

Molluscs of the Leschenault Inlet estuary: their diversity, distribution, and population dynamics

V Semeniuk¹ & P A S Wurm²

¹ 21 Glenmere Road, Warwick WA 6024

² Faculty of Science, Information Technology and Education,
Northern Territory University, Darwin NT 0909

Abstract

Thirty-one species of mollusc were collected in Leschenault Inlet during 1982-1987. Seven species were common, with the remaining 24 species occurring sporadically, rarely or only once during the study. These seven most common species in order of general abundance were: *Arthritica semen*, *Tellina deltoidalis*, *Nassarius burchardi*, *Spisula trigonella*, *Hydrococcus brazieri*, *Acteocina* sp and *Bedevea paivae*. The molluscs of Leschenault Inlet can be classified as follows: (1) a stenohaline marine component: *Bittium granarium*, *Mytilus edulis*, *Polinices conicus*, *Pholas australasiae*, *Nassarius nigellus*, *Solemya australis*, *Irus crenata*, and *Venerupis anomala*; (2) a euryhaline marine component: *Tellina deltoidalis*, *Tellina* sp, *Theora lubrica*, *Sanguinolaria biradiata*, *Philine angasi*, *Nassarius burchardi*, *Bedevea paivae*, *Spisula trigonella*, *Epicodakia* sp, and *Laternula creccina*; and (3) a true estuarine component: *Acteocina* sp, *Arthritica semen*, *Xenostrobus securis*, *Hydrococcus brazieri*, *Fluviolanatus subtorta*, *Assimineia* sp, and *Salinator* sp. Across the inlet in general, molluscs inhabited tidal sand or tidal mud, shallow water platform sand or muddy sand, or deep water basin mud, within lower, middle, or upper estuarine salinity fields. In this context, seven broadly recurring assemblages or populations of mollusc could be discerned: (1) a mixed molluscan assemblage inhabiting the tidally flushed environments of the Preston River Delta and the tidal delta leeward of "The Cut"; (2) a *Tellina* (\pm *Spisula*) assemblage inhabiting the deep water central muddy basin; (3) a *Tellina*-*Nassarius* (\pm *Bedevea*) assemblage inhabiting seagrass-vegetated platforms; (4) *Tellina* populations inhabiting shallow subtidal mud flats, (5) *Hydrococcus* populations inhabiting tidal sandy beaches; (6) *Acteocina* populations inhabiting tidal mud flats; and (7) *Arthritica* populations inhabiting low tidal to shallow subtidal sand flats. Population structures were found to be different for the three common genera. *Tellina* populations appeared to be maintained by a relatively continuous low level of juvenile recruitment. *Nassarius* populations were dominated by a mature age cohort, with a low intermittent level of juvenile recruitment. *Spisula* populations were numerically dominated by one age cohort, and were not maintained by further recruitment. This study provides a five-year perspective of changes in mollusc populations in Leschenault Inlet, providing insight into the variability and longevity of the fauna. Some species are consistently present in the estuary although abundances varied seasonally, while others fluctuated markedly in their presence or absence. While the overall character in terms of diversity/abundance, and population structure of the mollusc assemblages may have remained similar, there were also changes in composition from year to year and from season to season. For many species there was a decrease in abundance, such that the relative abundance of species within an assemblage changed with time. Abundances of each species fluctuated largely independently of other species or a given habitat, and did not apparently occur in response to seasonal patterns in oxygen concentration, temperature, or salinity.

Keywords: molluscs, Leschenault Inlet, estuary, population dynamics, south-western Australia.

Introduction

Estuarine molluscs have been studied to varying detail in south-western Australia (Ashman *et al.* 1969, Wilson 1969, Hughes 1973, Smith 1975, Wallace 1975, Chalmer *et al.* 1976, Poore & Rainer 1979, Brown *et al.* 1980, Wells *et al.* 1980, Rainer 1981, Wells & Threlfall 1981, 1982a,b,c; Chalmer & Scott 1984 Davey & George 1986). Specifically for Leschenault Inlet, molluscs were reported as part of a survey for benthic fauna in 1974 by Chalmer & Scott (1984), and by others who reported incidentally on them for comparative work (Smith 1975; Wells & Threlfall 1981). Most studies focused on the biology and occurrence of specific molluscs, and did not include details of habitats, molluscan assemblages in relation to habitat, or longer term population dynamics.

The dynamic physical and hydrochemical nature of the Leschenault Inlet estuary has developed a varied array

of habitats across the system and a poikilosaline range of salinity fields, and this provides a context for describing and interpreting the distribution and abundances of estuarine molluscs. In contrast with most other studies into estuarine mollusc autoecology (cited above), the habitat framework of Wurm & Semeniuk (2000) is used here to view mollusc diversity, distribution, and population dynamics. Thus, this paper describes the mollusc assemblages of Leschenault Inlet over 5 years in terms of species composition and their relationship to habitat, the population dynamics of the more common species, and for three common species the dynamics of their population size structure.

Methods

Field study

The study of Leschenault Inlet and its molluscan fauna involved a range of sampling strategies, locations, and times

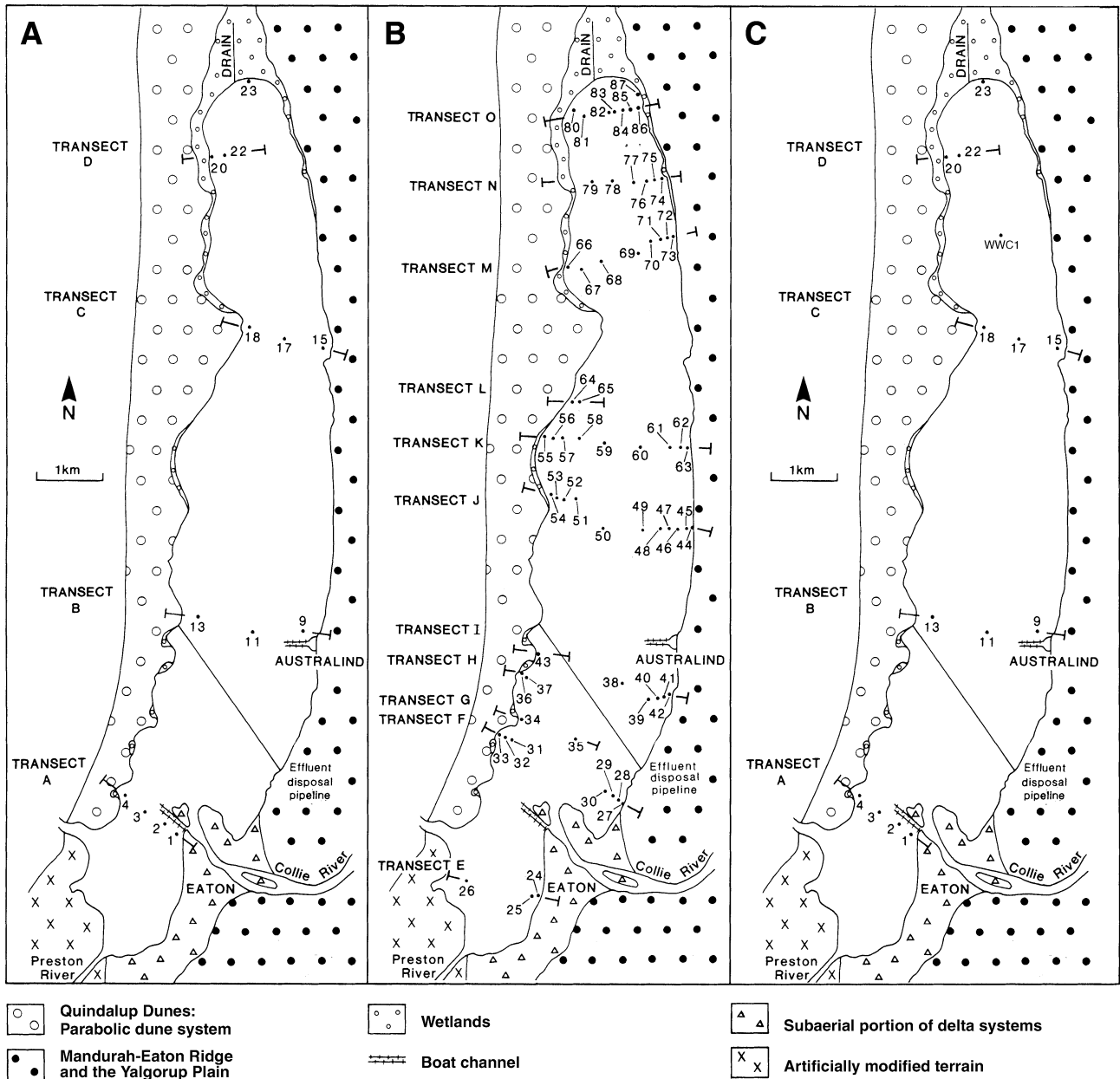


Figure 1. A: Location of the main fauna sampling transects and 22 sites. B: Location of the 63 supplementary fauna flora and substrate sampling sites. C: Location of the water sampling sites, and the estuarine salinity fields after Wurm & Semeniuk (2000).

over five years between 1982 and 1987. Physical and chemical habitat data were also collected and used to identify a number of habitats in the estuary (Wurm & Semeniuk 2000). A wide-ranging, reconnaissance survey was undertaken during February 1982 to identify the main habitat types, based on bathymetry, substrate, vegetation cover and hydrochemical setting. This survey was the basis for selection of 4 main east-west oriented sampling transects for molluscs (Fig 1A), representing various hydrochemical locations along the length of the estuary, and along which 22 main sampling sites were located and sampled between 1982 and 1987. The sampling sites were located at the most common habitat types. In December 1986, a supplementary survey of mollusc fauna was undertaken, involving an additional 63 sites located along a further 11 transects (Fig 1B).

During 1986 and 1987, estuarine water was sampled at sites along the 4 main transects. Salinity, oxygen concentration, and temperature were measured, as they were considered to be directly critical to benthos, and all samples and measurements were taken from the base of the water column. Initially, these water quality parameters were sampled at all 22 sites, but the number of sites was reduced later to between 2-4 per transect, comprising those sites considered representative of the general hydrochemical field for a given transect (Fig 1C). Water quality data, described in Wurm & Semeniuk 2000, also were used in this study.

Two methods were used for sampling molluscs. Except for the dedicated sampling of *Arthritica semen*, all species were sampled with a 25 cm x 25 cm x 25 cm box-corer.

Samples were washed in the field through a 1 mm mesh, and molluscs were counted, measured, and returned to the environment. Small species such as *Assimineia* sp and *Hydrococcus brazieri* were also counted by this method. *A. semen*, because of its small size and high abundance, was sampled with a cylindrical corer 10cm in diameter and 15cm long. Samples were washed through a 1 mm mesh, fixed in preservative, and counted in the laboratory to ensure that only live specimens were counted. From each site, replicate samples were collected within an homogeneous area of 5 m radius. Initially 10 replicate samples were collected, but for logistical reasons this was later reduced to five. At some sites where species density was very low, to obtain sufficient number of animals to construct population size frequency histograms, it was necessary to sample 20, and at times 40 replicates. For the survey in December 1986, only 3 replicate samples were taken as the data were used for mapping purposes and not population dynamics studies.

Population size structure was studied for *Nassarius burchardi*, *Tellina deltoidalis* and *Spisula trigonella*. These species were sufficiently abundant and large enough to readily allow investigation of juvenile recruitment and the relationship between population structure and abundance. Up to several hundred animals were typically measured

during each survey. When abundance was low, sampling usually persisted until a minimum of 20 animals were collected. For *Nassarius*, the length of the shell from the spire tip to the posterior end of the columella was measured, and for bivalves the greatest length of the shell between posterior and anterior margins was measured. Measurement was carried out in the field, with the animals returned to their habitat after measurement. Although *Arthritica semens* was numerically the most abundant molluscan species in the estuary, its small size precluded the field approach outlined above for the other species. Study of *Arthritica semen* thus was a combined field and laboratory exercise. Samples of the species collected in small cores were returned to the laboratory, separated from seagrass, algae and other fauna such as polychaetes and small crustaceans under a binocular microscope, and then counted. The population size structure of this species was not analysed because the mesh size adopted for this study was 1 mm, and small individuals < 1mm in size (which were numerous and critical to the construction of size-frequency histograms) were not systematically sampled.

Monitoring of molluscs and habitat parameters was carried out annually, quarterly, or monthly (Table 1). Given the large number of sites involved, the anticipated medium

Table 1: Sampling times of fauna monitoring programmes.

DATE	SITE																					
	A1	A2	A3	A4	A5	A6	A7	B8	B9	B10	B11	B12	B13	B14	C15	C16	C17	C18	C19	D20	D21	D22
1982	FEB	S	.	.	S	S	S
	MAY	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
	AUG	.	S	S	S	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
	DEC	.	S	S	S	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
1983	FEB	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
	MAY	.	S	S	S	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
	AUG	.	S	S	S	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	.
	DEC	.	S	S	S	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	.
1984	FEB	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
	MAY	.	S	S	S	.	.	.	S	.	S	.	.	.	S	.	S	.	S	.	.	.
	AUG	.	S	S	S	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
	DEC	.	S	S	S	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
1985	FEB	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
	MAY	.	S	S	S	.	.	.	S	.	S	.	.	.	S	.	S	.	S	.	.	.
	AUG	.	S	S	S	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
	DEC	.	S	S	S	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
1986	FEB	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
	MAY	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
	JUNES	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
	JUL	.	S	S	S	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
	AUG	.	S	S	S	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
	SEP	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
	OCT	.	S	S	S	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
	NOV	.	S	S	S	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
	DEC	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
	1987	JAN	.	S	S	S	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S
FEB		.	S	S	S	.	.	.	S	.	S	.	.	.	S	.	S	.	S	S	S	S
MAR		S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S

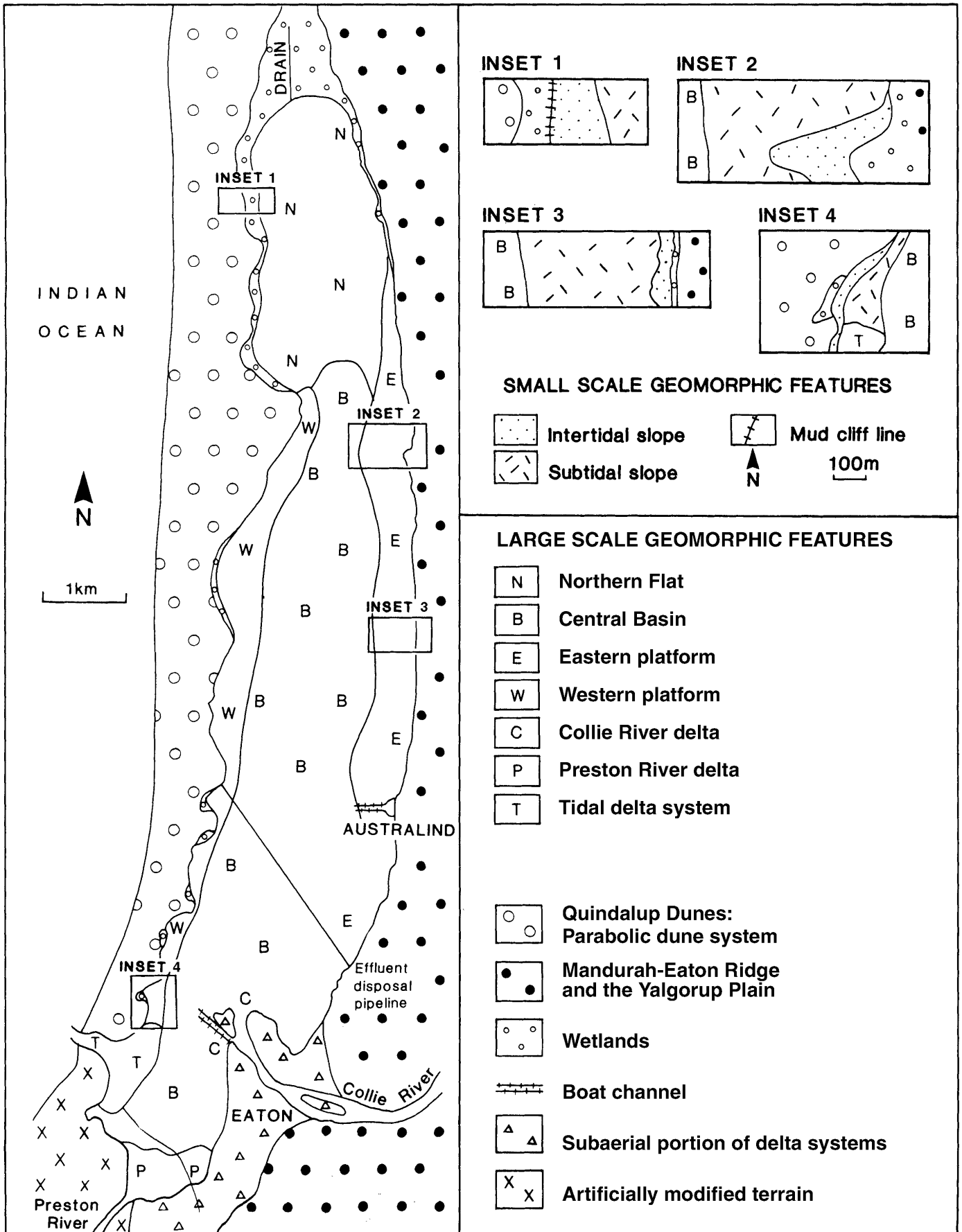


Figure 2. The large scale geomorphic/bathymetric units within Leschenault Inlet (after Wurm & Semeniuk 2000).

term faunal population monitoring proposed for this estuary dictated that a stratified sampling strategy be undertaken. After the initial reconnaissance survey in February 1982, for the period 1982-1986, all 22 sites were sampled in May 1982, representing an end-of-summer period, and thereafter sampled annually in February each year. Selected sites, representing examples of specific habitat settings in the four estuarine salinity fields, were sampled quarterly, representing seasonal sampling. After 1986, in the period February 1986 to March 1987, when the mollusc study became more intensive, the sites that were sampled yearly were then sampled quarterly, and the sites previously sampled quarterly were then sampled monthly. Monitoring sites thus can be categorised into two groups: those sampled frequently, *i.e.* quarterly between 1982 and 1986, and monthly between 1986 and 1987 (sites A2, A3, A4, B9, B11, B12, C15, C19, C17, D20, D21 and D22), and those sampled less frequently, *i.e.* yearly between 1982 and 1986, and quarterly between 1986 and 1987 (sites A1, A5, A6, A7, B8, B10, B13, B14, C16 and C18). Data presented in this paper focus on that derived from the frequently sampled sites (A2, A3, A4, B9, B11, B12, C15, C19, C17, D20, D21 and D22) for seven key species. Data on these species for sites A1, A5, A6, A7, B8, B10, B13, B14, C16 and C18 are presented in Appendix 1. The full data set for all sites and all species is presented in Wurm (1987). Sampling times are shown in Table 1.

Analytical methods

Abundances of animals, given as mean \pm standard deviation, were determined from the box cores (surface area 625 cm²) and the cylindrical corer (surface area *ca* 78 cm²). These estimates were multiplied appropriately to calculate abundances per square meter. While the database of this study is large, encompassing regular sampling of 22 sites, most often seasonally for more than 5 years, many species were too sparse or too patchy for detailed study. Preliminary analyses of the main species were undertaken using a General Linear Model with replications, with the five sampling years and four sampling seasons selected as 'inner subject' factors, with substrate types, salinity field and depth as 'between subject' factors. Due to the large number of samples containing no specimens, data distributions were highly skewed, and even after square-root transformations were not normal-distributed according to Kolmogorov-Smirnov and Shapiro-Wilk tests. There was significant inhomogeneity of variances. Accordingly, the emphasis in this study is to focus on the mean density determined by the five replicates, and to compare these spatially and temporally.

Sample lodgement and database

Species were identified by S Slack-Smith and F Wells of the Western Australian Museum, and R Black of the Department of Zoology, University of Western Australia. Specimens of the taxa have been lodged with the Western Australian Museum. Raw data from this study, have been lodged with the Royal Society of Western Australia Library, in Microsoft Excel 5.0 spreadsheet and are available for future researchers.

Habitats of the Leschenault Inlet estuary

This study was confined to the subtidal and tidal area below the supratidal zone fringing the Leschenault Inlet Estuary. Within this area, the estuary can be divided into five bathymetric and geomorphic units (Fig 2; Table 2): (1) a relatively deep water central basin, underlain by mud; (2) a northern shallow water subtidal to tidal flat, underlain by mud; (3) a tidal to shallow water western platform/ramp underlain by muddy sand; (4) an eastern tidal to shallow water platform underlain mainly by sand; and (5) a delta, with subtidal prodelta sand flats, shoals, channels, and muddy bays. The estuary itself is a microtidal wave-dominated estuarine lagoon, with diurnal tides (mean range 0.5 m and a maximum range of 0.9 m; Semeniuk & Meagher 1981; Wurm & Semeniuk 2000). Waters within the estuary are poikilosaline (Fig 3). To the north, salinity varies annually from hyposaline to hypersaline. In the middle estuary, salinity fluctuates within a range of mesosaline values. At the Collie River delta, salinity varies from hyposaline to mesosaline. In winter, the salinity generally decreases with fresh water inflow from rivers, drains, run-off, and groundwater seepages (*e.g.* dunes and deltas). After winter, evaporation (induced by higher summer temperatures and wind) and the continued exchange with the ocean increase the water salinities. To the north, furthest away from "The Cut", estuarine waters may become hypersaline. Salinity is not typically stratified, but there is a salinity gradient from south to north over most seasons. Weak stratification exists, however, during times of freshwater influx.

The waters of the estuary generally are well oxygenated throughout the year (Fig 3). The highest oxygen values occur at the well-vegetated sites of shallow depths. Overall, there was no clear correlation between oxygen concentration and other water parameters, and oxygen concentration appeared to vary independently of temperature and salinity. Dissolved oxygen concentration even in summer is generally > 5 mg L⁻¹. Water temperatures of the estuary in winter in deep water are frequently below 15 °C; summer temperatures are frequently at or above 25 °C, but generally around 22 °C. The deep water of the central basin has a temperature range of *ca* 10 °C, and is generally maintained at a lower temperature than shallower sites. Shallower water sites have winter water temperatures of *ca* 15 °C, and summer temperatures of *ca* 30 °C. They also exhibit greater temperature fluctuations. Shallow water sites, with dark muddy substrates had the highest temperatures, up to 32 °C.

The water body of the estuary can be divided into 4 gradational salinity fields based on mean salinity value and its variation throughout the year (Fig 4; Wurm & Semeniuk 2000). This also formed the basis for dividing the estuary into large scale habitat settings: (1) a deltaic field where mean salinity is slightly less than that of sea water but with a large variability about the mean (Transect A); (2) lower estuarine field in which mean salinity is slightly greater than that of sea water, with a small variability about the mean (Transect B); (3) a mid estuarine field in which mean salinity is higher than that of sea water, with a large variability about the mean (Transect C); and (4) an upper estuarine field in which mean salinity is much greater than

Table 2. Main features of the habitat types of Lescenault Inlet.

Habitat Type	Distribution across large scale geomorphic unit	Salinity field*	Vegetation cover	Depth	Substrate	Site samples and other features
deltaic inter-tidal sand	Collie River delta	hyposaline to mesosaline	none	0-0.25m	medium to coarse sand	A1, A6, A7
deltaic sand	Collie River delta	hyposaline to mesosaline	none	0.25-0.50m	Medium to coarse sand	A2
lower-estuarine basinal mud	central basin	mesosaline stable	none or patchy <i>Halophila ovalis</i>	1-2m	mud	B11, B12, G35
lower-estuarine basinal	central basin	mesosaline stable	none or patchy <i>Halophila ovalis</i>	1-1.5m	sandy mud	A3, H38, the sand fractions are comprised predominately of fossil gastropod shells
lower-estuarine platform sand	eastern platform as a shore-parallel ribbon to 500m; western platform as an apron emanating from front of parabolic dunes	mesosaline stable	continuous <i>Halophila ovalis</i> some <i>Ruppia megacarpa</i> , and <i>Gracilaria</i> sp, rare <i>Heterozostera tasmanica</i>	0.25 - 1m	medium sand to muddy medium sand	B8, E25, E26, F28, F29, F30, the western platform the unit is developed at the reworked front of encroaching dunes
lower-estuarine platform mud	western platform as an irregular shore-parallel ribbon	mesosaline, stable	continuous <i>Halophila ovalis</i> cover with <i>Gracilaria</i> sp	0.25-1m	mud to sandy- mud and shelly- mud	B14, F31, F32, H36, H37
lower-estuarine intertidal mud	western platform as an irregular shore-parallel ribbon to 50m wide	mesosaline stable	none	0-0.25m	mud; may overly sandy- mud	F33 developed in sheltered embayments pools of water are retained at low tide because of the undulating surface shallow
lower-estuarine intertidal sand	eastern platform, shore- parallel ribbon 50-100m; western platform shore-parallel ribbon or apron 10-30m wide	mesosaline stable	none	0-0.25m	medium sand	E24, F27, H42; on the western platform the unit is developed at the reworked front of encroaching dunes
lower-estuarine platform muddy-sand	western platform as an irregular shore- parallel ribbon	mesosaline stable	continuous <i>Halophila ovalis</i> cover with <i>Gracilaria</i> sp	0.25-1m	muddy medium sand	A4, A5, B9, B10, B13
mid-estuarine basinal mud	central basin	mesosaline fluctuating	none or patchy <i>Halophila ovalis</i>	1-1.6m	mud to sandy-mud	C17, J49, J50, K59, K60
mid-estuarine platform mud	western platform, shore-parallel ribbon to 500m	mesosaline, fluctuating	continuous <i>Halophila ovalis</i> cover with algae	0.25-1m	mud to sandy-mud	C18, J51, K56, K57, K58, L65

Table 2 (continued). Main features of the habitat types of Leschenault Inlet.

Habitat Type	Distribution across large scale geomorphic unit	Salinity field*	Vegetation cover	Depth	Substrate	Site samples and other features
mid-estuarine platform muddy-sand	western platform, shore-parallel ribbon to 300m wide; eastern platform, shore-parallel ribbon 300m wide	mesosaline, fluctuating	continuous <i>Halophila ovalis</i> cover with <i>Chaetomorpha</i> sp and <i>Gracilaria</i> sp	0.25-0.70m	muddy medium sand	C15, C16, J52, J53, J54
mid-estuarine platform sand	eastern platform, shore-parallel ribbon to 500m	mesosaline fluctuating	continuous <i>Halophila ovalis</i> with some algae	0.25-0.90cm	medium sand	J45, J46, J47, J48, K61, K62
mid-estuarine intertidal muddy-sand	western platform, apron or shore-parallel ribbon to 30m	mesosaline fluctuating	none	0-0.25m	muddy medium sand	K55, L64
mid-estuarine intertidal sand	eastern platform, shore-parallel ribbon to 100m wide	mesosaline fluctuating	none	0-0.25m	medium sand	C19, J44, K63
upper-estuarine flat sand	northern flat shore-parallel ribbon 100-200m wide	hyposaline to hypersaline	sparse <i>Acetabularia</i> sp	0.05-0.30m	medium sand to muddy medium sand	N72, N75
upper-estuarine flat mud	northern flat, the shallow centre wide	hyposaline to hypersaline	patchy to continuous cover of <i>Halophila ovalis</i>	0.30-0.55m	mud to sandy- mud	M68, M69, M70, M71, N76 N77, N78, N79
upper-estuarine intertidal sand	northern flat, shore-parallel ribbon to 150m wide	hyposaline to hypersaline	none	0-0.25m	medium sand to muddy medium sand	M72, M73, N74, N75, O86
upper-estuarine intertidal mud	northern flat as a shore-parallel ribbon up to 400m wide	hyposaline to hypersaline	none or sparse and patchy <i>Chaetomorpha</i> sp <i>Gracilaria</i> sp; or some <i>Ruppia megacarpa</i>	0-0.30m	mud and sandy mud	D20, D21, D22, M66, M67, O80, O81, O82, O83, O84, O85; because of the undulating surface shallow pools of water are retained at low tide.

*Terminology after Hammer (1986).

that of sea water, with a very large variability about the mean (Transect D).

In the descriptions of sampling sites that follow in relation to the molluscs, site numbers prefixed by A along Transect A are in the deltaic salinity field, those prefixed by B are along Transect B in the lower estuarine salinity field, those prefixed by C are along Transect C in the middle estuarine salinity field, and those prefixed by D are along Transect D in the upper estuarine salinity field.

Wurm & Semeniuk (2000) also divide the estuary into some 19 habitat units for benthic biota (Fig 4), based on

geomorphology, substrates, depth, and hydrochemistry. A summary description of habitat features of the 22 sampling sites is provided in Table 3.

The molluscs of Leschenault Inlet estuary

Diversity & Distribution

Thirty-one species of mollusc were collected in Leschenault Inlet during the study period (Table 4). Of these, only 14 were recorded by Wells & Threlfall (1981) in their survey of the Peel-Harvey Estuary, with 20 recorded

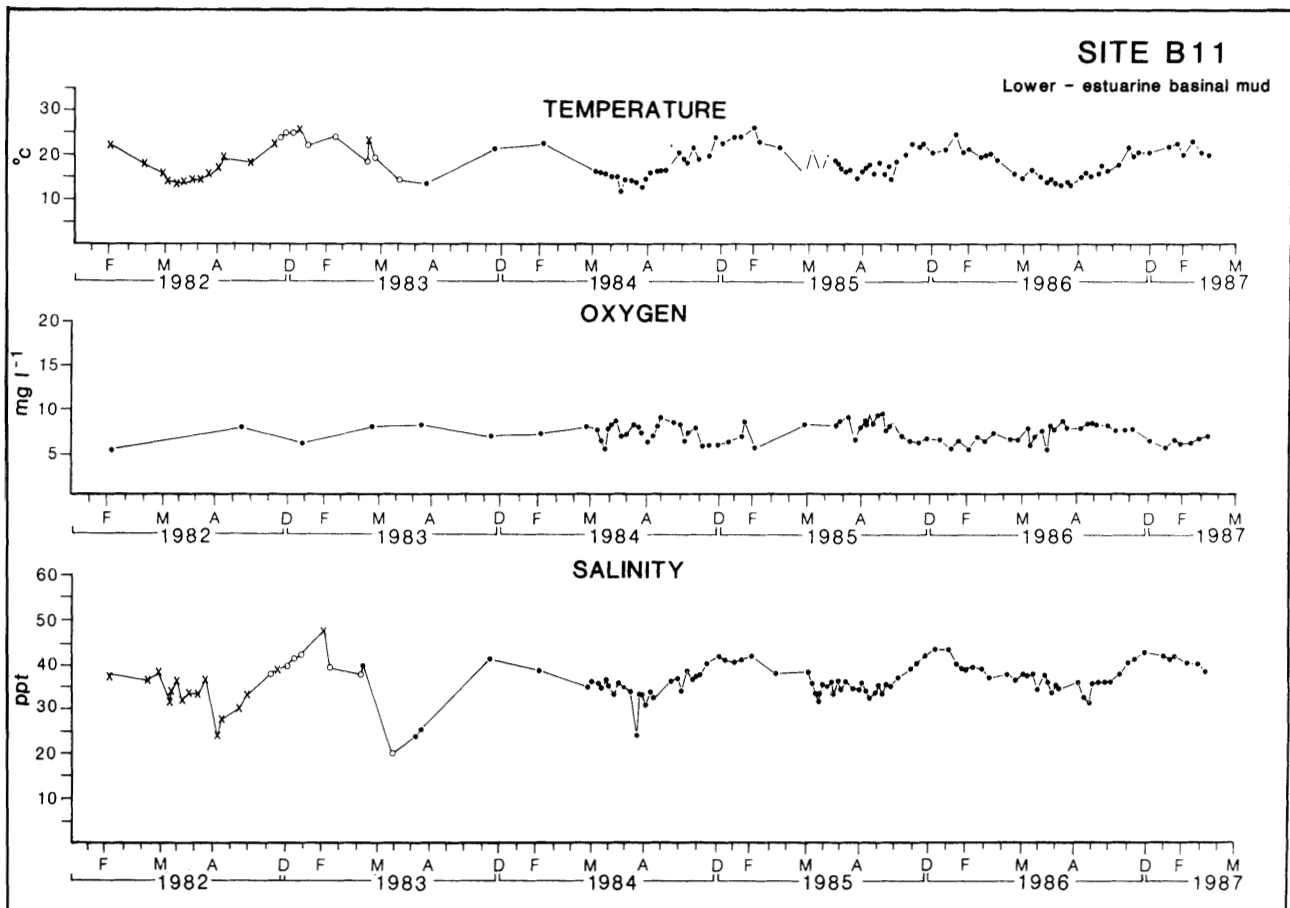


Figure 3. Typical variation of water temperature, oxygen, and salinity in the middle estuary, showing seasonal fluctuation of temperature and salinity. Data from site B11 (see Fig 1A; after Wurm & Semeniuk 2000).

by Chalmer *et al.* (1976) for the Swan River Estuary. In Leschenault Inlet, during this study, seven mollusc species were common, with the remaining 24 species occurring sporadically, rarely or only once during the study. In order of decreasing abundance, these seven most common species are: *Arthritica semen*, *Tellina deltoidalis*, *Nassarius burchardi*, *Spisula trigonella*, *Hydrococcus brazieri*, *Acteocina* sp, and *Bedevea paivae*. Although not common throughout the estuary, *Assimineia* sp and *Xenostrobus securis* were sufficiently abundant at all times or abundant sporadically to warrant a brief description in this paper. Most of the uncommon, rare, restricted, or sporadically occurring species fall into 5 groups:

1. Species occurring only in the marine-influenced southern sites of the estuary near the opening to the ocean (Transect A) frequently occurred only as juveniles. It is probable they have developed from oceanic larvae originating from outside the Inlet. This group included the largest number of species, *viz.* *Donax columbella*, *Epicodakia* sp, *Irus crenata*, *Maetra flindersi*, *Mytilus edulis*, *Nassarius nigellus*, *Pholas australasiae*, *Polinices conicus*, *cf Solemya australis*, and *Venerupis galactites*.

2. Species occurring infrequently or rarely, but not confined to sites near the opening of the estuary to the ocean, included *Fluviolanatus subtorta*, *Laternula creccina*, *Philine angasi*, *Salinator* sp, *Tellina* sp, *Theora lubrica*, and

Venerupis anomala.

3. Species which were present throughout the study period and across much of the estuary, but in low numbers, included *Assimineia* sp, *Bedevea paivae*, and *Sanguinolaria biradiata*.

4. Species forming small local populations at a single site for a short period include *Xenostrobus securis*, which occurred on deltaic sands of the Collie River delta at the beginning of the study, and *Bittium granarium* which was established late in the study along Transect C on the western platform.

5. One species (*Bembicium auratum*) forming small local populations over a long period at a single site (within local a mangrove environment along the intertidal shore of the estuary).

Abundance and age structure

Data on the abundance, temporal variation of the most common mollusc species, and the age structure of three species are shown in Figs 5-14, and described below in regard to environmental factors and population age structure for selected species. The description of mollusc abundances centres around the results of the most frequently monitored sites *i.e.* A2, A3, A4, B9, B11, C15,

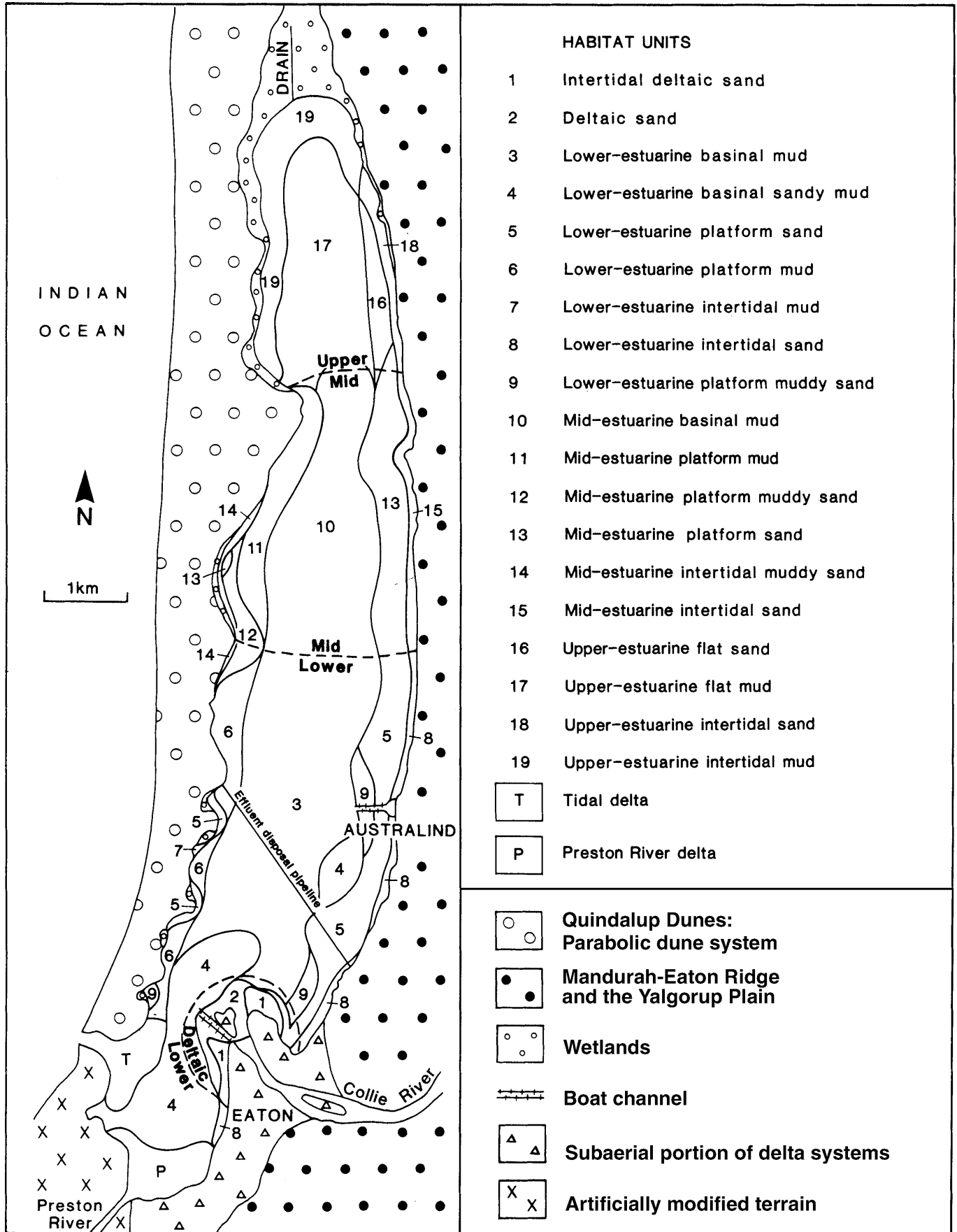


Figure 4. Distribution of habitats in the Leschenault Inlet estuary.

Table 3. Habitat features of sites on Transects A-D.

Site	Large-scale geomorphic unit	Habitat unit	Substrate	Flora	Salinity
A1	Collie River Delta	Deltaic inter-tidal sand	Medium & coarse sand	None	Deltaic
A2	Collie River Delta	Deltaic sand	Medium & coarse sand	None	Deltaic
A3	Central Basin	Lower estuarine basinal sandy mud	Sandy mud	Patchy <i>Halophila</i>	Lower
A4	Western Platform	Lower estuarine platform muddy sand	Muddy medium sand	<i>Halophila</i>	Lower
A5	Western Platform	Lower estuarine inter-tidal muddy sand	Muddy medium sand	Patchy algae & <i>Halophila</i>	Lower
A6	Collie River Delta	Deltaic inter-tidal sand	Medium & fine sand	Patchy algae & <i>Halophila</i>	Lower
A7	Collie River Delta	Deltaic inter-tidal sand	Medium & fine sand	Patchy algae & <i>Halophila</i>	Lower
B8	Eastern Platform	Lower estuarine platform sand	Medium sand	Patchy <i>Halophila</i> & algae	Lower
B9	Eastern Platform	Lower estuarine platform muddy sand	Medium sand	<i>Halophila</i>	Lower
B10	Eastern Platform	Lower estuarine platform muddy sand	Medium sand	<i>Halophila</i>	Lower
B11	Central Basin	Lower estuarine basinal mud	Mud	Patchy <i>Halophila</i>	Lower
B12	Central Basin	Lower estuarine basinal mud	Mud	Patchy <i>Halophila</i>	Lower
B13	Western Platform	Lower estuarine platform muddy sand	Muddy medium sand	<i>Halophila</i> & algae	Lower
B14	Western Platform	Lower estuarine platform sandy mud	Sandy mud	Patchy algae & <i>Halophila</i>	Lower
C15	Eastern Platform	Mid estuarine muddy sand	Muddy medium sand	<i>Halophila</i> & algae	Mid
C16	Eastern Platform	Mid estuarine muddy sand	Muddy medium sand	<i>Halophila</i> & algae	Mid
C17	Central Basin	Mid estuarine basinal mud	Mud	Patchy <i>Halophila</i>	Mid
C18	Western Platform	Mid estuarine platform sandy mud	Mud	<i>Halophila</i> & algae	Mid
C19	Eastern Platform	Mid estuarine inter-tidal sand	Medium sand	None	Mid
D20	Northern Flat	Upper estuarine inter-tidal sandy mud	Sandy mud	Patchy algae	Upper
D21	Northern Flat	Upper estuarine inter-tidal mud	Mud	Patchy algae	Upper
D22	Northern Flat	Upper estuarine inter-tidal mud	Mud	Patchy algae	Upper

C17, C19, D20 and D22. Data for the other sites are presented in Wurm (1987). The distribution and relative abundance of the main species with respect to the identified habitats are described in Table 4.

Figure 15 shows the distribution and relative abundance of key species during estuary-wide sampling in December 1986. This information presents a single time frame and was obtained when a number of species were increasing in their abundance within the estuary after a period of relatively low population densities over the period 1984 to mid 1986. The distribution of species with respect to habitat and setting in the estuary is summarised

in Figure 16, as based on the results of the longer term sampling. In December 1986, *Acteocina* was located mainly in the tidal to subtidal upper estuary, and to a less extent along the tidal shore of the eastern platform. *Arthritica semen* was located on the tidal and subtidal shallow water platform environments in all salinity fields, with local abundances reaching thousands per square metre. *Assimineia* was restricted to the tidal to shallow water upper estuary. *Hydrococcus brazieri* was located mainly in the tidal to subtidal upper estuary and patchily along the tidal and shallow water environments of the eastern platform. *Nassarius burchardi* was widespread throughout the estuary, but generally absent from the northern basin. *Tellina*

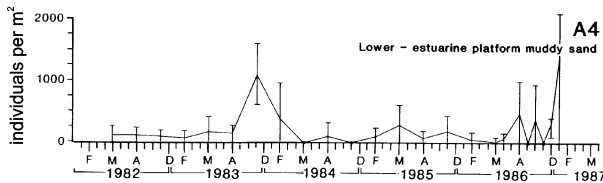
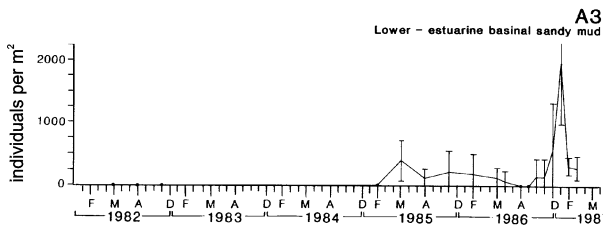
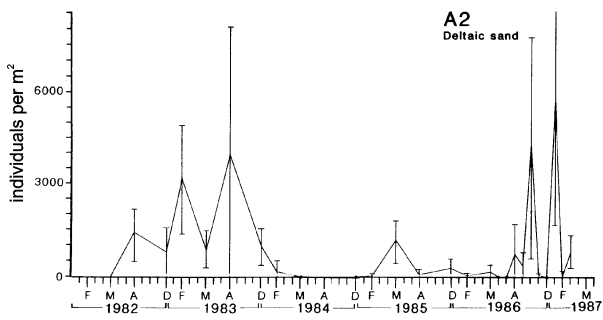
Table 4. Species listing and their main occurrence in habitats of the estuary.

Species	Main habitats	Relative abundance within habitat 1982-1987
AMPHIBOLIDAE <i>Salinator</i> sp	upper-estuarine intertidal mud; one recording at site D20.	uncommon
ASSIMINEIDAE <i>Assimineia</i> sp	upper-estuarine intertidal mud; mid-estuarine muddy-sand.	uncommon
CERTHIDAE <i>Bittium granarium</i> (Kiener, 1842)	lower-estuarine platform muddy-sand; at site A4.	uncommon, becoming common at that site during the monitoring
CERITHIOPSIDAE unidentified species	lower-estuarine platform muddy-sand; one specimen recorded at A4.	uncommon
DONACIDAE <i>Donax columbella</i> Lamarck, 1818	tidal delta; one recording.	uncommon
HYDROCOCCIDAE <i>Hydrococcus brazieri</i> (Tenison Woods, 1876)	upper-estuarine flat mud; mid-estuarine intertidal sand; mid-estuarine platform muddy-sand.	common
LATERNULIDAE <i>Laternula creccina</i> Reeve, 1860	mid-estuarine intertidal sand; one recording at site C19; lower-estuarine platform muddy-sand; one recording at site A4.	uncommon
LEPTONIDAE <i>Arthritica semen</i> (Menke, 1843)	upper-estuarine intertidal mud; mid-estuarine platform muddy-sand; mid-estuarine intertidal muddy-sand; lower-estuarine platform sand; lower-estuarine intertidal sand; lower-estuarine intertidal mud; deltaic sand; deltaic intertidal sand.	common
LITTORINIDIDAE <i>Bembicium auratum</i> (Quoy & Gaimard, 1834)	at the contact between marshlands and lower-estuarine intertidal deltaic sand, and in mangrove zone.	uncommon
LUCINIDAE <i>Epicodakia</i> sp	lower-estuarine basinal sandy-mud; one recording at site A3.	uncommon
MACTRIDAE <i>Mactra flindersi</i> Cotton, 1938	lower-estuarine platform muddy-sand; one recording at site A4.	uncommon
<i>Spisula trigonella</i> (Lamarck, 1818)	mid-estuarine basinal mud; mid-estuarine intertidal sand; lower-estuarine basinal initially common, mud, lower-estuarine basinal sandy-mud; deltaic sand.	common only at beginning of monitoring; later uncommon
MURICIDAE <i>Bedevea paivae</i> (Crosse, 1864)	upper-estuarine peripheral mud; mid-estuarine basinal mud; lower-estuarine platform sand; deltaic sand.	common-uncommon
MYTILIDAE <i>Mytilus edulis</i> (Lamarck, 1819)	deltaic sand, one recording at site A2.	uncommon

Table 4 (continued). Species listing and their main occurrence in habitats of the estuary.

Species	Main habitats	Relative abundance within habitat 1982-1987
<i>Xenostrobus securis</i> (Lamarck, 1819)	deltaic sand and deltaic intertidal sand.	common for a short period; no longer present at end of monitoring period
NATICIDAE		
<i>Polinices conicus</i> (Lamarck, 1822)	lower-estuarine basinal sandy-mud; several recordings of one or two individuals at site A3.	uncommon
NASSARIIDAE		
<i>Nassarius burchardi</i> (Philippi, 1849)	occurs in all subtidal habitats in the mid-estuarine and lower-estuarine salinity fields.	common
<i>Nassarius nigellus</i> (Reeve, 1854)	lower-estuarine platform sand; one recording in lower-estuarine basinal mud at site A3.	uncommon
PHILINIDAE		
<i>Philine angusi</i> (Crosse & Fischer, 1865)	lower-estuarine basinal sandy-mud one recording at site A3; mid-estuarine intertidal sand, one recording at site C19.	uncommon
PHOLADIDAE		
<i>Pholas australasiae</i> Sowerby, 1849	basinal sandy-mud, one recording at site A3; deltaic sand, one recording at site A2.	uncommon
SANGUINOLARIIDAE		
<i>Sanguinolaria biradiata</i> (Wood 1815)	mid-estuarine platform muddy-sand, lower-estuarine platform sand.	common-uncommon
SCAPHANDRIDAE		
<i>Acteocina</i> sp	upper-estuarine intertidal mud, mid-estuarine intertidal sand.	common
SEMELIDAE		
<i>Theora lubrica</i> Gould, 1861	mid-estuarine and lower-estuarine basinal muds, and lower-estuarine basinal sandy-mud.	uncommon
SOLEMYIDAE		
cf <i>Solemya australis</i> Lamarck, 1818	lower-estuarine platform mud and lower-estuarine basinal sandy-mud.	uncommon
TELLINIDAE		
<i>Tellina deltoidalis</i> (Lamarck, 1818)	common in all subtidal habitats, less common in upper-estuarine intertidal and flat mud.	common
<i>Tellina</i> sp	one recording in upper-estuarine intertidal mud.	uncommon
TRAPEZIIDAE		
<i>Fluviolanatus subtorta</i> (Laserson, 1956)	upper-estuarine intertidal mud; one recording at site D20.	uncommon
VENERIDAE		
<i>Irus crenata</i> (Lamarck, 1818)	deltaic sand, several recordings at site A2; single on lower-estuarine basinal mud, platform sand and platform mud.	uncommon
<i>Kateleysia</i> sp	one recording on lower-estuarine basinal sandy-mud.	uncommon
<i>Venerupis anomala</i> (Lamarck, 1818)	deltaic sand, two recordings at site A2; also single recordings on lower-estuarine basinal sandy-mud, sand and lower-estuarine platform mud.	uncommon
<i>Venerupis galactites</i> (Lamarck, 1818)	lower-estuarine basinal sandy-mud, one recording at site A3.	uncommon

LEPTONIDAE: *Arthritica semen*



LEPTONIDAE: *Arthritica semen*

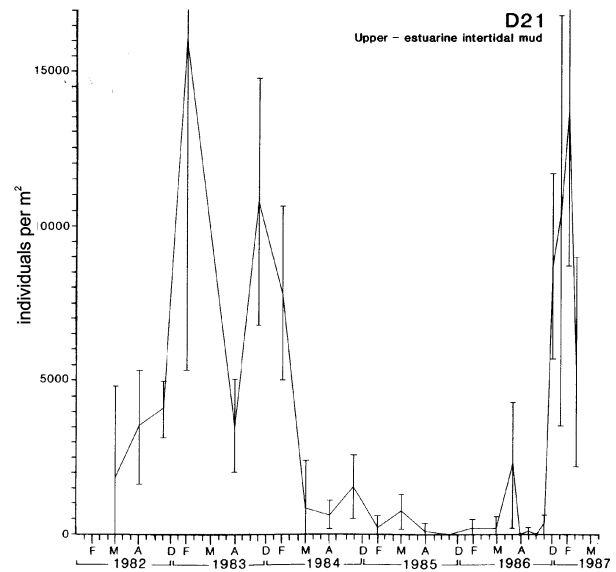
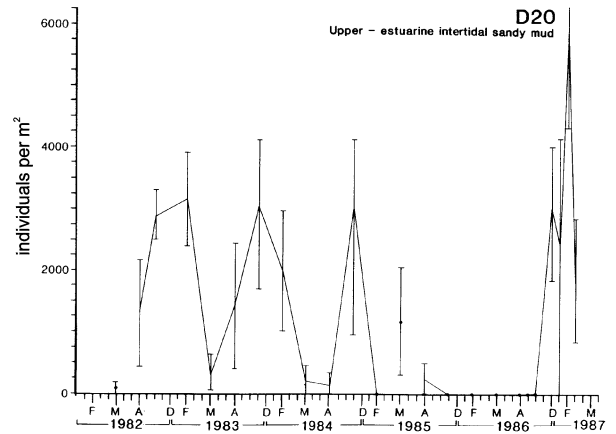
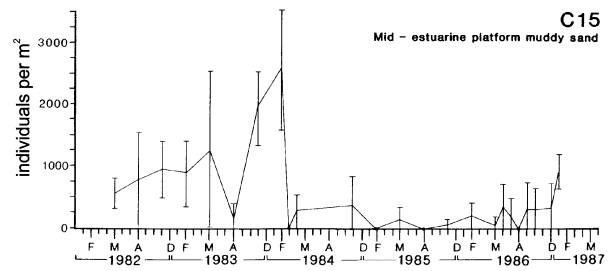
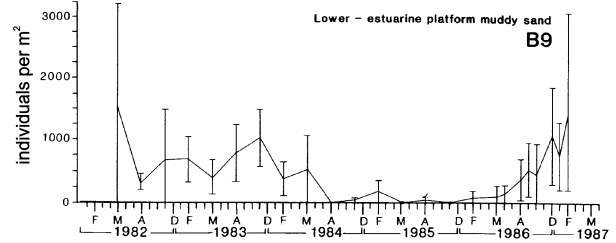
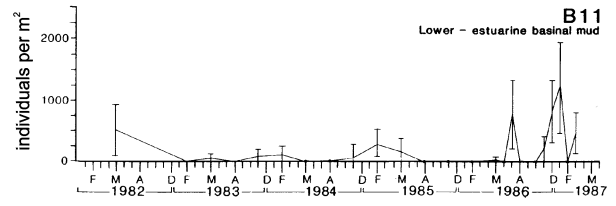
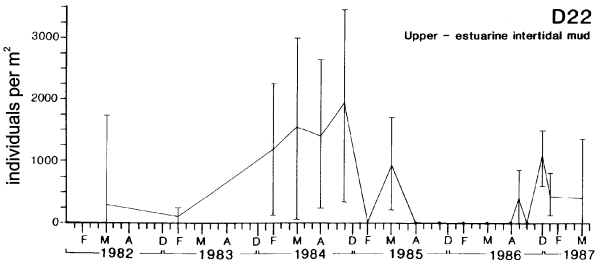
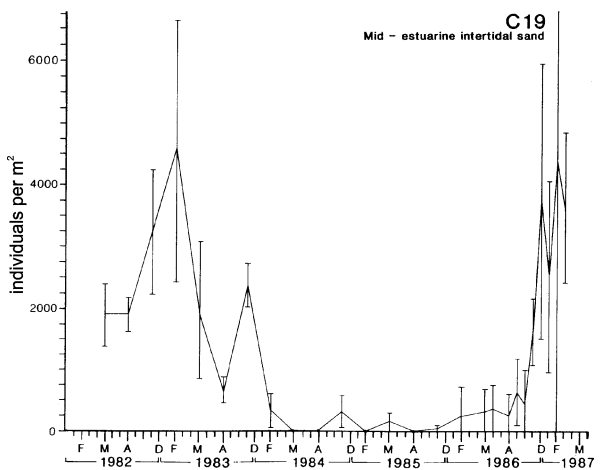
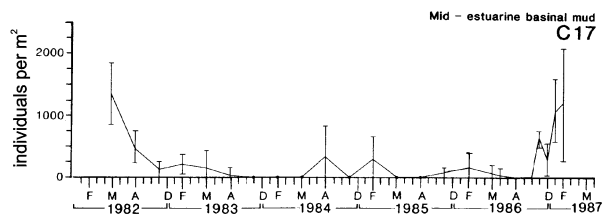


Figure 5. Abundance of individual per m² (mean ± sd) for *Arthritica semen* at the key sampling sites.

TELLINIDAE: *Tellina deltoidalis*

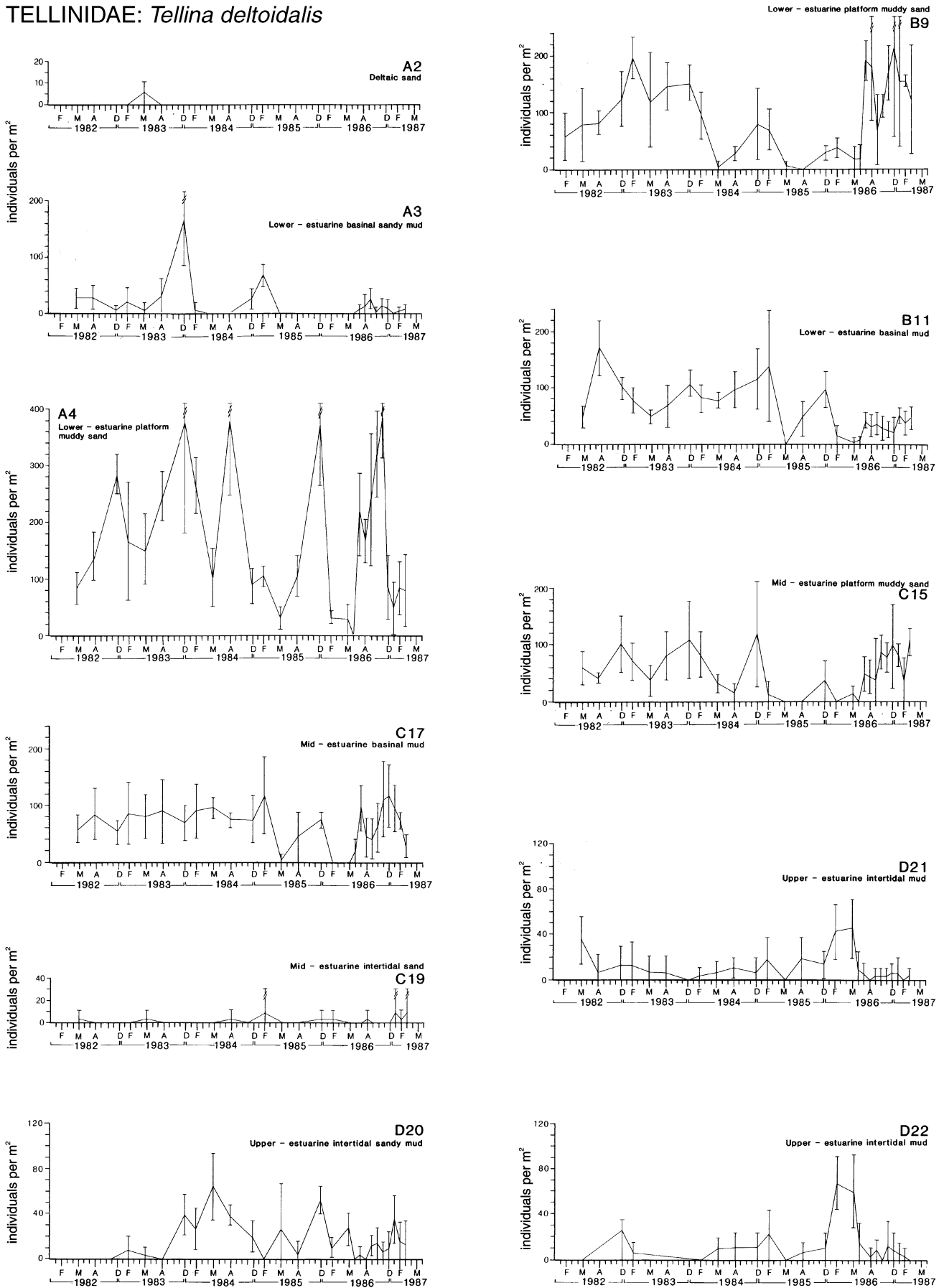


Figure 6. Abundance of individual per m² (mean ± sd) for *Tellina deltoidalis* at the key sampling sites.

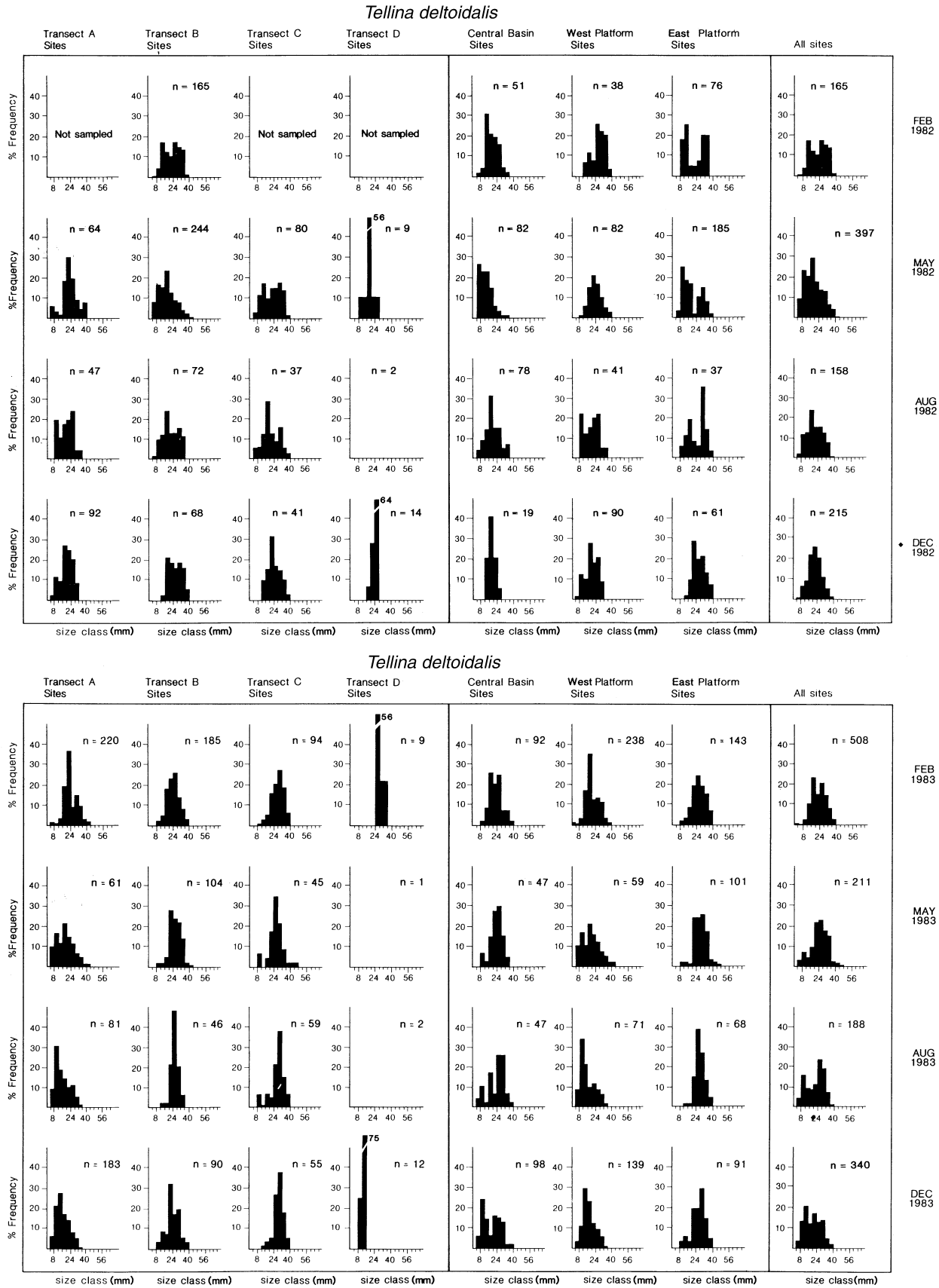


Figure 7. Histograms showing age structure of *Tellina deltoidalis* in relation to large scale habitats, in relation to the transects (reflecting the south to north gradient in the salinity fields), and aggregating all individuals sampled in the estuary. Data are presented only where $n > 3$. Histograms have been constructed where $n = 3$ to $n = 20$ only to show the size distribution of animals in these very low density populations. A value of $n = 0$ indicates the site was sampled but no animals were collected. Each histogram represents data aggregated from several sites, either along a transect, or within a large scale habitat.

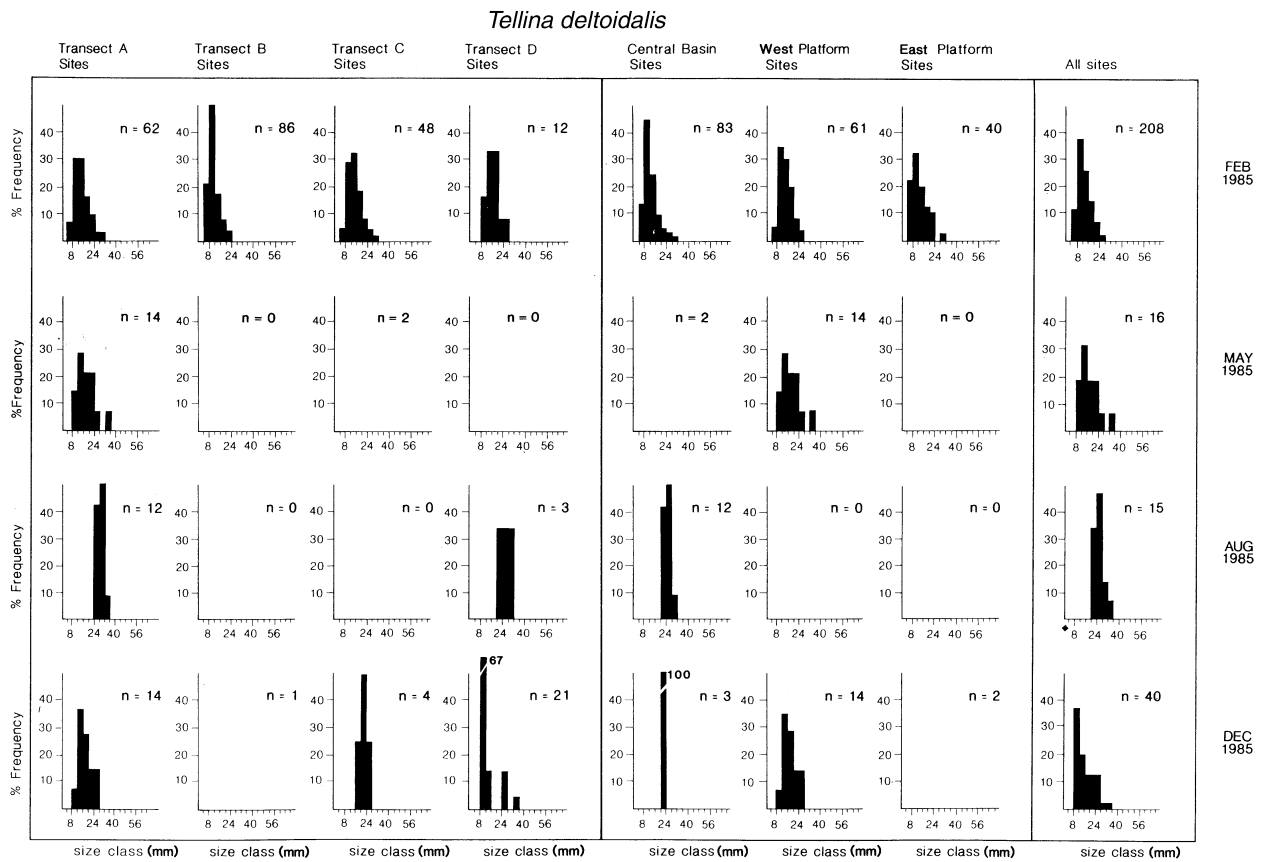
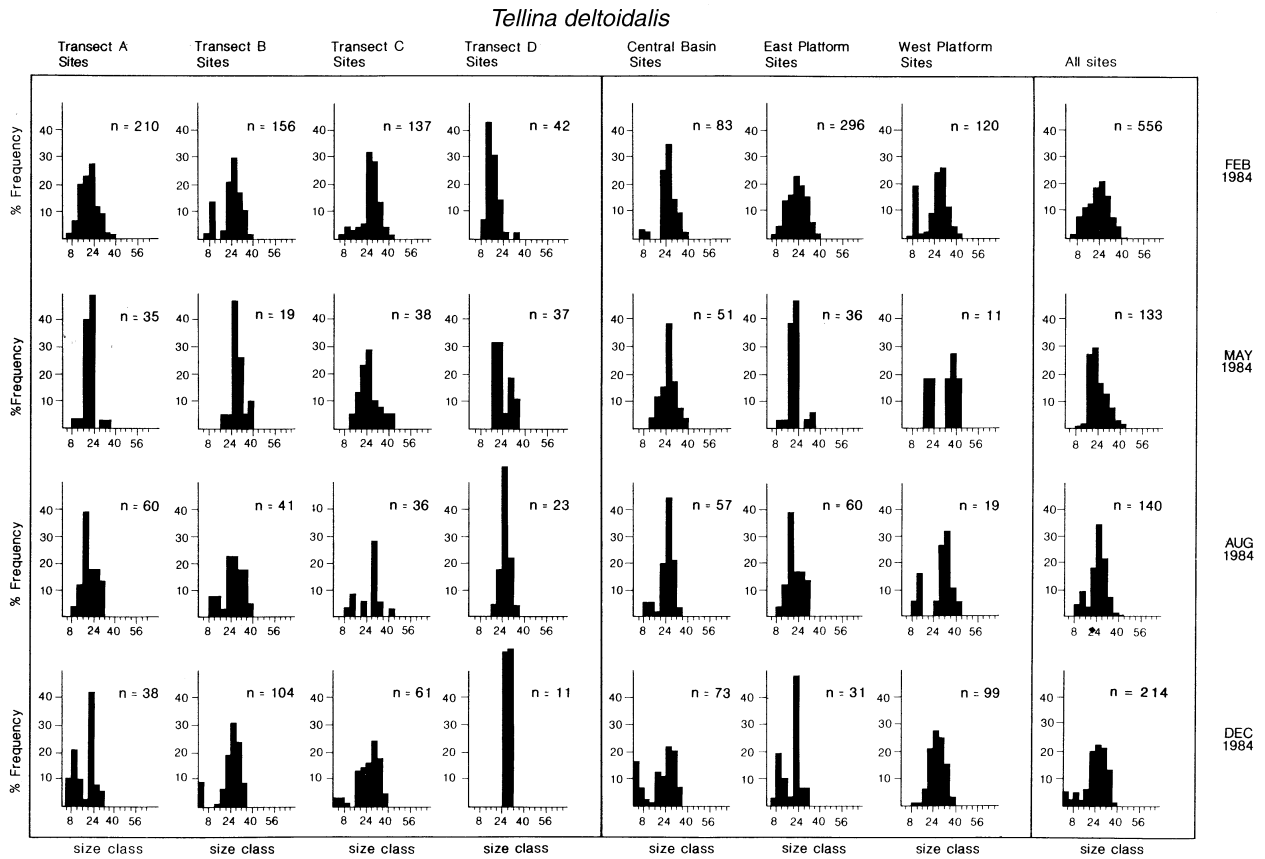


Figure 7 (continued).

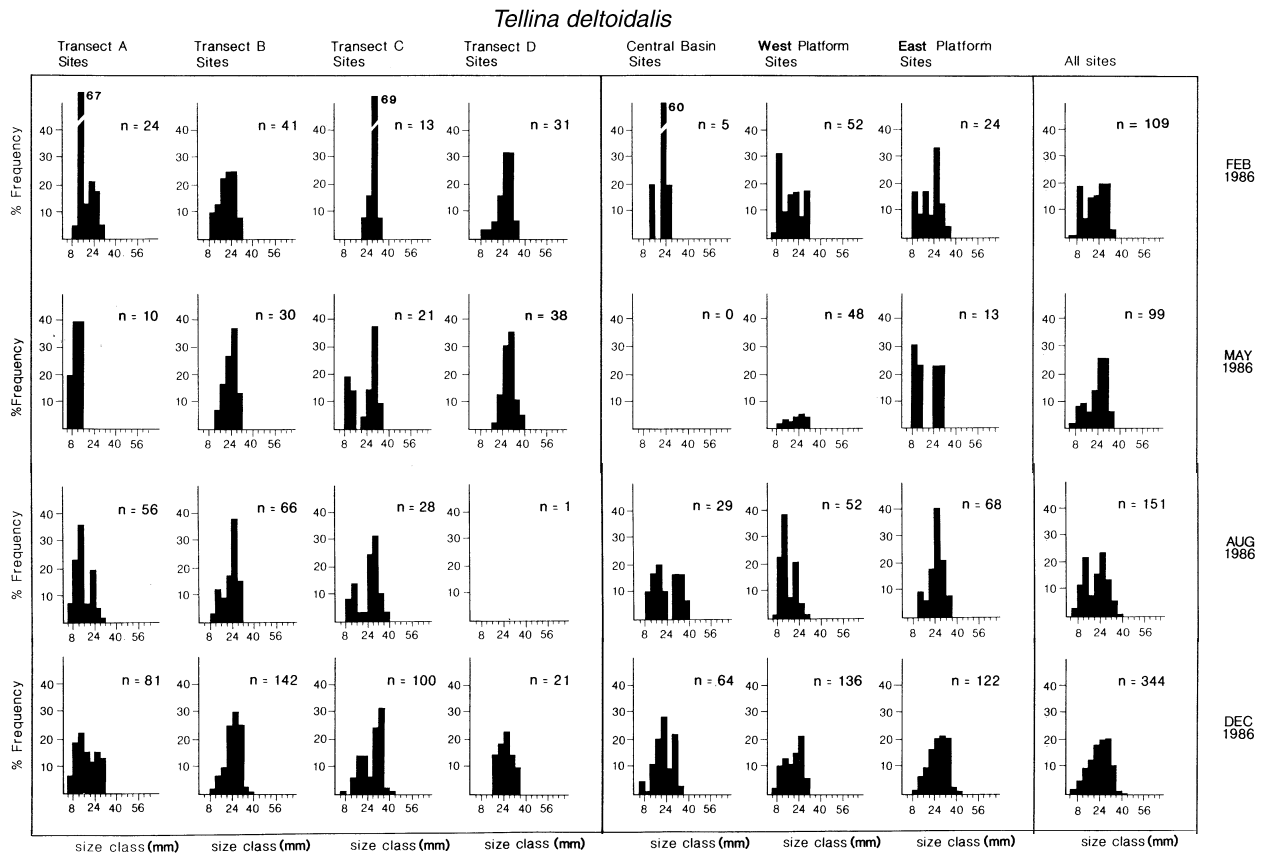


Figure 7 (continued).

deltoidalis was widespread subtidally throughout the estuary. *Bedevea paivae* was relatively widespread subtidally throughout the estuary and in low numbers. *Spisula trigonella* and *Sanguinolaria biradiata* were in low numbers and very scattered in occurrence. *Xenostrobus securis* was restricted to the lower estuary and in low numbers.

Species abundances varied markedly over the course of the study. Even populations of the most abundant and widespread species, such as *A. semen*, *T. deltoidalis* and *N. burchardi*, showed major fluctuations in density within and between sites. In some cases, such as for *T. deltoidalis* and *N. burchardi*, the fluctuations were approximately synchronous. In many cases, population fluctuations appear to have occurred independently of obvious changes in habitat characteristics such as temperature and salinity. For many species, there has been an overall decrease in abundance over the study period such that the relative proportion of species within an assemblage changed over time.

Histograms of size frequency distributions of *Nassarius burchardi*, *Tellina deltoidalis* and *Spisula trigonella* were aggregated in three ways (Figs 7, 9 & 11): from sites along the four monitoring transects, such that population age structures within the various estuarine salinity fields are compared; within large scale habitat sites, i.e. the western platform, eastern platform and central basin, such that population age structures between these habitat types determined by substrate/depth are compared; and as an aggregate of all sites for the whole estuary.

Arthritica semen

Arthritica semen was abundant in all salinity fields, typically occurring within 2 cm of the surface, with 100s to 1000s of individuals per square metre (Fig 5 & 15). It was particularly common on tidal sand (A1, A2, A7, B8, C17 and I43), and on tidal and shallow water mud and muddy-sand (M62, M63, J54, J53, K55, L64, F33 and C15). However, the species was periodically quite abundant within the mid-salinity field at C17, a basinal mud site.

The abundance of *A. semen* varied at almost all sites over the study period. At most of sites of its preferred habitat, *A. semen* was present in relatively large numbers during the initial one to two years of the study, after which population density declined. Populations increased again towards the end of 1986 and beginning of 1987. Sites A2, B9, C15, C17 and C19 best show this pattern. At different sites, abundances decreased markedly and variably during the period 1983 to 1987. Population densities also fluctuated abruptly (e.g. at C15 from December 1983 to February 1984). These longer term trends do not appear to correlate either with any observed trend in the physical and chemical parameters of the habitat, nor with gradients in habitats occurring across the inlet (e.g., in a given year, *A. semen* was most abundant in summer at C19, D20, and more abundant in winter at A2, A4).

NASSARIIDAE: *Nassarius burchardi*

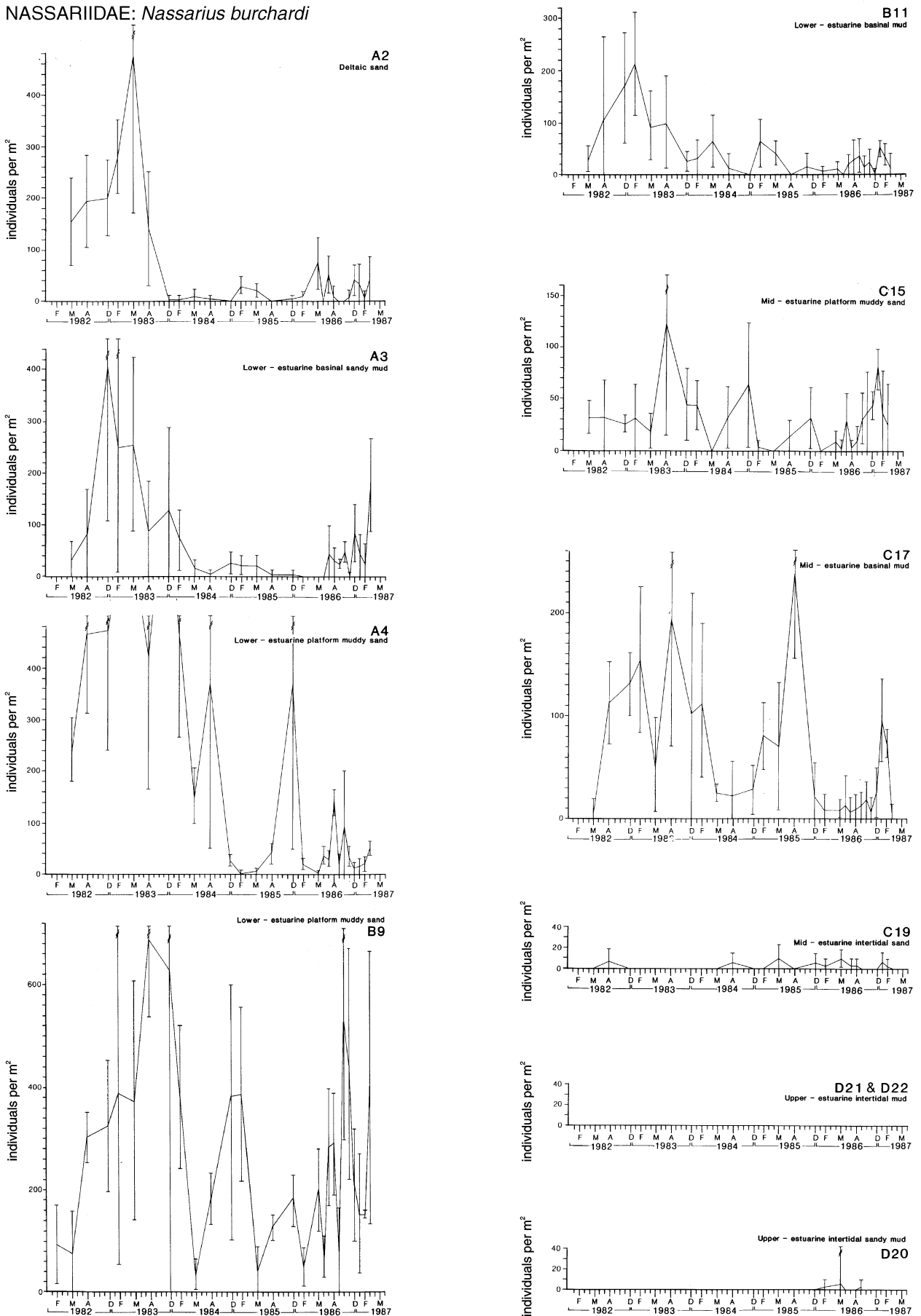


Figure 8. Abundance of individual per m² (mean ± sd) for *Nassarius burchardi* at the key sampling sites.

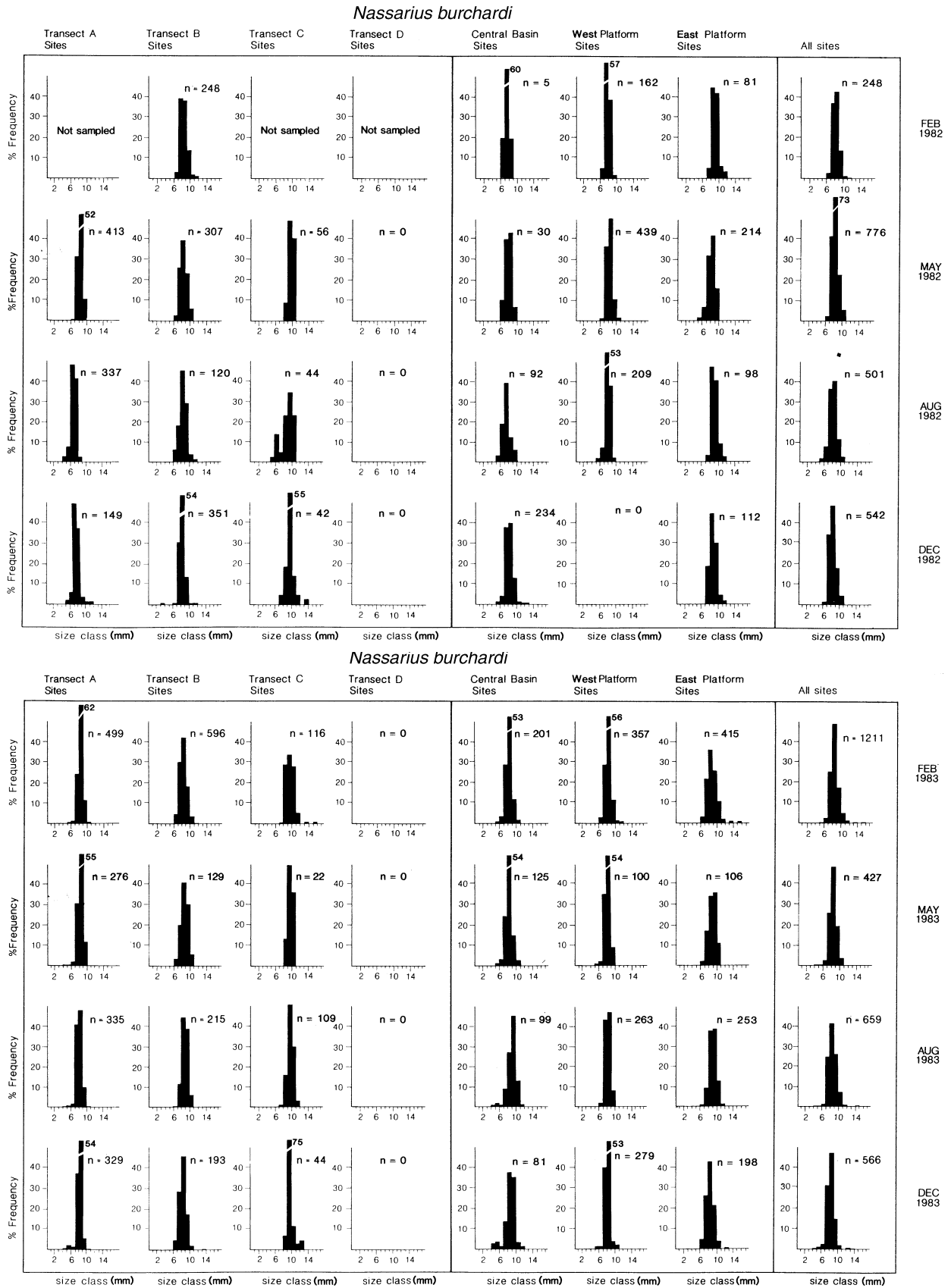


Figure 9. Histograms showing age structure of *Nassarius burchardi* in relation to large scale habitats, in relation to the transects (reflecting the south to north gradient in the salinity fields), and aggregating all individuals sampled in the estuary. Data are presented only where $n > 3$. Histograms have been constructed where $n = 3$ to $n = 20$ only to show the size distribution of animals in these very low density populations. A value of $n = 0$ indicates the site was sampled but no animals were collected. Each histogram represents data aggregated from several sites, either along a transect, or within a large scale habitat.

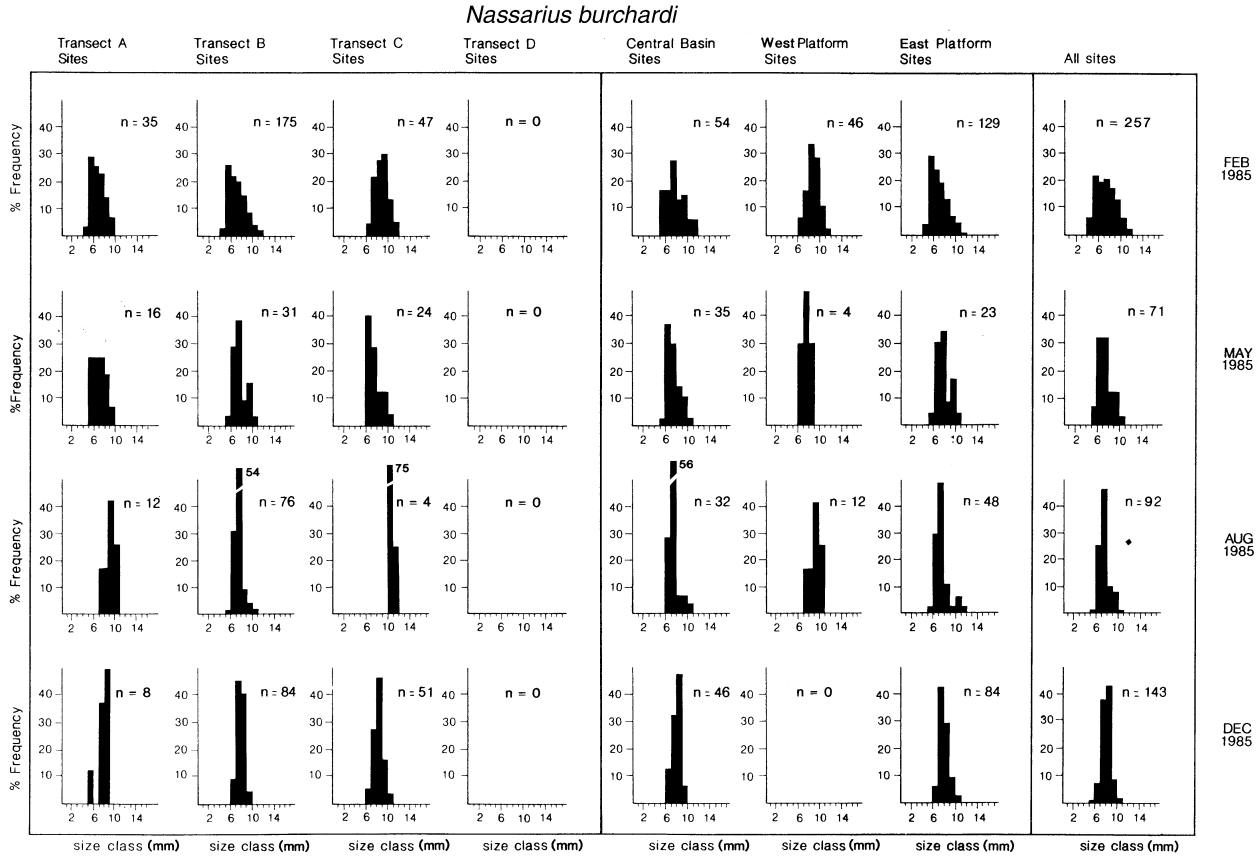
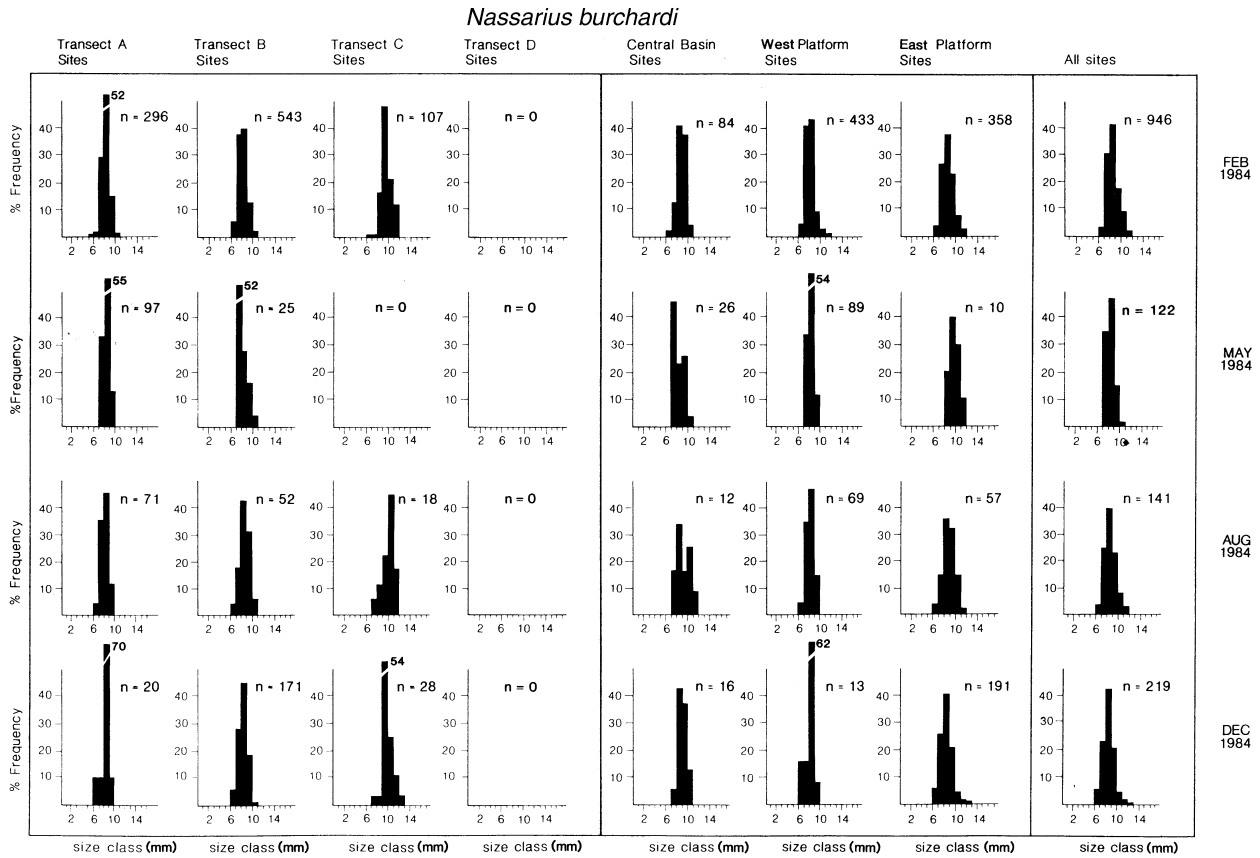


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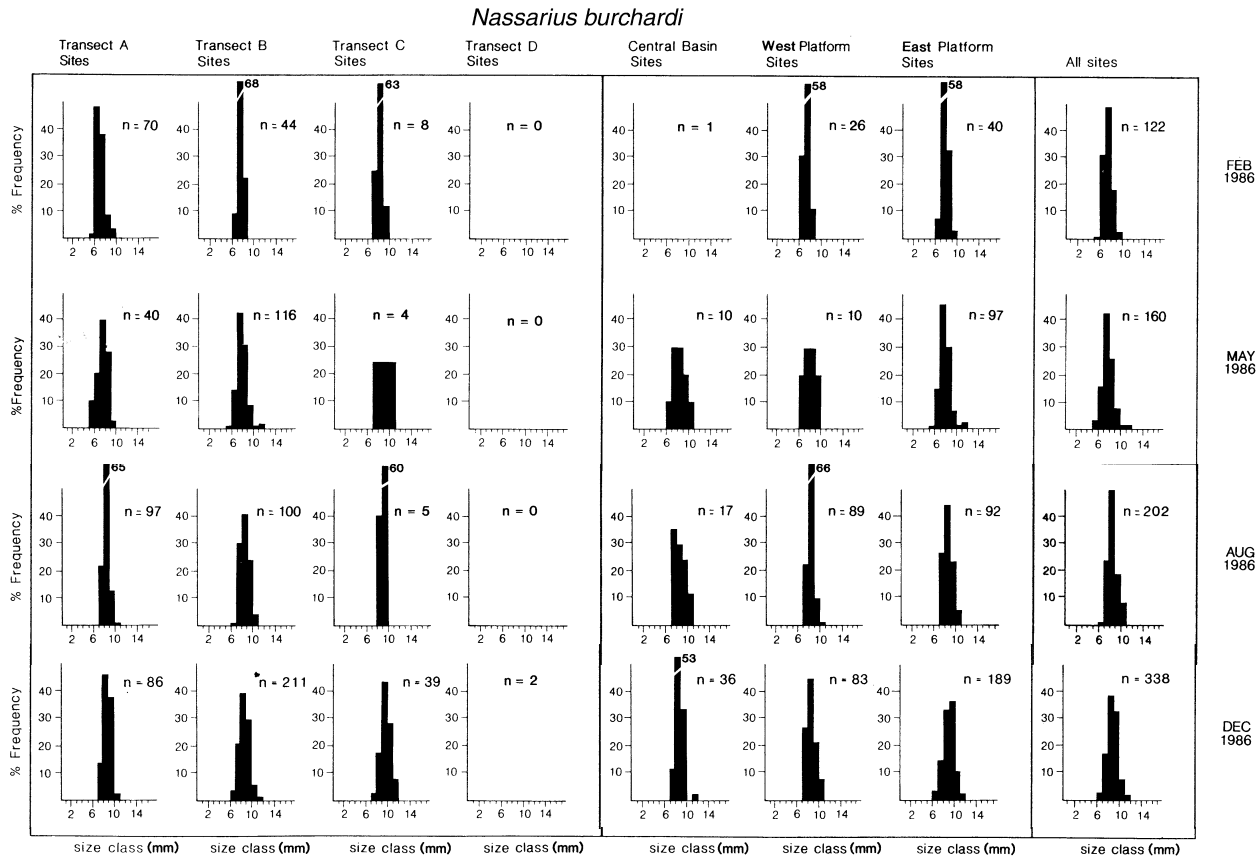


Figure 9 (continued).

Tellina deltoidalis

During the study period, *Tellina deltoidalis* was the most widespread mollusc in Leschenault Inlet, occurring mostly subtidally in almost all substrates, with 10s to 100s of individuals per square meter (Figs 6 & 15). It appears to be euryhaline, occurring in all salinity fields. It was buried to depths of up to at least 25 cm. While inhabiting both muddy and sandy substrates, it was most abundant in vegetated platform muddy-sand sites (A4, A5, E26, J52 and J53), vegetated muddy platform and flat sites (M69, L65, H36, H37, F31, F32), and on some patchily vegetated muddy basal sites (A3, B11, B12, C17, G35, J49 and K60). Although its relative abundance was lower in habitats of the generally depauperate northern flat, it was, nevertheless, a major component of the fauna of this habitat. The species was rarely found in the coarse deltaic sands, or in sites towards the shoreward edge of tidal slopes (e.g. C19, J44, N74, N75, K63, F33 and F42).

Tellina populations exhibit annual cycles of abundance, on lower estuary platform sites (A4 and B9), at a lower estuary basal site (B11), and at a mid-estuary platform site (C15). Seasonally, numbers reached a peak in late winter to early summer and declined during May with the input of fresh water during winter. Other sites show fluctuations in abundance but not in relation to seasonal patterns. Despite the proximity of some sites, fluctuations in population densities of *T. deltoidalis* did not necessarily correspond. For example, fluctuations in abundance at A3 were not synchronous with those at A4, and abundance

patterns at sites along Transect D did not follow the patterns observed along Transects A, B and C. In fact, they exhibited a counter trend to that observed elsewhere with relatively low peaks in abundance in the winter. Along Transect D, however, sites D21 and D22 had similar fluctuations in population density over the period February 1984 to February 1987.

Histograms of size classes of *T. deltoidalis* show four main patterns (Fig 7): the populations generally were primarily of mature individuals (centred on the 12-30 mm size range); juveniles (arbitrarily defined as < 12 mm long) were consistently present; there had been a continuous low-level of non-seasonal recruitment of juveniles during the study period; and although very small juveniles (ca 4 mm size) are generally present in low numbers, they occasionally comprised the majority of individuals at a given site. The size structures, and recruitment patterns were different on the large scale habitats (eastern platform vs western platform vs central basin), and different in relationship to the gradient in the south to north salinity fields. Three of these patterns are amplified with examples as follows: (1). juvenile recruits were found at sites along Transect A between May 1982 and December 1982, at sites along Transect C between May 1983 and August 1983, and at those along western platform between February 1984 and December 1984; (2). there was a change in population structure, with differing sizes and differing proportions of adults and juveniles from east to west across the estuary, as exemplified by the sites within the central basin, those

MACTRIDAE: *Spisula trigonella*

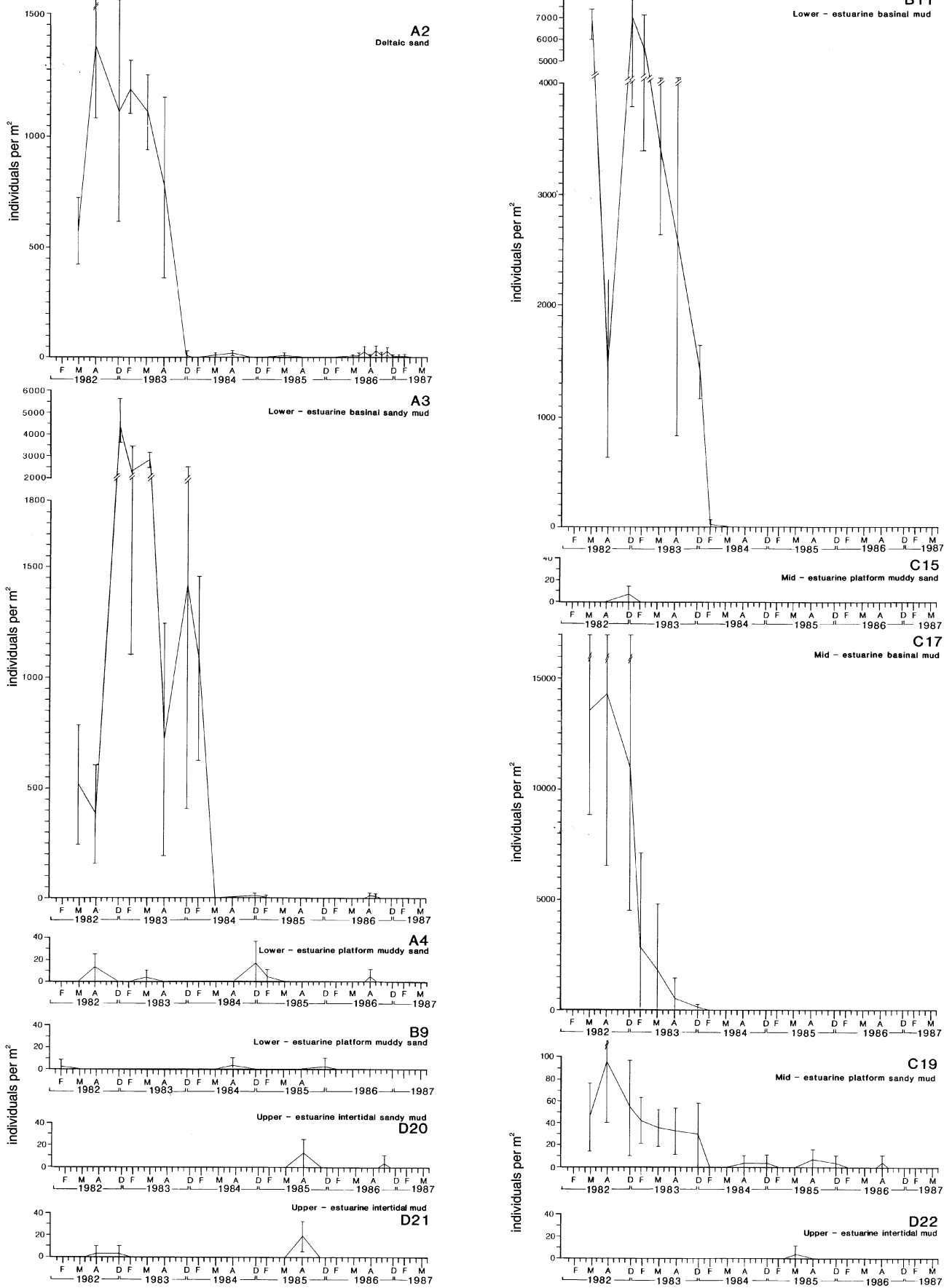


Figure 10. Abundance of individual per m² (mean ± sd) for *Spisula trigonella* at the key monitoring sites.

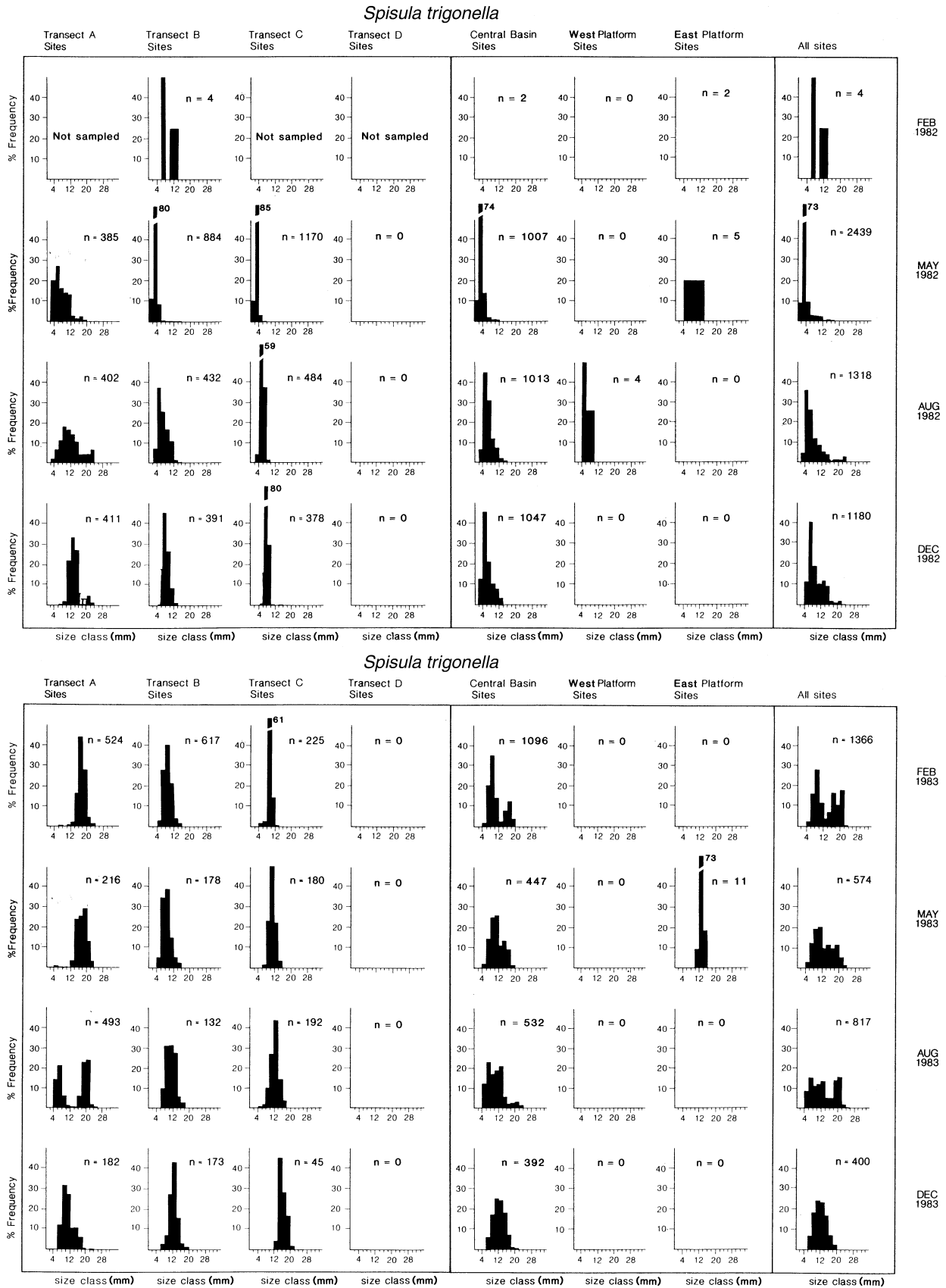


Figure 11. Histograms showing age structure of *Spisula trigonella* in relation to large scale habitats, in relation to the transects (reflecting the south to north gradient in the salinity fields), and aggregating all individuals sampled in the estuary. Data are presented only where $n > 3$. Histograms have been constructed where $n = 3$ to $n = 20$ only to show the size distribution of animals in these very low density populations. A value of $n = 0$ indicates the site was sampled but no animals were collected. Each histogram represents data aggregated from several sites, either along a transect, or within a large scale habitat.

HYDROCOCCIDAE: *Hydrococcus brazieri*

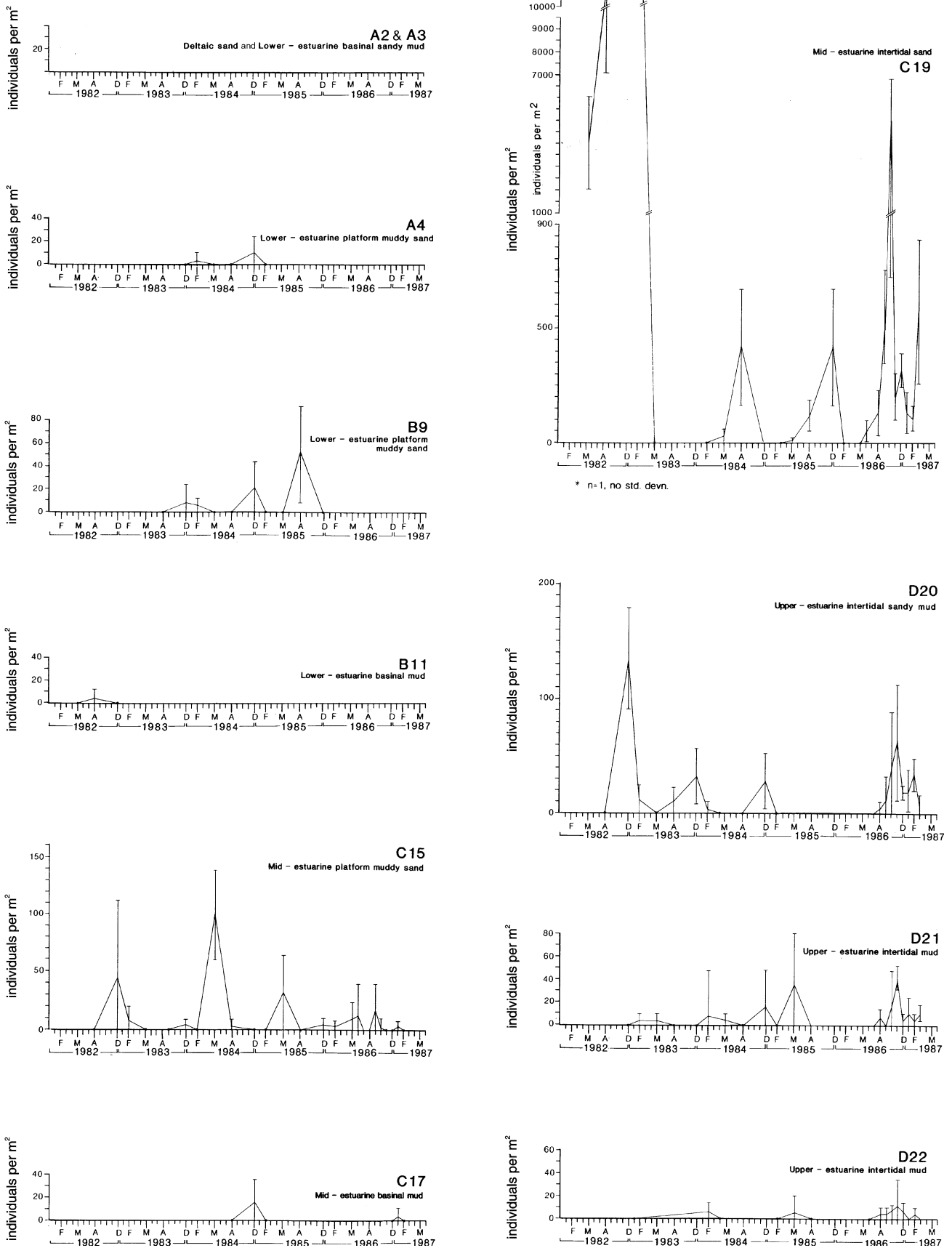


Figure 12. Abundance of individual per m² (mean ± sd) for *Hydrococcus brazieri* at the key monitoring sites.

SCAPHANDRIDAE: *Acteocina* sp.

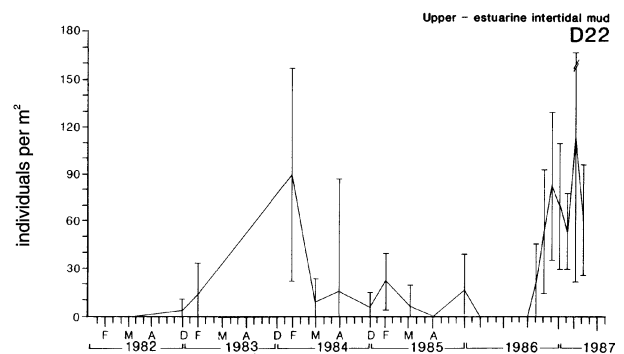
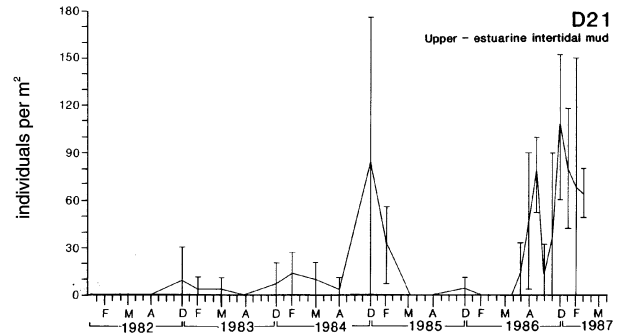
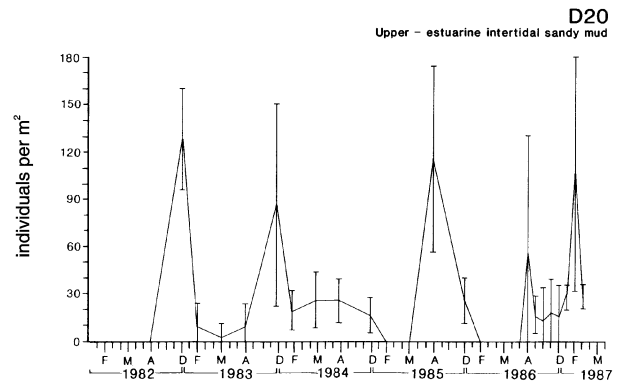
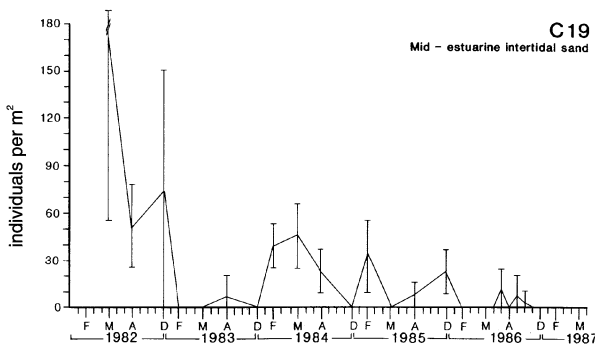
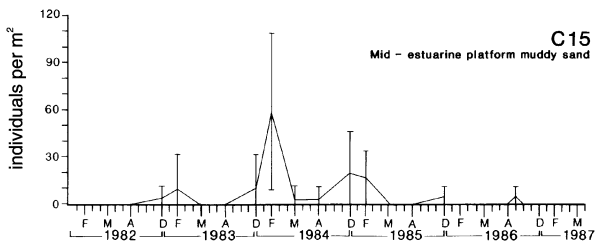
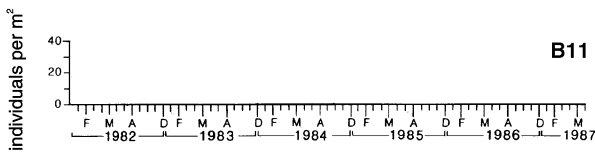
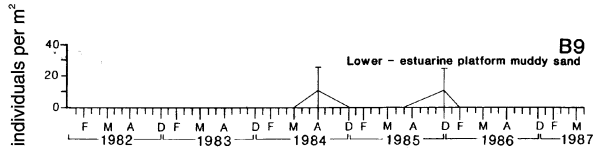
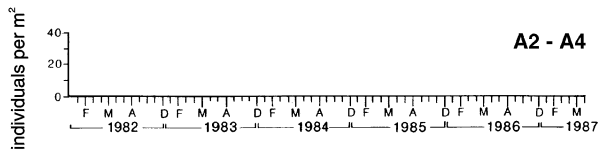


Figure 13. Abundance of individual per m² (mean \pm sd) for *Acteocina* at the key monitoring sites.

MURICIDAE: *Bedevea paivae*

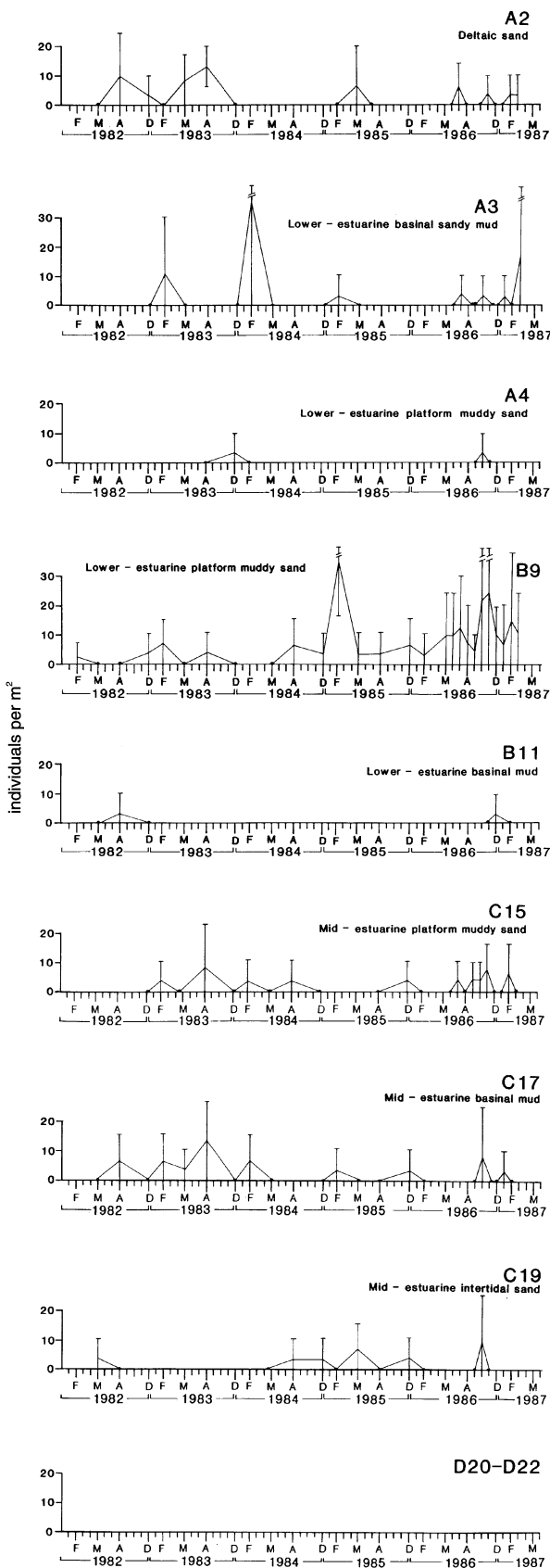


Figure 14. Abundance of individual per m^2 (mean \pm sd) for *Bedevea paivae* at the key monitoring sites.

along the western platform, and sites along the eastern platform for May and August 1982, and for August to December 1983; and (3). there was a progressive growth trend and a shift of the mode of the histogram over the year, as exemplified by sites along the eastern platform between February 1982 and February 1983, those along Transect C between February 1983 and February 1984, and all sites between May 1982 and May 1983.

Using age structure histograms from May 1982 to December 1982 to trace the progressive growth of juveniles over 7 months, and commencing with a clearly bimodal population of adults and recently recruited juveniles present in May 1982, *T. deltoidalis* appeared to have had a growth of *ca* 12 mm over that period, giving an average growth of 1.7 mm per month.

Nassarius burchardi

Nassarius burchardi was common throughout all subtidal habitats, and was consistently present during the study period (Figs 8 & 15). It was most abundant at vegetated sites on eastern and western platforms, occurring in 100s per metre square and was generally absent, or much less abundant, on substrates within the upper estuarine salinity field. There was a decrease in numbers of individuals within the estuary after the first two years of the study (e.g. A2, A3, A4, B10, B11 and B12).

Fluctuations in population density of the species were broadly similar for sites A2, A3, A4, B9, B11 and C17, albeit that the patterns were magnified at sites A4 and B9, and the timing of the peaks of abundance were not exactly in phase. At these sites, *N. burchardi* populations were dense over the period 1982-1983, declined in abundance thereafter, then increased slightly for a short period for part of 1985, and then increased over the period mid-1986 to mid-1987. There was some synchronicity in patterns of abundance for sites A2, A3, A4 and B11.

In this study, *N. burchardi* was more abundant at A4, on well vegetated muddy-sand on the western platform, than at any other site in the estuary. On deltaic sand (A2), the species was most abundant during early 1983; numbers then decreased abruptly after December 1983, and remained low throughout 1984 and 1985. This decline corresponded with a major fresh water influx (< 5 ‰ salinity at A3) during August 1983 (cf Kowarsky 1969; Smith 1975). Along Transect B there was a net decline in abundance from 1982 at all sites except B9 and B14. These latter sites showed reduced numbers during mid 1985 to mid 1986. Along Transect B, the species was most abundant at B9 (a vegetated platform sand habitat). The long-term population densities of the species here were largely maintained, apart from declines in abundance during May in 1984 and 1985. Trends in variation in abundance, however, were not ubiquitous, e.g. there was no net decrease in abundance at B8, B9 and B14, while concurrently there was marked decline in abundance at B10, B11, B12 and B13. Along Transect C, *N. burchardi* was most abundant at C15, C16 and C17, but generally less abundant than at sites along Transect B. At C15 and C17, there was some cyclicity to the fluctuations in its abundance, with a decline in numbers occurring during late summer to winter. Overall, there appeared to be a decrease in

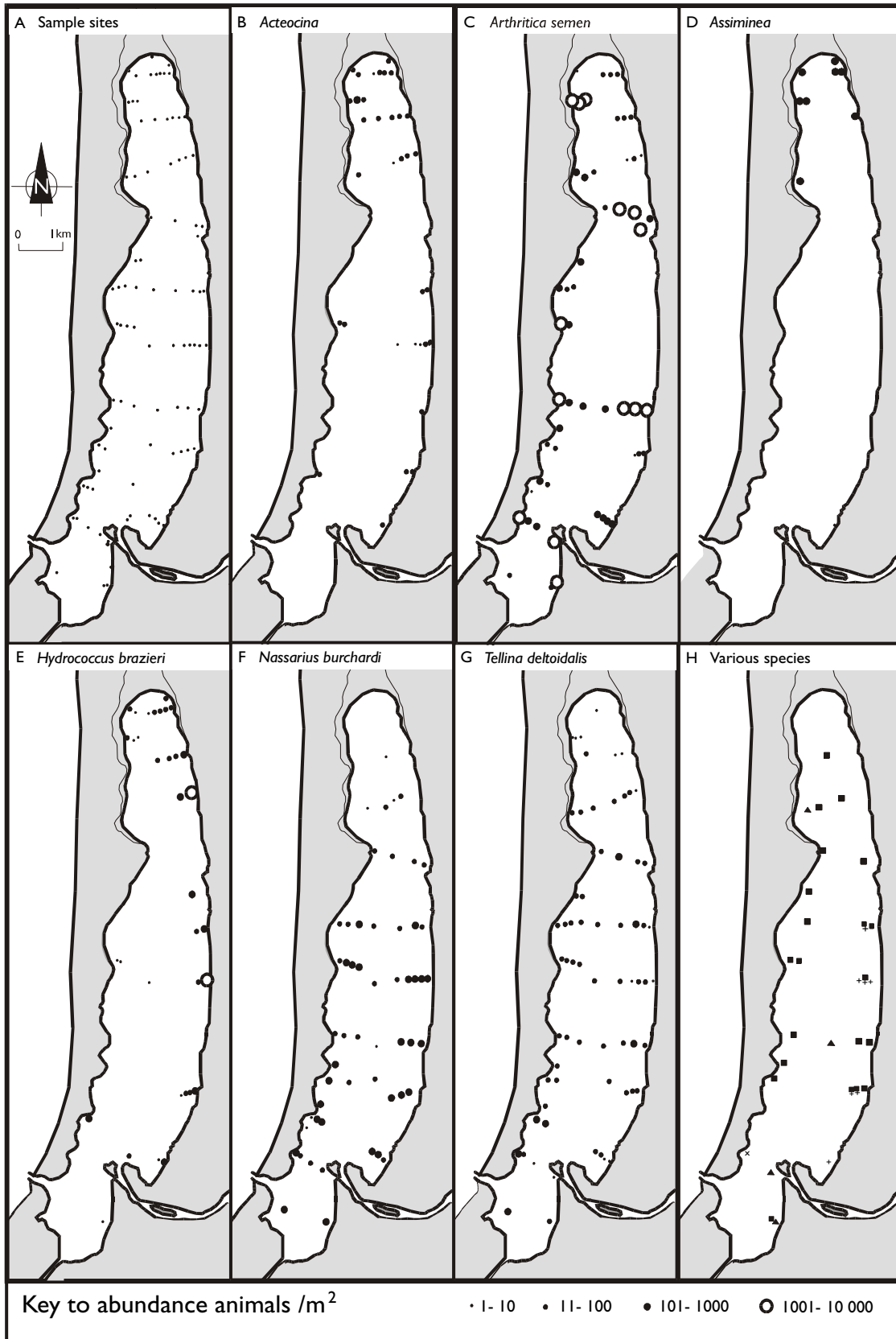


Figure 15. Distribution and relative abundance of key mollusc species in December 1986 (data from Wurm 1987). **A:** Sampling sites. **B-G:** Abundance of animals for a given species. Size of circle reflects relative abundance of animals based on three replicate samples. No symbol at a sampling site denotes zero animals. **H:** Occurrence of various other species, with local population density for each species < 10 / m² (see Appendix 1 for details): *Bedeva paivoe* (black square), *Sanguinolaria biradiata* (+), *Spisula trigonella* (black triangle), and *Xenostrobus securis* (x)

abundance of *N. burchardi*, relative declines in abundance in late summer to early winter, with peaks in abundance in late winter/summer, major fluctuations in abundance at some sites that did not correlate with extremes of salinity and temperature, and cyclicity in abundances.

Histograms of size classes for *N. burchardi* for the various sites show a fairly uniform pattern of unimodal populations, with a mode centred on the 8 mm size class for most of the years of sampling (Fig 9). This mode occurred within all salinity fields and at all sites on all large scale habitats, indicating no growth, and persistence over several years of individuals in the population. Occasionally, there was a minor mode due to the recruitment of juveniles, such as in August 1982 in sites along Transect C, and in August and December 1983 and December 1985 in sites of the central basin and along Transect A, and in September 1986 along Transect A.

Spisula trigonella

Spisula trigonella was very abundant at many sites at the beginning of the study, being most abundant in the basinal mud of the mid and lower estuary, with 1000s of individuals per square metre (Fig 10). *S. trigonella* was also abundant on the tidal and subtidal coarse sands of the Collie River delta system and in the mid tidal sand at C15. It was found only rarely on vegetated sites on the eastern and western platform, and in the upper estuarine salinity field of the northern flat. During the study, its overall abundance in the estuary dropped markedly, such that by 1987 it was uncommon to absent in all habitats.

Along Transect A, *S. trigonella* was most abundant in deltaic sand at site A2, and in basinal sandy-mud at site A3 in the lower estuary. Peak abundance occurred in May 1982. Numbers began to decline by August 1983 and the species was absent by December 1983. At A3, the peak of abundance was not reached until December 1982, three months later than at A2, and numbers declined by August 1983. Maximum decline in numbers did not occur until after February 1984, due to further recruitment of juveniles at the site. By May 1984, *S. trigonella* was almost entirely absent at this site also. At B11, there appeared to be two peaks in abundance, one in May 1982, the other from December 1982 to February 1983. These do not correlate with any observed pattern of juvenile recruitment and may be due to sampling of the spatial variability in animal density. The species was absent at site B11 by February 1984. Along Transect C, *S. trigonella* was most abundant at C17, a mid estuarine basinal mud site. It was more abundant here than elsewhere in the inlet. It also was relatively abundant at C19 on the mid estuarine tidal sand. Elsewhere in the estuary it was generally absent or uncommon on subtidal platform and tidal environments. A similar abrupt decline in abundance began after December 1982 at sites along Transect C and was complete by December 1983, almost a year earlier than at Transects A and B. Along Transect D, *S. trigonella* was most absent. Three patterns, however, are evident: the major recruitment in the lower to middle estuary is reflected in a small population at site D21; small populations of the species appear in May-August 1985, synchronous with site C19; and a small population appears at site D20 between August and December 1986, synchronous with some sites along Transect A.

Histograms of size classes for the species show the patterns of recruitment, and varying growth rates, depending on setting according to large scale habitats and in relation to the south to north gradient in salinity fields (Fig 11). Population structures are variable from eastern platform to western platform to central basin, depending on whether juvenile recruitment had occurred in the given habitat. There was a major juvenile recruitment mainly located in the central basin along all transects in May 1982. Following this, there was a progressive shift in the size mode of the population through time. By December 1982, the populations along all transects were numerically dominated by the age cohort arising from this single recruitment event. There also appeared to have been a smaller recruitment in August 1983 in the region of Transect A, and a possibly a small recruitment in the period between August and December 1985.

The size histograms for 1982 indicate growth rates of *S. trigonella* individuals along all three transects initially to be ca 0.6 mm per month. A difference in growth rate from south to north (Transect A to Transect C) is evident during 1982 and 1983. By December 1983, the numerically dominant age cohort, arising as juveniles at sites along Transect A in May 1982, was predominantly in the 18 to 22 mm range. However, the cohort along Transect B at the same time was 8-14 mm in size, and that along Transect C was 10-14 mm in size. The total population for the inlet in February 1983 showed a bimodal population structure. Traditionally, assessment of the total population from many sites in an estuary is often undertaken by researchers to determine regional population structures and recruitment patterns, and it is in this sense only that the total population was used, to highlight the invalidity of such an approach. The temporal sequence of histograms for *S. trigonella* in the estuary indicates there had been no further recruitment in the estuary, and that the bimodal size structure was due to the rates of growth of animals at Transect C differing from those at the other transects to the south. By May 1983, the two modes began to merge. In August 1983, the population of the estuary was again bimodal, due to the arrival of another cohort of juveniles only at Transect A. This influx of recruits this time is not clearly reflected in the abundance graphs. This latter cohort maintained the presence of *S. trigonella* at A3 into early 1984.

Six individuals of *S. trigonella*, 12-18 mm in size, were recorded along Transect D, in the upper estuarine salinity field, during August 1985. These were obtained from widespread sampling at site D22 (sampling continued until 40 box cores were obtained to ensure that determination of population density was valid). The results indicated that the population was of very low density, and consisted of residual adults. The size range of *S. trigonella* at this time corresponded to an age of approximately one year, based on interpreted growth rates along Transect C. However, the growth rate of individuals was probably even slower along Transect D. Some juveniles, 6 mm in size, were recorded at Transect A in February/May 1985 and in August 1986, indicating that there was some low level recruitment, although not at the scale of the major recruitment event in May 1982.

Hydrococcus brazieri

Hydrococcus brazieri occurred on, or was buried shallowly within substrates, particularly those on tidally exposed surfaces, but also locally on shallow subtidal sites (Figs 12 & 15). The species inhabited specific sites intermittently during the study period, occasionally increasing in abundance to 10s or 100s of individuals per square metre. It was most abundant in mid and upper estuarine salinity fields on tidal sand and muddy-sand (e.g. C19, N74, M73, J44, K63 and F27) but also inhabited some platform muddy-sand (e.g. C15, M72 and J45), and tidal mud in the upper estuarine salinity fields (e.g. D20, D21, D22, O85, O80, N76 and N77). In these latter habitats, it was less abundant and was not consistently present.

H. brazieri was most abundant at a mid estuarine tidal sand site (C19) and its occurrence there is described in detail to illustrate the dynamics in the population. Seasonal peaks in abundance occurred in winter or summer, and there was a consistent annual decline in population numbers during February and May. Overall, there was a general decrease in abundance of the species from a record of 1000s per square metre in 1982. Subsequently, the species was not recorded there between February 1983 and May 1984, and may have been eliminated between January and May 1983 as a result of high salinities (up to 45 ‰), coupled with high summer water temperatures. A search along the strand in the proximal vicinity of C19, to locate another populations, failed to find the species. Similar salinities during summer 1986/87 did not eliminate the species from the site C19, although numbers had decreased, but at this time the temperatures of the water, and of the air where the site was exposed, were lower than those during the 1983 period of high salinity.

At A7, between 1982 and 1985, the species was absent, but made its first appearance in winter 1986, steadily increasing in abundance up to summer 1987. Site A7, located at the distal edge of the Collie River delta, had been naturally modified in late 1985 by an incursion of a sheet of deltaic sand, which built the surface to a higher tidal level. This species progressively colonized the newly accreted surface. At C15, a mid estuary platform muddy-sand site, the abundance of the species varied over five years, with annual peaks occurring generally in mid- to late summer. However these were much lower than at C19. Similarly, at upper estuarine tidal sandy-mud and mud sites (D20, D21, and D22), its abundance varied over the study period, peaking generally in mid to late summer. Sites D21 and D22 appear to show sympathetic fluctuations in population density over the period February 1984 to February 1987.

Acteocina sp

Acteocina sp was most abundant in tidal mud in the upper estuarine salinity fields of the northern flat (e.g. at D20 and D21), forming populations of several to 10s to 100s of individuals per square metre (Figs 13 & 15). It also inhabited tidal sand (e.g. at C19, B8, H42 and F27). *Acteocina* was most consistently present at C15, C19, D20, D21 and D22. Its abundance fluctuated, generally being more abundant during summer, although locally reaching peak

abundance at some sites in winter or autumn. At C19, there was a nett decrease in abundance over the study period, with peaks in abundance occurring during late summer to winter. At C15, although *Acteocina* was in relatively low numbers, there was a general increase in abundance in summer.

Other less abundant species

Species which were present throughout the study period, but in low numbers, included *Assiminea* sp, *Bedevea paivae*, and *Sanguinolaria biradiata* (Fig 15). While overall *Assiminea* sp was not common in this study, in general it was consistently present in low numbers, mostly inhabiting tidal to shallow water sandy-mud and mud habitats along Transect D, and sites O87, O86, O85, O80, N74 and M66 in the upper estuary. The most southerly occurrence of the species was on shallow vegetated muddy-sand at C15. *Bedevea paivae* occurred in many habitat types, generally in low abundance (Figs 14 & 15). It mostly inhabited platform sites B9 and B10. Locally, it inhabited upper estuarine habitats (e.g. N77, M68 and M69). There was a continued presence in the estuary during the study period, with no correlation in fluctuations in abundance and measured environmental parameters. A localized population of *Xenostrobus securis* became established in coarse sands of the Collie River delta in August 1982. It increased in density the following summer, reaching a peak in abundance when surrounding salinity approximated sea water, and when the water temperature would have been high (ca 25-28 °C). The population was absent by August 1983. Other populations were found at A4 in December 1983 and A5 in December 1986. *Sanguinolaria biradiata* was present throughout the study period and across much of the estuary, but in low numbers, occurring most commonly on peripheral sand or muddy-sand substrates in the mid estuarine and lower estuarine salinity fields.

Discussion

Habitat type and mollusc distribution

The dynamic and varied nature of the Leschenault Inlet estuary has produced complex responses of the biota, in the patterns of abundance and population maintenance, and although most of the more abundant species occurred at least rarely in most habitat types, the relative abundance of a given species clearly corresponded with a habitat type(s) and substrate (Table 4). For example, *A. semen* and *H. brazieri* were predominantly tidal-substrate inhabitants in all salinity fields. *S. trigonella*, when abundant in the estuary, occurred selectively on substrate types which were unvegetated in the mid estuarine, lower estuarine, and deltaic salinity fields. *B. paivae* occurred in all salinity fields, predominantly on shallow water platform substrates, rather than on deep water basinal or tidal substrates (notably, *B. paivae* normally is found on hard substrates, but in Leschenault Inlet estuary it inhabits sandy and muddy sand substrates). *Tellina deltoidalis*, although common in all subtidal habitat types, occurred most abundantly in well vegetated platform substrates in the mid and lower estuarine salinity fields. *Nassarius burchardi* also was common in all subtidal habitats, being most

abundant in well vegetated platform habitats in the mid and lower estuarine salinity fields. *Sanguinolaria biradiata* occurred most commonly on peripheral sand or muddy-sand substrates in the mid estuarine and lower estuarine salinity fields. Ultimately the distribution of a particular species may be determined by smaller scale phenomena which may occur within those units identified at the large scale, however, species distribution may also transcend identified habitat boundaries, or occur as zones or mosaics within them.

Salinity and temperature generally are important factors limiting mollusc distribution. Salinities of 60 ‰ and temperatures of up to 32 °C occur in summer in the upper estuarine salinity field, and these would be limiting for even the truly estuarine species *A. semen* and *H. brazieri* (Wells & Threlfall 1982a). Elsewhere in the estuary, the range of salinities and water temperatures begin to delineate mollusc assemblages of marine affinity at one extreme, and those of truly estuary character at the other. Oxygen concentrations rarely fell below 6 mg L⁻¹ during this study, and thus does not appear to be a limiting factor. Even so, estuarine fauna are known to adapt to low oxygen tensions and cope with dynamic estuarine through an ability to conform their consumption to ambient oxygen levels or to rest during low oxygen concentrations (e.g. Hammen 1976).

The main distribution over the medium term of the key mollusc species with respect to bathymetry and habitat, and in relation to the estuarine hydrochemical field in the Leschenault Inlet estuary is summarised in Fig 16. Mixed mollusc assemblage occurred in the basin environment and *X. securis* occurred in shallow water, both in the lower estuary. *Acteocina* was restricted to the tidal and shallow tidal habitats mainly in the upper estuary. *H. brazieri* and *A. semen* were located mainly in tidal habitats throughout the estuary. *T. deltoidalis* and *N. burchardi* were widespread throughout the estuary, occurring in nearly all habitats. *B. paivae* was present on shallow water platforms in middle to lower estuary, and in the shallow water subtidal of the upper estuary. *S. biradiata* was mainly restricted to the eastern platform and intertidal of the middle estuary. *S. trigonella*, when it was abundant, inhabited the basin of the middle estuary and the basin of the lower estuary and shallow water to tidal zone of the delta.

Abundance and population dynamics

This study provides a perspective of changes in mollusc abundance over 5 years in the Leschenault Inlet estuary and an insight into their variability and longevity. For instance, some species have been consistently present, although abundances varied seasonally, whereas the presence of others fluctuated markedly. While the overall character of the mollusc assemblages in the estuary over the study period remained similar, there also have been significant changes from year to year, and from season to season. Despite the medium term nature of this study, the reasons behind the patterns of abundance in populations of the molluscs were not readily identified. In most cases, the abundances of a given species fluctuated independently of others, and for many species did not appear to directly relate to seasonal patterns in salinity, temperature, or oxygen concentration. For some short-lived species, the

timing of peaks in abundance occurring after a decline in population density may be determined by the rate of the extra estuarine recruitment of juveniles, which may not necessarily directly correlate with ideal environmental conditions in the estuary. Some of the variation in abundance in time may be an artifact of sampling patchy populations.

Population structures and their temporal variation were different for the three species investigated. *Spisula* was numerically dominated by one age cohort which progressed in time from juveniles to adults, and was not maintained significantly by further recruitment. *Tellina* appeared to be maintained by a relatively continuous low level of juvenile recruitment, and *Nassarius* was dominated by a persistent mature age cohort, with an intermittent low level of juvenile recruitment which did not maintain the size of the population at its initial level.

Population structures for a given species were also different in relation to habitats, viz. recruitment patterns could be different from western to eastern platforms, from the central basins to the shallow water platforms, in response to the south to north salinity fields, and even within the one habitat setting, from site to site. This indicates that there are significant intra-estuarine determining factors that can regulate the population dynamics of mollusc species on a habitat to habitat basis, and within a habitat, on a site to site basis. As such, it is clear that recruitment patterns and population maintenance patterns are not similar estuary-wide.

In summary, the interpretations and discussion that follow suggest that the various mollusc species are responding independently and in different ways to the varied estuarine environment. The mollusc fauna was comprised of a group of species sharing a common habitat but differing in their life strategies and population maintenance mechanisms (e.g., of a range of species cohabiting the same environment: *Bedevea* is a carnivore, *Tellina* is a detrital feeder, *Nassarius* is a scavenger; cf Morton & Britton 1991), a factor noted by Wells & Threlfall (1981). Although the distribution of a particular species was correlated with one or more habitat types, the size of the population of a given species, with time, varied markedly within habitats. Consequently, for a realistic indication of the presence and relative abundance of each species in a given assemblage or habitat, populations or habitats must be sampled through time at least over the medium term. For the more common mollusc species, patterns of distribution, abundance, and population dynamics, and summary of the literature on their autecology as it relates to Leschenault Inlet are discussed below.

Arthritica semen

In the Leschenault Inlet estuary, *A. semen* was abundant in all salinity fields, particularly in tidal mud and sandy-mud substrates. Its abundance varied over 5 years, from a peak early in the study, to low levels shortly thereafter, to an increased abundance late in the study. The species appeared tolerant of high salinities and temperatures, and patterns in its abundance did not correlate with extremes in water parameters. Clearly some other factors had influenced its abundance. Natural patchiness could be one

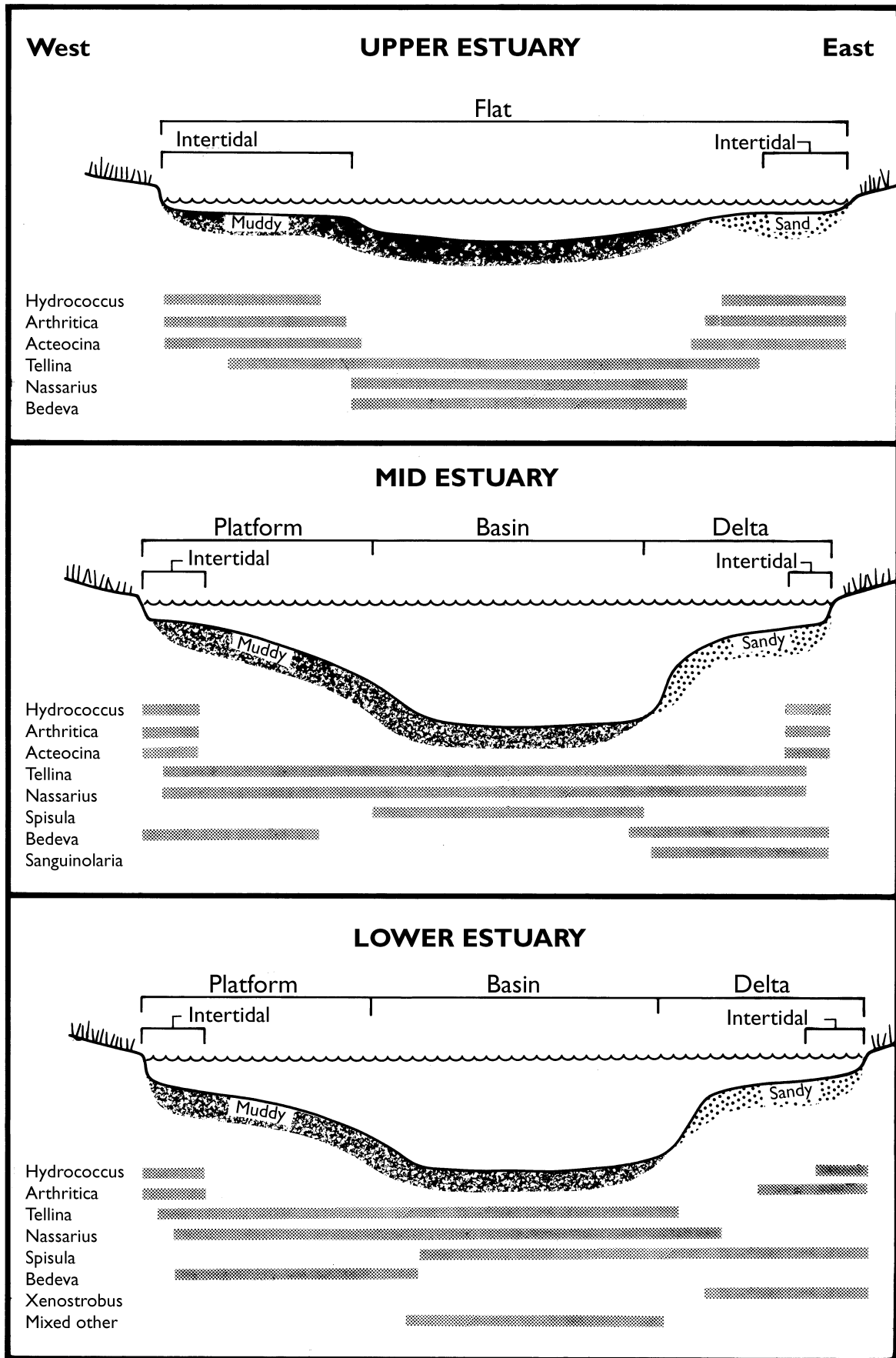


Figure 16. Summary schematic illustration showing the main molluscs and their distribution across the main habitats from lower estuary to upper estuary.

explanation, predation could be another. Fish, for example, are known to prey on small molluscs (Potter *et al.* 2000).

Studies of reproduction over two years in the nearby Peel-Harvey estuary system by Wells & Threlfall (1982b) showed no seasonality in breeding, with animals in the field reproducing almost continuously. The number of females brooding and the number of juveniles varied between months with no seasonal correlation. Larvae were found to undergo several developmental stages in the brood pouch, and shelled juveniles are released directly from the female, with individuals reaching maturity after 6 months and maximum size in 9 months, with a probability some animals surviving for a second year (Wells *et al.* 1980; Wells & Threlfall 1982c). This is relevant to the situation at Leschenault Inlet, as it explains the ever-present large numbers of individuals within the populations.

A. semen occurs elsewhere in south-western Australian estuaries, from Albany to Moore River. Information useful to interpreting the population dynamics of the species in the Leschenault Inlet estuary is provided by such studies elsewhere. For example, the species is abundant on shallow-water sand flats in the Swan River Estuary (Ashman *et al.* 1969; Chalmer *et al.* 1976) and in the Peel-Harvey Estuary (in densities up to thousands m⁻²; Wells & Threlfall 1982c). During monthly monitoring over 2 years in the Peel-Harvey Estuary, the density of individuals varied markedly from month to month with no apparent correlation with season. Changes in abundances were abrupt, with numbers of individuals dropping from 45 491 m⁻² to 4 893 m⁻² in several months (Wells & Threlfall 1982c). In laboratory experiments, *A. semen* tolerated a wide range of temperatures and salinities (Ashman *et al.* 1969; Wells & Threlfall 1982a), remaining active between 18 °C and 32 °C, and at salinities of 10 ‰ to 54 ‰, though the effects of high temperature and high salinity act synergistically to cause inactivity. The species was also able to survive salinities < 10 ‰ and a median lethal temperature of 37 °C, simulating the extremes in winter and summer conditions. These results corroborate and help explain the patterns of the population dynamics of the species in the Leschenault Inlet estuary.

Tellina deltoidalis

Tellina deltoidalis was widespread in the estuary in all subtidal habitats except that of the Collie River delta. It was less abundant in the upper estuarine salinity field but was still a dominant component of the low intertidal and subtidal habitats there. The species was most abundant in vegetated muddy substrates of the eastern and western platforms in the mid and lower salinity fields. The distribution of the species suggests a tolerance of a considerable range of salinities, *e.g.* in the period 1986-1987, in the northern part of the estuary the species tolerated salinities from 21-62 ‰, while in an area marginal to the deltaic field in the southern estuary it experienced salinities of 21.5-32.5 ‰. At most sites, at some sampling times, there was a general trend of declining abundances during May, which correlated with winter fresh water influx. However, the low level of recruitment makes fluctuations in abundance at the various sites difficult to interpret, as they may not be due to mortality and subsequent replenishment

of the population by juvenile recruits. Some apparent fluctuations in population density may be an artifact due to the heterogeneous distribution of the species within a habitat, rather than true fluctuations through time, however, changes in mean abundance and lack of overlap in the standard deviation at many sites, and the synchronous nature of the fluctuations between some sites suggests otherwise. The synchronous fluctuations in population density at sites D21 and D22 over 1985 to 1987 may be due to the fact that the northern basin, with more restricted circulation generates a relatively homogeneous large scale habitat that results in similar widespread response in the species. Unlike many other species in the estuary, *T. deltoidalis* did not exhibit a decline in the abundance during the study.

The histograms indicate that there is periodic juvenile recruitment, and a progressive shift in the mode of shell sizes as the individuals grow and mature. Further, the age structures from the different environments (*e.g.* platforms sites *vs* basins, lower estuarine sites *vs* middle or upper estuarine sites) show slightly to markedly varying structure and history, suggesting there is a range of factors regulating the populations (*viz* the varying relative importance of mortality due to factors of the physical environment, mortality due to disease, predation, and possibly migration between habitats). The appearance of juveniles in August 1982 along Transect C, in August and December 1983 along Transect A and in the central basin, in August 1985 along Transect A, and in September 1986 along Transect A appears to correlate with some peaks in population density for those times (*e.g.*, the August 1982 recruitment coincides with increases in population density at sites A3, A4, B11, C17; the the August and December 1983 recruitment appears to coincide with a lagged increase in population densities at sites A3, A4 and C17; the December 1985 recruitment appears to coincide an increase in population density at A4). For the most part, however, the appearance of juveniles did not always correlate with peaks in population abundance, and so it is difficult to interpret some of the abundance variations. Population age structures indicate that the populations were maintained by a continuous but sporadic low level of juvenile recruitment.

Tellina deltoidalis is common from Queensland to Western Australia, including Tasmania (Wells & Bryce 1985). Chalmer *et al.* (1976) listed *T. deltoidalis* as a continuous and common resident of the sand flats of the lower and middle parts of the Swan Estuary, and also noted that it is occasionally collected in the sea near Fremantle. Wells & Threlfall (1981) recorded it on shallow water sand flats in the Peel-Harvey Estuary. Chalmer & Scott (1984) recorded it in Leschenault Inlet during their 1974 survey. The seasonal pattern of decline in abundance of the species is probably not related to seasonal senescence of mature individuals but perhaps to predation, as their shallow subtidal habitats do not exhibit extremes of temperature and salinity. Also, studies in the Peel-Harvey Estuary show a seasonal pattern of microalgal blooms in late winter to early summer, driven by an influx of nutrient-rich fresh water during winter (*e.g.* Lukatelich & McComb 1983; Lukatelich 1986). This pattern of algal response to an influx of nutrients may occur in Leschenault Inlet although at a

reduced level, *i.e.* nutrients are imported into the estuary, and generate short term phytoplankton blooms seasonally, or phytoplankton are transported into the estuary from the drainage basin during winter (Hosja & Deeley 2000). If so, nutrient influx, or fluvial delivery of phytoplankton, would result in a seasonality in food supply for suspension and deposit feeders, and may explain the apparent seasonal trends observed for the species. For the northern sites, along Transect D, the conditions during summer of high salinities and temperatures would presumably be an additional limiting factor for the species in this hydrochemical zone.

Nassarius burcharidi

Nassarius burcharidi was ubiquitous in the Leschenault Inlet estuary, even moving into tidal habitats during high tide, but was uncommon in the upper estuarine salinity field. Population densities of *N. burcharidi* fluctuated independently of trends in environmental parameters. Also, there was a decline in the abundance of the species in the estuary since the beginning of the study, particularly noted along Transect A. The population had been composed primarily of mature individuals, and the sporadic, low level juvenile recruitment which occurred but was insufficient to maintain the population at its original levels of abundance. This pattern of population maintenance contrasts with the results of Smith (1975) in the Swan Estuary where populations were maintained by two spawning seasons per year, despite an annual decrease in numbers following seasonal fresh water input. The population structures in Leschenault Inlet suggest that the species is relatively long lived, with stable adults and low levels of recruitment, or that its juvenile phase is a short-lived, rapidly-growing phase (similar to that proposed by Wells & Keesing 1997 for *Haliotis roei*).

N. burcharidi is common elsewhere in many south-western Australian estuaries and locally in marine environments (Smith 1975; Chalmer *et al.* 1976; Wallace 1975; Chalmer & Scott 1984). The species was recorded in Leschenault Inlet in 1973 by Smith (1975) and in 1974 by Chalmer & Scott (1984). Kowarsky (1969) and Smith (1975) studied *N. burcharidi* in the Swan River Estuary, where it inhabited all substrate types at all depths, though it was eliminated from the shallow sand flats by fresh water during winter where salinities are > 7 ‰. Smith (1975) suggested that deep water populations provided adult and sub-adult immigrants and larvae which repopulate the shallow water flats during spring. *N. burcharidi* spawns twice annually, in late autumn and in early spring (Smith 1975). The smallest observable individual in the field was 5 mm in shell length; in the laboratory, animals reached adult size in eleven weeks, with a growth rate of 2 mm month⁻¹ (Smith 1975), and growth rates determined from populations in the field were 1.4 mm month⁻¹. Growth rates of *N. burcharidi* were affected also by temperatures, with adult size reached in 24 weeks at 15 °C, and in 11 weeks at 20-25 °C. In most *Nassarius* species, when the adult maximum size is reached the outer lip and callus thicken.

In laboratory experiments, Smith (1975) found that the species tolerates a wide range of salinities at all stages of its life cycle. Smith's results were applied to the Swan River Estuary, with the experiments involving only salinities

lower than sea water. No eggs hatched below 10.5 ‰, implicating salinity as an environmental regulator of the species, as the success rate of laying/hatching increased with increasing salinity. In adults, 7 ‰ was the minimum salinity for activity, and animals which were acclimatized to 35 ‰ were able to tolerate instantaneous drops to 17 ‰ (withdrawal of the animal into the shell serving as a mechanism for avoidance). Whereas an instantaneous reduction in salinity from 35 ‰ to 13 ‰ results in temporary retraction from which the animal recovers after acclimatization, a drop from 35 ‰ to 10 ‰ results in death (Kowarsky 1969; Smith 1975), implicating fresh water as a potentially lethal factor. In summary, *N. burcharidi* populations in the Swan River Estuary had two breeding periods per year, a rapid growth rate (taking 5 months to develop from egg to sexually mature adults), a tolerance of wide salinity ranges by eggs and adults, and a high mobility of individuals enabling migration (Smith 1975). These aspects enabled the species to adapt to the estuarine environment.

The significance of the laboratory and autoecological results, described above, for the Leschenault Inlet situation is that mortality due to salinities of < 7 ‰ may occur at some sites and not at others, migration between sites may occur and juvenile recruitment may be frequent. In the Leschenault Inlet estuary, however, the vast majority of adult *N. burcharidi* examined had a thickened outer lip and callus, indicating that they were mature and had ceased growing. Juvenile recruitment was generally low, with individuals < 6 mm in size rarely comprising more than 2% of the population. Juvenile recruitment alone did not account for the local increases in abundances, and given the decrease in population numbers since the beginning of the study, it appears this level of recruitment was insufficient to maintain the population density first encountered in the study. These results suggest a gradually depleting population of mature *N. burcharidi* over the period of study.

There are no data for Leschenault Inlet on spawning times and growth rates of juveniles for *N. burcharidi*, and so the Swan River Estuary data (Smith 1975) are used to interpret patterns in the Leschenault Inlet estuary. It must be borne in mind, however, that patterns for the species in the Swan River Estuary (with its own set of environmental parameters) could be different to those of the Leschenault Inlet estuary. In the Leschenault Inlet estuary, there had been some generally low levels recruitment of juveniles of *N. burcharidi* from 1982 to 1984, *e.g.* along Transect A in February 1984, and significant recruitment along Transects A and B by February 1985. Extrapolating the data of Smith (1975), juveniles of 5-6 mm size would have developed from eggs laid 10-11 weeks earlier, suggesting a spawning the previous mid-December. Juveniles of 5.0-5.9 mm in size taken along Transect A in May 1985 would have developed from eggs laid during the previous mid-March. By December 1985, the populations along Transect A were unimodal with a mode centred around 9 mm, as they had been for most of the study period, implicating rapid juvenile growth. In seven months, the juveniles of May 1985 (< 6 mm) had joined the adult population of 8-9 mm, indicating a growth rate of *ca* 0.6 mm per month. Some juvenile recruitment occurred along Transect A in May 1986 and

September 1986, arising from spawning in mid-March and mid-to late July, respectively. Juveniles were not recorded for the remainder of the study.

The trends in population age structures of *N. burchardi* in Leschenault Inlet estuary indicate firstly that recruitment, albeit at low levels, occurred primarily in the lower estuary, and rarely in mid-estuary (possibly due to the higher salinities there), and secondly, that recruitment of juveniles could occur in any month. No juveniles were recorded at Transect D, where the species is generally absent. Recruitment of juveniles does not appear to correlate with changes in population abundances at various sites (e.g. there was a peak in abundance between December 1984 and February 1985 at B9 but no juvenile recruitment).

Spisula trigonella

Spisula trigonella occurred at all water depths and on all substrate types, from the coarse sands of the Collie River delta to the mud of the central basin, but it was extremely abundant in specific habitats such as the central basin muds in the estuary at the beginning of study. The populations, however, were not maintained at their original densities. Toward the end of the study period the species was uncommon, or rare, or absent at the study sites. Given that elsewhere in south-western Australia *Spisula* is considered to be of marine affinity (Chalmer & Scott 1984), individuals comprising the estuarine populations here would have derived as plankton from the (oceanic) Koombana Bay populations.

Chalmer & Scott (1984) recorded the species in the Leschenault Inlet estuary in 1974 but in low abundance. Similarly, during the initial reconnaissance survey of this study, in February 1982, the species was present but not abundant. However, by May 1982, juvenile *S. trigonella* were very abundant in some habitats. Just as abruptly, their numbers fell by late 1983 and the species was again uncommon in the estuary by the end of the study period.

The decline in numbers of *S. trigonella* between December 1983 and February 1984 is difficult to explain. Laboratory studies suggest the species tolerates quite low salinities (Hughes 1973), but low salinity does not fully account for decreases in population densities in Leschenault Inlet, as the decline in numbers at many sites occurred despite fluctuating seasonal salinity. At C17, for instance, the peak of *Spisula* abundance occurred between May and December 1982, a period which includes the winter freshening of the estuary, and began to decline by February 1983. However, there was a decline in population numbers at Sites A2 and A3 that might have been linked to a particularly heavy input of fresh water from the Collie River during the 1983 winter, and a consequent generally low salinity during early July of that year, perhaps beyond the level of the salinity tolerance of the species. There also was low salinity along Transect B during July 1983, which persisted until August 1983, during which time when the populations of *S. trigonella* declined. However this decline in *Spisula* numbers appears as a continuation of a trend from February 1983. Further, one of the sampling sites distant from "The Cut", along Transect C, supported the greatest density of individuals, implicating fresh water as a regulatory factor in areas near the Collie River delta.

Marked and dramatic fluctuations in abundance of *S. trigonella*, as recorded in this study, have been noted elsewhere in Australia by Wilson & Kendrick (1968), Stephenson *et al.* (1977), Stejskal (1985) and Rose (1994). It would appear that this pattern of marked population changes is typical of the species, although the reasons underlying these short term invasions of estuaries are unclear.

Throughout this study, populations of *S. trigonella* were dominated by the same age cohort at all times and were not maintained by further recruitment. This population probably originated from larvae outside the estuary, but once established, the greatest density of individuals occurred in localities towards the north of the inlet, away from the marine source. Since the species is a suspension feeder, its food supply is not related to the occurrence of other molluscs. However, the species itself may be prey for carnivorous molluscs. Although predation may account in part for some of the decline in numbers of *S. trigonella* over the study period, it does not explain the overall decline of the population. Clearly, other factors may be operating (e.g. breeding biology, fecundity, disease, and a short life span). Interestingly, as the population throughout the estuary of *Spisula*, which was derived from the *Spisula* recruitment in 1982, grew in size, a bimodal size structure of the total population emerged due to different growth rates of individuals in the estuary: in 18 months, the southern populations attained sizes of 18-22 mm, while the northern populations with slower growth rates attained sizes of 10-14 mm. This slower growth may be due to stunting induced by the generally slightly higher salinities in the mid estuarine salinity field, or by a lack of food resources. In contrast, the bimodality of populations evident in August 1983 was due to an influx of juveniles along Transect A, superimposed on an established adult population. In this context, the bimodality of the estuary-wide populations evident in February 1983 was due to differing growth rates from south to north along the estuary, while that in August 1983 was due to a genuine juvenile recruitment.

The Mactridae have a world-wide distribution in all waters. *S. trigonella* is found around the entire Australian coast from a range of marine and estuarine habitats including shoals and flats at the mouths of rivers (Wilson & Kendrick 1968; Stephenson *et al.* 1977; Stejskal 1985). Lamarck (1818) first recorded the species in Western Australia at Shark Bay. It was also collected off Troughton Island in the far north in 1962. In Western Australian estuaries, the species has been recorded in the Swan River Estuary since 1965 (Wilson & Kendrick, 1968; Chalmer *et al.* 1976), and in Nornalup Inlet (Hodgkin & Clarke 1988). In the Leschenault Inlet estuary, *S. trigonella* was recorded in relatively low numbers in 1974 (Chalmer & Scott 1984) and in Koombana Bay near Bunbury in 1982 (Anon 1982b).

In the Swan River Estuary, the species was recorded as being most abundant on unvegetated sandy substrates, but was also abundant in muddier substrates of deeper water (Hughes 1973). It showed a gradient in size of individuals from upstream to downstream and from deep to shallow water sites, with smaller individuals in upstream and deeper water sites. This was attributed to differential

settlement patterns, arising largely due to salinity gradients in the estuary (Hughes 1973), though the Leschenault data implicates differing growth rates as an explanation. Winter fresh water appears to eliminate much of the population. Laboratory studies suggest that 3-4 ‰ is a "lethal minimum salinity", and that juveniles are more tolerant of lower salinities than adults (Hughes 1973). The relevance of these results from the Swan River Estuary to the populations in Leschenault Inlet is that salinity may not be a major factor in regulating *Spisula* populations.

Hydrococcus brazieri

Hydrococcus brazieri is a very shallow water to tidal species that inhabits sandy or muddy sand sites, with a preference for tidal sand habitats in the mid and upper estuarine salinity fields. There was an overall decrease in the abundance of this species from the beginning of the study. Decreases in abundance also occurred intra-annually at any time of year. At some sites this occurred in late summer to early winter, which would seem to implicate high salinities (at the end of summer) and freshwater (at the beginning of winter) as regulating factors. However, the experimental evidence would suggest otherwise (see later), and overall, in the Leschenault Inlet context, *H. brazieri* appeared to be tolerant of high salinities and temperatures, as the changes in its population densities did not correlate with extremes in these water parameters. Variation in its population numbers, however, may also be due to natural patchiness, or to predation.

H. brazieri occurs around the Australian coastline from New South Wales to Tasmania and to Western Australia, including many Western Australian estuaries (Wells & Threlfall 1981). It was found in shallow-water sand in the Peel-Harvey Estuary, in densities of up to 10 000/m² (Wells & Threlfall 1982a,b,c). There, animal densities fluctuated markedly but apparently not in direct response to any seasonal pattern similar to that observed in Leschenault Inlet. It was recorded in Leschenault Inlet in 1974 by Chalmer & Scott (1984).

Laboratory experiments show that the species is tolerant of a wide range of salinities and temperatures, with preferences for certain combinations of temperatures and salinity between 10 ‰ and 50 ‰ (Wells & Threlfall 1982a). During summer in the period of highest water salinity, the species is active at salinities between 25 ‰ and at least 54 ‰. During winter in times of lowest salinity, the species is active at salinities between 15 ‰ and 35 ‰. Also, *H. brazieri* is tolerant of temperatures between 8 °C and 32 °C. These experimental results indicate that winter conditions would not necessarily eliminate *H. brazieri* from estuaries, and that moderate summer conditions are favorable for the species. In the context of Leschenault Inlet, this means that the species is able to tolerate summer temperature conditions and salinities developed on the tidal flats, and also is able to survive the winter freshening in these environments.

Field studies over two years in the Peel-Harvey Estuary showed *H. brazieri* reproducing continuously, with no obvious seasonality (Wells & Threlfall 1982b). Females attach eggs to any suitable hard surface. Embryos emerge from eggs as crawling juveniles, with individuals reaching maturity in 4 months, reaching maximum size in 7-8

months. Some individuals perhaps might survive for a second year. In this context, the patterns of population fluctuations in Leschenault Inlet may be related to this type of ongoing recruitment.

Other species

The main occurrence of *Acteocina* sp in the tidal, upper estuary field indicates it is tolerant of a wide range of salinities and high temperatures. Its abundance fluctuated markedly temporally, but this did not occur in synchrony with trends in environmental factors. *Acteocina* consumes foraminifera (Burn & Thompson 1998), and fluctuations in foraminifera densities, related to variation in micro-environmental factors such as detritus content (cf Hottinger 1983) may well determine the densities of this species. Although fluctuating, the overall level of abundance of the species had been maintained during the study period.

The remaining species were either quite widespread (e.g. *Bedevea paivae* and *Sanguinolaria biradiata*), occurred in low numbers in consistent but restricted distributions (e.g. *Assimineia*), or formed temporary localized but quite dense populations or became established as low density populations later in the study period (e.g. *X. securis* colonising the Collie River delta for one year, and a small population of *Bittium granarium* of a mixed-size structure locally colonising the lower estuary). In the context of the numerically more dominant species discussed above, these less common species appeared to have little effect on the overall ecosystem of Leschenault Inlet, regardless of their trophic level.

For *Bedevea paivae*, the data suggest a continuous presence during the study period. Due to its low density, fluctuations in abundance of the species may be an artifact of sample area and sample number, rather than population dynamics. Biogeographically, *B. paivae* is widespread (Wells & Bryce 1985). Chalmer *et al.* (1976) record it in the Swan River Estuary, and Wells & Threlfall (1981) recorded it in the Peel-Harvey Estuary. In this study, in contrast to its occurrence in rocky estuarine settings elsewhere in southwestern Australia, *B. paivae* inhabited muddy to sandy subtidal shallow water platforms.

Xenostrobus securis occurs throughout southern Australia (Wilson 1968). It was recorded in the Peel-Harvey Estuary (Wells & Threlfall 1981), and is a sporadic and temporary resident of the Swan River Estuary (Chalmer *et al.* 1976). Studies of the species in the Swan River Estuary was within the context of a freshwater to marine gradient (Wilson 1968) and not under conditions of salinities above that of sea water. Consequently, the results are not applicable to the Leschenault Inlet estuary where salinities rise above that of seawater, but only to the Collie River to estuary transition. Normal development of embryos of *X. securis* occurs between a salinity of 8 ‰ and 17.5 ‰, which would preclude the possibility of marine dispersal of larvae between estuaries (Wilson 1968). If so, then populations resident in the Collie River delta in 1982 would have originated from populations further upstream.

There is little information on *Assimineia* sp. Its distribution in this study indicates a tolerance of a range of salinities and temperatures. Wells (1984) notes *Assimineia*

sp as inhabiting salt marshes in several south-western Australian estuaries, although its full geographic range is unknown, and Chalmer *et al.* (1976) note it in the Swan River Estuary.

Classification of estuarine molluscs

There is a wide range of approaches to the classifying of estuarine fauna. Day (1981) presents a classification based on the salinity tolerance of the species and its occurrence, or otherwise, in the marine environment, and divides estuarine fauna into six categories. Of these, four are relevant to the mollusc fauna of the Leschenault Inlet estuary:

- the stenohaline marine component - including species which are represented in the marine environment and which can tolerate salinities of between 25-40 ‰;
- the euryhaline marine component - including species which are represented in the marine environment and which tolerate salinities of 5-50 ‰;
- the true estuarine component - including species which have no representation in the marine environment and which tolerate salinities of 20-60 ‰; and
- the euryhaline fresh water component - including species primarily derived from fresh water but which are able to tolerate salinities greater than 5 ‰.

Based on available marine records to determine occurrence of a given species with the marine to estuarine transition (Chalmer *et al.* 1976; Wells 1984; Wells & Bryce 1985), studies of the salinity tolerances of individual species (Wells & Threlfall 1982a; Wilson 1968; Hughes 1973; Smith 1975), as well as the distribution of species within Leschenault Inlet in relation to the salinity fields documented during this study, the molluscs of the Leschenault Inlet estuary are classified as follows (an * indicating a tentative assignment due to absence of distribution information and limited occurrence in Leschenault Inlet):

- the stenohaline marine fauna: *Bittium granarium*; *Cerithiopsidae sp, **Macra flindersi*, *Mytilus edulis*, *Polinices conicus*, *Pholas australasiae*, *Nassarius nigellus*, *Solemya australis*, *Irus crenata*, *Venerupis anomala*.
- the euryhaline marine fauna; *Tellina deltoidalis*, *Tellina* sp, *Theora lubrica*, *Sanguinolaria biradiata*, *Philine angasi*, *Nassarius burchardi*, *Bedevea paivae*, *Spisula trigonella*, *Epicodakia* sp, *Laternula creccina*, and
- the true estuarine fauna; *Acteocina* sp, *Arthritica semen*, *Xenostrobus securis*, *Hydrococcus brazieri*, *Fluviolanatus subtorta*, *Assimineia* sp, *Salinator* sp.

This study has shown that species populations vary markedly in the long and short term, largely independently of seasonal trends in habitat features. Further, the general trends in abundance are different for each species. Obviously, data from different times would result in different assemblages being identified (*cf* Cresswell *et al.* 2000). However, using long-term data available in this study, seven molluscan assemblages/populations, determined by the most abundant and/or temporally persistent components, are provisionally noted below as

to their occurrence in the various habitats (minor molluscan components of an assemblage or population are not incorporated into the nomenclature):

- a mixed assemblage, of the tidally flushed environments of the Preston River delta and the tidal delta;
- a *Tellina* (\pm *Spisula*) dominated assemblage inhabiting the deep water central muddy basin;
- a *Tellina-Nassarius* (\pm *Bedevea*) dominated assemblage inhabiting seagrass-vegetated platforms;
- a *Tellina*-dominated population inhabiting shallow subtidal mud flats.
- a *Hydrococcus*-dominated population inhabiting tidal sandy beaches;
- an *Acteocina*-dominated population inhabiting tidal mud flats;
- an *Arthritica*-dominated population inhabiting low tidal to very shallow subtidal sand and muddy sand flats.

The full picture of associations and population occurrences in time and space is more complex, but generalised distributions of the main mollusc species are shown diagrammatically for the various habitats in lower, middle and upper parts of the estuary in Figure 16. The relative abundance of species of each assemblage will vary.

The results of this study suggest a complexity of biological responses among species of the estuarine mollusc fauna. However, despite the medium-term nature of this study, and the fact that a habitat framework types was used within which to interpret patterns in the species abundances, much of the population dynamics of mollusc species still remains unexplained in detail. While various large scale and macroscopic features of the estuary were identified as a habitat framework for benthos, it may be that many species respond to micro-environmental features only indirectly related to the macroscopic setting, *e.g.* microscopic algal distribution related to substrate grain size. A fuller explanation of the autecology of the various species in the Leschenault Inlet estuary must await research on its micro-habitat features, examining the relationship between macroscopic setting and benthos through factors such as water temperature, salinity, oxygen concentration, substrate texture and detritus content, substrate temperature, pore water characteristics, and bathymetry, at smaller temporal and spatial scales.

While the abundance of some species could be related to seasonal changes in salinity, there was a general lack of direct correlation between evident annual salinity patterns and the abundance of many of the commonly occurring species. This suggests that the species are adapted to cope with fluctuations in salinity in the estuary. The patterns of population abundance may be influenced by parameters such as food supply, and predator/prey relationships (*e.g.*, predators such as birds and fish). These aspects of the estuarine ecology require investigation in order to fully understand the mollusc population dynamics. While studies have been already carried out on species such as *Arthritica semen*, *Hydrococcus brazieri*, *Nassarius burchardi*,

Spisula trigonella, and *Xenostrobus securis*, the reproductive biology and the variation of autecology between these and other species in the Leschenault Inlet estuary needs to be understood to explain the population dynamics of mollusc species specifically in this estuary.

In summary, the range of potential factors that control the abundance and composition of the molluscs, and hence composition of assemblages in Leschenault Inlet estuary are manifold, and appear to be complex in their interaction. Firstly, there is the effect of the physical environment. This may affect species distribution through features of the habitat such as substrate, depth, and salinity field (e.g. *Arthritica* in shallow water to tidal sand, *Acteocina* in tidal mud), and hydrochemically by seasonally regulating the populations of some species (e.g. freshwater influx annually may eliminate or trigger migration of populations of *Nassarius*, and cause mortality of *Spisula*). The significance of substrate in directly or indirectly determining distribution of benthic molluscs is well established (Parker 1975; Yonge 1976). For instance, the distribution of deposit feeders can be related to particle size as it affects their food source and feeding (Tunncliffe & Risk 1977). In another example, the control on mollusc distribution and abundance of depth, grain size, salinity and temperature was investigated by Wells (1978) who found that of eight environmental variables investigated, depth and grain size were the most important in controlling the density of the mud snail *Hydrobia* on a Nova Scotia salt marsh.

Other factors regulating composition of mollusc assemblages include the effects of predators, local population explosions, style of recruitment, the various mechanisms of population maintenance, and the interactions of long term population patterns between the species. In regard to the effects of local population explosions, clearly, rapid increases in population numbers can have a marked effect on assemblage composition as exemplified by *Spisula* which exhibited a major increase in numbers, and then subsided. Similar patterns of population explosions exhibited by other species in this estuary are afforded by an ophiuroid species (cf Unno 2000) and polychaetes (e.g. *Capitella capitata*; cf TA Semeniuk 2000), and in concert, can result in varying and complex faunal associations through time. The varying types of population dynamics and maintenance is exemplified by the contrasting patterns shown by *Tellina*, *Spisula*, and *Nassarius*. The varying styles of recruitment i.e. juvenile recruitment vs adult or post-juvenile migration, and the effects of recruitment from intra-estuarine larvae vs marine-derived larvae and how they influence population maintenance, is afforded by examples of *Tellina* which exhibited recruitment throughout the study, and *Nassarius* which did not appear to exhibit recruitment but rather inter-site migration. Finally, composition of assemblages can be markedly affected where there were long term trends of population decline superimposed on the annual input/output of the species, operating synchronously with another species that maintains its populations albeit with seasonal fluctuations. This all creates, within the appropriate salinity and habitat fields, population size and compositional complexities even at the one site, and differences in response and complexity between sites.

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Appendix 1. Mean abundance of key species of mollusc per square metre (abundances > 10/m² are rounded off) at the various sites (see Fig 1).

<i>Acteocina</i> sp																						
	A1	A2	A3	A4	A5	A6	A7	B8	B9	B10	B11	B12	B13	B14	C15	C16	C17	C18	C19	D20	D21	D22
Feb-82	*	*	*	*	*	*	*	0	0	*	*	0	*	0	*	*	*	*	*	*	*	*
May-82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	170	0	0	0
Aug-82	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	51	0	0	*
Dec-82	*	0	0	0	*	*	*	*	0	*	0	*	*	*	3.2	*	0	*	74	128	9.6	3.2
Feb-83	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9.6	0	0	0	0	9.6	3.2	13
May-83	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	3.2	3.2	*
Aug-83	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	6.4	9.6	0	*
Dec-83	*	0	0	0	*	*	*	*	0	*	0	*	*	*	9.6	*	0	*	0	86	6.4	*
Feb-84	0	0	0	0	0	0	0	3.2	0	0	0	0	0	0	58	0	0	0	38	19	13	90
May-84	*	0	0	0	*	*	*	*	0	*	0	*	*	*	3.2	*	0	*	45	26	9.6	9.6
Aug-84	*	0	0	0	*	*	*	*	9.6	*	0	*	*	*	3.2	*	0	*	22	26	3.2	16
Dec-84	*	0	0	0	*	*	*	*	0	*	0	*	*	*	19	*	0	*	0	16	83	6.4
Feb-85	0	0	0	0	0	0	0	29	0	0	0	0	0	0	16	0	0	0	32	0	32	22
May-85	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	6.4
Aug-85	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	6.4	115	0	0
Dec-85	*	0	0	0	*	*	*	*	9.6	*	0	*	*	*	3.2	*	0	*	22	26	3.2	16
Feb-86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May-86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jun-86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jul-86	*	0	0	*	*	*	*	*	0	*	0	*	*	*	0	*	0	*	9.6	0	16	*
Aug-86	*	0	0	*	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	54	46	0
Sep-86	0	0	0	0	0	0	9.6	3.2	0	0	0	0	0	0	3.2	0	0	0	6.4	16	76	22
Oct-86	*	0	0	*	*	*	*	*	0	*	0	*	*	*	0	*	0	*	3.2	13	13	54
Nov-86	*	0	0	*	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	19	35	83
Dec-86	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	16	106	70	
Jan-87	0	0	0	0	0	0	0	*	0	*	0	*	*	*	0	*	0	*	0	29	80	54
Feb-87	0	0	0	0	0	0	0	*	0	*	0	*	*	*	0	*	0	*	0	106	67	112
Mar-87	0	0	0	0	0	0	0	3.2	0	0	0	0	0	0	0	0	0	0	0	29	64	61

<i>Arthritica semen</i>																						
	A1	A2	A3	A4	A5	A6	A7	B8	B9	B10	B11	B12	B13	B14	C15	C16	C17	C18	C19	D20	D21	D22
Feb-82	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
May-82	815	0	0	127	688	0	3440	2319	1529	561	510	0	255	306	662	25	1885	1350	25	51	1885	255
Aug-82	*	1376	0	127	*	*	*	*	331	*	0	*	*	*	764	*	1885	484	*	1350	3593	*
Dec-82	*	815	0	102	*	*	*	*	669	*	0	*	*	*	943	*	3236	102	*	2892	4026	*
Feb-83	12689	3159	0	76	2777	382	510	459	688	51	0	0	306	1529	917	102	4637	229	*	3159	16052	127
May-83	*	892	0	178	*	*	*	*	408	*	51	*	*	*	1248	*	1885	178	*	382	*	*
Aug-83	*	3949	0	153	*	*	*	*	790	*	0	*	*	*	178	*	713	51	*	1401	3516	*
Dec-83	*	1019	0	1096	*	*	*	*	1045	*	76	*	*	*	1987	*	2344	0	*	3026	10854	*
Feb-84	0	178	0	382	25	25	178	688	382	586	102	0	0	76	2675	1198	357	0	408	1987	7924	1223
May-84	*	0	0	0	*	*	*	*	535	*	0	*	*	*	0	*	0	0	*	229	994	1554
Aug-84	*	0	0	102	*	*	*	*	0	*	0	*	*	*	280	*	0	357	*	178	357	1427
Dec-84	*	0	0	0	*	*	*	*	25	*	51	*	*	*	357	*	331	0	*	3007	1631	1809
Feb-85	459	51	0	102	0	0	101	204	178	0	306	0	178	357	0	0	0	229	0	0	153	0
May-85	*	1147	408	280	*	*	*	*	0	*	153	*	*	*	153	*	153	0	*	1172	815	917
Aug-85	*	102	127	76	*	*	*	*	25	*	0	*	*	*	0	*	0	0	*	255	76	0
Dec-85	*	306	229	178	*	*	*	*	0	*	0	*	*	*	25	*	25	51	*	0	0	0
Feb-86	178	51	204	51	0	178	255	204	76	0	0	0	76	153	229	0	255	178	0	0	127	0
May-86	153	204	153	25	0	178	127	178	96	25	25	0	51	51	76	0	280	76	0	0	127	0
Jun-86	0	0	76	51	0	178	510	102	127	153	0	*	0	0	357	0	382	51	127	0	0	0
Jul-86	*	0	0	0	*	*	*	*	0	*	764	*	*	*	204	*	0	0	*	0	2344	*
Aug-86	*	739	0	459	*	*	*	*	382	*	0	*	*	*	0	*	255	0	*	0	0	0
Sep-86	459	433	0	0	0	0	0	1045	535	815	0	25	204	255	331	255	662	0	280	0	51	357
Oct-86	*	4255	178	357	*	*	*	*	459	*	0	*	*	*	280	*	484	0	*	0	0	0
Nov-86	*	51	178	0	*	*	*	*	0	*	204	*	*	*	0	*	1682	662	*	0	229	0
Dec-86	7364	0	586	255	3414	0	0	2089	1096	3083	815	586	586	2548	306	1198	3796	280	1274	2956	8791	1198
Jan-87	*	5657	1987	1350	*	*	*	*	764	*	1198	*	*	*	917	*	2548	1045	*	2370	10217	484
Feb-87	*	76	357	0	*	*	*	*	1427	*	0	*	*	*	0	*	4383	1274	*	11415	13606	0
Mar-87	0	866	331	0	0	178	14422	1198	0	0	459	1121	0	0	0	1529	3618	0	357	1784	5657	484

Appendix 1 (continued).

Bedevea paivae

	A1	A2	A3	A4	A5	A6	A7	B8	B9	B10	B11	B12	B13	B14	C15	C16	C17	C18	C19	D20	D21	D22
Feb-82	*	*	*	*	*	*	*	0	1.6	*	*	0	*	1.6	*	*	*	*	*	*	*	*
May-82	0	0	0	0	0	0	0	0	0	0	0	0	3.2	3.2	0	0	6.4	0	3.2	0	0	0
Aug-82	*	9.6	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	*
Dec-82	*	3.2	0	0	*	*	*	*	3.2	*	0	*	*	*	0	*	6.4	*	0	0	0	0
Feb-83	0	0	9.6	0	0	0	3.2	0	6.4	16	0	0	9.6	0	3.2	0	3.2	0	0	0	0	0
May-83	*	9.6	0	0	*	*	*	*	0	*	0	*	*	*	0	*	13	*	0	0	0	*
Aug-83	*	13	0	0	*	*	*	*	3.2	*	3.2	*	*	*	9.6	*	0	*	0	0	0	*
Dec-83	*	0	0	3.2	*	*	*	*	0	*	0	*	*	*	0	*	6.4	*	0	0	0	*
Feb-84	0	0	35	0	0	0	0	0	0	3.2	0	0	0	3.2	3.2	3.2	0	0	0	0	0	0
May-84	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	3.2	*	3.2	0	0	0
Aug-84	*	0	0	0	*	*	*	*	6.4	*	0	*	*	*	3.2	*	0	*	3.2	0	0	0
Dec-84	*	0	0	0	*	*	*	*	3.2	*	0	*	*	*	0	*	3.2	*	0	0	0	0
Feb-85	0	0	3.2	0	0	0	3.2	0	32	19	0	3.2	0	6.4	0	0	0	0	6.4	0	0	0
May-85	*	6.4	0	0	*	*	*	*	3.2	*	0	*	*	*	0	*	0	*	0	0	0	0
Aug-85	*	0	0	0	*	*	*	*	3.2	*	0	*	*	*	0	*	3.2	*	3.2	0	0	0
Dec-85	*	0	0	0	*	*	*	*	6.4	*	0	*	*	*	3.2	*	0	*	0	0	0	0
Feb-86	0	0	0	0	0	0	0	0	3.2	3.2	0	0	0	0	0	6.4	0	0	0	0	0	0
May-86	0	0	0	0	0	0	3.2	0	9.6	0	0	0	0	0	0	0	0	0	0	0	0	0
Jun-86	0	0	0	0	0	0	0	0	9.6	9.6	0	0	0	0	0	0	0	0	0	0	0	0
Jul-86	*	6.4	3.2	0	*	*	*	*	13	*	0	*	*	*	3.2	*	0	*	0	0	0	*
Aug-86	*	0	0	0	*	*	*	*	6.4	*	0	*	*	*	0	*	0	*	0	0	0	0
Sep-86	0	0	0	0	0	0	0	3.2	3.2	0	0	0	0	16	3.2	6.4	0	0	0	0	0	0
Oct-86	*	0	3.2	3.2	*	*	*	*	22	*	0	*	*	*	3.2	*	9.6	*	0	0	0	0
Nov-86	*	3.2	0	0	*	*	*	*	26	*	0	*	*	*	6.4	*	0	*	0	0	0	0
Dec-86	0	0	0	0	0	0	0	3.2	9.6	0	0	0	3.2	0	0	3.2	0	0	0	0	0	0
Jan-87	*	0	3.2	0	*	*	*	0	6.4	0	3.2	0	*	*	0	*	3.2	*	0	0	0	0
Feb-87	*	3.2	0	0	*	*	*	*	16	*	0	*	*	*	6.4	*	0	*	0	0	0	0
Mar-87	0	3.2	16	0	0	0	0	0	9.6	0	0	0	3.2	3.2	0	0	0	3.2	0	0	0	0

Hydrococcus brazieri

	A1	A2	A3	A4	A5	A6	A7	B8	B9	B10	B11	B12	B13	B14	C15	C16	C17	C18	C19	D20	D21	D22	
Feb-82	*	*	*	*	*	*	*	*	0	0	*	*	0	*	0	*	*	*	*	*	*	*	
May-82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3974	0	0	0
Aug-82	*	0	0	0	*	*	*	*	*	*	3.2	*	*	*	0	*	0	*	16944	0	0	*	
Dec-82	*	0	0	0	*	*	*	*	*	*	0	*	*	*	45	*	0	*	16176	134	0	0	
Feb-83	0	0	0	0	22	0	3.2	0	0	0	0	0	0	0	6.4	0	0	0	15008	9.6	3.2	0	
May-83	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	3.2	*	
Aug-83	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	9.6	0	*	
Dec-83	*	0	0	0	*	*	*	*	9.6	*	0	*	*	*	3.2	*	0	*	0	32	0	*	
Feb-84	0	0	0	3.2	0	0	0	3.2	3.2	0	0	0	0	0	3.2	0	0	0	0	3.2	9.6	6.4	
May-84	*	0	0	0	*	*	*	*	0	*	0	*	*	*	99	*	0	*	32	0	3.2	0	
Aug-84	*	0	0	0	*	*	*	*	0	*	0	*	*	*	3.2	*	0	*	416	0	0	0	
Dec-84	*	0	0	0	*	*	*	*	22	*	0	*	*	*	0	*	16	*	0	29	19	0	
Feb-85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6.4	0	0	0	0	0	0	
May-85	*	0	0	0	*	*	*	*	0	*	0	*	*	*	32	*	0	*	9.6	0	38	6.4	
Aug-85	*	0	0	0	*	*	*	*	51	*	0	*	*	*	0	*	0	*	118	0	0	0	
Dec-85	*	0	0	0	*	*	*	*	0	*	0	*	*	*	3.2	*	0	*	416	0	0	0	
Feb-86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3.2	9.6	0	0	0	0	0	0	
May-86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9.6	6.4	0	0	0	0	0	0	
Jun-86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	54	0	0	0	
Jul-86	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	*	
Aug-86	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	131	3.2	6.4	3.2	
Sep-86	0	0	0	0	0	0	38	0	0	0	0	0	0	0	19	0	0	0	547	16	0	3.2	
Oct-86	*	0	0	0	*	*	*	*	0	*	0	*	*	*	3.2	*	0	*	1386	42	19	6.4	
Nov-86	*	0	0	9.6	*	*	*	*	0	*	0	*	*	*	0	*	0	*	205	61	42	13	
Dec-86	0	0	0	0	0	0	64	0	0	0	0	0	0	0	0	0	0	0	317	19	3.2	6.4	
Jan-87	*	0	0	0	*	*	*	*	0	*	0	*	*	*	3.2	*	3.2	*	131	19	9.6	0	
Feb-87	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	109	35	3.2	3.2	
Mar-87	0	0	0	0	0	0	224	13	3.2	0	0	0	0	0	0	0	0	0	570	6.4	13	0	

Appendix 1 (continued).

Nassarius burcharadi

	A1	A2	A3	A4	A5	A6	A7	B8	B9	B10	B11	B12	B13	B14	C15	C16	C17	C18	C19	D20	D21	D22
Feb-82	*	*	*	*	*	*	*	48	93	*	*	6.4	*	674	*	*	*	*	*	*	*	*
May-82	6.4	154	32	486	461	0	61	80	77	106	29	42	378	179	32	128	6.4	3.2	0	0	0	0
Aug-82	*	195	83	931	*	*	*	*	304	*	102	*	*	*	32	*	112	*	6.4	0	0	*
Dec-82	*	202	407	944	*	*	*	*	323	*	166	*	*	*	26	*	131	*	0	0	0	0
Feb-83	6.4	285	250	1446	1907	0	755	170	387	611	211	198	944	128	32	186	154	3.2	0	0	0	0
May-83	*	474	256	1338	*	*	*	*	374	*	93	93	*	*	19	*	51	*	0	0	0	*
Aug-83	*	141	90	845	*	*	*	*	688	*	99	*	*	*	122	*	189	*	0	0	0	*
Dec-83	*	3.2	131	2051	*	*	*	*	627	*	29	*	*	*	45	*	102	*	0	0	0	*
Feb-84	0	3.2	74	938	624	0	230	154	381	410	32	38	749	214	45	122	115	26	0	0	0	0
May-84	*	9.6	16	301	*	*	*	*	35	*	64	*	*	*	0	*	26	*	0	0	0	0
Aug-84	*	3.2	3.2	733	*	*	*	*	182	*	13	*	*	*	32	*	22	*	6.4	0	0	0
Dec-84	*	0	26	58	*	*	*	*	381	*	0	*	*	*	64	*	29	*	0	0	0	0
Feb-85	0	32	22	3.2	470	0	64	48	387	339	61	22	32	106	3.2	51	80	19	0	0	0	0
May-85	*	22	19	13	*	*	*	*	42	*	42	*	*	*	0	*	70	*	9.6	0	0	0
Aug-85	*	0	3.2	83	*	*	*	*	128	*	0	*	*	*	13	*	237	*	0	0	0	0
Dec-85	*	3.2	3.2	733	*	*	*	*	182	*	13	*	*	*	32	*	22	*	6.4	0	0	0
Feb-86	0	9.6	0	42	77	45	150	9.6	48	48	6.4	*	19	16	0	32	9.6	3.2	3.2	0	0	3.2
May-86	26	74	0	6.4	0	0	29	38	202	86	9.6	*	45	9.6	9.6	9.6	9.6	0	9.6	0	0	6.4
Jun-86	3.2	0	0	74	122	0	19	86	70	58	0	*	0	0	3.2	6.4	13	0	0	0	0	0
Jul-86	*	51	42	51	*	*	*	*	285	*	16	*	*	*	29	*	6.4	*	3.2	0	0	*
Aug-86	*	9.6	29	285	*	*	*	*	291	*	26	*	*	*	3.2	*	9.6	*	3.2	0	0	0
Sep-86	0	0	26	42	128	0	19	70	80	42	32	9.6	51	154	9.6	38	13	3.2	0	0	0	3.2
Oct-86	*	0	51	186	*	*	*	*	528	*	16	*	*	*	32	*	19	*	0	0	0	0
Nov-86	*	6.4	3.2	72	*	*	*	*	445	*	22	*	*	*	38	*	6.4	0	0	0	0	0
Dec-86	0	45	86	26	122	0	0	192	211	118	3.2	48	74	35	45	42	26	13	0	0	0	0
Jan-87	*	35	45	29	*	*	*	*	154	*	51	*	*	*	80	*	96	*	6.4	0	0	0
Feb-87	*	6.4	26	42	*	*	*	*	154	*	38	*	*	*	38	*	74	*	3.2	0	0	0
Mar-87	0	45	186	102	115	0	0	141	400	106	13	48	48	48	26	93	6.4	3.2	0	0	0	0

Spisula trigonella

	A1	A2	A3	A4	A5	A6	A7	B8	B9	B10	B11	B12	B13	B14	C15	C16	C17	C18	C19	D20	D21	D22
Feb-82	*	*	*	*	*	*	*	3.2	1.6	*	*	3.2	*	*	*	*	*	*	*	*	*	*
May-82	83	570	512	0	0	0	179	16	0	0	6682	11958	0	1.6	0	6.4	13504	0	45	0	0	0
Aug-82	*	1402	384	13	*	*	*	*	0	*	1446	*	*	*	0	*	14186	*	93	0	3.2	*
Dec-82	*	1120	4499	0	*	*	*	*	0	*	6925	*	*	*	6.4	*	10902	*	54	0	3.2	0
Feb-83	3.2	1222	2326	0	3.2	0	157	0	0	0	5570	4384	0	0	0	0	2880	0	42	0	0	0
May-83	*	1107	2774	3.2	*	*	*	*	0	*	3456	3296	*	*	0	*	1760	*	35	0	0	*
Aug-83	*	874	723	0	*	*	*	*	0	*	2691	*	*	*	0	*	504	*	32	0	0	*
Dec-83	*	13	1418	0	*	*	*	*	0	*	1434	*	*	*	0	*	125	*	29	0	0	*
Feb-84	0	0	1078	0	0	0	22	0	0	0	38	3.2	3.2	0	0	0	0	0	0	0	0	0
May-84	*	9.6	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	0
Aug-84	*	16	0	0	*	*	*	*	3.2	*	3.2	*	*	*	0	*	0	*	3.2	0	0	0
Dec-84	*	0	9.6	16	*	*	*	*	0	*	0	*	*	*	0	*	0	*	3.2	0	0	0
Feb-85	3.2	0	3.2	3.2	0	0	13	0	0	0	3.2	3.2	0	0	0	0	0	0	0	0	0	0
May-85	*	9.6	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	3.2
Aug-85	*	0	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	6.4	13	19	0
Dec-85	*	0	0	0	*	*	*	*	3.2	*	3.2	*	*	*	0	*	0	*	3.2	0	0	0
Feb-86	0	0	0	0	0	3.2	9.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May-86	0	6.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jun-86	0	6.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jul-86	*	26	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	*
Aug-86	*	3.2	9.6	3.2	*	*	*	*	0	*	0	*	*	*	0	*	0	*	3.2	0	0	0
Sep-86	6.4	30	6.4	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oct-86	*	13	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	3.2	0	0
Nov-86	*	29	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	0
Dec-86	0	3.2	0	0	0	0	0	0	0	3.2	0	0	0	0	0	0	0	0	0	0	0	0
Jan-87	*	3.2	0	0	*	*	*)	0	0	0	0	0	0	0	*	0	*	0	0	0	0
Feb-87	*	3.2	0	0	*	*	*	*	0	*	0	*	*	*	0	*	0	*	0	0	0	0
Mar-87	0	0	0	0	0	0	0	0	0	0	0	3.2	0	0	0	0	0	0	0	0	0	0

Appendix 1 (continued).

Tellina deltoidalis

	A1	A2	A3	A4	A5	A6	A7	B8	B9	B10	B11	B12	B13	B14	C15	C16	C17	C18	C19	D20	D21	D22
Feb-82	*	*	*	*	*	*	*	8	59	*	*	94	*	130	*	*	*	*	*	*	*	*
May-82	0	0	29	83	109	0	3.2	13	80	147	48	154	90	192	61	54	58	74	3.2	0	35	0
Aug-82	*	0	29	138	*	*	*	*	83	*	170	*	*	*	42	*	83	*	0	0	6.4	*
Dec-82	*	0	6.4	285	*	*	*	*	125	*	99	*	*	*	102	*	51	*	0	0	13	26
Feb-83	0	0	22	166	509	0	80	45	198	108	77	102	7.4	362	70	80	86	77	0	6.4	13	6.4
May-83	*	3.2	6.4	154	0	*	*	*	123	*	48	*	*	*	38	*	80	0	3.2	3.2	6.4	*
Aug-83	*	0	32	243	0	*	*	*	147	*	67	*	*	*	80	*	91	0	0	0	6.4	*
Dec-83	*	0	163	371	0	*	*	*	154	*	109	*	*	*	109	*	70	0	0	38	0	*
Feb-84	0	0	6.4	266	400	0	19	16	96	6.4	80	83	54	61	83	102	90	96	0	26	3.2	0
May-84	*	0	0	102	*	*	*	*	6.4	*	77	*	*	*	32	*	96	*	0	64	6.4	9.6
Aug-84	*	0	0	378	*	*	*	*	29	*	96	*	*	*	16	*	74	*	3.2	38	9.6	9.6
Dec-84	*	0	26	90	*	*	*	*	80	*	115	*	*	*	118	*	77	*	0	19	6.4	9.6
Feb-85	0	0	67	106	256	0	32	9.6	70	16	138	67	26	35	13	45	118	42	6.4	0	18	22
May-85	*	0	0	32	*	*	*	*	6.4	*	0	*	*	*	0	*	6.4	*	0	26	0	0
Aug-85	*	0	0	106	*	*	*	*	0	*	45	*	*	*	0	*	45	*	0	4.4	18	6.4
Dec-85	*	0	0	362	*	*	*	*	29	*	96	*	*	*	35	*	74	*	3.2	53	13	9.6
Feb-86	0	0	0	32	102	0	9.6	32	38	38	16	67	32	26	0	9.6	0	38	3.2	9.6	42	67
May-86	0	0	0	29	6.4	0	0	9.6	19	3.2	3.2	61	90	26	13	19	0	42	0	26	45	61
Jun-86	0	0	0	0	35	0	0	3.2	9.6	70	6.4	*	9.6	16	0	3.2	19	29	0	0	9.6	16
Jul-86	*	0	6.4	214	*	*	*	*	192	*	42	*	*	*	48	*	96	*	0	3.2	6.4	*
Aug-86	*	0	13	170	*	*	*	*	182	*	32	*	*	*	42	*	45	*	3.2	0	0	3.2
Sep-86	0	0	26	240	173	0	6.4	0	70	0	35	26	96	93	38	102	42	32	0	22	3.2	9.6
Oct-86	*	0	3.2	320	*	*	*	*	112	*	29	*	*	*	86	*	64	*	0	13	3.2	0
Nov-86	*	0	13	384	*	*	*	*	170	*	26	*	*	*	77	*	112	*	0	6.4	3.2	13
Dec-86	3.2	0	9.6	86	147	0	0	29	211	29	22	61	61	90	96	67	118	42	0	9.6	6.4	9.6
Jan-87	*	0	0	48	*	*	*	*	154	*	51	*	*	*	80	*	96	*	6.4	35	6.4	6.4
Feb-87	*	0	3.2	83	*	*	*	*	154	*	38	*	*	*	38	*	74	*	3.2	16	0	3.2
Mar-87	0	0	6.4	80	131	0	0	3.2	125	19	45	58	102	102	106	160	29	32	6.4	13	3.2	0

Xenostrobus securis, *Assimineia* sp and *Sanguinolaria*

	A1	A2	A3	A4	A5	A6	A7	B8	B9	B10	B11	B12	B13	B14	C15	C16	C17	C18	C19	D20	D21	D22
Feb-82	*	*	*	*	*	*	*	0	0	*	*	0	*	0	*	*	*	*	*	*	*	*
May-82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6.4	0	0
Aug-82	*	13	0	0	*	*	*	3.2	*	0	*	*	*	*	0	*	0	*	0	0	0	*
Dec-82	*	58	0	0	*	*	*	0	*	0	*	*	*	*	3.2	*	0	*	0	0	0	0
Feb-83	141	58	0	0	0	0	0	0	0	6.4	0	0	0	0	0	0	0	0	3.2	0	0	0
May-83	*	6.4	0	0	*	*	*	0	*	0	*	*	*	*	0	*	0	*	0	0	0	*
Aug-83	*	3.2	0	0	*	*	*	0	*	0	*	*	*	*	0	*	0	*	0	0	0	*
Dec-83	*	0	0	3.2,3.2	*	*	*	0	*	0	*	*	*	*	3.2	*	0	*	0	0	0	*
Feb-84	0	0	0	0	0	0	45	0	0	3.2	0	0	0	0	0	0	0	0	0	0	0	0
May-84	*	0	0	0	*	*	*	0	*	0	*	*	*	*	0	*	0	*	0	0	0	0
Aug-84	*	0	0	0	*	*	*	0	*	0	*	*	*	*	0	*	0	*	0	0	0	0
Dec-84	*	0	0	0	*	*	*	0	*	0	*	*	*	*	3.2	*	0	*	0	9.6	3.2	0
Feb-85	0	0	0	0	0	0	0	0	3.2	0	0	0	0	0	0	0	0	0	0	0	0	0
May-85	*	0	0	0	*	*	*	0	*	0	*	*	*	*	0	*	0	*	0	0	0	0
Aug-85	*	0	0	0	*	*	*	0	*	0	*	*	*	*	3.2	*	0	*	0	0	0	0
Dec-85	*	0	0	0	*	*	*	0	*	0	*	*	*	*	0	*	0	*	0	0	0	0
Feb-86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May-86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jun-86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jul-86	*	0	0	0	*	*	*	3.2	*	0	*	*	*	*	0	*	0	*	0	0	0	*
Aug-86	*	0	0	0	*	*	*	0	*	0	*	*	*	*	0	*	0	*	0	0	0	0
Sep-86	0	3.2	0	0	0	0	0	0	3.2	0	0	0	0	0	0	0	0	0	0	0	0	0
Oct-86	*	0	3.2	3.2	*	*	*	0	*	0	*	*	*	*	0	*	0	*	0	0	0	3.2
Nov-86	*	0	0	0	*	*	*	3.2	*	0	*	*	*	*	0	*	0	*	0	3.2	0	0
Dec-86	0	0	0	0	3.2	0	0	0	0	0	0	0	0	0	3.2	6.4	0	0	0	6.4	3.2	0
Jan-87	*	9.6	3.2	0	*	*	*	0	0	0	0	0	0	0	3.2	*	0	*	0	13	6.4	3.2
Feb-87	*	0	0	0	*	*	*	3.2	*	0	*	*	*	*	0	*	0	*	0	0	0	0
Mar-87	0	0	0	0	0	0	0	3.2	0	9.6	0	0	0	0	3.2	3.2	0	0	0	0	9.6	0

* *Xenostrobus* in bold, *Assimineia* in normal font, *Sanguinolaria* in italics.