

INFLUENCE OF WATER DEPTH, SEASON, HABITAT AND ESTUARY LOCATION ON THE MACROBENTHIC FAUNA OF A SEASONALLY CLOSED ESTUARY

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The macrobenthic invertebrates in the shallow (<0.5 m), medium-depth (0.75–1.0 m) and deep (2.0–2.5 m) waters of the lower and upper regions of the large basin of the seasonally closed Wilson Inlet were sampled, using corers, in each season between the winters of 1989 and 1990. The fauna was dominated by capitellid, spionid and nereid polychaetes and mytilid, venerid and tellinid molluscs. Almost 75% of the total numbers were contributed by the polychaetes *Heteromastus filiformis* (Claparède) (30.2%), *Capitella capitata* (Fabricius) (17.4%), *Prionospio cirrifera* (Wirén) (7.9%) and *Boccardia chilensis* (Blake & Woodwick) (5.4%), and the gastropod *Hydrococcus brazieri* (Tenison Woods) (12.4%). The numbers of species recorded in Wilson Inlet (41) were relatively very low for an estuary. This presumably reflects (i) the low salinities, which would restrict colonization by stenohaline marine species, (ii) the prevention of recruitment from the sea by the closure of the estuary mouth during the summer, at which time many macrobenthic species are producing pelagic larvae, (iii) the very limited tidal movements, and thus mechanisms for transporting larvae from the sea, when the estuary mouth is open, and (iv) the lack of a pronounced salinity gradient and the small variation in sediment composition along the estuary. Characteristics (ii–iv), together with the dispersal of pelagic larvae within the basin by wind mixing, would also account for the fact that faunal composition was influenced less by the region within the basin than by water depth. The densities of species, such as *Ceratonereis aquisetis* (Augener), *Capitella capitata* and *H. brazieri*, were greater in the shallow and medium depths than in deeper water, while the reverse pertained with *P. cirrifera*. Since densities of the first three species are correlated with the biomass of *Ruppia megacarpa* Mason, the greater amounts of this aquatic macrophyte in the shallow and medium-depth waters may thereby provide more food and/or protection from predators in those waters than would be the case in deep water. In contrast, *P. cirrifera*, which is a detritivore, would benefit from the greater proportion of particulate organic material in the deep waters. The greater habitat complexity in the shallow and medium-depths, that is provided by the greater amounts of *R. megacarpa* and shell debris in those waters, was associated with a greater species richness, diversity, density and biomass of benthic invertebrates. The composition of the fauna underwent cyclical changes, which were related, in part, to the patterns of recruitment of certain major taxa following spawning.

INTRODUCTION

The macrobenthic communities of estuaries, which comprise mainly polychaetes, gastropod and bivalve molluscs and amphipod crustaceans, vary in composition both

spatially and seasonally (e.g. Holland et al., 1987; Kalejta & Hockey, 1991). Spatial differences in the composition of these communities along the length of the estuary have often been related to changes that occur in the salinity and type of sediment along those systems (de Decker & Bally, 1985; Castel et al., 1989; Junoy & Viéitez, 1990). The composition of the communities may also be related to characteristics associated with water depth (Maurer & Vargas, 1984; Holland et al., 1987). For example, some species are more abundant in shallower waters, which contain greater amounts of aquatic macrophytes and shell debris and thereby increase habitat complexity (e.g. Orth et al., 1984; Castel et al., 1989), whereas others are more numerous in deeper waters where the substratum is less subject to wave action and thus tends to contain finer particles (e.g. Read, 1984). The greater complexity of habitat provided by such features as the presence of vegetation, shell debris and heterogeneous substratum is also often accompanied by increased species richness and diversity (Dauer et al., 1982; Castel et al., 1989; Junoy & Viéitez, 1990). The composition of the estuarine macrobenthic communities also undergoes temporal changes, reflecting seasonality in the reproduction of certain species and therefore the timing of the recruitment of those species (e.g. Rainer, 1981; Kalejta & Hockey, 1991; Sardá et al., 1995).

The estuaries of south-western Australia typically contain a large basin that opens to the ocean by a narrow entrance channel (Hodgkin & Lenanton, 1981). The formation of sand bars at the mouths of many of the estuaries on the southern coast of south-western Australia leads to these systems becoming closed, either seasonally or for longer periods (Hodgkin & Lenanton, 1981). In Wilson Inlet, the resultant absence of tidal exchange when the estuary mouth is closed, and the limited tidal influence even when the mouth is open, combines with the presence of shallow water and a high exposure to wind action to produce a salinity regime that is atypical for an estuary (Hodgkin & Clark, 1988b). For example, the salinity for much of the year is relatively uniform throughout most of the 14 km length of the basin of this system and does not exceed 30‰ (Potter et al., 1993). The combination of the, at best, limited tidal exchange with the sea and the large input of nutrients from surrounding agricultural land has resulted in Wilson Inlet becoming moderately eutrophic and, as a consequence, the aquatic macrophyte *Ruppia megacarpa* has flourished (Hodgkin & Hamilton, 1993).

Since estuarine faunas are essentially marine or derived from marine populations (Kennish, 1990), the closure of the mouth of Wilson Inlet during the warmer and drier period of most years means that there is, at those times, no opportunity for the recruitment of the larvae of those many macrobenthic species that spawn during that period and have a pelagic larval phase (e.g. Kalejta & Hockey, 1991; Sardá et al., 1995). Furthermore, the low salinities throughout the basin for much of the year will discourage colonization by more stenohaline marine species at those times when the estuary mouth is open. The present study was therefore undertaken firstly to test the hypothesis that, for the above reasons, the number of macrobenthic species in Wilson Inlet will be relatively low. The study has also tested the hypothesis that, because opportunities for the recruitment of organisms into the lower basin from the sea are limited and there is only a weak salinity gradient along the basin, the species richness, diversity and

faunal composition of the benthic invertebrate assemblage of Wilson Inlet will be less likely to be influenced by location in the estuary than by differences associated with water depth and the seasonal patterns of recruitment of those organisms that breed within the estuary. The hypothesis was also tested that species which feed on plant material would be most abundant in areas where *R. megacarpa* is present, whereas detritivores would be most numerous in more stable areas where there is an abundance of particulate organic material. The question of whether areas with extensive shell debris are colonized differentially by certain species, and whether species richness and diversity were related to habitat complexity, were also investigated.

MATERIALS AND METHODS

Study area

Wilson Inlet comprises a large basin (48 km²), which is fed by the Hay and Denmark rivers and smaller tributaries, and opens to the sea by a short entrance channel (Figure 1). The mouth of the entrance channel is typically closed for three to seven months by a sand bar, which is breached artificially when the water in the Denmark River reaches a specified level (Hodgkin & Clark, 1988b). Since astronomical tides are small in southwestern Australia (Hodgkin & di Lollo, 1956) and the entrance channel is short and shallow, the tides cause little water movement within the basin when the estuary mouth is open (Hodgkin & Clark, 1988b). Although the water in a few central parts of the basin can reach 4–5 m in depth, most of the basin is <2.5 m deep. Since rainfall in this region is highly seasonal, with cool, wet winters and warm, dry summers, the volume of fresh water discharged into the basin undergoes marked seasonal changes.

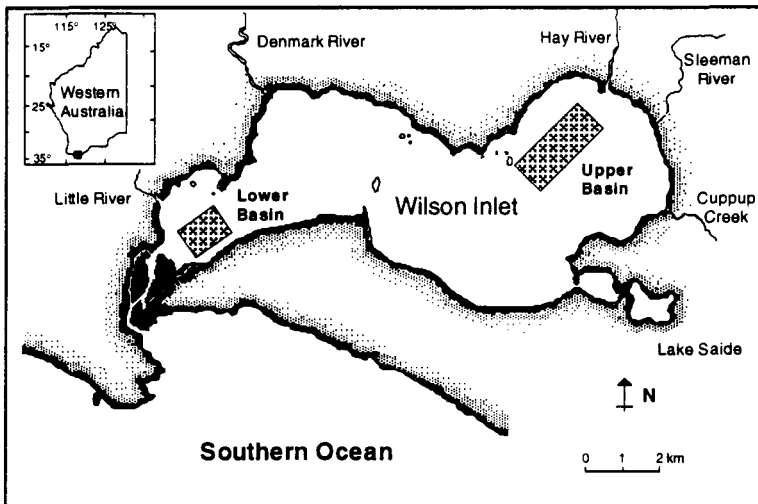


Figure 1. Map showing the regions (shaded rectangles) in the lower and upper basin of Wilson Inlet in which macrobenthic invertebrates were sampled.

Macrobenthic sampling

The macrobenthic communities in shallow (0.3–0.5 m), medium (0.75–1.0 m) and deep waters (2–2.5 m) in both the lower and upper region of the basin of Wilson Inlet (Figure 1), were sampled in August and October of 1989 and in January, April and June of 1990, thereby providing data for five consecutive seasons between the winters of 1989 and 1990. The three water depths, i.e. sites, which were sampled in both regions, were aligned in a transect from shallow to deep at right angles to the estuary shoreline. These sites were approximately 100 m apart in the lower basin but, due to the shallower incline of the basin floor in the upper basin, approximately 1000 m apart in the latter region (Figure 1). The depths sampled in the lower and upper basin were considered representative of the shallows, medium-depth and deeper waters in those regions of the estuary. The sand bar was breached in July 1989 and then closed in March 1990, before being breached again in July 1990.

A pole-mounted corer of 11-cm diameter (cross sectional area, 96 cm²) was used to sample sites in shallow and medium depth waters, whereas SCUBA equipment and a hand-held corer of 9-cm diameter (63 cm²) were employed to sample deeper water. The use of slightly differently-sized corers to sample different depths was based on preliminary experiments aimed at elucidating the best way to sample the shallow and medium depths, where thick mats of *Ruppia megacarpa* rhizomes were present, and to sample deep water, in which SCUBA diving had to be employed. All core samples penetrated at least 15 cm, and thus below the depth in which the benthic fauna is found in southwestern Australian estuaries (Rose, 1994). On the first sampling occasion, i.e. the winter of 1989, the effectiveness and economy of effort of the sampling procedure were assessed. Thus ten cores were taken from each sampling depth and sieved through firstly 1.0-mm mesh and then 0.5-mm mesh. The organisms retained by the two sieves were sorted, counted and weighed. The 1.0-mm mesh contained all the species, and on average nearly 75% of the individuals and 98% of the biomass that were retained using both 0.5- and 1.0-mm meshes. Since the construction of cumulative species/area curves also indicated that six cores consistently provided a representative sample, all later samples at each depth used only the 1.0 mm mesh and employed six replicate cores. The organisms obtained in the cores were converted to a density, i.e. numbers per 100 cm² in the sediment.

All macrobenthic core samples were preserved in 10% buffered formalin with estuary water. During the sieving of each macrobenthic sample, any pieces of *R. megacarpa* and any shell fragments >1 cm were removed and wet-weighed to 10 mg. Each sample was sorted under a dissecting microscope and the number of individuals and biomass (weighed to 0.1 mg after blotting) of each species recorded. This enabled the total density and biomass in each sample to be estimated.

Bottom water temperature, salinity and dissolved oxygen, and the Secchi disc depth were recorded at each depth on each sampling occasion.

Sediment analysis

Three sediment cores were taken from each sampling depth in both the lower and upper basin in the late winter of 1989 and in the summer and early winter of 1990. Cores

were frozen and cut in half vertically to provide material for separate analyses. Macrofauna and macroflora were removed from the two halves of each core. The sediments were then oven-dried at 80°C for 12 h to a constant weight, prior to analysing grain size and particulate organic material (POM) content.

Each dried sample was weighed to 0.1 mg. After wet-sieving through a graded series of standard sieves (2000, 1000, 600, 180 μm), the fractions retained by each sieve were dried and reweighed (Buchanan, 1984). The fraction that was not retained on the 180 μm mesh was calculated by subtraction. Following a slight modification of the Wentworth grade classification (see Buchanan, 1984), the five component fractions are termed granules (>2000 μm), very coarse sand (1000–1999 μm), coarse sand (600–999 μm), medium and fine sand (180–599 μm) and very fine sand, silt and clay (<180 μm). The second half of each dried sample was weighed to the nearest 0.1 mg, ashed at 550°C for 6 h, and subsequently reweighed to obtain the ash-free dry weight (AFDW). Particulate organic material, which represents the difference between the AFDW and the original weight of the dried sample, is expressed as a percentage of that original weight.

Data analysis

Species richness (i.e. number of species) and the Shannon-Wiener diversity index (H') were calculated for each sample. The bottom salinity and temperature, biomass of both shell-debris and *R. megacarpa*, the species richness and diversity, and the density and biomass of the total benthic fauna and its most abundant benthic species were tested for heteroscedasticity using Cochran's C test (Underwood, 1981). Where there were significant departures from homogeneity, the data were log-transformed ($\log_{10}(n+1)$), which generally resulted in homoscedasticity. Three-way fixed-factor analyses of variance (ANOVA) were used to detect whether these variables differed among regions (lower and upper basin), water depths (shallow, medium and deep) and seasons (winter 1989, spring 1989, summer 1990, autumn 1990, winter 1990). Those factors and their interactions, which were shown to be significant by ANOVA, were further analysed using an a posteriori Scheffé test to determine which values were significantly different at $P < 0.05$ (Day & Quinn, 1989). Whenever significant interactions and main effects were found in the same ANOVA, the means for the significant main effect(s) were explored within each level of the appropriate alternative main factor(s) (see Underwood, 1981). Pearson correlation coefficients were used to examine the relationship between the macrobenthic faunal variables and the bottom temperature, bottom salinity, wet biomass of shell debris and wet biomass of *R. megacarpa*.

The densities of individuals of each species were classified using flexible unweighted, pair-group, arithmetic averaging (UPGMA, $\beta=0$) (Belbin, 1988), and ordinated using multi-dimensional scaling (MDS) (Clarke & Warwick, 1994). Prior to analysis, the density of each species was log-transformed ($\log_{10}(n+1)$). The Bray-Curtis measure was used to produce the association matrix for these procedures (Clarke & Green, 1988). Stress level for the two-dimensional solution for the ordination was 0.15. The groupings produced were tested for significant differences using analysis of similarities (ANOSIM), and the similarity percentages (SIMPER) program was used to identify those species

which contributed most to the differences between the various groups (Clarke & Warwick, 1994).

RESULTS

Environmental conditions

Mean salinity in the lower basin declined from 21.6‰ in winter 1989 to 18.3‰ in spring 1989, before rising to 23.5‰ in summer 1990 and then falling to 15.6‰ in winter 1990 (Figure 2). Although the mean salinity followed the same trend in the upper basin, it was appreciably lower in this region in the winter of 1989. Mean temperatures in both regions rose from ~14–15°C in winter 1989 to ~22°C in summer and autumn 1990, and then declined to ~12°C in winter 1990 (Figure 2). The bottom dissolved oxygen concentration was always at saturation and the Secchi disc could always be seen, even at the deep sites.

The very fine sand, silt and clay fraction and the medium and fine sand fraction in the winter of 1989 and the summer and winter of 1990 collectively contributed over 80% to the sediments at all depths, except for those in the deep water of the upper basin in the winter of 1990 (Figure 3). In the last case, the coarse sand, very coarse sand and granules together contributed 45%. The very fine sand, silt and clay fraction was greater in deep water than in the shallow and medium depths of the lower basin in the winter of 1989 and the summer and winter of 1990, whereas the reverse trend was observed in the deep water of the upper basin in the winter of 1990 (Figure 3).

The amount of particulate organic material (POM) was greatest in the deep waters in both the lower and upper basins. However, POM was also 3–8 times greater in deep water in the lower basin than in deep water in the upper basin in each season, presumably reflecting the fact that the sampling region in the lower estuary is more protected. The amount of POM peaked in the summer of 1990, with mean values in the deep water being 18.2% in the lower basin and 1.9% in the upper basin.

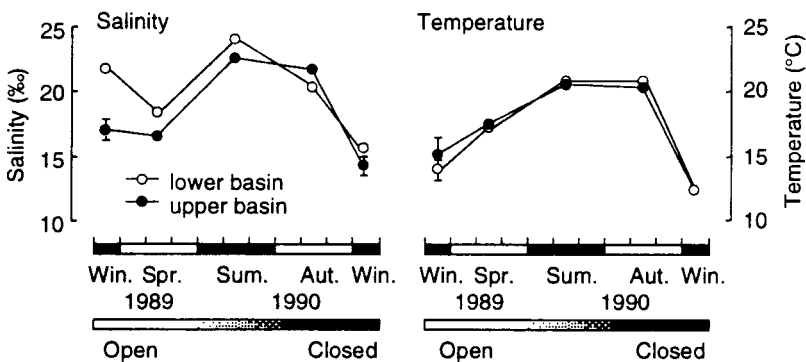


Figure 2. Mean bottom salinities and water temperature ± 1 SE. in the lower and upper basin of Wilson Inlet in the five seasons between the winters of 1989 and 1990. On the abscissa, the black rectangles represent winter and summer months and the open rectangles the spring and autumn months. The lower abscissa shows state of closure of the estuary mouth. Open, estuary open to the sea; partially stippled, estuary open but water flow at a minimum; stippled, estuary closed to the sea.

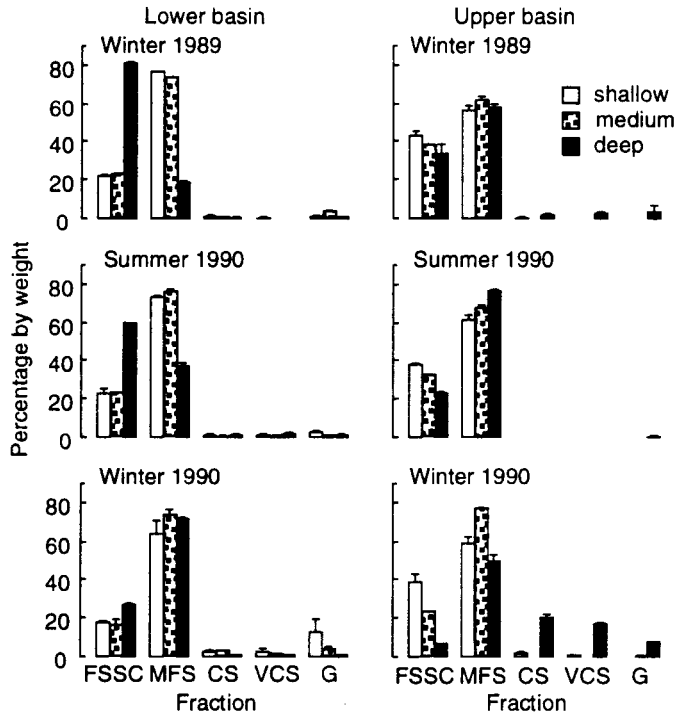


Figure 3. Mean percentage contribution (+1 SE) of the different sediment fractions at different depths in the lower and upper basin of Wilson Inlet in the winter of 1989 and in the summer and winter of 1990. FSSC, very fine sand, silt and clay; MFS, medium and fine sand; CS, coarse sand; VCS, very coarse sand; G, Granules.

Table 1. Mean squares and significance levels for three-way ANOVA of the biomass of shell debris and *Ruppia megacarpa*, recorded in regions (lower and upper basin), depths (shallow, medium and deep water) and seasons in Wilson Inlet between the winters of 1989 and 1990.

Factors	df	Shell debris	<i>R. megacarpa</i>
Region (R)	1	85.70***	2.84***
Depth (D)	2	2.06***	8.01***
Season (S)	4	0.52***	0.80***
R x D	2	4.04***	0.66***
R x S	4	0.38**	0.65***
D x S	8	0.37***	0.46***
R x D x S	8	0.38**	0.30***
Within cells	146	0.10	0.08

df, degrees of freedom; ** $P < 0.01$; *** $P < 0.001$.

Analysis of variance showed that the biomass of shell debris varied significantly with region, depth and season, with region having by far the highest mean square (Table 1). There were also significant interactions between the above factors, these being strongest between region and depth (Table 1). The mean biomass of shell debris in each season was far greater in the lower basin (max, 20.56 g 100 cm⁻²) than upper basin (max, 0.97 g

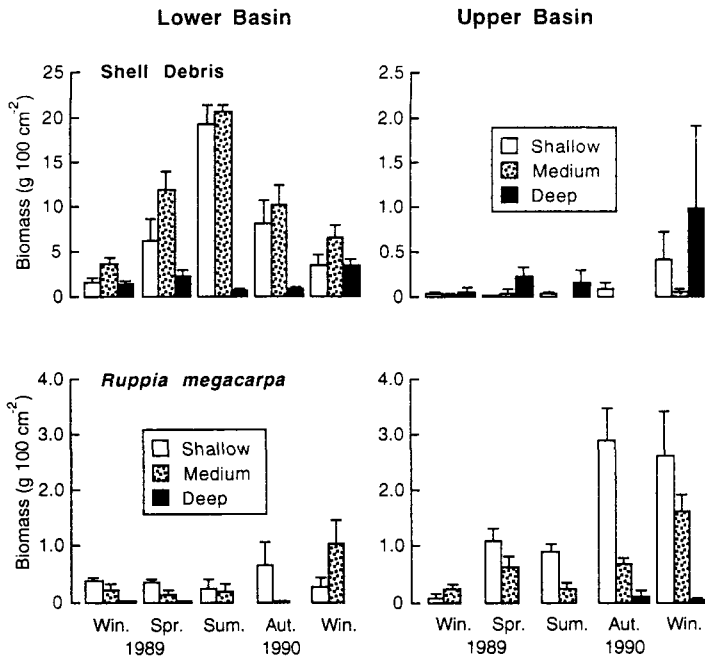


Figure 4. Mean biomass of shell debris and *Ruppia megacarpa* (+1 SE) at different depths in the lower and upper basin of Wilson Inlet between the winters of 1989 and 1990. Note that the scale on the ordinate for shell debris is an order of magnitude greater in the lower basin than in the upper basin.

100 cm⁻²) (Figure 4). In the lower basin the biomass of shell debris was greater in shallow and medium depths than in deep waters in all seasons, and was also significantly greater in medium depths than in deep water in the spring of 1989 and in the summer and autumn of 1990 (Figure 4).

The biomass of *Ruppia megacarpa* differed significantly between depth, region and season and there were significant interactions between each of these factors (Table 1). The mean squares were greater for depth than region, which in turn were far greater than for season and for each of the interactions (Table 1). The weight of *R. megacarpa* in each region was greatest at the shallow depths in each of the five seasons, except in the lower basin in the winter of 1990 and in the upper basin in the winter of 1989, when in both cases it was greatest in medium depths (Figure 4). *Ruppia megacarpa* was either absent or in very low abundance in the deep waters of both estuarine regions in all seasons. The biomass of *R. megacarpa* was significantly greater in the upper than in the lower basin in all but the first of the five seasons. It reached a seasonal maximum of 2.91 g 100 cm⁻² in the upper basin in autumn 1990 (Figure 4).

Species composition

A total of 19,554 individuals and 41 species were recorded from the three depths (sites) in each of the lower and upper estuarine regions of Wilson Inlet (Table 2). These

Table 2. List of all macrobenthic invertebrate taxa collected using corers from Wilson Inlet between the winters of 1989 and 1990.

Polychaetes	Gastropods	Crustaceans
<i>Anaitides longipes</i>	<i>Hydrobia buccinoides</i>	<i>Haplostylus</i> sp.
<i>Podarke</i> sp.	<i>Tatea preissii</i>	<i>Sphaeroma</i> sp.
<i>Ceratonereis aequisetis</i>	<i>Salinator fragilis</i>	<i>Melita</i> sp.
<i>Ceratonereis amphidonta</i>	<i>Hydrococcus brazieri</i>	<i>Corophium minor</i>
<i>Neanthes vaalii</i>	<i>Nassarius burchardi</i>	<i>Paracorophium excavator</i>
<i>Nephtys</i> sp.	<i>Philine</i> sp.	<i>Macrobrachium intermedium</i>
<i>Scoloplos simplex</i>	<i>Liloa brevis</i>	<i>Palaemonetes australis</i>
<i>Prionospio cirrifera</i>		
<i>Boccardia chilensis</i>	Bivalves	Other Arthropods
<i>Capitella capitata</i>	<i>Mytilus edulis planulatus</i>	<i>Pontomyia</i> sp.
<i>Heteromastus filiformis</i>	<i>Xenostrobus pulex</i>	
<i>Branchiomaldane</i> sp.	<i>Xenostrobus inconstans</i>	
? <i>Oriopsis</i> sp.	<i>Arthritica semen</i>	
<i>Armandia</i> sp.	<i>Spisula trigonella</i>	
	<i>Tellina deltoidalis</i>	
	<i>Donax columbella</i>	
Nemertines	<i>Sanguinolaria biradiata</i>	
unidentified sp.	<i>Dosinia sculpta</i>	
	<i>Irus crenata</i>	
	<i>Katelysia scalarina</i>	

comprised 14 species of polychaete and 18 species of mollusc (gastropods and bivalves collectively), which contributed 76 and 18% to the total numbers of individuals, respectively, while the remaining nine species, consisting of seven species of crustacean and one species each of nemertean and chironomid, collectively contributed only 6% to the total abundance. Five species accounted for almost 75% of the total numbers, namely *Heteromastus filiformis* (30.2%), *Capitella capitata* (17.4%), *Hydrococcus brazieri* (12.4%), *Prionospio cirrifera* (7.9%) and *Boccardia chilensis* (5.4%). Six species accounted for ~75% of the total biomass, namely *Spisula trigonella* (Lamarck) (29.0%), *Tellina deltoidalis* (Lamarck) (14.4%), *Katelysia scalarina* (Lamarck) (11.9%), *Nassarius burchardi* (Philippi) (10.7%), *Heteromastus filiformis* (4.7%) and *Ceratonereis aequisetis* (4.7%). Each of the 41 species was found on at least one occasion in both the upper and lower basin, except for *Podarke* sp., *Armandia* sp., *Donax columbella* Lamarck and *Dosinia sculpta* (Hanley) which were found only in the lower basin.

Community variables

Species richness and the density and biomass of all organisms each differed significantly between region, depth and season and, in each case, there were significant interactions between at least two of these variables (Table 3). Species diversity differed significantly between depth and season, but not region, and interactions occurred between region and depth and between depth and season (Table 3).

The mean squares for species richness were greatest for depth, followed by region, and there was a strong interaction between these terms (Table 3). Season and the region-by-season interaction were also highly significant. Species richness was almost invari-

Table 3. Mean squares and significance levels for three-way ANOVA of species richness, diversity (H'), and the density (no. 100 cm^{-2}) and biomass (g 100 cm^{-2}) of all macrobenthic organisms recorded in regions (lower and upper basin), depths (shallow, medium and deep water) and seasons in Wilson Inlet between the winters of 1989 and 1990.

Factors	df	Richness	Diversity	Density	Biomass
Region (R)	1	100.15***	0.09	0.23*	2.25***
Depth (D)	2	316.14***	6.93***	0.52***	4.85***
Season (S)	4	35.29***	0.97***	1.95***	0.61**
R x D	2	72.38***	2.62***	2.26***	1.86***
R x S	4	30.49***	0.19	0.43***	1.07***
D x S	8	12.14	0.98***	0.13***	0.76***
R x D x S	8	11.10	0.12	0.38**	1.03***
Within cells	146	5.14	0.12	0.03	0.15

df, degrees of freedom; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

ably greater in the shallow and medium depths than in the deep waters in both regions of the estuary, and in several seasons these differences were significant (Figure 5). In the upper basin, species richness in the shallow water was also significantly higher than in the medium depth in the winter of 1989. Species richness underwent marked seasonal changes in the deep water of the lower basin, with values declining from ~10 in the winter and spring of 1989 to 3.8 in the autumn of 1990, before subsequently increasing markedly to 9.8 in the winter of 1990 (Figure 5). The lowest seasonal species richness in the medium depth was also recorded in autumn. At both the shallow and medium depths in the upper basin, richness fell to its lowest seasonal level in the summer of 1990, whereas in deep water it reached its maximum in that season (Figure 5). Species richness was positively correlated with the biomass of both shell debris ($P < 0.001$) and *R. megacarpa* ($P < 0.01$) (Table 4).

Table 4. Pearson correlation coefficients between species richness, diversity, density and biomass of all macrobenthic organisms, and the density of the eight most abundant macrobenthic species in Wilson Inlet, and the values for bottom salinity and temperature and biomass of shell debris and *Ruppia megacarpa*, using data collected seasonally between the winters of 1989 and 1990.

	Salinity	Temperature	Shell debris	<i>R. megacarpa</i>
Species richness	-0.066	-0.081	0.403***	0.221**
Species diversity	0.093	0.084	0.182*	0.253**
Density	-0.474***	-0.465***	0.152*	0.232**
Biomass	0.116	-0.004	0.361***	-0.036
<i>Ceratonereis aquisetis</i>	-0.471***	-0.299***	-0.083	0.348***
<i>Capitella capitata</i>	-0.435***	-0.353***	0.107	0.264***
<i>Hydrococcus brazieri</i>	-0.282***	-0.388***	0.020	0.277***
<i>Arthritica semen</i>	-0.414***	-0.201**	-0.132	0.330***
<i>Prionospio cirrifera</i>	-0.176*	-0.274***	-0.097	-0.219**
<i>Scoloplos simplex</i>	-0.108	0.019	0.016	0.166*
<i>Boccardia chilensis</i>	0.064	0.045	0.526***	0.035
<i>Heteromastus filiformis</i>	-0.076	-0.106	0.118	-0.082

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

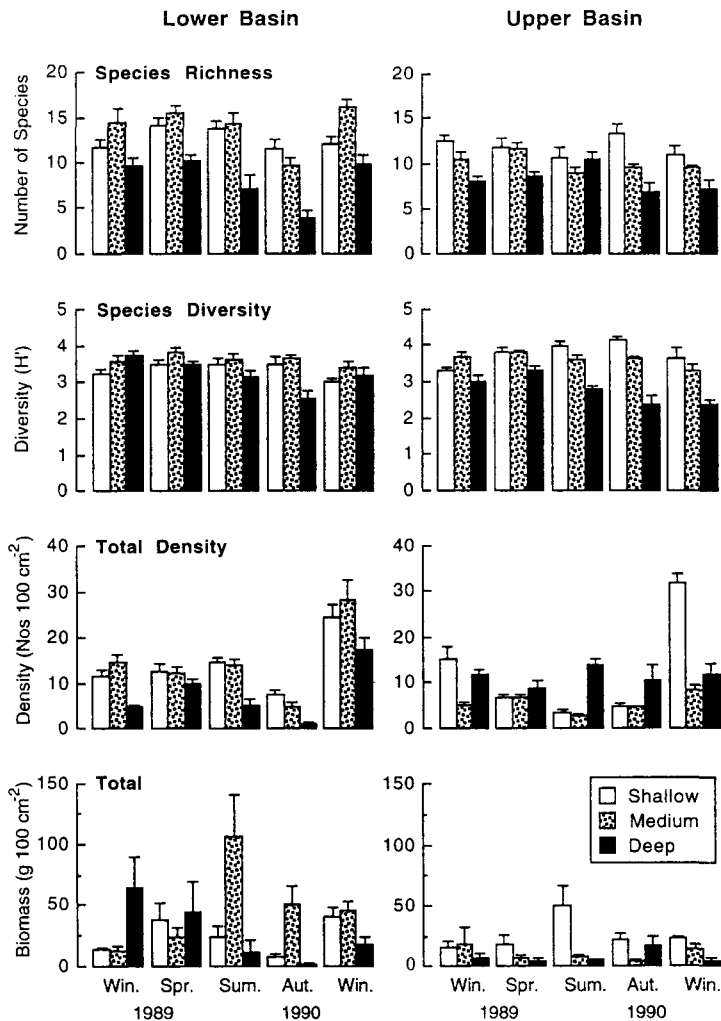


Figure 5. Mean values (+1 SE) for species richness, diversity (H'), density and biomass of the macroinvertebrate fauna at different depths in the lower and upper basin of Wilson Inlet between the winters of 1989 and 1990.

The mean squares for species diversity were by far the highest for depth, followed by the region-by-depth and depth-by-season interactions, and season (Table 3). While diversity in the upper basin was almost always significantly greater in the shallow and medium depths than in the deep water in all seasons, this was the case only in autumn in the lower basin (Figure 5). Furthermore, in the winter of 1989, the diversity was significantly greater in the deep water than in both the shallow and medium depths of the lower basin. In the lower basin, diversity in the deep water declined from 3.7 in the winter of 1989 to 2.5 in the autumn of 1990, and then increased sharply to 3.2 in the winter of 1990 (Figure 5). Although a similar but less pronounced trend occurred in the upper basin, no such comparable trends were seen in the shallow and medium depths

of either the lower or upper basin (Figure 5). Species diversity was positively correlated with the biomass of both shell debris ($P<0.05$) and *R. megacarpa* ($P<0.01$) (Table 4).

The mean squares for the density of all organisms were greatest for the region-by-depth interaction and season, followed by depth and the region-by-season interaction (Table 3). In the lower basin the mean density was lower in the deep water than in either the medium or shallow depths in all seasons, and these differences were frequently significant (Figure 5). However, in the upper basin the mean density in the deep water was greater than in the medium depth in all seasons. Although the mean density was also greater in the deep water than in the shallows in three of the five seasons, the highest seasonal means in any depth in the upper estuary were recorded in the shallows of those other two seasons, i.e. in the winters of 1989 and 1990. Densities increased markedly in the early winter of 1990 at all three depths in the lower basin, and in the shallow and medium depths of the upper basin (Figure 5). Density was negatively correlated with salinity and temperature ($P<0.001$), and positively correlated with the biomass of both shell debris ($P<0.05$) and *R. megacarpa* ($P<0.01$) (Table 4).

The mean squares for the biomass of all organisms were greatest for depth, followed by region and the region-by-depth interaction (Table 3). The mean biomass in the upper basin was low in all seasons in the medium and deep waters, i.e. <23 g 100 cm², and the same was true for the shallows in all seasons except the summer of 1990 (Figure 5). In contrast, the mean biomass in the shallow, medium-depth and deep waters of the lower basin exceeded 37 g 100 cm² in either two or three seasons. The maximum seasonal values for biomass of 106.3 g 100 cm² and 64.8 g 100 cm² were recorded in the medium-depth and deep waters of the lower basin, respectively (Figure 5). Total biomass was significantly correlated with the biomass of shell debris ($P<0.001$) (Table 4).

Density trends of the most abundant species

Analysis of variance showed that at least two of the three factors (region, depth and season) always had a highly significant ($P<0.001$) effect on the density of the eight most abundant macrobenthic species (Table 5), which collectively contributed nearly 85% to the numbers of all organisms. There were also very highly significant interactions between one or more of these factors. The mean squares for depth were the greatest of the main effects in the case of five species (*Ceratonereis aequisetis*, *Capitella capitata*, *Hydrococcus brazieri*, *Arthritica semen* (Menke) and *Prionospio cirrifera*) and were only slightly lower than the maximum for a sixth species (*Scoloplos simplex* (Hutchings)). The mean squares were greatest for region in the case of this last species and *Boccardia chilensis*. The region-by-depth interaction was most important for *Heteromastus filiformis* and was of similar importance to depth in the case of *A. semen*. The seasonal effect was significant for seven of the eight species, and particularly for *Ceratibereus aequisetis*, *Capitella capitata*, *Hydrococcus brazieri* and *A. semen* (Table 5).

Ceratonereis aequisetis, *Capitella capitata* and *H. brazieri* were either absent or in very low densities in the deep waters of both regions of the estuary (Figure 6). The greatest densities of both *Ceratonereis aequisetis* and *Capitella capitata* were recorded in the shallow waters in the winters of 1989 and 1990 (Figure 6). The density of *H. brazieri* in

Table 5. Mean squares and significance levels for three-way ANOVA of the densities of the 8 most abundant macrobenthic species recorded in regions (lower and upper basin), depths (shallow, medium and deep water) and seasons in Wilson Inlet between the winters of 1989 and 1990.

Factors	df	<i>Ceratonereis aequisetis</i>	<i>Capitella capitata</i>	<i>Hydrocooccus brazieri</i>	<i>Arthritica semen</i>	<i>Prionospio cirrifera</i>	<i>Scoloplos simplex</i>	<i>Boccardia chilensis</i>	<i>Heteromastus filiformis</i>
Region (R)	1	0.45**	0.82**	1.15***	1.22***	0.59**	2.01***	7.20***	1.42***
Depth (D)	2	5.12***	12.65***	14.39***	2.24***	14.43***	1.61***	1.32***	0.19
Season (S)	4	2.30***	2.51***	3.71***	1.75***	0.65***	0.14	1.15***	1.04***
R x D	2	0.49***	2.08***	0.24	2.29***	1.15***	0.36**	1.39***	7.46***
R x S	4	0.41***	0.96***	1.06***	0.59***	0.84***	0.39***	0.86***	0.67***
D x S	8	0.34***	0.78***	1.39***	0.78***	0.36***	0.16**	0.68***	0.46***
R x D x S	8	0.23***	0.36***	0.70***	0.74***	0.23***	0.10	0.56***	0.19
Within cells	146	0.06	0.09	0.06	0.02	0.07	0.06	0.08	0.08

df, degrees of freedom; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

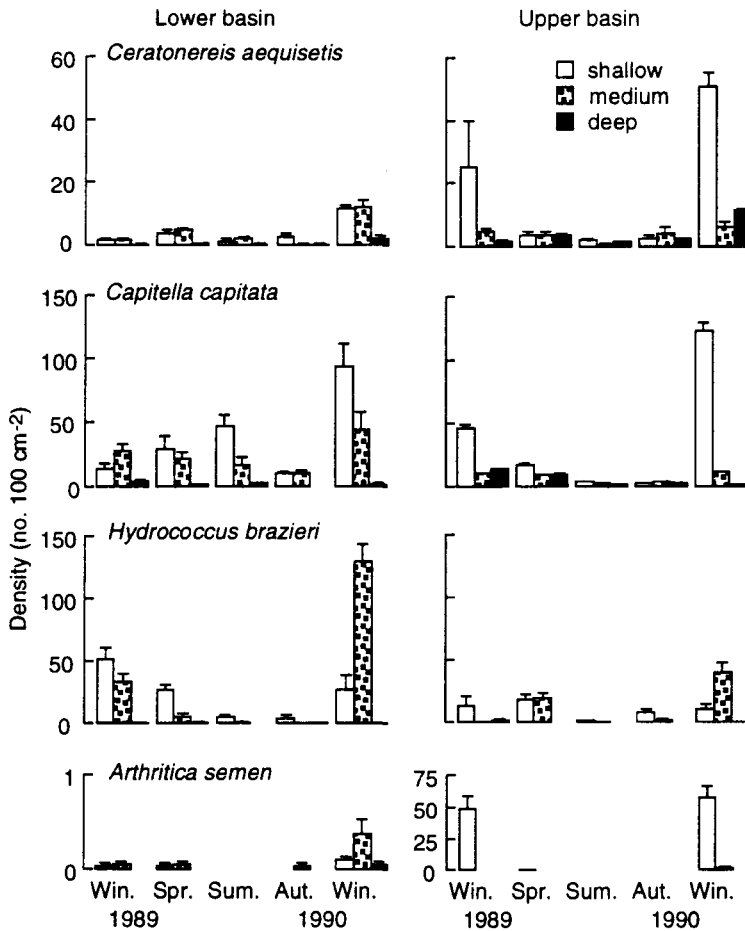


Figure 6. Mean density (+1 SE) of *Ceratonereis aequisetis*, *Capitella capitata*, *Hydrocooccus brazieri* and *Arthritica semen* at different depths in the lower and upper basin of Wilson Inlet between the winters of 1989 and 1990.

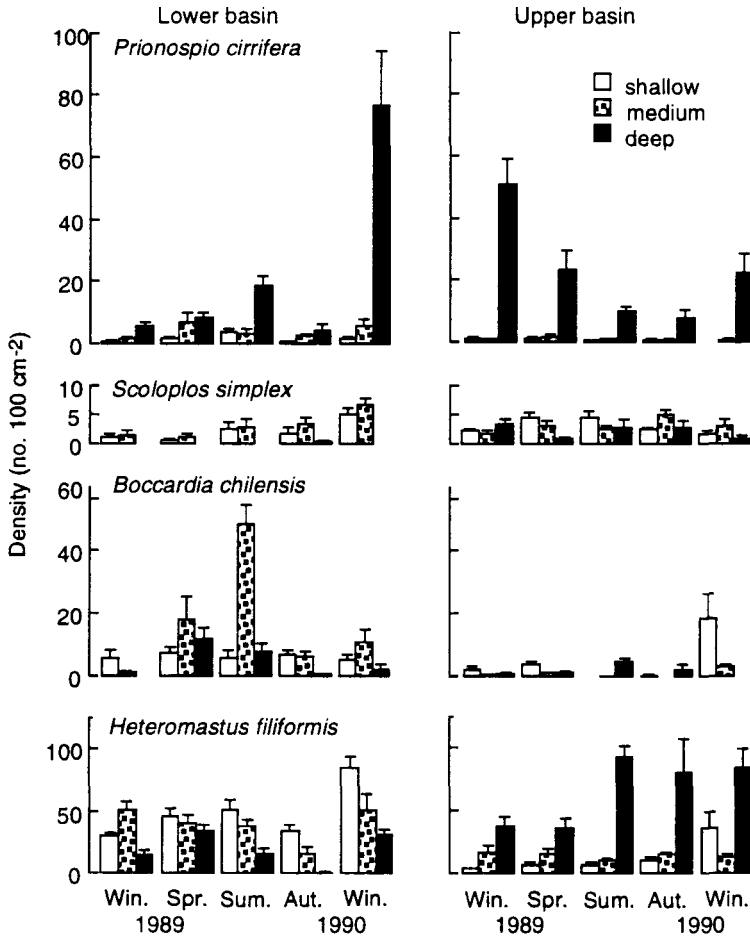


Figure 7. Mean density (+1 SE) of *Prionospio cirrifera*, *Scoloplos simplex*, *Boccardia chilensis* and *Heteromastus filiformis* at different depths in the lower and upper basin of Wilson Inlet between the winters of 1989 and 1990.

the lower basin declined between the winter of 1989 and the autumn of 1990, before rising sharply in the winter of 1990, whereas no such trends were seen in the upper basin (Figure 6). The density of *P. cirrifera* was greatest in the deep waters in both regions of the estuary in all seasons (Figure 7).

The density of *B. chilensis* was greater in the lower than in the upper basin, while the reverse was true for *S. simplex* in most seasons (Figure 7). The region-by-depth differences for *B. chilensis* can be related to the fact that the highest densities in the lower basin were recorded in the medium depth, while those in the upper basin were found in the shallows. Furthermore, and in contrast to the situation in the upper basin, *S. simplex* was absent in deep water in the lower basin in all but one season, and even in that season was in very low densities (Figure 7).

The densities of *Heteromastus filiformis* in shallow and medium depths were significantly greater than in the deep water in the lower basin, whereas the reverse was the

case in the upper basin (Figure 7). *Arthritica semen* was always absent or in very low densities in the lower basin, while it was very abundant in shallow waters during the winters of 1989 and 1990 in the upper basin (Figure 6).

The densities of five of the eight most abundant species (*Ceratonereis aequisetis*, *Capitella capitata*, *Hydrocooccus brazieri*, *A. semen* and *P. cirrifera*) were inversely correlated with both bottom salinity and temperature (Table 4). *Boccardia chilensis* was the only species whose density was positively correlated with biomass of shell debris ($P < 0.001$). The densities of five species (*Ceratonereis aequisetis*, *Capitella capitata*, *H. brazieri*, *A. semen* and *S. simplex*) were positively correlated with the biomass of *R. megacarpa*, while that of only one species, *P. cirrifera*, was negatively correlated with the biomass of this macrophyte (Table 4).

Classification and ordination

Classification separated the fauna of the deep waters from those in shallow and medium depths (Figure 8). Moreover, the samples from the deep water in the upper basin showed a marked tendency to cluster separately from those in the deep water of the lower basin. The samples from the shallow and medium depths in the upper basin were separated from those in the corresponding depths in the lower basin. The samples from the shallow and medium depths separated according to season, with, for example, in the lower basin, one group containing the samples from the winter and spring of 1989 and the winter of 1990, and another containing the samples from summer and autumn 1990. Classification separated the samples from the shallow depths in the upper basin

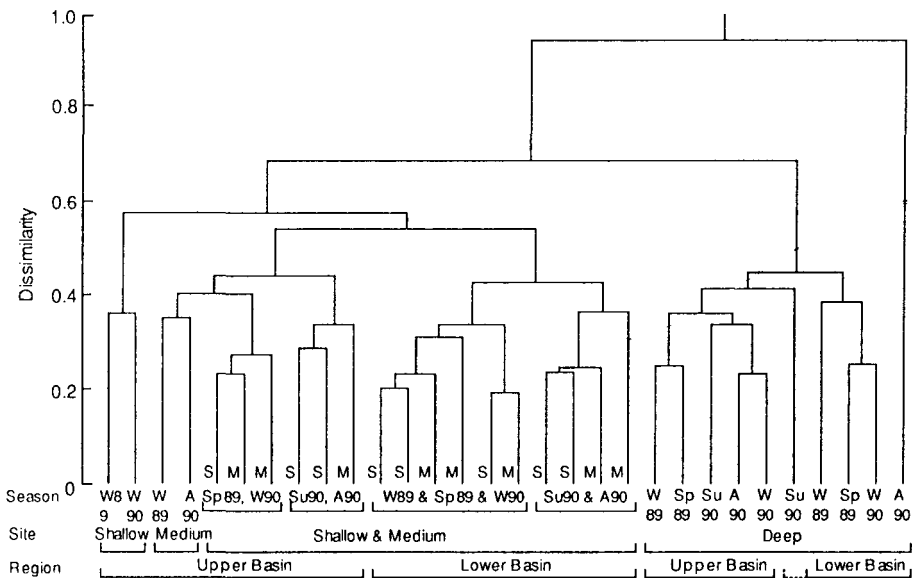


Figure 8. Classification of the densities of the macrobenthic species in samples collected from Wilson Inlet in each season between the winters of 1989 and 1990. S, shallow; M, medium.

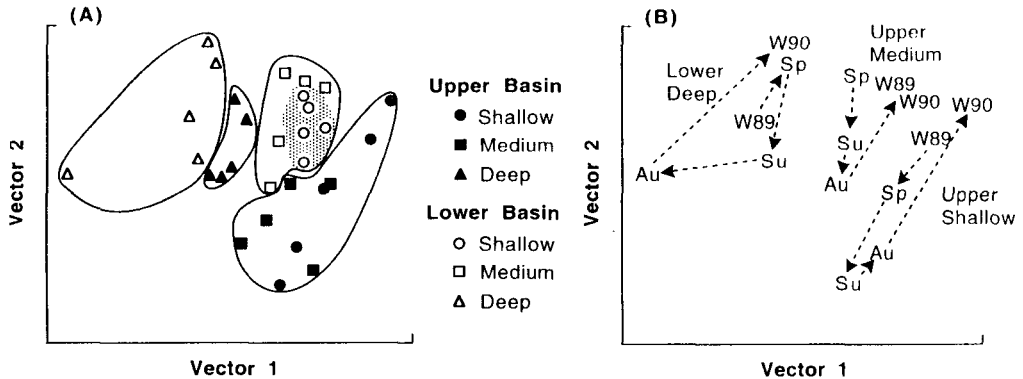


Figure 9. A two-dimensional ordination plot produced by multi-dimensional scaling analysis, using mean densities of the macrobenthic species collected from different depths in the lower and upper basin of Wilson Inlet between the winters of 1989 and 1990. (A) Shows grouping of sites and (B) shows selected, cyclical seasonal changes.

during the winters of 1989 and 1990 from all other samples (Figure 8).

The results of the MDS ordination complemented those produced by classification (cf. Figures 8 & 9A). Thus samples from the deep waters of both the lower and upper basins formed groups that were distinct from those in the medium and shallow depths of the two regions, and samples in medium and shallow depths in the upper basin clustered separately from those in these depths in the lower basin (Figure 9A). The samples from the shallow waters in the lower estuary formed a particularly close cluster (shaded area, Figure 9A). Analysis of similarities demonstrated that all the groups encircled in Figure 9A are significantly different from each other. Samples from the shallow and medium depths in the upper basin and from deep water in the lower basin showed a pronounced cyclical change with season (Figure 9B).

The similarity percentages (SIMPER) program demonstrated that, in comparison with the deep waters, the shallow and medium-depth waters are characterized by greater densities of species such as *Hydrococcus brazieri*, *Boccardia chilensis*, *Capitella capitata* and *Nassarius burchardi*. The separation by region within these groupings is due to the greater densities of the first two species in the lower basin, and of *Ceratonereis aequisetis*, *Arthritica semen* and *Nephtys* sp. in the upper basin. The deeper waters are distinguished from these two groups by the presence of much higher densities of *Prionospio cirrifera*, while differences between regions are mainly due to the presence of greater densities of *Oriopsis* sp., *Liloa brevis*, and *B. chilensis* in the lower basin, and of *Scoloplos simplex* in the upper basin.

DISCUSSION

Faunal composition

The macrobenthic community of the seasonally closed Wilson Inlet is dominated by capitellid, spionid and nereid polychaetes and mytilid, venerid and tellinid molluscs, as is typically the case in permanently open estuaries in temperate regions of the northern

and southern hemispheres (e.g. Gaston et al., 1988; Steimle & Caracciolo-Ward, 1989; Junoy & Viéitez, 1990; Kalejta & Hockey, 1991). However, extensive sampling of the shallow and deeper waters of this seasonally closed system over five seasons yielded only 41 species of macrobenthic invertebrate. This is a far lower number than the 90–204 species recorded in several different studies of temperate estuaries in eastern Australia (Rainer & Fitzhardinge, 1981; Poore, 1982; Rainer, 1982; Jones et al., 1986) and the northern hemisphere (Steimle & Caracciolo-Ward, 1989; Junoy & Viéitez, 1990; Warwick et al., 1991).

Since the majority of species found in estuaries also occur in marine waters or are derived from marine species (Kennish, 1990), the relatively very low numbers of species in Wilson Inlet may be related, at least in part, to the fact that salinities in all but the entrance region of this system never reach 30‰ and are frequently below 17‰ (Figure 2; Potter et al., 1993). These low numbers must also reflect the fact that the closure of the estuary mouth during the drier months would prevent recruitment of the larvae of the many marine macrobenthic invertebrate species which typically spawn in summer (Kalejta & Hockey, 1991; Quijón & Jaramillo, 1993; Sardá et al., 1995). Indeed, even when the estuary mouth is open, tidal water movement in Wilson Inlet is very small, which means that, as with larval fish (Neira & Potter, 1992), the transport mechanisms for recruitment of invertebrates as larvae from the sea are very limited. It should also be recognized that, for much of the year, there is essentially no salinity gradient throughout the long basin of Wilson Inlet (Potter et al., 1993), and that such a characteristic in northern and southern hemisphere estuaries is associated with a relatively low number of species (see e.g. Stoner & Acevedo, 1990; de Decker & Bally, 1985). Since, in other systems, a high number of species has been associated with variability in the sediment composition along the estuary (e.g. Junoy & Viéitez, 1990), it is also relevant that the composition of the sediments is similar throughout the length of the basin of Wilson Inlet. The proposal that the above factors contribute to the low number of macrobenthic invertebrate species in Wilson Inlet is entirely consistent with the observation that Hodgkin & Clark (1988a) recorded over 50% more species during a far less intensive sampling regime in the nearby Nornalup-Walpole Estuary, which, in contrast to Wilson Inlet, is permanently open, reaches high salinities and has a marked longitudinal salinity gradient (Potter & Hyndes, 1994).

Influence of water depth

Classification and ordination demonstrated that the composition of the macrobenthic invertebrate community within the large basin of Wilson Inlet was strongly related to water depth, with the composition in medium depths being far more similar to that of shallow than deeper waters. The conclusion that water depth has an even greater influence on this fauna, than either region or season, is borne out by the results of ANOVA. Thus the mean squares for water depth were greater than those for estuarine region or season in the case of species richness, diversity, total density and biomass of all individuals, as well as for the densities of five of the eight most abundant species. The abundant species, whose densities were conspicuously greater in shallow and

medium depths than in deeper waters, were *Ceratonereis aequisetis*, *Capitella capitata* and *Hydrococcus brazieri*. It may thus be relevant that the densities of these three species, and also that of the less abundant *Arthritica semen*, were positively associated with the biomass of the aquatic macrophyte *Ruppia megacarpa*, which was far greater in the shallow and medium depths than in deeper waters. Colonization of the substratum in beds of *R. megacarpa* by *Ceratonereis aequisetis* would also enable this species both to feed directly on plant material, which forms part of its diet (Hutchings, 1984), and to obtain protection from the teleost *Atherinosoma elongata* Klunzinger, which is one of its predators (Humphries & Potter, 1993). Since *Capitella capitata* and *H. brazieri* are deposit feeders (Fauchald & Jumars, 1979; Wells & Threlfall, 1982a), the decaying *R. megacarpa* present in the substratum would also be of value to these species. In contrast to the situation with the above four species, the density of the spionid *Prionospio cirrifera* was far greater in deeper waters than in the shallow and medium depths of both the upper and lower estuary, and the same is true for *Heteromastus filiformis* in the upper estuary. Since these two species are deposit feeders, which utilize fine detrital particles as a food source (Fauchald & Jumars, 1979), it is relevant that the amount of particulate organic material was greatest in the deeper waters. The fact that the latter species was not more abundant in the deeper water than in medium and shallow depths in the lower estuary may be due to these waters being less exposed to the prevailing wind action than in the upper estuary.

Diversity was almost invariably greater in shallow and medium depths than in deeper waters. It is thus noteworthy that, in both the lower and upper estuary, the growths of *R. megacarpa* were most prolific in the shallow and medium-depth waters and that, in the lower estuary, the amount of shell debris was most abundant in these water depths. Furthermore, diversity was correlated with the amount of both *R. megacarpa* and shell debris. The greater diversity in shallow and medium depths may therefore be related to the increased complexity of habitat provided by the presence of beds of *R. megacarpa* and/or shell debris. Such a view would be consistent with the results of studies in the northern hemisphere, which have shown that species diversity is greater in areas occupied by macrophytes and shell remains (Dauer et al., 1982; Castel et al., 1989).

Influence of region

All but four of the 41 species recorded in this study were found in both the upper and lower estuary, and the eight most numerous species were at least moderately abundant in both of these regions. Although samples from these regions did tend to cluster separately with classification and ordination, the differences were not as marked as they were with water depth. The less marked influence of region than water depth on community composition is presumably related to the fact that, at any one time, the salinity regime is similar throughout the basin, a feature which results from the influence of wind mixing on the waters of this shallow system and the, at best, very limited tidal action. This contrasts with the distinct salinity gradient that is typically found in temperate northern hemisphere estuaries (e.g. Holland et al., 1987; Warwick et al.,

1991).

Despite the broad similarities between the faunal composition in the lower and upper estuary, the densities of each of the eight most abundant species were significantly greater in one or other of the two regions. This applied particularly to *Boccardia chilensis*, whose density was greater in the lower estuary, and to *Scoloplos simplex* and *H. filiformis*, which were more abundant in the upper estuary. Since *B. chilensis* builds tubes, it is probably important that shell debris, which helps stabilize the substratum (Kennish, 1990), was more abundant in the lower than upper estuary. The greater amount of subsurface shell debris in the lower estuary may have inhibited colonization by the highly mobile *S. simplex* and *H. filiformis*, whereas the presence of the surface rhizomes of *R. megacarpa* in the upper estuary was not sufficient to prevent these species burrowing in this region.

Seasonality of the macrobenthic fauna

Ordination showed that the composition of the macrobenthic invertebrate fauna changed cyclically throughout the year, which implies that there is a sequential pattern of recruitment and/or mortality. It has sometimes been possible to relate seasonal changes in macrobenthic invertebrate communities in other estuaries to seasonality in the reproduction of certain members of those communities (Rainer, 1982; Holland et al., 1987). It is thus relevant that in Wilson Inlet the densities of polychaete and gastropod larvae rise from low levels in the winter to reach their maxima between mid-spring and mid-autumn, and between mid-summer and late autumn, respectively (Gaughan & Potter, 1995). Furthermore, the density of bivalve larvae shows a similar but less marked seasonal trend to that of polychaete larvae. These seasonal changes in the larvae of polychaetes are reflected by the marked increases that occur in the densities of the juveniles and adults of species such as *Ceratonereis aequisetis* and *Capitella capitata* in winter.

Some of the most abundant macrobenthic invertebrates in Wilson Inlet do not produce pelagic larvae. This applies, for example, to the micromolluscs *Hydrococcus brazieri* and *A. semen*, whose young stages are benthic in the first case and brooded by their adults in the second (Wells & Threlfall, 1982b). The densities of these two mollusc species exhibited seasonal changes in Wilson Inlet, with numbers being highest in winter and spring. The very low densities of *Ceratonereis aequisetis*, *Capitella capitata*, *H. brazieri* and *A. semen* in summer imply that these species are subject to mortality during the spring when salinities are lowest.

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