Ecology of southern African estuaries: Part XIII. The Palmiet River estuary in the south-western Cape

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The Palmiet estuary is only 1,67 km in length, but has a relatively large catchment of 539 km^2. Rain falls largely during winter when it scours the estuary and widens the mouth, but by late summer the mouth narrows and, in some years, may close. The estuary never closes for more than a few months, and salinities are normal. The entire estuary has clear bottom water and high bottom salinities, but the surface waters are usually fresh and darkly stained with humic acid. This permanent stratification allows many marine species to penetrate the estuary.

Owing to the scouring in winter, the sediments are coarse, >98% consisting of sand and gravel, with a low organic content. *In situ* primary production is low, contributing only about one fifth of the organic material in the system, the rest being imported from the river and the sea. Species richness is low, only 28 species of invertebrates being recorded, but many of these occur in enormous numbers. *Callianassa kraussi* plays a crucial role, trapping fine particles around its burrows and locally enhancing the organic content of the sediments. Its faeces are an important vehicle for the concentration and turnover of organic matter.

Four of the 19 species of fish recorded breed in the estuary, the rest being represented largely by juveniles or small adults. Only three species occurred in the estuary year-round, the other species being absent during the period that the estuary is in flood.

Floods and a relatively high flow of river water are critical to keeping the estuary open. If, as proposed, a dam is built on the river, steps will have to be taken to ensure that the mouth is kept open. A related problem will be the reduction of organic material entering the estuary from the river and the sea.

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Alhoewel die Palmiet-getyrivier slegs 1,67 km lank is, het dit 'n betreklike groot opvanggebied van 539 km^2. Dit reën hoofsaaklik gedurende die winter en dan word die getyrivier uitgeskuur en die monding verbreed, maar teen die einde van die somer vernou die monding weer en kan in sommige jare selfs toegaan. Die getyrivier is egter nooit langer as 'n paar maande toe nie, met soutgehaltes wat normaal varieer. Die hele getyrivier het helder bodemwater met hoë soutgehaltes, terwyl die oppervlakwater vars is en verdonker deur humussuur. As gevolg van hierdie permanente stratifikasie, kan baie mariene spesies die getyrivier binnedring.

Die uitskuureffek van die wintervloede veroorsaak dat die sedimente grof is en hoofsaaklik uit sand en gruis (>98%) met 'n lae organiese inhoud bestaan. Primêre produktiwiteit is laag en is verantwoordelik vir slegs een vyfde van die organiese materiaal in die sisteem, terwyl die res hoofsaaklik van die rivier en die see afkomstig is. Spesierykheid is laag, en slegs 28 invertebraatspesies is aangeteken, maar baie hiervan kom in groot getalle voor. *Callianassa kraussi* speel 'n uiters belangrike rol deur klein partikels om hul gate te versamel en so die sedimente plaaslik organies te verryk. Hierdie spesie se faeces is belangrik vir die konsentrasie en omset van organiese materiaal.

Negentien visspesies is aangeteken, waarvan vier in die getyrivier broei en die res hoofsaaklik as jongvis of klein vissies voorkom. Slegs drie spesies is dwarsdeur die jaar aangeteken, terwyl die ander spesies die getyrivier vanaf April of Mei tot September, die periode wanneer die rivier in vloed is, verlaat.

Vloedtoestande en betreklike sterk riviervloei is uiters noodsaaklik om die mond oop te hou. Indien, soos voorgestel, daar 'n dam hoër in die rivier gebou word, sal maatreëls getref moet word om te verseker dat die monding oop bly. 'n Verdere probleem is die vermindering van die invoer van organiese materiaal vanaf die rivier en die see.

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The Palmiet River estuary (34°20'S/18°59'E) is situated about 75 km south-east of Cape Town between Betty's Bay and Kleinmond. Although neither the estuary nor its catchment area is large, they incorporate a number of unusual features. Between the Berg and the Breede Rivers, a distance of some 350 km, the Palmiet is the only estuary which is normally open to the sea and which receives a large permanent inflow of fresh water. This has important consequences for the fauna of the estuary and for those species of fish whose juveniles feed in estuaries. Owing to high human population densities in the extreme south-western Cape and the resultant heavy demand for water, most of the local rivers are extensively dammed as well as receiving considerable nutrient enrichment from agricultural run-off. Despite its upper reaches being surrounded by apple orchards and forestry plantations (largely *Pinus* spp.) the Palmiet is the least disturbed of the water courses in the area and there is no heavy industry on its banks. Further, the catchment area includes the Kogelberg State Forest, which is renowned for the large number of species of indigenous terrestrial plants belonging to the small, threatened Cape Floral Kingdom.

Owing to the heavy demand for water in the area, there is a proposal to dam the Palmiet River within 2 km of the head of the estuary. The present study was commissioned by the then Department of Environmental Planning and Energy to study the ecology of the estuary and the factors maintaining it in its present condition. In particular, we examined the patterns of water flow which normally keep the mouth open; the nature and distribution of the primary production; the distribution and abundance of the fauna; the sources and standing stocks of detritus, organic material and nutrients and the trophic status of the system in relation to import and export of food and nutrients.

Methods

The Palmiet River estuary was visited on seven occasions: in April, August and December 1979 and in March, April, July and September 1980, giving a total of 28 days field work. On most occasions the authors were assisted by staff and students of the University of Cape Town.

Two-litre water samples were collected at each of six stations (A to F in Figure 1), situated in the deepest part of the channel. *In situ* measurements were made of oxygen and temperature, using a portable Beckman meter, and of salinity using an American Optics refractometer. pH was estimated by using universal indicator paper. The water samples were frozen for further analyses. NO_3-N, NH_3-N, reactive PO_4-P and

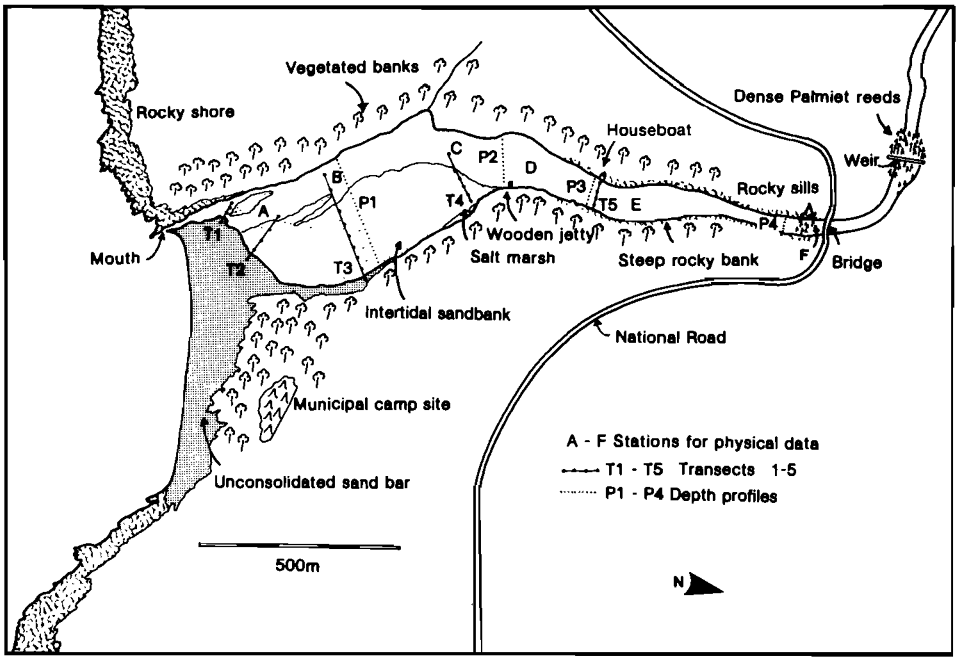

Figure 1 Map of Palmiet River estuary showing positions of sampling stations for physical data, transects and the profiles given in Figure 2.

SiO_2 – Si were determined by the Sea Fisheries Institute using an autoanalyser. Chlorophyll (as a measure of phytoplankton standing stock) was determined by the method of Strickland & Parsons (1968), total particulate matter (TPM) by filtering the water samples through a 0,45-μm mesh and drying, and particulate organic matter (POM) by ashing the TPM at 540 °C for 6 h.

A further series of 1 ℓ water samples was taken in conjunction with current readings at the mouth over four full tidal cycles in order to determine import and export of phytoplankton, TPM and POM through the mouth. On one of these occasions a series of 20 ml water samples was taken very near the bottom in order to determine the extent of mass transport of sediment and its relation to current velocity.

Figures for rainfall and river flow were supplied by the Department of Water Affairs, and the current at the mouth measured with a digital battery-operated current meter. Water flow at the weir (Figure 1) was calculated according to the equation

$$Q = cLH^{1,5}$$

where Q is the flow rate in $m^3 s^{-1}$, L is the width of the weir in metre, H is the height of the water flowing over the weir in metres and c is a constant where, for sharp-edged weirs,

$$c = 1,80 + (0,22 \times \frac{H}{h})$$

and h is the height of the downstream wall of the weir in metres.

Tidal ebb and flood were determined by surveying the profile of the mouth and multiplying the cross-sectional area by an integrated value for the mean rate of water flow out of and into the estuary. These flows were measured at hourly intervals in the centre of the mouth, at the surface, and at depth intervals of one third and two thirds of the water depth. Flushing time was calculated for the conditions prevailing during spring-tides in March and July 1980 and for a neap-tide in April 1980. The modified tidal prism method (Dyer 1973) was used to calculate flushing time, with adjustments to allow for incomplete mixing.

Particle sizes of sediment samples were determined by dry-sieving through a nest of sieves graduated at 0,5-ϕ intervals and the organic content by combustion of samples at 540 °C for 6 h. Separate analyses were undertaken for sediment surrounding *Callianassa* burrows. Faecal production by *Callianassa* was measured by collecting faeces released from the burrows between one low tide and the next, and the organic content and particle sizes of the faeces similarly measured. A more detailed analysis of the sedimentology of the estuary is being prepared by Dr J.P. Willis of the Deparment of Geochemistry, University of Cape Town.

Five transects, T1 to T5 in Figure 1, situated at intervals of approximately 300 m up the length of the estuary, were undertaken to assess the nature, distribution and biomass of the macroflora and fauna. On each transect 10 to 15 duplicate random samples were taken using quadrats with an area of 0,25 m^2. Samples were initially taken to a depth of 30 cm but this was later reduced to 10 cm after it had been determined that all fauna, with the exception of *Callianassa*, occurred only within the upper layers of sediment. The sediment was passed through a sieve of mesh-size 0,25 mm and the animals extracted and dried at 60 °C; all biomass figures are given as grams dry mass per square metre. A mean production : biomass ratio of 3,6 was assumed for all invertebrates excluding *Callianassa*. This value was obtained by averaging the P:B ratios of comparable animals, given in Burke & Mann (1974), Chambers & Milne (1975), Warwick & Price (1975) and Puttick (1977).

Callianassa holes were counted and, based on previous experience, the numbers of *Callianassa* were calculated on the assumption that two holes visible on the surface of the sand correspond to one animal. The dry biomass of *Callianassa* was calculated from the average body weight (0,30 g) of 36 individuals collected at random. A production : biomass ratio of 2,0 was estimated for *Callianassa*, being derived from Robertson's (1979) regression of P:B against lifespan, and assuming the lifespan of *Callianassa* to be three years.

The relative quantities of benthic diatoms were determined in December 1979 and July 1980 by measuring the concentration of total chlorophyll extracted from 1 g of sediment and analysed according to the method of Strickland & Parsons (1968) for phytoplankton. Triplicate samples were taken at six stations on four transects (T1 – T4: Figure 1). After integrating these values for the estuary as a whole, standing stocks of diatoms were estimated by assuming that the chlorophyll values could be multiplied by a conversion factor of 200 (R. Carter, pers. comm.) and by converting the mass of sand to a measure of area by using the specific gravity of sand (2,98 g cm^{-3}).

Rough estimates of the dry biomass of zooplankton were obtained from three hauls using a N-70 plankton net with a diameter of 0,4 m towed at two knots for 5 min.

The mass of decomposing plant detritus was determined by collecting, drying and weighing all the solid material present in a series of 48 replicated 0,25 m^2 quadrats across all five transects. The samples were taken between December 1979 and April 1980.

Twenty-nine hauls of fish were made, two or three in each of the months December 1979 and April 1980 to April 1981, all near Transects T3 and T4. A small seine-net with a 1 cm stretched mesh length and a 100 m long gill-net with a 5 cm stretched mesh length were used. All fish were weighed and measured and the gonads and gut contents examined. A more detailed analysis of the fish in the Palmiet, Kleinmond and Bot Estuaries is being undertaken by B. Bennett of the Zoology Department, University of Cape Town.

Seaweed and debris imported and exported through the mouth were caught in a large net with a stretched mesh length of 5 cm, strung right across the mouth. Two subsidiary nets, each 0,5 × 0,5 m, with a stretched mesh length of 1 cm, collected the smaller pieces of detritus. This material was all dried and weighed.

Results

Description

The catchment of the Palmiet River lies in the mountainous Kogelberg, Paarde, Groenland and Hottentots Holland Ranges, covering an area of 539 km^2. The Palmiet itself, about 65 – 70 km long, rises in the Kogelberg Range and is joined by two major tributaries and several minor feeder-streams, some seasonal, before reaching the estuary. The river bed is very steep, resulting in a strong flow. The coastal plain is extremely narrow so that the river changes from mountain stream to estuary with no intervening stretch typical of a lower river; such systems have been classified by Noble & Hemens (1978) as 'South Cape acid rivers'.

The mountains are composed almost entirely of sandstone of the Table Mountain Series (TMS), consisting largely of quartzite and feldspar with some tillite derived from Bokkeveld shale in the valleys. The hardness of these rocks results in low levels of erosion and, consequently, in relatively low nutrient and sediment loads in the water.

The prevailing winds are north-westerly in winter and south-easterly in summer, resulting in rainfall of 700 – 1 200 mm $year^{-1}$ in the upper catchment, mostly in winter. Owing to high winds, evaporation may reach 1 250 to 1 500 mm $year^{-1}$, mostly in summer, but nonetheless the mean annual run-off, measured at the weir immediately above the head of the estuary, is 310 × 10^6 m^3 $year^{-1}$. The estuary, lying in the rain shadow of the mountains, has a mean annual rainfall of 700 – 800 mm $year^{-1}$.

The river and its tributaries flow for the most part through undisturbed mountain fynbos (macchia), with the result that the water is 'black' and darkly stained with humic substances (King, Day & van der Zel 1979).

Estuarine conditions prevail as far inland as the road bridge (Figure 1) so that the estuary stretches 1,67 km from the bridge to the mouth. Its maximal width is 282 m; it covers an area of about 230 000 m^2 and at high tide has a volume of approximately 360 000 m^3.

The position of the mouth on the western bank is fixed by a rocky promontory and the mouth is no more than 30 m wide at high tide owing to an extensive, mobile sand spit to the east. This spit is built up by the prevailing westerly longshore currents in the sea together with the prevailing SSW to WSW swells and high-energy waves (Harris 1978). This type of estuary is classified by Heydorn & Tinley (1980) as 'type A: single spit with rock on the opposite bank'. The profile of the mouth is uneven and very variable, changing virtually from hour to hour owing to the very strong tidal currents. For the same reason the sediment, which is of recent marine origin, is very coarse and unstable. On the outgoing tide the depth of water at the mouth varies from a few centimetres in late summer to almost 2 m in winter, when it may carve a shifting vertical cliff a metre high in the unstable, sandy, east bank. The mouth is usually open but may close briefly in January or February, approximately once every two years. The upper limit of estuarine conditions is determined by a series of rocky sills (Figure 1) which reaches the surface in places. At this point the estuary is 50 m wide, gently increasing to a width of 150 m about half-way towards the mouth. This entire stretch lies within steep rocky banks which gradually become lower and less steep downstream. Near the head of the estuary the channel reaches a depth of 4 m close to the east bank but half-way down it moves across towards the west bank, leaving a wide sand-flat, which is exposed at low tide, on the east bank (Figure 2). This sand-flat has an area of 110 000 m^2 and is densely populated by the sand-prawn *Callianassa kraussi*. The channel becomes less pronounced towards the mouth, where sand from the spit is brought into the estuary on the high tide and is deposited as a bar immediately inside the mouth.

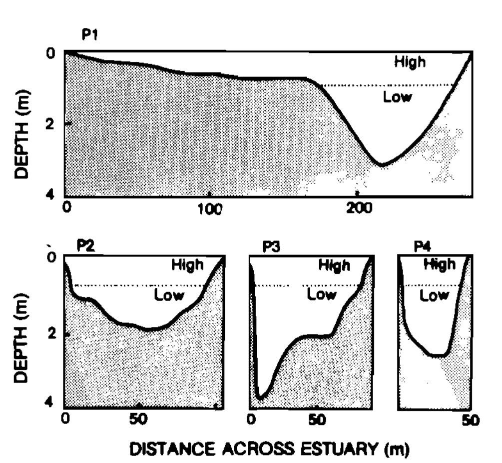

Figure 2 Profiles P1 – P4 taken at various points along the Palmiet River estuary (see Figure 1). The western bank of the estuary is on the right of each profile.

Water flow

The pattern of mean monthly flow in the Palmiet River for the period 1967 to 1980 is summarized in Figure 3, which shows the strongly seasonal nature of flow, the peak occurring in July to August and minimal flow in the summer months. However, flow is usually maintained throughout the year, which may be an important feature contributing towards keeping the

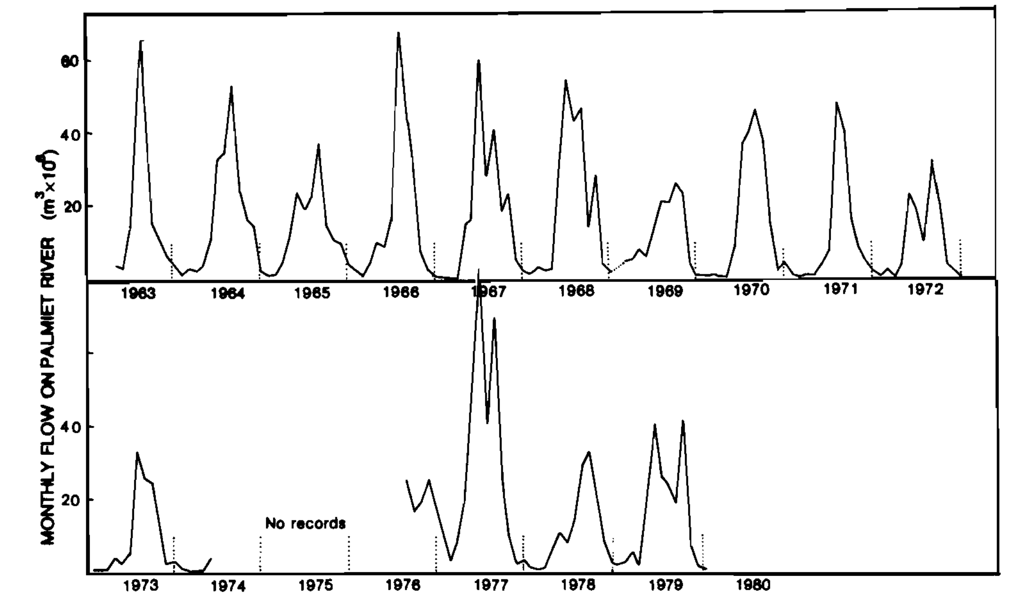

Figure 3 Mean monthly flow of water at the weir on the Palmiet River. Data supplied by Department of Water Affairs, Forestry and Environmental Conservation.

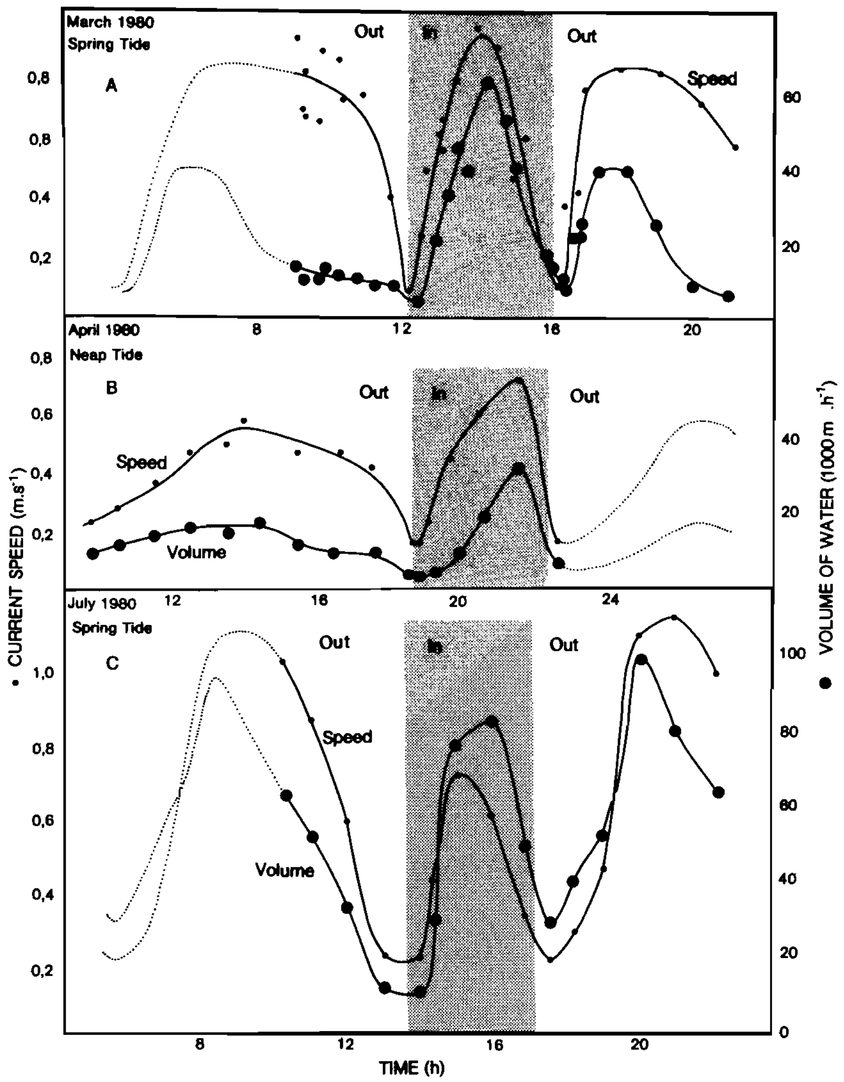

Figure 4 The pattern of current speed and volume of flow at the mouth over three contrasting tidal cycles. Shading indicates periods of inflow. Dotted lines are extrapolations and are inserted only for comparison; they were not used in calculating flow over the tidal cycle.

mouth open. Considerable fluctuation occurs from year to year, 1969 being the lowest in the last 17 years, but even in this year the mouth closed for only a brief period.

Figure 4 illustrates the pattern of flow at the estuary mouth over three complete but contrasting tidal cycles. During a spring-tide in March 1980, river flow at the weir was minimal, resulting in an estimated flow into the estuary of 9 802 m^3 over the 12,3 h tidal cycle; the tide accounted for an input of 136 794 m^3 from the sea, while the total outflow through the mouth was 143 775 m^3. Maximal speed of flow occurred during the flood-tide, reaching 0,96 m s^{-1} at mid-tide, while both speed and volume per unit time were lower during the outflowing ebb-tide (Figure 4A). This pattern is partly due to the constricted mouth configuration, coupled with the fact that the bottom of the mouth is about 1 m above the level of low water spring-tide. This means the tidal range immediately inside the estuary mouth is only about 87 cm and that the estuary only begins to fill when the tide rises above the mid-tide level. Hence the estuary fills over a period of only 3,5 h, while the ebb-tide lasts 9 h, low tide in the estuary lagging 3 h behind that in the sea. As a result currents are greatest during the flood-tide. This has important consequences in terms of sediment transport.

During the neap-tide observations in April 1980 the pattern was similar although flow rates and volumes were depressed (Figure 4B). By this stage river flow at the weir had increased since the seasonal winter rains had begun and accounted for an input of 65 605 m^3 of fresh water per tidal cycle. Tidal flow on the other hand contributed only 62 669 m^3 to the inflow while the total outflow was 119 711 m^3.

Flow in July 1980, during spring-tides, was strikingly different (Figure 4C), for the river was in full spate, contributing 290 088 m^3 per tidal cycle to the estuary while tidal input was 188 271 m^3 and total outflow 464 772 m^3. Not surprisingly the current speed was highest during outflow, reaching 1,14 m s^{-1}, while during inflow a maximum of only 0,68 m s^{-1} was recorded (Figure 4C). Even these conditions must be taken as moderate, for the flow rate of the river was only about half of that during peak floods. It is worth contrasting conditions during the low summer river flow with those in winter when the river runs strongly: in the summer, tidal flow predominates and current speeds are greatest on the rising tide, while in winter the reverse is true with river flow being more important and speeds highest during the ebb.

Sediments

The sediment is unusually coarse for an estuary, although this is not surprising in view of the scouring action of floods. Sediments are coarsest at the head of the estuary, comprising 65% gravel and 34% sand, but the gravel component declines towards the mouth, where sand makes up almost 99% of the sediment (Figure 5). The mud fraction (<64 μm) is insignificant throughout the estuary, forming less than 3% of the sediment even in the lagoon where water movement is lowest. Organic content is always low in coarse sediments (see Branch & Grindley 1979) and the Palmiet is no exception, organic matter never exceeding 0,6% (Figure 5). Near the head of the estuary the sediments are derived mainly from quartzitic and feldspar sandstone mixed with tillite from Bokkeveld shale, all of riverine origin, but in the lagoon and at the mouth finer marine sands predominate. Throughout the estuary the levels of trace elements are extremely low, concentrations of Zn, Cu and Ni being generally less than 2 ppm and most often less than 1 ppm (J. Willis, pers. comm.).

The dense populations of sand-prawn, *Callianassa kraussi*, that occupy most of the estuary have a dramatic influence on the sediments and on the turnover of organic material. The burrows of *Callianassa* are lined by a layer, about 2 – 3 mm thick, of remarkably fine, black sediment. In strong contrast with the surrounding sediment, this layer consists of very fine

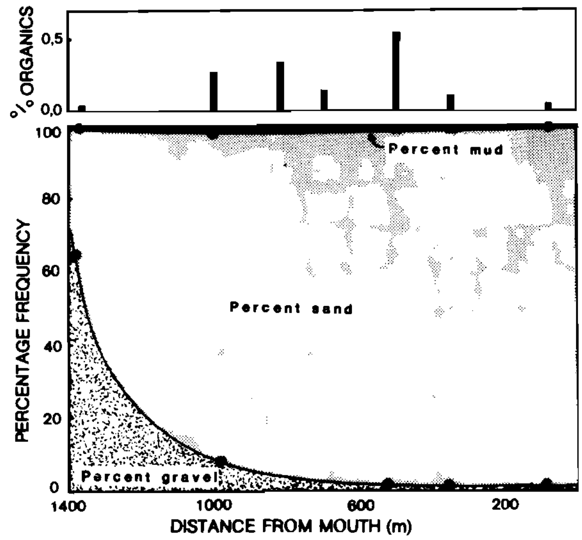

Figure 5 The composition of the sediment and the percentage organic material in the sediment, down the length of the estuary. (Size composition from data supplied by Dr J. Willis.)

particles, 98,91% being <90 μm and having a high organic content (4 to 10%). The ability of *Callianassa* to concentrate fine particles from the water column must thus be formidable. Furthermore each *Callianassa* hole yields an average of 1,50 ± S.D. 0,37 g dry mass of faeces per tidal cycle. These faeces have a similarly fine composition and a 35% organic content, representing a 165-fold concentration over that of the surrounding sediment.

The import or export of sediment into the estuary is clearly of central interest in this study since the rate at which sediment is banked up at the mouth or swept into the estuary will determine the vulnerability of its mouth to closure. On two occasions total particulate matter (TPM) and particulate organic matter (POM) were monitored at the weir and at the mouth of the estuary over complete tidal cycles (Figure 6). On both occasions the TPM levels were much higher on the flood than on the ebb-tides, reflecting the higher levels in seawater (up to 38 mg ℓ^{-1}) as compared with river water (usually 4 mg ℓ^{-1}). As a result there was a net import of TPM which amounted to 867 kg per tidal cycle during the April neap-tide and 1 873 kg during the July spring-tide.

This measure of TPM includes inorganic sediment particles in transport, and an organic fraction which amounts to about 14% of the imported material. Furthermore it takes into account only the suspended particles. In terms of sediment transport the scouring action of currents close to the substratum may be more important, briefly suspending and shifting larger particles. Samples of water taken close to the bottom in the mouth confirm this (Figure 7) and also show that a huge sediment load can be carried in this manner. During the ebb-tide monitored in July 1980, levels of 18 g ℓ^{-1} were recorded, and there was a striking correlation between sediment load and speed of water movement (Figure 7). For this particular sampling period it is clear that there can be an enormous export of sediment during the winter floods, although we cannot calculate in absolute terms how much this may be since the sand particles are not uniformly suspended throughout the water column. Equally important is the fact that water speeds of less than about 0,75 m s^{-1} result in little movement of sand, so that it can be anticipated that during the summer, when river flow is minimal, the stronger flowing incoming tide (Figure 4A) will import more sand than is exported.

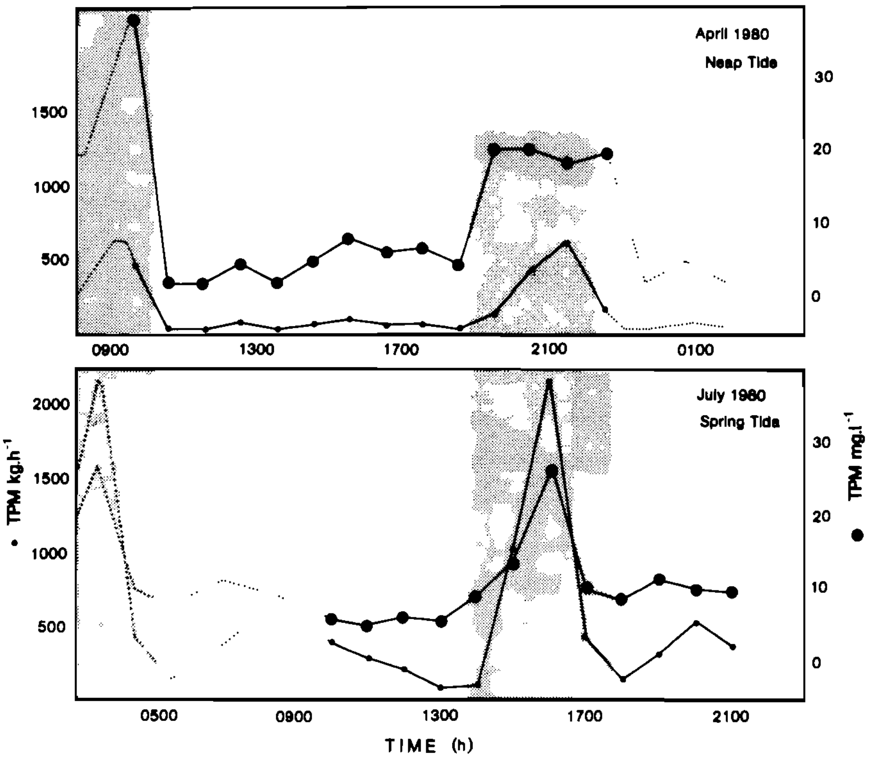

Figure 6 Concentration of total particulate matter in the water at the mouth (TPM mg ℓ^{-1}) and rate of import or export (kg h^{-1}) over two tidal cycles in April and in July. Shading indicates the period of inflow; unshaded areas show outflow. Dotted lines are extrapolations inserted only for comparison but not used in calculating import or export.

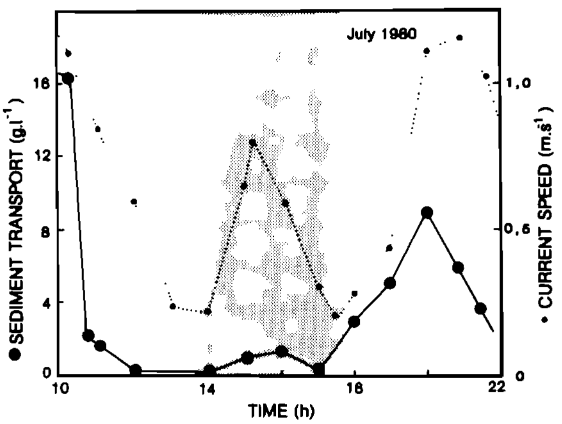

Figure 7 The amount of sand (g ℓ^{-1}) transported by tidal action. Samples were taken 10 cm from the bottom and show mass transport over a complete tidal cycle. Current speeds (dotted line) are also shown; shading shows the period of inflow.

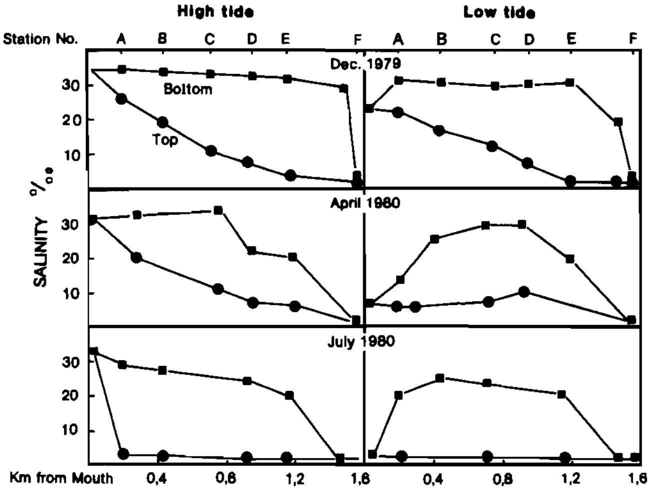

Figure 8 Salinity gradient down the length of the estuary. Samples were taken at the surface and 10 cm from the bottom at high and low tides. The differences between top and bottom samples reflect the stratification of the estuary.

Physico-chemistry of the water

Salinity declines from the mouth to the head of the estuary (Figure 8). The estuary is unusually well stratified. In summer (December) the bottom water of the estuary was between 31 and 35‰ (except at Site F) while the top layer increased from 0‰ at the head to 35‰ at the mouth. By April the river flow was greater and the difference between high and low tide salinities more obvious, but stratification remained a dominant feature. Even in July when the river was running strongly, and the upper layers of the entire estuary were fresh, the bottom remained saline, being between 20‰ and 35‰ except at the head and in the mouth. The result is that salinities remain remarkably constant throughout most of the estuary, fresh water forming a blanket over the saline water. Only at the mouth does salinity fluctuate widely over each tidal cycle, being 35‰ during flood-tides when seawater enters, but dropping to between 25‰ (in summer) and 0‰ (in winter) during the ebb-tide, when the upper layers of less saline water flow out (Figure 8). The halocline is clearly defined, and made more obvious by the fact that the fresh river water, almost the colour of black tea, forms a distinctive layer over the clear seawater. The penetration of seawater up the estuary is halted abruptly at the series of rocky sills that rises from the bed to the surface just below the bridge, so that all samples taken at Site F were entirely fresh (Figure 8) even though the river is relatively deep (up to 5 m) at this point.

The pattern of water temperatures is given in Figure 9. In summer the river was warmer than the sea and consequently

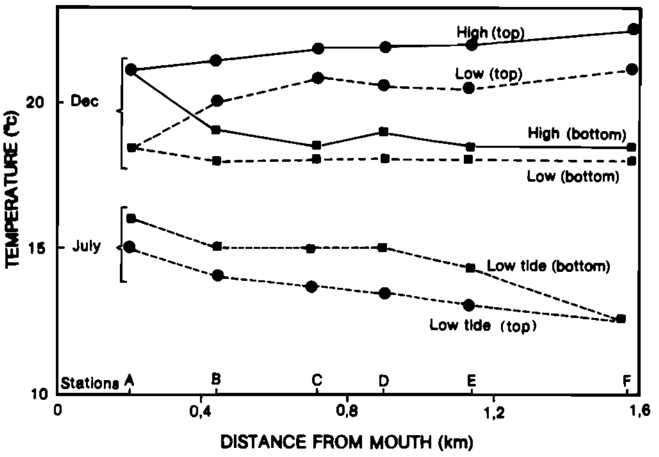

Figure 9 Water temperature gradients from the mouth to the head of the estuary, measured at the surface and 10 cm from the bottom, for high and low tides in December and for a low tide in July.

the surface waters were warmer than the bottom; but in winter the reverse condition existed, the sea being warmer than the river and the bottom layers warmer than the surface. Here again the stratification between top and bottom is clearly defined and results in the bottom layers having a comparatively constant temperature (Figure 9).

Dissolved oxygen levels were high at all surface stations throughout the year, being between 85 and 104% saturated. Bottom samples were consistently lower, ranging from 58 to 90% saturated, as might be expected from the permanent stratification.

Values for pH were interesting, the river water being acid (pH 4,0 – 4,5) and very poorly buffered while the pH rose rapidly in the estuary owing to the buffering action of the salts in seawater. From the head to the mouth pH rose from 6,5 to 7,0 in bottom waters and from 5,0 to 7,0 in surface waters, which were always slightly more acid than the underlying, more saline, water.

Table 1 summarizes the nutrient levels in the estuary in December 1979. Nitrates ranged from 3,09 to 35,71 μg atoms N ℓ^{-1}, being clearly greater in the surface waters than at the bottom in all instances and, in general, showing an increase from the mouth to the head, suggesting a riverine origin for most of the nitrates. Ammonia varied from 0,95 to 5,64 μg atoms N ℓ^{-1}, bottom samples without exception being markedly higher than surface samples. This presumably reflects the more reducing conditions on the bottom. Reactive phosphate was low, ranging from 0,68 to 1,85 μg atoms P ℓ^{-1}; once again bottom samples were higher than those at the surface, a condition that is common in estuaries since the sediments trap organic material which later releases phosphates. In this instance, however, the organic content of the sediments is so low that other sources of phosphate must be sought; it probably originates from the decaying detritus that accumulates in the basin of the channel.

Levels of $PO_4 - P$, $NO_3 - N$ and $NH_3 - N$ fall within the range given by Day (1981) for the Berg and Breede River estuaries. However it is interesting that values for combined $NO_2 - N$ and $NO_3 - N$ in the river some kilometres above the estuary are very much higher at times, ranging from <2 to 300 μg atoms N ℓ^{-1}. At the same time, levels of $PO_4 - P$ do not appear to exceed 2 μg atoms P ℓ^{-1} anywhere along the river (data pers. comm. from R. de Decker and from the Directorate of Water Affairs). This suggests that most nitrogen from agricultural fertilizers is rapidly removed from the river in its course to the sea, presumably by volatilization. On the other hand, either levels of phosphorus are low in the fertilizers applied or are complexed extremely rapidly by the humic substances in the highly acid, black waters of the river.

Levels of $SiO_4 - Si$ (0,84 – 26,25 μg atoms Si ℓ^{-1}) fall within the normal range for estuaries. In most cases the surface water was richer in silicates than was the bottom water, although Station F had the lowest values. Figures for water from higher up the river average about 35 μg atoms Si ℓ^{-1}, suggesting that much of the silicate in the estuarine water is imported from the river.

Primary producers

The Palmiet estuary is unusual in that there are practically no attached macrophytes in the system. *Cladophora* sp. was present for a short period of the year, first appearing in December and reaching a peak in April, after which it died away completely; none was recorded between May and November. The maximal biomass, recorded in April, is shown in Figure 10. *Cladophora* was most abundant in the deeper parts of the channel where salinities were high and water movement slow. Since this weed is so strongly seasonal, its annual production is conservatively estimated as being equal to the maximal standing stock, which is about 30 360 kg for the entire estuary.

Although there is a small salt marsh near the jetty (Figure 1), the steep banks and rapid water flow preclude formation of salt marshes in the rest of the system. A surprising variety of plant species occurs in the salt marsh (see Appendix 1), but their contribution to the total flow of energy in the system is negligible.

The standing stock of microflora, such as diatoms, in the sediment, was determined by measuring chlorophyll levels (Figure 11A). Chlorophyll levels were low in the turbulent area at the mouth and at the head of the estuary, where the sediment

Table 1 Nutrient levels in Palmiet estuary in December 1979

	Nitrate μg atoms N ℓ^{-1}				Ammonia μg atoms N ℓ^{-1}				Reactive phosphate μg atoms P ℓ^{-1}				Silicates μg atoms Si ℓ^{-1}			
	High tide		Low tide		High tide		Low tide		High tide		Low tide		High tide		Low tide	
Station	Top	Bottom	Top	Bottom	Top	Bottom	Top	Bottom	Top	Bottom	Top	Bottom	Top	Bottom	Top	Bottom
A	6,23		7,00		0,95		1,67		0,68		0,80		14,71		20,00	
B	6,95	3,14	7,76	4,97	3,50	3,25	1,17	2,15	0,76	1,10	0,72	1,27	18,24	8,24	13,75	10,00
C	7,38	3,65	11,43	6,28	1,23	2,55	1,17	2,43	0,34	1,35	0,59	1,31	13,53	8,82	11,88	2,50
E	10,10	4,02	35,71	4,08	1,77	–	1,13	5,64	0,76	–	0,97	1,35	26,25	–	15,63	12,50
F	12,33	3,09	7,29	3,09	1,93	3,87	1,59	2,88	0,29	1,23	0,58	1,85	1,39	8,82	0,84	3,57

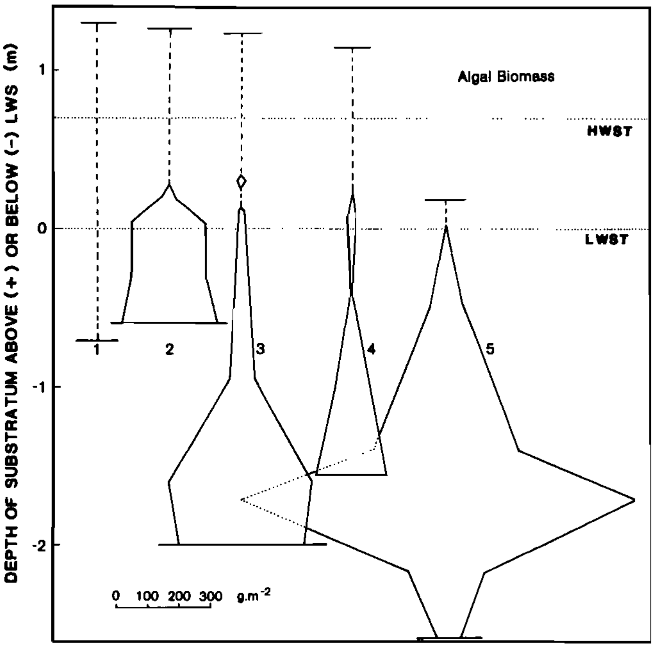

Figure 10 Standing stock (g dry mass m^{-2}) of algal biomass (mainly *Cladophora*) on the five transects in April, when algal biomass was at its greatest. Horizontal bars indicate limits of transects; dashed lines indicate absence of algae.

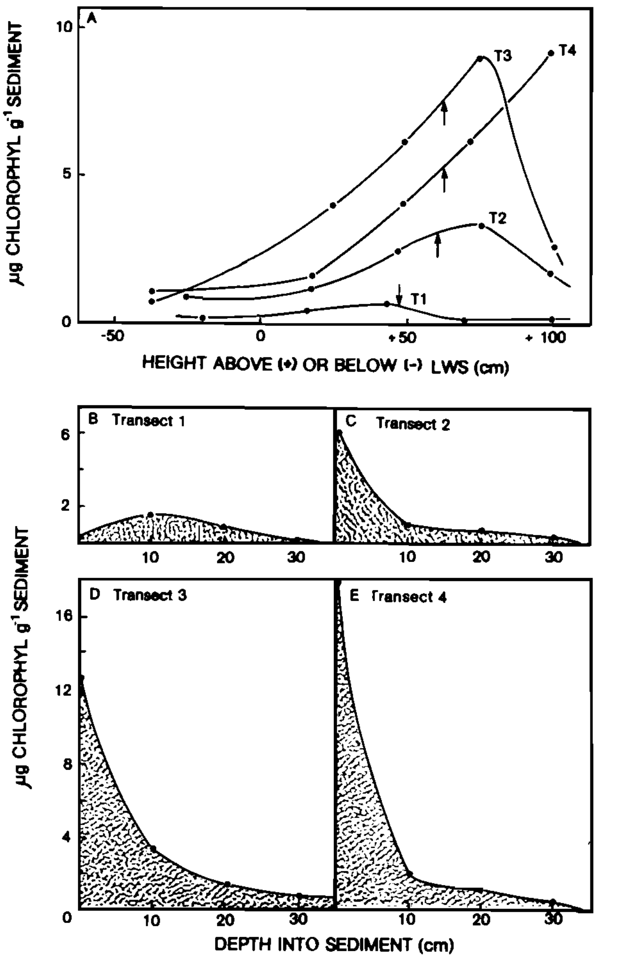

Figure 11 (A) Chlorophyll levels in the top 5 cm of sediment (µg g^{-1} sediment) on Transects T1 – T4, in December 1979. Each data point is the mean of three samples. (B) – (E) Chlorophyll levels in cores sunk 30 cm into the sediment. Points at which the samples were taken are shown by arrows in (A).

is coarse. Maximal levels were found on the sandbanks just above the mid-tide level, decreasing down the shore and being very low subtidally. Cores were taken to a depth of 30 cm and showed that chlorophyll declined with depth into the substratum, as expected (Figures 11B – E), although some chlorophyll was found down to 30 cm, probably due to living diatoms carried down by the activities of *Callianassa*. Rather cautiously chlorophyll values were converted to a total standing stock of 7 000 kg (dry mass) of microflora in the estuary as a whole. A conversion from chlorophyll to production of carbon has been obtained for Langebaan by P. Fielding and K. Damstra (pers. comm.): Production (mg C m^{-2} h^{-1}) = 3,17 + 5,625 (chlorophyll mg m^{-2}). This can be used to estimate the production of diatoms in the Palmiet estuary as about 350 kg (dry mass) per year for the whole estuary.

Table 3 summarizes the chlorophyll levels in the water column. Although not exceptional, these values are higher than might be expected in an estuary with such a fast flow. Values range from 2,12 to 8,40 µg chlorophyll ℓ^{-1} in December and from 1,48 to 4,82 µg chlorophyll ℓ^{-1} in April. A rough estimate of the standing stock for the whole estuary is 232 kg (dry mass). Insignificant though this may appear, phytoplankton may turn over once every two days if nutrients are not limiting.

Import and export

Figure 12 shows the standing stock of detritus in the estuary. Two features are of interest. Firstly, detritus tends to accumulate in the deeper, calmer parts of the channel, below the halocline, and particularly massive amounts (in excess of 5 000 g m^{-2}) are present in the deeper parts of the lagoon on Transect 3 (Figure 12). Secondly, on all but the sheerest banks

Table 2 Levels of total particulate matter (TPM) and particulate organic matter (POM) in the Palmiet River estuary

	TPM mg ℓ^{-1}								POM mg ℓ^{-1}							
	December				April				December				April			
	High tide		Low tide		High tide		Low tide		High tide		Low tide		High tide		Low tide	
Station	Top	Bottom	Top	Bottom	Top	Bottom	Top	Bottom	Top	Bottom	Top	Bottom	Top	Bottom	Top	Bottom
A	7,20		4,50		6,63		1,78		2,70		1,48		2,52		1,74	
C	10,58	–	9,08	–	8,14	–	1,40	3,48	4,20	–	3,40	–	2,13	–	1,55	1,66
D	–	–	–	–	2,11	5,56	5,44	24,98	–	–	–	–	1,63	2,22	2,31	7,22
E/F	5,02	3,48	5,40	–	2,09	0,84	1,18	2,18	2,44	1,76	2,76	–	2,84	0,78	1,99	2,20
Weir	4,88				1,96				2,52				0,78			

Table 3 Chlorophyll levels in the water column of the Palmiet River estuary

	Chlorophyll $\mu g\ \ell^{-1}$							
	December				April			
	High tide		Low tide		High tide		Low tide	
Station	Top	Bottom	Top	Bottom	Top	Bottom	Top	Bottom
A	2,126		3,41		2,16		4,21	
C	3,51	–	5,04	–	2,36	3,35	4,82	3,26
D	–	–	–	–	2,97	3,61	2,19	2,65
E/F	7,76	–	6,05	–	1,52	2,47	1,48	2,24
Weir	8,40				1,48			

there is a deposit of detritus, well above the high tide mark, left behind after the annual floods in winter. This flood-level detritus is almost entirely riverine in origin and consists largely of blades of the palmiet reed, *Prionum serratum*, which lines the river and forms dense beds around the weir. The detritus on the bed of the estuary comes from two sources, that in the narrow upper half of the estuary being mainly *Prionum* from the river, while kelp (*Ecklonia maxima*) washed in through the mouth forms a dense mat in the channel of the lagoon. The kelp seems more important quantitatively, and it also clearly decomposes more readily than does *Prionum*.

Attempts were made to monitor the gains and losses of organic matter over two contrasting tidal cycles. Kelp was imported on both occasions, 188 g (dry mass) during the April neap-tide, and 3 740 g during the spring-tide cycle in July. If these figures are representative of neap and spring-tides, this import could amount to an annual input of 1 400 kg (roughly estimated by multiplying the average tidal input by 712 tides per year). In relation to the measured standing stock of 270 kg (Table 4), this means that kelp must decay and be dispersed as particles within about 68 days of its introduction into the estuary (estimated by dividing the mean standing stock by the annual input).

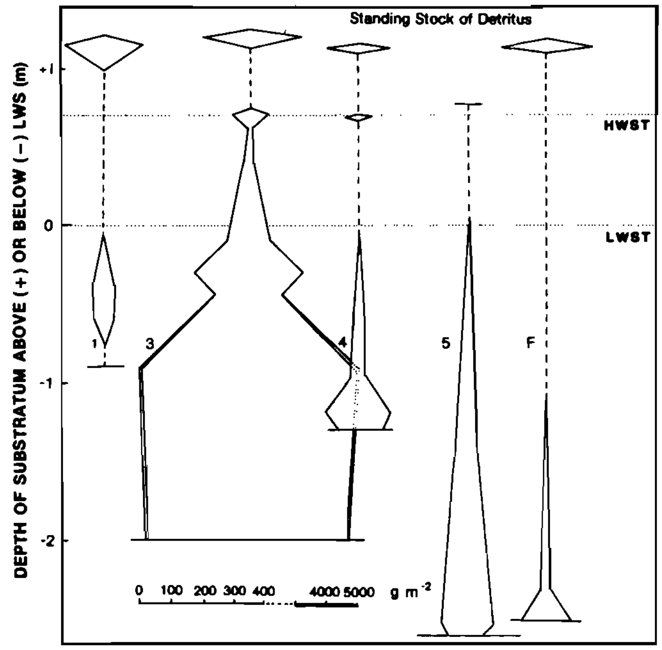

Figure 12 Standing stock (g ash-free dry mass m^{-2}) of detritus on Transects 1, 3, 4 & 5 and at Station F. The double line on Transect 3 refers to the expanded scale relating to stations where standing stock exceeded 4 000 g m^{-2}. Dashed lines indicate an absence of detritus and horizontal bars the limits of the transects.

No quantitative figures are available for the import of *Prionum* and although large quantities are introduced it would appear that the material does not decay easily and is probably not readily used as food.

Except at times of flood, little of the *Cladophora* is exported; between 18 and 37 g (dry mass) were recorded passing out of the mouth on the two tidal cycles that were monitored.

The particulate organic matter is the most interesting component in terms of import and export. Over two tidal cycles POM occurred at higher levels in the incoming than in the outgoing water and, because of the different rates of water transport during the ebb and flood, the rate at which POM

Table 4 Standing stocks and estimated rates of turnover of various sources of organic material in the Palmiet River estuary. Mean standing stocks are derived from actual measurements whereas total standing stocks and turnover rates have been estimated

Source	Mean standing stock	Total standing stock for estuary kg (dry mass)	Estimated turnover per year kg (dry mass)
Kelp[a]	1,17 g m^{-2}	270	1 400
Cladophora[a]	132 g m^{-2} [f]	30 360	30 360
Detritus[b]	390 g m^{-2}	89 764	?
Callianassa faeces[a]	84 g m^{-2}	19 347	>235 000
Particulate organic matter[c]	2,40 g m^{-3}	715,6	140 000
Phytoplankton[c]	2,7 – 5,1 mg Chl m^{-3}	232	? 8 000
Zooplankton[c]	16 mg m^{-3}	4,78	?
Benthic diatoms[d]	0,305 g Chl m^{-2}	7 000	348
Organics in sediments[d]	899 g m^{-2}	206 963	?
Callianassa[e]	9,0 g m^{-2}	2 070	4 140[g]
Invertebrates other than *Callianassa*[d]	5,7 g m^{-2}	1 329	4 784[h]

[a] = measured from surface collections; [b] = measured from surface collection and top 10 cm of sediment; [c] = measured from water samples; [d] = measured in top 10 cm of sediment; [e] = estimated from number of holes and average mass; [f] = maximum for the year: taken as being equal to production; [g] = assuming a production : biomass ratio of 2,0; [h] = assuming a mean P:B ratio of 3,6.

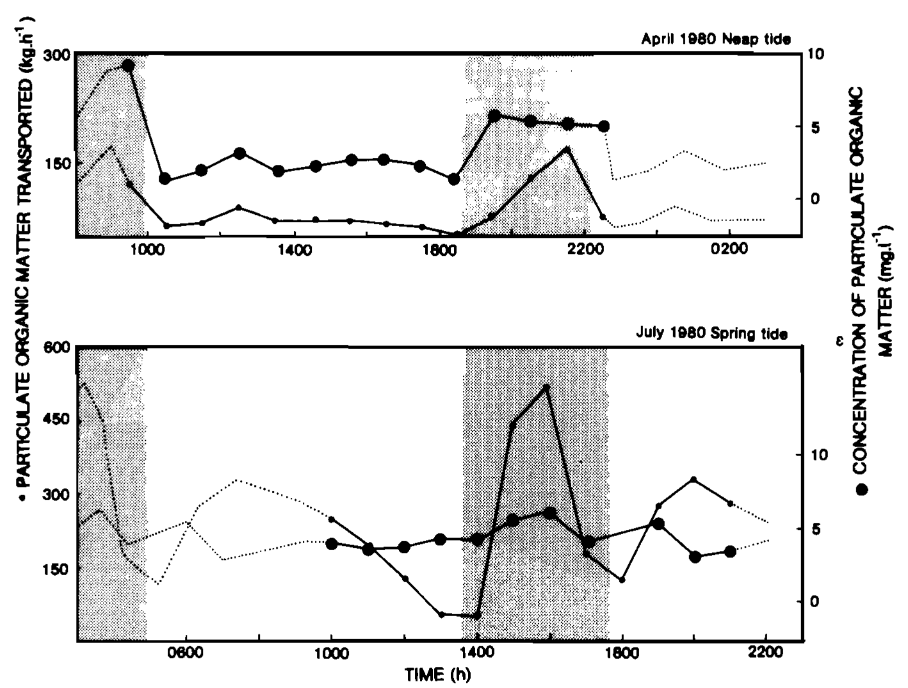

Figure 13 The concentration of particulate organic matter (mg ℓ^{-1}) and its rate of transport (kg h $^{-1}$) through the mouth over the tidal cycles. Shading shows the period of inflow into the estuary.

was introduced at the mouth far exceeded its rate of loss (Figure 13). During the April neap-tide, 337 kg of POM were imported into the estuary from the sea and 51 kg from the river, while only 262 kg were exported with the ebbing tide. Thus in a single tide there was a net import of 126 kg of POM. During the July spring-tide the figures were even more dramatic, 1 092 kg coming in from the sea and 883 kg from the river, while losses from the mouth accounted for 1 707 kg, resulting in a net import of 268 kg. If these figures are representative, there may be a net annual import of POM of over 140 000 kg.

Chlorophyll levels in the water were measured over the same two tidal cycles, and fluctuated between 1,5 and 3,8 μg ℓ^{-1}; even being generous in converting this to a biomass of organic material, phytoplankton would only account for 0,3% of the POM.

Fauna

Invertebrates

Five transects were laid across the estuary at various points (Figure 1) but only three of these are described here since Transects 2 and 4 were intermediate in nature between those on either side. Transect 1, across the mouth (Figure 14), contained three sets of organisms. Firstly, batches of kelp deposited above the high tide mark by extremely high spring-tides supported a wrack fauna including several beetles (*Pachyphaleria capensis* and a staphylinid being the most common), larvae of the kelp fly *Coelopea africana*, and the amphipod *Talorchestia quadrispinosa*. Secondly, two isopods, *Excirolana natalensis* and *Euridice longicornis*, were present on the steeply sloping bank. Finally, with the exception of a few *Callianassa*, no animals were found in the unstable sediment at the mouth.

Transect 3 was typical of much of the lagoon area, a broad inter-tidal sandbank ending at a well-defined channel (Figure 15). A restricted wrack fauna still existed at the highest levels, but the sandbank itself supported remarkably dense populations of a small number of species. *Callianassa* holes reached a density of 135 m^{-2}. The importance of *Callianassa* in modifying the sediment and in producing highly organic faeces

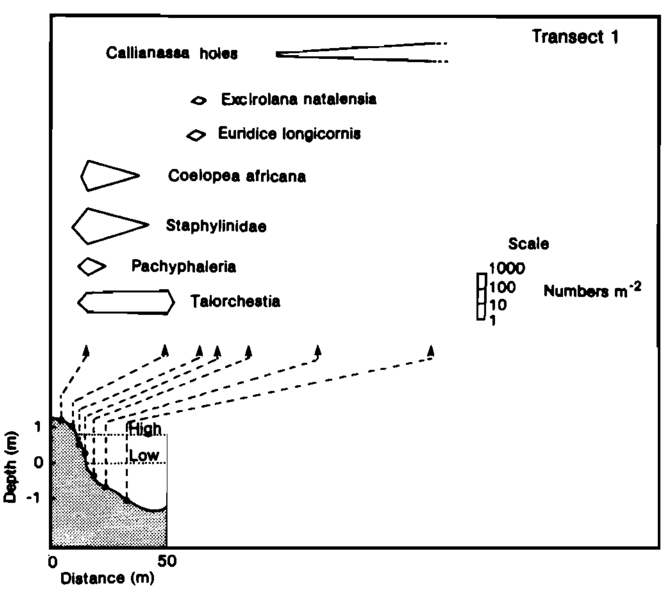

Figure 14 Distribution and abundance of invetebrates on Transect 1. Densities are accurately plotted on a logarithmic scale.

has been mentioned above. The polychaete *Ceratonereis keiskamma* was common at lower levels and extending into the channel. Small *Hydrobia* snails, common over most of the flats, reached particularly high numbers in the channel, where they feed on the decaying kelp. The amphipod *Grandidierella bonnieroides* epitomized the high densities that are reached by most of the species, achieving maximal numbers of over 100 000 m^{-2}. The polychaete *Prionospio* cf. *tenuis* was common in local patches in the channel.

Transect 4 was very similar to Transect 3 except that the uppermost stations fell in the small salt-marsh; a large number of halophytes (see Appendix 1) and two species of animals (*Orchestia rectipalma* and *Assiminea globulus*) were confined to this salt-marsh.

Transect 5 (Figure 16) ran across the narrow upper reaches between steep rocky cliffs, with a sloping bed that dropped

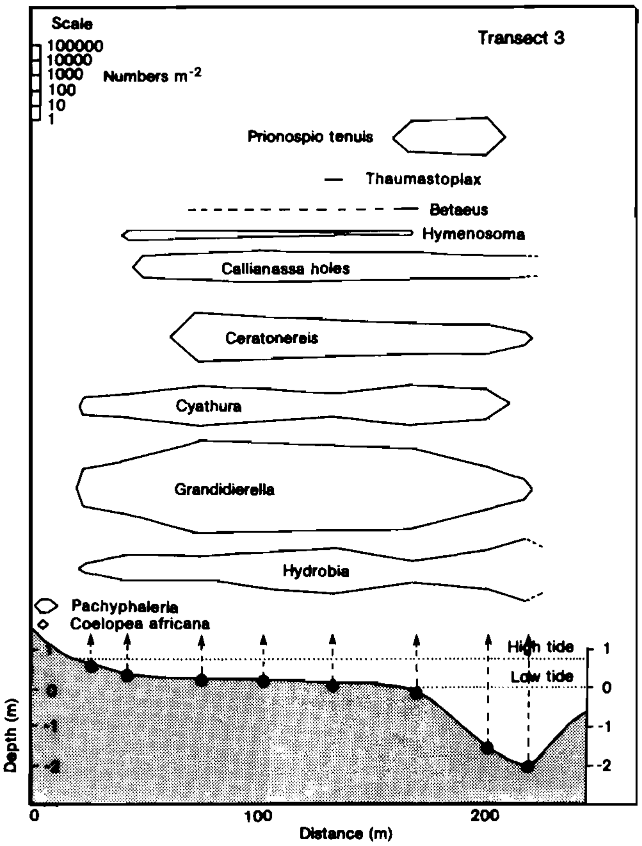

Figure 15 Distribution and abundance of invertebrates on Transect 3. Densities are accurately plotted on a logarithmic scale.

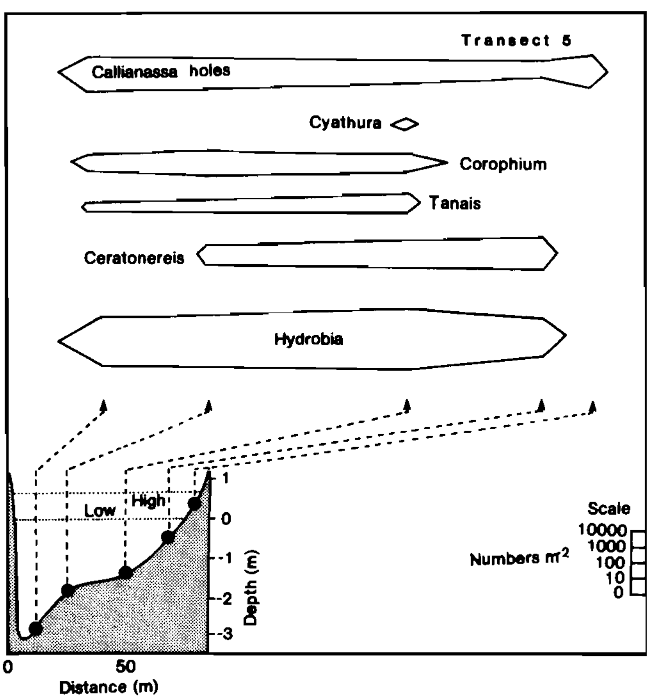

Figure 16 Distribution and abundance of invertebrates on Transect 5. Densities are accurately plotted on a logarithmic scale.

to a depth of 3,2 m. Intertidal banks were so steep that they supported no life. Despite the fact that the sediment is much coarser, the subtidal fauna remained remarkably similar to that of Transect 3, with numerous *Callianassa*, *Hydrobia* and *Ceratonereis*. This is probably due to the salt wedge extending up the estuary. *Grandidierella* was present but not common, being replaced by the tube-dwelling amphipod *Corophium triaenonyx. Tanais philataerus* also occurred in fair numbers. This community extended right to the rocky sills below the bridge.

Much of the western bank is lined with rock, as are both banks in the upper third of the estuary, where the bed is also strewn with boulders. Rocky substrata make up only about 5% of the total area, but there were several species which occur only on rock. A small group of euryhaline species, including *Choromytilus meridionalis, Natica tecta, Oxystele variegata* and *O. sinensis*, occurred inside the mouth, even penetrating the estuary as far as the jetty: a tribute to the permanence of the stratification, for this last species is strictly stenohaline and is usually excluded from estuaries. Throughout the estuary practically every stone supported groups of isopods, *Exosphaeroma hylocoetes* in the lower two thirds of the estuary and *Pseudosphaeroma barnardi* higher up. *Melita zeylanica* also populated rocks and debris in the lower parts of the estuary.

The biomass of invertebrates in the top 10 cm of sediment (Figure 17) is highest at the mid-tide level on the sand-flats, reaching surprisingly high values of up to 35 g m^{-2}; most of this biomass is due to the high numbers of *Grandidierella*. Subtidally *Hydrobia* contributes substantially to the high values recorded in the channel, where the snails assemble densely to feed on the rotting kelp. The mean biomass of invertebrates was 5,7 g m^{-2}, to which an estimated 9 g m^{-2} of *Callianassa* can be added (Table 4).

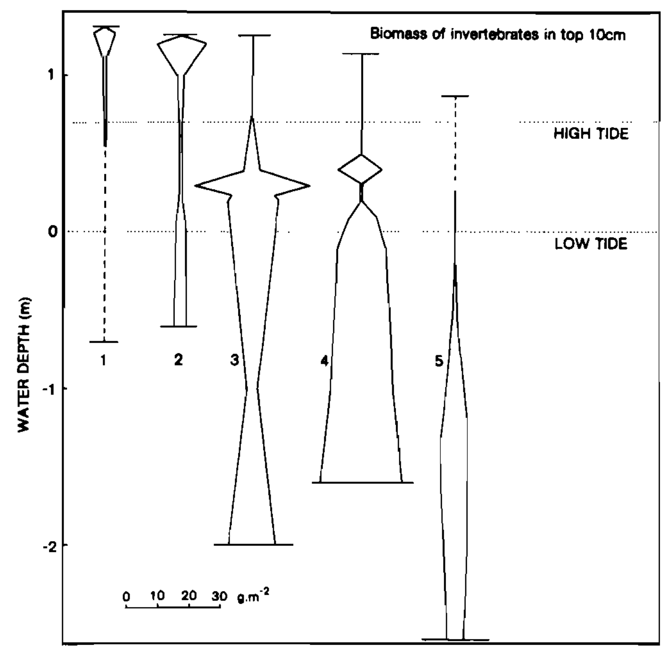

Figure 17 Biomass of invertebrates (g dry mass m^{-2}) in the op 10 cm of the sediments on Transects 1 – 5. Horizontal lines indicate the limits of each transect, and dashed lines an absence of invertebrates.

There are thus two striking features about the invertebrate fauna: one is the paucity of species, and the other is the remarkably high densities achieved by many of those species which do occur in this estuary.

Fish

Nineteen species of fish (Appendix 2) have been collected in the estuary in a series of 29 samples spread throughout the year. Generally the number of fish caught was rather small and very variable; for instance 7 870 *Hepsetia breviceps* were caught in one haul while in almost all other hauls over the same area it was absent. Monthly sampling of fish has been completed and will be reported in more detail by B.A. Bennett of the Zoology Department, University of Cape Town.

Of the fish, *Caffrogobius multifasciatus, Gilchristella aestuarius* and *Psammogobius knysnaensis* are all confined to shallow, quiet waters, particularly estuaries, where they breed. *Hepsetia breviceps* breeds both in the sea and in estuaries. Individuals of all of these species had reached adult size and were sexually mature. Their diets closely reflected their feeding habits and the abundance of benthic invertebrates in the system, *Hepsetia* and *Psammogobius* feeding mainly on bottom-dwelling amphipods (in particular *Grandidierella*) and tanaids. *Caffrogobius* had a varied diet, feeding on amphipods, crabs, isopods and fish. Too few individuals of *Gilchristella, Monodactylus* and *Solea* were caught to warrant discussing their feeding habits.

Most of the remaining fish are species which migrate in and out of estuaries. The five species of mullet, *Liza dumerili, L. richardsoni, L. tricuspidens, Mugil cephalus* and *Myxus capensis*, all commonly occur in estuaries but breed in the sea (Wallace, Kok, Beckley, Bennett, Blaber & Whitfield 1984). All but *L. richardsoni* and *M. capensis* were represented only by young individuals with undeveloped gonads. The gonads of these two species varied from undeveloped to very ripe and many of the fish had reached adult size. In many cases these fish had voided their gut contents but the remainder contained large quantities of sediment, sometimes mixed with large numbers of copepods and *Hydrobia* (which are seldom eaten by mullet in other estuaries).

Lithognathus lithognathus and *Rhabdosargus holubi* are largely dependent on estuaries as nursery feeding-grounds, while *Lichia amia, Rhabdosargus globiceps* and *Pomatomus saltatrix* visit estuaries on a more casual basis (Wallace *et al.* 1983). Only juveniles of these species were captured in the Palmiet estuary.

The Palmiet may thus be important in being the only estuary that is normally open in 350 km of coastline, for it can act as a nursery for vulnerable young fish which can then escape to the sea to breed.

Monthly samples of the fish reveal that only three species (*Liza richardsoni, Psammogobius knysnaensis* and *Myxus capensis*) occurred in the estuary throughout the year. The remaining 16 species were found there from September or October to April or May — the months when the estuary is not in flood. This emphasizes the flood-driven nature of the estuary.

Discussion

Physical interactions

The Palmiet River estuary is clearly a current-driven system, the floods and strong tidal surges having profound effects on the hydrology and sediments and hence on the flora and fauna.

Even in summer, when river flow is minimal, the tidal exchange of water with the sea may be as much as 50% of the total volume at neap-tides and flushing time in March was between 2,54 days and 5,96 days, depending on how mixed the estuary was. When river flow is high, during winter, the outflow through the mouth may amount to some 150% of the total volume of the estuary. In July the flushing time was only 8 h, indicating complete exchange of the surface layers during each ebb-tide. Even in April, before the onset of rains, flushing time was 24 h. Thus retention times of surface waters are extremely short, explaining the very low levels of zooplankton and the fact that virtually all of it is of marine rather than of estuarine origin. Phytoplankton values may be fairly high relative to those in the sea, but once again their retention must be short. Even in December, when river flow is low, the high levels of phytoplankton coming in from the river are diluted four-fold within the estuary and most phytoplankton is eventually lost to the sea (Table 3). Presumably the riverine phytoplankton derives largely from a small dam behind a gauging weir 800 m upstream of the bridge, since there is little evidence of phytoplankton in the river above the weir.

The deep channel, protected by rocky banks for a large part of its length, is not affected to any great extent by the currents, so that the salt wedge is maintained throughout the year. This in turn allows the benthic invertebrates in the area to live in almost constant, quiet conditions despite the considerable movement of water above them. This stratification further means that the physico-chemical conditions in the channel also differ from those nearer the surface; phosphate and ammonia tend to be higher and oxygen lower, while large quantities of decaying macrophytes are retained on the bottom rather than being swept out of the system.

Sediments are also greatly affected by the currents. The Palmiet estuary has unusually coarse sediments in comparison with those of most southern African estuaries, (see Branch & Grindley 1979; Day 1981 & references therein) while the amount of mud is extremely small. This coarse sediment, combined with the strong currents, precludes many animals from living in the system; many mud dwellers require a high organic content in the mud as a food source and others require a soft, stable mud for burrowing. Those which do occur are either physically able to withstand the abrasive action of moving sand particles or are large and able to burrow deeply, below the level of maximal sand movement. *Callianassa*, by cementing its tube with fine, richly organic mud, is able to stabilize the sediment.

Most attached macrophytes are unable to maintain their positions owing to the instability of the sediment. Exceptions are *Cladophora*, which is only found in summer when current velocities are lowest, and *Enteromorpha*, which grows on rocky substrata near the mouth.

The small salt-marsh occurs in the most sheltered corner of the lagoon, on the opposite bank from the channel and protected from the full force of the currents; even here the edge is constantly being eroded.

Physically, then, surface waters remain in the system for a short time while deeper waters remain relatively unaffected by currents. The surface sediments are highly unstable on the sand-flats and at the mouth but are more stable in deeper areas because of reduced current velocities. Presumably extreme flood conditions may destroy the stratification or scour the bottom of the estuary, but we have no evidence of this; stratification remained a dominant feature even in July, when the river was running strongly.

The mouth

One of the most unusual and important characteristics of the estuary is the fact that the mouth is almost always open. This is due to a combination of topographical and hydrological features. On a high-energy coast such as this, most estuaries close because the highly seasonal river flow drops to a minimum in summer at the same time that the southerly swell and tradewind-driven waves have maximal onshore force. Thus there is a build-up of sediment at the mouth at just that time when river flow is too weak to force a channel to the sea. It is only during winter spates that there is sufficient force of water to break through the bar and open the estuary. In the Palmiet estuary the combined effect of a rocky spit on the west bank, which turns the longshore current away from the mouth and out to sea, and a permanently running river, maintain a small unstable channel throughout most years. Added to this the tidal lag, which forces all the imported seawater to enter the estuary during a very short period of 3 h, ensures that the current velocity during the flood tide is far stronger than it would otherwise be. This high velocity tends to import sediments, particularly during spring-tides when the volume of water imported from the sea is greatest. It is the annual build-up of this sediment which closes the mouths of most of the neighbouring rivers.

Presumably when the Palmiet estuary does close it is due to a combination of minimal river flow and particularly strong wave action. As far as we can ascertain the mouth usually stays closed for no longer than a month at a time, opening in about March or April when rainfall in the mountains causes increased river flow.

Production

The relatively small size of the estuary and its narrow mouth have allowed us to make very rough estimates of the total standing stocks and turnover rates of the major components of the system.

The high flow rate in winter makes it almost impossible for attached plants to establish themselves. *Cladophora* thrives for a brief period in late summer, when the flow is least, producing an average standing stock of 132 g m^{-2} (Table 4), mainly concentrated in the basin and the deeper parts of the channel below the halocline. Since this weed is absent for the rest of the year, we can assume that its annual production is equal to its maximal biomass, i.e. 30 360 kg for the whole system.

Phytoplankton standing stocks (2,7 to 5,1 mg chlorophyll m^{-3}) are relatively high for an estuary, although much lower than the range of 4,9 to 32,9 recorded for Saldanha Bay by Henry, Mostert & Christie (1977). From the conversion equation given by these authors, it can be estimated that this is equivalent to a production for the whole estuary of 44 kg C day^{-1} or over 16 000 kg C $year^{-1}$. This will be roughly equal to 8 000 kg dry mass $year^{-1}$ (Table 4). Thus the small standing stock of phytoplankton may be capable of significant productivity.

Benthic diatoms and other microflora are abundant in the more stable sediments and are largely confined to the intertidal sandbank. As light penetration is confined to the top few millimetres of sand, production by this microflora is low, probably not exceeding 400 kg $year^{-1}$ (Table 4). Since nutrient levels are moderate, they are unlikely to be limiting to plant growth, and again the current-driven nature and the low retention time of the estuary are probably the major factors restricting plant productivity.

Production within the estuary should be viewed in relation to possible import and export. Although our data are based on a limited number of observations and must therefore be treated cautiously, they show quite clearly that a substantial amount of kelp and probably also of *Prionum* is imported and, more particularly, that particulate organic matter brought in at the mouth and from the river may contribute a massive 143 000 kg $year^{-1}$ to the estuary (as estimated by multiplying the mean input per tidal cycle by 712 cycles per year) (Table 4). The sediments (down to a depth of 10 cm) contain about 900 g m^{-2} of organic materials, and thus there would seem to be over 200 000 kg in the estuary as a whole (Table 4). However, the concentration of organics in the sediment is so low (less than 0,5%) that it is doubtful whether infaunal deposit-feeders could feed profitably on the sediment; indeed there are no macroinvertebrate species filling this niche in the Palmiet estuary. Again, the importance of *Callianassa* in concentrating organic material and packaging it into faeces is obvious.

Thus if we compare the sources of production within the estuary with the net import of organic material (Table 4), it is obvious that import outweighs production *in situ* by a factor of about 3,6, since the net import of kelp and particulate matter amounts to about 141 400 kg $year^{-1}$, and the production of *in situ Cladophora*, benthic diatoms and phytoplankton contributes only about 39 800 kg $year^{-1}$.

Invertebrates

The current-swept nature of the estuary, the annual flooding, the possibility of the mouth closing (albeit briefly), the coarse sediment and its low organic content are all factors militating against the establishment of invertebrate populations, so that their low diversity is not surprising. Only 28 species were recorded; this compares with 89 species in the Klein River estuary, Hermanus (Scott, Harrison & MacNae 1952) and 34 species in Milnerton Lagoon (Millard & Scott 1954), despite the fact that both of these estuaries are closed more often and for longer periods than is the Palmiet. Knysna Lagoon, a large, permanently open estuary, supports over 360 species (Day 1967). On the other hand many of the species which do occur in the Palmiet seem to thrive there, judging by their numbers. *Callianassa* achieves a density that is exceeded only in Langebaan Lagoon (C. Gaigher, pers. comm.) while the amphipod *Grandidierella* reaches a density of over 100 000 m^{-2} and *Hydrobia*, *Cyathura* and *Ceratonereis* are all abundant. Furthermore the biomass averages 5,7 g m^{-2} and its upper value of 35 g m^{-2} (Figure 17) equals that of many other estuaries and lagoons, including such rich systems as Langebaan Lagoon (Christie & Moldan 1977; Puttick 1977) and Mngazana estuary (Branch & Grindley 1979). The success of these species must be due at least in part to the salt wedge that maintains constant conditions in the deeper waters of the channel. Many of the species are debris- or detritus-feeders, accumulating around the decaying kelp deposited at the bottom of the lagoon or at the high-tide mark; there are no invertebrate predators except for isolated individuals of *Natica* on rocks and small numbers of *Excirolana* and *Eurydice* near the high-tide mark, all in the vicinity of the mouth.

Callianassa has an important effect in the system, concentrating fine particles and organic material to line its tubes. Without this action much of the particulate material would probably be lost from the system. The turnover of organic material in the faeces of *Callianassa* is prodigious. On average 1,4 g of dry faeces (with up to 35% organic matter) are produced per hole per tidal cycle. As the mean density of holes throughout the whole estuary is 60 m^{-2}, and 35% of the holes are surrounded by faeces during any one tidal cycle, over the whole estuary *Callianassa* could potentially turn over $1,7 \times 10^6$ kg organic material in its faeces each year. Further research is needed to confirm and quantify these findings more accurately, but the importance of the animal is unquestionable, as Frankenberg, Coles & Johannes (1967) have shown elsewhere.

Faunistically there are three major zones to the estuary. The mouth is unstable and supports only a high-shore isopod fauna feeding in the water column at high tide, a fauna associated with cast-up seaweed and, subtidally, a few *Callianassa*. In the lagoon where conditions are more stable there are large numbers of *Grandidierella, Callianassa, Hydrobia* and *Cyathura*, together with a few other species. Towards the head of the lagoon *Grandidierella* is replaced by *Corophium* and *Exosphaeroma hylocoetes* by *Pseudosphaeroma barnardi* but the rest of the fauna remains remarkably similar although it becomes sparser as the sediment becomes coarser. These three zones reflect the stability of the substratum rather than changes in salinity since, as discussed above, stratification maintains remarkably constant salinities.

Management

This report was commissioned because of the proposal to dam the Palmiet River very close to the sea. It is clear from the survey that the construction and operation of such a dam will have profound consequences for the estuary. Two features are worth singling out. Firstly, the Palmiet estuary is one of the few in the western Cape which is normally open. On average, it closes every other year, but only briefly for periods of between one and three months. Any reduction in the flow of fresh water into the estuary will certainly close the mouth, either permanently or for more prolonged periods. When the river flow reduces in summer, there is a net import of marine sediments at the mouth which will block the mouth in the absence of winter flooding. Stagnation, a break-down of stratification, and greater long-term fluctuations of salinity will ensue. Recruitment of juvenile fish will be prevented or curtailed, and adult fish will no longer be free to migrate in and out of the estuary to feed. Dense growths of the alga *Cladophora* choke the estuary when it is closed. Almost all the invertebrates in the estuary are of marine origin and many of them thrive only in open estuaries, so that mouth closure will lead to a further impoverishment of the fauna.

The construction of a dam will also reduce the input of organic particles to the estuary from the river. This problem will be compounded if the mouth closes, for substantial amounts of organic material, in the form of particulate matter, detritus and whole kelp plants, enter the estuary from the sea. This survey has shown that production within the estuary accounts for only about a third of that imported from the sea and river. If the proposed dam is built, it is critical that attention be paid to the volume and periodicity of water release from the estuary. Sufficient flooding will be required to open, and preferably keep open, the mouth, while smaller, more regular, discharges will be necessary to offset salinity increases owing to evaporation. H. Swart (pers. comm.) has calculated that a minimum release of 50 $m^3 s^{-1}$ for 15 h, simulating winter floods, will be necessary to open the mouth after it closes, and that further regular releases, amounting to $0,3 \times 10^6 m^3 year^{-1}$, should balance evaporative water losses. It must, however, be stressed that these are minimal releases which can only ensure that the estuary is not permanently closed: they will not maintain the estuary in its present condition.

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Appendix 1 Species list of the invertebrates and plants of the Palmiet River estuary. Station numbers refer to the physical stations shown in Figure 1

Species	Abundance[a,b] at Stations A – F						Habitat[c]
	A	B	C	D	E	F	
Invertebrates							
Polychaeta							
Ceratonereis keiskamma	P	A	A	A	A		Sa
Prionospio cf. *tenuis*	C	A					Sa
Ostracoda	A	A	A				Sa
Copepoda	A						Sa
Amphipoda							
Corophium triaeonyx	R			P	A	P	Sa
Grandidierella bonnieroides	A	A	A	A	P		Sa
Melita zeylanica	P	P	R				Sa
Orchestia rectipalma			C				Sa
Talorchestia quadrispinosa	A	A					Sa
Isopoda							
Cyathura estuaria	P	A	A	P	P		Sa
Eurydice longicornis	R	P					Sa
Excirolana natalensis	P						Sa
Exosphaeroma hylecoetes	R	P	P	P			Ro
Pseudosphaeroma barnardi					P	P	Ro
Tanaidacea							
Tanais philetaerus	A				C		Sa, Ro
Decapoda							
Betaeus jucundus		P	P				Sa
Callianassa kraussi	C	A	A	A	A		Sa
Cleistostoma edwardsii		P					Sa
Hymenosoma orbiculare		P	C	P			Sa
Ocypode ceratophthalmus	R						Sa
Thaumastoplax spiralis		R				R	Sa
Insecta							
Chironomid larvae (Diptera)	C	A					Sa
Coelopea africana (Diptera)	C	A					Sa
Pachyphaleria capensis (Coleoptera)	C	A					Sa
Staphylinid (Coleoptera)	A	C					Sa
Gastropoda							
Assiminea globulus			A				SM
Hydrobia sp.	A	A	A	A	A		Sa
Natica tecta	R						Ro
Oxytele sinensis				R			Ro
Oxystele variegata	P						Ro
Bivalvia							
Choromytilus meridionalis	P						Ro

Appendix 1 (continued)

Species	Abundance[a,b] at Stations A – F						Habitat[c]
	A	B	C	D	E	F	
Plants							
Algae							
Enteromorpha sp.	C						
Cladophora sp.		C	P	C	A		Sa
Angiospermae							
Arctotheca calendula			R				SM
Cotula coronopifolium			C				SM
Crassula sp.			R				SM
Chenopodium sp.			R				SM
Filicina sp.			R				SM
Juncus kraussii kraussii			C				SM
Orphium fructescens			P				SM
Plantago carnosa			R				SM
Prionum serratum						P	R
Samolus porosus			C				SM
Scirpus verruculosus			P				SM
Sporobolus virginicus			P				SM
Triglochin striatum			P				SM

[a]Relative abundance of invertebrates is indicated by the number of specimens m^{-2} at a particular site: R = 1 – 2 (rare); P = 3 – 20 (present); C = 21 – 100 (common); A = >100 (abundant).
[b]Abundance of plants is rated according to percentage cover: R = 0 – 5%; P = 5 – 20%; C = 21 – 50%; A = >50%
[c]Habitat types are rock (Ro), Sand (Sa), Salt-marsh (SM) or River bank (R).

Appendix 2 Fish species list for the Palmiet River estuary and numbers caught in 12 monthly samples between May 1980 and April 1981

Species	Common name	Number caught	Seasonal occurrence
Arius feliceps	Sea catfish	24	Late summer
Caffrogobius multifasciatus	Prison goby	96	Spring to summer
Gilchristella aestuaria	Estuarine round herring	78	Summer
Hepsetia breviceps	Cape silverside	7887	Spring & autumn
Lichia amia	Leervis	5	Summer
Lithognathus lithognathus	White steenbras	384	Summer
Liza dumerili	Groovy mullet	81	Autumn
Liza richardsoni	Southern mullet	8729	Year round
Liza tricuspidens	Striped mullet	1	–
Monodactylus falciformis	Cape moony	4	–
Mugil cephalus	Flathead mullet	10	–
Myxus capensis	Freshwater mullet	88	Year round
Pomatomus saltatrix	Elf	5	Summer
Psammogobius knysnaensis	Knysna sandgoby	464	Year round
Rhabdosargus globiceps	White stumpnose	23	Summer
Rhabdosargus holubi	Cape stumpnose	27	Late summer
Solea bleekeri	Blackhand sole	3	–
Syngnathus acus	Longnose pipefish	1	–
Therapon jarbua	Thornfish	1	–