.06	0.50 ± 0.06	1.28 ± 0.21	1.90 ± 0.18	0.84 ± 0.13	2921
grazer	0.06 ± 0.02	0.01 ± 0.01						0.02 ± 0.01			0.01 ± 0.01	0.02 ± 0.01		26
parasite		0.01 ± 0.01		0.01 ± 0.01	0.01 ± 0.01								6
Sum of Means	24.40 ± 1.25	19.96 ± 0.91	15.86 ± 0.77	10.01 ± 0.60	14.45 ± 0.80	5.96 ± 0.40	8.12 ± 0.51	6.05 ± 0.37	6.43 ± 0.39	11.97 ± 0.56	22.24 ± 0.83	18.49 ± 0.83	35421

Table 1B. Change in mean species richness (N per $0.1m^2$ ± s.e.) of infaunal groupings (based on taxonomic affinity and feeding type) at 16-30 sampling stations surveyed on 12 sampling dates between November 1995 and April 2001.

	Nov-95	Apr-96	Nov-96	Apr-97	Nov-97	Apr-98	Nov-98	Apr-99	Nov-99	Apr-00	Nov-00	Apr-01	Total Species
Taxonomic affinity													
Molluscs	3.75 ± 0.18	3.50 ± 0.17	3.62 ± 0.14	2.78 ± 0.12	3.69 ± 0.16	2.17 ± 0.14	2.72 ± 0.12	2.18 ± 0.13	2.17 ± 0.13	2.88 ± 0.16	3.36 ± 0.16	3.81 ± 0.28	110
Polychaetes	4.56 ± 0.28	3.10 ± 0.19	2.47 ± 0.15	1.39 ± 0.11	1.77 ± 0.11	0.43 ± 0.04	1.03 ± 0.07	0.76 ±0.06	0.93 ± 0.06	2.12 ± 0.14	3.01 ± 0.14	1.98 ± 0.16	128
Crustaceans	1.74 ± 0.14	1.22 ± 0.10	1.36 ± 0.12	0.65 ± 0.06	1.12 ± 0.08	0.38 ± 0.04	0.56 ± 0.05	0.46 ±0.05	0.47 ± 0.05	1.13 ± 0.10	1.39 ± 0.09	0.72 ± 0.08	103
Chordates	0.62 ± 0.05	0.37 ± 0.04	0.35 ± 0.04	0.10 ± 0.02	0.30 ± 0.04	0.05 ± 0.01	0.08 ± 0.02	0.08 ±0.02	0.05 ± 0.01	0.17 ± 0.03	0.46 ± 0.04	0.58 ± 0.06	12
Echinoderms	0.74 ± 0.07	0.69 ± 0.07	0.36 ± 0.05	0.20 ± 0.03	0.21 ± 0.03	0.05 ± 0.01	0.13 ± 0.02	0.11 ±0.02	0.17 ± 0.03	0.52 ± 0.06	0.70 ± 0.07	1.16 ± 0.13	33
Cnidarians	0.09 ± 0.02	0.08 ± 0.02	0.09 ± 0.02	0.06 ± 0.02	0.08 ± 0.02	0.03 ± 0.01	0.01 ± 0.01	0.02 ±0.01		0.03 ± 0.02	0.07 ± 0.01	0.02 ± 0.01	9
Sipunculids	0.02 ± 0.01	0.01 ± 0.01	0.01 ± 0.01			0.01 ± 0.01				0.04 ± 0.02	0.06 ± 0.01		5
Pycnogonids	0.05 ± 0.02	0.03 ± 0.01	0.04 ± 0.01	0.01 ± 0.01							0.01 ± 0.01	0.01 ± 0.01	5
Nemerteans	0.04 ± 0.02	0.02 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.01						0.01 ± 0.01	0.01 ± <.01	2
Platyhelminthes	0.01 ± 0.01	0.01 ± 0.01											1
Nematodes							0.01 ± <.01						1
Feeding type													
suspension	4.33 ± 0.21	3.60 ± 0.18	3.75 ± 0.16	2.58 ± 0.13	3.59 ± 0.17	1.99 ± 0.13	2.14 ± 0.12	2.06 ± 0.13	1.79 ± 0.12	2.84 ± 0.16	3.33 ± 0.16	4.11 ± 0.26	113
deposit	4.34 ± 0.22	3.36 ± 0.19	2.50 ± 0.14	1.47 ± 0.10	1.86 ± 0.10	0.56 ± 0.05	1.28 ± 0.08	0.69 ± 0.05	0.95 ± 0.06	2.08 ± 0.14	3.17 ± 0.14	2.51 ± 0.19	149
predator	1.63 ± 0.12	1.03 ± 0.08	1.01 ± 0.07	0.60 ± 0.05	0.89 ± 0.07	0.27 ± 0.03	0.66 ± 0.05	0.48 ± 0.04	0.63 ± 0.05	1.13 ± 0.08	1.51 ± 0.08	1.12 ± 0.10	50
scavenger	1.26 ± 0.10	0.99 ± 0.08	1.03 ± 0.09	0.53 ± 0.06	0.83 ± 0.07	0.30 ± 0.03	0.45 ± 0.05	0.38 ± 0.05	0.41 ± 0.04	0.83 ± 0.09	1.04 ± 0.07	0.53 ± 0.07	92
grazer	0.06 ± 0.02	0.01 ± 0.01					0.01 ± 0.01			0.01 ± 0.01	0.02 ± 0.01		3
parasite		0.01 ± 0.01		0.01 ± 0.01	0.01 ± 0.01								2
Sum of Means	11.61 ± 0.48	8.99 ± 0.39	8.29 ± 0.37	5.20 ± 0.26	7.18 ± 0.35	3.11 ± 0.19	4.54 ± 0.25	3.61 ± 0.20	3.78 ± 0.20	6.88 ± 0.30	9.06 ± 0.38	8.27 ± 0.36	409

Table 2A. Results of two-way ANOVA on differences in the abundance of benthic organisms at thirty Port Curtis sampling stations surveyed on twelve dates between November 1995 and April 2001.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Power(a)
Corrected Model	465.891(b)	259	1.799	14.236	< 0.001	1.000
Intercept	4910.198	1	4910.198	38860.065	< 0.001	1.000
DATE	139.964	11	12.724	100.700	< 0.001	1.000
STATION	118.959	29	4.102	32.464	< 0.001	1.000
DATE * STATION	175.497	219	.801	6.342	< 0.001	1.000
Error	295.673	2340	.126			
Total	8326.294	2600				
Corrected Total	761.564	2599				

a Computed using alpha = 0.1
b R Squared = .612 (Adjusted R Squared = .569)

Table 2B. Results of Student-Newman-Keuls (SNK) post-hoc multiple comparisons test for differences in mean species abundance ($\sqrt{\sqrt{}}$ transformed) between sampling dates.

Date	N	1	2	3	4	5	6	7	8
					Subset				
APR 98	240	1.3240							
APR 99	240	1.3377							
NOV 99	240		1.4136						
NOV 98	240			1.5698					
APR 97	240				1.6426				
APR 00	160					1.7319			
NOV 97	240						1.8338		
NOV 96	200							1.9068	
APR 01	140							1.9170	
NOV 00	300							1.9504	
APR 96	200							1.9722	
NOV 95	160								2.1207
Sig.		.695	1.000	1.000	1.000	1.000	1.000	.241	1.000

Table 2C. Results of Student-Newman-Keuls (SNK) post-hoc multiple comparisons test for differences in mean species abundance (√√ transformed) between sampling stations.

Station	N	Subset 1	2	3	4	5	6	7	8	9	10	11	12
23	70	1.2168											
22	70	1.2862	1.2862										
17	90	1.4083	1.4083	1.4083									
18	90	1.4250	1.4250	1.4250	1.4250								
21	70	1.4338	1.4338	1.4338	1.4338	1.4338							
7	110		1.5102	1.5102	1.5102	1.5102	1.5102						
20	90			1.5339	1.5339	1.5339	1.5339	1.5339					
3	120			1.5451	1.5451	1.5451	1.5451	1.5451					
2	120			1.5654	1.5654	1.5654	1.5654	1.5654					
1	120			1.5677	1.5677	1.5677	1.5677	1.5677					
24	70			1.5897	1.5897	1.5897	1.5897	1.5897					
5	120			1.5934	1.5934	1.5934	1.5934	1.5934					
29	10				1.6812	1.6812	1.6812	1.6812	1.6812				
4	110					1.6996	1.6996	1.6996	1.6996	1.6996			
14	120						1.7549	1.7549	1.7549	1.7549			
26	10						1.7709	1.7709	1.7709	1.7709			
8	120							1.7868	1.7868	1.7868			
10	120							1.7897	1.7897	1.7897			
19	90							1.7941	1.7941	1.7941			
13	120							1.8116	1.8116	1.8116			
11	120							1.8138	1.8138	1.8138			
25	10							1.8216	1.8216	1.8216			
15	120								1.8689	1.8689			
16	120								1.8752	1.8752			
9	120								1.9250	1.9250			
6	120								1.9285	1.9285			
28	10									1.9789			
30	10										2.1542		
12	120											2.3360	
27	10												2.6921
Sig.		.073	.059	.453	.070	.050	.070	.050	.159	.055	1.000	1.000	1.000

Table 3A. Results of two-way ANOVA on differences in benthic species richness at thirty Port Curtis sampling stations surveyed on twelve dates between November 1995 and April 2001.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Power(a)
Corrected Model	238.045(b)	259	.919	11.356	< 0.001	1.000
Intercept	3676.565	1	3676.565	45427.987	< 0.001	1.000
DATE	74.615	11	6.783	83.814	< 0.001	1.000
STATION	57.688	29	1.989	24.579	< 0.001	1.000
DATE * STATION	85.693	219	.391	4.835	< 0.001	1.000
Error	189.380	2340	.081			
Total	6093.147	2600				
Corrected Total	427.425	2599				

a Computed using alpha = 0.1
b R Squared = .557 (Adjusted R Squared = .508)

Table 3B. Results of Student-Newman-Keuls (SNK) post-hoc multiple comparisons test for differences in mean species richness (√√ transformed) between sampling dates.

		Subset					
Date	N	1	2	3	4	5	6
APR 98	240	1.1623					
APR 99	240	1.2112					
NOV 99	240		1.2734				
NOV 98	240			1.3917			
APR 97	240			1.4183			
APR 00	160				1.5340		
NOV 97	240				1.5666		
APR 01	140					1.6323	
NOV 96	200					1.6369	
NOV 00	300					1.6421	
APR 96	200					1.6622	
NOV 95	160						1.7878
Sig.		.080	1.000	.342	.244	.710	1.000

Table 3C. Results of Student-Newman-Keuls (SNK) post-hoc multiple comparisons test for differences in mean species richness (√√ transformed) between sampling stations.

Station	N	Subset 1	2	3	4	5	6	7	8	9	10	11
22	70	1.1130										
23	70	1.1192										
21	70	1.2066	1.2066									
17	90	1.2840	1.2840	1.2840								
24	70	1.2848	1.2848	1.2848								
18	90		1.3082	1.3082	1.3082							
7	110		1.3179	1.3179	1.3179	1.3179						
3	120		1.3836	1.3836	1.3836	1.3836	1.3836					
1	120		1.3994	1.3994	1.3994	1.3994	1.3994					
20	90		1.4047	1.4047	1.4047	1.4047	1.4047					
2	120		1.4082	1.4082	1.4082	1.4082	1.4082					
4	110			1.4335	1.4335	1.4335	1.4335	1.4335				
5	120			1.4363	1.4363	1.4363	1.4363	1.4363				
14	120			1.4977	1.4977	1.4977	1.4977	1.4977	1.4977			
29	10				1.5095	1.5095	1.5095	1.5095	1.5095			
19	90					1.5258	1.5258	1.5258	1.5258			
25	10						1.5457	1.5457	1.5457			
11	120						1.5477	1.5477	1.5477			
10	120						1.5539	1.5539	1.5539			
13	120						1.5559	1.5559	1.5559			
8	120						1.5592	1.5592	1.5592			
15	120						1.5616	1.5616	1.5616			
16	120						1.5853	1.5853	1.5853	1.5853		
26	10						1.5857	1.5857	1.5857	1.5857		
6	120							1.6536	1.6536	1.6536		
9	120								1.6759	1.6759		
28	10									1.7701	1.7701	
30	10									1.7737	1.7737	
12	120										1.8933	
27	10											2.0488
Sig.		.079	.068	.057	.082	.062	.181	.064	.279	.057	.159	1.000

Table 4. Pearson correlation coefficients between: A) long-term series (November 1995 - April 2001) of the Southern Oscillation Index (SOI), rainfall in the Calliope catchment, freshwater discharge to Port Curtis, turbidity at Wiggins Island, chlorophyll *a* concentration at the Calliope River mouth, phosphate concentrations at Clinton wharf, and benthic species richness and abundance; B) Pearson correlations with a delay of 4 months in all parameters except for species richness and abundance. Significant correlations are denoted at the: ** 1% level and *5% level.

	SOI	Rain	Flow	Turbidity	Chlorophyll	Phosphate	Richness
(A) - no lag							
SOI	-	-	-	-	-	-	-
Rain	0.20	-	-	-	-	-	-
Flow	0.16	0.66**	-	-	-	-	-
Turbidity	-0.01	-0.05	0.06	-	-	-	-
Chlorophyll	-0.19	0.44**	0.48**	0.11	-	-	-
Phosphate	0.01	0.44*	0.20	0.09	0.46*	-	-
Richness	0.13	0.33	0.21	0.16	0.43	-0.19	-
Abundance	0.13	0.39	0.34	0.17	0.56	-0.17	0.98**
(B) - 4 month lag							
Richness	-0.08	-0.09	-0.03	0.80**	0.12	0.24	-
Abundance	-0.04	-0.10	-0.09	0.82**	0.15	0.28	0.98**

Appendix 1. Mean infaunal species abundances at two depth strata in Port Curtis. Levels of species contributions to regional differences are given here as the percentage contributions of individual dissimilarity measures to the overall average dissimilarity (87.64). Note that species have been ranked here according to total species abundances at all sampling stations and sampling periods.

Rank	Species	Subtidal	Intertidal	Dissim.	% Contr.	Rank	Species	Subtidal	Intertidal	Dissim.	% Contr.
1	Carditella torresi	21.17	0.17	2.71	3.09	78	Pharella wardi	0.30		0.27	0.31
2	Ascidia sydneiensis	5.49		1.03	1.18	79	Goniadidae 2	0.26	0.20	0.35	0.40
3	Corbula tunicata	5.36	0.60	1.62	1.84	80	Cuspidaria sp. 1	0.27	0.10	0.37	0.42
4	Acidiacea sp. 5	5.17		0.14	0.16	81	Maldanidae 2	0.28		0.14	0.16
5	Mimachlamys gloriosa	4.89		1.29	1.47	82	Bivalvia 33	0.07	1.63	0.29	0.33
6	Eunice vittata	4.80	0.03	1.21	1.38	83	Amphipoda 3	0.27		0.16	0.18
7	Leionucula superba	4.65	1.00	1.65	1.88	84	Gobiidae 1	0.27		0.36	0.42
8	Mactra abbreviata	2.60	9.23	1.83	2.09	85	Pitar trevori	0.25	0.13	0.28	0.32
9	Placamen tiara	3.18	0.40	1.67	1.90	86	Sabellidae 2	0.21	0.43	0.43	0.49
10	Alpheus sp.	2.73	1.40	1.49	1.70	87	Streblosoma sp.	0.26	0.03	0.15	0.17
11	Myochamidae	2.84	0.13	1.32	1.51	88	Arabellidae 1	0.25	0.07	0.31	0.35
12	Eunice sp. 1	2.62	0.40	1.42	1.62	89	Gari anomula	0.26		0.06	0.07
13	Lumbrineris sp. 2	2.28	2.40	1.39	1.58	90	Syllidae 2	0.26		0.13	0.15
14	Maldanidae 6	2.26		0.44	0.50	91	Tellina sp. 5	0.21	0.40	0.46	0.53
15	Aloidis hydropica	1.91	1.17	1.35	1.54	92	Trypauchen microcephalus	0.25	0.07	0.39	0.44
16	Bivalvia 30	0.72	10.07	1.95	2.22	93	Cumacea 1	0.24		0.28	0.31
17	Ophiuroidea 5	1.76	0.43	0.78	0.89	94	Polynoidae 3	0.25		0.20	0.23
18	Modiolus sp. 1	1.75	0.03	0.64	0.73	95	Sigalion sp. 1	0.19	0.47	0.41	0.46
19	Arca tortuosa	1.68		1.00	1.14	96	Capitellidae 1	0.24		0.21	0.23
20	Atylus falcatus	1.49	0.17	0.82	0.94	97	Isopoda 7	0.24		0.26	0.30
21	Cuspidaridae 1	1.38	1.03	0.92	1.05	98	Eupanthalis sp. 1	0.24		0.06	0.07
22	Dexaminidae 1	1.46	0.07	0.76	0.86	99	Lumbrineris sp. 1	0.24		0.20	0.23
23	Ophiuroidea 11	1.41		0.27	0.31	100	Holothuroidea 3	0.23		0.29	0.33
24	Pectinidae 1	1.39		0.23	0.26	101	Amphipoda 1	0.23	0.03	0.20	0.22
25	Trichobranchidae 1	1.38	0.07	0.52	0.59	102	Bivalvia 27	0.22		0.08	0.09
26	Anodontia omissa	1.18	1.33	1.10	1.26	103	Nereididae 9	0.03	1.50	0.18	0.20
27	Solecurtidae 1	1.32		0.43	0.49	104	Ceriatharia 2	0.22		0.02	0.02
28	Ophelina sp. 1	1.22	0.60	1.10	1.25	105	Porcellanidae 1	0.21	0.03	0.23	0.26
29	Antigona materna	1.24	0.03	0.85	0.97	106	Ampharete sp. 1	0.21		0.02	0.02
30	Ascidiacea 2	1.17		0.48	0.55	107	Bivalvia 19	0.21	0.03	0.08	0.09
31	Thoracica 1	1.15		0.29	0.33	108	Branchiomma nigomasculata	0.21		0.19	0.22
32	Diopatra denata	0.94	1.10	1.01	1.15	109	Veneridae 1	0.19	0.13	0.23	0.27
33	Alpheus nr. pacificus	0.88	1.37	0.99	1.13	110	Gari sp. 1	0.06	1.13	0.35	0.40
34	Eunice sp. 4	1.03	0.03	0.45	0.51	111	Thoracica 2	0.20		0.08	0.10
35	Cardita incrassata	1.02		0.20	0.23	112	Marphysa sp. 2	0.12	0.60	0.34	0.39
36	Orbiniidae 1	1.02		0.64	0.73	113	Nereididae 8	0.17	0.20	0.26	0.30
37	Azorinus sp. 2	0.02	7.57	1.66	1.89	114	Nothria sp. 1	0.19		0.16	0.18
38	Nematoneris unicornis	0.96	0.20	0.67	0.77	115	Sigalionidae 1	0.18	0.07	0.28	0.32
39	Soletellina sp. 1	0.87	0.50	0.74	0.84	116	Ophiuroidea 10	0.18		0.09	0.10
40	Glycera sp. 1	0.80	0.97	0.94	1.07	117	Ophiuroidea 15	0.18		0.10	0.12
41	Isopoda 1	0.88	0.17	0.74	0.84	118	Spionidae 4	0.18		0.10	0.11
42	Amphipoda 4	0.86	0.07	0.52	0.60	119	Ophiuroidea 13	0.18		0.13	0.15
43	Tellina sp. 3	0.62	1.87	0.65	0.74	120	Sabellariidae 1	0.18	0.03	0.28	0.32
44	Pahies heterodon	0.80	0.23	0.66	0.75	121	Eunice sp. 2	0.18		0.14	0.16
45	Nephtys sp. 1	0.76	0.23	0.55	0.62	122	Modiolus modiolus	0.17		0.20	0.23
46	Tanaidacea 1	0.75	0.33	0.59	0.67	123	Sabellidae 5	0.18		0.09	0.11
47	Corbula sulcata	0.77	0.13	0.57	0.65	124	Spionidae 2	0.18		0.09	0.10
48	Ophiuroidea 1	0.75		0.44	0.50	125	Notomastus sp. 2	0.17		0.12	0.13
49	Tellina sp. 7	0.08	5.23	1.53	1.75	126	Nereididae 4	0.17		0.16	0.18
50	Eunice sp. 5	0.73	0.07	0.54	0.62	127	Isopoda 6	0.17		0.10	0.11
51	Maldanidae 3	0.72		0.31	0.36	128	Polynoidae 4	0.16	0.03	0.23	0.26
52	Isopoda 2	0.71		0.32	0.37	129	Haploscoplos sp. 1	0.16		0.13	0.15
53	Arcidae 1	0.62	0.67	0.99	1.13	130	Semelidae 1	0.16		0.12	0.14
54	Amphipoda 2	0.63	0.10	0.35	0.40	131	Tellina sp. 6	0.07	0.70	0.39	0.45
55	Papha undulata	0.57	0.37	0.60	0.68	132	Bivalvia 31	0.14	0.13	0.20	0.23
56	Armandia sp. 1	0.61		0.24	0.28	133	Nereididae 10	0.12	0.27	0.22	0.25
57	Ophiuroidea 8	0.59		0.38	0.43	134	Xanthidae 1	0.14	0.10	0.38	0.43
58	Goniadidae 3	0.53	0.27	0.61	0.70	135	Ophiuroidea 4	0.15		0.10	0.11
59	Ophiuroidea 14	0.56	0.03	0.44	0.50	136	Bivalvia 43	0.00	1.10	0.18	0.20
60	Tellina sp. 1	0.50	0.37	0.37	0.42	137	Ophiuroidea 12	0.15		0.10	0.12
61	Lumbrineris sp. 3	0.45	0.60	0.67	0.77	138	Amphipoda 9	0.12	0.20	0.23	0.26
62	Sternapis scutata	0.50	0.10	0.57	0.64	139	Tellina sp. 9	0.14	0.07	0.11	0.12
63	Strigilla euronia	0.35	1.10	0.91	1.03	140	Ophiuroidea 20	0.14		0.09	0.10
64	Paphies sp. 1	0.49	0.03	0.40	0.46	141	Paphies sp. 2	0.13	0.07	0.17	0.20
65	Ceriatharia 1	0.49		0.20	0.22	142	Marphysa sp. 1	0.08	0.43	0.29	0.33
66	Lamaria sp. 1	0.47		0.39	0.45	143	Sabellidae 7	0.14		0.10	0.12
67	Mytilidae 1	0.44	0.03	0.34	0.39	144	Ophiuroidea 9	0.13		0.06	0.06
68	Nereididae 5	0.41	0.03	0.31	0.36	145	Notomastus sp. 1	0.13		0.09	0.11
69	Ophiuroidea 18	0.40		0.24	0.28	146	Sabellidae 4	0.13		0.07	0.08
70	Tellina sp. 4	0.27	1.03	0.43	0.49	147	Dorvilleidae 1	0.11	0.13	0.21	0.24
71	Isolda pulchella	0.38		0.29	0.33	148	Paphies cunata	0.12	0.03	0.16	0.18
72	Tanaidacea 1	0.35	0.17	0.37	0.42	149	Euidotea sp. 1	0.12	0.03	0.13	0.15
73	Azorinus sp. 3	0.35	0.13	0.25	0.29	150	Anthozoa 1	0.12		0.08	0.10
74	Tellina sp. 2	0.28	0.47	0.51	0.59	151	Leocratides filamentosa	0.12		0.11	0.13
75	Syllidae 1	0.33	0.03	0.24	0.27	152	Azorinus sp. 1	0.07	0.33	0.35	0.40
76	Maldanidae 1	0.31		0.10	0.11	153	Ophiuroidea 2	0.11		0.11	0.13
77	Ogyrides delli	0.29		0.25	0.28	154	Tanaidacea 3	0.09	0.17	0.32	0.37

Rank	Species	Subtidal	Intertidal	Dissim.	% Contr.
155	Ostracoda 1	0.03	0.60	0.30	0.34
156	Bivalvia 24	0.11		0.06	0.07
157	Ophiuroidea 6	0.11		0.09	0.10
158	*Callianassa* sp.	0.07	0.27	0.34	0.39
159	Decapoda 3	0.04	0.50	0.15	0.17
160	Phyllodocidae 3	0.10		0.06	0.06
161	Veneridae 2	0.10		0.13	0.15
162	Bivalvia 53	0.10		0.11	0.13
163	*Laternula constricta*	0.06	0.30	0.18	0.20
164	Capitellidae 3	0.09	0.03	0.09	0.10
165	Flabelligeridae 1	0.09		0.14	0.16
166	Hippolytidae 1	0.08		0.12	0.13
167	Isopoda 8	0.09		0.06	0.07
168	Terebellidae 1	0.09		0.08	0.09
169	Ampharetidae 1	0.09		0.06	0.07
170	Holothuroidea 1	0.09		0.07	0.08
171	Palaemonidae 2	0.09		0.06	0.07
172	Xanthidae 14	0.02	0.53	0.24	0.28
173	*Alpheus richardsoni*	0.09		0.11	0.12
174	Bivalvia 35	0.04	0.37	0.39	0.44
175	Polynoidae 1	0.09		0.10	0.11
176	*Eupolymnia* sp.	0.09		0.05	0.06
177	Asteroidea 1	0.08		0.12	0.14
178	Serpulidae 1	0.08		0.08	0.09
179	*Samytha* sp. 1	0.07		0.10	0.11
180	Bivalvia 25	0.08		0.04	0.05
181	Sipuncula 6	0.08		0.06	0.07
182	Bogueidae 1	0.01	0.47	0.23	0.27
183	Nemertea 1	0.06	0.07	0.13	0.14
184	Bivalvia 45	0.03	0.30	0.36	0.41
185	Decapoda 1	0.07		0.04	0.05
186	Isopoda 3	0.07		0.03	0.04
187	Sabellidae 9	0.07		0.02	0.02
188	*Virgularia* sp.	0.06	0.07	0.14	0.16
189	Xanthidae 11	0.03	0.37	0.29	0.33
190	Arcidae 2	0.06	0.10	0.26	0.29
191	Goniadidae 1	0.07		0.07	0.08
192	*Macrobranchium intermedium*	0.07		0.06	0.07
193	*Metapenaeus* sp. 1	0.04	0.20	0.35	0.40
194	Polynoidae 4	0.07		0.07	0.08
195	Xanthidae 2	0.07		0.10	0.12
196	*Notomastus* sp. 3	0.06		0.05	0.06
197	Majidae 1	0.06		0.07	0.08
198	Phyllodocidae 1	0.06		0.10	0.12
199	Sabellidae 1	0.06		0.05	0.06
200	*Pista typha*	0.03	0.27	0.21	0.23
201	Anthozoa 4	0.06		0.03	0.04
202	*Enders strangham*	0.06		0.06	0.06
203	Nereididae 1	0.06		0.06	0.06
204	Stomatopoda 1	0.05	0.10	0.28	0.32
205	Sipuncula 1	0.06		0.08	0.09
206	*Soletellina petalina*	0.06		0.05	0.06
207	Amphinomidae 1	0.06		0.07	0.08
208	Bivalvia 28	0.06		0.04	0.05
209	Polyplacophora 2	0.06		0.05	0.06
210	Diogenidae 2		0.40	0.24	0.27
211	Maldanidae 5	0.06		0.05	0.05
212	Tellinidae 1	0.06		0.04	0.05
213	*Tellina* sp. 8	0.04	0.10	0.10	0.11
214	Bivalvia 29	0.05		0.08	0.09
215	Nereididae 6	0.05		0.04	0.05
216	Cirratulidae 2	0.04		0.08	0.09
217	Nuculanidae 1	0.05		0.03	0.03
218	*Scoloplos madagascariensis*	0.05		0.04	0.04
219	Spionidae 1	0.05		0.06	0.07
220	*Paphia gallus*	0.05		0.05	0.06
221	Ascidiacea 7	0.04		0.08	0.09
222	Bivalvia 26	0.04		0.04	0.04
223	Cephalopoda 1	0.04		0.02	0.03
224	Diogenidae 1	0.03	0.10	0.20	0.22
225	Decapoda 2	0.04		0.05	0.05
226	Pinnidae 1	0.04		0.05	0.05
227	Polynoidae 5	0.04		0.05	0.06
228	Porcellanidae 3	0.03	0.07	0.14	0.16
229	Caprellidae	0.04		0.05	0.06
230	Sabellidae 8	0.04		0.05	0.05
231	Bivalvia 21	0.04		0.05	0.05
232	Ophiuroidea 16	0.04		0.05	0.06
233	Ophiuroidea 21	0.04		0.04	0.05
234	Majidae 3	0.04		0.06	0.07
235	Alcoyonacea 1	0.04		0.04	0.05
236	Astropectinidae 1	0.04		0.07	0.08
237	*Volachlamys singaporinus*	0.04		0.03	0.04

Rank	Species	Subtidal	Intertidal	Dissim.	% Contr.
238	Phyllodocidae 4	0.04		0.05	0.06
239	Sabellidae 6	0.04		0.04	0.04
240	Tellinidae 3	0.02	0.17	0.08	0.09
241	Xanthidae 12	0.02	0.17	0.17	0.20
242	Bivalve 81	0.03		0.02	0.02
243	Bivalvia 41	0.03	0.03	0.09	0.11
244	Bivalvia 47	0.03		0.03	0.03
245	Bivalvia 51	0.03		0.06	0.07
246	Ophiuroidea 3	0.03		0.03	0.04
247	Polyplacophora 1	0.03		0.04	0.04
248	*Marphysa* sp. 3	0.03		0.05	0.06
249	Nereididae 2	0.03		0.04	0.05
250	Amphipoda 8	0.03	0.07	0.11	0.13
251	*Polyodontes australiensis*	0.03	0.03	0.11	0.13
252	Anthozoa 3	0.03		0.03	0.03
253	Pycnogonida 2	0.03		0.04	0.04
254	Pycnogonida 4	0.03		0.01	0.01
255	Ascidiacea 3	0.03		0.04	0.05
256	Ascidiacea 4	0.03		0.04	0.04
257	*Leiochrides* sp. 2	0.03		0.02	0.03
258	*Cardita* sp. 2	0.03		0.04	0.05
259	Nephtyidae 1	0.03		0.03	0.04
260	Nereididae 3	0.03		0.03	0.03
261	Amphipoda 5	0.03		0.03	0.03
262	Decapoda 4	0.01	0.17	0.09	0.10
263	Amphipoda 7	0.03		0.03	0.03
264	Sipuncula 2	0.03		0.05	0.05
265	Paraonidae 1	0.03		0.04	0.04
266	Scalibregmidae 1	0.03	0.03	0.07	0.08
267	Xanthidae 20	0.03		0.04	0.04
268	Crinoidea 1	0.03		0.05	0.05
269	Capitellidae 2	0.02		0.07	0.07
270	Capitellidae 4	0.03		0.02	0.02
271	*Metapenaeopsis endeavori*	0.02	0.03	0.06	0.07
272	*Metapenaeopsis novaeguineae*	0.02	0.07	0.15	0.17
273	Syllidae 3	0.02	0.03	0.07	0.08
274	Tellinidae 2	0.03		0.02	0.02
275	Xanthidae 8	0.01	0.13	0.25	0.28
276	Aphroditidae 1	0.02		0.03	0.04
277	Oligochaeta 1	0.02		0.02	0.03
278	Bivalvia 17	0.02		0.03	0.04
279	Bivalvia 50	0.01	0.10	0.12	0.13
280	Bivalvia 52	0.02	0.03	0.07	0.09
281	Ophiuroidea 17	0.02		0.02	0.02
282	Polyplacophora 3	0.01	0.10	0.09	0.10
283	*Leiochrides* sp. 1	0.02		0.03	0.03
284	*Clibanarius taeniatus*	0.01	0.07	0.14	0.16
285	Echinometridae 1	0.02		0.03	0.04
286	Flabelligeridae 2	0.02		0.04	0.05
287	Portunidae 1	0.02		0.04	0.04
288	Portunidae 2	0.01	0.07	0.11	0.12
289	Pteriidae 1	0.02		0.03	0.03
290	Xanthidae 5	0.01	0.10	0.13	0.15
291	Ampharetidae 2	0.02		0.03	0.03
292	*Amphicteis* sp. 1	0.02		0.03	0.03
293	Bopyridae 1	0.02		0.02	0.03
294	Anthozoa 2	0.02		0.02	0.02
295	Nemertea 2	0.02		0.03	0.03
296	Pycnogonida 1	0.02		0.02	0.02
297	Pycnogonida 3	0.02		0.02	0.02
298	Asteroidea 3	0.02		0.03	0.04
299	Bivalve 78	0.02		0.02	0.02
300	Bivalvia 13	0.02		0.01	0.01
301	Bivalvia 20	0.02		0.02	0.02
302	Bivalvia 23	0.02		0.02	0.02
303	Bivalvia 38	0.02		0.03	0.03
304	Bivalvia 44	0.01	0.07	0.11	0.13
305	Cirratulidae 1	0.02		0.02	0.02
306	*Archaeus* sp. 1	0.02		0.03	0.03
307	Nematoda 1	0.02		0.02	0.03
308	Amphipoda 6	0.02		0.03	0.03
309	Astropectinidae 2	0.02		0.02	0.03
310	Astropectinidae 3	0.01		0.06	0.07
311	Isopoda 5	0.02		0.03	0.03
312	*Smilium* sp. 1	0.02		0.03	0.03
313	Pandalidae 1	0.02		0.02	0.02
314	*Phyllodoce malmgreni*	0.02		0.02	0.02
315	Pilargiidae 1	0.02		0.02	0.02
316	Xanthidae 15	0.01	0.07	0.15	0.17
317	Acrocirridae 1	0.01	0.03	0.08	0.09
318	Arabellidae 2	0.01		0.01	0.01
319	Ostracoda 2	0.01		0.02	0.02
320	Asteroidea 2	0.01		0.03	0.03

Rank	Species	Subtidal	Intertidal	Dissim.	% Contr.
321	Bivalvia 36	<0.01		0.06	0.07
322	Bivalvia 42	0.01	0.03	0.07	0.09
323	Bivalvia 54	0.01		0.01	0.01
324	Bivalvia 56	0.01		0.01	0.01
325	Ophiuroidea 19	0.01		0.01	0.02
326	Callianassidae 1	0.01		0.01	0.01
327	Dasybranchus sp. 1	0.01		0.01	0.02
328	Echinoidae 1	0.01		0.02	0.02
329	Hesionidae 1	0.01		0.01	0.01
330	Elamenopsis lineata	0.01		0.05	0.05
331	Majidae 4	0.01		0.03	0.03
332	Majidae 5	0.01		0.02	0.02
333	Decapoda 6	0.01		0.03	0.03
334	Polycladida 1	0.01		0.02	0.02
335	Ocypoda 2		0.07	0.13	0.15
336	Chordata 1	0.01		0.01	0.01
337	Sipuncula 3	0.01	0.03	0.11	0.13
338	Penaeidae 1	0.01		0.02	0.02
339	Pilumnidae 2	0.01		<0.01	0.01
340	Portunidae 4	0.01		0.02	0.03
341	Portunidae 5	0.01		0.02	0.02
342	Sabellidae 10	0.01		0.01	0.02
343	Spionidae 3	0.01		0.01	0.02
344	Trichobranchidae 2	0.01		0.02	0.02
345	Trichochaetidae 1	0.01		0.02	0.02
346	Veneridae 3	0.01		0.02	0.02
347	Xanthidae 7	<0.01	0.10	0.16	0.19
348	Artus graeffei	<0.01	0.03	0.10	0.11
349	Oligochaeta 2	0.01		0.01	0.02
350	Bivalvia 40	0.01		0.01	0.01
351	Bivalvia 55	0.01		0.01	0.01
352	Remipedia 1	0.01		0.01	0.01
353	Notomastus sp. 4		0.07	0.07	0.08
354	Cardiidae 1	0.01		<0.01	<0.01
355	Chamidae 1	0.01		0.01	0.01
356	Corbula sp. 2	0.01		0.01	0.01
357	Orseis sp. 1	0.01		0.01	0.01
358	Maldanidae 4	0.01		0.01	0.01
359	Maldanidae 7	0.01		0.01	0.01
360	Malleidae 1	0.01		0.01	0.01
361	Mictyridae 1		0.07	0.05	0.05
362	Isopoda 4	0.01		0.01	0.01
363	Ocypoda 3	<0.01	0.03	0.07	0.08
364	Phyllodocidae 2	0.01		0.01	0.01
365	Eumida sanguinea	0.01		0.01	0.01
366	Processa dimorpha	0.01		0.01	0.01
367	Sabellidae 3	0.01		0.01	0.01
368	Pseudoscalibregma sp. 1	0.01		0.01	0.01
369	Sygnathidae 1	<0.01	0.03	0.05	0.06
370	Psammotreta sp. 1	0.01		0.02	0.02
371	Braesma sp. 1	0.01		0.02	0.02
372	Xanthidae 10	0.01		0.01	0.01
373	Xanthidae 16		0.07	0.05	0.05
374	Xanthidae 4	0.01		0.01	0.01
375	Ampharetidae 3	<0.01		0.01	0.01
376	Ascidiacea 6	<0.01		0.01	0.01
377	Asteroidea 4	<0.01		0.01	0.01
378	Bivalvia 32	<0.01		0.01	0.01
379	Bivalvia 46	<0.01		0.01	0.01
380	Bivalvia 48	<0.01		0.02	0.02
381	Callianassidae 2	<0.01		<0.01	<0.01
382	Capitellidae 5	<0.01		0.05	0.06
383	Capitellidae 6	<0.01		0.01	0.01
384	Carditidae 3	<0.01		0.01	0.01
385	Pterasteridae	<0.01		0.01	0.01
386	Hesionidae 2	<0.01		<0.01	<0.01
387	Latreutes pygmaeus	<0.01		0.01	0.01
388	Isopoda 13	<0.01		<0.01	<0.01
389	Magelonidae 1	<0.01		<0.01	<0.01
390	Majidae 7	<0.01		0.01	0.01
391	Nereididae 7	<0.01		0.01	0.01
392	Alcoyonacea 2	<0.01		0.01	0.01
393	Amphipoda 11		0.03	0.06	0.07
394	Amphipoda 27	<0.01		<0.01	<0.01
395	Decapoda 5		0.03	0.06	0.06
396	Decapoda 8	<0.01		0.01	0.02
397	Amphipoda 10	<0.01		0.01	0.01
398	Ocypoda 1		0.03	0.06	0.06
399	Ocypoda 6	<0.01		0.01	0.02
400	Ostracoda 6	<0.01		0.01	0.01
401	Sipuncula 4	<0.01		0.01	0.01
402	Phyllodocidae 5	<0.01		0.01	0.01
403	Pteriidae 2	<0.01		0.01	0.01

Rank	Species	Subtidal	Intertidal	Dissim.	% Contr.
404	Scyllaridae 1	<0.01		0.01	0.01
405	Xanthidae 17	<0.01		0.01	0.01
406	Xanthidae 18	<0.01		0.01	0.01
407	Xanthidae 19		0.03	0.06	0.07
408	Xanthidae 3	<0.01		0.01	0.01
409	Xanthidae 6	<0.01		0.01	0.01