

Long-term spatial dynamics of polychaetes in Leschenault Inlet estuary

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Abstract

Long-term abundance and distribution changes of benthic polychaetes in the Leschenault Inlet estuary were monitored over a period of five years from February 1982 to May 1987. A total of fifteen polychaete species were recorded, one of which was a new species (*Ampharetidae* sp). Spatial distributions of the dominant species could be linked to environmental factors, particularly to salinity, water depth and substrate. These specific habitat preferences indicate three polychaete assemblages. Long-term abundance changes of the three most common species, *Ceratonereis aequisetis*, *Nephtys gravieri* and *Capitella cf capitata*, followed rather complex patterns. Average circa-annual periodicity in abundance at a single site was typically unimodal, with a peak in late summer to autumn. There was no obvious circa-annual periodicity for the overall populations of given species, probably because large year-to-year variability at single sites and phase differences between sites masked the average pattern. Coincident long-term trends observed for *C. aequisetis* at neighbouring sites revealed a persistent synchronicity after disturbance, but a lack of coupling to seasonal variation in abiotic factors. This suggests the spatial and temporal changes in polychaete distribution within the Leschenault Inlet estuary mostly reflect local scale environmental conditions.

Keywords: estuarine polychaetes, Leschenault Inlet, estuary, south-western Australia.

Introduction

Few studies of estuarine macrobenthic infauna have been carried out in Western Australia, hence the polychaete fauna is poorly known (Hodgkin & Clark 1987-1990; Phillip & Lavery 1997; Platell & Potter 1996). Augener (1913, 1914) lists about 160 species of polychaetes from south-western Australia. Although most specimens were collected from marine sites, there are a few important estuarine records contained in this work. Hodgkin & Clark (1987-1990) compiled polychaete fauna lists for estuaries in south-western Australia from recent literature records and from cursory collection of material from locations where no previous work had been carried out. The latter inventory provides a taxonomic working-list with some 20 estuarine species of polychaetes noted for estuaries in the southwest region. Only three previous studies specifically identified polychaetes from the Leschenault Inlet estuary; Anon (1983) identified three species of polychaete, Chalmer & Scott (1984) recorded six species, and Deeley (Murdoch University *pers. comm.* 1998) recorded 13 species, six of which were identified only to the family level.

However, very little is known about estuarine polychaete biology and autecology apart from their pres-

ence at particular sites. Ecological studies investigating the preferences of particular polychaete species for various substrates and salinity ranges within estuarine environments of Western Australia are even sparser. Notable exceptions are the works by Platell & Potter (1996) at Wilson Inlet and Phillip & Lavery (1997) at Waychincup estuary. Long-term studies that allow assessment of circa-annual patterns in the population dynamics of particular species over several years have not been carried out in Western Australia.

A number of long-term studies on polychaete population dynamics, however, have been carried out in both marine and estuarine environments (*e.g.* Hutchings 1984; Kaleijta 1992; Beukema *et al.* 1993), but usually the reported temporal patterns can not be easily linked to environmental factors present in different habitats. This paper specifically attempts to address this problem within the context of the Leschenault Inlet estuary in south-western Australia, because of the high-resolution spatial and temporal sampling over several years. We provide an inventory of species compiled from five years of sampling benthic polychaete infauna of the Leschenault Inlet estuary. Moreover, we correlate polychaete distribution patterns to environmental factors, and show the temporal and spatial fluctuations in abundance and distribution of the three main species found in this estuary on short to long-term time frames.

Methods

Regional setting

Physical, chemical, habitat, and sedimentological aspects of the Leschenault Inlet estuary are described in Semeniuk V (2000) and Wurm & Semeniuk (2000). These studies document the range of estuarine habitats along four cross-inlet transects, which provide representative shallow and deep water sites in each of the four salinity fields of this estuary (Transects A-D; Fig. 1). Since the polychaetes described in this study were collected along the same transects, only a brief description of the range in salinity, substrate and aquatic vegetation along these transects is reiterated here. Salinity regimes are described after the Venice system for brackish waters (Anon 1959).

Transect A (sites A1-7) was located in the deltaic salinity field, where salinity varied from mesohaline in winter to euhaline in summer. Substrates comprised sands in shallow areas and sandy mud in the deeper basin area (sites A4 and A5). Most sites had the seagrass *Halophila ovalis* present (except sites A1 and A2 located on the delta front). Green (*Acetabularia*, *Chaetomorpha*), red (*Gracilaria*) and brown algae (two unidentified species) also were present at sites A5, A6 and A7.

Transect B (sites B8-14) was located in the lower estuarine salinity field, where salinity was euhaline throughout the year. Substrates were sandy in shallow regions on the western and eastern margins, with mud present in the deeper basin region (sites B11 and B12). *Halophila* was present at all sites, although in low abundance at sites B11 and B12. Algae were only found at sites B13 and B14 on the western margin.

Transect C (sites C15-19) was located in the mid-estuarine salinity field, where salinity was polyhaline in winter and euhaline in summer. Substrates comprised sandy mud on the eastern margin and were muddy in the deeper basin and western margin regions. *Halophila* was present at all sites. Algae occurred along the shore margins.

Transect D (sites D20-22) was located in the upper estuarine salinity field, where salinity was polyhaline in winter and hyperhaline in summer. Substrates were typically mud-dominated. Algae occurred patchily at all sites.

Methodology

Polychaetes were identified and counted from samples collected during seasonal benthic surveys of the Leschenault Inlet estuary in the years 1982-1987. Samples were collected quarterly at 22 sites along Transects A-D from May 1982 to May 1987 (Fig. 1 B, C). Additionally, eleven of these sites (sites

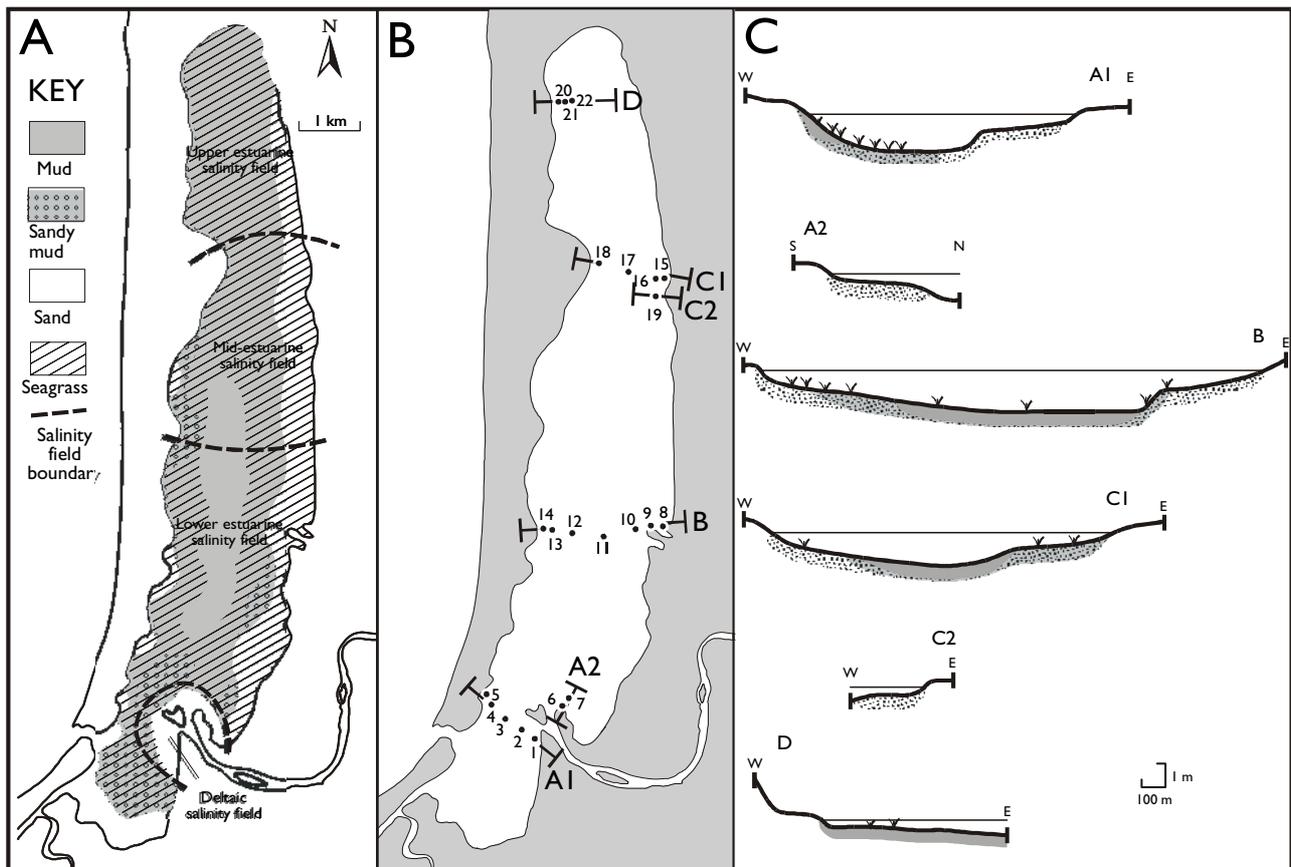


Figure 1. A: Habitat framework of Leschenault Inlet estuary after Wurm & Semeniuk (2000) with superimposed distribution of the seagrass *Halophila* after Lukatelich (1993). Major determinants of habitat classification are salinity regime (deltaic, lower, mid- and upper salinity field) and substrate composition (sand, muddy sand, sandy mud, mud). B: Sampling transects and sites in Leschenault Inlet estuary. Four transects were chosen according to prior habitat classification by Wurm & Semeniuk (2000). Transects A, B, C and D run across the deltaic/ lower, lower estuarine, mid-estuarine and upper estuarine salinity fields, respectively. C: Schematic cross-sections are redrawn after Wurm & Semeniuk (2000). Seagrass is recorded only at sampling sites. Dots (sand) and grey shading (mud) indicate substrate type.

A2, A3, A4, B9, B11/12, C15, C17, C19, D20, D21 and D22) were monitored monthly during the period May 1986 to May 1987 as part of a more detailed faunistic study (Wurm & Semeniuk 2000). Each site was sampled by retrieval of five randomly placed sediment cores; each core was 78.5 cm² in surface area and 15 cm depth. In May 1982, 10 samples per site were taken. The core was sieved with a 1 mm mesh. Retained specimens were immediately fixed in formaldehyde and fragments of menthol were added for the first few hours after collection in order to make the polychaete mouthparts accessible. Later, samples were washed and subsequently stored in 10% phenoxytol solution. More detailed information about the sampling strategy and sampling history is given by Semeniuk & Wurm (2000).

Specimens were identified and counted from each sample. However, field sieving, heat exposure, storage time and either the persistence of menthol in samples or insufficient fixation resulted in preservation problems for a number of samples. Deterioration of specimens in samples from August 1982 limited identification of species to those possessing chitinous mouthparts e.g. families Nereidae and Nephtyidae. Minor deterioration of specimens also occurred in May and December 1982. These circumstances affected the data on temporal variation and quantitative analyses of *Capitella cf capitata* for August 1982, and to a lesser extent for the sampling times of May 1982 and December 1982. Some problems with identification were also encountered due to fragmentation of the specimens during sieving, especially for *Capitellidae*, where setae patterns along the body length are important. In spite of the large sample base underlying this study, it is therefore possible that the reported species list is not exhaustive.

Additional samples collected in 1997 were used to provide fresh material for taxonomic work. Taxonomic reference standards were established using the keys and species de-

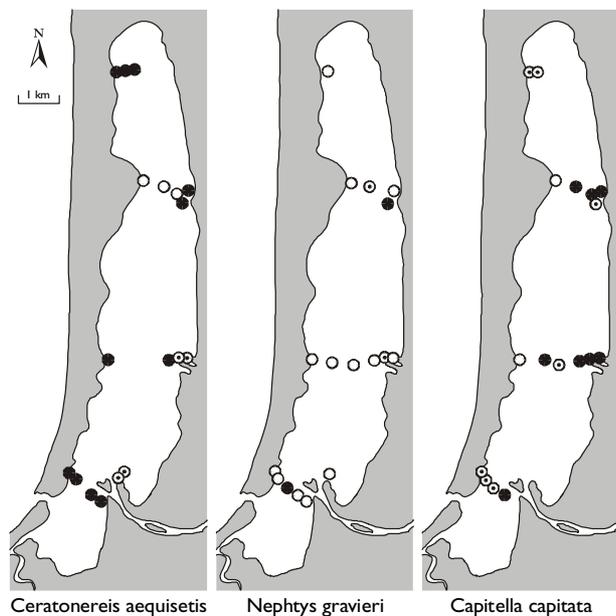


Figure 2. Distributions of the three main polychaete species of Leschenault Inlet estuary, based on maximum abundance at monitored sites between 1982-1987. Abundance is depicted for each site and rated as 'very common' (● > 10 specimen per site), common (⊙: 5-10 specimens per site) and uncommon (○: 1-5 specimens per site).

scriptions of Augener (1913, 1914), Day (1967), Rainer & Hutchings (1977), Hutchings & Murray (1984) and Hutchings & Glasby (1985). Some of our reference standards were cross-checked by P Hutchings (Australian Museum). Comparison of our reference standards with sample material enabled identification of most specimens.

Statistical analyses were attempted using a general linear model with replication (SPSS V8.0). The five sampling years and four sampling seasons were selected as 'inner subject' factors, with substrate (sand, muddy sand, sandy mud and mud), salinity (estuarine, lower, mid- and upper salinity field) and depth (intertidal and subtidal) as 'between subject' factors. However, due to the large number of samples containing no specimens, data distributions were highly skewed and even after square-root transformation were not normal-distributed according to Kolmogorov-Smirnov and Shapiro-Wilk Tests. Moreover, neither Levene's Test for homogeneity of variances, nor Mauchly's Test for sphericity were significant. This suggests the data were not suitable for analysis of variance. As a consequence, statistical analysis was limited to calculation of mean and standard error. Mean species abundance and standard error are always given for the sample area of a single core (except for Fig 7). Mean species abundance for the core area can be converted to species abundance per square meter by multiplying by 127.4. Thus abundance is used synonymously to population density.

Results

Inventory of species and diversity

Fifteen polychaete species were recorded for the Leschenault Inlet estuary in this study (Table 1). Most species were recorded over the interval 1982-1987 with three additional species recorded only in 1997. *Ampharetidae* sp represents a new species, possibly even a new genus (P Hutchings, Australian Museum, *pers. comm.*), but preservation was not adequate for an original description. The preservation state of the delicate Phyllodoceidae also did not allow us to distinguish between the genera *Phyllodoce* and *Anaitides*, both of which have been recorded from southwestern Australian estuaries before. To our knowledge, *Glycera cf americana* and *Lumbrineris cf latreilli* were recorded for the first time from Western Australia.

Table 1. Polychaete species list for Leschenault Inlet

Name	Family
<i>Ampharetidae</i> sp	Ampharetidae
<i>Capitella cf capitata</i> (Fabricius 1790)	Capitellidae
<i>Mediomastus</i> sp*	Capitellidae
<i>Caulleriella</i> sp*	Cirratulidae
<i>Glycera cf americana</i> (Leidy 1855)	Glyceridae
<i>Lumbrineris cf latreilli</i> (Adouin and Milne-Edwards 1834)	Lumbrineridae
<i>Nephtys gravieri</i> (Augener 1913)	Nephtyidae
<i>Australonereis ehlersi</i> (Augener 1913)	Nephtyidae
<i>Ceratonereis aequisetis</i> (Augener 1913)	Nereidae
<i>Neanthes oxyopoda</i> (Marenzeller 1879)	Nereidae
<i>Diopatra dentata</i> (Kinberg 1865)	Onuphiidae
<i>Scoloplos simplex</i> (Hutchings 1974)	Orbiniidae
<i>Harmothoe praeclara</i> (Haswell 1883)	Polynoidae
<i>Phyllodoce</i> or <i>Anaitides</i> sp	Phyllodoceidae
<i>Prionospio cf cirrifera</i> (Wiren 1883)*	Spionidae

* recorded in 1997 only.

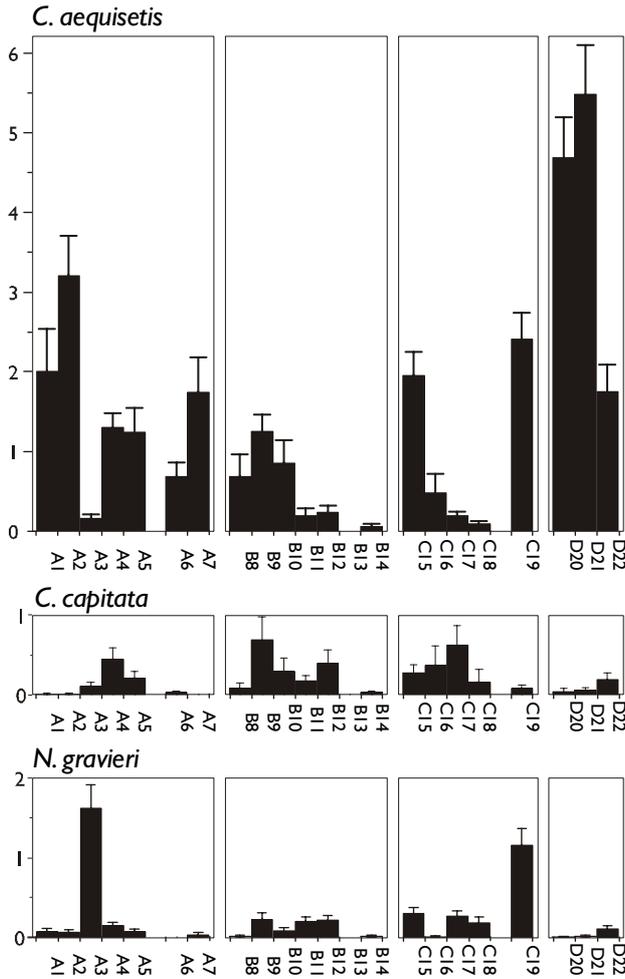


Figure 3. Average abundance of the three main polychaete species of Leschenault Inlet estuary between 1982 and 1987. Values are mean number of specimens per sample \pm standard error for *C. aequisetis*, *C. cf capitata* and *N. gravieri*, for each site along the four transects (n=140 for sites A2, A3, A4, B9, B11, B12, B14, C16, C18, C19, D20, D21 and D22, otherwise n=105). Spacing of bars within the 1st and 3rd columns separate sub-transects A1-5, A6-7 and C15-18, C19.

Over the period of the study, the most abundant species in the Leschenault Inlet estuary were *Ceratonereis aequisetis*, *Nephtys gravieri* and *Capitella cf capitata*. *Scoloplos simplex* was also commonly recorded in samples from sandy regions of the lower and middle estuary. Other species were recorded only rarely or only in 1997.

Overall species diversity for this estuary was low and samples were typically mono-specific. Highest diversity was recorded along Transect A where up to five species per sample were retrieved from deep basinal mud of the lower estuarine field (site A4; see Fig. 2). Diversity decreased from the lower estuary towards the upper estuarine regions. The upper estuarine field was dominated by a single species, *C. aequisetis* (see Fig. 2).

Spatial patterns of species

Quantitative analyses of spatial and temporal abundance change were restricted to the three main species of

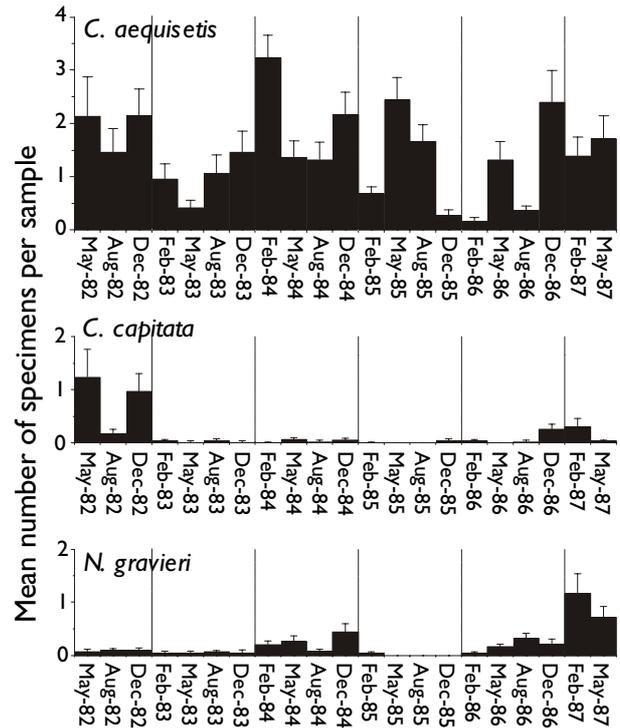


Figure 4. Overall mean abundance of the three main species indicates total biomass attributed to a single polychaete species through time. Species counts were pooled for all sites at a given month. Only quarterly samples are calculated for 1986-1987. Values are mean \pm standard error.

the Leschenault Inlet estuary, *C. aequisetis*, *N. gravieri*, and *C. cf capitata*. All other species occurred too patchily or infrequently to give a reliable account of their spatio-temporal population dynamics. For the three main species, maximum abundance at a given site was used as an indication of the maximal extent of their distribution within the estuary (Fig. 2). Additionally, mean abundance of these species was plotted along each transect to display average distribution for a given site (Fig. 3).

Ceratonereis aequisetis was recorded at all but one of the 11 sites monitored monthly. Highest abundances were recorded on the upper estuarine mud flat at sites D20-22 (Transect D), where there were up to 50 individuals per sample. Maximum abundance (Fig. 2) indicates that this species was very common at shallow sandy sites A1 and A2 in the Collie Delta region, sites C15 and C19 on the mid-estuarine eastern platform and shallow sandy mud (B14) or muddy sand sites (A4, A5, B10) of the lower estuarine region. *C. aequisetis* was common *i.e.* 2-5 individuals per sample maximum, at other sites in the Collie Delta region (sites A6, A7) and at shallow sandy and muddy sand sites in the lower estuarine region (sites B8, B9). *C. aequisetis* appeared to favour shallow and intertidal regions of the estuary with no specific preference for sediment type. Average abundance along transects reflected this preference for shallow sites (Fig. 3), since the species typically showed a drop in abundance with increasing depth along a transect (*e.g.* C15, C19 vs C16; D20, D21 vs D22). This pattern was most pronounced along Transect D, where the species was by far the dominant taxon. At the shallow site D21, mean abundance was more than 100 times those of *C. cf capitata* and more than 300 times

those of *N. gravieri* in the intertidal mud, whereas the relative dominance of *C. aequisetis* was reduced by a factor of ten at the slightly deeper water site D22. The decrease in abundance of *C. aequisetis* was paralleled by an increase in abundance of the other two species. Interestingly, in sandy sites of the deltaic region (along Transect A) this relationship with depth was reversed (Fig. 3), with lower abundances of *C. aequisetis* in the shallow intertidal zone than in the deeper subtidal zone (e.g. A2 vs A1; A7 vs A6). This reversal may have been due to the effect of freshwater input at these sites, or to the absence of seagrass. Since this species occurred throughout the lower to upper estuarine salinity fields, the latter explanation is more likely.

Capitella cf capitata was recorded at all but one of the 11 sites monitored monthly, but occurred most commonly within the lower and mid-estuarine salinity fields sampled along Transects B and C (Fig. 2). Highest abundances were recorded at sites B9 and C17, with up to 20 individuals per sample. *C. cf capitata* was abundant in lower to mid-estuarine basinal mud and less abundant on the adjacent eastern sandy platform and western muddy platform (Fig. 3). *C. cf capitata* was rare on both the deltaic front and on the upper estuarine muddy flat. It had a salinity preference for the lower to mid-estuarine fields and to favour mud or muddy sand substrates.

Nephtys gravieri was not recorded at all sites (Fig. 2). It was notably uncommon or absent in the deltaic region (sites A1-2, A6-7) and upper estuarine region (sites D20-22), and sparse at shallow muddy sites on the western platform (B14, C18). Mean abundance was highest at basinal sites of the lower and mid estuarine region (A3, B10-12, C17) and at sandy sites along the western platform margin of the lower and mid-estuarine field (B9, C15, C19). *N. gravieri* reached highest abundance at the lower estuarine basin site A3, with up to 20 individuals per sample. From these data the species appeared to have no clear preference for substrate or depth, but preferred the stable salinity regime of the mid-estuarine region.

Scoloplos simplex was recorded mainly at sites A1, A6-7, B8-10 and C19, which correspond to sandy areas of the eastern platform margin (data not shown). Abundances were typically 1-2 individuals per sample. It was notably absent from the upper reaches of the estuary, and appeared to favour intertidal sandy sites of the lower to middle estuary.

The distributions of the remaining polychaete species were more difficult to delineate, since their low abundances did not always guarantee collection during the various sampling surveys. *Ampharetidae* sp was only recorded along Transect D at sites D21 and D22. *Glycera cf americana* was recorded only from muddy sand on the lower estuarine western platform (site A4). *Lumbrineris cf latreilli* was recorded in the lower estuarine field at sandy mud and muddy sand sites A3-5. *Australonereis ehlersi* was recorded at sites A1-4, B11, C15 and C17, which are sand, muddy sand and mud sites in the lower to mid-estuarine fields. Low numbers of *Neanthes oxyopoda* were consistently recorded at sites A2 and A4. *Diopatra cf dentata* was recorded from deep basinal mud at site A3. *Harmothoe praeclara* was recorded at most muddy sand sites of the eastern platform (B9, B10, and C16) and at site A4. *Phyllodoce* sp was only recorded from basinal mud at sites A3, A4 and B11/12 in the lower estua-

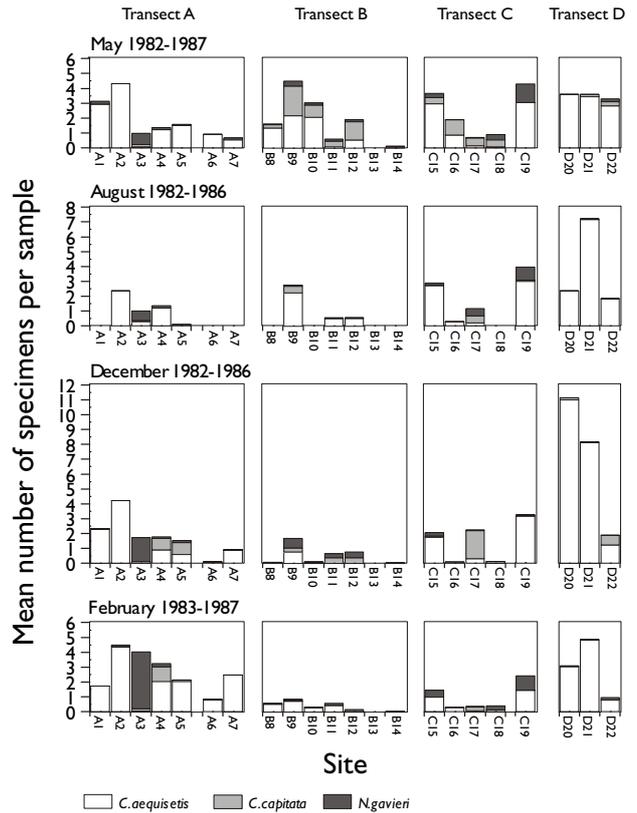


Figure 5. Average seasonal change in abundance of the three main species. Mean species abundance was pooled for a given season, but calculated separately for each site. Site data are arranged in columns, corresponding to sampling transects. Spacing of bars within the 1st and 3rd column separate sub-transects A1-5, A6-7 and C15-18, C19.

rine field. *Prionospio cf cirrifera*, *Mediomastus* sp and *Caulleriella* sp were only recorded in 1997 at sites C15 and C17 on the eastern platform margin within the mid estuarine region.

Long-term abundance

To present a measure of the overall biomass attributable to a given species of polychaete and its change through time, the temporal sequence of mean species abundance was examined (Fig. 4). There was no consistent circa-annual pattern over the five-year sampling period for any of the three main species. Mean species abundance of *C. aequisetis* showed some periodic change, in that for four out of five years it was lower in February than in December, and again lower in August than in May. However, the amplitude of the fluctuation was of the same order of magnitude as the underlying putative pattern, so variability masked any consistent periodicity.

Seasonal abundance

Average species abundances over the five years for the months of May, August, December and February for each site (Fig. 5). were typically a unimodal circa-annual pattern for each of the three main species at single sites. However, it is evident from comparing different sites that

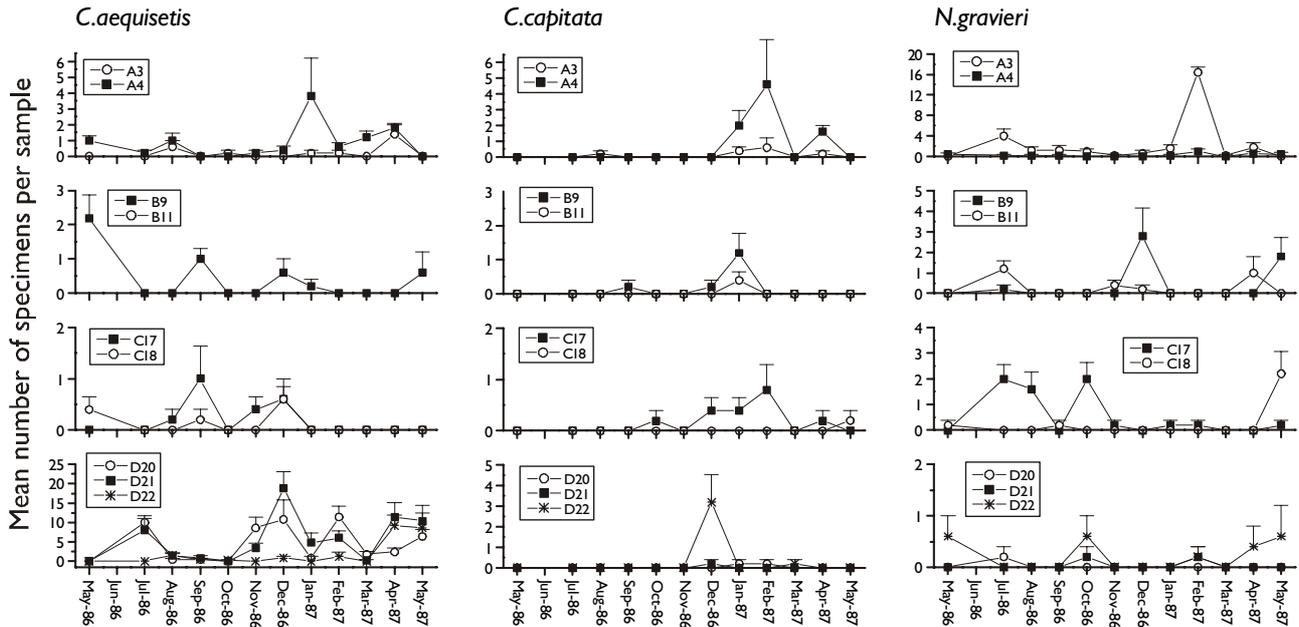


Figure 6. Temporal variation of species abundance on a monthly basis from May 1986 to May 1987. Mean species abundance per sample was calculated for nine sites and grouped according to transects (rows) and species (columns). Values are mean \pm standard error; note different scales of the ordinates.

the maximum of this unimodal pattern occurs in different months. For example, average abundance of *C. aequisetis* reached a maximum in December at upper and mid-estuarine sites D20, D21 and C17; in February at deltaic and lower estuarine sites A2, A4, A5 and A7; in May at lower and mid-estuarine sites B8-10, B12, C15, C16, C19), but also at deltaic and upper estuarine sites A1, A6 and D22 (Fig. 5). At sites dominated by other species, it appears the average abundance of *C. aequisetis* may even have peaked in August, when the dominant species was least abundant (e.g. specimen numbers of *C. aequisetis* were anti-cyclic with *N. gravieri* at A3, and *C. cf. capitata* at B11; Fig. 5). Similar observations could be made for the other two species.

The magnitude of abundance changes varied significantly between sites. At some sites, seasonal changes were relatively small (e.g. *C. aequisetis* at A2; Fig. 5), whereas at nearby sites populations varied from a moderate abundance of 1-2 individuals per sample to total absence (e.g. *C. aequisetis* at site A7; Fig. 5). Highest abundances were recorded in February or May at most sites *i.e.* late summer to autumn. It is obvious that the varying amplitudes and phase shifts of local, unimodal dynamics are unlikely to superimpose into a simple circa-annual pattern (Fig. 4). Hence, two questions emerge; (1) how variable were seasonal abundance changes at a given site within a single year *i.e.* could more frequent sampling reveal more complex patterns?; and (2) how variable were these seasonal patterns from year-to-year *i.e.* is the average seasonal pattern long-lasting and consistently present?

Short-term spatio-temporal variation

To address the first question, circa-annual abundance changes were examined for nine sites sampled monthly from July 1986 to May 1987 (Fig. 6). In some cases, such as for *C. aequisetis* at upper estuarine sites D20-22, monthly

changes of abundance were remarkably similar (Fig. 6). There were also several instances of concurrent abundance peaks at different sites along the same transect for a given species, as well as concurrent abundance peaks for different species at the same site. For example, abundance of *C. aequisetis* had coincident local maxima in December 1986 at sites B9, C17, C18, and D20-22 (Fig. 6). In this month, coincident peaks were recorded for *N. Gravieri* at site B9 and *C. cf. capitata* at site D22. Other months typically showed fewer coincidences of peaks. Peak abundances for *C. cf. capitata* almost always occurred between December and February at all of the nine sites, a pattern that was less pronounced for *C. aequisetis* and *N. gravieri* (Fig. 6). Hence, it appears that circa-annual abundance patterns varied a great deal between sites and between species, although there were some coincident short-term trends.

Long-term spatio-temporal variation

To address year-to-year variability, quarterly species abundance was plotted for four sites of the western platform and three sites of the central basin (Fig. 7). Sites were grouped such that they show a transition through different salinity fields at different depths (*i.e.* a deep-water and a shallow-water site from each Transect A-D). All sites had muddy substrates.

The long-term temporal variation of abundances at these sites showed both coincident events and pronounced variability, similar to the observations made for the one-year cycle (Fig. 6). Generally, year-to-year variability between samples of the same month was enough to mask the average unimodal pattern (Fig. 5), but some long-term trends could still be recognised at different sites for particular species. For instance, there were periods of high abundance of *C. aequisetis* at sites A4, B11, C17 and D22 from February 1984 to August 1985 (Fig. 7). A similar trend

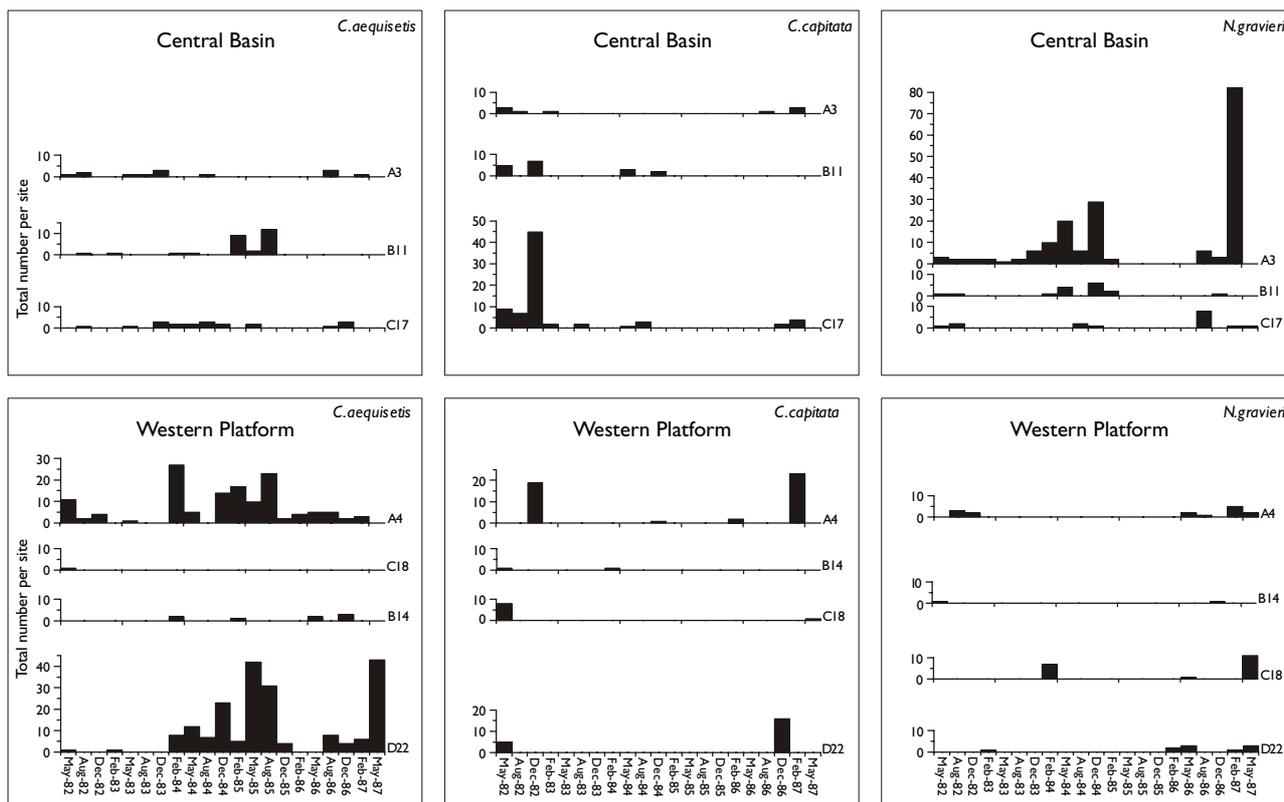


Figure 7: Long-term temporal variation of species abundance on a quarterly basis from May 1982 to May 1987. Total species counts from five samples per site and date, were calculated for seven sites. These are grouped according to depth (rows), salinity (sequence within single box) and species (columns).

was observed for *N. gravieri* at sites in the central basin; coincident peaks could be seen during May 1982 to December 1982 and December 1986 to February 1987. *N. gravieri* exhibited only irregular peaks at site A3 in 1984 and 1986/87. These peaks appeared to post-date mesohaline periods at site A3, suggesting that this was either a population stress response or an opportunistic response to fluctuating environmental conditions, or due to mass mortality of other species. The grouping of sites again emphasises the preference of species for particular habitats; *C. aequisetis* was most abundant at shallow-water sites of the lower to upper estuary; *N. gravieri* was most abundant at deep-water sites of the lower estuary; and *C. cf. capitata* had peak abundance in the mid-estuarine basin, but occurred with moderate abundances in both lower and upper estuarine sites of the western platform.

Small-range spatial changes of species.

Small-range spatial fluctuations in a single species population were investigated for the *C. aequisetis* along Transect D (Fig. 8). Mean abundance changes along Transect D were mainly determined by the population dynamics occurring at sites D20 and D21. However, the periodic pattern of the initial two years of sampling was markedly different at these two sites. In 1982 and 1983 the abundance of *C. aequisetis* at site D20 showed a single prominent peak each year (December collections), while the abundance at site D21 peaked four months earlier (August collection) and settled down to a medium level for the following six months (December and February collections).

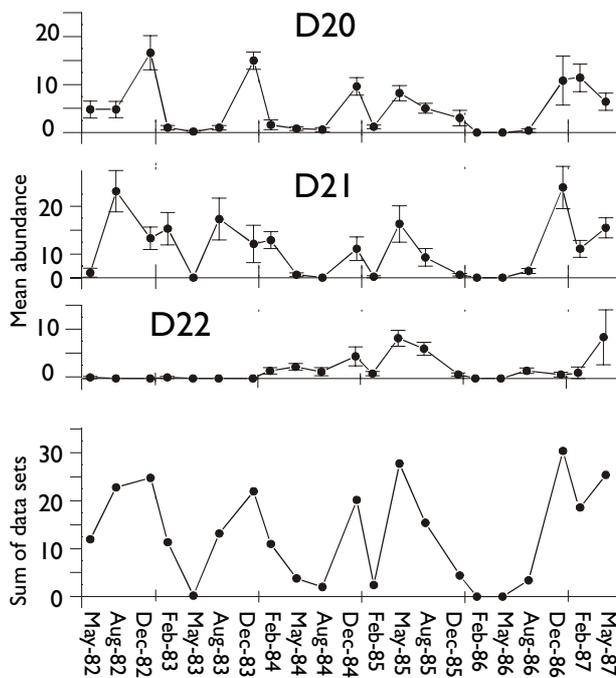


Figure 8. Temporal abundance change of *C. aequisetis*, recorded over a sequence of five years. Values are mean \pm SE for five replicate samples collected at sites D20-22 from the upper estuary. The bottom panel shows the sum of the three data sets.

The earlier rise and broader base of this second peak may reflect spreading of the *C. aequisetis* population from the more central regions of the mud flat near site D21 towards site D20. Changes to this circa-annual pattern occurred post-February 1984, with a notable increase in abundance changes at site D22. A sharp 'disturbance' in February 1985 characterised by a drop in abundance was recorded at all Transect D sites. The following peak and trough in 1986 was also observed at all sites. The circa-annual pattern of the years 1982 to 1984 were synchronous with marked salinity and temperature changes that occurred in the upper estuarine flat (Wurm & Semeniuk 2000). However, the decrease in abundance in February 1985 lacked a corresponding change in abiotic factors.

Discussion

Faunal composition

Our record of fifteen benthic polychaete species for the Leschenault Inlet estuary appears to be rather low given the mainly euhaline marine environment of this estuary, particularly when compared with polychaete diversity in estuaries of New South Wales (Hutchings & Murray 1984) or South Africa (Day 1981), where over 200 species have been recorded. However, our records are comparable with the fourteen species recorded from Wilson Inlet by Platell & Potter (1996) and agree well with the total species number for south-western Australian estuaries (Hodgkin & Clark 1987-90). The relatively low polychaete diversity may be due to the absence of seagrasses from the family Potamogetonaceae (*Posidonia*, *Zostera*, *Ruppia*). *Posidonia* meadows in the Hawkesbury River and other southern estuaries of New South Wales are the habitat most preferred by polychaetes (Hutchings & Murray 1984). Similarly, the presence of eelgrass *Zostera* affects diversity or abundance of benthic polychaete fauna both in South Australian estuarine (Conolly 1997) and marine environments (Hutchings *et al.* 1993). Platell & Potter (1996) also report a significant positive correlation of species diversity and the presence of *Ruppia megacarpa*. Whether seagrasses from Hydrocharidaceae, such as *Halophila* lack this positive effect on polychaete diversity remains to be investigated. A second factor possibly contributing to low diversity in our study area was the shallow sampling depth of 15 cm. Deeply burrowing species might have been missed or inadequately sampled in our study. For example, the deeply burrowing eunicid *Marphysa sanguinea* recorded for the Swan-Canning-System (Thurlow *et al.* 1986) was not recorded in our study.

All species listed in Table 1, with the exceptions of *Ampharetidae* sp, *Glycera cf americana*, *Lumbrineris cf latreilli* and *Nephtys gravieri*, have been previously recorded from the Leschenault Inlet estuary (*e.g.* Anon 1983) or from other estuaries from south-western Australia (Hodgkin & Clark 1987-1990). The most dominant benthic polychaete species found throughout the Leschenault Inlet estuary during this study, was *C. aequisetis*. Both *N. gravieri* and *C. cf capitata* had moderate local abundances. The only other species frequently recorded was *S. simplex*. Except for *N. gravieri*, these species also are dominant benthic components in other south-western Australian estuaries including Wilson In-

let, Wellstead Inlet, Broke Inlet and Beaufort Inlet (Hodgkin & Clark 1987-90; Platell & Potter 1996). Surprisingly, *N. gravieri* has never been listed for south-western Australian estuaries, although it was originally described from a marine site off Fremantle (Augener 1913) and could easily migrate into local estuaries.

There were a number of notable differences between the polychaete fauna of other south-western Australian estuaries and the Leschenault Inlet estuary. Polychaete families that are absent from Leschenault Inlet estuary but are found in other south-western Australian estuaries include Eunicidae (Swan-Canning System; Thurlow *et al.* 1983), Arenicolidae (Wilson Inlet; Hodgkin & Clark 1987-90), and Opheliidae, Sabellidae and Hesionidae (Wilson Inlet; Platell & Potter 1996). For example, *Boccardia chilensis* and *Heteromastus filiformis* are both very common in Wilson Inlet, but were not found in Leschenault Inlet estuary. Platell & Potter (1996) argued that the preferred environment of *B. chilensis* is deep sandy sediment containing a high amount of shell debris. Since this habitat does not occur in Leschenault Inlet estuary, the absence of this species is perhaps not surprising. No such explanation can be given for the capitellid *H. filiformis*, which occurs in shallow-water sands of Wilson Inlet. Possibly, this species is replaced by *Mediomastus* sp in the Leschenault Inlet estuary.

There were three polychaete species recorded from the Leschenault Inlet estuary that, to our knowledge, have never been found in south-western Australian estuaries before: *Lumbrineris cf latreilli*, *Glycera cf americana*, and *Ampharetidae* sp This is likely due to sparse sampling in many earlier studies. Augener (1914) gives a description of an ampharetid, *Isolda warnbroensis* that bears some similarity to our specimens. However, it is likely that the species from Leschenault Inlet estuary is yet undescribed.

Three species previously recorded for the Leschenault Inlet estuary were not retrieved in our study. Anon (1983) listed *Eunereis* sp and Deeley (Murdoch University, *pers. comm.*) recorded *Boccardiella limnicola* and *Leitoscoloplos normalus* in 1991. The latter species were recorded from oligohaline regions of the estuary not sampled in this study. Furthermore, Anon (1983) records *Ceratonereis erythraensis* as the dominant species of Leschenault Inlet estuary, constituting 9-15% of the total benthic fauna. We suggest that this species was really *C. aequisetis*. This possible mis-identification highlights the general problem of polychaete identification, particularly since there is no recent taxonomic work available on the polychaetes of south-western Australia.

Spatial patterns

Most of the fifteen polychaete species present in the Leschenault Inlet estuary may be regarded as euryhaline marine species. They are frequently recorded from marine sites and appear to be restricted by salinity within the estuary. This is reflected in the decreasing polychaete species diversity from lower to upper salinity fields. However, records of *C. aequisetis* are restricted to estuaries (Augener 1913; Hutchings & Murray 1984) so it appears to be able to withstand large changes in salinity.

Spatial distributions of particular species were linked

to salinity, depth and substrate. Salinity appeared to affect the distributions of *N. gravieri*, *C. cf capitata* and *S. simplex* which showed a preference for the mid- to lower estuarine fields that is typical for euryhaline marine species within estuaries (Kennish 1990). *C. aequisetis* had a shallow depth preference (which may have been a function of temperature, oxygen or seagrass distribution) resulting in a depth-controlled, concentric distribution pattern within the estuary. Abundance of *C. cf capitata* showed some correlation with substrate; it had highest abundances in mud to muddy sand substrates. *C. capitata* is known to tolerate the low oxygen regime of muddy sapropel in seagrass swards (Remane & Schlieper 1971) which could account for its high abundance in the basinal muds of the Leschenault Inlet estuary. In contrast, *N. gravieri* showed no clear substrate preference since it was common in substrates ranging from sandy intertidal to basinal mud.

Hutchings & Murray (1984) recorded detailed environmental parameters for species found in the Hawkesbury River and southern New South Wales estuaries. In general, their habitat remarks for particular species agree well with our distribution data, as discussed below. *C. aequisetis* was the most widespread estuarine species recorded in southern estuaries of New South Wales, which is consistent with distribution and abundance data for this species in Leschenault Inlet estuary. *C. capitata* was found in sandy muds with salinity greater than 30‰, which is corroborated by our records which restrict this species to the lower to mid-estuarine fields where salinity rarely drops to mesohaline values. Similarly, both Hutchings & Murray (1984) and this study recorded *S. simplex* most commonly from intertidal areas. Both studies found that species of

the genera *Phyllodoce*, *Neanthes*, *Glycera*, *Diopatra* and *Lumbrineris* were restricted to muddy sands in salinity regimes comparable to marine environments. Finally, Hutchings & Murray (1984) found *A. ehlersi* restricted to sand and muddy sand in salinities ranging from 5-37‰, which is consistent with our records of this species from deltaic sands to mid-estuarine central basin mud.

Habitat associations

Wurm & Semeniuk (2000) recognised nineteen habitat types within the estuary, of which fourteen were sampled in this study. Maximum abundance of the main polychaete species with respect to this habitat classification is shown in Table 2.

C. aequisetis was most common in intertidal and shallow platform habitats, but showed no substrate preference. *N. gravieri* typically occurred in muddy basinal habitats in the lower to mid-estuarine fields. *C. cf capitata* was most abundant in the muddy sand to mud habitats in mid- to lower estuary. *S. simplex* was restricted to the lower to middle estuary, where it appeared to favour intertidal sand habitats (Table 2).

Site data on polychaete diversity and abundance indicate that the habitat framework correlates fairly well with polychaete distributions, since there are only minor differences in abundance between sites representing the same habitat. For example, *C. aequisetis* shows some differences between intertidal habitats in the Collie Delta region of Transect A (sites A1, A2 vs A6, A7) which could be attributed to factors such as food source, grain size preference

Table 2. Maximal abundance of species with respect to individual site within the habitat framework of Wurm & Semeniuk (2000).

Habitat (sites)	Site	<i>Ceratonereis aequisetis</i>	<i>Nephtys gravieri</i>	<i>Capitella cf capitata</i>	<i>Scoloplos simplex</i>
deltaic intertidal sand	1	***	*	-	*
	6	*	-	-	*
	7	**	*	-	*
deltaic sand	2	***	*	*	*
lower estuarine intertidal muddy sand	5	***	*	**	*
lower estuarine platform muddy sand	4	***	*	**	-
	9	**	*	***	*
	10	***	*	***	*
	13	-	-	-	-
lower estuarine platform sand	8	**	*	***	*
lower estuarine platform sandy mud	14	***	*	*	-
lower estuarine basinal sandy mud	3	-	***	**	*
lower estuarine basinal mud	11	-	*	**	*
	12	-	*	***	-
mid-estuarine intertidal sand	19	***	***	**	*
mid-estuarine platform sandy mud	18	*	*	*	*
mid-estuarine platform muddy sand	15	***	*	***	-
	16	*	-	***	-
mid-estuarine basinal mud	17	*	**	***	-
upper estuarine intertidal sandy mud	20	***	-	-	-
upper estuarine intertidal mud	21	***	-	**	-
	22	***	*	**	-

Species are classified as: very common (***; typically >10 specimens per site); common (**; typically between 5-10 specimens per site); and uncommon (*; typically less than 5 specimens per site).

or aquatic vegetation. Differences in abundance of this species also occurred between sites C15 and C16 and between site B13 and other lower estuarine platform muddy sand habitats that may be attributed to differences in water depth. However, since polychaetes were never recorded from site B13 and only low numbers were collected from site B14, the differing numbers at these sites may have been related to disturbance caused by their vicinity to the effluent disposal pipeline. Since the habitats of the dominant polychaete species appear to be well defined, they can be used to define assemblages which characterise three different regions of the estuary.

1. Sediments in the deltaic region and the lower to mid-estuarine sections of the western platform margin characteristically had high numbers of *C. aequisetis*, with less common occurrences of other species including *C. cf capitata* and *N. gravieri*. We use this characteristic to define a *Ceratonereis-Capitella-Nephtys* assemblage found mainly in shallow-water sands with salinities ranging from 15-40‰.
2. Lower to mid-estuarine deep-water basinal mud was characterised by *C. cf capitata* and *N. gravieri*, with *C. aequisetis* being least abundant. Here, we delineate a *Capitella-Nephtys* assemblage for muds with salinities from 35-45‰.
3. The northern part of the estuary was largely dominated by *C. aequisetis*, with less common occurrences of *C. cf capitata*, defining a *Ceratonereis-Capitella* assemblage for shallow muds with salinities from 25-60‰.

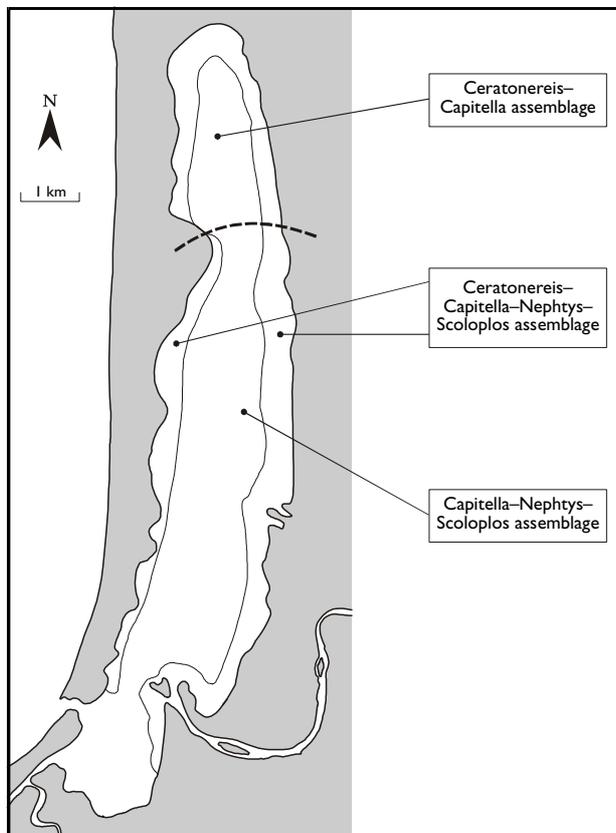


Figure 9: Polychaete assemblages for Leschenault Inlet estuary (linked to salinity, depth and substrate), based on habitat classification of Wurm & Semeniuk (2000).

We suggest that the habitat preferences of the three major polychaete species in Leschenault Inlet estuary (Figs 2, 3; Table 2) are sufficient to distinguish lower to mid-estuarine shallow- and deep-water assemblages and an upper estuarine assemblage. Figure 9 illustrates the expected spatial ranges of these assemblages, based on the habitat mapping by Wurm & Semeniuk (2000).

Temporal variation

Average seasonal abundance throughout the five-year period revealed that all three main species typically show unimodal circa-annual periodicity in population abundance (Fig. 5). Although average peak abundances were mostly recorded in February or May *i.e.* late summer to autumn, the exact timing of the peak varied from site to site. For example, *C. aequisetis* peaked in abundance in December at shallow upper estuarine sites D20 and D21, which were also the sites where highest abundances of this species occur (Fig. 5). This may indicate preferred recruitment of this species in shallow warm, muddy substrate of the upper estuary. However, since neither body size nor abundance of larvae was recorded, we can not strictly separate adult migration from juvenile recruitment in temporal patterns.

Kaleijta (1992) presented a detailed study of the population dynamics of *Ceratonereis keiskama* and *Ceratonereis erythraeensis* from a South African estuary. Maximum annual recruitment of *C. keiskama* occurred in December, whereas the recruitment timing of *C. erythraeensis* varied both between years and between sites. Our data suggest that the life cycle of *C. aequisetis* is similar to that of *C. erythraeensis*. Kaleijta (1992) also reported size-dependent stratification of young animals in superficial (<5 cm) and larger animals in deeper regions of the substrate (5-30 cm) for *C. erythraeensis*. A similar tendency in *C. aequisetis* would have caused under-sampling of adult specimens in this study due to shallow coring, particularly during winter.

Overall seasonal abundance changes for the whole population of polychaetes in Leschenault Inlet estuary appear to be highly unpredictable (Fig. 4). Given the rather stable circa-annual pattern of chemical and physical parameters such as temperature, salinity or oxygen content (Wurm & Semeniuk 2000), this result implies that the effect of seasonally varying abiotic factors can only be recognised on smaller spatial scales. In general, population dynamics at different sites were asynchronous (Fig. 5). Hence, locally determined amplitude and phase relationships of population dynamics masked any regular circa-annual periodicity in the average overall abundances of a given species. In addition, large variability in species abundance within a single year (Fig. 6) and from year to year (Fig. 7) limited detection of underlying dynamics.

Beukema *et al.* (1993) argued that variability of abundances could be interpreted as a genuine species characteristic. In their twenty-year record of benthic infauna of the Wadden Sea, coefficients of variation in year-to-year sampling were larger than 0.8 for *Nephtys* and *Nereis*, and even larger than 1.2 for *Harmothoe* and *Anaitides*. In our study, variability was similarly high and more importantly, lacked any obvious habitat dependency. Future studies on seasonal abundance will have to take into account that large numbers of samples are required to give a robust estimate of

average abundance and that long-term monitoring is required to determine whether the observed temporal pattern is due to variability or due to other factors.

Finally, coincident anti-cyclic patterns at neighbouring sites indicate that, in spite of all the variability between sites, nearby populations may be subjected to the same environmental stresses and follow rather similar long-term abundance fluctuations (Fig. 8 e.g. August 1984 to August 1986). Such coherent phase shifts in the timing of peaks and troughs in abundance recorded at different sites did not necessarily relate to abiotic factors.

At some sites there appeared to be an anti-cyclic population pattern between two species (e.g. at A3, where *C. aquisetis* was most abundant when *N. Gravieri* is least abundant; Fig 6). In spite of such examples, there was no consistent proportional or inverse relationship between abundances of different species. The impact of predators on polychaete populations was not investigated in this study, and may also be a factor contributing to temporal variation on annual and longer time scales.

During the sampling period T A Semeniuk (2000) recognised a long-term decline in abundance of small benthic Crustacea, and Semeniuk & Wurm (2000) noted a similar long-term decline in numbers of some mollusc species. The data presented for the polychaetes in this paper supports this overall trend. However, the marked drop in crustacean numbers over the period 1984-1985 was not reflected in the polychaete abundance. Rather, at some sites, polychaetes were relatively more abundant during this period (see Fig. 8). Hence, benthic faunal groups show different sensitivity to environmental change, and would appear to have different potential as environmental indicators.

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