Distribution and abundance of the macrobenthic fauna of the Kariega estuary

A.N. Hodgson
Department of Zoology and Entomology, Rhodes University, Grahamstown, 6140 Republic of South Africa

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The Kariega estuary is an open estuary which is about 18 km in length. The freshwater inflow into the estuary is very sporadic and consequently the water is often hypersaline at the head. Quantitative and qualitative sampling has been undertaken to describe the distribution and abundance of the macrobenthos along the estuary. Of the 107 species that have been recorded, 80% can be classified as euryhaline. One of the possible reasons for the high species diversity, when compared to other eastern Cape estuaries, is the growth of *Zostera capensis* along the entire length of the estuary. The major contributors to the macrobenthic biomass are the crustaceans, *Cleistostoma edwardsii, C. algoense, Upogebia africana, Sesarma catenata* and *Uca urvillei* and the bivalve *Solen cylindraceus*. The latter is particularly abundant in the middle reaches of the estuary where it can reach densities of 400 m^{-2}. Its successful colonization is attributed to food availability and stable physical conditions within the estuary which in turn can be linked to the low freshwater input.

Die Karieganviermond is 'n oop riviermonding ongeveer 18 km lank. Die varswaterinstroming in die monding geskied baie sporadies en die water aan die bopunt is gevolglik dikwels hipersoutagtig. Die verspreiding en voorkoms van die makrobentos in die monding is deur kwantitatiewe en kwalitatiewe monsterneming bepaal. Van die 107 spesies wat opgeteken is, kan 80% as eurihalien beskryf word. Een van die moontlike redes vir die hoë spesiesverskeidenheid, vergeleke met ander Oos-Kaaplandse riviermondings, is die voorkoms van *Zostera capensis* langs die hele lengte van die riviermonding. Die grootse bydrae tot die makrobentos word deur die krustacea, *Cleistostoma edwardsii, C. algoense, Upogebia africana, Sesarma catenata* en *Uca urvillei* en die tweekleppige *Solen cylindraceus* gemaak. Laasgenoemde kom veral in die middelste gedeelte van die monding voor, waar dit digthede van 400 m^{-2} kan bereik. Die suksesvolle kolonisasie van die monding deur *Solen cylindraceus* kan veral toegeskryf word aan die bestendige fisiese toestande binne die monding vanweë die lae varswaterinstroming.

Considerable ecological research has been carried out on many South African estuaries (see Day 1981 for review). However the estuaries of the eastern Cape have to a large extent been overlooked. In a report on the S.A.N.C.O.R. estuaries programme (1983), only the Kromme and Swartkops were categorized as estuaries with a good data base. Apart from the pollution survey of Gardner, Connell, Eagle, Moldan & Watling (1985), who determined that the water of the Kariega had no metal pollution, there have been no published studies on this estuary.

The Kariega estuary (33°41'S/26°42'E) is situated 120 km north-east of Port Elizabeth, its mouth opening just east of Kenton-on-sea (Figure 1). The characteristic features of the Kariega, which ultimately affect the physical conditions and therefore faunal distribution within the estuary, are a mouth which is always open to the sea, and a freshwater input which is very sporadic. Prior to October 1985, there had not been any significant freshwater inflow for four years. A number of factors have contributed to this insignificant freshwater inflow; poor rainfall in the catchment, the small catchment area (685 km^2) and finally the fact that there are two major reservoirs in the catchment.

Although the catchment of the Kariega estuary has been greatly disturbed by the construction of dams, the estuary itself is undisturbed. Recreational activities are almost restricted to one month of the year (mid-December to mid-January), and unlike the adjacent Bushmans estuary, farming activities have not encroached upon the intertidal banks. The Kariega therefore provided an opportunity to study an undisturbed, open estuary with a sporadic freshwater input. This paper reports on the distribution of invertebrates within the estuary and is intended as a base-line study for future research. In addition the paper is one of several (to be published by other workers from Rhodes University) dealing with the ecology of the Kariega estuary.

Materials and Methods

Ten transects (T1 to T10) were undertaken during December 1983 to February 1984. Further sampling was carried out in September 1984 and 1985. The transects were spaced at approximately 1-km intervals from the mouth to the head of the estuary (Figure 1). A preliminary survey had shown that from LWS to HWS, four distinct zones or habitats, characterized by plant species, could be recognized on the intertidal banks. Zone I, lowest down the bank, consisted of a band of *Zostera capensis*, Zone II of mud or sand which lacked macrophytes, Zone III a belt of *Spartina maritima* and Zone IV of *Sarcocornia* sp. Although the width of these zones varied along the length of the estuary, each zone was present for most of the length. For each transect, two quantitative samples were taken within each of the four zones. Quantitative samples were obtained from a 0,25-m^2 quadrat dug to a depth of about 60 cm, and sieved through a 1-mm mesh sieve. Each transect was continued into the subtidal area to the middle of the channel, samples being taken with a Van Veen grab which sampled an area of 0,026 m^2. Qualitative sampling was undertaken from the rocky areas of the estuary (R1 to R7, Figure 1). At each of these areas random collections were made from HWS to LWS.

The collected samples were immediately frozen and stored until sorting. After sorting to determine species composition, specimens were dried at 60°C to constant weight. All biomass figures are expressed as dry weight.

Results

Summary of physical conditions

The following account of the physical conditions within the estuary includes personal observations and a summary of information provided by Dr G. Read and Mr D. Taylor of Rhodes University.

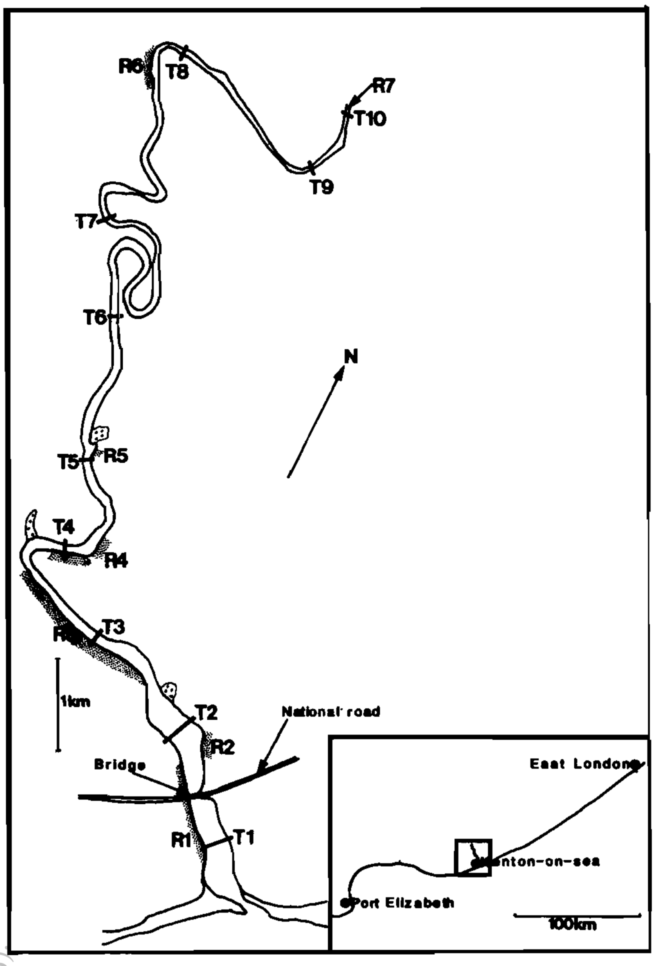

Figure 1 The Kariega estuary in the eastern Cape showing transects and sampling stations. T1 – T10 transects taken in sand or mud. R1 – R7 rocky areas sampled. Heavy stipple indicates areas of rocky shore. Light stipple identifies larger areas of salt marsh not sampled in this study.

In winter, water temperatures are stable at 15 – 16°C within the water column and along the estuary. During summer, the water temperature reaches a maximum of 23°C at the mouth, whereas in the upper reaches, temperatures are about 5°C higher. The salinity throughout the water column of the lower reaches has remained stable at 35 – 36°/oo except during a brief period of floods in 1981. In the upper reaches, however, the salinity has increased slowly to 40 – 42°/oo. Oxygen concentrations within the water column range from 7 – 8 mg $O_2\ l^{-1}$.

The intertidal banks of the lower reaches of the Kariega estuary have a shallow gradient. The sediments for the first 2,5 km are of well sorted marine sands which are clean and have a low organic content (< 0,6%). The sand flats at Transect 1 are about 300 m wide. Three hundred metres above the national road bridge (Transect 2, Figure 1), the sediments are slightly finer with a greater proportion of mud. Further upstream the intertidal mud banks narrow; at Transect 3 they are 30 m wide, Transect 4, 10 m and thereafter (T5 – 10) 5 m wide. In addition the banks become steeper. For most of the length of the estuary the banks are composed of soft sediments, but a number of rocky areas run down to the water's edge (Figure 1).

Vegetation

The sea grass, *Zostera capensis* Setchell, occurs as a 2 – 6 m wide band just below and above low water springs (LWS) along the length of the estuary. Using a combination of aerial photographs and on site measurements it is estimated that there is approximately 24 ha of *Zostera* within the Kariega. The plant's biomass (leaves and roots) is greatest in the middle reaches of the estuary, between T5 and T8 (Figure 2), with a maximum value of 391 g m^{-2}. The mean biomass for the entire estuary of 190 g m^{-2} is only slightly lower than that recorded by Grindley (1978) for *Zostera* in Knysna lagoon (206 g m^{-2}) but is over 100 g m^{-2} lower than that recorded (Hodgson, unpublished data) in the adjacent Bushmans estuary (Table 1). Just below the *Zostera*, and only exposed on the lowest spring tides, are small patches of *Halophila ovalis* (R.Br.).

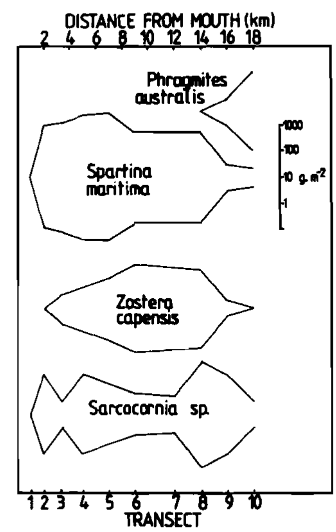

Figure 2 Distribution and biomass of four macrophytes along the Kariega estuary.

Towards the top of the intertidal zone is a belt of rice grass *Spartina maritima* (Curtis), which occupies approximately 22 ha of mud bank. *Spartina* has its greatest biomass (c. 2100 g m^{-2}) in the lower and middle reaches (T2 – 6) of the estuary (Figure 2). Such a standing biomass is similar to that recorded in the adjacent Bushmans (Table 1). Towards the head of the estuary (above T8), *Spartina* is more patchy in its distribution and is gradually replaced by *Scirpus litoralis* Schrad. and *Phragmites australis* (Cav.) (Figure 2).

Table 1 Mean and maximum biomasses (g m^{-2} dry weight) of *Zostera capensis, Spartina maritima* and *Sarcocornia* sp. recorded in the Kariega and Bushmans estuaries

	Zostera		*Spartina*		*Sarcocornia*	
	Mean	Max	Mean	Max	Mean	Max
Kariega	190	391	1186	2194	522	1469
Bushmans	319	409	1570	2558	400	490

Above the *Spartina*, the salt-marsh vegetation is dominated by *Sarcocornia perennis* (Miller) which in places can have a biomass of about 1500 g m^{-2}. At a higher level, *Sarcocornia pillansae* (Moss) is found. In addition to *Sarcocornia, Chenolea diffusa* Thunb., *Cotula coronopifolia* Linn., *Triglochin* *bulbosa* Linn. and *Limonium scabrum* Kubtze are also common. These plants are flooded only by very high spring tides.

One of the striking features of the intertidal banks of the middle and upper reaches of the estuary is the overhanging terrestrial vegetation. The lower branches and some roots of trees and bushes are nearly always submerged at high tide. The trees and bushes are dominated by four species; *Sideroxylon inerme* L., *Rhus glauca* Thunb., *Schotia afra* (L) Thunb. var. *afra* and *Cussonia spicata* Thunb. The distribution of the major aquatic and marginal plant species is indicated in Table 2.

Table 2 Distribution of aquatic and marginal vegetation along the Kariega estuary (the presence of a species at or near a station is indicated by (▲); S = subtidal; I = intertidal; M = salt-marsh; O = overhanging marginal)

Species		Transect number 1	2	3	4	5	6	7	8	9	10
Spartina maritima	M	▲	▲	▲	▲	▲	▲	▲	▲	▲	▲
Sarcocornia sp.	M	▲	▲	▲	▲	▲	▲	▲	▲	▲	▲
Zostera capensis	I/S	–	▲	▲	▲	▲	▲	▲	▲	▲	–
Chenolea diffusa	M	–	▲	▲	▲	▲	▲	▲	▲	▲	▲
Halophila ovalis	S	–	–	▲	▲	▲	▲	▲	▲	▲	–
Limonium scabrum	M	–	▲	▲	▲	▲	–	–	–	▲	–
Triglochin bulbosa	M	–	–	▲	▲	▲	–	–	–	▲	–
Codium sp.	S	–	▲	▲	▲	–	–	–	–	–	–
Protasparagus sp.	O	–	–	–	–	▲	▲	▲	–	–	–
Cussonia spicata	O	–	–	–	–	▲	▲	▲	–	–	–
Sideroxylon inerme	O	–	–	–	–	▲	▲	▲	–	–	–
Schotia afra var. *afra*	O	–	–	–	–	▲	▲	▲	–	–	–
Rhus glauca	O	–	–	–	–	▲	▲	▲	–	–	–
Azima tetracantha	O	–	–	–	–	▲	▲	▲	–	–	–
Euclea sp.	O	–	–	–	–	▲	▲	▲	–	–	–
Sporobolus virginicus	M	–	▲	–	–	–	–	–	▲	▲	▲
Atriplex vestita	M	–	–	▲	–	–	–	–	–	▲	–
Cotula coronopifolia	M	–	–	–	–	–	–	–	–	▲	▲
Scirpus litoralis	M	–	–	–	–	–	–	–	–	▲	▲
Phragmites australis	M	–	–	–	–	–	–	–	–	▲	▲
Apium graveolus	M	–	–	–	–	–	–	–	–	–	▲
Stenotaphrum secundatum	M	–	–	–	–	–	–	–	–	–	▲

Fauna of soft substrates

Day (1951) divides estuaries into four regions, namely, mouth, lower, middle and upper reaches. In the Kariega the greatest faunistic changes occur in the lower reaches of the estuary (Transects 1 – 3). Consequently data from all three transects of the lower reaches are represented. Thereafter data from two transects represent the faunal distribution of the middle and upper reaches.

Transects at the mouth and the lower reaches of the estuary (Transects 1 – 3)

Transect 1 was positioned close to the mouth of the estuary. Here the intertidal banks are composed of clean sand, and therefore have a fauna which is quite distinct from that of the rest of the estuary. Subtidally there is a very poor fauna, with only the polychaete *Glycera tridactyla* being found

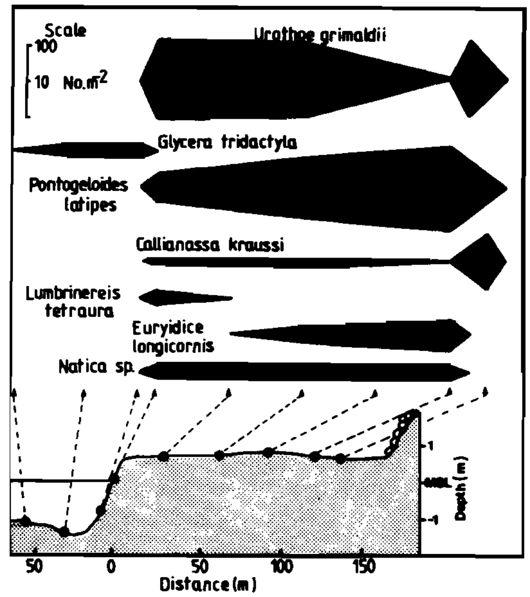

Figure 3 Transect 1 across the sand bank near the mouth.

(Figure 3). Above LWS the diversity increases.

The lower shore is dominated by the amphipod *Urothoe grimaldii*, this being replaced at higher levels by *Pontogeloides latipes* and *Eurydice longicornis*. Near the centre of the sand bank, and at the high-water mark, numerous staphylinid beetles burrow into the top layers of the sand. A few predatory gastropods, *Natica tecta* and *N. gualteriana* are found scattered about the sand banks. The sand prawn, *Callianassa kraussi*, gradually increase in numbers from the LWS mark, reaching their greatest abundance of 50 m^{-2}, 0,8 m above the low-tide mark. The fauna is therefore typical of unstable sand banks which have a low organic content.

Transect 2 (Figure 4) was sited 3 km from the mouth. Subtidally no animals are found. This is undoubtably a result of the strong tidal currents in the channel and coarse subtidal sediments.

Intertidally the banks are of a more stable sediment and thus support a more diverse fauna. At LWS there is an area on which *Zostera* grows. The *Zostera* here has short leaves (100 – 150 mm long) and a patchy distribution. Associated with the leaves of the macrophyte are small numbers of the brachyuran crab *Hymenosoma orbiculare*, and the herbivorous gastropod *Haminea alfredensis* (Figure 4). These species are found on *Zostera* along the length of the estuary. On and just below the surface of the mud, large numbers (> 150 m^{-2}) of the scavenging gastropod *Nassarius kraussianus* are found. The dominant infaunal animals are the mud prawn, *Upogebia africana*, the brachyuran crab *Cleistostoma edwardsii* and the polychaete *Ceratonereis erythraeensis*. *Upogebia* and *C. edwardsii* reach densities of between 100 – 150 m^{-2}. Beyond the *Zostera* is a mud bank 150 m wide which does not support any macrophytes. Only *C. edwardsii* appears to be able to colonize this area successfully with large numbers of the crabs moving over the surface of the mud at low tide to feed.

Towards the high-tide mark there is a large stand of *Spartina*. Species diversity is low with only the crabs *Sesarma catenata*, *C. edwardsii* and the gastropod *Assiminea bifasciata* being recorded. Within the *Sarcocornia* at the top of the shore, the numbers of *A. bifasciata* increase to over 1000 m^{-2}. The densities estimated for this gastropod are probably under-

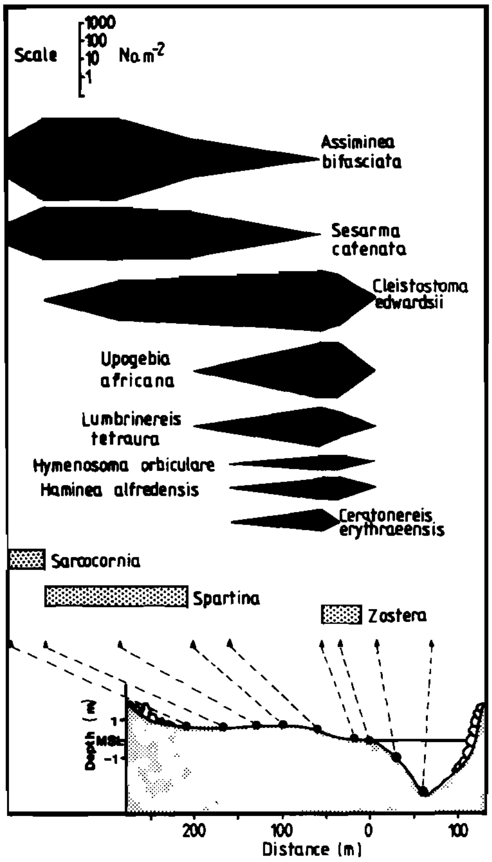

Figure 4 Transect 2 across a mud bank above the national road bridge. Stippled bars indicate limits of macrophyte distribution.

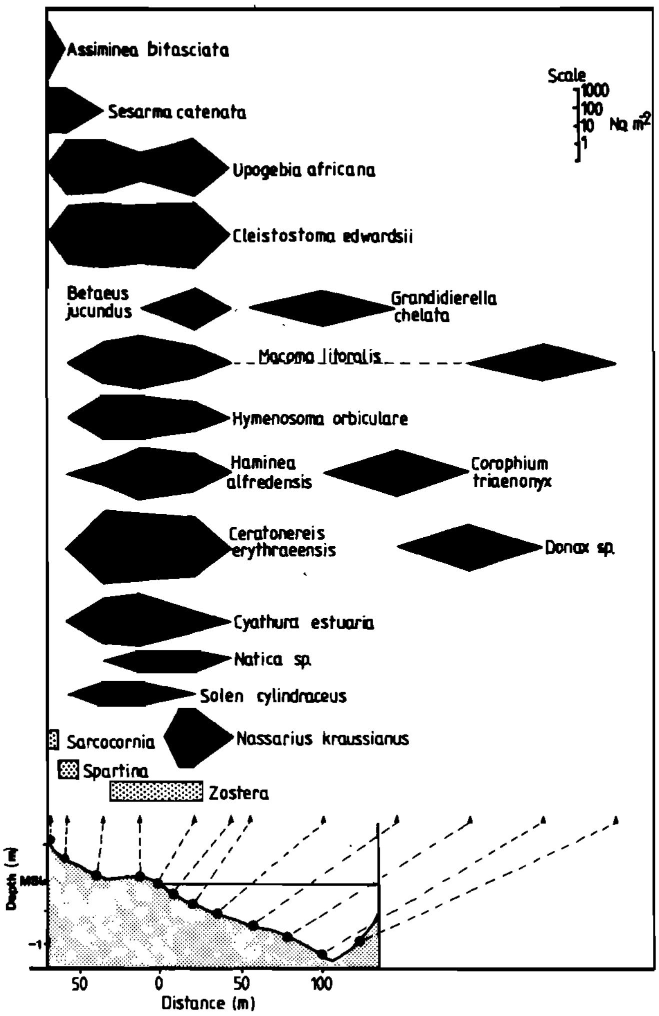

Figure 5 Transect 3, 3 km from the mouth of the estuary. Stippled bars indicate limits of macrophyte distribution.

estimated as many individuals are small enough to pass through a sieve with a 1-mm mesh.

Transect 3 ran from the middle of the channel, across a 30 m wide stand of *Zostera*, and into salt marsh vegetation (Figure 5). Compared with T2, the *Zostera* is not as patchy in its distribution, and it supports a large diversity of invertebrates (Table 3). The distribution of some of the more abundant animals is illustrated in Figure 5. *Cleistostoma edwardsii* is particularly abundant reaching densities of > 900 m^{-2}. Also found in large numbers are *U. africana*, and *C. erythraeensis*. Increasingly abundant are the bivalves *Solen cylindraceus* and *Macoma litoralis*, the latter extending into the channel.

Towards high water, *S. catenata* replaces *C. edwardsii* as the dominant animal. The burrows of *S. catenata* can be found amongst the *Spartina* and *Sarcocornia*. Also present in the salt-marsh vegetation are large numbers (> 1000 m^{-2}) of *A. bifasciata*.

The main channel is still poor in invertebrates, with only specimens of the amphipods *Corophium triaenonyx*, *Grandidierella chelata* and the bivalve *M. litoralis* being found.

Transects in the middle reaches of the estuary

Transects 4 – 7 were undertaken in the middle reaches of the estuary, and Figure 6 represents the results from one such transect (T6). The intertidal banks are steep and only about 5 m wide. At the HWM the mud banks are riddled with the burrows of brachyuran crabs, *S. catenata* and *C. edwardsii* being particularly abundant. Other species of *Sesarma*, *S. eulimene* and *S. meinerti*, are also present. In addition the fiddler-crab, *Uca urvillei* also inhabits the mud banks with densities of 28 m^{-2}, which approach those found in many mangroves (Day 1981). *Uca urvillei* tends to inhabit east-north-east-facing banks, favouring the morning sun. Another species of fiddler-crab, *U. annulipes* is occasionally found in the mud banks. Within the *Sarcocornia*, living on the surface of the mud are large numbers (> 100 m^{-2}) of a shell-less pulmonate, *Onchidella* sp. It has a wide distribution along the estuary being found from Transect 4 to the head. Below the salt marsh vegetation the mud of the intertidal area supports large populations of *U. africana* (particularly Transects 4 and 5), *S. cylindraceus* and *M. litoralis* (T5 – 8). Densities of *U. africana* (500 m^{-2}) are equivalent to those reported for the Swartkops and Kowie estuaries (Table 4).

A number of species extend from the LWS mark subtidally. Among them are *N. kraussianus*, *C. triaenonyx*, *Scolelepis squamata*, *Cleistostoma algoense* and *Cyathura estuaria*. The scouring action of the water during the ebb and flow of the tide is not as strong in the middle reaches and therefore the sediments of the channel are of fine muds. These have a high organic content (Taylor, pers. comm.) and provide a stable habitat for many animals.

Transects in the upper reaches of the estuary

Transect 8 (Figure 1) represents many of the features of the upper reaches of the estuary. Subtidally there is an increasingly diverse fauna which is able to inhabit the fine muds. Common species include the bivalves *M. litoralis* and *Eumarcia paupercula*, the amphipods *C. estuaria* and *C. triaenonyx*, the

Table 3 Abundance and biomass of species recorded in *Zostera* at T3

Species	No. m^{-2}	Dry weight g m^{-2}
Crustacea		
Upogebia africana	130	14,76
Cleistostoma edwardsii	604	11,40
Alpheus crassimanus	2	2,20
Hymenosoma orbiculare	24	1,86
Cyathura estuaria	45	0,22
Betaeus jucundus	15	0,06
Exosphaeroma hylocoetes	7	0,04
Melita zeylanica	128	0,03
Mollusca		
Macoma litoralis	43	1,06
Haminea alfredensis	40	0,69
Nassarius kraussianus	4	0,21
Solen cylindraceus	4	0,20
Natica tecta	3	0,20
Arcuatula capensis	13	0,04
Polychaeta		
Ceratonereis erythraeensis	268	0,76
Glycera tridactyla	5	0,01
Lumbrinereis tetraura	3	0,01
Tanaidacea		
Apseudes digitalis	84	0,01
Nemertea		
Polybrachiorhynchus dayi	1	0,04
Total number of species = 19		T = 34,02

Table 4 Abundance of *Solen cylindraceus* and *Upogebia africana* in some South African estuaries; all figures are number of animals per m²

Estuary	*S. cylindraceus*	*U. africana*	Reference
Kromme	5 – 15	10 – 110	Baird *et al.* 1980
Swartkops	120	156 – 500	Day 1981
Sundays	No data	90 – 180	Day 1981
Bushmans	10 – 20	120	Hodgson unpublished data
Kariega	10 – 400	120 – 500	Present study
Kowie	150	600	Day 1981
Mngazana	64	up to 90	Branch & Grindley 1979
St Lucia – Gillys point	498	–	Blaber *et al.* 1983
St Lucia – other sites	49 – 151	–	Blaber *et al.* 1983

polychaete, *Dendronereis arborifera* and the tanacian, *Apseudes digitalis*. Intertidally the brachyuran and anomuran crabs which are common in the lower and middle reaches of the estuary, are no longer present. The polychaete *C. erythraeensis* and the bivalve *S. cylindraceus* are the dominant species. *A. bifasciata* and *Talorchestia australis* are common in the salt-marsh vegetation. Figure 7 illustrates the distribution of the more common species at Transect 8.

Fauna of rocky shores

Rocky outcrops which run down from HWS to LWS occur at seven areas along the estuary (Figure 1). Collections were made at each of these areas. As rocks form a small proportion only (< 10%) of the total intertidal substrate, their fauna is

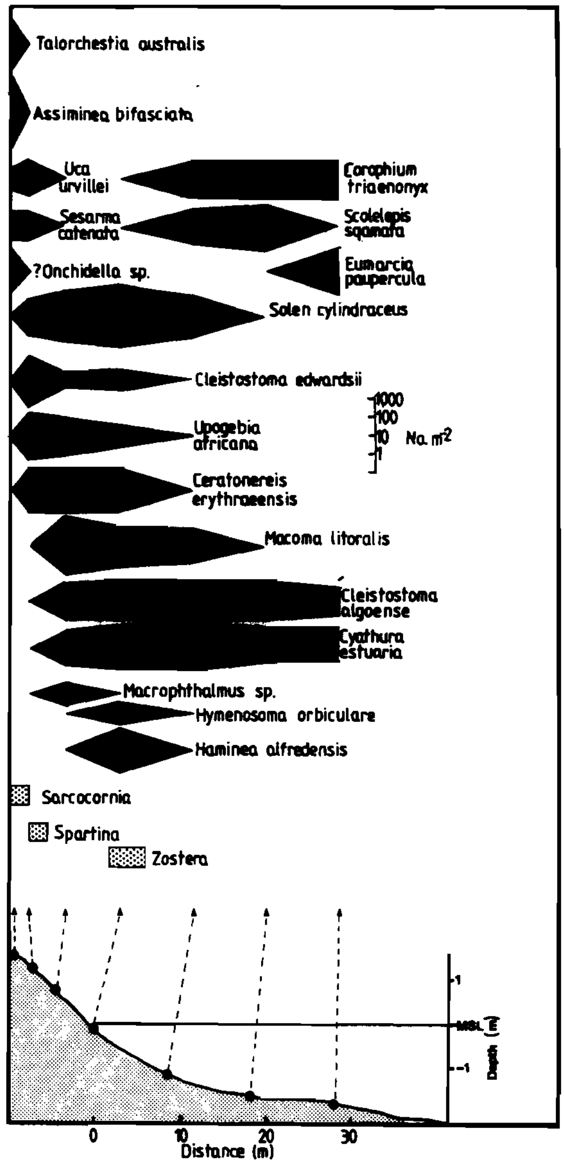

Figure 6 Transect 6 from the middle reaches of the estuary. Stippled bars indicate limits of macrophyte distribution.

discussed briefly (see Appendix I for a complete list of species). At stations R1 – R4 the rocky substrate consists of small boulders interspersed with flat rock surfaces. The boulders tend to decrease in size towards low tide. Most of the fauna found here is typical of the open rocky shores of the eastern Cape. At HWS there are abundant populations of *Littorina africana africana* and *L. a. knysnaensis*. Under rocks *Cyclograpsus punctatus* is common. At the upper balanoid zone the barnacle *Chthamalus dentatus* is abundant along with the siphonariid limpets *Siphonaria capensis, S. concinna* and *S. oculus*. In the lower balanoid zone the oyster *Saccostrea margaritacea* can be found. The under-sides of rocks and rock crevices house a variety of fauna, the commonest being the gastropods *Oxystele variegata, O. tigrina* and *Patella oculus*; the bivalves *Arcuatula capensis* and *Ostrea algoensis* and the polychaete *Thelepus plagiostoma. Upogebia africana* is also found burrowing in the mud which is trapped in between boulders.

Further upstream, at R5 and R6, the fauna is poor. Most of the littorinids are still abundant and in addition *L. scabra* is common. Specimens of *Nerita albicilla* and the mangrove snail *Cerithidea decollata* are found and *S. oculus* is the

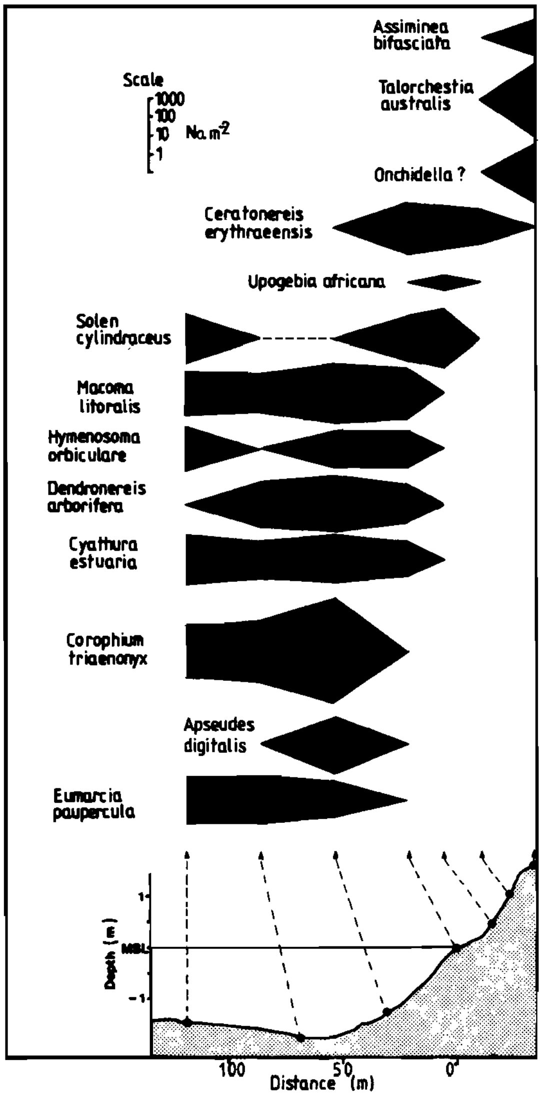

Figure 7 Transect 8 from the upper reaches of the estuary.

dominant limpet. Under boulders, populations of *A. capensis* exist and a few species of *Brachidontes virgillae* can be found. The barnacle *Balanus amphitrite* is abundant at LWS. The number of *B. virgiliae* increase towards the head of the estuary and *B. amphitrite* is gradually replaced by the estuarine barnacle *B. elizabethae*.

At station R7, the bed consists of a mixtures of sand, mud, small stones and boulders. Here the fauna consists of *B. virgiliae*, the tube-dwelling polychaete *Ficopomatus enigmatica* and *Balanus elizabethae*.

Discussion

The physical conditions in the Kariega estuary have been very stable for a number of years (Allanson and Read pers. comm.), the salinity has remained at between 35 and 40‰ and the input of fine silt from freshwater inflow has been very low. It is therefore not surprising that the estuary has a high species diversity. When compared to other eastern Cape estuaries, only the larger Swartkops has as great a number of invertebrate species (Table 5). The diversity of species in the Kariega can be partly attributed to *Zostera* which extends for the length of the estuary and provides microhabitats for many species. The low silt load and marine conditions in the Kariega have undoubtedly allowed *Zostera* to colonize all 18 km of the estuary. By comparison in the adjacent Bushmans, *Zostera* only penetrates 5 km up the estuary (pers. obs.)

Table 5 Number of macrobenthic invertebrates recorded from eastern Cape and southern Transkei estuaries; O indicates estuary open for most of the year, C indicates estuary normally closed

Estuary	Type	Freshwater inflow	Number of invertebrate species recorded	Reference
Kromme	O	Low	31	Baird *et al.* 1980 Hanekom 1982
Swartkops	O	Low	122	Baird *et al.* 1986
Bushmans	O	Low	79	University of Cape Town records
Kariega	O	Very sporadic	107	Present study
Kleinemond	C	Very sporadic	34	Brown 1953
Keiskamma	O	Low	51	University of Cape Town records quoted by Branch & Grindley 1979
Haven area (Bashee, Mbanyana Haven)	O	Moderate	70	Branch & Grindley as above

and Day (1981) notes that in those estuaries which often have a heavy silt load, *Zostera* may be completely absent. Figure 8 illustrates the change in numbers of species down the estuary. Branch & Grindley (1979) state that for most estuaries the normal pattern of species distribution is for a large number of species to occur at the mouth, with a steady decline in numbers towards the head. This pattern is not immediately

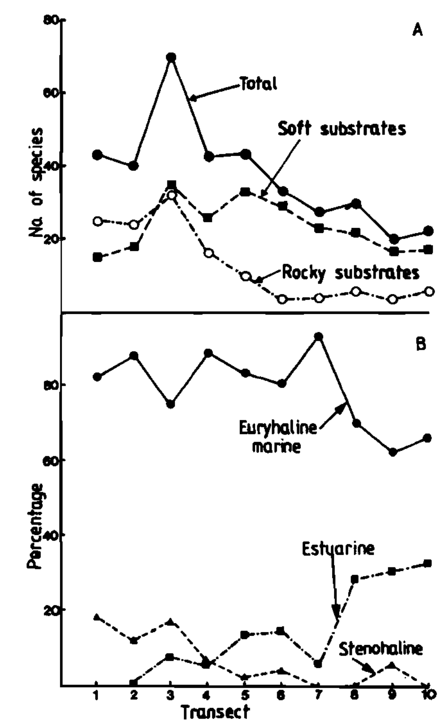

Figure 8 A. Change in numbers of species found along the length of the Kariega estuary. B. Analysis of the faunal components of the estuary. Data is expressed as a percentage of the total number of species found.

apparent in the Kariega, where the greatest number of species is found 3 km from the mouth, with species numbers increasing from 40 to 70 (Figure 8A). This increase is probably linked to the greater diversity of habitats available in this region of the estuary, there being both stable rock and mud banks, the latter being covered with extensive stands of *Zostera*. Thereafter species diversity follows the general trend i.e., decreasing towards the head.

When the invertebrate fauna is divided into soft substrate and rocky substrate species the two show differing trends. The number of species on the rocky substrates is highest in the lower reaches, after which species numbers decline rapidly, remaining at a low level to the head. It can only be speculated as to the reason for such decline. Branch & Grindley (1979) suggested that in the Mngazana estuary siltation prevents many rock-dwelling species from colonizing such habitats towards the head of the estuary. With the reduced freshwater input, siltation is not as problematical for animals living in the Kariega, except during the occasional floods. The effect of episodic salinity changes could have a far greater impact, the rocky shore animals bearing the full brunt of such fluctuations. Nearly all the rocky shore animals living at the head of the estuary are truly estuarine species e.g. *Ficopomatus enigmaticus* and *Brachidontes virgiliae*.

In contrast to the fauna of the rocks, the number of species found living in soft substrates increases from the mouth to the middle reaches of the estuary (Figure 8A), with only a small decline towards the head. At the mouth the animals living in the marine sands must be limited by the low organic content and the instability of the sand-banks. Above the national road bridge the muds of the intertidal banks are more stable, and they have a higher organic content (Taylor, pers. comm.).

When the invertebrate fauna is analysed in terms of the faunal components defined by Day (1951, 1981), most of the species are found to fall within the category of euryhaline marine with only a small percentage which are truly estuarine (Figure 8B). Branch & Grindley (1979) and Day (1964, 1981) have shown that this is so for other South African estuaries. The number of estuarine species increases from the mouth to the head of the estuary, whereas the euryhaline marine and stenohaline marine species show a steady decrease although some stenohaline species do exist towards the upper reaches of the estuary, undoubtedly a result of the sea-water conditions there.

The distribution and biomass of the more dominant invertebrates is illustrated in Figure 9. The lower reaches of the estuary are dominated by the detritivores *Upogebia africana, Cleistostoma edwardsii* and *Sesarma catenata*. However in the middle reaches the filter-feeding bivalves, *Solen cylindraceus* and *Macoma litoralis* are far more abundant. The numbers of *S. cylindraceus* (400 m^{-2}) are three times higher than those reported within other eastern Cape estuaries (Table 4). Such densities approach those recorded by Blaber, Klure, Jackson & Cyrus (1983) at Gillys point in Lake St Lucia. The large numbers of *Solen* in St Lucia were attributed to the high salinities which had predominated there for several years. The large populations of *Solen* in the Kariega can also be attributed to several years of high salinities. However the success of *Solen* may also be linked to food availability. *Solen* is most abundant in those regions of the estuary (T4–7) where the total particulate matter in the water column is highest (Allanson & Reid, in preparation). Such a correlation clearly warrants further investigation. It is estimated that 51% of the intertidal biomass in the middle reaches of the Kariega are

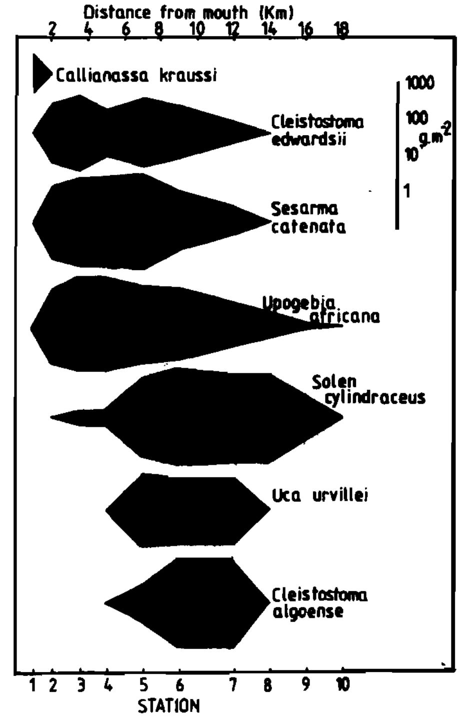

Figure 9 Biomass and distribution of dominant macrobenthic invertebrates in the Kariega.

filter-feeders. These animals must make a considerable impact on the particulate content of the estuarine water. In many other estuaries that have been studied it is the detritivores which are dominant, for example Branch & Grindley (1979) found that in the Mngazana estuary 80–100% of the fauna were detritivores. Nichols (1985) has shown that in San Francisco Bay the filter-feeders became very abundant during a period of drought with the result that the salinity of the water increased. A similar situation would appear to have developed in the Kariega estuary, with the marine conditions favouring the filter-feeders.

The distribution of several species of crab found in the estuary has been extended further south, in particular that of *S. meinerti, U. urvillei* and *U. annulipes. Uca chlorophthalmus* has also been recorded in the Kariega (Neethling & Jubb 1972). However a re-examination of their photographs suggests that in all probability what were reported to be *U. chlorophthalmus* were in fact *U. urvillei*. All the aforementioned species are more associated with subtropical and tropical estuaries where mangroves occur (Day 1981). Their presence may be a result of several factors but the stable salinity, warm temperature and overhanging vegetation must all aid the survival of these species. The sesarmid crabs may utilize the leaf litter produced by the overhanging terrestrial vegetation. Branch & Grindley (1979) report that *S. meinerti* will scavenge mangrove leaves and coarse detritus at low tide.

Figure 10 illustrates the distribution of invertebrate biomass on 4 transects. In the lower reaches, the marine sands support a low biomass. Above the national road bridge (see Figure 1), in the lower and middle reaches of the estuary, the sediments support an increasingly higher invertebrate biomass. The biomass declines once more towards the head. The *Zostera* beds contain the highest biomass (34 g m^{-2}), especially in the middle reaches of the estuary. Such a biomass is similar to that found for *Zostera* beds in other southern African estuaries (Grindley 1978; Branch & Grindley 1979; Day 1981).

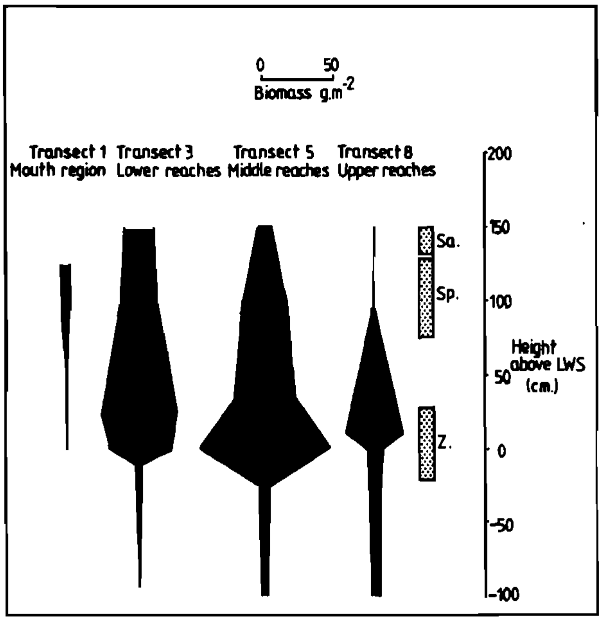

Figure 10 The distribution of biomass of invertebrates (g m^{-2}) on 4 transects in the Kariega estuary. Stippled bars represent limits of macrophyte distribution. Sa, *Sarcocornia*; Sp, *Spartina*; Z, *Zostera*.

The potential effects of reduced freshwater inflow into an estuary are demonstrated in the Kariega. It has allowed a macrophyte such as *Zostera* to penetrate deep into the upper reaches of the estuary which in turn has aided the development of a rich macrobenthic fauna. In particular the filter-feeders appear to benefit from such conditions dominating the fauna of the middle and upper reaches. As only standing stocks were measured in this study the productivity of the estuary as compared to other estuaries has still to be determined. Workers from the Zoology department at Rhodes University are currently undertaking productivity studies within a number of eastern Cape estuaries.

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Appendix 1 List of invertebrates occurring in the Kariega estuary. Distribution up the estuary is given for Stations 1 – 10, Station 1 being close to the mouth and Station 10 the head. Relative abundance is indicated by the number of specimens collected at each site: R = 1 – 2; P = 3 – 20; C = 21 – 100; A > 100. Substrate types: S = clean sand; M = mud; R = attached to rocks; P = planktonic. Geographical distribution: C = cold temperate, west coast; W = warm temperate, south coast Cape point to East London; S = subtropical, Transkei to southern Mozambique; T = tropical; U = ubiquitous. Asterisks indicate an extension of known records as given by Day 1981. Component: St.m = stenohaline marine; Eur, euryhaline marine; Est. estuarine

	Distribution down the estuary 1 2 3 4 5 6 7 8 9 10	Substrate	Geo. Dist.	Component
Porifera				
Unidentified sponges	P P P	R		
Cnidaria				
Hydractinia kaffraria	P P P P P P P	Shell	W-T	Eur.
Pseudactinia flagellifera	R P	M	W*	St.m.
Nemertea				
Polybrachiorhynchus dayi	R R R	M	W-T	Eur.
Platyhelminthes				
Planocera gilchristi	P	R		St.m.

Appendix 1 Continued

	Distribution down the estuary												
	1	2	3	4	5	6	7	8	9	10	Substrate	Geo. Dist.	Component
Echiuroida													
Ochaetostoma capense					R	R					M		Eur.
Polychaeta													
Arenicola loveni		R									M	W*	Eur.
Ceratonereis erythraeensis		P	A	A	A	C	C	A			M	T	Eur.
Dendronereis arborifera						P		C	C	P	M	S-T*	Eur.
Ficopomatus enigmatica			C	C		C	C	C	C	A	R	W-S	Est.
Glycera tridactyla	R		P	P	P						S	U	Eur.
Lepidonotus semitectus			P								R		
Lumbrinereis tetraura	P	P	P				R				S/M	C-S	Eur.
Marphysa sanguinea		P	P				R				M		Eur.
Perinereis nuntia vallata			C								M	W-T	Eur.
Scolelepis squamata					P	P			P		S	U	St.m.
Spirorbis sp.	P	P	P	P							R		
Thelepis plagiostoma			C								R	W-T	St.m.
Crustacea													
Amphipoda													
Corophium triaenonyx			P		P	P		A	A	P	M	W-T	Est.
Grandidierella chelata			P		P	P		A	A	P	M		
Melita zeylanica			A		P						S/M	C-T	Eur.
Talorchestia australis		P				C	A	A	A	A	M		Eur.
Urothoe grimaldi	A										S		St.m.
Isopoda													
Cirolana fluviatilis					P			P			M	W-S	Est.
Cirolana sp.							P				M		
Cyathura estuaria			C	C	P	C		C	C	P	M	W-T	Est.
Exosphaeroma hylocoetes			C		P				P		M	W-T	Est.
Ligia natalensis	C	C	C				P				R	C-W	Eur.
Pontogeloides latipes	A										S/P	U	St.m.
Eurydice longicornis	P							P	P		S/P	C-S	Eur.
Anilocra capensis	On head of fishes											W	
Cirripedia													
Balanus amphitrite	P	P	C	C			C	C	P	P	R	W-T	Eur.
Balanus elizabethae					C	P		P	P		R	W-S	Est.
Chthamalus dentatus	P	P	P	P							R	U	St.m.
Tanaidacea													
Apseudes digitalis			A					A	C	P	M-P	W-S	Est.
Macrura													
Alpheus crassimanus			P	R	R						M	W-T	Eur.
Betaeus jucundus	P		C	P							M/P	C-S	Eur.
Palaemon pacificus	C	A	A	A	A	A	P	P			P/S/M	C-T	Eur.
Penaeus semisulcatus			R								P	S-T*	Eur.
Anomura													
Callianassa kraussi	C								P		S	C-S	Eur.
Diogenes brevirostris	P	P	P	P	P						S/M	W-S	Eur.
Upogebia africana		A	A	A	A	C	P	P			M	C-T	Eur.
Brachyura													
Cleistostoma algoense				A	C	C					M	W-T	Eur.
Cleistostoma edwardsii		A	A	A	A	P	P				M	C-T	Eur.
Cyclograpsus punctatus	P	C	C	C	C	P					R/M	C-S	Eur.
Hymenosoma orbiculare			C	P	P	P		P	P	R	M	C-S	Eur.
Macrophthalmus sp.				P	P	P	P				M	S-T*	Eur.
Ocypoda madagascariensis			P	P			P				S/M	S-T	Eur.
Sesarma catenata		C	C	A	C	C	C				M	W-T	Eur.
Sesarma eulimene					R	P		P			M	S-T*	Eur.
Sesarma meinerti				P		P	P				M	S-T*	Eur.
Scylla serrata					P	P	P	P	P	P	M	W-T	Eur.
Thaumastoplax spiralis	P			P	P						S/M	C-S	Eur.
Uca urvillei					P	C	C	P			M	S-T*	Eur.
Uca anulipes						P	R				M	W-T*	Eur.
Insecta													
Anurida maritima	P	P	P	P		A					R	U	Eur.
Staphylinid	A										S		
Mollusca													
Polyplacophora													
Acanthochiton garnoti	P	P	C								R	C-S	Eur.
Chiton tulipa			P								R	C-S	St.m.
Ischnochiton oniscus			P								R	S-T	St.m.
Bivalvia													
Anomia achaeus		R	R								R		
Arcuatula capensis		C	C	C	P		P		R		R	W-T	Eur.
Barbatia obliquata			P								R	W-T	Eur.
Crassostrea margaritacea	R	P	C	R							R	W-S	Eur.
Donax sp.			R								S		St.m.
Dosinia hepatica		P				P	R	P	P		M	C-T	Eur.
Eumarcia paupercula			P		P	P	P	P	P	P	M	W-T	Eur.
Macoma litoralis		P	A		P	C	C	C	C	P	S/M	W-T	Eur.
Ostrea algoensis		P	P								R	W-S	Eur.
Saccostrea cucullata	P	P	P	P							R	S-T*	Eur.
Solen capensis		R									S	W	St.m.
Solen cylindraceus			P	P	C	A	C	C	P	P	M	W-T	Eur.
Gastropoda													
Aplysia sp.	R										R		St.m.
Assiminea bifasciata		A	P		P	P	C	C	P	P	M	W-S	Eur.

Appendix 1 Continued

	Distribution down the estuary												
	1	2	3	4	5	6	7	8	9	10	Substrate	Geo. Dist.	Component
Berthella granulata			P								R		St.m.
Cerithidea decollata			P	P	C						R	W-T	Eur.
Crepidula porcellana				R	R						R		Eur.
Haminea alfredensis			C	P	P	P					M	W-S*	Eur.
Helcion pectunculus	P										R		St.m.
Helcion pruinosus	P										R		St.m.
Littorina africana africana	C	C	C	C	P						R		Eur.
Littorina africana knysnaensis	A	A	A	A	A	C					R		St.m.
Littorina scabra		P		C	C					P	R/M	S-T	Eur.
Nassarius kraussianus			A	P	C	C		A	C	R	M	C-T	Eur.
Natica gualteriana		P	P	P							S/M	S-T*	Eur.
Natica tecta	P		P	P							S/M	C-S	Eur.
Nerita albicilla			P	P	P						R	S-T	Eur.
Notarchus leachii	In weed beds August & September as far as T6.												
Onchdella sp.				R	C	C	P	A	A	A	M/R	?	Est ?
Oxystele sinensis	P	P									R		St.m.
Oxystele tigrina	P	P	C								R		St.m.
Oxystele variegata	C	C	C								R	C-S	Eur.
Patella oculus	P	P	P								R	C-S	Eur.
Siphonaria concinna	C		C								R	W-S	Eur.
Siphonaria oculus			C	C	C						R	W-S	Eur.
Thais dubia			P	P	P	P					R	C-W	Eur.
Cephalopoda													
Octopus granulatus	Single specimens observed up to station 7												
Sepia officinalis	P	P	P										
Sepia tuberculata			R										
Echinodermata													
Ophiothrix fragilis			P								R		
Parechinus angulosus		P	P								R		
Patiriella exigua	P	P	P								R	C-S	Eur.
Brachiopoda													
Kraussiana rubra			C								R		St.m.
Tunicata													
Pyura sp.			P								R		
Unidentified sp.			C								R		