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SEASONAL CHANGES IN THE MACRO-ZOOBENTHOS OF A TROPICAL MUDFLAT

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The cover shows the pindan-red northern shore of Roebuck Bay, just off the Broome Bird Observatory, where the intertidal benthic monitoring programme was carried out, together with a biological visualization of the local tropical seasons.

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Seasonal changes in the macrozoobenthos of a tropical mudflat

Report on *MONROEB* — *MON*itoring *ROE*buck Bay *B*enthos, 1996-2001

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ABSTRACT

Roebuck Bay in the Kimberley region of northwest Australia is especially famous for the tens of thousands of shorebirds that spent the tropical winter here. Shorebirds are attracted to the richness of benthic invertebrates living in and on the intertidal flats.

To find out which benthic animals are present throughout the year, and from year to year, a benthic monitoring programme was started in 1997. The aim of *MONROEB* (*MON*itoring *ROE*buck Bay *B*enthos) was to unravel the seasonality of the benthic life on a tropical intertidal flat in order to compare this to the better studied intertidal flats of temperate northwest Europe. To the best of our knowledge this is the first long-term study of the seasonal dynamics of intertidal benthos in the tropics.

From March 1996 two sites in the bay were sampled almost monthly. One site is a sandy place off Fall Point , the other is a very muddy place off One Tree , at the eastern end of Crab Creek Road. At these two sites the benthic invertebrates were monitored at two stations, respectively 150 m and 250 m offshore. The sampling was carried out by the Broome Bird Observatory wardens assisted by volunteers. At each of the four stations (two sites with two stations each), four samples each consisting of six cores of 83 cm^2 to a depth of 20 cm were taken. Each sample was sieved over a 1-mm mesh, which thus yielded the macrozoobenthic animals . The sieved samples were directly sorted in trays with salt water. All animals were conserved in formalin, stored in ethanol and sent to the Royal Netherlands Institute for Sea Research (NIOZ) for identification. The sampling programme is still continuing, but the analysis includes samples up to May 2001.

In the laboratory, all molluscs and crabs (to species level), the polychaete tubeworms Oweniidae and Chaetopteridae (to family level), the ostracods (three taxa), the brachiopods (one species *Lingula*), the echinoderms, the pygnogonids (sea spiders), anemones, tunicates and fish were distinguished, counted and, if possible, their lengths measured to the nearest mm. The remaining polychaetes were not analysed yet.

In the process almost 23,000 macrozoobenthic animals were sorted and assigned names. A total of 139 different taxa were encountered, including 40 different species of bivalve, 26 gastropods, 2 scaphopods, 7 echinoderms and 17 crab species. The total number of species was much higher in the sands off Fall Point than in the soft mud off One Tree. There were hardly any differences between the relatively nearshore and offshore stations.

At Fall Point the most common species were the bivalves *Anodontia omissa*, *Divaricella ornata* and *Tellina piratica*, the gastropods *Vexillum radix* and Eulimidae spec., the scaphopod *Laevidentalium* cf. *lubricatum*, the crab taxon *Macrophtalmus* spec., the spidercrab

Halicarcinus cf. *australis*, the crabs *Hexapus* spec. and *Myrodes eudactylus*, the polychaete tubeworms Chaetopteridae and Oweniidae, an ostracod, hermit crabs, the brachiopod *Lingula* spec., brittlestar *Amphiura tenuis* and starfish *Astropecten granulatus*. At One Tree the most common species were the bivalves *Tellina* cf. *exotica* and *Siliqua pulchella*, the gastropods *Tornatina* spec., *Salinator* cf. *burmana* and the small *Nassarius* spec., the scaphopod *Dentalium* cf. *bartonae*, hermit crabs and mudskippers Periophthalmidae.

Of the 15 numerically dominant taxa, most of which were bivalves, the seasonal changes are given. In contrast to the clear and regular annual rhythmicity in the numbers of most species on temperate intertidal flats, the species in Roebuck Bay show a great variety of density changes, with little evidence for clear circannual cycles. Bloody cockles *Anadara granosa* had the highest densities from early to mid 1997 with lower numbers since. The lucinid bivalve *Anodontia omissa* reached peak densities in late 1997 and again in late 1999. Another lucinid bivalve, *Divaricella irpex*, showed peaked numbers every two years. The razorclam-like *Siliqua pulchella* peaked in mid 1997, with a gradual decline in numbers since. The tellinid *Tellina capsoides* peaked in late 1996-1997 and also declined since. In contrast, *Tellina piratica* peaked three times over the six year of study. *Tellina exotica* has been in decline since the start of the monitoring programme, with quite low numbers from 1999 onwards.

The Ingrid-eating snail *Nassarius dorsatus* showed repeated peak numbers after the cold (dry) seasons. Neither of the tusk shells showed any sign of regular circannual changes in numbers, nor did the tubeworms Chaetopteridae and Oweniidae. Of the two crab taxa that could be examined, *Halicarcinus* cf. *australis* peaked four times in the middle of the year, whereas *Macropthalmus* spec. peaked three times in the middle of the year. The brittlestar *Amphiura tenuis* showed no large changes over time.

For the seven most abundant bivalves and one gastropod, aspects of settlement of new cohorts and the possibility of movements of animals over the intertidal flats were examined by looking at the size-frequency distributions. Unlike the temperate species, there is no single time period of settlement. Settlement of the different species in the Bay took place at different times of the year. *Anadara granosa* settled in the course of some of the wet seasons. Both lucinids, *Anodontia omissa* and *Divaricella irpex* settled early in the wet, *Siliqua pulchella* probably settled late in the wet. The tellinids settled in the middle of the wet (*Tellina capsoides*), after the wet (*Tellina piratica*) or at the beginning and the end of the wet season (*Tellina exotica*).

For one bivalve species, *Siliqua pulchella*, there were clear indications that these animals make movements over the intertidal flats after settlement.

SAMENVATTING

Roebuck Bay, gelegen in noord-west Australi vlakbij Broome, is vooral beroemd om de tienduizenden wadvogels die daar de tropische winter doorbrengen. De wadvogels worden aangetrokken door de rijkdom aan voedsel: de benthische bodemdieren die in en op het wad leven.

Om uit te vinden hoeveel en welke bodemdieren er door het jaar heen aanwezig zijn en hoe de aantallen en van jaar op jaar verschillen, zijn we in 1997 gestart met een onderzoeksprogramma waarin de aanwezigheid en aantallen van bodemdieren op een viertal plekken werd gevolgd. Het doel van MONROEB (*MON*itoring *ROE*buck Bay *B*enthos) was om een vergelijking te maken tussen de seizoenscycli van bodemdieren in en op een tropisch wad en die van de bodemdieren in de uitvoerig bestudeerde waddengebieden in noord-west Europa. Voorzover ons bekend, is dit is de eerste langdurig volgehouden studie van het benthos van een getijdegebied in de tropen.

Vanaf maart 1996 zijn bijna iedere maand op twee locaties in de baai monsters genomen. De ene locatie is een zandige plek bij Fall Point , vlakbij het Broome Bird Observatory (BBO). De andere locatie betreft twee hele modderige plekken bij One Tree , aan het oosteinde van de Crab Creek road . Op deze twee locaties werden de benthische bodemdieren gemonsterd op twee plekken, respectievelijk 150 en 250 meter vanaf het zandstrand. De bemonsteringen werd uitgevoerd door de beheerders van BBO met hulp van vele vrijwilligers. Op elk van de vier stations (twee locaties, ieder twee plekken) werden vier monsters van de wadbodem genomen. Ieder monster bestond uit zes steken met een steekbuis van 83 cm^2 tot een diepte van 20 cm. Ieder monster werd gezeefd over een 1 mm zeef. Dat wat op de zeef achterblijft is het macrozoobenthos . De gezeefde monsters werden direct uitgezocht in bakken met zout water. Alle dieren werden geconserveerd in formaline, opgeslagen in ethanol en ter identificatie opgestuurd naar het Koninklijk Nederlands Instituut voor Onderzoek der Zee (NIOZ). Het bemonsteringsprogramma gaat nog steeds door. In dit verslag worden de resultaten gepresenteerd van de monsters die tot en met mei 2001 zijn verzameld.

In het laboratorium werden de volgende soorten en groepen onderscheiden: alle schelpdieren en krabben (tot op soortniveau), de borstelwormen Oweniidae en Chaetopteridae (tot op familieniveau), de ostracoden (drie typen), de brachiopoden (n soort, *Lingula*), de stekelhuidigen, zeespinnen, anemonen, manteldieren en vissen. Alle dieren werden geteld en indien mogelijk opgemeten tot op een millimeter nauwkeurig. De overgebleven wormpjes en kleine kreeftachtigen zijn nog niet geteld, gemeten en op naam gebracht.

Bijna 23.000 dieren werden gesorteerd en van een werknaam voorzien. In totaal werden er 139 soorten onderscheiden, waarvan 40 verschillende soorten tweekleppige schelpdieren, 26 slakken, 2 olifantstanden, 7 stekelhuidigen, en 17 krabben. Het totaal aantal soorten was veel hoger op de zandige locaties van Fall Point dan op de modderige locaties van One Tree. Er waren nauwelijks verschillen tussen de plekken die 150 m en 250 m van het strand lagen.

De meest algemene soorten van Fall Point waren de tweekleppige schelpdieren *Anodontia omissa*, *Divaricella ornata* en *Tellina piratica*, de slak *Vexillum radix* en Eulimidae spec., de olifantstand *Laevidentalium* cf. *lubricatum*, de krabben *Macrophtalmus* spec., *Halicarcinus* cf. *australis*, *Hexapus* spec., het solda-

tenkrabje *Myrodes eudactylus*, de kokerwormen Chaetopteridae and Oweniidae, een roeipootkreeftje of ostracode, heremietkreeften, de brachiopode *Lingula* spec., de brokkelster *Amphiura tenuis* en de zeester *Astropecten granulatus*. De meest algemene soorten van One Tree waren de tweekleppigen *Tellina* cf. *exotica* en *Siliqua pulchella*, de slakken *Tornatina* spec., *Salinator* cf. *burmana* en *Nassarius* spec., de olifantstand *Dentalium* cf. *bartonae*, heremietkreeften en slijkspringers Periophthalmidae.

Van de 15 meest voorkomende taxa, met name tweekleppige schelpdieren, zijn de seizoensveranderingen weergegeven. In tegenstelling tot de duidelijke en regelmatige jaarlijkse ritmiek in de aantallen van de meeste soorten bodemdieren van gematigde getijdegebieden zoals de Waddenzee, vertonen de soorten in Roebuck Bay een grote variatie aan dichtheidsveranderingen. Er zijn weinig aanwijzingen voor het bestaan van duidelijke jaarcycli. De bloedkokkel, *Anadara granosa*, kwam in de hoogste dichtheden voor van begin tot halverwege 1997 en daarna alleen in lage aantallen. De tweekleppige *Anodontia omissa*, een oogje , vertoonde piekdichtheden aan het eind van zowel 1997 en 1999. Een ander oogje , *Divaricella irpex*, vertoonde iedere twee jaar een piek in aantallen. De op een kleine mesheft lijkende *Siliqua pulchella* piekte halverwege 1997 en nam daarna geleidelijk in aantallen af. De nonnetjesachtige *Tellina capsoides* piekte aan het einde van 1996 en begin 1997 en is sindsdien eveneens afgenomen. In tegenstelling hiertoe vertoonde een ander soort nonnetje, *Tellina piratica*, in de zes jaar van het onderzoek, drie keer een piek. De platschelp *Tellina exotica* is sinds de start van het monitorprogramma in aantal afgenomen en kwam na 1999 nog slechts in zeer lage aantallen voor.

De Ingrid-etende slak , *Nassarius dorsatus*, vertoonde ieder jaar piekaantallen na het koude (droge) seizoen. Geen van de twee olifantstanden (scaphopoda) toonde een teken van regelmatige jaarlijkse veranderingen in aantallen, en dat geldt ook voor de kokerwormen Chaetopteridae en Oweniidae. Van de twee krabben die in voldoende aantallen voorkwamen, piekte *Halicarcinus* cf. *australis* vier keer midden in het jaar en *Macropthalmus* spec. drie keer. De brokkelster *Amphiura tenuis* vertoonde geen grote veranderingen in aantallen.

Voor de zeven meest voorkomende tweekleppigen en de slak *Nassarius dorsatus* is de vestiging van nieuwe jaarklassen, de groei en de mogelijkheid van migratie van dieren over de wadplaten onderzocht door naar de lengteverdelingen van die dieren over de jaren te kijken. In tegenstelling tot de soorten uit gematigde streken, is er niet n specifiek moment waarop de jonge dieren zich vestigen. In Roebuck Bay vestigde het broed van de verschillende soorten zich op verschillende momenten van het jaar. De bloedkokkel *Anadara granosa* vestigde zich in de loop van enkele van de natte seizoenen. De beide oogjes, *Anodontia omissa* en *Divaricella irpex*, vestigden zich vroeg in het natte seizoen. *Siliqua pulchella* vestigde zich hoogstwaarschijnlijk laat in het natte seizoen. De nonnetjesachtigen vestigden zich midden in (*Tellina capsoides*), net na (*Tellina piratica*) of zowel aan het begin als aan het einde van het natte seizoen (*Tellina exotica*).

Alleen voor de mesheftachtige tweekleppige *Siliqua pulchella* waren er duidelijke aanwijzingen dat deze dieren over de wadplaten migreren nadat ze zich als jong dier ergens gevestigd hadden.

1. INTRODUCTION

In northwest Europe, where there is a long tradition in intertidal benthic studies, the biomass of animals living in soft sediments shows a pronounced seasonal cycle (Fig. 1). The biomass is the lowest in the northern winter (November through February) and reaches a peak in midsummer (June-August) (Beukema 1974). These seasonal changes in total biomass are a reflection of the settlement of new cohorts of benthic animals in late spring and early summer (March-June), the growth of these and older animals, the death and disappearance of animals of all sizes and ages and the changes in individual body condition (Zwarts & Wanink 1993). Obviously, such seasonal changes in the abundance of intertidal benthic animals are important to all predators, notably the shorebirds, which make a living of eating macrozoobenthos (benthic animals retained by a 1 mm sieve). In July-August when the northern migrant shorebirds come back from the Arctic to places like the Wadden Sea (The Netherlands), they find their larder refilled after a spring and summer of benthic growth and reproduction.

Many shorebirds do not stay for the whole nonbreeding season in northern temperate latitudes, but instead continue their migrations further south. Indeed, the great majority of shorebirds seem to overwinter in tropical regions, and Roebuck Bay in the Kimberley region of northwest Australia is a typical and numerically important tropical 'wintering' area for migrants from northern Asia (Lane 1987, Watkins 1993). In the eyes of many north-temperate shorebird ecologists, tropical nonbreeding areas would have the advantage of offering a more constant food supply because the tropics would (a) be less seasonal and (b) have a greater variety of animals with variable and compensatory recruitment and growth cycles (Wolff 1991, Piersma 1994, Van de Kam *et al.* 1999).

Probably as a consequence of smaller seasonal changes in daylength and irra-

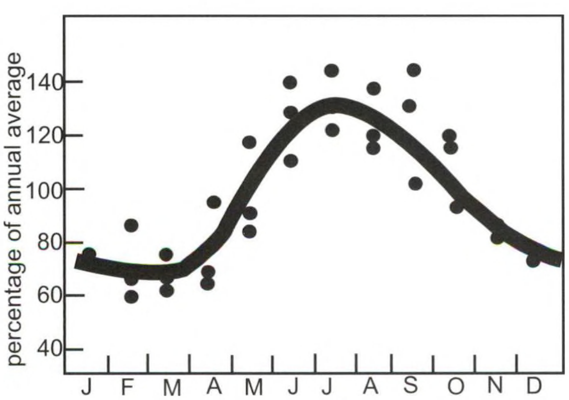


Figure 1. Seasonal cycle of the relative macrozoobenthic biomass in the Dutch Wadden Sea. After Beukema (1974); data from three different sampling stations are presented.

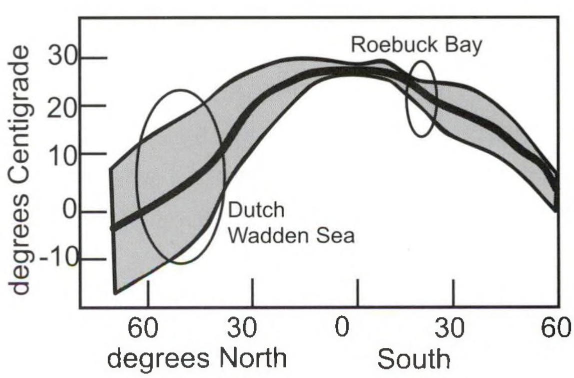


Figure 2. Annual range of mean monthly temperatures (shaded area) as a function of latitude. The approximate positions of the Dutch Wadden Sea (53°N) north of the equator and Roebuck Bay (18°S) south of the equator are indicated by the ellipses. After Fig. 9-5 in Ricklefs (1990), based on data in Clayton & Clayton (1947).

diation at tropical latitudes, the variation in air temperatures is much less than at temperate latitudes (Fig. 2). If the seasonality in benthic biomass found in temperate latitudes is a consequence of climatic factors, then it seems logical to argue for a more constant benthic food supply in the tropics (Piersma 1980). What we really are saying here is that reproduction and/or growth of benthic animals would be much more constant in the tropics than at temperate latitudes, but to the best of our knowledge there is little testing of this hypothesis or establishing this for a fact (Alongi 1990). Although Broom (1982; for a mudflat in Malaysia) and Vargas (1989; for a mudflat in Central America) did find some species-specific responses to wet and dry seasons, Dittmann (2002) found no seasonal changes in benthic abundance for a tropical mudflat in northeast Australia.

Actually, there is of course seasonality with respect to climatic conditions and biotic responses in many tropical areas, and the Kimberley region of northwest Australia is no exception (Kenneally *et al.* 1996). For shorebird-oriented naturalists, the seasons in Roebuck Bay are obvious because of the presence and absence of particular groups of birds, together with the changing weather conditions in which these various birds can be observed (Fig. 3A). From December to March heavy rains occur during a time that is otherwise characterised by the large numbers of northern migrants which moult into breeding plumage and depart north around March-May. The departure

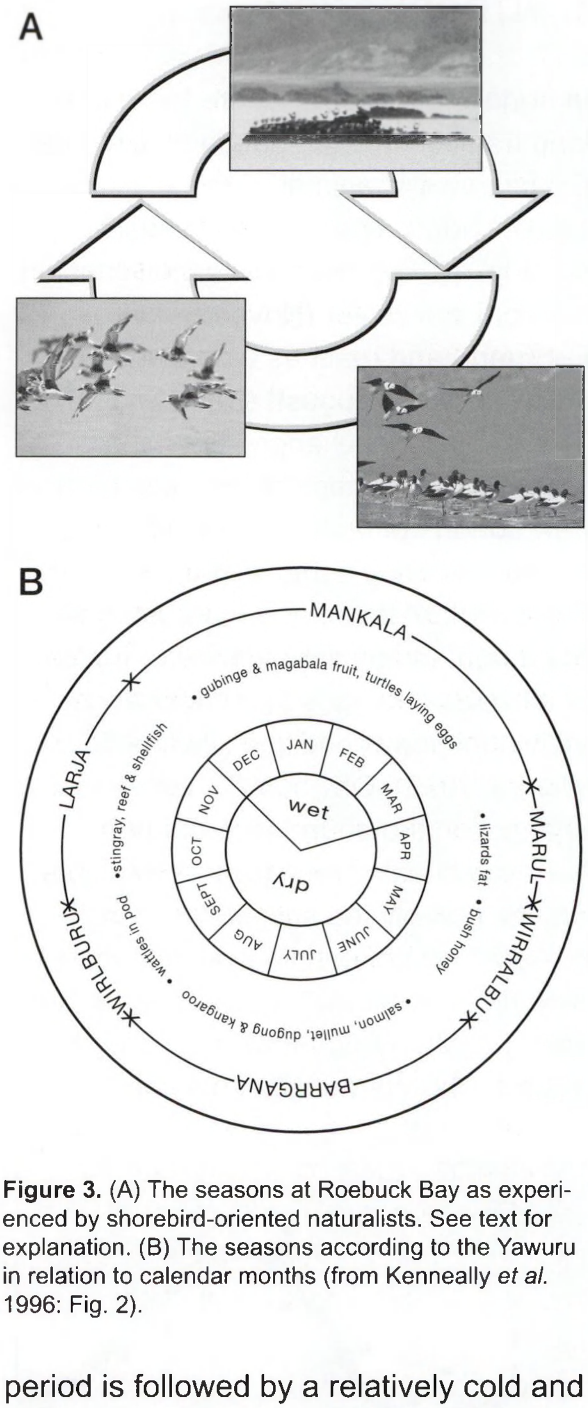


Figure 3. (A) The seasons at Roebuck Bay as experienced by shorebird-oriented naturalists. See text for explanation. (B) The seasons according to the Yawuru in relation to calendar months (from Kenneally *et al.* 1996: Fig. 2).

period is followed by a relatively cold and dry period when birds from inland wetlands, such as Black-winged Stilts *Himantopus himantopus*, come to the bay. When the temperatures increase in July and August the northern migrants start to return, and the naturalists notice that the northern migrants commence a moult from breeding into nonbreeding plumage. This includes the replacement of flight feathers, as indicated in Fig. 3A by the gaps in the wings of the Grey Plovers *Pluvialis squatarola*.

The Yawuru people from the lands east of Roebuck Bay have always distinguished their seasons on the basis of the varying resources (Fig. 3B). Based on the information assembled by Merrilee Lands and Maria Mann (in Kenneally *et al.* 1996), the Yawuru seasons consist of *Mankala* (December-March), *Marul* (April), *Wirralburu* (May), *Barrgana* (June-August), *Wirlburu* (September) and *Larja* (October-November). *Mankala* is the wet season, with northwesterly winds and the occasional cyclone. The shellfish are skinny and the sea turtles lay their eggs. *Marul* is the hot period after the wet when the mangrove *Avicenna marina* is in fruit, but when the reef fish are skinny. During *barrgana* the winds come from the southeast, the nights are cold and the stars are bright. Threadfin salmon, mullet, catfish and dugong are fat. During *wirlburu* the west winds and the warmer nights return. The reef fish and the shellfish are getting fat. *Larja* is the time before the wet. Turtles are mating and stingray, reef fish and shellfish are fat.

Based on the Yawuru seasons, there may be as much seasonality in the marine biota of Roebuck Bay as there is in the Dutch Wadden Sea. Although we do not know to which species of shellfish the Yawuru refer (the bloody cockle *Anadara granosa* is likely to be among them), it is clear that during *wirlburu* they grow, during *larja* they are fat and during *mankala* they are skinny. Doesn t this suggest a period of growth during the dry season, before a period of spawning (and slimming down) at the start of the wet?

Here we report on studies aimed to verify whether a north-temperate perspective on tropical intertidal macrozoobenthos has any merit, or, as the names and meanings of the seasons observed by the Yawuru and other Aboriginal groups in the Kimberley region suggest, that the north-temperate perspective is much too simplified. Over a period of five years at approximate monthly intervals, volunteers from the Broome Bird Observatory have collected quantitative samples of macrozoobenthic animals from two sites in the north of Roebuck Bay: (1) offshore at the eastern end of Crab Creek Road at One Tree in the deep mud of Kraken Corner (Pepping *et al.* 1999) and (2) offshore from Fall Point, just west of the beach entrance to the Broome Bird Observatory, on the rather narrow band of sandy sediment. We will examine weather patterns during these five years (3.1), look at changes in the abundances of particular groups, with a focus on bivalves, gastropods and crustaceans (3.2), establish when the settlement of the small cohorts takes place, and whether macrozoobenthic animals in Roebuck Bay move around during early life (3.3), and will round up with an assessment of the research strategy followed so far. Do we get good value for the enormous volunteer effort, or can we rationalize the programme for an even better scientific yield (3.4)?

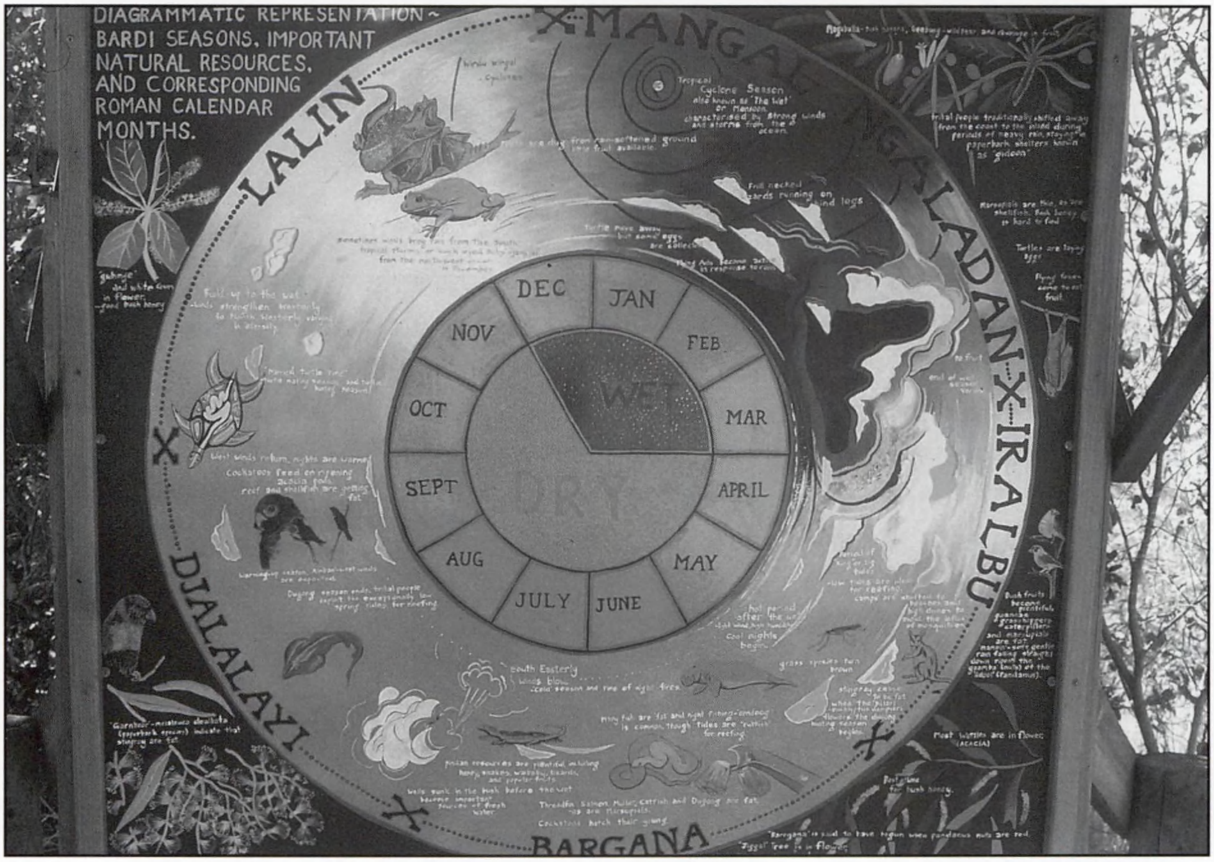


Plate 1. The calendar of seasons of the Bardi people of the Dampier Peninsula, photographed at Cape Leveque by Marc Lavaleye.

2. STUDY SITES AND METHODS

2.1. STUDY SITES

Roebuck Bay is a marine embayment with a fringe of mudflats in the north, and with extensive intertidal mudflats in the east and south (Fig. 4). The bay regularly supports over 100,000 shorebirds, which makes it one of the most important intertidal areas in Australia (Watkins 1993). All these birds depend on the benthic animals living on and in the mud. A study of the food of Great Knots *Calidris tenuirostris* (Tulp & de Goeij 1994) and a study mapping the intertidal benthos of the north-shore mudflats (Pepping *et al.* 1999) both indicated that the benthic life of Roebuck Bay is very diverse and rich.

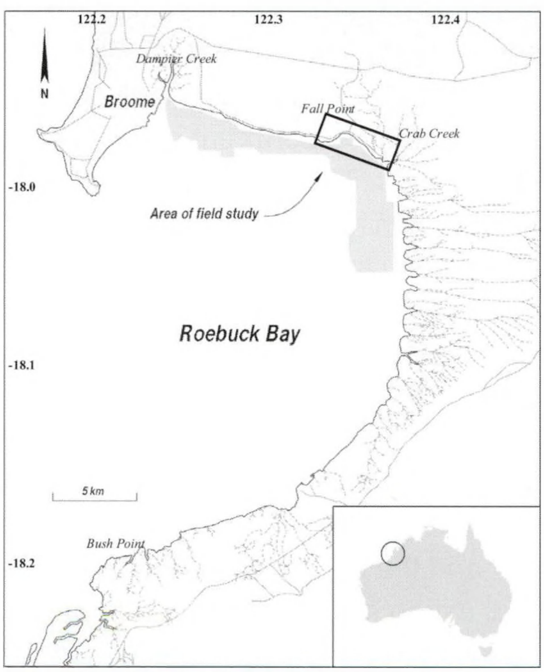


Figure 4. Location of Roebuck Bay and the town of Broome on the Dampier Peninsula on the Australian continent (inset) and map of Roebuck Bay with the area of intertidal flat mapped by Pepping *et al.* (1999) outlined in grey and the core sites where the benthic monitoring took place from 1996-2001 indicated by the short sides of the rectangle between Fall Point and Crab Creek (see Fig. 5).

In March 1996 two sites were selected (called 'Fall Point' and 'One Tree', near Crab Creek, Fig. 4), and at each of these sites two sampling stations were positioned approximately 150 m and 250 m offshore (perpendicular to the beach, more or less directed due south), named A and B (Fig. 5). The approximate geographical position of the Fall Point stations is 17°59'S, 122°21'E and for the One Tree stations 17°60'S, 122°22'E. The One Tree site is slightly longer exposed per tidal cycle than the Fall Point site, especially during neap tides.

2.2. METHODS

The two sites (= four stations) were sampled almost every month in the period March 1996 to May 2001. At each station 4 samples were taken, each consisting of 6 standard cores with a diameter of 10.3 cm and a surface of 1/120 m^2 (= 0.083 m^2 = 83 cm^2), taken to a depth of 20 cm. Each sample was sieved on location over a sieve with a mesh-size of 1 mm. Each sample thus represented a mud-surface of 6*1/120 = 1/20 m^2, and each station represented a sampled surface of 4*1/20 = 1/5 m^2; to obtain a density per m^2, the number of animals per station was multiplied by 5. To obtain overall densities per sampling date, the average of the station-specific densities was calculated.

The sieved samples were transferred to the Broome Bird Observatory where they were sorted in trays with salt water,

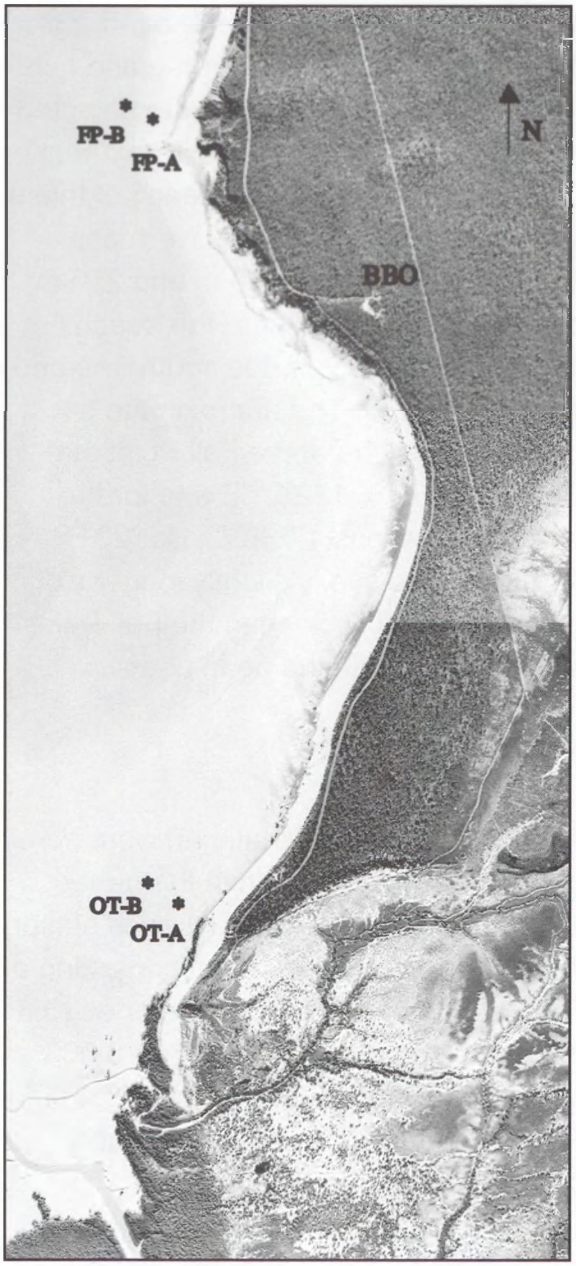


Figure 5. Composite of two aerial photo s showing the study area, the two sites (FP = Fall Point and OT = One Tree) and the four sampling stations (A and B at each site) in the northeastern corner of Roebuck Bay (see Fig. 4 for orientation). BBO = Broome Bird Observatory.

on most occasions on the day of sampling. All animals were picked out and fixed with 4% formaldehyde. After a few days the formaldehyde was removed and replaced by 70% ethanol. The samples were then sent to the Royal Netherlands Institute of Sea Research (NIOZ) for detailed analysis. To prevent both leakage and the dehydration of specimens, before the samples were packed and sent the ethanol was removed and replaced by ethanol-saturated paper tissue. After arrival in the Netherlands the vials were filled again with 70% ethanol.

In our laboratory analyses so far we have distinguished (and counted!) all molluscs and crabs (to species level), other crustacean groups to order level but sometimes to species level, the polychaete tubeworms Oweniidae and Chaetopteridae (to family level), the ostracods (three taxa), the brachiopods (one species of *Lingula*), the echinoderms, pygnogonids (sea spiders), anemones, tunicates and fish. This leaves the many families of polychaete worms and an assortment of small crustacean forms. The sorted, counted and measured animals have been kept for further study and so have the unsorted animals. All specimens were counted and their length was measured with callipers to the nearest 0.5 mm. The length of bivalves is defined as the length of the anterior-posterior axis, the length of the gastropods as the distance between the apex and the tip of the anterior (siphonal) canal (when present) or to the farthest edge of the aperture, and the length of the scaphopods as the length of the straight line between both tips of the shell. The size of the crabs was defined as their carapace width. The length of all other specimens is given by the longest body length.

Identifications were made with the help of a stereo-microscope, using among other sources Edgar (1997), Faucauld (1977), Janssen (1995), Jones & Morgan (1994), Lamprell & Whitehead 1992, Lamprell & Healy 1998, Shepherd & Thomas (1989) and Wilson (1993, 1994). Although it was possible to assign some species a proper scientific name (mainly the bivalves), for many specimens a field name was given for preliminary use (see Table 1). Note that these field names are not intended to be used in the nomenclature within the meaning of International Committee of Zoological Nomenclature (ICZN). In the process we have so far sorted and assigned names to 22,946 macrozoobenthic animals of at least 144 species. Given the taxonomic gaps, true diversity is likely to be much higher.

Plate 2 (A, B and C). Early efforts at monitoring the benthos of Roebuck Bay. Sampling at the One Tree stations in March 1996 when we found a yellow sea snake in one of the mudskipper burrows! Photo's by Theunis Piersma.

3. RESULTS AND DISCUSSION

3.1. TROPICAL SEASONS

The intertidal macrozoobenthic animals of Roebuck Bay (as well as the birds, the wallabies and the people) encounter strong seasonal changes in rainfall and air temperature (Fig. 6). Rainfall peaks in January, February or March, with two of the six years (1996 and 2000) showing a single peak and the other four a second period with rain in either May or June. Although monthly average maximum air temperatures varied with 7°C only from 28 to 35°C, there were brief excursions to the lowest part of the temperature range during the middle of each year, with broader bands of higher temperatures from October through April. The monthly average minimum air temperatures varied twice as much, with lows down to 12°C in June and highs of up to 27°C in December or January. During these five years Roebuck Bay was visited by a cyclone one time. In late January 1998 a category 1 cyclone had some striking effects on some of the outlets of Crab Creek whereas in April 2000 the cyclone 'Rosita' passed 40 km south of Broome, coming on land between Bush Point and the Ecobeach tourist resort (which was completely destroyed). The latter cyclone is thought to be responsible for the disappearance of most of the seagrass cover on the northern shore of Roebuck Bay (D.I. Rogers pers. comm.).

3.2. OVERALL BIODIVERSITY

Excluding the polychaetes (except two taxa), a total of 139 different taxa were encountered among the 23,000 animals retrieved from the core-samples taken at the One Tree and Fall Point stations

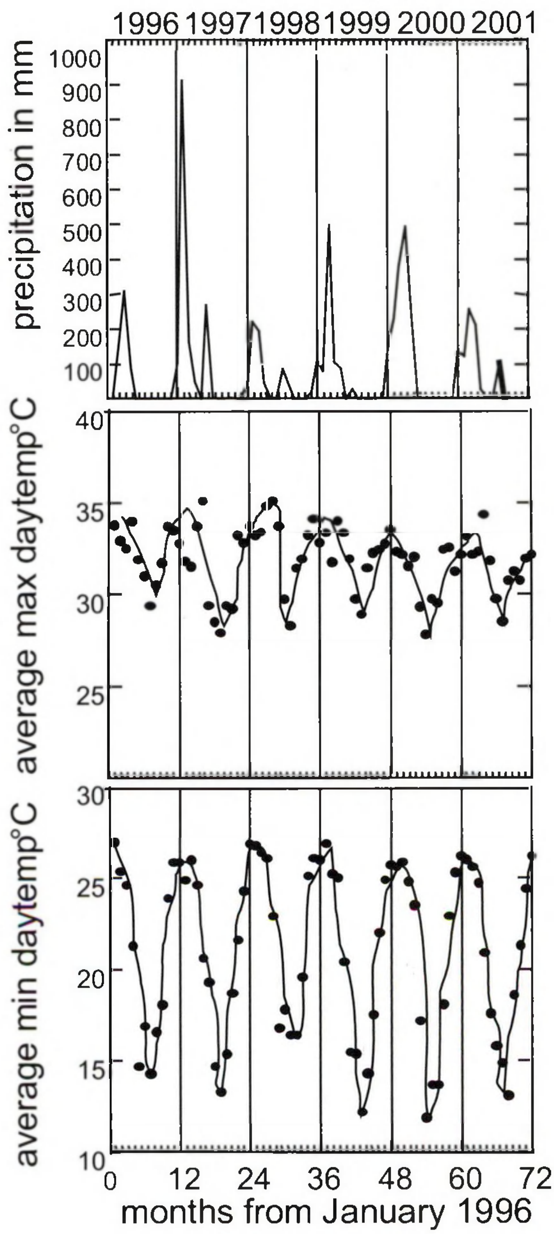


Figure 6. Seasonal patterns of rainfall, average maximum and average minimum air temperature at Broome over the entire period of study, 1996-2001. The data are presented as monthly sums (precipitation) or averages (temperature), and were kindly made available by the Bureau of Meteorology in Perth.

Table 1. For all different macrozoobenthic taxa found during MONROEB the numbers are given per site (Sum) and over all sites (Total sum). FP-A= Fall Point-A, FP-B= Fall Point-B, OT-A= One Tree-A, OT-B= One Tree-B

Species name	Group	Sum FP-A	Sum FP-B	Sum OT-A	Sum OT-B	Total sum
juvenile bivalve	Bivalvia	2	1	4	2	9
Nucula cf. *astricta*	Bivalvia	36	18	2		56
Ledella spec.	Bivalvia	4	1	3		8
Solemya cf. *terraereginae*	Bivalvia	14	24			38
Anadara granosa	Bivalvia		1	39	47	87
Modiolus micropterus	Bivalvia	1	2			3
Atrina spec.	Bivalvia		1			1
Anodontia omissa	Bivalvia	184	398	1		583
Divaricella irpex	Bivalvia	280	208	1	4	493
Ctena "rough"	Bivalvia	49	61			110
Ctena "smooth"	Bivalvia	1				1
Montacuta spec.	Bivalvia	1	2			3
Mysella "curva"	Bivalvia	3	1			4
Pseudopythina macrophthalmensis	Bivalvia	7	5	3	7	22
Scintilla spec.	Bivalvia	2	22	2		26
Heterocardia gibbosula	Bivalvia		3	15	21	39
Mactra spec. 1	Bivalvia	1				1
Mactra?	Bivalvia	1	4	4	7	16
Mactra grandis	Bivalvia	2	2		1	5
Raeta spec.	Bivalvia	2				2
Cultellus cultellus	Bivalvia	15	2			17
Siliqua pulchella	Bivalvia	22	6	138	137	303
Tellina capsoides	Bivalvia			141	140	281
Tellina piratica	Bivalvia	236	188	5	7	436
Tellina inflata	Bivalvia	3	2			5
Tellina amboynensis	Bivalvia	18	2	1	2	23
Tellina oval	Bivalvia			1		1
Tellina pointed	Bivalvia			7	1	8
Tellina cf *remies*	Bivalvia				1	1
Mud *Tellina*	Bivalvia			1	9	10
Tellina "mysia"	Bivalvia			1	12	13
Tellina ìexoticaî	Bivalvia	39	48	110	117	314
Tellina "exotica rose"	Bivalvia	15	5			20
Gari lessoni	Bivalvia	3	3		1	7
Solen spec.	Bivalvia	1	2		1	4
Anomalocardia squamosa	Bivalvia	4	2	1		7
Veneridae spec.	Bivalvia	1	2			3
Placamen gravescens	Bivalvia		2			2
Tapes spec.	Bivalvia		1			1
Laternula creccina	Bivalvia	6				6
Stenothyra spec.	Gastropoda				7	7
Vitrinellidae spec.	Gastropoda	1				1
Nerita spec.	Gastropoda	1	3			4
Epitoniidae spec.	Gastropoda		3	2	8	13
Cerithidea cingulata	Gastropoda	1			8	9
Eulimidae spec.	Gastropoda	19	40			59
Polinices conicus	Gastropoda	21	14	3	6	44
Natica "dull colored"	Gastropoda	2	2			4
Natica "with brown band"	Gastropoda				4	4
Columbellidae spec.	Gastropoda				1	1
Nitidella essingtonensis	Gastropoda	3		7	2	12
Nassarius dorsatus	Gastropoda	14	21	364	323	722
Nassarius "small Ingrid"	Gastropoda		1	22	21	44
Vexillum radix	Gastropoda	33	54			87
Turridae spec.	Gastropoda	2	4			6
Terebridae spec.	Gastropoda		3			3
Haminoae "green"	Gastropoda		7			7
Acteon spec.	Gastropoda	1				1

Tornatina spec.	Gastropoda	4	1	40	42	87
Salinator cf. *burmana*	Gastropoda	1		32	24	57
Pyramidellidae spec.	Gastropoda	2	1			3
Leucotina spec.	Gastropoda		1		4	5
Chrysallida spec.	Gastropoda			6	5	11
Syrnola spec.	Gastropoda	3	2			5
Odostomia spec.	Gastropoda	1				1
Tiberia spec.	Gastropoda		1			1
Laevidentalium cf. *lubricatum*	Scaphopoda	57	74	8	22	161
Dentalium cf. *bartonae*	Scaphopoda	2		114	131	247
Chaetopteridae spec.	Polychaeta	2426	2450			4876
Oweniidae spec.	Polychaeta	3433	771	16	26	4246
Ostracoda "oval, smooth"	Crustacea	489	565	10	7	1071
Ostracoda "square, sculptured"	Crustacea	26	61			87
Ostracoda "denticulated"	Crustacea	63	59	2	1	125
Gammariidae spec.	Crustacea	11	41	3	1	56
Anthura spec.	Crustacea	4	12			16
Tanaidacea spec.	Crustacea	34	22			56
Cumacea spec.	Crustacea	1			2	3
Mantis Shrimp (Squillidae)	Crustacea	6	8	4	1	19
Caridae (shrimp)	Crustacea	11	23	15	33	82
Gourretia coolibas	Crustacea	2	1		2	5
Callianassa spec.	Crustacea	2				2
hermit crab	Crustacea	108	44	13	18	183
Dorippe cf. *australiensis*	Crustacea	4	4			8
Raninidae spec.	Crustacea	1				1
Matuta planipes	Crustacea	10	3			13
cf. *Myrodes eudactylus*	Crustacea	3	14	3	2	22
Nursia abbreviata	Crustacea	9	1	2	1	13
Ebalia spec.	Crustacea	3				3
Leucosia spec.D	Crustacea	2				2
Portunidae spec.	Crustacea	4	5			9
Halicarcinus cf. *australis*	Crustacea	278	286	2	1	567
Mictyris longicarpus	Crustacea	5	5	1		11
Pinnotheres cf *cardii*	Crustacea	3	2	1	3	9
Pilumnidae spec.	Crustacea				2	2
Hairy crab (Pilumnidae)	Crustacea	2	3	1		6
Hexapus spec.	Crustacea	12	13	1	4	30
Macrophthalmus spec.	Crustacea	170	217	230	256	873
Uca spec.	Crustacea				1	1
Edwardsia spec.	Anthozoa	2	4	2	1	9
Shell anemone	Anthozoa			2	1	3
Pycnogonida spec.	Pycnogonida	4	6			10
Lingula spec.	Brachiopoda	118	80	1		199
Amphiura (*Ophiopeltis*) *tenuis*	Ophiuroidea	1882	1742	6	6	3636
Astropecten granulatus	Asteroidea	83	7			90
Peronella tuberculata	Echinoidea	1	1			2
Holothuroidea spec.	Holothuroidea	2				2
Leptopentacta grisea	Holothuroidea	1	5			6
Holothuria A	Holothuroidea	5	2	5	1	13
Stolus buccalis	Holothuroidea	2				2
Rooted Tunicate	Tunicata		46			46
Sandy Colonial Tunicate	Tunicata	52	751			803
Mudskipper (Periophthalmidae)	Pisces	9	9	57	60	135
Fish (Gobiidae)	Pisces	12	20	17	54	103

(Table 1). The taxon-list includes 40 different bivalves, 26 gastropods, 2 scaphopods, 7 echinoderms and 17 crabs. The total number of macrozoobenthic species is much higher in the sands off Fall Point than in the blue muds off One Tree (Fig. 7), and this is true also for the diversity of bivalves, gastropods and crabs. It is also clear that there are hardly any differences between the relatively nearshore station and the one further off, at both sites the station further offshore accumulated a few more species (Fig. 7).

Among the bivalves the most common species at the Fall Point stations were *Anodontia omissa* (583 animals were found in total, Table 1), *Divaricella irpex* (493) and *Tellina piratica* (436). The most common bivalves at the One Tree stations were *Tellina* exotica (227), *Tellina capsoides* (281) and *Siliqua pulchella* (275). *Tellina* exotica and *Siliqua pulchella* were also found in fair numbers at the Fall Point stations, but by and large each bivalve species occurred at one of the two sites rather than both (Table 1).

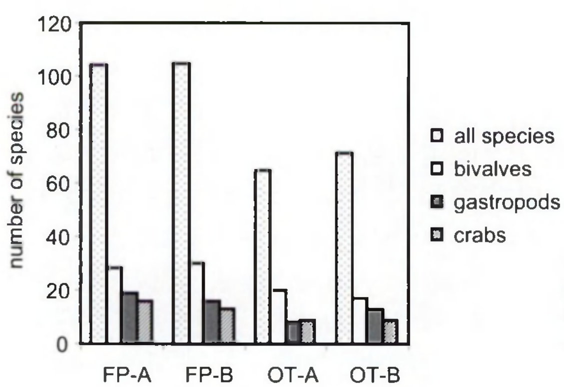


Figure 7. Total number of taxa (here called species) encountered during the MONROEB-sampling and sorting efforts between 1996 and 2001, with separate columns for the bivalves, gastropods and crabs.

The most common gastropod was the scavenger *Nassarius dorsatus* (722 animals in total), which occurred most abundantly at the One Tree stations. Other abundant gastropods were *Vexillum radix* (87; Fall Point only), *Tornatina* spec. (87; One Tree only), Eulimidae spec. (59; Fall Point only) and *Salinator* cf. *burmana* (57; One Tree only), *Polinices conicus* (44), and *Nassarius* small Ingrid (44; One Tree only). Two different scaphopods were found: *Dentalium* cf. *bartonae* (247 animals in total) that was only found at the One Tree stations and *Laevidentalium* cf. *lubricatum* (161) that was most abundant at the Fall Point stations but was also occasionally found at One Tree.

The most common crab taxon, found at all stations in almost equal numbers, were sentinel crabs *Macrophthalmus* spec. (873 animals in total). It is likely that this taxon comprises different species of *Macrophthalmus*. Another abundant crab near Fall Point was the spider crab *Halicarcinus* cf. *australis* (567). Two other crabs from the Fall Point stations found in reasonable numbers were *Hexapus* spec. (30; mostly Fall Point) and cf. *Myrodes eudactylus* (22).

Of the polychaete worms we sorted and counted, the two most obvious groups were the Chaetopteridae and Oweniidae. A total of 4876 Chaetopteridae were found at Fall Point. Most of the 4246 Oweniidae were also found at Fall Point, but lower numbers occurred at the One Tree stations. Three different Ostracoda were found, with the smooth form from Fall Point being the most common. Hermit crabs (183) occurred at both the Fall Point and One Tree stations, but species identity might differ between the two sites. Some 10 times a seaspider Pycnogonida was found in the Fall Point samples. The brachiopod *Lingula* spec. (199) occurred only at Fall Point. The brittlestar *Amphiura tenuis* was very common (3636) and almost completely restricted to Fall Point. The starfish *Astropecten granulatus* (90) was only found at Fall Point. Two tunicates were found, again at the Fall Point stations. Mudskippers Periophtalmidae (135) ended up mostly in some of the samples taken near One Tree. Gobiid fishes (103) came from all stations.

3.3. SEASONAL CHANGES IN ABUNDANCE

In a series of figures (Fig. 8 to Fig. 22) we will now present the seasonal changes in average densities (per m¯) over all four stations of the 15 numerically dominant taxa, most of which are bivalves. Densities are plotted as date-specific average densities over time, through which a kind of running average (the LOWESS routine of SYSTAT, tension 0.2) was fitted to lead the eye in our search for evidence for seasonal cyclicity (also called circannual rhythmicity).

Figure 8 shows the density changes of the bloody cockle *Anadara granosa*. Highest densities were found in early to mid 1997, with little evidence of clearly repeated circannual variations. Apart from two high values in late 1996 that do not show up in the LOWESS routine, the Lucinid eye-shell *Anodontia omissa* (Fig. 9) peaked in late 1997 and early 1998, with a second smaller peak in late 1999. Another Lucinid, *Divaricella irpex* (Fig. 10), showed clear cyclicity, but on a bi-annual rather than an annual basis. Over the time series, peak densities were reached three time, in late 1996, early 1998 and early 2000. The thin-shelled *Siliqua pulchella* which mostly occurred in the soft deep mud off One Tree, showed a single peak density in mid 1997 (at the time of the mapping effort by Pepping *et al.* 1999) and has been in decline since with no outspoken rhythmicity (Fig. 11).

A similar pattern to *Siliqua* was found in the Tellinid bivalve *Tellina capsoides* which occurred in the muds off One Tree rather than the sands off Fall Point (Fig. 12). After a single peak in late 1996- early 1997, the species went into decline and had completely disappeared by late 1999. Again, there was no evidence for any kind of circannual ryhthmicity in numbers. Just as *Divaricella irpex* (Fig. 10), the second Tellinid, *Tellina piratica*, occurred in peak numbers three times over the six years of this study (Fig. 13). The timing of the peaks also coincided with those of *Divaricella*, with high numbers in late 1996, mid 1998 and early to mid 2000. The third Tellinid was *Tellina* exotica , which occurred at both the sandy and the muddy site (Fig. 14). From the very start of the study in early 1996, it went into decline to reach a level of low numbers from 1999 onwards. This pattern resembles the numerical changes in *Tellina capsoides* (Fig. 12).

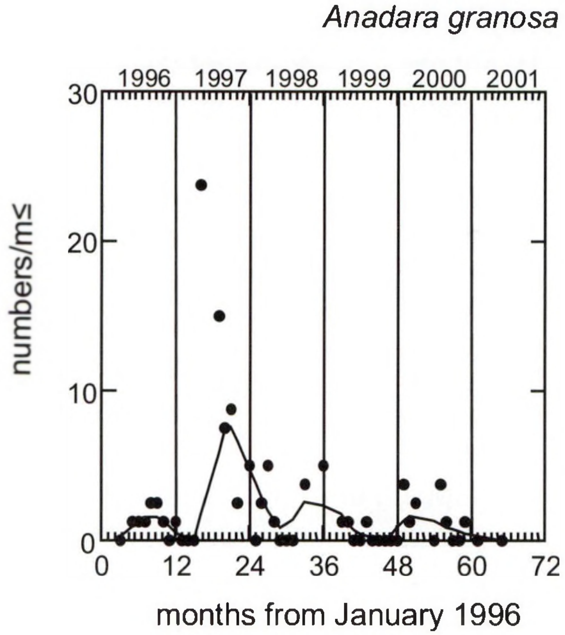
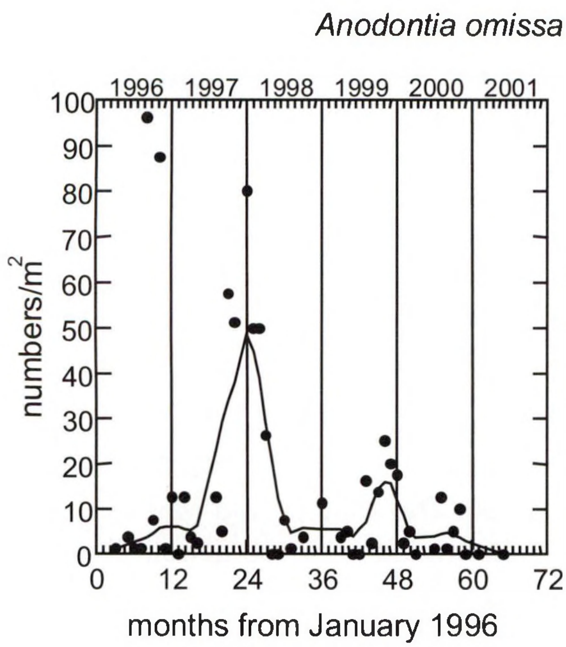


Figure 8. Changes in average density of *Anadara granosa* from early 1996 to mid 2001.



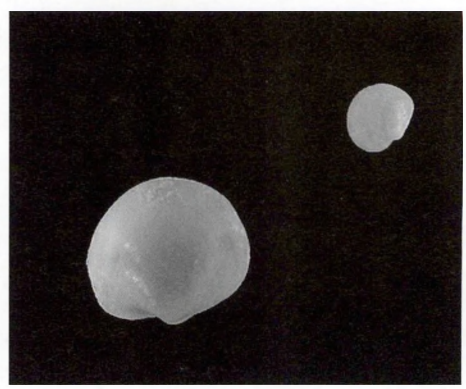
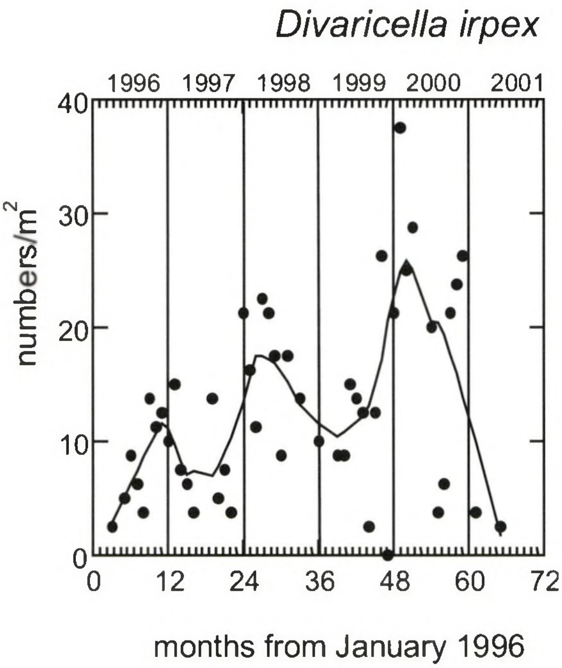


Figure 9. Changes in average density of *Anodontia omissa* from early 1996 to mid 2001.



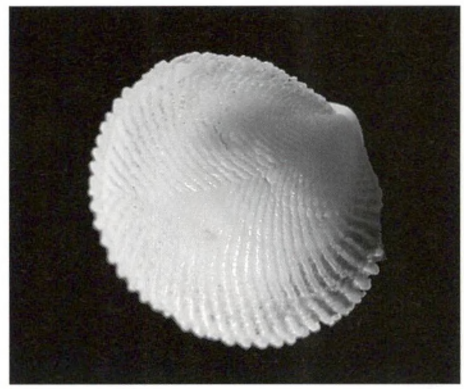
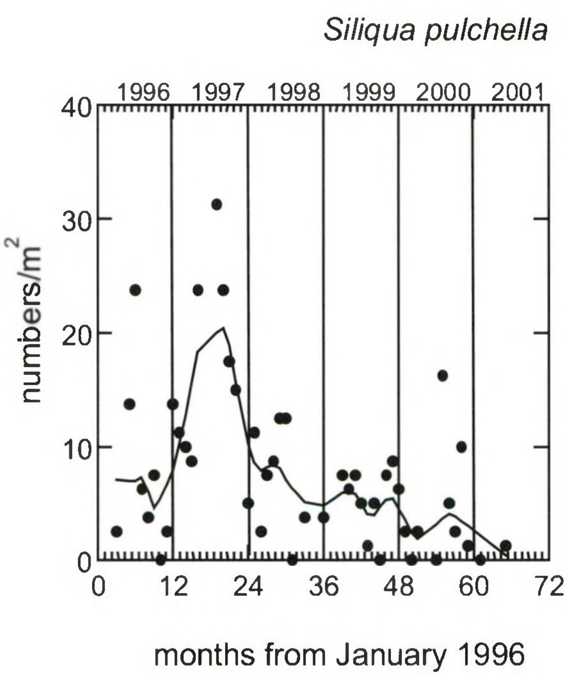


Figure 10. Changes in average density of *Divaricella irpex* from early 1996 to mid 2001.



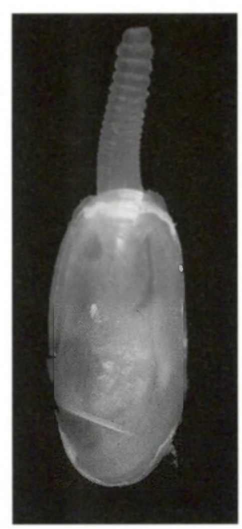


Figure 11. Changes in average density of *Siliqua pulchella* from early 1996 to mid 2001.

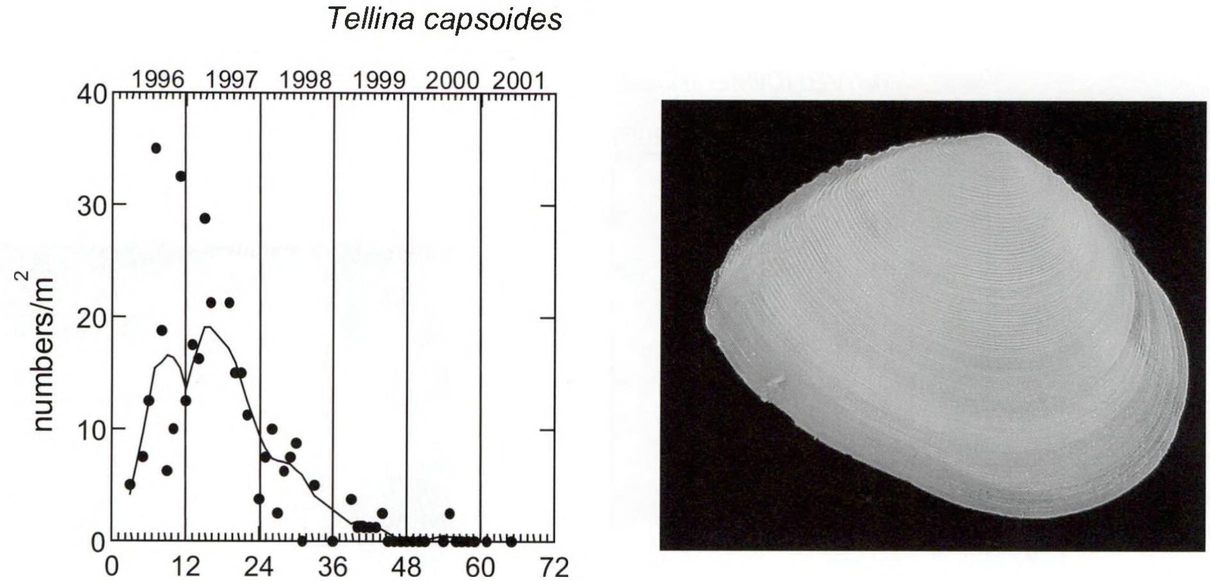


Figure 12. Changes in average density of *Tellina capsoides* from early 1996 to mid 2001.

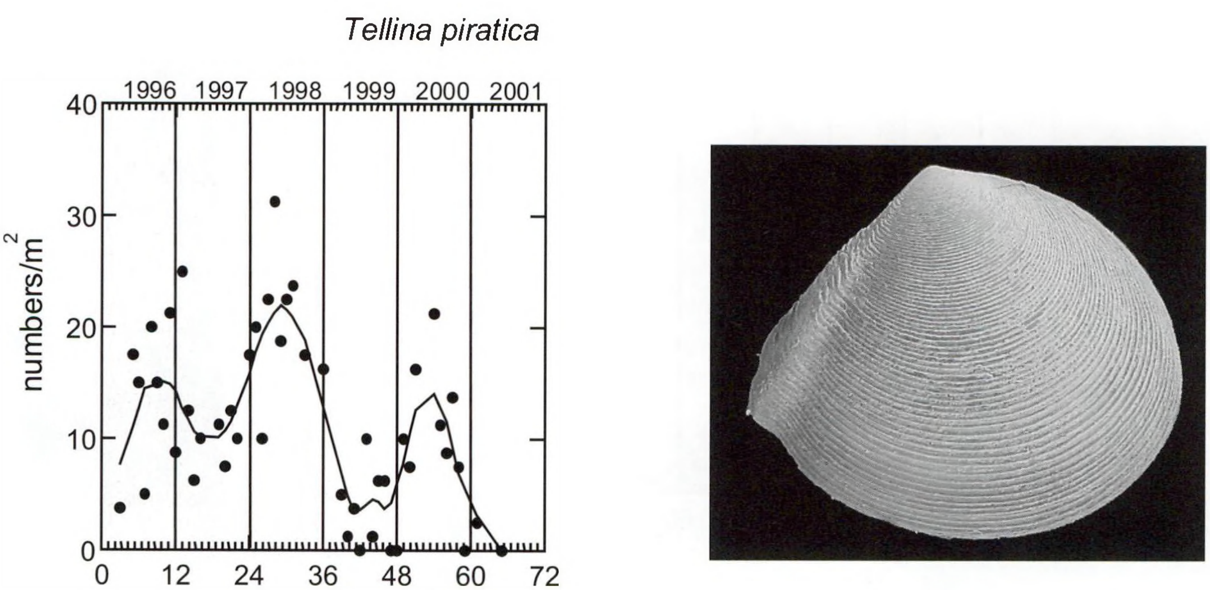
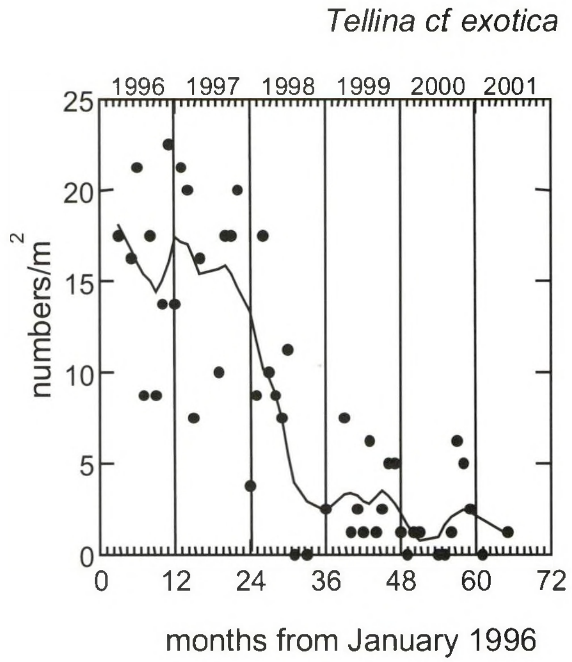


Figure 13. Changes in average density of *Tellina piratica* from early 1996 to mid 2001.



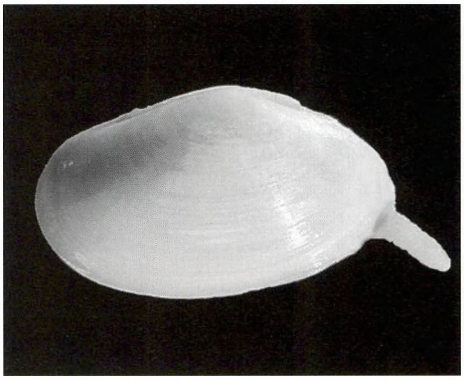


Figure 14. Changes in average density of *Tellina* exotica from early 1996 to mid 2001.

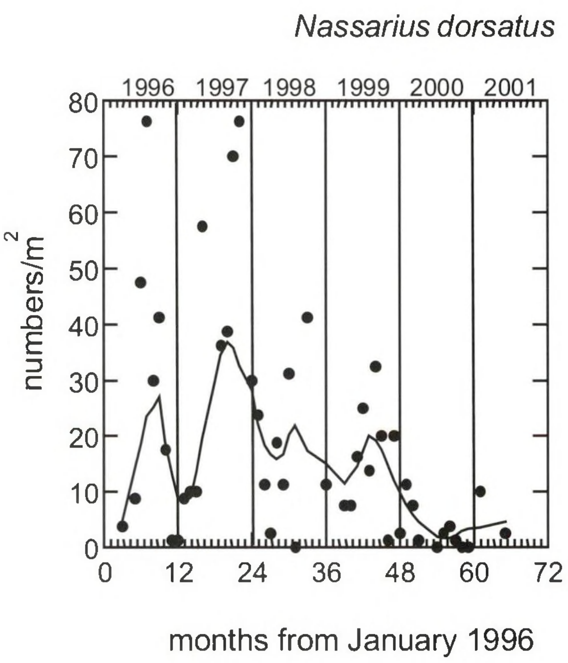


Figure 15. Changes in average density of *Nassarius dorsatus* from early 1996 to mid 2001.

The single gastropod that occurred in large enough numbers to examine seasonality was the Ingrid-eating snail *Nassarius dorsatus* (Fig. 15). Apart from a decline in the last two years of observation this species showed peak numbers repeatedly after the cold season, in mid 1996, 1997, 1998 and 1999, suggesting repeated settlements of new cohorts.

The first tusk-shell or scaphopod, the smoothly textured *Laevidentalium* cf. *lubricatum* had a rather indistinct pattern of numerical abundance, with high numbers in 1996 and 1997 and again in late 2000 (Fig. 16). The second, grooved, tusk-shell *Dentalium* cf. *bartonae* started off with low numbers and ended with low numbers as well, and peaked in 1998 (Fig. 17). In neither of the tusk-shells was there any sign of circannual rhythmicity.

The abundant plastic tubeworms Chaetopteridae that were such a sorting problem during the mapping effort in June 1997 (Pepping *et al.* 1999), now appear to only have been that abundant in mid 1997, being absent before and after that year (Fig. 18)! The tubeworms Oweniidae peaked in early 1997, again almost a year later in December 1997 and once more in October 2000 (Fig. 19). Both these polycheate worm taxa therefore had strong and erratic occurrences, where high numbers alternate with period of absence. In neither case was there any evidence for a seasonal effect.

The two crab taxa that can be examined, the tiny spider crab *Halicarnus* cf. *australis* (Fig. 20) and the sentinel crabs belonging to the genus *Macrophthalmus* (Fig. 21) both showed great variations

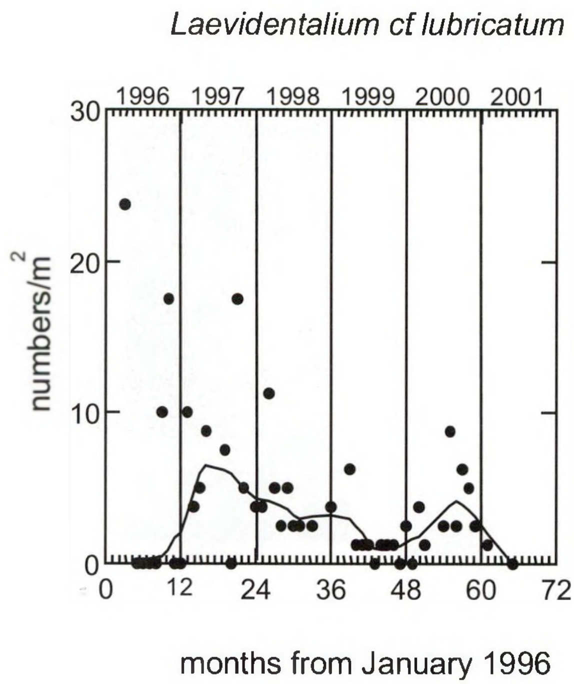


Figure 16. Changes in average density of *Laevidentalium* cf. *lubricatum* from early 1996 to mid 2001.

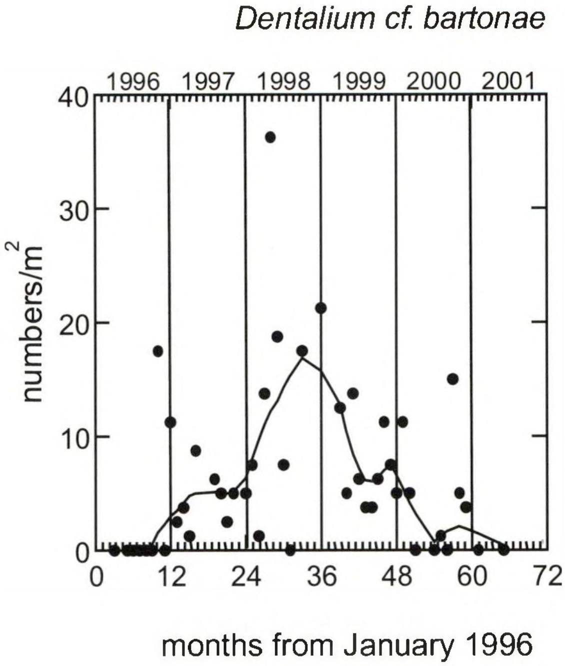
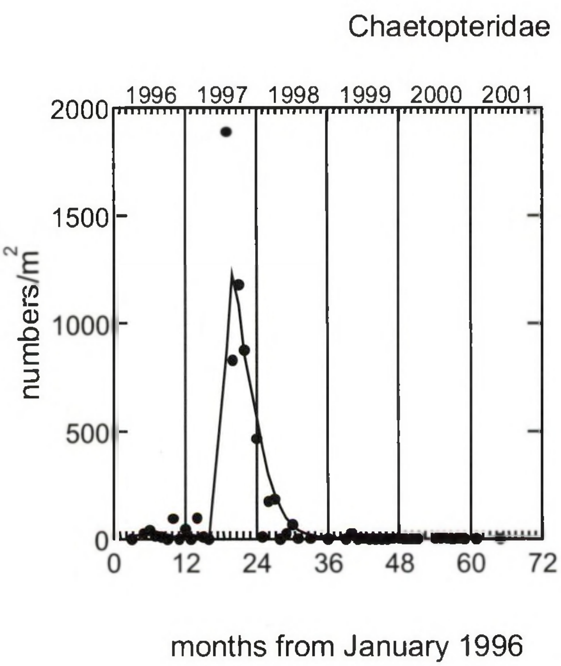


Figure 17. Changes in average density of *Dentalium* cf. *bartonae* from early 1996 to mid 2001.



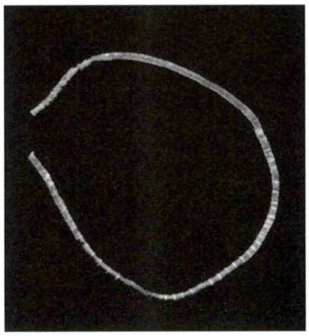
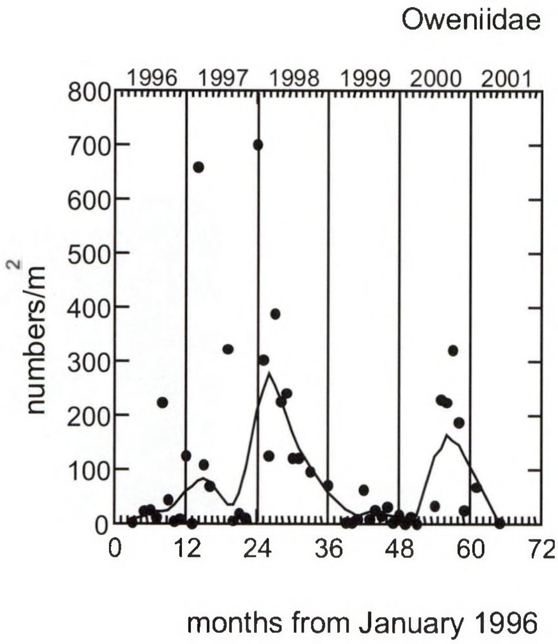


Figure 18. Changes in average density of plastic tubeworms Chaetopteridae from early 1996 to mid 2001.



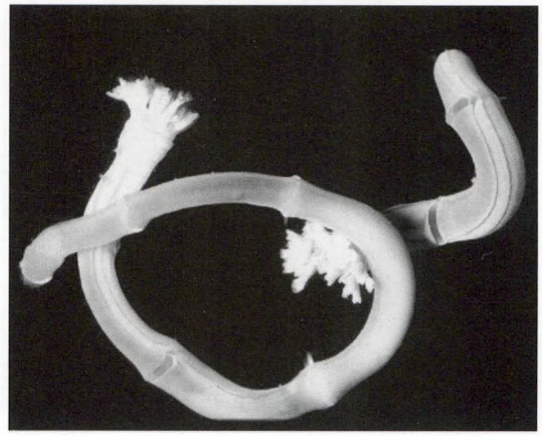


Figure 19. Changes in average density of tubeworms Oweniidae from early 1996 to mid 2001.

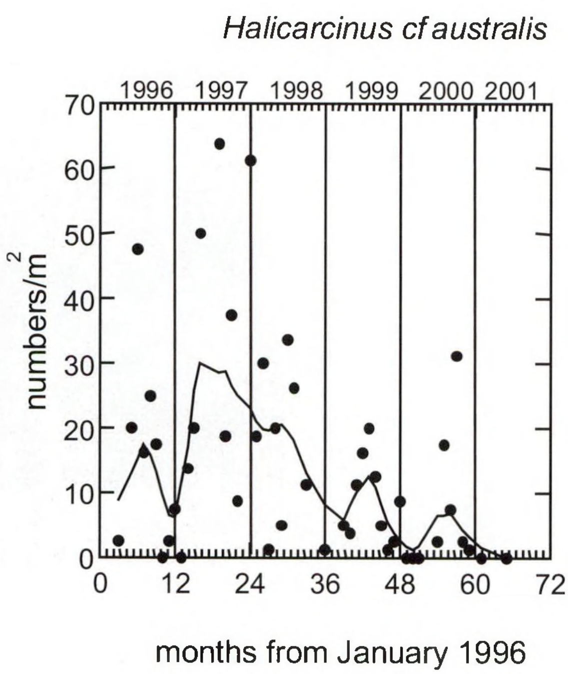
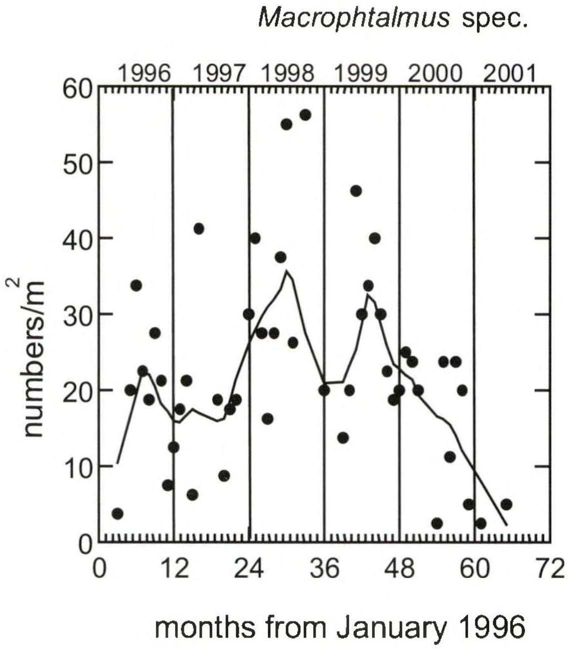


Figure 20. Changes in average density of the crab *Halicarninus* cf. *australis* from early 1996 to mid 2001.



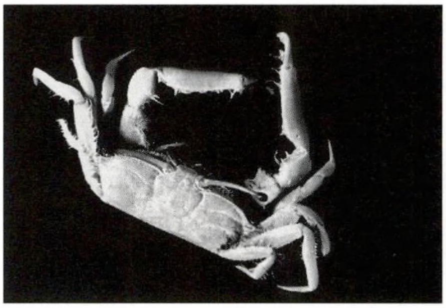
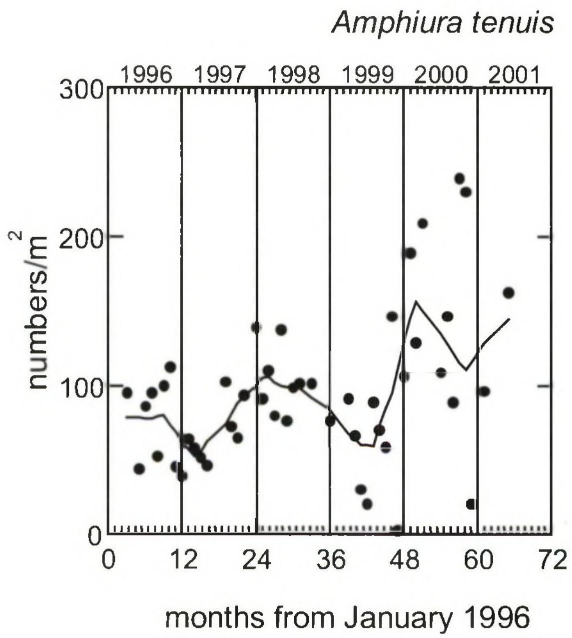


Figure 21. Changes in average density of sentinel crabs *Macrophthalmus* spec. from early 1996 to mid 2001.



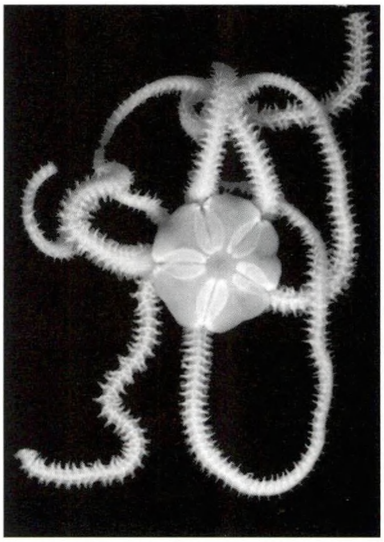


Figure 22. Changes in average density of the brittle star *Amphiura tenuis* from early 1996 to mid 2001.

between successive sampling dates, but quite clear seasonal patterns of numerical change. *Halicarcinus* peaked four times in the middle of the year (1996, 1997, 1999 and 2000), whereas *Macrophthalmus* peaked three times in the middle of the year (1996, 1998 and 1999). The abundant brittle star of Fall Point *Amphiura tenuis*, showed a gradual increase in numbers over the study period, with peak numbers in late 2000 (Fig. 22).

3.4. RECRUITMENT PATTERNS

To generate some insight into aspects of settlement of new cohorts and the possibility of movements by larger macrozoobenthic animals we have constructed hypothetical (but roughly realistic; see e.g. van der Meer *et al.* 2000) curves for the density and body size changes as a function of time of a single cohort, and the size-frequency distribution over the entire study period of this particular cohort assuming that they stay put (Fig. 23). If the size-frequency distributions that we generate on the basis of the 6 years of monitoring data roughly conform to the pattern given there (i.e. peak numbers at small body size and a gradual decline with a long tails thereafter), under the assumption that we have fairly sampled one or more cohorts over their entire lifetime, we can conclude that this indicates a stationary, growing population that is unlikely to exhibit mass movement over the mud- and sandflats later in life.

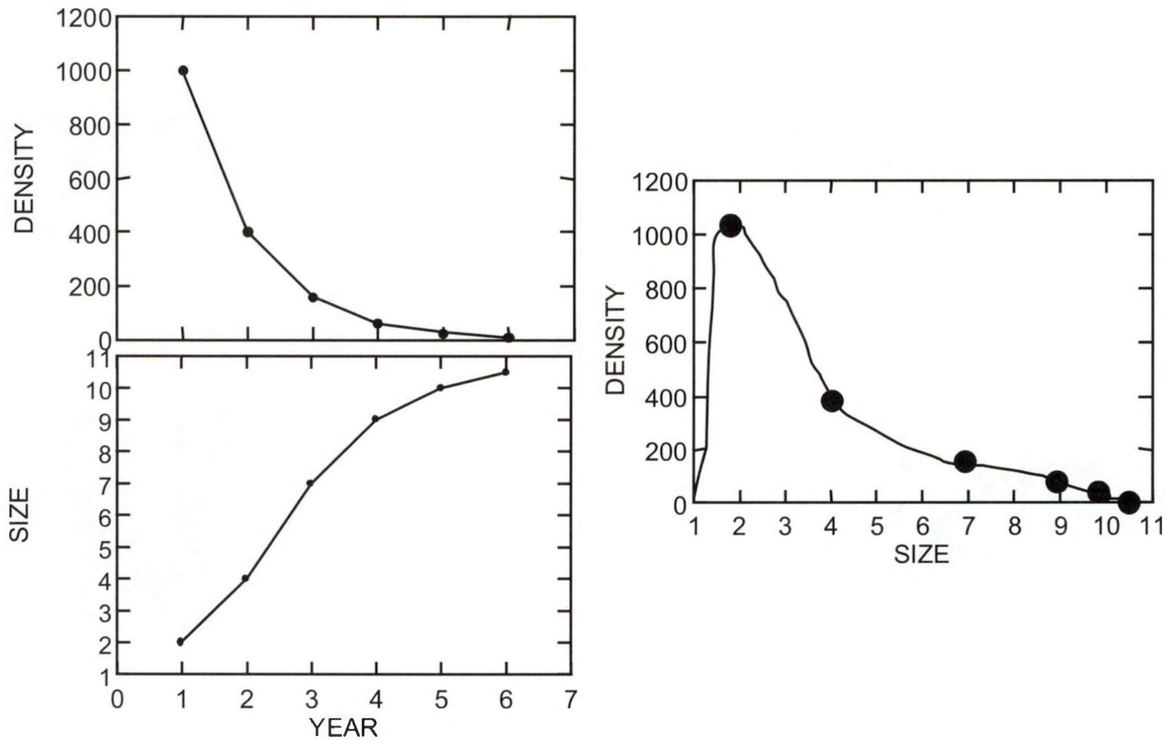


Figure 23. Hypothetical changes in the density and body size (left two panels) of a macrozoobenthic animal that settles in a density of 1000/m² at a body size of 2 mm, incurs an annual survival of 40% and shows a logistic type growth over its lifetime. The expected size-frequency distribution is given in the right panel and shows a density peak at small sizes and increasingly gradual disappearance thereafter.

The right panel of Fig. 23 thus gives us a shape that we can compare our data with.

As a second step, at a (somewhat arbitrary) value in the size distribution we made cut-off to examine if there exist any differences in changes in numerical abundance of the smallest and larger animals in the population. This exercise may tell us when settlement took place, and whether these settlement patterns bear any resemblance to seasonal (climatic) factors.

The bloody cockle *Anadara granosa* beautifully obeyed the size-frequency distribution expected from single settlement and growth (Fig. 24). Particularly large numbers occurred in early and mid 1997, after the wet season (Fig. 25). A smaller settlement of *Anadara* may have taken place after the wet of 2000. There is much variation in the density of larger *Anadara*, with the decline over the years probably reflecting the disappearance of the strong 1997 cohort.

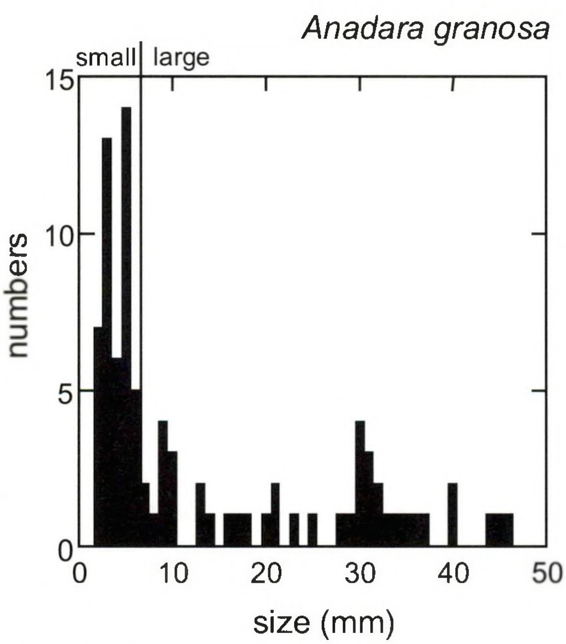


Figure 24. Size-frequency distribution of *Anadara granosa* on the basis of animals found in the monitoring samples between 1996 and 2001.

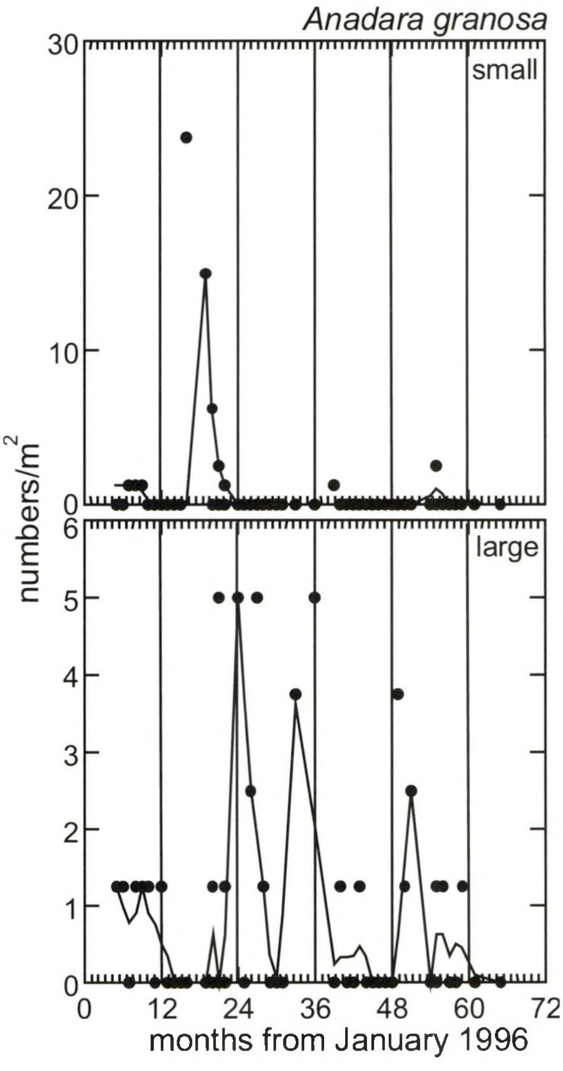


Figure 25. Changes in the densities of small and large *Anadara granosa* (as based on the size-frequency distribution of Fig. 24) from early 1996 to mid 2001.

The deeply buried and small-footed lucinid *Anodontia omissa* also showed the expected size-frequency distribution for a sedentary species (Fig. 26). There appeared to have been recruitment events late in most years, but these events were most pronounced in 1996, 1997 and 1999 (Fig. 27). In fact, the three clear peaks in the density of small *Anodontia* were all followed by peaks in the density of larger *Anodontia*, suggesting fast growth and a life span that is little longer than a year.

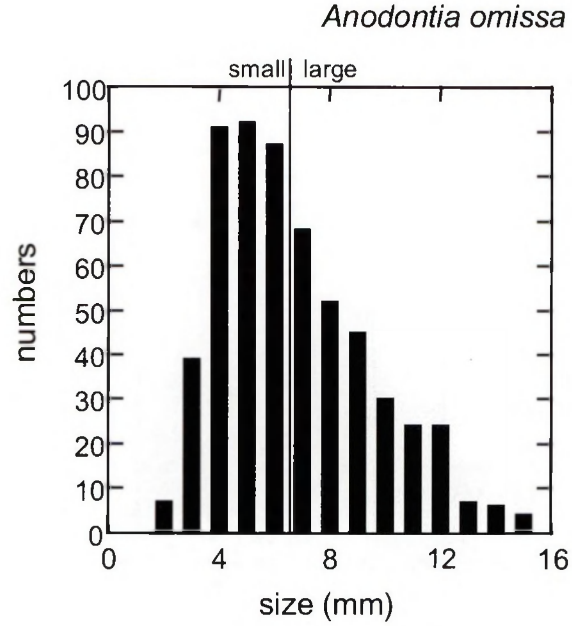


Figure 26. Size-frequency distribution of *Anodontia omissa* on the basis of animals found in the monitoring samples between 1996 and 2001.

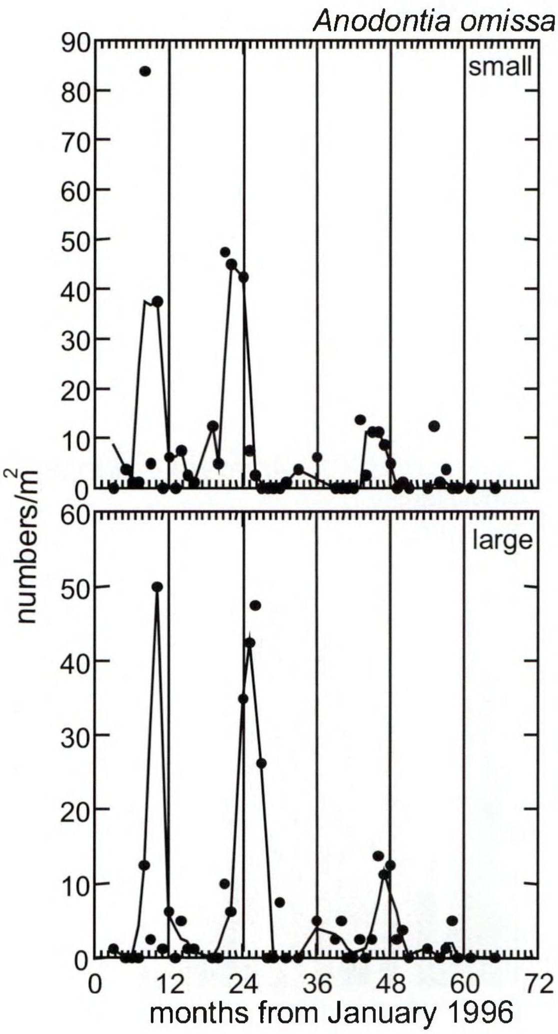


Figure 27. Changes in the densities of small and large *Anodontia omissa* (as based on the size-frequency distribution of Fig. 26) from early 1996 to mid 2001.

The size-frequency distribution of the second lucinid, *Divaricella irpex* (Fig. 28), resembles that of *Anodontia omissa* but shows more irregularity. Despite this irregularity, the picture appears consistent with what we would expect of a sedentary species. The density figures are also more irregular (Fig. 29), but nevertheless suggest that recruitment occurred somewhat later than *Anodontia* in most years and especially in 1996, 1997, 1999 and 2000. Each of these recruitment events appears to have been followed by an increase in the population of larger-sized *Divaricella*. Both species of Lucinidae settled late in the year (i.e. just before the wet season) with growth during the subsequent wet season and little survival beyond one year of life.

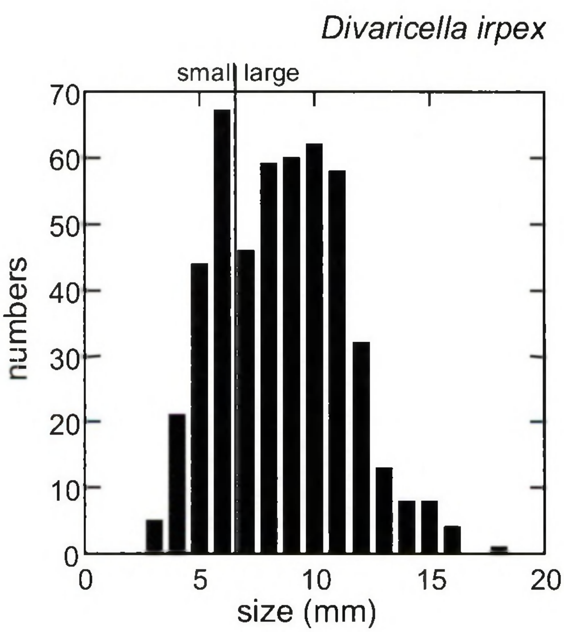


Figure 28. Size-frequency distribution of *Divericella irpex* on the basis of animals found in the monitoring samples between 1996 and 2001.

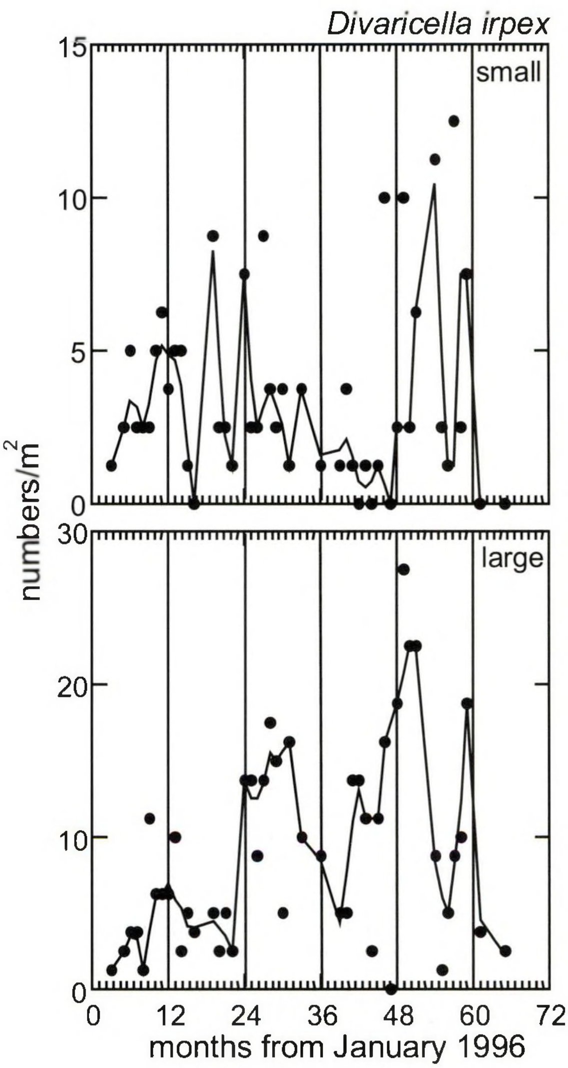


Figure 29. Changes in the densities of small and large *Divaricella irpex* (as based on the size-frequency distribution of Fig. 28) from early 1996 to mid 2001.

The size-frequency distribution of *Siliqua pulchella* (Fig.30) bears little resemblance to the hypothetical size-frequency distribution of a resident species (Fig. 23). Although this could be due to the presence, at the start of the study, of a strong cohort of individuals with body sizes that were not subsequently achieved again (see below for *Tellina capsoides*), this does not seem to be the case as *Siliqua* is probably a rather short-lived species (Fig. 31). The latter is suggested by the presence of a strong cohort of small-sized animals in early 1997 followed by a similarly strong cohort of larger animals later that year, which then declined and disappeared in early 1998. Nevertheless, the size-frequency distribution does suggest movements of larger individuals over the area of intertidal flats, and the fact that the densities of larger-sized *Siliqua* are much higher than the densities of small-sized *Siliqua* is consistent with this. Thus, *Siliqua* settled early in the calendar-year (late in the wet season), showed massive movements after settlement and did not become much older than 1.5 to 2 years.

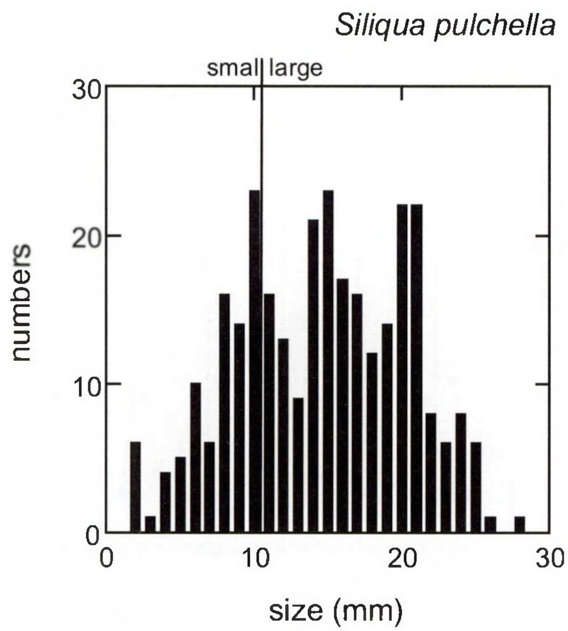


Figure 30. Size-frequency distribution of *Siliqua pulchella* on the basis of animals found in the monitoring samples between 1996 and 2001.

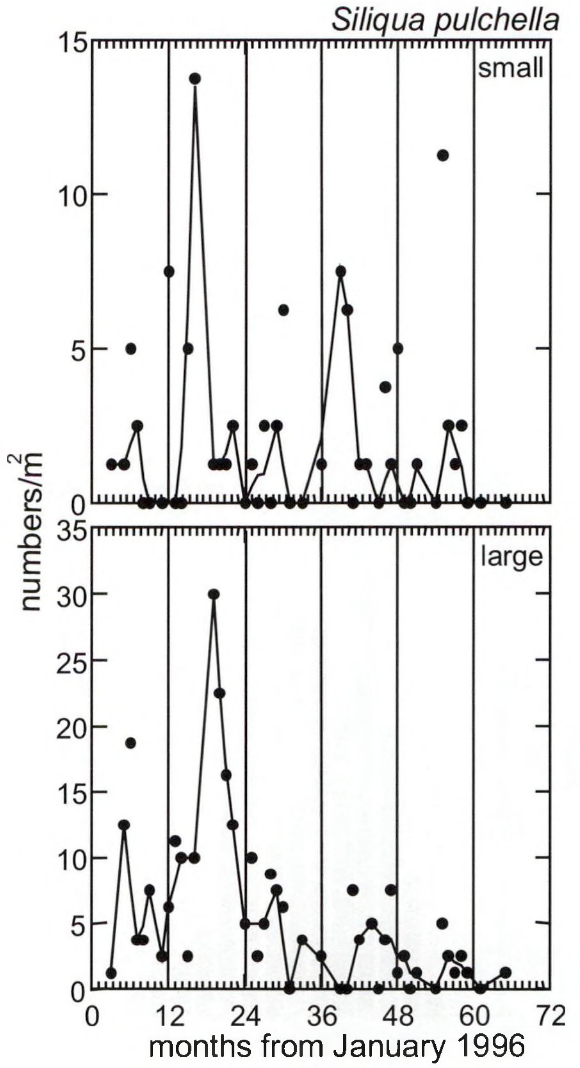


Figure 31. Changes in the densities of small and large *Siliqua pulchella* (as based on the size-frequency distribution of Fig. 30) from early 1996 to mid 2001.

Although the size-frequency distribution of *Tellina capsoides* at first sight suggests massive movement at large size (Fig. 32), the high frequency of bivalves longer than 35 mm is due to a large cohort of old animals being present in our study area (offshore from One Tree) in early 1996, at the beginning of our study. Although there was some recruitment late in 1996, a recruitment event which translated in increasing densities of larger specimens early in 1997 (Fig. 33), the strong cohort of older animals present in early 1996 was never replaced and *Tellina capsoides* thus gradually disappeared from the One Tree stations (see Fig. 12). *Tellina capsoides* probably can live some 2-3 years.

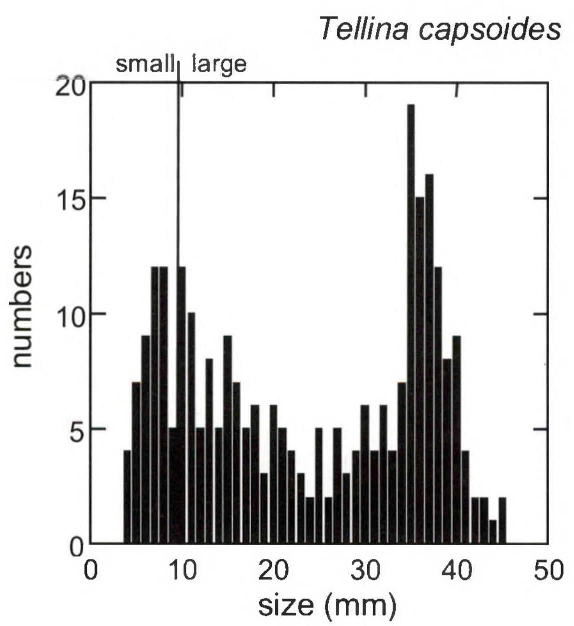


Figure 32. Size-frequency distribution of *Tellina capsoides* on the basis of animals found in the monitoring samples between 1996 and 2001.

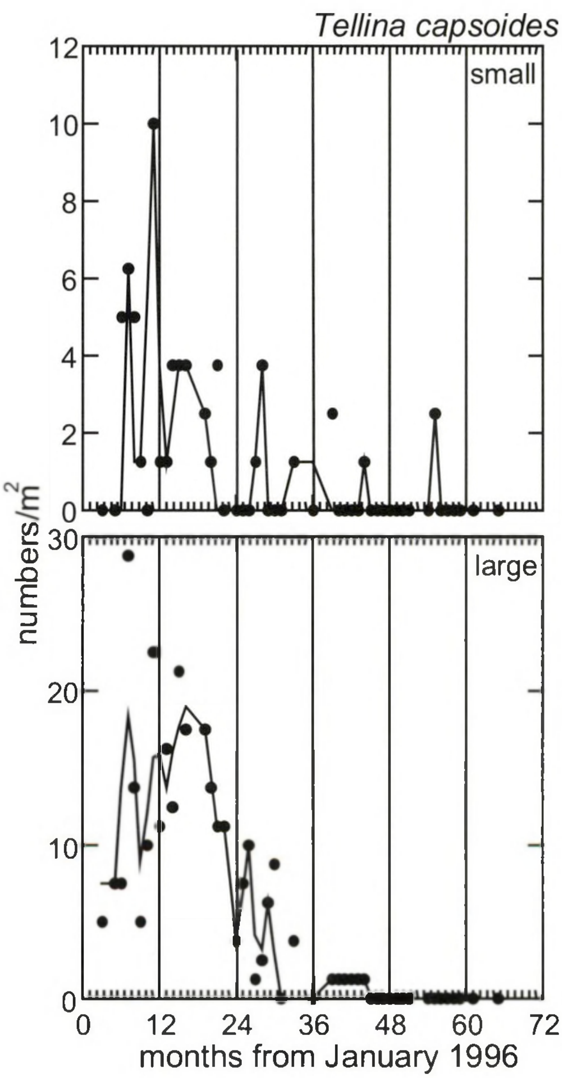


Figure 33. Changes in the densities of small and large *Tellina capsoides* (as based on the size-frequency distribution of Fig. 32) from early 1996 to mid 2001.

The size-frequency distribution of *Tellina piratica* (Fig. 34) is consistent with a sedentary life-style (i.e. no movements after settlement) and a lifespan somewhat longer than 2 years. This fact and their low densities overall may be the reason that it is hard to interpret the numerical changes over time (Fig. 35). Recruitment appeared to have occurred in the middle of the year (i.e. after the wet season), with reasonable recruitment in 1997 leading to a build-up of larger animals in early and mid 1998. The subsequent collapse is a bit strange as it is not preceded by a similar low in the densities of small animals. A recruitment-peak in mid 2000 to some extent restored the population of *Tellina piratica*.

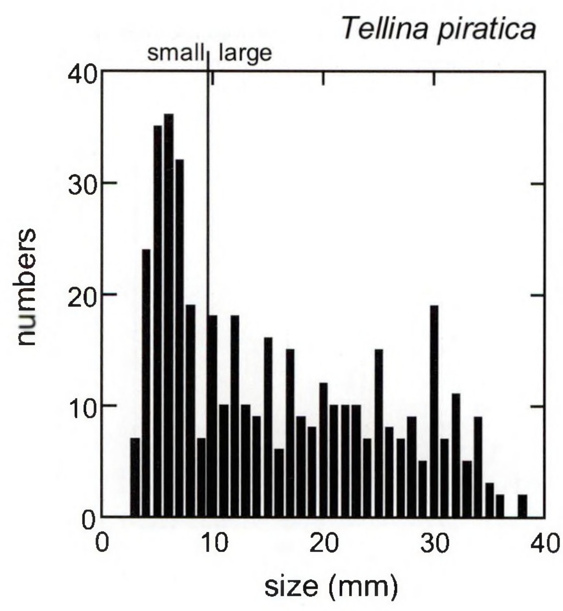


Figure 34. Size-frequency distribution of *Tellina piratica* on the basis of animals found in the monitoring samples between 1996 and 2001.

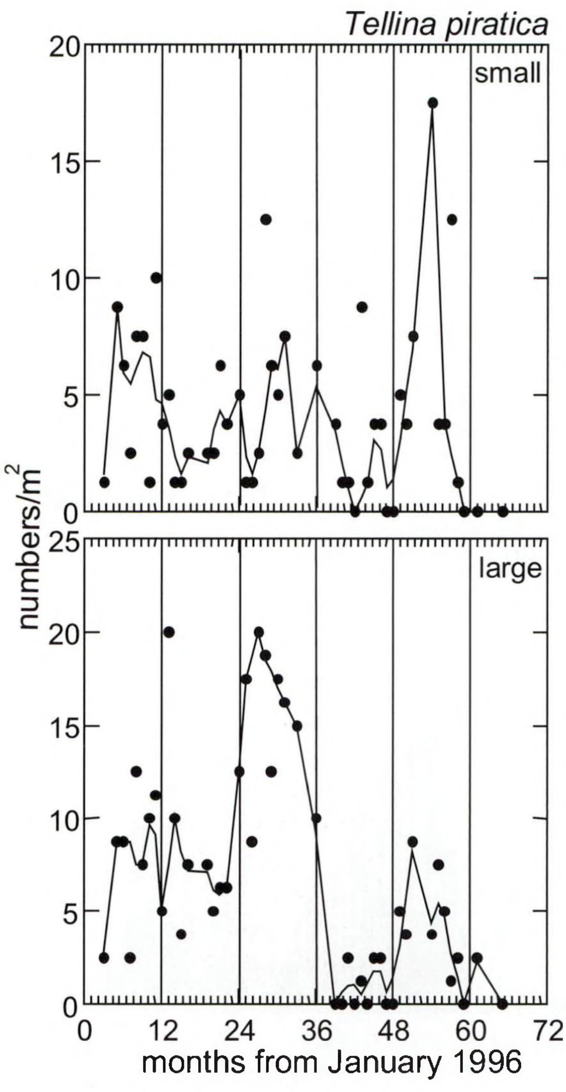


Figure 35. Changes in the densities of small and large *Tellina piratica* (as based on the size-frequency distribution of Fig. 34) from early 1996 to mid 2001.

Tellina exotica is a small (Fig. 36) and probably short-lived species that showed increases in densities of small animals both early and late in the year (i.e. at the beginning nd the end of the wet season; Fig. 37). Good recruitment in 1996 led to a build-up of larger animals in early 1997, but this cohort disappeared rapidly to be replaced immediately by a new cohort that settled in late 1997. The latter cohort disappeared in the course of 1998. Since, recruitment of *Tellina* exotica has been low, so that total densities have remained low as well (see Fig. 14).

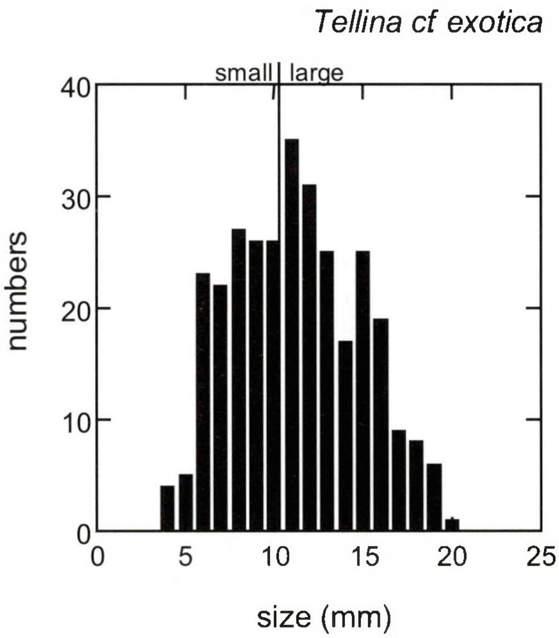


Figure 36. Size-frequency distribution of *Tellina* exotica on the basis of animals found in the monitoring samples between 1996 and 2001.

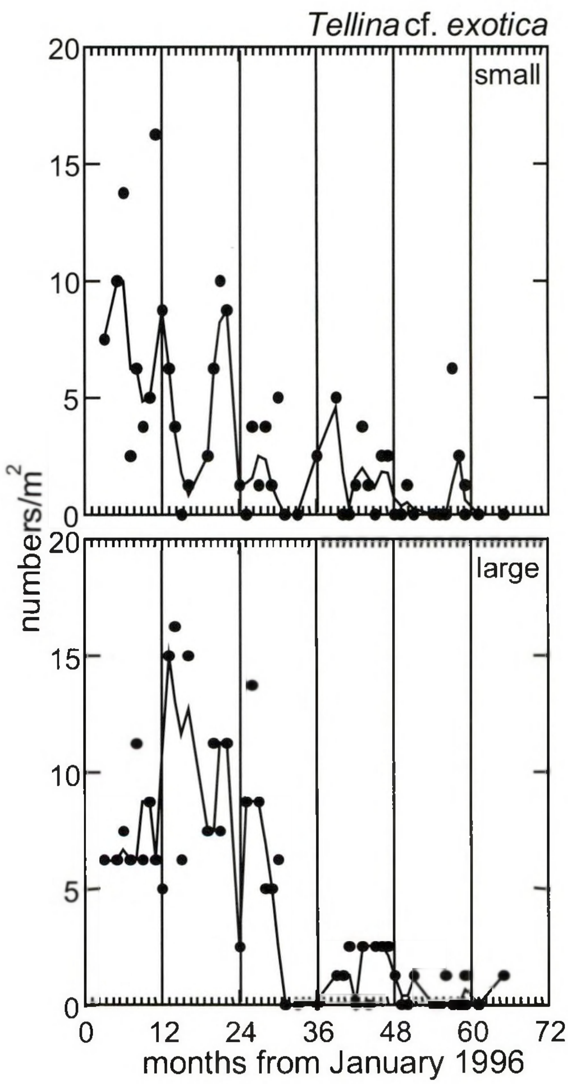


Figure 37. Changes in the densities of small and large *Tellina* exotica (as based on the size-frequency distribution of Fig. 36) from early 1996 to mid 2001.

The scavenging and predatory gastropod *Nassarius dorsatus* (Ingrid-eating snail) has all the characteristics of sedentary species (Fig. 38), with recruitment taking place in the middle of the year (the cold season; Fig. 39), rapid growth and a life span little longer than a year. Peak recuitment in mid 1996 and mid 1997 (Fig. 39) was immediately followed by increased densities of the larger animals. Recruitment has been somewhat lower in 1998 and 1999 and was virtually absent in 2000 (even though densities of large animals were good in January 2001: displacement of older individuals from elsewhere?).

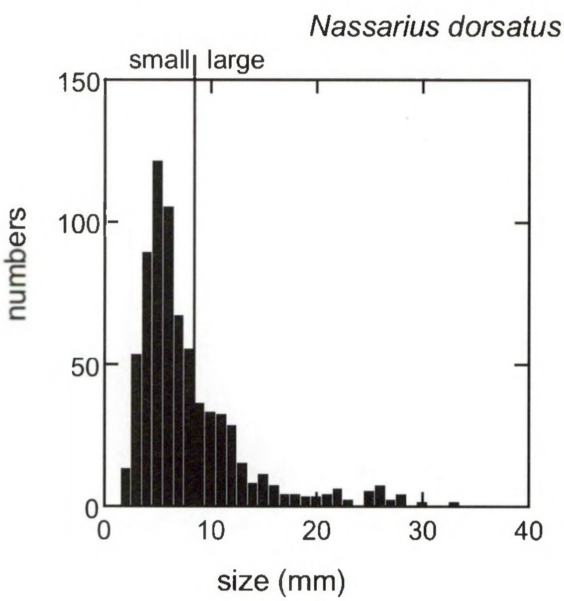


Figure 38. Size-frequency distribution of *Nassarius dorsatus* on the basis of animals found in the monitoring samples between 1996 and 2001.

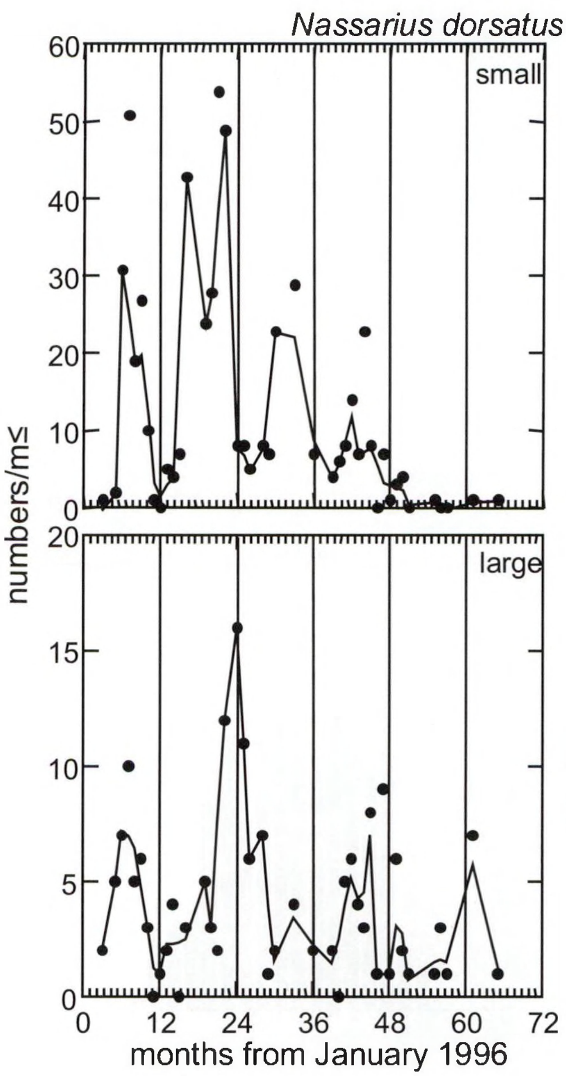


Figure 39. Changes in the densities of small and large *Nassarius dorsatus* (as based on the size-frequency distribution of Fig. 36) from early 1996 to mid 2001.

3.5. OPTIMIZING FUTURE BENTHIC MONITORING

From 1996 to 2001 the BBO-wardens and the volunteers helping with MONROEB not only visited the two sites (Fall Point and One Tree) in the course of each sampling day, at each of the sites they also went to two stations, a relatively nearshore and a relatively offshore one. On the sandy sediment off Fall Point this is not a big issue, but at One Tree it does take a lot of effort to get to the second station at 250 m from the shoreline. Table 1 and Fig. 7 already showed the congruence in species diversity and total numbers of animals collected among the two stations at each of the site. Here we have made a further comparison among the data for bivalves to see whether changes in densities over time are also comparable between sites. In order to do so we have plotted densities over time for the nearshore and offshore stations for the sites where the seven most numerous species selected were most common (Figs. 40-46). We also calculated the correlations between the numbers found at each of the sites.

The result is that samples taken at the relatively nearshore and offshore stations give very similar answers. Figures 40 to 46 show that the patterns are clearly comparable and all correlations are positive. In 5 of the 7 cases the r-value is also significantly greater than zero (Table 2). The correlations are highest for the One Tree stations, which in our experience is a particularly homogenous area of mud.

This means that in the future we can do with a single station at each of the two sites. The general congruence also means that the precise location of this site is not very important, and that it can be in the vicinity of the nearshore sites,

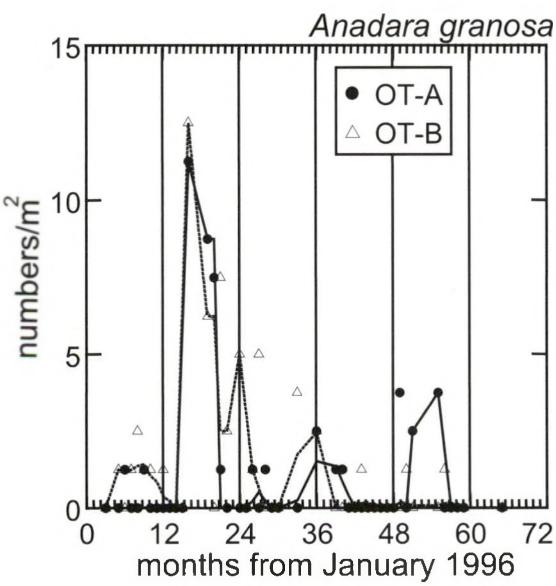


Figure 40. Comparison of the changes in density of *Anadara granosa* at the nearshore (A) and offshore (B) stations off One Tree.

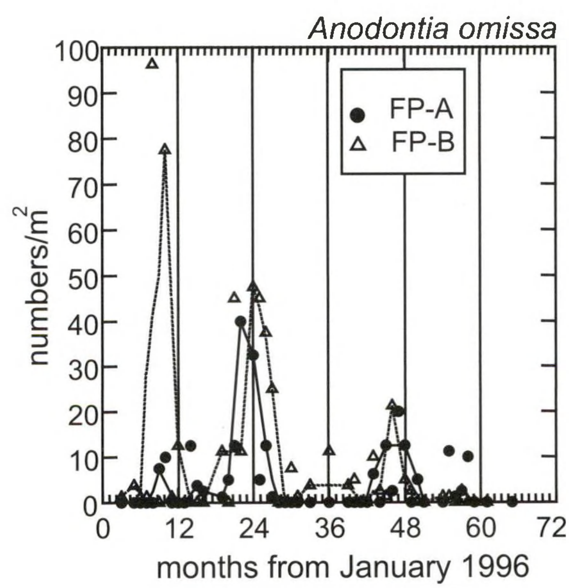


Figure 41. Comparison of the changes in density of *Anodontia omissa* at the nearshore (A) and offshore (B) stations off Fall Point.

to reduce workload. Nevertheless, the same total of 8 samples consisting of 6 (1/120 m²) cores should be taken, as reductions in the number of individuals collected per date would lead to less interpretable results (i.e. less interpretable results for more taxa than at present).

Table 2. Pearson product-moment correlations between the densities measured on different occasions during MONROEB (n indicating the number of comparisons) on the nearshore (A) and offshore (B) sites.

Species	Pearsons r	p	n	Site
Anadara granosa	**0.568**	**<0.005**	45	One Tree
Anodontia omissa	0.237	>0.5	48	Fall Point
Divaricella irpex	**0.368**	**<0.01**	48	Fall Point
Siliqua pulchella	**0.549**	**<0.005**	45	One Tree
Tellina piratica	0.238	>0.5	48	Fall Point
Tellina capsoides	**0.679**	**<0.005**	45	One Tree
Tellina "exotica"	**0.415**	**<0.005**	48	One Tree

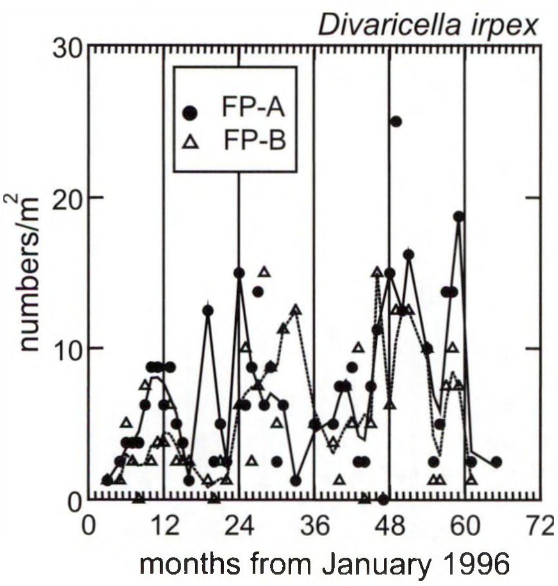


Figure 42. Comparison of the changes in density of *Divaricella irpex* at the nearshore (A) and offshore (B) stations off Fall Point.

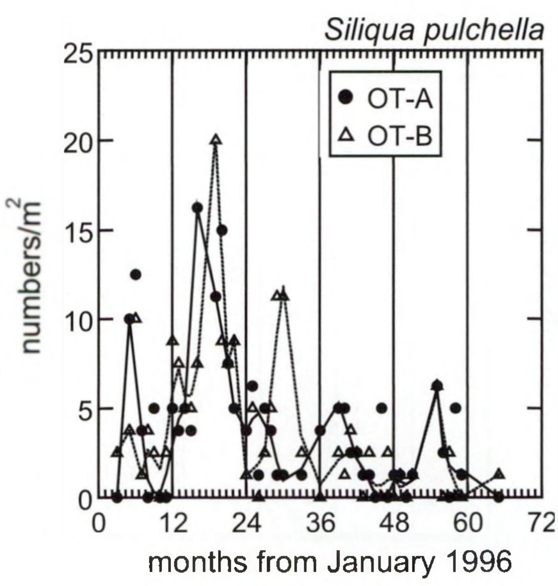


Figure 43. Comparison of the changes in density of *Siliqua pulchella* at the nearshore (A) and offshore (B) stations off One Tree.

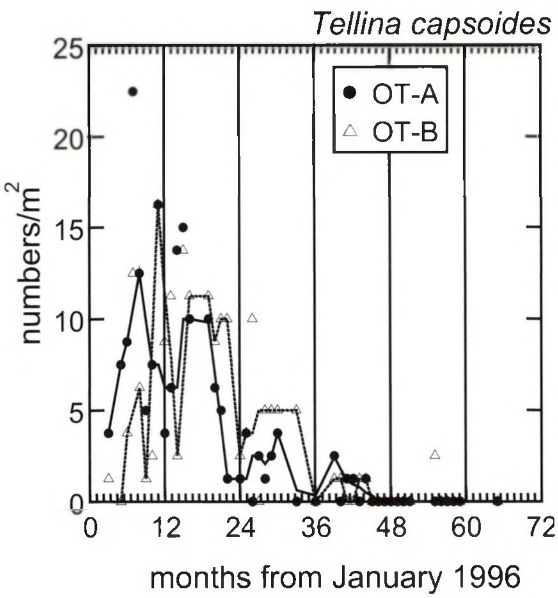


Figure 44. Comparison of the changes in density of *Tellina capsoides* at the nearshore (A) and offshore (B) stations off One Tree.

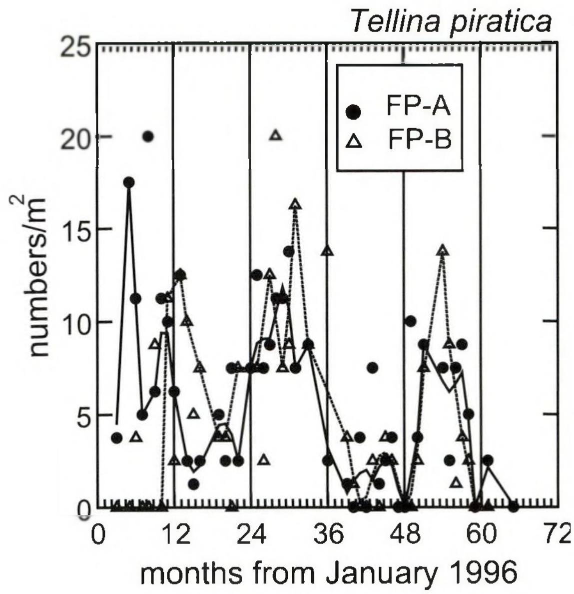


Figure 45. Comparison of the changes in density of *Tellina piratica* at the nearshore (A) and offshore (B) stations off One Tree.

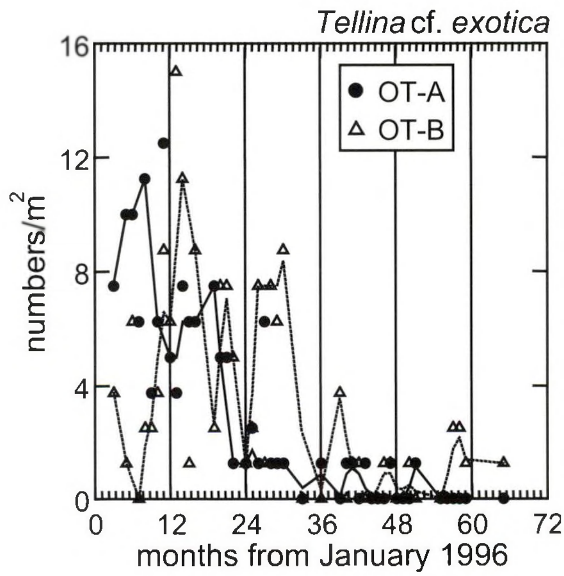


Figure 46. Comparison of the changes in density of *Tellina* exotica at the nearshore (A) and offshore (B) stations off One Tree.

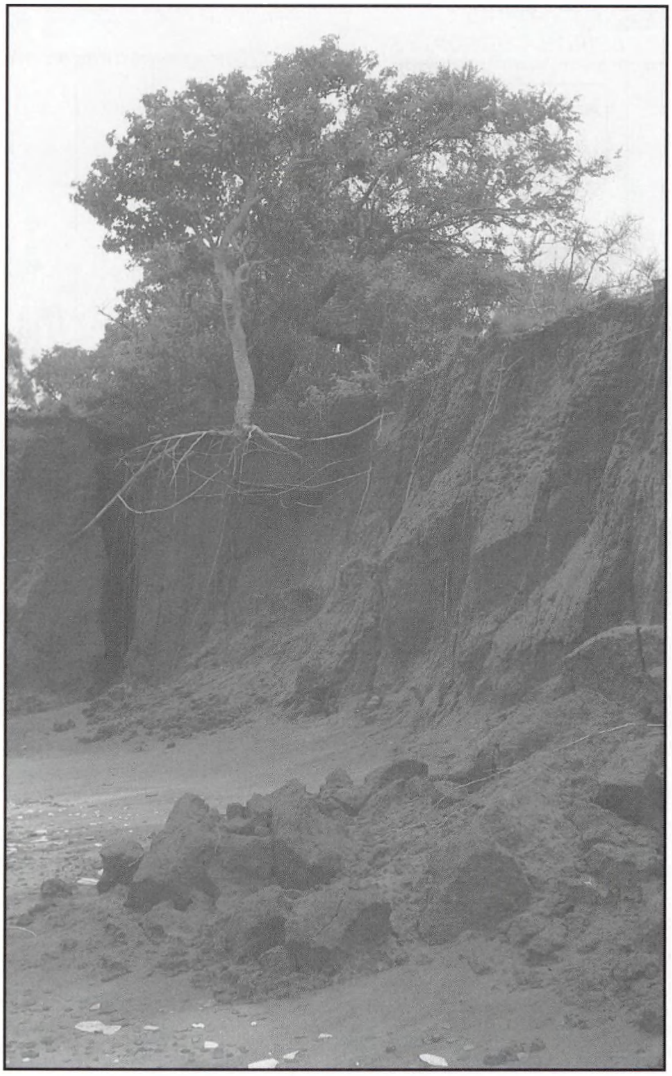


Plate 3. The pindan cliffs near the One Tree stations after a rainstorm in March 1996. Photograph by Theunis Piersma.

4. GENERAL DISCUSSION

A reasonable concern shared by several people repeatedly involved in the monthly mudsampling was whether the repeated sampling effort would disturb the local sediments so much that this would have reduced numbers of macrozoobenthic animals in the course of the years. We would expect fragile sedentary species to be most easily affected. That one such species, the brittle star *Amphiura tenuis*, together with the lucinid bivalve *Divaricella irpex*, were the only taxa that showed a steady increase over time since early 1996, suggests that the role of disturbance could only have been a minor factor. We also like to note that the precision with which the stations were located (counting steps by different team leaders, rather than the consistent use of modern, high precision GPS) was not very high, which would have been a concern in itself was it not for the fantastic congruence in species composition and densities among the two stations at each site. Thus, we believe that the area over which the monitoring samples were collected was perfectly able to cope with the disturbance inflicted by the human observers.

In fact, it is rather gratifying to see that trend apparent from other mudsampling efforts, notably the repeated mapping efforts of the northern shores in June 1996 (Pepping *et al.* 1999), March 2000 (Rogers *et al.* 2000) and June 2002 (SROEBIM, report in prep.) came up with similar impressions on the abundance of various macrozoobenthic taxa as did MONROEB. For a start, there is the great abundance of plastic tubeworms Chaetopteridae that made life so difficult during ROEBIM-97 (Pepping *et al.* 1999); plastic tubeworms were absent during both the March 2000 and the June 2002 efforts, a picture fully consistent with the MONROEB results. Then there is the relative abundance of *Siliqua pulchella* on the soft muds of Kraken Corner in June 1997 and the near-absence there in both March 2000 and June 2002 (Rogers & Taylor 2002). Again this is consistent with the results of MONROEB. The relative scarcity of Ingrid-eating snails *Nassarius dorsatus* reported during June 2002 was reflected well by the MONROEB results. We conclude that the monitoring has done a fine job in generating interpretable seasonality data for about 15 different taxa.

This bring us back to the questions we set out to answer with MONROEB: to which extent are settlement and growth seasonally structured and is the level of seasonality comparable to what we find at well-studied north temperate mudflats? To structure the discussion, we have prepared a summary table (Table 3) outlining the basic biological features for 7 bivalves and 1 gastropod as discovered during this study. Half of the species are particularly short-lived, with the others having lifespans typical of mollusks from north temperate mudflats. Like the north temperate situation, recruitment is highly seasonal with a tendency for one recruitment period to occur within each year (two events in the case of the small tellinid bivalve *Tellina* exotica).

Table 3. Summary of the traits of 7 bivalve and 1 gastropod species as derived from the MONROEB observations.

Species	Max shell length	Approximate lifespan	Timing of settlement	Movement after settlement?
Anadara granosa	50 mm	3-4 yrs	Late or just after the wet season	No
Anodontia omissa	15 mm	1 yr	Early in the wet season	No
Divaricella irpex	18 mm	1 yr	Before the wet season	No
Siliqua pulchella	28 mm	1.5-2 yrs	Late in the wet season	Yes
Tellina capsoides	46 mm	2-3 yrs	Early in the wet season?	No
Tellina piratica	38 mm	2 yrs	After the wet, in the cold season	No
Tellina ìexoticaî	20 mm	1 yr	Beginning ·nd end of wet season	No
Nassarius dorsatus	32 mm	2 yrs?	After the wet, in the cold season	No

However, *un*like the north temperate situation, there is little correspondence between species in when recruitment takes place. In fact, recruitment takes place year-round, with some species settling (or appearing in our samples) before the wet, others in the early wet, yet others in the late wet and some after the wet in the cold season (Table 3). Only for the highly mobile species *Siliqua pulchella* is there evidence for large-scale movement of older animals, with large animals turning up in fair numbers at the One Tree stations especially in late 1997 and early 1998 (Fig. 31).

In summary, in a sense, the mudflats of Roebuck Bay as a larder for migratory shorebirds is less dependable than the mudflats of the Wadden Sea (Zwarts & Wanink 1993). Timing of settlement is much more variable, and what is more important, there is great temporal variability in the presence/absence of potential prey species. For example, *Siliqua pulchella* were so abundant in June 1997 that we thought them to comprise the staple in the diet of great and red knots. Unpredictability in species presence also explains the observations of Tulp & de Goeij (1994) who in February-April 1991 found that a mussel species *Modiolus micropterus* then was both abundant and an important food item for great knots. We have only found a few large specimens in surveys since, indicating that Tulp & de Goeij (1994) observed what may have been a one-off heavy spatfall of *Modiolus*.

Of course the Yawuru are right when they tell us that during *willburu* (September) shellfish are getting fat and that during *larja* (October-November, just before the wet) the shellfish are fat. As we have seen, the first small bloody cockles *Anadara granosa* turn up in our samples just after the wet, and by then they have experienced a time as a free-swimming pelagic larva and a time of early growth as a tiny settled shell on the sediment. If fat shellfish indicate cockles that are ready to spawn, and spawning is triggered by the fresh water running over the intertidal flats after the first big rainstorm in December or early January (brackish water is known to trigger spawning in the long-lived estuarine West-African species *Anadara senilis*; Wolff *et al.* 1987), then there would be 2-3 months left for the pelagic and early settlement phases before we would find them in our sieves. This seems perfectly reasonable.

Plate 4. Innovation on the deep blue mud near the One Tree stations in 1997: the first and last use of skis! Photograph by Grant Pearson.

5. ACKNOWLEDGEMENTS

It happened during a tropical downpour in mid March 1996: GBP and TP were crawling on their knees in the mud, amazed at the variety of creeping crawlies and realizing how little we know about what was out there. This was the incentive to start a monitoring scheme of macrobenthic animals of the intertidal flat of Roebuck Bay on 24 March 1996, which was to be run by wardens and volunteers from the Broome Bird Observatory (BBO) with in-kind and logistic support from the Western Australian Department of Conservation and Land Management (CALM) and the (now Royal) Netherlands Institute for Sea Research (NIOZ). The monitoring scheme was named MONROEB. BBO and its wardens have played a major role in continuing this sampling programme. Due to the immense effort of many participants over five years now, a truly unique record of temporal and seasonal changes on a tropical mudflat could now be presented in this report.

A huge number of people (at least 126) have been involved in this project in one way or another. During the first 18 months, Ali Pentelow from Broome took the lead and provided a solid foundation that established the monitoring program during the first difficult months . From that time on the Broome Bird Observatory (BBO) wardens took the responsibility for carrying out the programme: thanks a million Becky Hayward and John Fallaw, Janet Sparrow and Chris Hassell, Alistair Dermott and Tracy Stolman, Andr Joubert, Paula and Bill Rutherford. Special thanks to Phil Joy for his extraordinary fill-in role between wardens that kept the process rolling.

Special thanks also to the many officers from the West Kimberley Branch of The Department of Conservation and Land Management, especially Allen Grosse, Mike Lapwood, Tim Willing, Kingsley Miller and Jill Green. It is important to note that West Kimberley District through the then District Manager, Allen Grosse, contributed the initial seed capital that enabled the monitoring to begin.

Environs Kimberley provided ongoing support for the project and assisted from time to time with collections and processing of samples. It was not an easy task to get volunteers in the mud every month, especially not the mud of One Tree. It is peculiar kind of enjoyment to go over your knees in the soft mud! Lots of people tried once. Sorting the samples as soon as they got back from the field was another onerous job which requirement a kind of determination. The following list gives the names of all people who helped in one way or another to get the poor benthic creatures from the mud into the vials. Some names are incomplete, as some helpers were passing through BBO too quickly to get their names properly registered. However, they have to be thanked too!

In chronological order: Ali Pentelow, Becky Hayward, Jon Fallaw, Janet Sparrow, Chris Hassell, Sheila Foster-Nixon, Claas, Tim Willing, Kathryn from CALM, Jenny Noble, Janet Lankester, Helen MacArthur, Rosemary MacArthur, Robert Kirwan, Heather Beswick, John Curran, Phil Joy, Robert Van Leeuwen, David Baker-Gabb, Peter West, Raoul Broughton, Christine McNamara, Shapelle McNee, Ray Lyons, Oliver Vachez, Kathy Fletcher, Mavis Russell, Darlene, Sarah and Tim Cantrill and their children, Shirley Cook, Barbara Lake, Mary Councillor, Ian Snadden, Paul and Jake Botwell, Brenda, Michelle McDonald, Jean, Mike, Dick and Pam Smith, Jeromy, Danny Rogers, Kerry Duff, Sharon, J. Woods, Clare Howard, Magnolia Howard, Wilyarti Howard, Matt Gillis, Jacquie and Nigel Clark, B. Hart, A. Hart, M. Tarry, C. Tarry, A. Dunn, Nicole Grenfell, Sandie McCaig, Macafee, Julie Deleyev, Hunter, Blyth, Shirley Slack-Smith, Pieter Honkoop, eight Australian Wader Study Group members, A. Mayer, Adrian Boyle, Al Dermer, Yus Rusila Noor, H. Rambiak, W. Gebse, Susan, Tracey Stolman, P. Michele, Cass Hutton, S. Hartvigsen, D. Secombe, Jacquie Cochran, Ruth Bonser, Maria Pedersen, Jan Lewis, Astrid and Guido Gomes, Liz Cochran, Persine Ayersberg, Andr Joubert, M. Slattery, Terry Strong, Jaenet, Peter Tucker, Jun Matsui, Michael Curran, Jane Rusden, John Peterson, Diane Sherman, Sharin Mullaly, Magie Kurcz, Josh van Dijke, Melinda Glace, Andrea Feldpausch, Kelly Millenbah, Max Tishler, and 15 other anonymous BBO-guests. Rob Van Leeuwen of the Met-station at Broome helped in the mud as well as behind the computer by regularly sending us weather data reports.

Plate 5. The second time monitoring at the Fall Point stations in April 1996: instructions by Theunis Piersma before entering the flats, with the Russian shorebird scientist Pavel Tomkovich on the right. Photograph by Petra de Goeij.

In The Netherlands, especially in the lab, Pieter Honkoop had great input during the first year. Later we received help from Mavis Russell and Danny Rogers during occasional visits to The Netherlands. Danny also read the draft report and made many useful suggestions.

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Plate 6. Sorting the samples outside the Pearson Laboratory at Broome Bird Observatory in July 2002. Helen MacArthur on the left and Mavis Russell on the right, share the table with mollusk-specialist Shirley Slack-Smith. Photograph by Petra de Goeij.

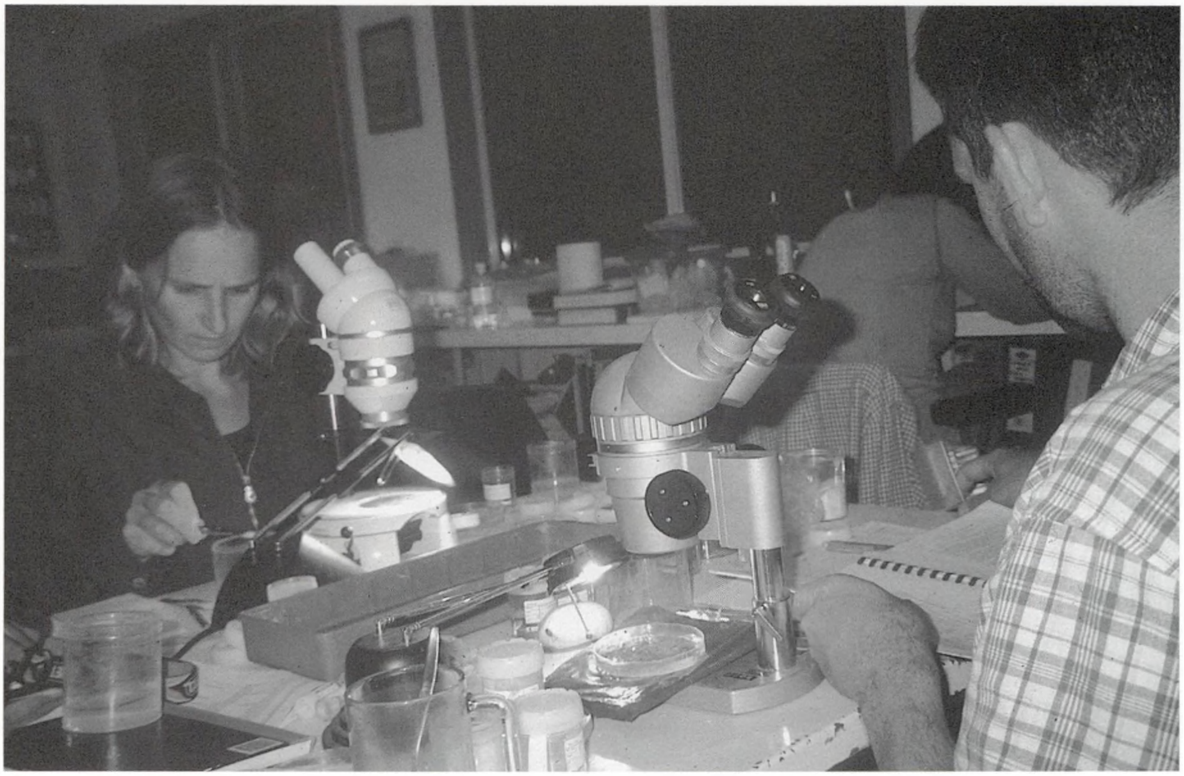

Plate 7. Identification of invertebrates in the Pearson Laboratory at Broome Bird Observatory in July 2002, with Petra de Goeij on the left, and Pieter Honkoop on the right. Photograph by Theunis Piersma.

Plate 8. Pleasurable monitoring on the go at Fall Point, July 2002. Photograph by Theunis Piersma.

Plate 9. The challenges of monitoring the benthos at the One Tree Stations: an adventure with the Police Cadets in July 2002. Photographs by Theunis Piersma.

A: inaugural photograph, everybody optimistic and clean,

B: off we go!,

C: some are faster than others,

D: first problems, but Grant is chatting up the strugglers,

E: first samples, first fun,

F: mothers of invention: the breast crawl works!,

G: steady progress at the nearest station,

H: I am greyer than you,

I: wrestling and sampling, it all happens at the same time, J: the crawl back to the beach,

K: we have achieved!,

L: carted off for a good rinse.

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Plate 10. A potential new monitoring site? Dampier Flats in the Rain, March 2000. Photograph by Theunis Piersma