COMMUNITY METABOLISM AND PHOSPHORUS DYNAMICS IN A SEASONALLY CLOSED SOUTH AFRICAN ESTUARY

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Frontispiece - the Swartvlei estuary. Original photography: Professor D.A. Scogings, University of Natal.

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ABSTRACT

The effects of seawater inflows and macrophyte beds on community metabolism and phosphorus dynamics in the seasonally-closed Swartvlei estuary were investigated. Metabolic rates were determined by diurnal oxygen curve analysis. Gross primary production ranged from 0,7 to 14,9 g O_2 m^{-2} day^{-1}, and respiration from 0,9 to 25,2 g O_2 m^{-2} day^{-1}. The highest production rates were recorded inside the dense beds of *Zostera capensis* Setchell ($\bar{x}$ = 7,8 g O_2 m^{-2} day^{-1}). Metabolism was positively correlated to submersed macrophyte cover, and decreased upstream of the mouth region. No seasonal variation in gross production could be detected, and mouth closure had no detectable effect on metabolic rates. Growth of the green alga *Enteromorpha* sp. in winter, and the effect of decay of this alga on dissolved oxygen, total inorganic carbon and total dissolved phosphorus in the water column is discussed.

High day-time respiration values, measured in a darkened polythene enclosure, indicate that photorespiration occurs in *Zostera*. Apparently the annual amount of oxygen respired throughout the estuary exceeded that produced by 2 7100 tonnes, i.e. the estuary was heterotrophic. This is discussed in relation to the effectiveness of the diurnal curve method as a way of measuring metabolic rates, and to the possibility of organic matter input via river inflows.

There is a net gain of up to 17,4 kg of particulate phosphorus over mean tides. Diurnal phosphorus studies indicate that *Zostera* releases phosphate into the water column in the light. *Enteromorpha* takes up phosphate in the morning, which it appears to release over the rest of the day. The cycling of phosphorus between seawater, sediments, macrophytes and the water column is discussed.

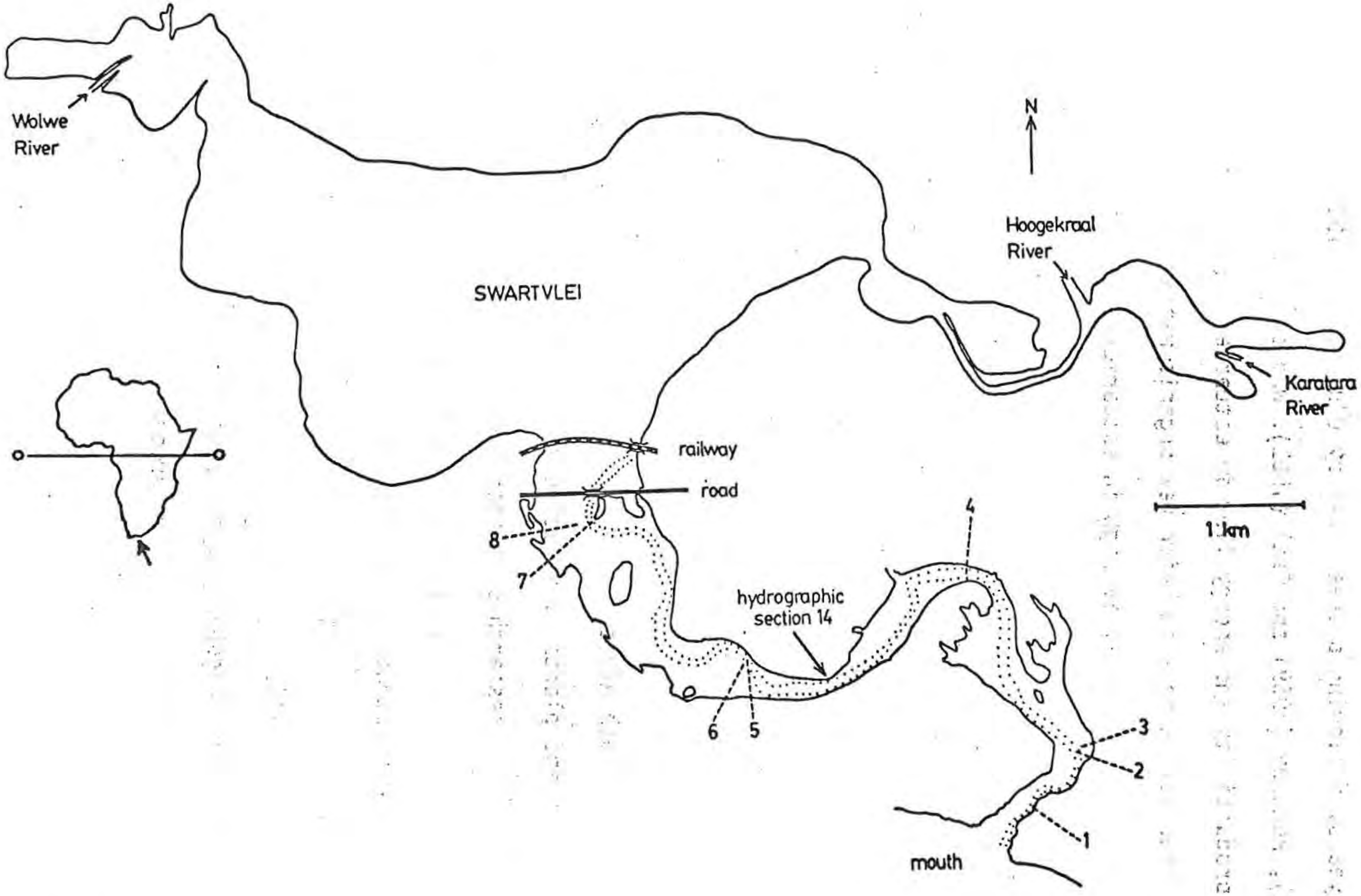

Fig. 1. Map of Swartvlei and the Swartvlei estuary, showing sampling Stations 1 - 8, and the position of the main channel (dotted lines). The three main river inflows (Karatara, Hoogekraal and Wolwe Rivers) are also shown. Insert: Africa, indicating position of estuary.

INTRODUCTION

Estuarine studies in the northern hemisphere have expanded tremendously in the last twenty years, following pioneer work by Odum (1956; 1957), Odum and Hoskin (1958), Pomeroy (1959) and Teal (1962), who devised ways to measure primary productivity and energy flow in estuaries. Primary productivity, defined as the rate at which new organic matter is created by photosynthesis (Westlake, 1963), is high in estuaries. Along with swamps, marshes, algal beds and coral reefs, estuaries are among the most productive ecosystems in the world (Whittaker and Likens, 1975).

This high productivity has been attributed to the ability of an estuary to trap nutrients, the presence of diverse resident autotrophs and also to tidal action (Odum, 1971). Tides act as energy subsidies by distributing food and nutrients, and preventing an accumulation of waste products (Odum, op.cit.,; Field et al., 1977).

Preliminary research on South African estuaries concentrated on the distribution of animals and plants in relation to their surrounding physico-chemical conditions. This research developed into detailed physiological studies on important animal species, and laid the foundations for the more recent work on primary and secondary productivity. Although primary productivity has been measured in other South African coastal aquatic ecosystems, e.g. Lake Sibaya (Allanson and Hart, 1975), a west coast kelp bed (Field et al., 1977) and Langebaan Lagoon (Christie, 1976; Henry et al., 1977), research on estuarine primary productivity has been confined to Swartvlei (Fig. 1). Robarts (1976) measured the production rates of the phytoplankton in the pelagic zone, and Howard-Williams (in press) studied growth of the submersed macrophytes in the littoral zone.

The Swartvlei estuary is one of the few South African estuaries possessing a prolific growth of the eelgrass, *Zostera capensis* Setchell. Mann (1972) considers *Zostera* to be one of the most productive groups of aquatic macrophytes in coastal waters, and to form a basis for detrital food chains. Also, *Zostera* is extremely important as food and shelter for various fish species (e.g. Adams, 1976a, b).

In common with the majority of South African estuaries, the mouth of the Swartvlei estuary is unstable and shows seasonal closure (Moes, 1976). South-westerly winds in May-June displace the longshore current close to the beach. This deposits sand at the mouth, forming a bar which isolates the estuary from the sea. The subsequent rise in water level usually inundates the partially-developed floodplain before the sand bar is breached, and hence the estuary is often opened artificially by local residents.

The closure of an estuary mouth can be deleterious to the estuarine fauna, resulting in death or stunting of many benthic animals (Day, 1967), even when there is no appreciable change in the salinity (Scott *et al*., 1952). Day (*op.cit*.) proposed the absence of tidal action to be the main cause of impoverishment, with the consequent formation of anaerobic conditions in the sediments, and a reduction in seston transport. These views, however, were not substantiated by quantitative data.

The Institute for Freshwater Studies (I.F.W.S.) has maintained an extensive research programme at Swartvlei since 1971, to assess the contributions of the different components of the system to energy flow and nutrient cycling. Apart from a preliminary survey of the Swartvlei estuary (Howard-Williams *et al*. 1975), research has concentrated on the ecology of the pelagic and littoral zones of the upper lake-like reaches.

Measurements of the seasonal fluctuations of major nutrients in Swartvlei showed that nitrate was found in relatively large concentrations (4-70 $\mu g \ell^{-1}$) in the water column. Phosphate, however, was often undetectable and apparently river water provides only a minor supply of phosphate (Robarts, 1976). This raised the question of the possible significance of seawater as a phosphorus source. Also, the abundant submersed macrophytes could be important in phosphorus release from the sediments, as has been demonstrated in North America (McRoy *et al.*, 1972).

In the present study, the water column along the estuary was sampled on a tidal, diurnal and seasonal basis in an attempt to:

(1) estimate the effect of both seawater inflow and the macrophyte beds on physico-chemical characteristics of the water column, and, in particular, dissolved phosphorus;

(2) measure the rates of energy fixation and utilization (community metabolism) throughout the estuary.

It is hoped that the completion of these objectives will contribute to a greater understanding not only of phosphorus dynamics and energy flow in an estuary, but also the effect of removal of tidal action on these processes.

PART 1 - DESCRIPTION OF THE STUDY AREA

The Swartvlei estuary ($34^{o}S$; $22^{o}46'E$) is situated on the south coast of the Cape Province, and forms part of the Knysna-Wilderness Lakes complex. There are two connected, but morphometrically distinct components of the Swartvlei estuarine system:

a. the humic-stained, lake-like upper reaches (Swartvlei);

b. the shallow, sinuous middle and lower reaches (the Swartvlei estuary).

Swartvlei 'lake' is subject to fluctuations in salinity due to seawater influence, and is hence strictly an estuary (Robarts, 1973). However, the region referred to in this text as 'Swartvlei estuary' or 'the estuary' is the 7,2 km long channel extending from the rail bridge to the mouth (Fig. 1), which links Swartvlei to the sea.

The estuary lies in a valley of Quaternary sands bounded by sand ridges (Martin, 1962). It is thought by Martin to have arisen in the Pleistocene as a tidal lagoon, and became drowned during a marine transgression probably within the last 7 000 years. This hypothesis is supported by Hill (1975). Sediments in the estuary mostly lie in the 180 to 600 μm particle size range, having a maximum silt/clay (< 63 μm) content of 14% in the dense seagrass beds. Rocky pinnacles and ledges of dune rock in the mouth region are the only natural hard substrates in the estuary.

Swartvlei has a water surface area of 8,2 km^2, and the estuary, 2,0 km^2. The catchment area, which is predominantly Table Mountain Sandstone (Martin, loc.cit.), covers 337,3 km^2 and drains an annual volume of 38 x 10^6 m^3 through the Wolwe, Hoekraal and Karatara Rivers (Howard-Williams, pers.comm.). This water, which enters Swartvlei in the north-western and north-eastern basins (Fig. 1), has a low pH (4,6 - 5,5), a low conductivity and a low light transmission. The latter is caused by humic acids, which stain the

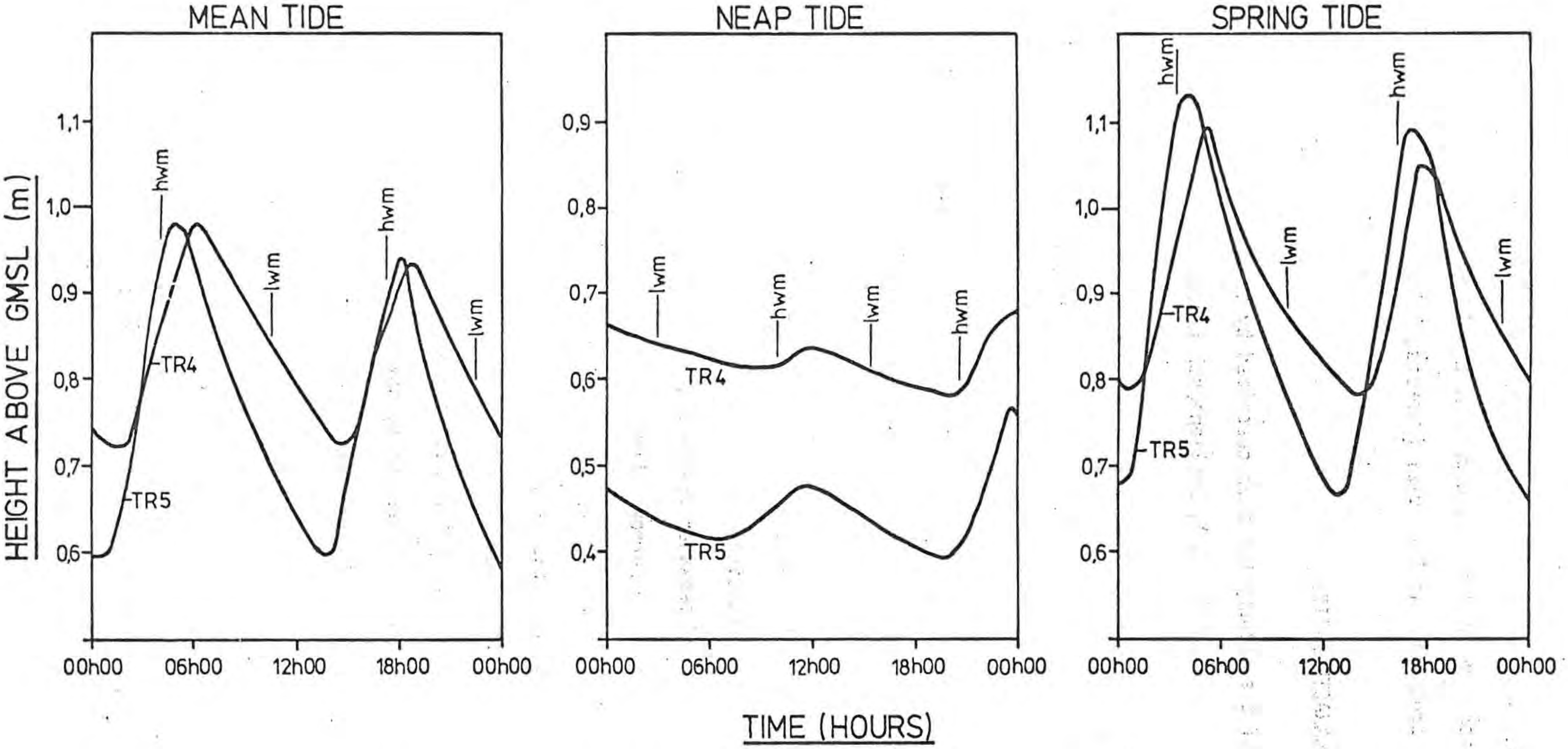

Fig. 2. Water levels at tide recorders 4 and 5 (respectively 4,8 and 1,1 km from the mouth) over mean, neap and spring tidal cycles. hwm - high water at the mouth; lwm - low water at the mouth; GMSL - geodetic mean sea level; mean tide: 30 April 1976; neap tide: 7 May 1976; spring tide: 14 May 1976.

water a characteristic brown colour. This humic material reduces the level of the euphotic zone due to light attenuation, and is a major factor in limiting primary production in Swartvlei (Robarts, 1976).

HYDROGRAPHICAL CHARACTERISTICS

The hydrography of the estuary has been described by the National Research Institute for Oceanology (N.R.I.O.), Stellenbosch (Anon, 1975; Moes, 1976).

The estuary can be divided into two sections (Fig. 1):

(1) the area upstream of hydrographic section 14, shallower than the rest of the estuary and having a maximum depth of 0,5 m below G.M.S.L. (geodetic mean sea level) with extensive tidal flood plains;

(2) Downstream of section 14, with a deeper main channel (maximum 2,5 m below G.M.S.L.), and a narrow tidal flood plain.

Analysis of the tidal data has established that, in general, water surface slopes in the estuary are negative, i.e. towards the sea, at all states of the tide. Large inflows of seawater create a surge in which water travels up the estuary and through the narrows (hydrographic section 14, Fig. 1). By virtue of the momentum developed by the surge, the water level in the upper section of the estuary rises rapidly. Due to the barrier formed by the rail bridge, this causes water to continue to flow into Swartvlei lake, even though the tide has turned at the mouth and lower section of the estuary. Consequently there is a time during spring, mean and some neap tidal cycles when estuarine water flows in two directions simultaneously.

Tide recorders, installed by N.R.I.O. and maintained by the C.P.A. Department of Nature and Environmental Conservation, gauge changes in water level at four points along the estuary. Data from two of these recorders are plotted in Fig. 2, and summarised in Table 1. There is a clear decrease in tidal amplitude both with increase in distance from the mouth, and from spring to neap tidal cycles.

Table 1. Tidal amplitudes 1,1 and 4,8 km from the mouth during a spring, a mean and a neap tidal cycle (from data shown in Fig. 2).

Date	Tidal cycle	Amplitude (m) (1,1 km from mouth)	 (4,8 km from mouth)
7 May 1976	Neap	0,09	0,05
30 April 1976	Mean	0,35	0,22
14 May 1976	Spring	0,42	0,27

The tidal surge mentioned above also means that the times of high and low water along the estuary occur later than at the mouth (Table 2), the differences increasing with distance from the mouth, and from spring to neap tides:

Table 2. Difference in times of high and low water between the mouth and stations 1,1 and 4,8 km upstream of the mouth (minutes).

Date	Tidal cycle	Distance from mouth (km)	High water	Low water
7 May 1976	Neap	1,1	+120	+240
		4,8	+150	+270
30 April 1976	Mean	1,1	+ 55	+180
		4,8	+ 85	+260
14 May 1976	Spring	1,1	+ 30	+180
		4,8	+ 90	+260

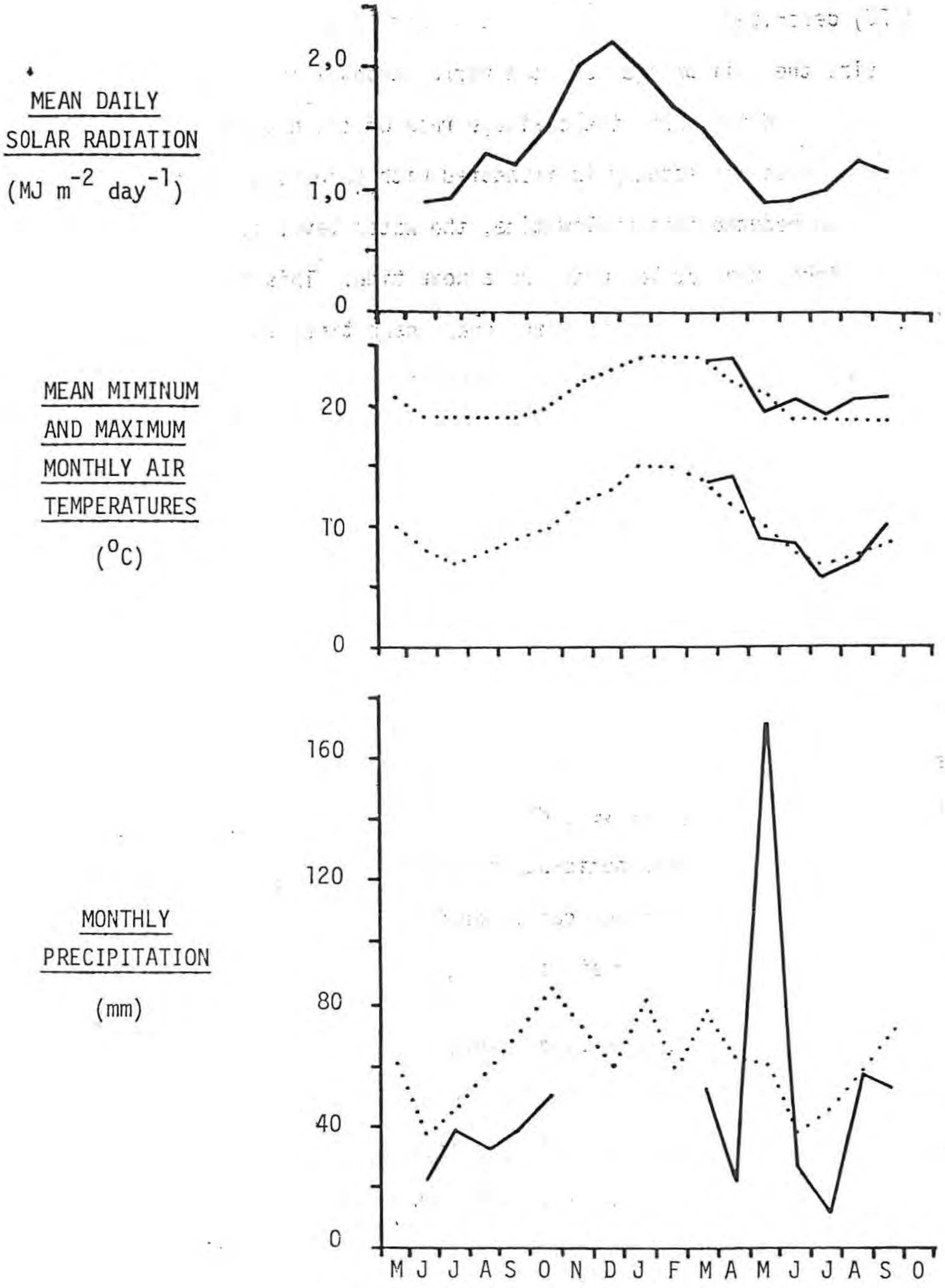

Fig. 3. Mean values of solar radiation, air temperatures and precipitation in the southern Cape and those measured at Swartvlei in 1976-1977.

— data from Swartvlei; ····· data for southern Cape from Schulze (1965).

Moes (1976) described two areas that had a particularly high resistance to flow, viz. the rail bridge, and the narrow channel at the mouth. These constrictions tend to dampen the drainage rate of the estuary. During spring tides, when the estuary is inundated with seawater, drainage at ebb tide is so reduced that at low tide, the water level is almost invariably higher than at low water of a neap tide. This results in a greater intertidal area being exposed over neap tides than over spring tides, a situation that has also been described in the Kosi Bay estuary (Day, 1951), and the Umlalazi estuary (Hill, 1966).

METEOROLOGICAL CHARACTERISTICS

20-year climate records compiled by Schulze (1965) for the southern Cape, show that annual precipitation can vary between 523 and 993 mm. Mean monthly rainfall is fairly constant, although the winter months (June-August) tend to have less rain (Fig. 3). The area is often subject to aperiodic heavy rainfall, however, during which the estuary is flooded with low salinity (< 5^{o}/oo), humic-stained water e.g. in May, 1977 when 169 mm rain fell. These floods can be sufficient to raise the water level of the closed estuary by at least 2 m within 12 h (Martin, 1962).

Mean monthly maximum air temperatures range from 19-24^{o}C, whereas the mean minimum air temperatures range from 7-15^{o}C (Fig. 3). The warmest and coolest months (February and July respectively) are those which follow the months receiving the highest and lowest solar radiation (January and June respectively).

BIOLOGICAL CHARACTERISTICS

The most striking feature of the estuary is the presence of extensive tracts of two seagrasses, <u>Zostera capensis</u> Setch. and <u>Ruppia spiralis</u> L.

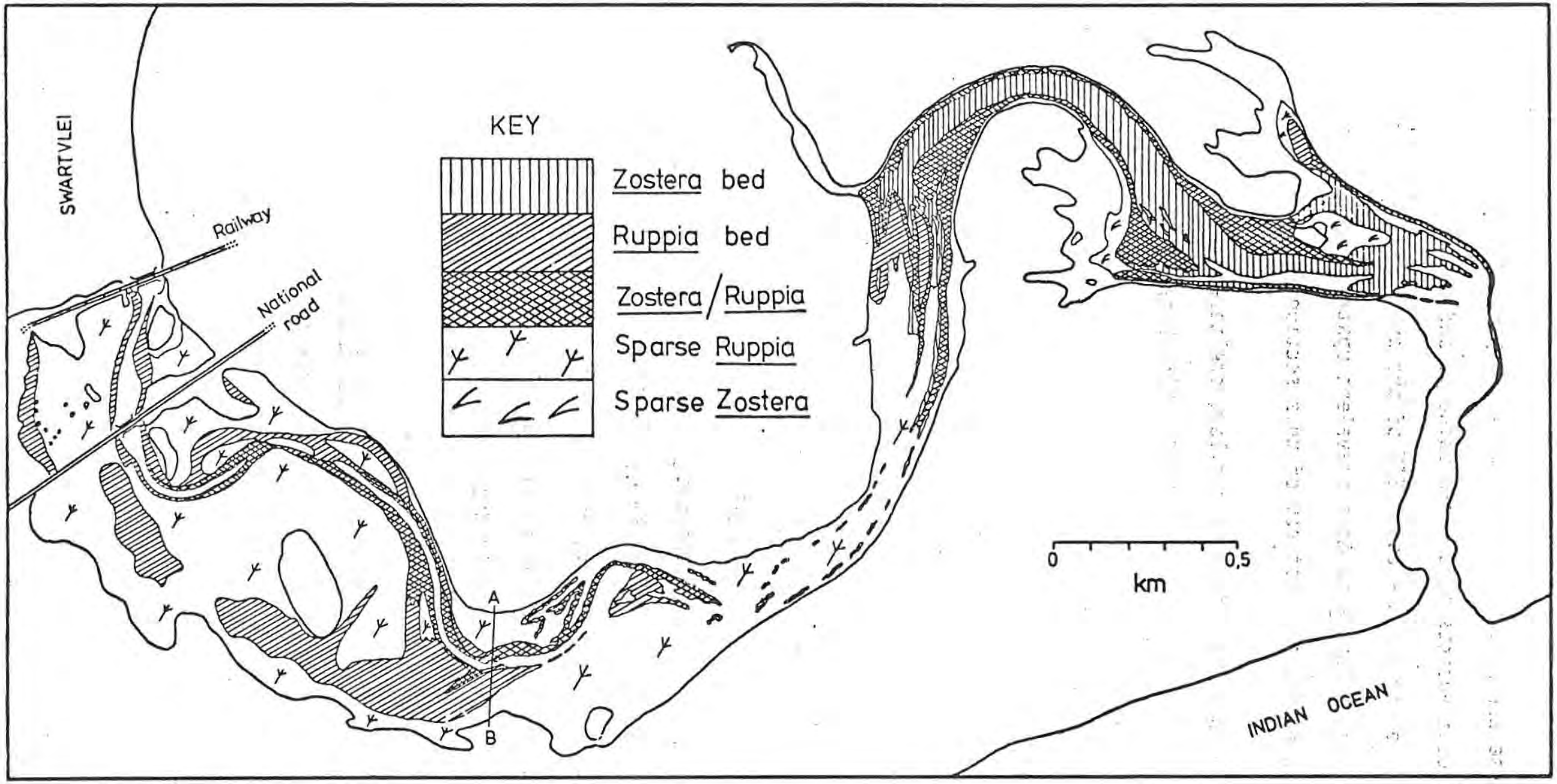

Fig. 4. The distribution of _Zostera capensis_ and _Ruppia spiralis_ in the Swartvlei estuary. The distribution west of A-B was determined by Howard-Williams _et al._ (1975).

ex Dum. These are present in mixed beds and pure stands. Examination of the N.R.I.O. transects across the estuary, and aerial photographs shows that these macrophytes cover 81% of the area below the salt marsh fringe (Table 3). Ruppia is more prevalent upstream of the 'narrows', and Zostera is dominant downstream of this section (Fig. 4, 5b).

Dense Ruppia beds are confined to shallow, sheltered regions that are permanently submerged (0,6 m below HWST - High Water Spring Tide). Thick Zostera beds occur between 1,0 m and 2,5 m below HWST. The macrophyte cover between 0,4 m and 0,5 m below HWST is sparse, as it is exposed at low water of neap tides. A typical zonation pattern is shown in Fig. 5a.

The macrophytes, particularly Zostera, support a large epiphytic population. The main species are shown in Table 4. The biomass of these epiphytes is usually about 25% of that of its supporting leaf, although it occasionally exceeds 100%. This is particularly true of the green alga, Enteromorpha sp. Initially an attached epiphyte, this alga forms mats of entangled filaments over the Zostera beds in winter (Fig. 6a). The mats are distributed by wind throughout the estuary, where they develop over shallow, sheltered regions, in particular, adjacent to Sedgefield village (Fig. 5c). These mats decay rapidly in spring (Fig. 6b).

Large populations of microphagous invertebrates are found in the estuary, both in the sediments (the sand prawn, Callianassa kraussi Stebbing; the mud prawn, Upogebia africana Ortmann; the razor shell, Solen capensis Fischer) and on the submerged macrophytes (the spirorbid polychaete, Janua brasiliensis Grube).

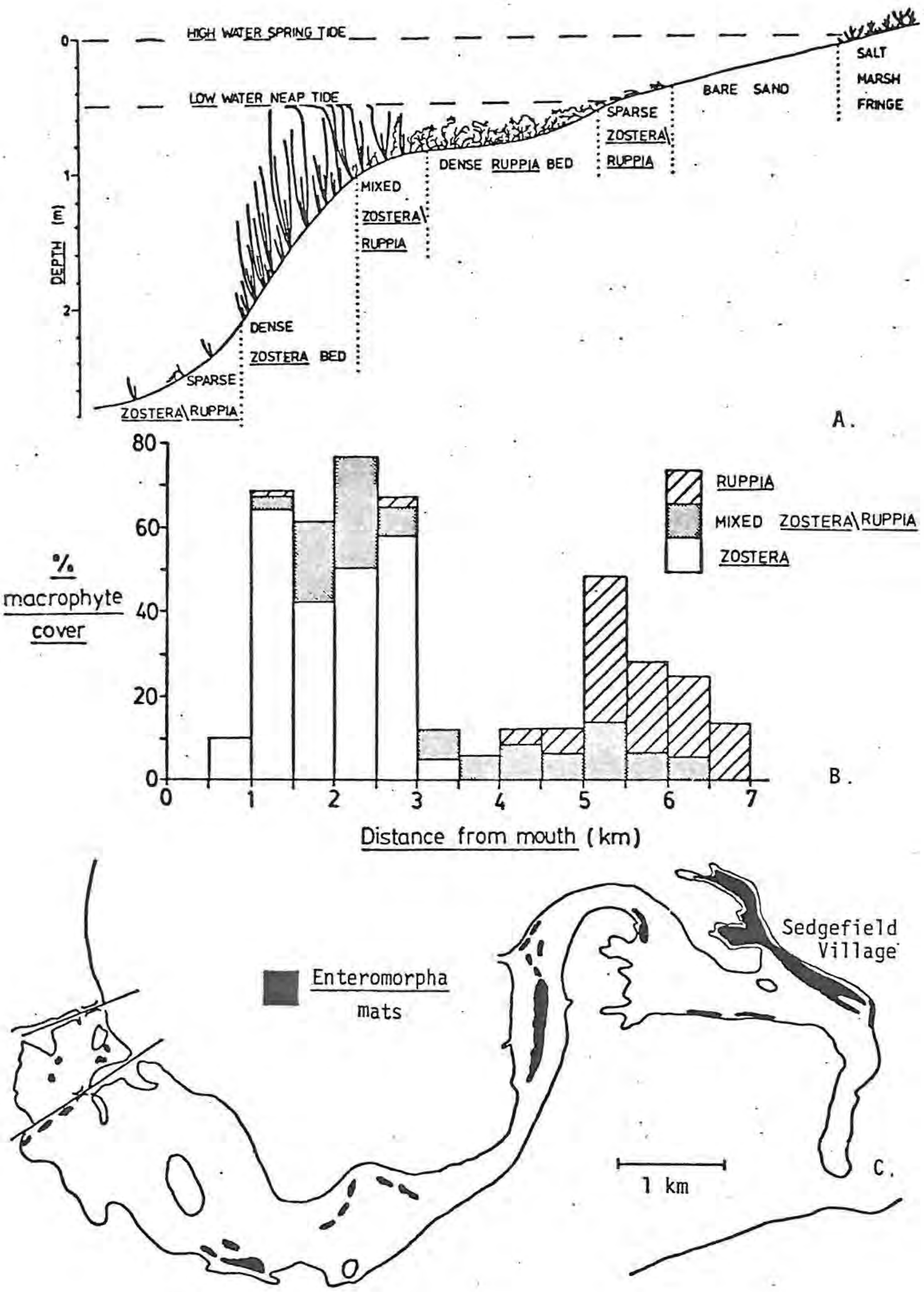

Fig. 5: A. Profile diagram of a typical transect across the Swartvlei estuary, showing zonation of the macrophytes. B. The percentage area covered by Zostera and Ruppia below high water spring tide in each 0,5 km section of the estuary. C. Distribution of Enteromorpha mats in the lagoon phase, 2 July 1976.

A

B

Fig. 6: A. The Swartvlei estuary in September, 1977, showing the extensive development of floating mats of the green alga, Enteromorpha sp. at Station 4 (Fig. 1). The alga is a recreational nuisance, and decomposes rapidly in spring. This results in localised anaerobic conditions and a generation of H_2S. B. A portion of the decomposing alga, with entangled Zostera leaves.

Table 3. Extent of cover of _Zostera capensis_ and _Ruppia spiralis_ in the Swartvlei estuary determined from aerial photographs and transect measurements.

Vegetation type	Area covered (hectares)	% Area covered
Z.capensis beds	20,3	10,4
R.spiralis beds	25,0	12,8
Mixed _Zostera/ Ruppia_ beds	23,3	11,9
Sparse _Ruppia_	87,6	44,2
Sparse _Zostera_	3,2	1,6
Bare sand*	37,3	19,1
Total area below salt marsh fringe	196,7	
Total area covered by macrophytes	159,4	80,9

* below the salt marsh fringe and at the bottom of the main channel.

Table 4. A list of common epiphytes associated with submerged aquatic macrophytes in the Swartvlei estuary during 1976-1977.

Division	Species	Occurrence
Cyanophyta	Lyngbia sp.*	Found occasionally in winter
Chlorophyta	Enteromorpha sp.*	Abundant throughout estuary, especially in winter
	Cladophora sp.*	Common
	Percursaria sp.	Common
Bacillariophyta	Cocconeis sp.	Abundant
	Pennate diatoms	Common on Zostera from deeper parts of channel
Phaeophyta	Ectocarpus sp.*	Very common
Rhodophyta	Polysiphonia sp.*	Abundant
	Chondria sp.*	Common
	Acrochaetium sp.*	Common in upper reaches only
	Hypnea rosea (Papenf.)	Locally common in sheltered lower reaches

* Identified by R. Simons, Seaweed Research Unit, Sea Fisheries Branch, Cape Town.

PART 2 - PHYSICO-CHEMICAL CHARACTERISTICS OF THE WATER COLUMN

Vollenweider (1969) pointed out that data on physico-chemical properties of the water column could enable the basis of primary production to be understood. These data could also indicate the effect of mouth closure on the estuary. With these aims in mind, a programme to monitor the water column was established. The parameters measured were temperature, salinity, dissolved oxygen, pH and total alkalinity. Phosphorus data are reported in Part 3, and the effect of physico-chemical parameters on community metabolism is described in Part 4.

In this section, the general physico-chemical characteristics of the water column are described first. Investigations into two important phenomena encountered in the estuary, viz. the rise in total inorganic carbon during the lagoon phases and flocculation of humic material, are then reported.

2.1: The general physico-chemical features

The eight stations established along the Swartvlei estuary are shown in Fig. 1. Each one was representative of the different aquatic habitats (Table 5). The stations were sampled during both the lagoon (i.e. mouth closed) and tidal phases from April, 1976 until October, 1977. A total of 15 diurnal cycles (in both lagoon and tidal phases), and 6 tidal cycles were monitored. In addition, 26 mid-day readings (11h00 ± 20 mins) were taken for a seasonal comparison of data.

The mouth was closed on three occasions during the study period: from 20 May 1976 to 5 October 1976; from 26 June 1977 until 10 July 1977; and from 17 July 1977, when it remained closed until December, 1977.

Table 5. A description of the eight stations established along the estuary. Their positions are shown in Fig. 1.

Station	Distance from mouth (km)	Description	Depth at high water spring tide (m)
1	0,4	Main channel, sandy bottom with rocky outcrops. No macrophytes present	1,7
2	1,1	Main channel, adjacent to thick *Zostera* bed. Sandy bottom	2,6
3	1,1	Dense *Zostera* bed with abundant *Janua*, *Enteromorpha*	1,2
4	2,6	Main channel, sandy bottom with sparse *Zostera*	2,8
5	4,4	Main channel, sandy bottom	2,0
6	4,4	Mixed *Zostera*/*Ruppia*/ *Enteromorpha* bed	0,9
7	6,7	Main channel, sandy bottom with sparse *Ruppia*	1,5
8	6,7	Upper tidal flats Sparse/medium *Ruppia* cover	0,6

METHODS

Water samples were collected at each station from the surface, middle and bottom of the water column with a Friedinger bottle. Samples were stored in 350 ml polythene bottles for 2-4 h in the dark before pH and total alkalinity analysis; this storage time did not affect the pH by more than 0,02 units, and had no detectable effect on the total alkalinity.

Salinity was measured in situ with an A.O. Instruments Co. refractometer, which is accurate to within 1 °/oo. Dissolved oxygen and temperature were determined in situ with a Y.S.I. Model 51B oxygen meter. Oxygen readings were found to be within 0,5 ppm (parts per million), when checked against Winkler analysis. pH was measured with a Beckman Expandomatic pH meter, which was checked regularly with standard buffers. Total alkalinity was determined using the method of Strickland and Parsons (1968). Total carbon dioxide and total inorganic carbon concentrations were computed from data on pH, the temperature at which the pH was measured, salinity, total alkalinity and the first and second apparent dissociation constants of CO_2, using a computer programme designed by Allanson and Rudd (in press).

RESULTS

Seasonal trends in the different parameters monitored at mid-day along the estuary are shown in Fig. 7. This overall pattern is first described for each parameter, and then the results of the tidal and diurnal sampling are given. The results are presented in this way in order to deduce the effects of both seawater penetration and mouth closure on seasonal, tidal and diurnal fluctuations of physico-chemical parameters throughout the estuary.

1. Water depth

Water levels during the tidal phase have been described in Part 1. After mouth closure, the water level usually rose steadily throughout the estuary, to a level above that encountered during spring tides

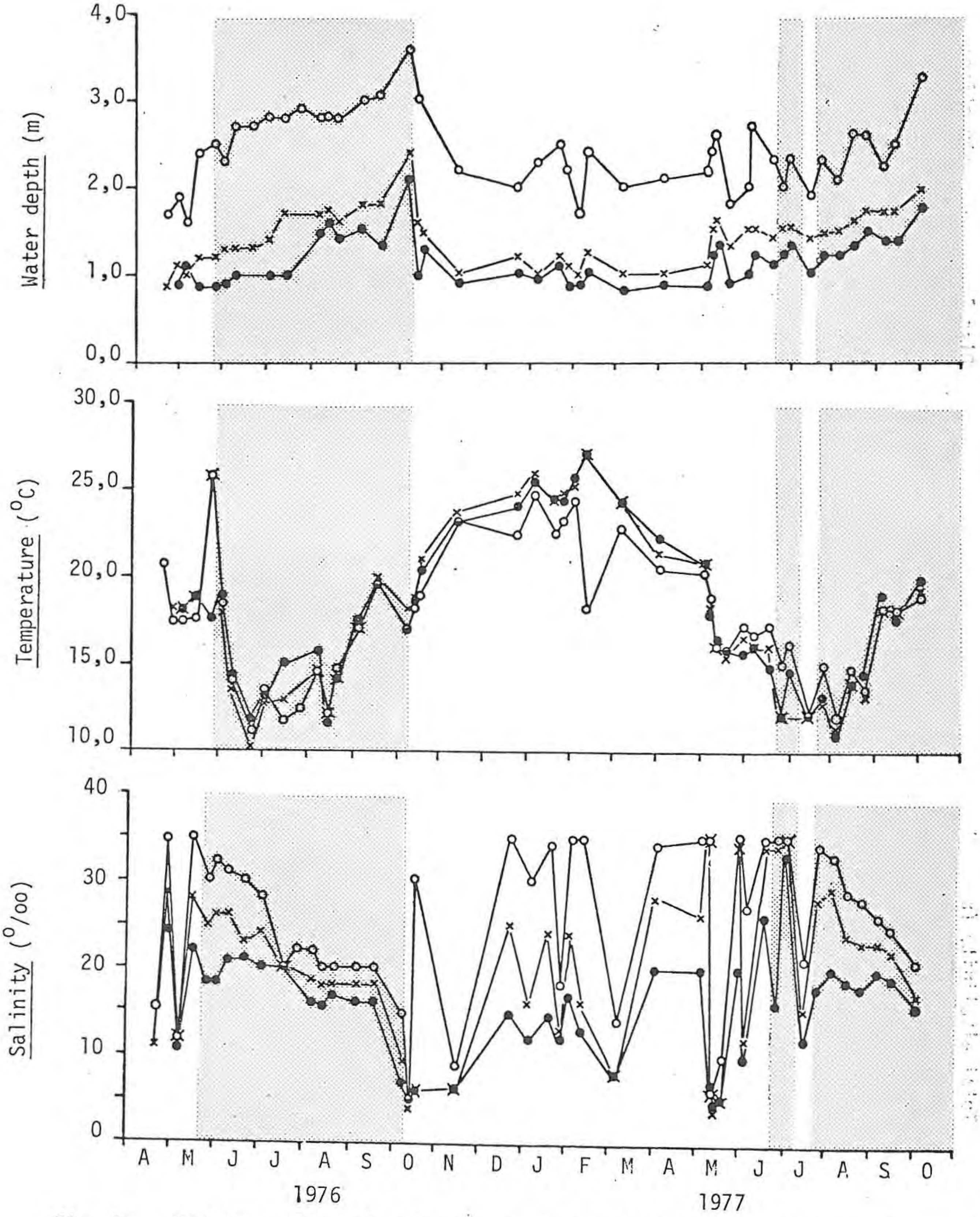

Fig. 7. Mid-day values of water depth, and surface values of temperature and salinity measured at Stations 2 (o), 5 (x) and 7 (●) in 1976 - 1977.

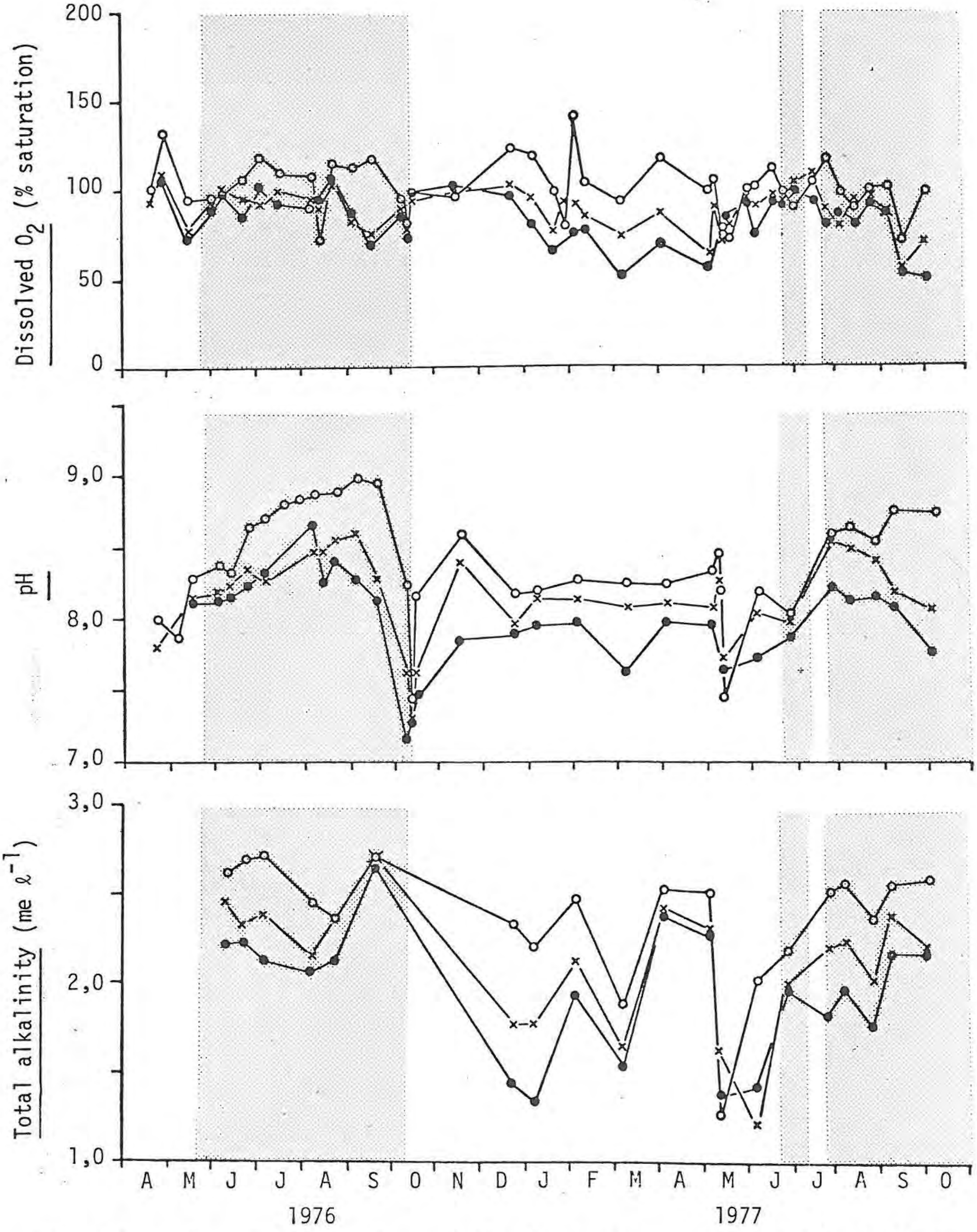

Fig. 7 (cont.). Mid-day values of dissolved oxygen, pH and total alkalinity measured in the surface waters of Stations 2 (o), 5 (x) and 7 (●) in 1976-1977. Shading indicates when mouth was closed.

(Fig. 7). This resulted in the flooding of salt marsh communities that were normally exposed. Rapid rises in water level e.g. October, 1976, and September 1977 (Fig. 7) were associated with high rainfall (Fig. 3). In the tidal phase, however, heavy precipitation did not result in an appreciable rise in water level, e.g. in May, 1977.

2. Water temperature

Temperatures showed a seasonal pattern which closely followed trends in both solar radiation and air temperatures (Figs 3 and 7), and did not appear to be affected by mouth closure. Unseasonally high surface water temperatures in May 1976 (Fig. 7) were caused by a warm Berg wind, which raised surface temperatures to a mean of 7,1°C above those of the midwater and bottom of the water column. In summer, seawater penetration tended to depress temperatures in the lower reaches of the estuary (Station 2, Fig. 7). The highest (29.1°C) and lowest (10,0°C) temperatures were recorded at the surface of Station 3, on 27 January 1977 and 13 July 1977 respectively.

In general, temperatures showed a diurnal, rather than tidal pattern, with minimum values recorded shortly after dawn, and maximum values in mid- to late afternoon. This pattern was reflected in both the tidal (Fig. 8) and lagoon phases (Fig. 9).

3. Salinity

Following mouth closure, salinities in the lower and middle reaches (Stations 2 and 5, respectively) gradually fell as the estuary became filled with low salinity (8-10 °/oo) water from Swartvlei (Fig. 7). Initially, both vertical and horizontal salinity gradients were marked, as shown by salinity profiles (Fig. 10). These gradients decreased with time, due to wind-induced mixing. At some stations, e.g. Station 7,

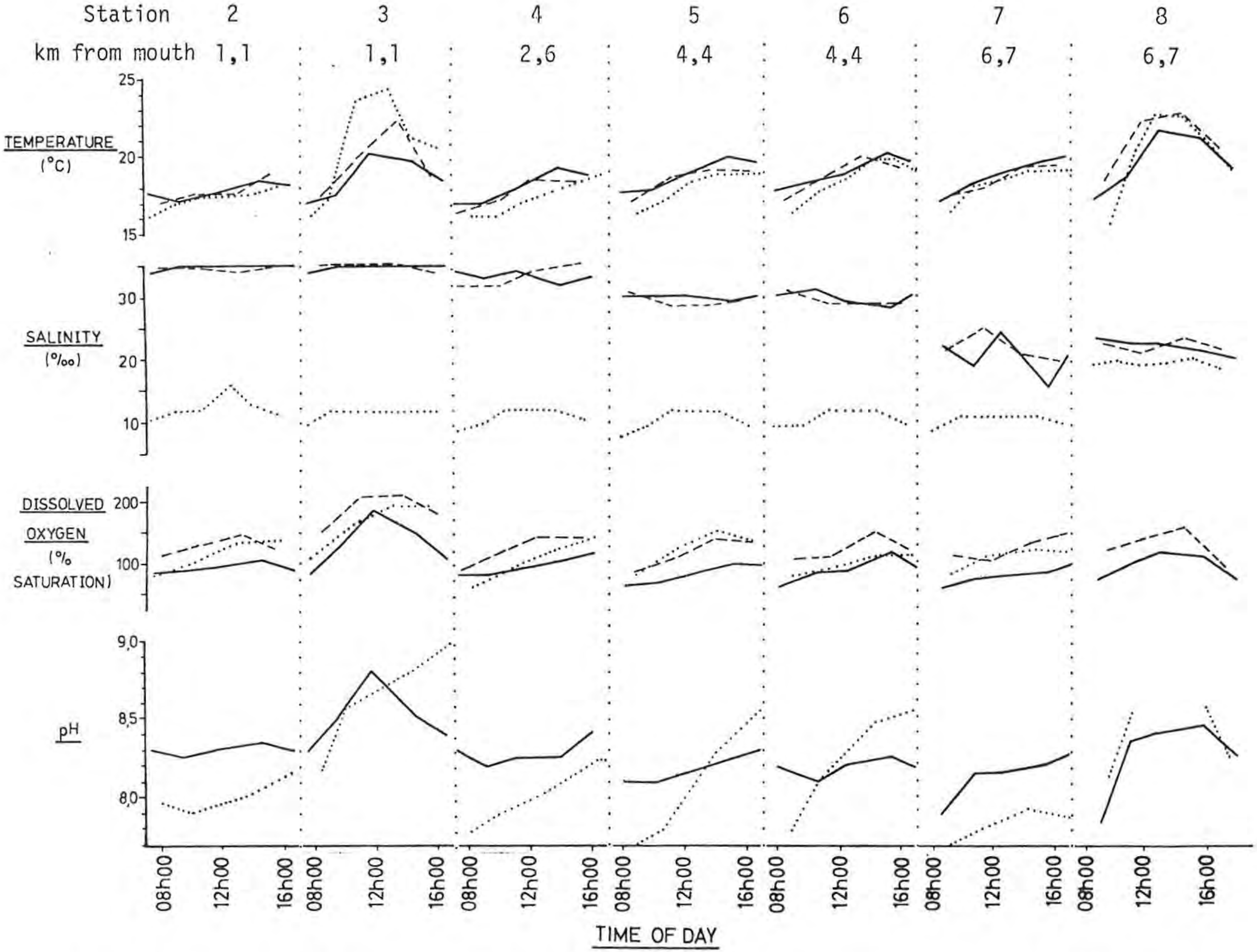

Fig. 8. Salinity, temperature, dissolved oxygen and pH of surface water at Stations 2 - 8 over three tidal cycles. —— spring tide; ---- mean tide; .... neap tide.

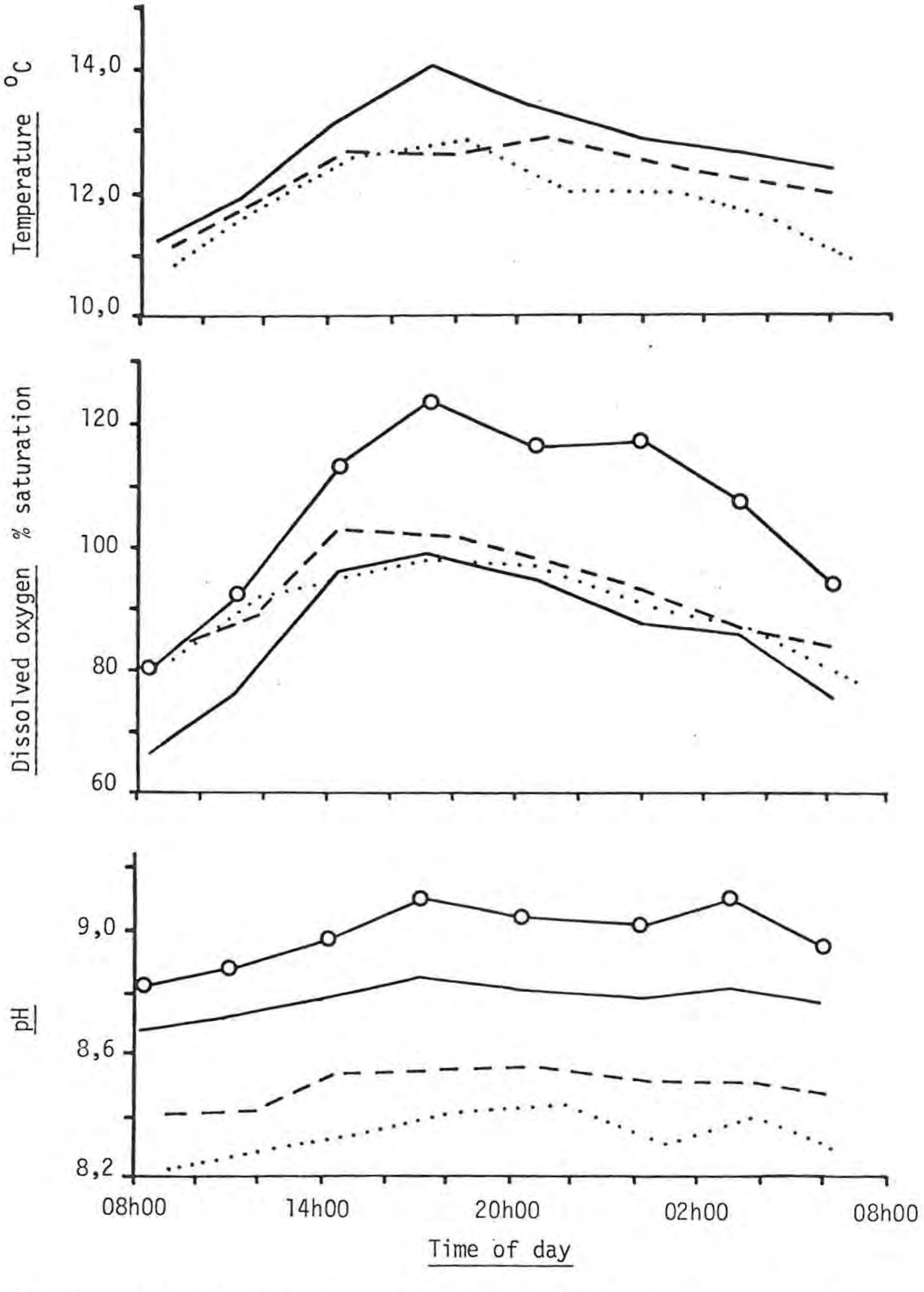

Fig. 9. Diurnal fluctuations in temperature, dissolved oxygen and pH at Stations 2, 3, 5 and 7 in the Swartvlei estuary on 12-13 August 1976, during the lagoon phase. Each point is the mean of surface, midwater and bottom water samples. —— Station 2; o—o Station 3; ---- Station 5; .... Station 7.

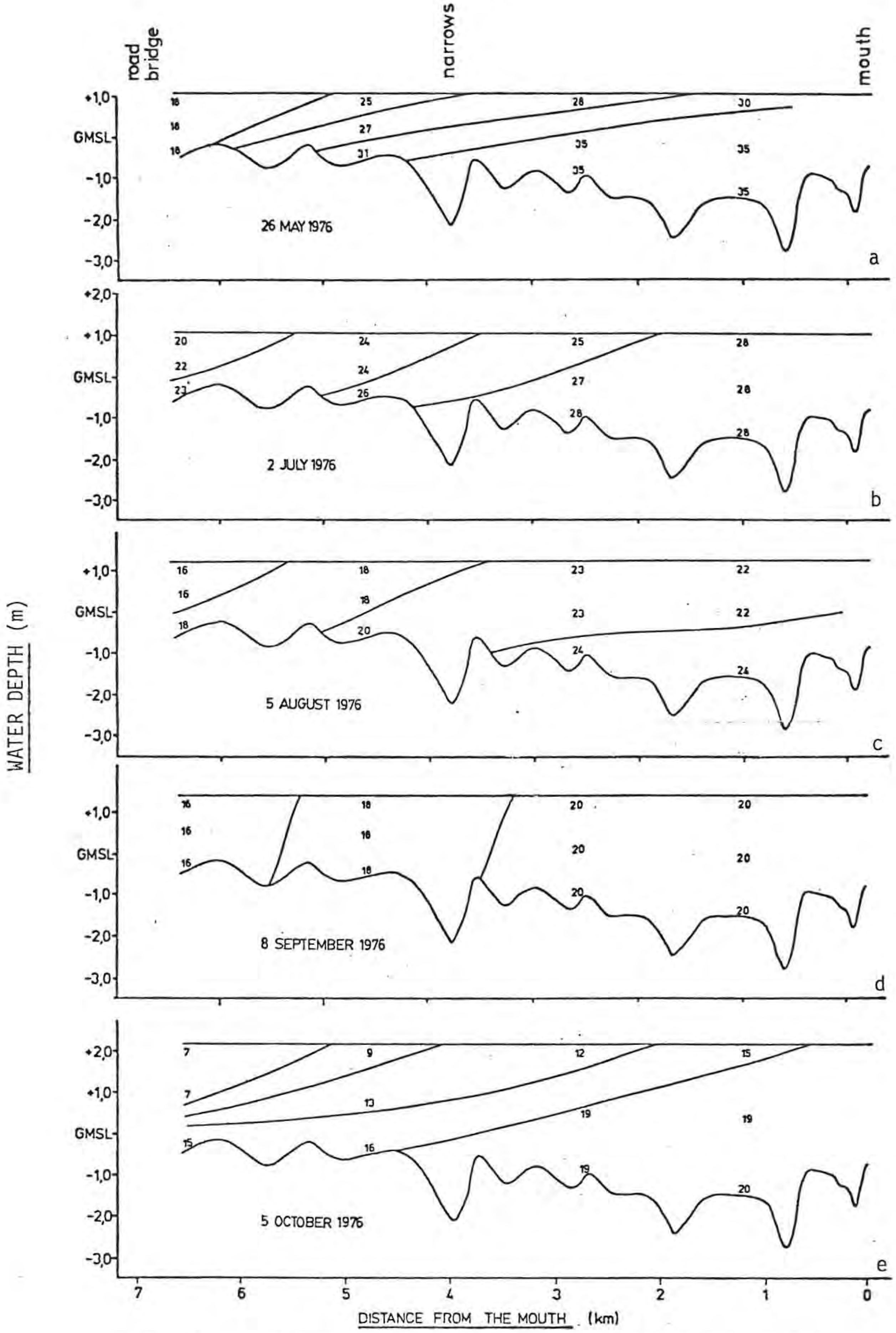

Fig. 10. Salinity profiles of the Swartvlei estuary in the 1976 lagoon phase. Mouth closed: 20 May 1976; mouth opened: 5 October 1976. Salinity values in parts per thousand; GMSL - geodetic mean sea level.

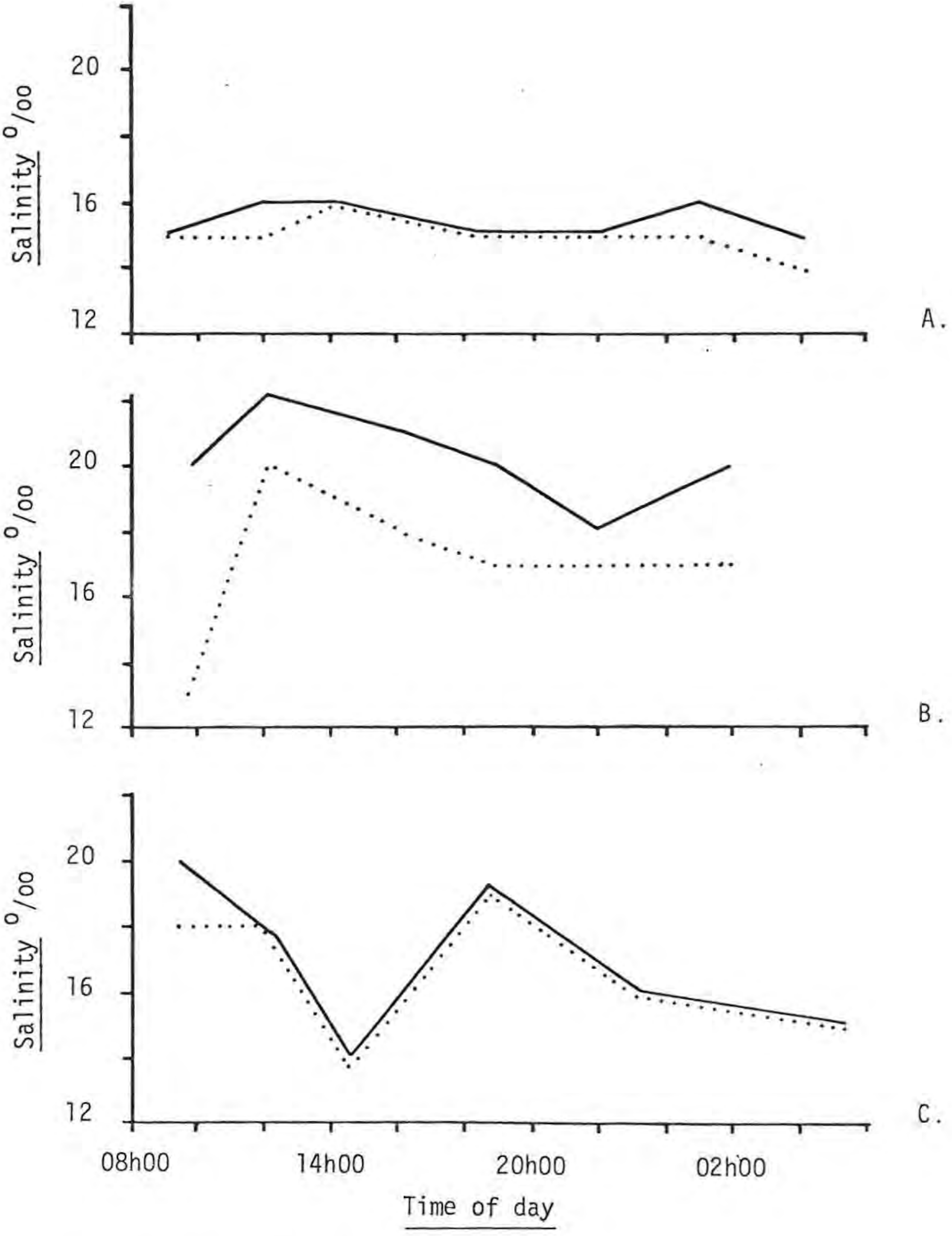

Fig. 11. Diurnal changes in salinity in the Swartvlei estuary at Station 7 in tidal and lagoon phases. A. Lagoon phase, minimal wind stress, 12-13 June 1976; B. Lagoon phase, high wind stress, 14-15 July 1976; C. Tidal phase, spring tidal cycle, 20-21 January 1977. .... surface water; —— bottom water.

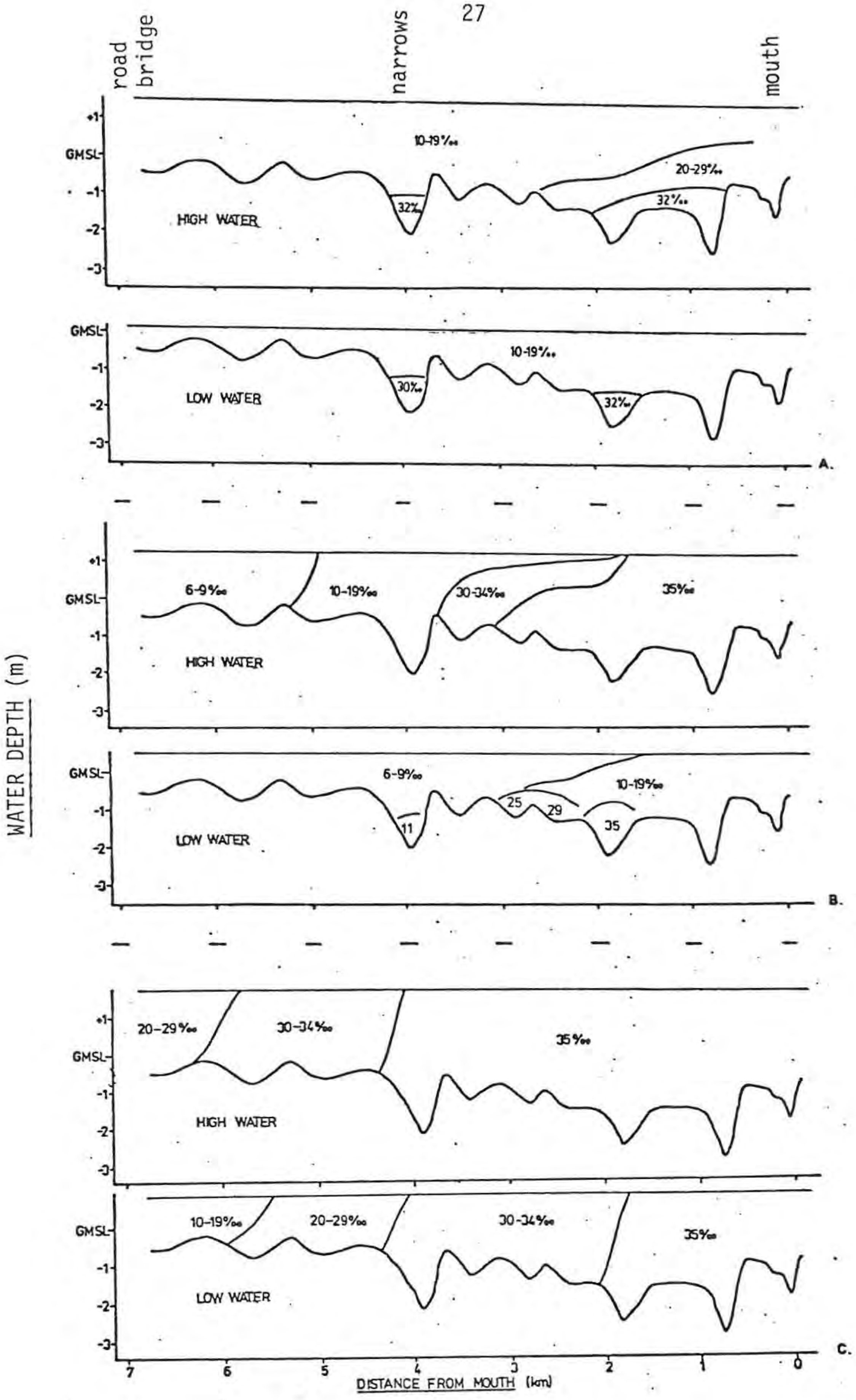

Fig. 12. Salinity profiles of the Swartvlei estuary over high and low water of a neap (27 January 1977); mean (17 November 1976) and spring (22 November 1976) tidal cycle
A - neap; B - mean; C - spring. GMSL - geodetic mean sea level.

movement of water by wind action caused salinity fluctuations over one day to be as marked as those measured during a spring tidal cycle. In calm weather, changes at the same station were minimal (Fig. 11). Salinity strata were re-formed at the end of the lagoon phase after heavy rain and consequent inundation with Swartvlei water (Fig. 10e).

In the tidal phase, seawater penetration along the estuary increased from neap to spring tides, and 'normal' seawater (having a salinity of 35 ^{o}/oo) was once recorded 6,4 km from the mouth on 5 May 1977 (Table 6). This was not an equinoctial tide, but the previous two days were marked by south-westerly (onshore) gales and unseasonally low barometric pressure (1009 millibars). These meteorological conditions appear to assist seawater penetration.

During heavy rainfall when the rivers were in spate and outflow from Swartvlei was strong, seawater penetration was negligible e.g. on 17 May 1977, when penetration was less than 1,1 km (Table 6). The mean maximum distance of travel of the seawater front was found to be 3,9 km from the mouth, i.e. to the 'narrows' (Fig. 1).

Typical salinity profiles of the three tidal regimes (neap, 'mean' and spring tides, Fig. 12) show that:

1. salinity decreases from the road bridge to the mouth, and from spring to neap tides;

2. Vertical mixing of the water column is greatest during spring tides;

3. A substantial volume of water is retained within the estuary over a tidal cycle.

Table 6. Extent of seawater penetration along the Swartvlei estuary during neap, mean and spring tidal cycles.

Tidal cycle	Date	Extent of seawater (35 ^{0}/oo salinity) penetration (km from mouth)
Neap	23 April, 1976	< 1,1
	7 May, 1976	< 1,1
	15 December, 1976	3,1
	27 January,1977	< 1,1
Mean	30 April, 1976	> 1,1 < 2,6
	17 November,1976	3,8
	10 February, 1977	2,6
	22 June, 1977	3,8
	13 July, 1977	1,5
Spring	14 May, 1976	> 1,1 < 2,6
	22 November, 1976	5,2
	20 January, 1977	3,1
	5 May, 1977	6,4
	17 May, 1977	< 1,1
	2 June, 1977	5,9

This latter point is interesting as it means that over a period of several tidal cycles, water in the middle reaches of the estuary will be shunted back and forth, with the seawater front acting as a 'piston'. Water in the lower reaches is constantly replaced by new seawater, whereas in the upper reaches, estuary water is exchanged with Swartvlei water.

Minimum salinities in the estuary occurred when the mouth was open and the rivers were in flood. Over these periods, there was very little salinity stratification as the estuary water was completely flushed out with floodwater and salinities dropped below 8 ^{o}/oo. In May, 1977, rivers remained in spate for three days, and a minimum salinity of 3 ^{o}/oo was recorded at Station 7.

4. Dissolved oxygen

Mid-day values of dissolved oxygen, expressed as percentage saturation (Fig. 7), varied from 47% to 150% along the main channel. These data were analysed to determine if there were any significant differences between: (1) values obtained in the tidal and the lagoon phases; (2) values obtained in the different regions (lower, middle and upper reaches) of the estuary at different salinities (3-10 ^{o}/oo, 11-25 ^{o}/oo and 26-35 ^{o}/oo). The results, with the statistical tests used, are shown below. At the 95% level of probability:

(1) there was no significant difference between the values obtained in the lagoon phase and those obtained in the tidal phase (Fisher-Behrens test);

(2) oxygen values were significantly higher in the lower reaches than in the middle and upper reaches in the 26-35 ^{o}/oo salinity range (Wilcoxon's signed rank test);

(3) there were no significant differences between the oxygen values along the estuary in the 3-10 ^{o}/oo and 11-25 ^{o}/oo salinity ranges (Wilcoxon's signed rank test).

Marked diurnal fluctuations in dissolved oxygen were recorded in both the tidal and lagoon phases (Figs 8 and 9, respectively). The highest

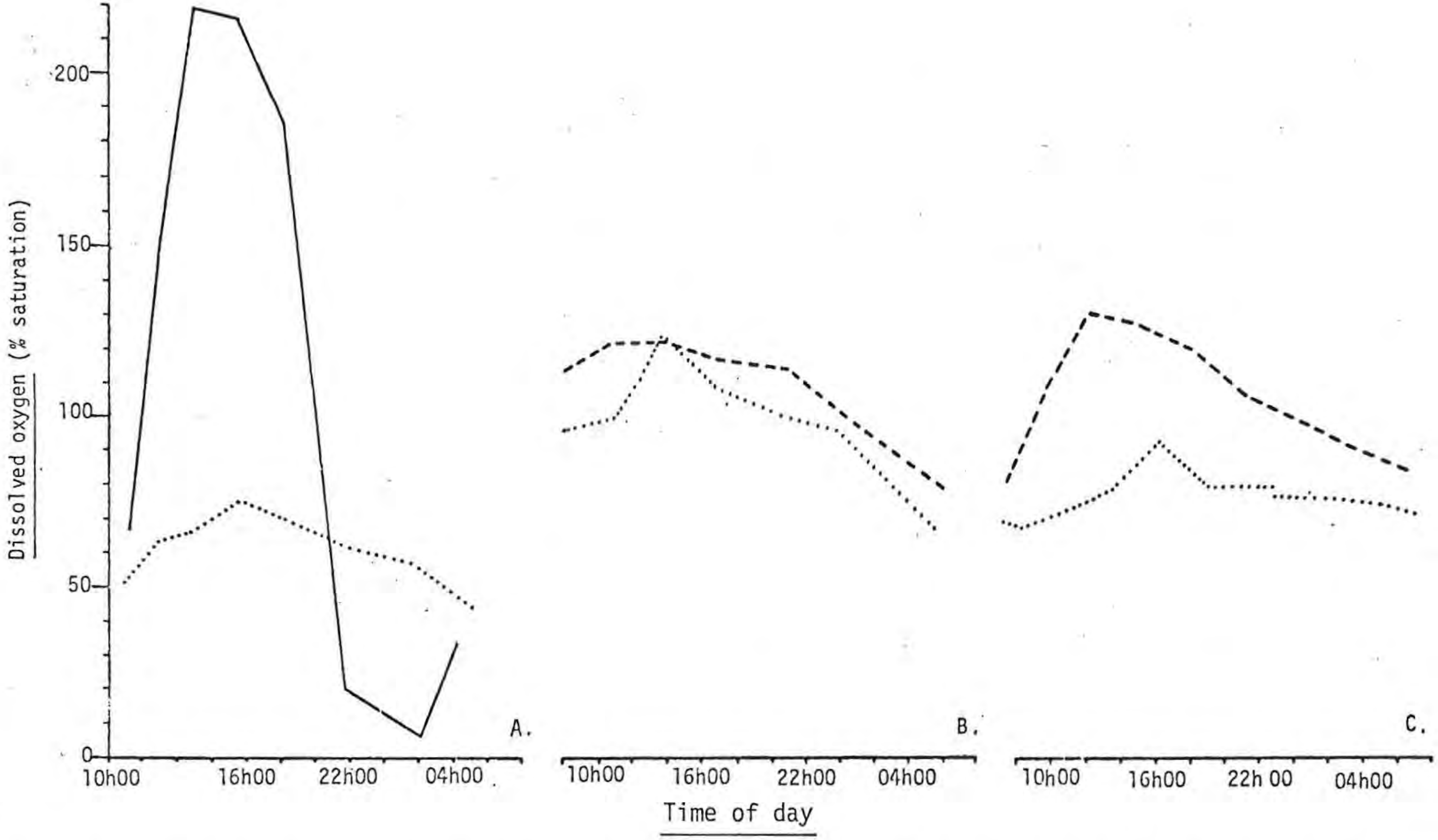

Fig. 13. Diurnal oxygen variations in A. an *Enteromorpha* mat (——) and the adjacent main channel (····). 10-11 February 1977. B. A *Zostera* bed (----) and the adjacent channel (····) when wind stress was high. 14-15 July 1976. C. A *Zostera* bed after floods (····) when the mean salinity was 14°/oo (2-3 June 1977) and after marked seawater penetration (----) when the mean salinity was 35°/oo (17 May 1977).

dissolved oxygen values were found in the dense Zostera bed at Station 3 and in the Enteromorpha mats throughout the estuary, where saturation values in excess of 200% were occasionally recorded. The means of the diurnal values ranged from 136% oxygen saturation during the period of rapid growth of Enteromorpha, to 37% saturation, which coincided with the time of rapid decomposition of the alga. In general, diurnal oxygen fluctuations were higher in the macrophyte beds than in the adjacent channel (Figs 9 and 13a). Differences between these two habitats were often small, however, in the tidal phase or windy conditions when water movement through the macrophyte beds was pronounced (Fig. 13b). After floods when low-salinity, humic-stained water drained through the estuary, diurnal fluctuations were small (67-91% saturation) when compared to those recorded during extensive seawater penetration (80-120% saturation) (Fig. 13c). The mean dissolved oxygen value after floods (77% saturation) was also lower than during seawater inflow (92% saturation).

Fig. 14 shows a summary of the means and ranges of the diel values along the estuary. Application of the Fisher-Behrens test indicated that, at the 95% probability level, there were no significant differences between the means, or the ranges, obtained in the tidal and lagoon phases. Both the means and ranges were significantly higher in the lower reaches of the estuary than in the middle and upper reaches (by Wilcoxon's signed rank test, $P < 0,05$) and suggest that more oxygen is produced in the lower reaches than upstream of this region.

Lower mid-day oxygen values ($\bar{x}$ = 80% saturation) were obtained during September-October than in the rest of the lagoon phase ($\bar{x}$ = 97% saturation), and coincided with the die-off of Enteromorpha mats, when anaerobic conditions developed along the sides of the channel. In the 1977

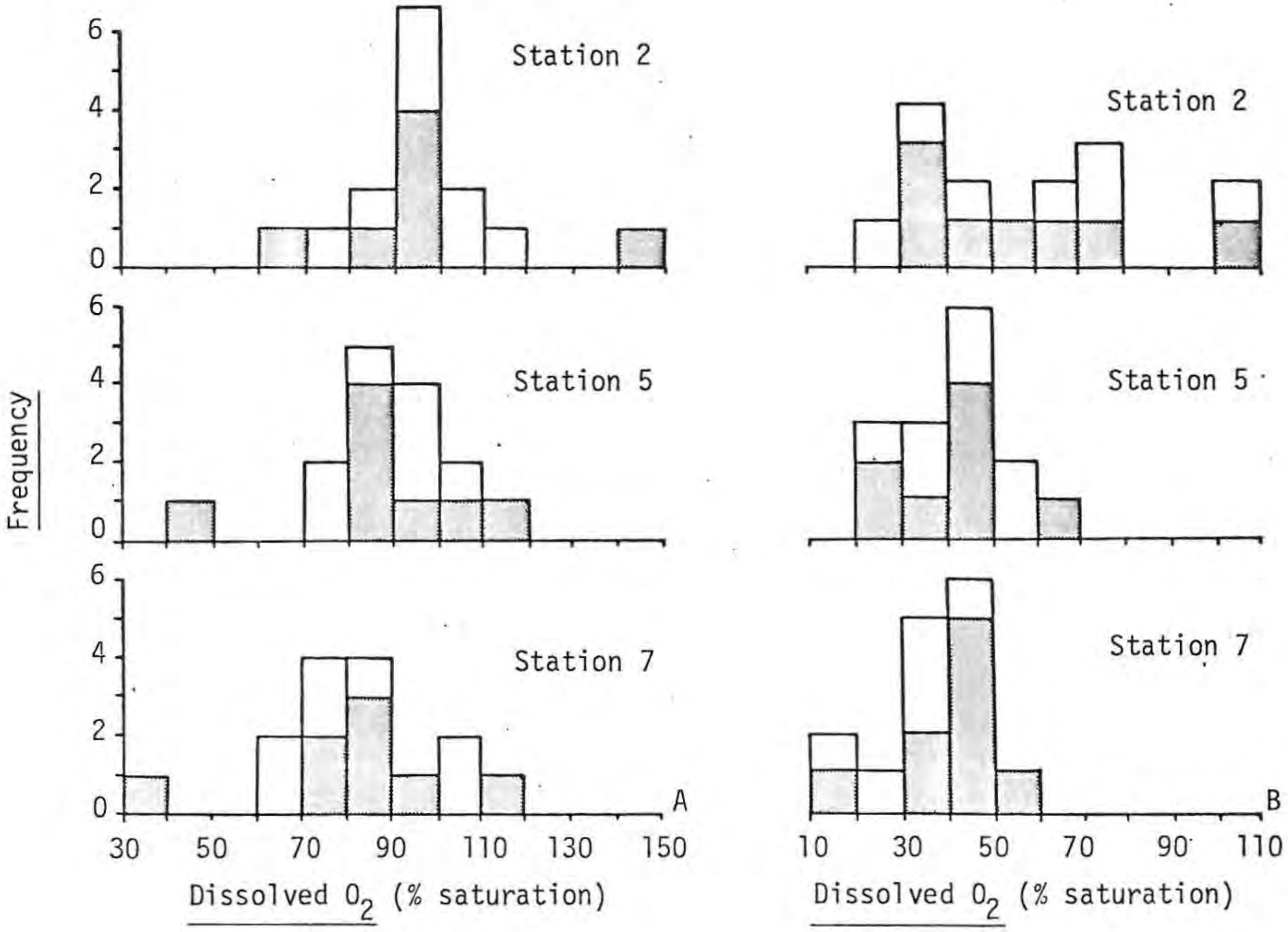

Fig. 14. Frequency histograms of A. the means, and B. the ranges of the % saturation of diurnal dissolved oxygen values recorded on 15 different days between June 1976 and September 1977 at Stations 2, 5 and 7. Range-difference between maximum and minimum saturation values. Shaded bars indicate means and ranges recorded when the mouth was closed.

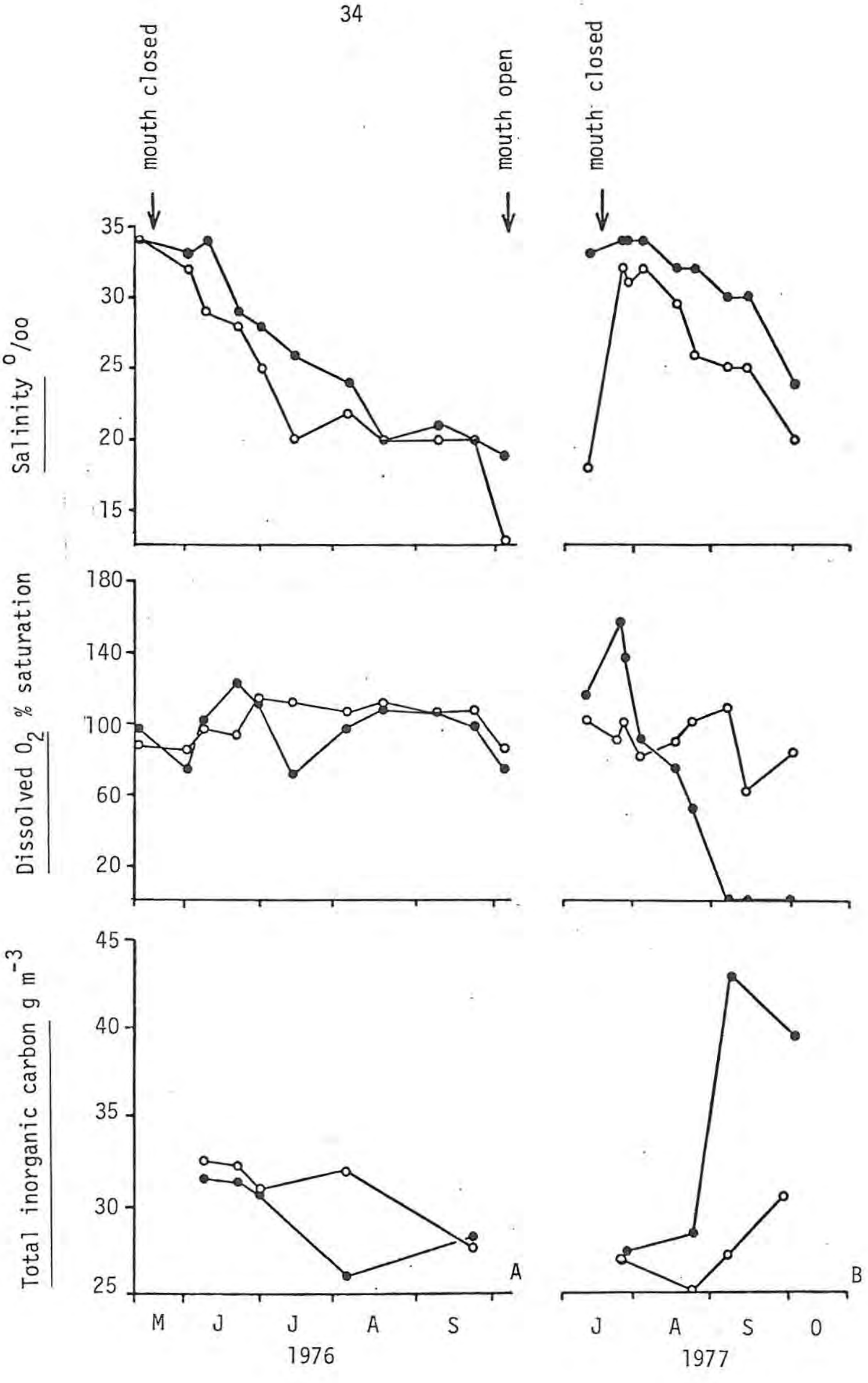

Fig. 15. Mid-day values of salinity, dissolved oxygen and total inorganic carbon at Station 4 in the 1976 (A) and 1977 (B) lagoon phases, at the surface (o) and bottom (●) of the water column. Note the development of anaerobic conditions in the 1977 lagoon phase.

lagoon phase (18 July 1977 onwards), anoxic conditions were also found in parts of the main channel, including Station 4. At the start of the lagoon phase, the water below the halocline was supersaturated with oxygen. This oxygen was gradually depleted until, after seven weeks, anaerobic conditions were formed (Fig. 15b). Salinity data showed that there was very little mixing of surface and bottom water; this was not so in 1976, when mixing occurred and the water column remained well oxygenated (Fig. 15a). Investigation of the anaerobic regions, using SCUBA, revealed that large amounts of decomposing Zostera and Enteromorpha were present below the halocline.

5. pH

After mouth closure, mid-day pH values along the estuary tended to increase above those values normally experienced in the tidal phase (Fig. 7). The mean values obtained at the main channel stations in the lagoon phase (8,2-8,7), were significantly higher ($P > 0,05$) than those measured in the tidal phase (7,7-8,0), using Fisher-Behrens test. The increase was particularly marked in the lower reaches (Station 2, Fig. 7). As with dissolved oxygen, pH values were depressed during inflow of low salinity water (Fig. 7, October 1976; May 1977) and decomposition of Enteromorpha (Fig. 7, September, 1976; October, 1977).

pH values showed a diurnal pattern (Figs 8 and 9) that was to a certain extent affected by tidal action. Ingress of seawater at spring tides raised the mean pH value from 8,09 units (recorded during a neap tide) to 8,26, while at the same time, the range of values decreased from 1,30 pH units (7,70-9,00) to 0,95 units (7,85-8,80). Mid-day pH values were always higher, and diel fluctuations more pronounced in the macrophyte beds than in the adjacent main channel (Figs 8 and 9). Also, pH values decreased from the mouth to the road bridge in both tidal and lagoon phases (Table 7).

The lowest pH, 7,32, was recorded at Station 7 during the floods in May, 1977, and the highest value recorded was 9,81 in an Enteromorpha mat at mid-day on 5 January, 1977, adjacent to Station 7.

6. Total alkalinity

The pattern of seasonal change in total alkalinity was not distinct (Fig. 7). However, the general trends followed those of pH:

i. there was a significant decrease ($P < 0,05$) in mid-day alkalinity values from the mouth to the road bridge, in both the tidal and lagoon phases (Table 7) as indicated by Wilcoxon's signed rank test;

ii. the mid-day alkalinity values were significantly higher ($P < 0,05$) in the lagoon phase ($\bar{x} = 2,3$ me ℓ^{-1}) than in the tidal phase ($\bar{x} = 2,0$ me ℓ^{-1}), using Fisher-Behrens test.

Table 7. Mean mid-day values for pH and total alkalinity at Stations 2, 5 and 7 in the tidal and lagoon phases.

Parameter	Station	Tidal phase	Lagoon phase
pH	2	8,0	8,7
	5	7,9	8,4
	7	7,7	8,2
Total alkalinity me ℓ^{-1}	2	2,20	2,52
	5	1,82	2,24
	7	1,68	2,11

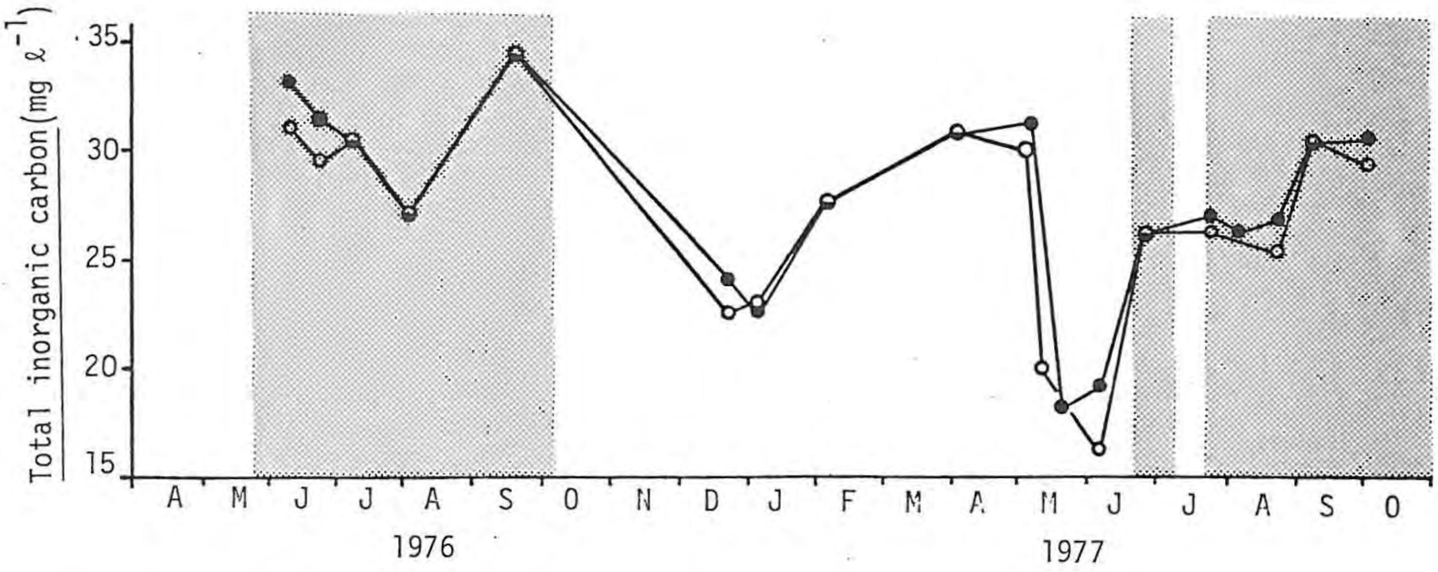

Fig. 16. Total inorganic carbon concentrations at the surface (o) and bottom (●) of Station 5 in 1976-1977. Note fall and then rise in concentrations in the lagoon phases. Shaded area indicates when mouth was closed.

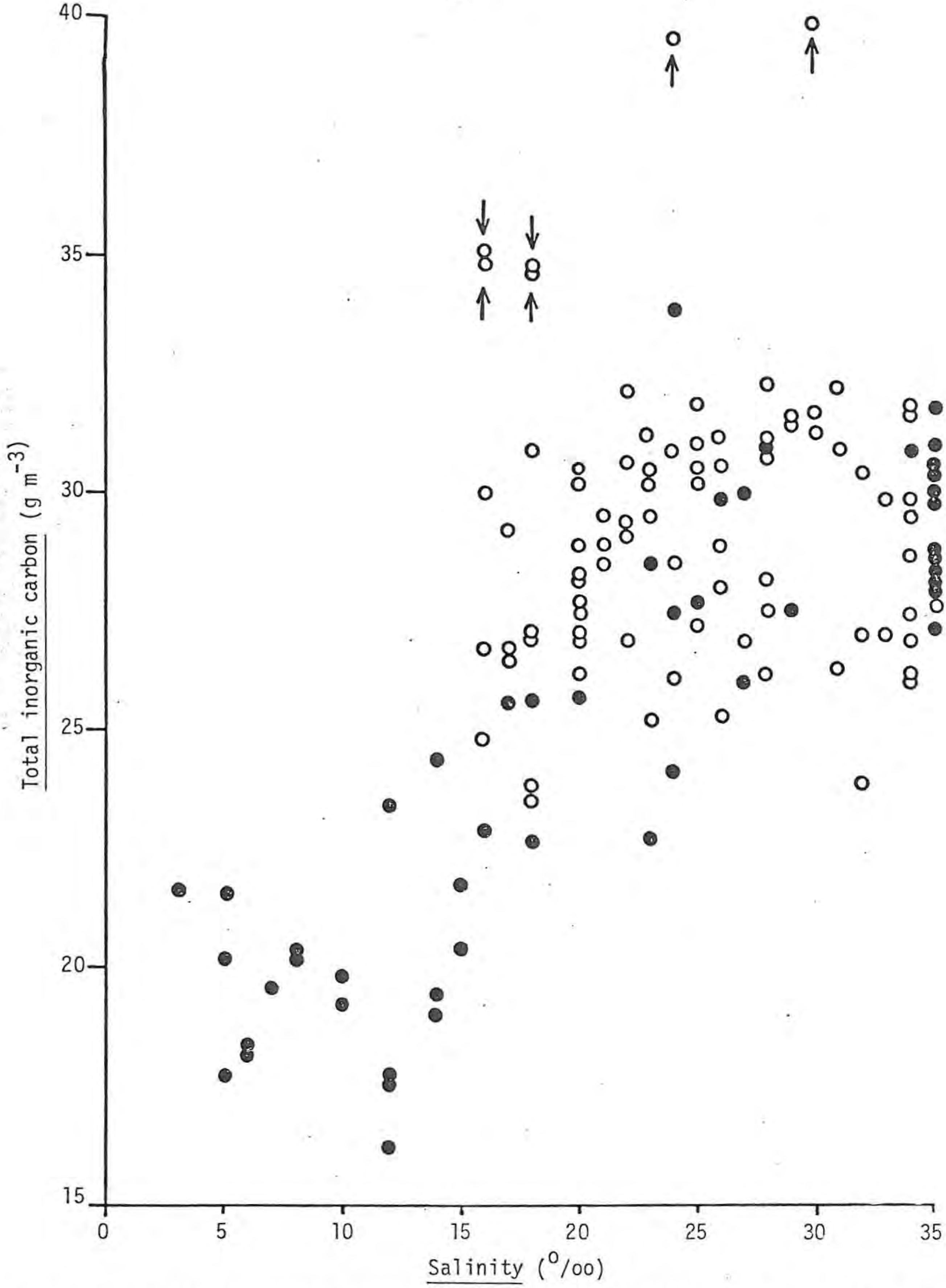

Fig. 17. Total inorganic carbon concentrations at Stations 2, 4, 5 and 7 during the tidal (●) and lagoon (○) phases of 1976 and 1977. The arrowed values were recorded in August and September of the lagoon phases. Note that, in general, the concentration decreases with a decrease in salinity.

The lowest values were measured during the floods in May, 1977, when the values were all lower than 1,6 me ℓ^{-1}. The highest value, 3,2 me ℓ^{-1}, was recorded from the anaerobic bottom waters of Station 4 in the 1977 lagoon phase.

7. Total inorganic carbon and total carbon dioxide

Trends in both of these parameters were identical; therefore, only the fluctuations in total inorganic carbon will be described here. The seasonal changes in total inorganic carbon depicted in Fig. 16 were typical of all the stations: a decrease was measured at the start of the lagoon phases, reaching a minimum in August. Then there was a sharp rise from the period August-October. In the tidal phase, there was also a considerable variation. Could these fluctuations be explained by changes in salinity?

Fig. 17 shows the total inorganic carbon content plotted against salinity: in general, there was a decrease in carbon with a decrease in salinity. Assuming that in the lagoon phase the estuary is diluted with surface water from Swartvlei, which had a mean salinity of 10 $^{o}/oo$, then the drop in total inorganic carbon from June 1976 to August 1976 could be explained mostly by dilution (Table 8). However, from August onwards in both lagoon phases there was a rise in total inorganic carbon despite a decrease in salinity. This rise, therefore, must be due to other factors. The decay of *Enteromorpha* mats in this period suggests that the alga could be responsible for the rise in inorganic carbon content of the water.

Table 8. Theoretical and actual total inorganic carbon values along the Swartvlei estuary in the 1976 lagoon phase.

Station	Date	Salinity	Total inorganic carbon values gm^{-3}	
			Theoretical*	Actual
2	10 June, 1976	33	-	32,0
	5 August, 1976	23	26,0	27,4
4	10 June, 1976	32	-	31,9
	5 August, 1976	23	26,0	28,2
5	10 June, 1976	28	-	32,7
	5 August, 1976	19	26,3	27,1
7	10 June, 1976	24	-	31,0
	5 August, 1976	17	25,5	26,1

* Assuming dilution with water of salinity 10 $^{o}/oo$ and total inorganic carbon content of 20,0 gCm^{-3}).

2.2: The effect of decaying Enteromorpha on total inorganic carbon in the water column

The results of the regular sampling programme showed that a rise in total inorganic carbon along the estuary occurred at the same time as the rapid decomposition of Enteromorpha. This suggested that the two processes were related. Therefore, the effect of decay of this alga on the pH and total alkalinity of the water column was investigated.

MATERIALS AND METHODS

Two experiments were performed. In the first experiment, each of four 15 ℓ plastic bowls was filled with 8 ℓ of unfiltered estuary water

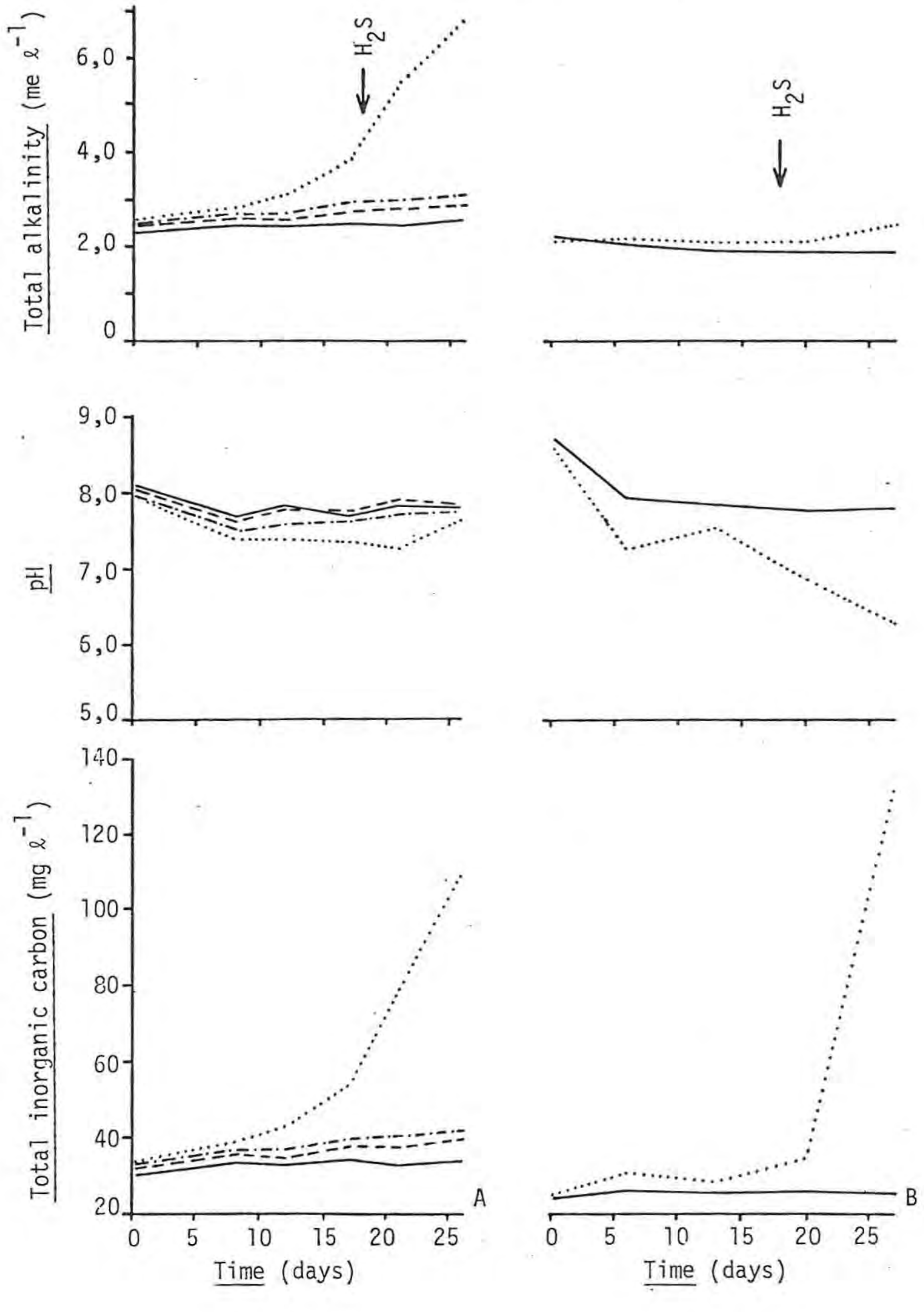

Fig. 18: A. The effect of sediment, dead Zostera and Enteromorpha on the total alkalinity, pH and inorganic carbon content of estuary water. For explanation see text. —— estuary water; ---- estuary water and sand; -·-·- estuary water, sand and Zostera; ..... estuary water, sand, Zostera and Enteromorpha. B. The effect of decaying Enteromorpha on the total alkalinity, pH and inorganic carbon content of estuary water. For explanation see text. —— estuary water; .... estuary water and Enteromorpha.

(S = 26 ^{o}/oo). 1 kg wet weight of sand from the lower tidal flats was placed in three of the bowls. 20 g air-dry weight of Zostera, collected from the eulittoral at Station 4, were placed in two of these three bowls. 100 g wet weight of apparently healthy Enteromorpha, also from Station 4, was put in one of the bowls containing Zostera. The bowls were monitored for temperature, pH and total alkalinity at 0, 8, 12, 17, 21 and 26 days after commencement. Water lost via evaporation was replaced with distilled water.

In the second experiment, each of two 15 ℓ bowls was filled with estuary water (S = 26 ^{o}/oo) and 100 g wet weight of Enteromorpha were placed in one of the bowls. The bowls were monitored in the same way as in the first experiment.

All bowls were kept in the laboratory out of direct sunlight.

RESULTS

The results of the two experiments are shown in Fig. 18. In both experiments, the pH values were lower, and the total alkalinity values higher in the bowls containing Enteromorpha. A distinct smell of H_2S was noticeable in these bowls after about 18 days. In the bowl with Enteromorpha, Zostera and sand, a black layer of reduced sediment was present underneath the rotting Enteromorpha, where the alga was in contact with the sand. The upper layer of Enteromorpha, which floated on the surface of the water, remained bright green and apparently healthy.

Calculation of the total inorganic carbon content in the bowls revealed that values were always higher in the bowls containing Enteromorpha. Values reached a maximum when the state of decay was advanced (Fig. 18). Therefore the decay of Enteromorpha, in which organic carbon is converted to inorganic carbon, increases the total inorganic carbon content of the surrounding water. This decay is probably a major causative factor in the rise of inorganic carbon throughout the closed estuary between August and October.

2.3: Precipitation of humic material

Another important phenomenon that occurs in the estuary is the precipitation of humic material. Evidence for this precipitation is as follows:

i. the catchment area enclosed by the Swartvlei estuary is 9,1 km^2, about 3% of the total catchment area of the Swartvlei system. The increase in water volume in the lagoon phase must therefore be largely due to water entering from Swartvlei. This would result in dilution of the estuary by humic-stained water with a salinity of about 10 ^{o}/oo. The estuary water could therefore be expected to become progressively darker after mouth closure. Measurements of P.A.R. (photosynthetically active radiation) in the 1976 lagoon phase, using a Lambda Instruments Corp. LI-185 quantum/radiometer, showed the opposite: there was a general rise in the percentage of P.A.R. reaching the bottom of the estuary after mouth closure (Fig. 19).

ii. Observations in both the tidal and lagoon phases using SCUBA revealed that bands of dark brown water were present in the middle of the water column, usually associated with haloclines.

Precipitation of humic material could explain why there is a wide scatter of percentage light transmission values at different salinities (Fig. 20). Preliminary experiments at Swartvlei indicated that humic acids were flocculated from Karatara River water by the addition of concentrated

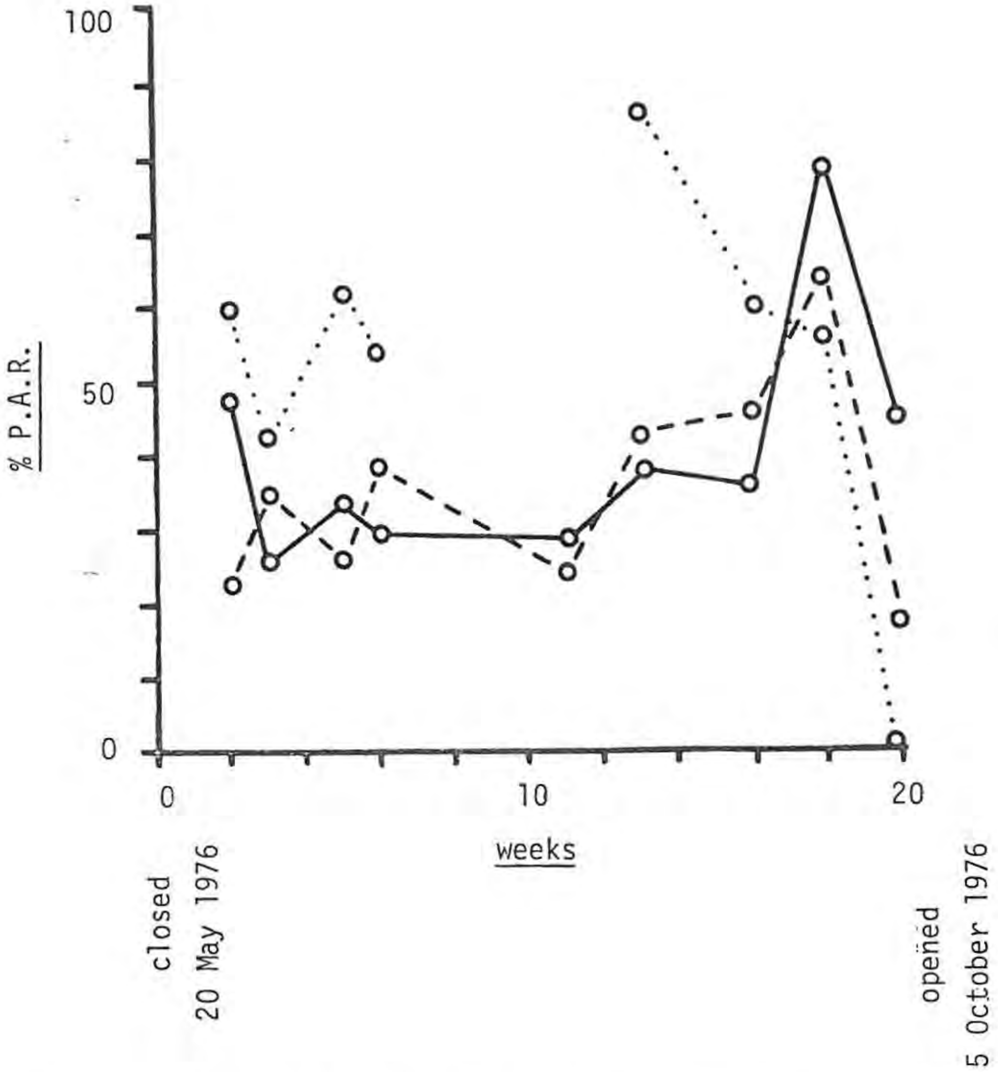

Fig. 19: Percentage of P.A.R. (photosynthetically active radiation) reaching the bottom of the estuary at Stations 2 (o——o), 4 (o--o) and 7 (o····o) during the 1976 lagoon phase.

hydrochloric acid (Dr C. Howard-Williams, pers.comm.). Addition of sodium hydroxide is reported to have the same effect (Weber, 1975). Humic material is also flocculated when mixed with seawater. Reduction of the negative charges on the humic complexes by cations in seawater, decreases repulsion between the complexes. Hence there is a tendency to flocculate when the particles collide (Burton, 1976).

It was decided, therefore, to investigate the effects of both salinity and pH on water from the largest inflow into Swartvlei, the Karatara

River. The amount of organic matter present in this water was also measured, to give some idea of the possible importance of river inflow as a potential source of allochthonous organic material.

MATERIALS AND METHODS

Unfiltered seawater (S = 35 ^{o}/oo) was diluted to 25 ^{o}/oo and 15 ^{o}/oo with distilled water. 50 ml of each of the 35 ^{o}/oo, 25 ^{o}/oo, 15 ^{o}/oo and 0 ^{o}/oo (distilled water) samples were added to 50 mℓ Karatara River water (S = < 0,5 ^{o}/oo, pH = 4,6) in 100 ml boiling tubes. The pH was then adjusted to 6,0 ($\pm$ 0,1) using dilute ($\pm$ 1N) HCl and NaOH. This

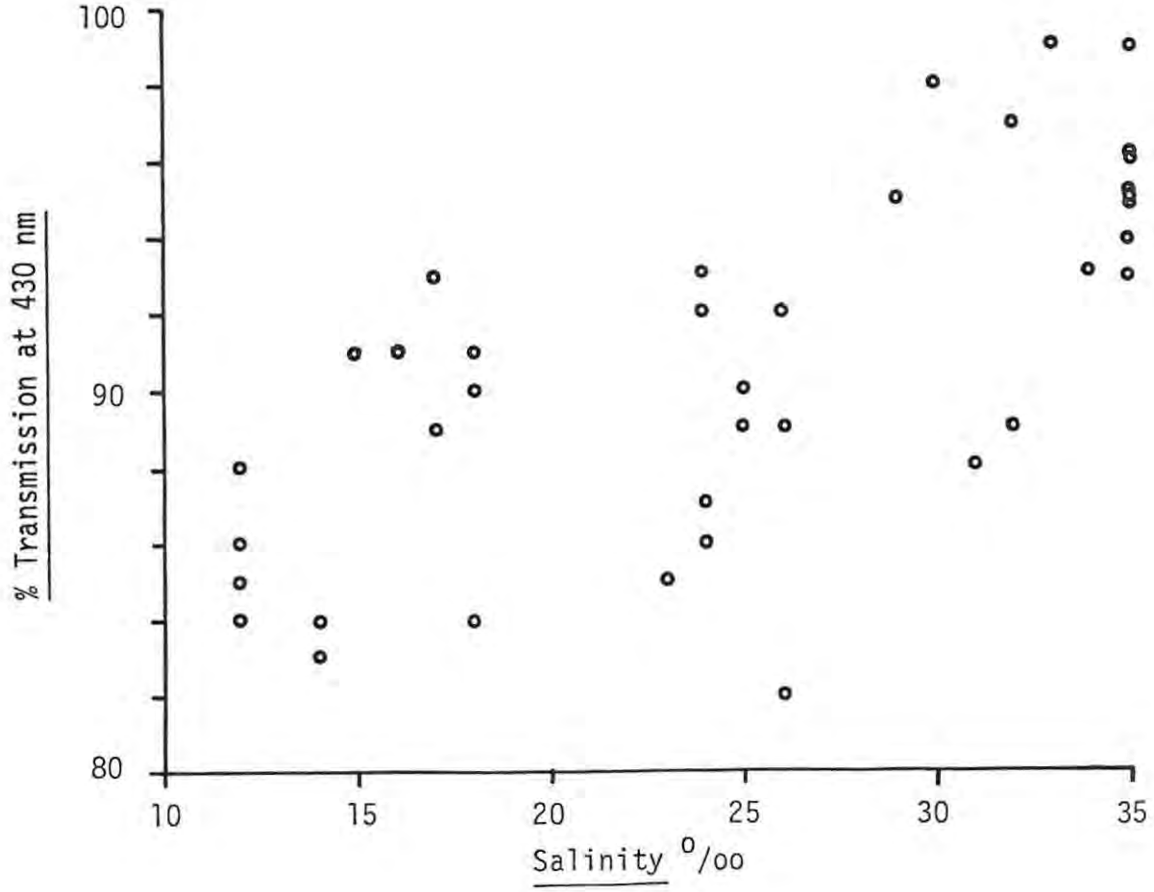

Fig. 20: The percentage light transmission at 430 nm of Swartvlei estuary water at different salinities, in 1977.

process was repeated to obtain pH values of 7,0, 8,0, 9,0 and 10,0 in each of four further sets of tubes. The tubes were then kept in a dark cupboard, and the % transmission of the samples at 430 nm was read after 10 days using a Pye Unicam 6000 spectrophotometer. The presence or absence of a precipitate was noted at the same time.

For the determination of the amount of organic material present in the river water, 200 ml of unfiltered Karatara water was evaporated to dryness on a steam bath. The residue was cooled in a dessicator and weighed, and then ashed in a muffle furnace at 500°C for 2 h. The weight of organic matter was calculated by difference.

RESULTS

Precipitates were noted in 6 of the 20 tubes after ten days (Table 9). Precipitation was dependent on both salinity and pH: the higher the salinity, the lower the pH at which flocculation occurred. In none of the tubes was flocculation complete. The % transmission of the mixtures remained at 30% in the tubes where no flocculation had occurred, and was 59% in the tube with the most precipitate i.e. in Karatara water plus 35 ^{o}/oo seawater at a pH of 10. Therefore, a maximum of half the humic material had been flocculated at the end of ten days.

Karatara River water was found to contain 39,7 mg of residue in 200 mℓ. Of this amount, 16,0 mg was present as organic material. In 1 ℓ, therefore, there would be 80 mg of organic matter.

Salinities above 17,5 ^{o}/oo and pH values above 8,0 are almost invariably present in the estuary during most tidal cycles and also in the lagoon phases. It is not unreasonable to conclude that humic material is being precipitated continuously, and estimating from the amount present in river water, could represent a significant input of organic matter into the estuary.

Table 9. The results of the experiment to determine the effect of pH and salinity on flocculation of humic material. For explanation see text. - no precipitate; P - precipitate.

			pH		
Karatara + distilled water	6	7	8	9	10
Karatara + distilled water	-	-	-	-	-
Karatara + 15 ^{o}/oo S	-	-	-	-	P
Karatara + 25 ^{o}/oo S	-	-	-	P	P
Karatara + 35 ^{o}/oo S	-	-	P	P	P

2.4: Discussion

The hydrographical studies (Moes, 1976) and salinity data in the present study have shown how the estuary fills up with seawater from neap to spring tides, and then drains slowly from spring to neap tides. The residence time of some of the water in the estuary could be as long as 10-14 days. The 'piston' effect of the seawater front ensures that plant material produced at any one point in the estuary is slowly distributed throughout the whole estuary. Fronds of Zostera found at the rail bridge had grown in the lower reaches of the estuary, as indicated by their periphyton.

After mouth closure, wind-induced water movement ensured that both horizontal and vertical salinity gradients were reduced (Fig. 10).

When vertical mixing was incomplete, e.g. in the second lagoon phase of 1977, anaerobic conditions developed in the deeper regions of the estuary. This indicates the importance of wind to induce turbulence in the absence of tidal action.

The effects of seasonal mouth closure have been studied in two other Cape estuaries: the Klein River Estuary at Hermanus (Scott *et al.*, 1952) and Milnerton Estuary, Cape Town (Millard and Scott, 1954). In the former, freshwater inflow balanced evaporation, so normal salinity gradients were maintained. In the latter, evaporation exceeded inflow, resulting in marked salinity increases. During closure the salinities in the Milnerton Estuary reached 56 $^{o}/oo$ at the mouth and 375 $^{o}/oo$ in the upper reaches (seawater = 35 $^{o}/oo$). This resulted in marked changes in the biota. In the Swartvlei estuary, freshwater inflow exceeded evaporation, and hence there was a decline in salinity. After nearly twenty weeks of isolation from the sea in 1976, salinities along the estuary were still within the limits experienced in the tidal phase, and there was no sign of impoverishment of the fauna. The submersed vascular macrophytes also appeared to remain healthy, except for those under the rotting *Enteromorpha* mats.

Inflow of water from Swartvlei 'lake' could provide a substantial energy subsidy in the form of humic material, which is flocculated in moderately saline water (7,5-17,5 $^{o}/oo$) and high pH (8,0-10,0). At a concentration of organic matter of 80 mg l^{-1}, and an estimated inflow of 38 x 10^{6} m^{3} yr^{-1}, river water would annually provide the Swartvlei system with 3 400 tonnes of dissolved and particulate organic matter. The relevance of this input is discussed in the Final Comments (p.112).

The results of this study stress the importance of the macrophytes in regulating physico-chemical conditions in the Swartvlei estuary, particularly dissolved oxygen. The diurnal range of % oxygen saturation values can be almost as large as the seasonal range in mid-day values e.g. at Station 3, a Zostera bed (Table 10). Of the macrophytes present in the estuary, Enteromorpha appears to have the greatest influence on dissolved oxygen and total inorganic carbon. Floating mats of this alga developed in June and reached maximum cover at the end of July, in both the lagoon phase of 1976 and the tidal phase of 1977. Therefore, mouth closure is purely incidental to mat development, and merely prevents large amounts of the alga from being flushed out of the estuary.

A possible factor that influences growth of Enteromorpha is temperature. The rapid growth in June occurs when mid-day water temperatures are about 16°C (Fig. 7).

Table 10. A comparison between the seasonal and diurnal values for temperature, salinity, dissolved oxygen and pH obtained at Station 3 (a Zostera bed).

	Temperature °C		Salinity °/oo		O_2 % Saturation		pH	
	Min	Max	Min	Max	Min	Max	Min	Max
Seasonal* range	10,0	29,1	6	35	43	205	7,45	9,17
Diurnal** range	17,9	28,0	15	35	75	208	8,45	9,44
Date	10 February 1977		27-28 January 1977		22-23 June 1977		13-14 September 1977	

* Values recorded during mid-day sampling programme in different seasons.

** Values recorded on dates shown, at different times of the day.

The temperature remains below 16°C until the end of August, when a rise above this temperature coincides with the decay of *Enteromorpha*. It is possible, therefore, that the mats only thrive when the temperature is less than 16°C. Low temperature growth ($< 16^{\circ}C$) is also recorded for *E.clathrata* (Roth) J.Ag. in a Massachusetts estuary (Conover, 1958), and winter growth is noted in *E.intestinalis* L. (Link.) and *E.prolifera* J.Ag., in New South Wales (Baas Becking and Mackay, 1956).

PART 3 - PHOSPHORUS DYNAMICS

With the realisation of the importance of phosphorus as a limiting nutrient, a wealth of literature has accrued on its cycling in different ecosystems. As pointed out by Correll et al. (1975) however, there have been few field studies of phosphorus cycling and flux in estuaries.

South African estuaries are no exception. Information on the dynamics of phosphorus in these estuaries is confined to a description of seasonal changes of phosphorus in the water column e.g. in St. Lucia estuary (Johnson, 1976) and in Swartvlei 'lake' (Robarts, 1973). Other studies which give measurements of phosphorus in the water column, though not on a seasonal basis, are those by Korringa (1956) for the Wilderness Lakes and the Keurbooms Lagoon, and a series of unpublished reports by the National Institute for Water Research (N.I.W.R.) on physico-chemical parameters of Kosi Bay estuary, Richards Bay estuary, Amanzimtoti Lagoon, Ifafa Lagoon, Bashee Estuary and Swartkops Estuary.

Due to the paucity of data on phosphorus cycling in estuary, particularly on the roles of seawater inflow and the macrophyte beds, it was decided to investigate phosphorus dynamics in the Swartvlei estuary. This estuary presents an ideal opportunity for such a study, as there is no evidence to suggest that artificial phosphorus enrichment occurs under normal conditions.

In general, seawater is far more important than river water in providing estuaries with phosphorus (Odum, 1971). This conclusion was also reached by Leach (1971), who demonstrated that in the Ythan estuary in Scotland, the bulk of the phosphorus entered the estuary via large volumes of seawater. This was despite the fact that inflowing river water had a far higher phosphorus concentration than seawater.

Macrophytes are reported to play an important role in phosphate transfer in other aquatic ecosystems. For example, McRoy and Barsdate (1970) and McRoy *et al*. (1972) showed that *Zostera marina* L. absorbed phosphate from the sediments and then released it into the overlying water via the leaves, i.e. was a nutrient pump. This could encourage the growth of epiphytes on *Zostera* (Harlin, 1975). Non-attached macrophytes, e.g. the alga *Enteromorpha* have been shown to accumulate phosphate from the water column (Baas Becking and Mackay, 1956).

Sandbar formation and subsequent closure of the mouth of the Swartvlei estuary prevents import of nutrients from the sea and export of material from the estuary. In the tidal phase, large amounts of *Zostera* leaves are flushed out of the estuary with ebb tides. McRoy *et al*. (1972) considered export of *Zostera* leaves from Izembek Lagoon, Alaska, to be a "substantial contribution of phosphorus to the open sea", although the magnitude of this export was not determined.

The present study attempts to assess the importance of both tidal exchange, and the resident aquatic macrophytes, on phosphorus flux in the Swartvlei estuary from data on the following processes:

1. tidal import and export of phosphorus, including loss of particulate phosphorus in the form of *Zostera* leaves;

2. changes in the phosphorus concentration of the water column following mouth closure;

3. diurnal phosphorus variations in the water column inside *Zostera* beds, *Enteromorpha* mats and the main channel.

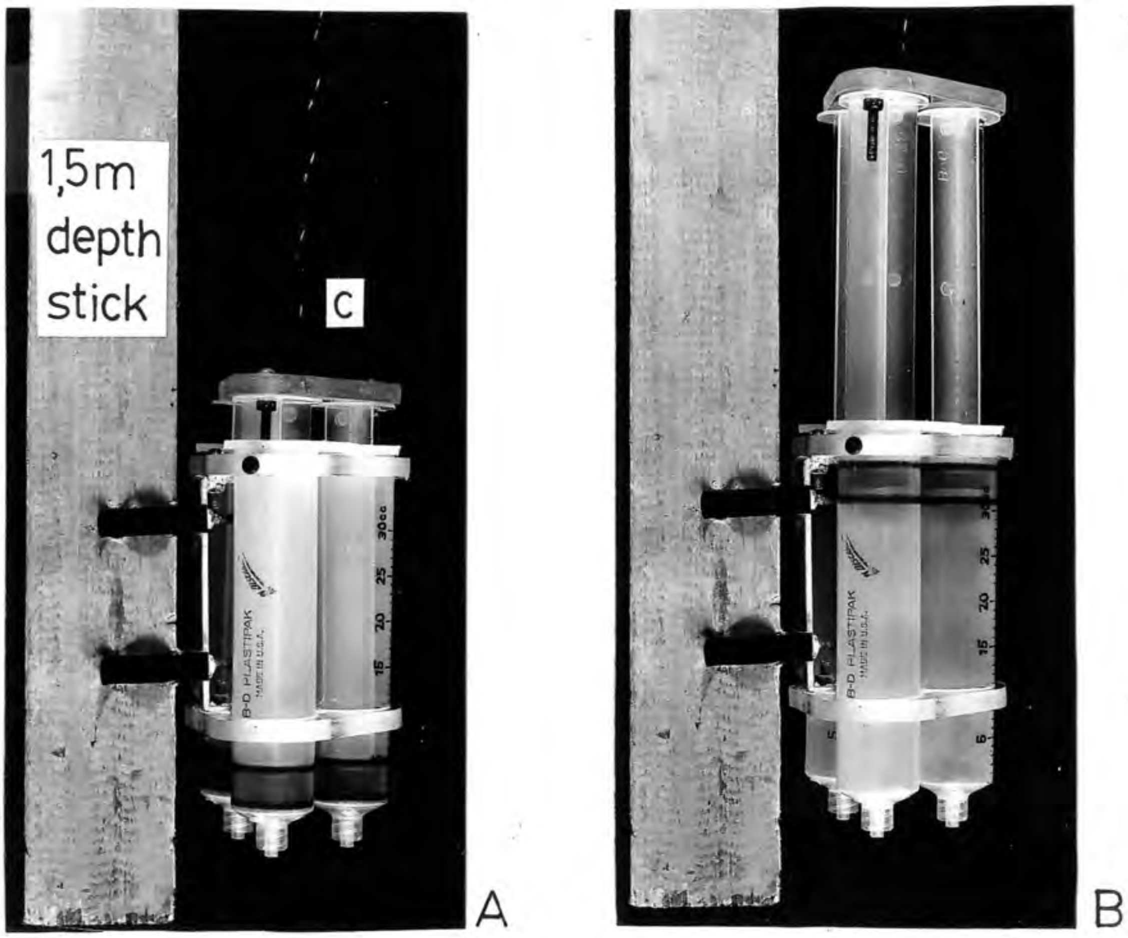

Fig. 21: Syringe apparatus which was used to sample water from inside and below Enteromorpha mats. A - before, and B - after filling. The apparatus, operated manually by a cable (c), was designed by A. Bruton.

MATERIALS AND METHODS

1. Sampling of the water column

Water for phosphorus analysis was collected using a Friedinger bottle. 350 ml polythene bottles, rinsed with ambient water prior to filling, were used to store samples. Samples were kept in the dark until being filtered at the field laboratory, approximately 3 hours after collection. If the samples could not be analysed on the date collected, as in the diurnal studies, they were frozen and analysed after 1 or 2 days.

Water from amongst and below the Enteromorpha mats was collected with a group of syringes attached to a depth stick. The syringes were filled by manual operation of a cable (Fig. 21).

2. Determination of soluble reactive, total dissolved and total phosphorus

a. Soluble reactive phosphorus (SRP)

Determined by the method of Golterman and Clymo (1969), modification 'c', in which the sample is passed through a 0,45 μm Millipore filter and allowed to react with an ascorbic acid-molybdate-tartrate mixture. The blue complex obtained is then extracted with hexanol, and its extinction measured at 690 nm.

b. Total phosphorus (TP)

Determined by the method of Strickland and Parsons (1968) in which the unfiltered sample is digested with perchloric acid, liberating phosphorus as inorganic phosphate. This is then allowed to react with an ascorbic acid-molybdate tartrate mixture, and the extinction measured at 885 nm.

c. Total dissolved phosphorus (TDP)

Determined by the same method as for total phosphorus, except that the sample was first passed through a 0,45 μm Millipore filter.

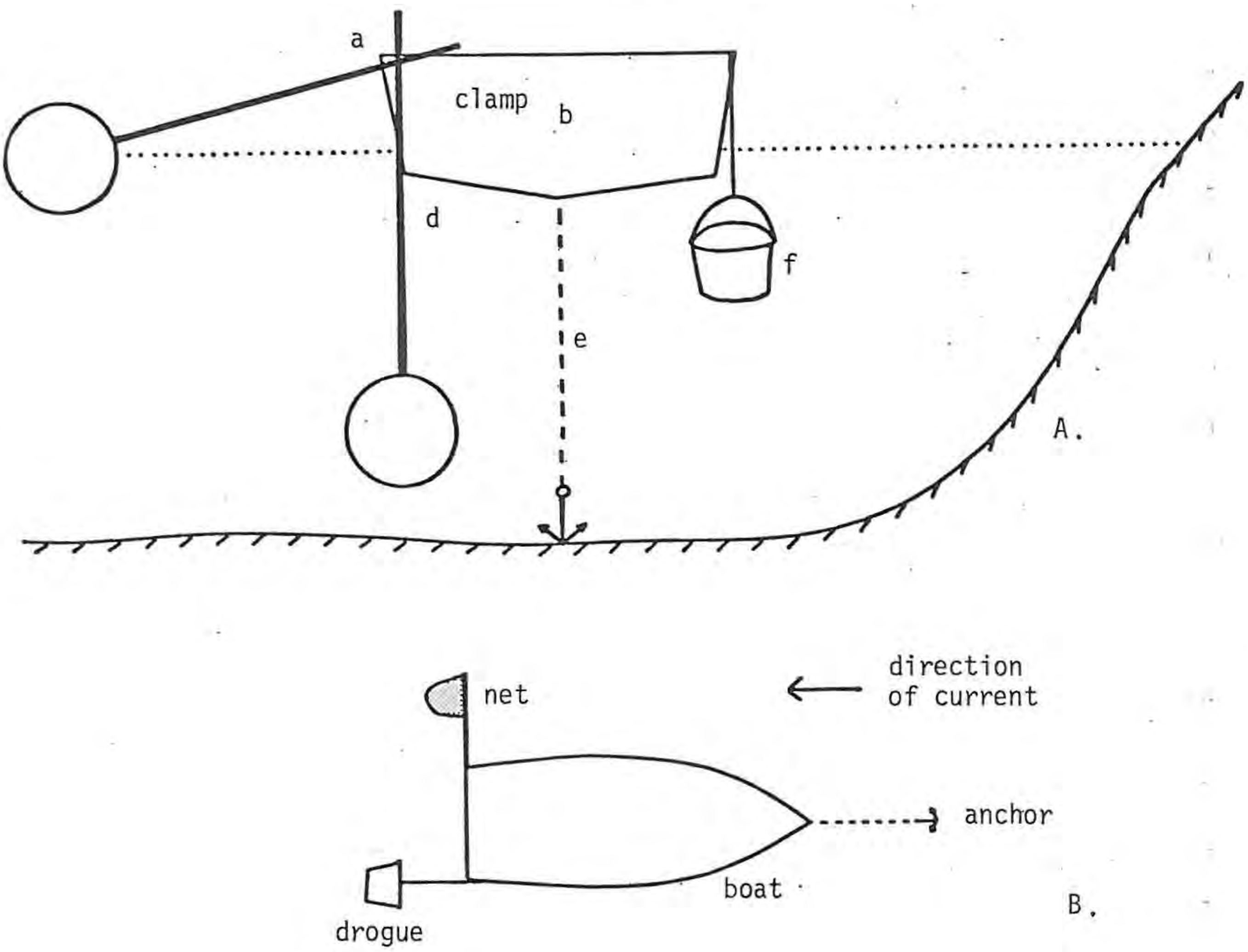

Fig. 22. Collection of floating vegetation in the tidal phase.
A. The handle of the net (a) was clamped to the stern of the boat (b) so that the mouth of the net was half submerged (c). Midwater samples were collected by clamping the handle at right angles to the surface (d). Care was taken not to align the net with the anchor rope (e). This was achieved by tying a large plastic bucket (f) to the opposite side of the boat, so that the bucket acted as a drogue.
B. A plan of the boat with the net and drogue in position. Collections were made 1,1 km from the mouth, over 4 tidal cycles in February and March, 1977.

3. Phosphorus flux due to tidal exchange

Hourly samples over one complete tidal cycle were collected at the surface, midwater and bottom of the water column, in the main channel 1,05 km from the mouth. Samples collected during ebb tide were pooled and analysed for TP and TDP, for comparison with the integrated flood tide sample. Data on water levels from the adjacent tide recorder, and estimates of water volumes throughout the estuary at different water levels (provided by N.R.I.O.) were used to determine the volume of tidal inflow. These data, along with the TP and TDP concentrations during the ebb and flood tides, were used to calculate the amount of phosphorus entering and leaving the estuary on three tidal cycles in February-March, 1977.

4. Export of Zostera from the estuary

a. Collection of leaves

Collections of loose Zostera in the water column were made at the same site, and throughout the same tidal cycles as those monitored for exchange of phosphorus. In addition, one spring tidal cycle was monitored. Drifting vegetation was found both on the surface and suspended in the middle of the water column. A method was therefore designed to sample both of these components.

A net, with a mesh size 2 mm and a diameter of 0,312 m, was clamped to the anchored boat. The mouth of the net was positioned in the centre of the channel, at right angles to the direction of flow and with the greatest width at the surface of the water (Fig. 22). After 15 minutes, the net with the trapped vegetation was carefully removed. Any fronds wrapped around the mouth, but not entirely inside the net, were broken off and material outside the circumference of the mouth was discarded. This procedure was repeated with the net clamped at midwater level.

Samples were taken every hour throughout ebb and flood tides from 05h00 to 17h30.

Collections at five different points across the section showed that at the particular site chosen for the tidal studies, the amount of vegetation collected was 70% of the mean value obtained for all the sites. The collection site was therefore regarded as being fairly representative of the whole section. Analysis of samples collected at the bottom and midwater of the water column, using Wilcoxon's signed rank test, showed that there was no significant difference ($P < 0,05$) between the masses of the two samples. Samples collected at midwater were therefore considered to be representative of the sub-surface component of the loose vegetation.

b. Calculation of net loss of leaves

The amount of vegetation collected per hour for the whole section was estimated using the equation:

$$\text{Mass of vegetation section}^{-1}\ h^{-1} = \left[(W/0{,}312) \times Ms \times 4\right] + \left[(A/0{,}072) \times Mm \times 4\right] \qquad (1)$$

where W = width of section in metres

0,312 = width of net in metres

Ms = mass of vegetation collected on the surface

4 = conversion of 15 minute sample to 1 h

A = cross-sectional area of section in m^2

0,072 = area of mouth of net in m^2

Mm = mass of vegetation collected at midwater.

The width of the section and its cross-sectional area were calculated for each hour using the morphometry of the section (Anon, 1975) and water level data from the adjacent tide recorder. The amount of vegetation collected in the flood tide was subtracted from that collected in the ebb, to calculate the total amount of vegetation that was lost from the system.

c. Analysis of Zostera leaves for phosphorus

Each of five 2,0000 g samples of Zostera leaves, with the periphyton attached, were mineralised (Anon, 1971). The total phosphorus was then determined colorimetrically, using the mixed reagent described on p. 54.

5. Changes in the phosphorus concentration of the water column after mouth closure

Water samples were collected for TDP analysis from the established stations in the main channel at mid-day, and at a depth of 1 m. Sampling frequency was increased from once a month in the 1976 lagoon phase to every two weeks in the 1977 lagoon phase.

The amounts of phosphorus present in the water column on different dates were calculated from data on phosphorus concentration and water levels, as described on p. 56.

6. Phosphorus concentrations in the sediments and in Enteromorpha

Sediment samples from Stations 1-8 were collected on 19 September 1977 (lagoon phase), with a 120 mm long, 105 mm diameter cylindrical corer. Interstitial water was removed by Büchner filtration through Whatman GF/C glass fibre filter paper. SRP and TDP concentrations were then determined by the methods described on p. 54.

In addition, the biomass of the Enteromorpha mats in the 1976 lagoon phase was estimated. This was done so that the amount of phosphorus present in the alga could be calculated. The biomass estimate was undertaken immediately prior to the opening of the mouth (5 October 1976), when the area covered by Enteromorpha mats was 9,8 hectares. Ten random 0,0225 m^2 quadrat samples were collected from the mats along the estuary. The samples were dried to constant weight in a drying oven at $100^{o}C$, allowed to cool in a desiccator, and then weighed. The alga was then analysed for phosphorus by the same method as for Zostera (p.58).

7. Diurnal variations inside the macrophyte communities

a. Sampling sites

Diurnal studies were conducted in the Zostera beds and Enteromorpha mats at Station 3, and in the adjacent main channel at Station 2, in both the tidal and lagoon phases between 29 June and 14 September, 1977.

b. Enclosure of sampling sites

The results of the diurnal studies (p.32) indicated that tidal- and wind-induced water movement through the macrophyte beds was often pronounced. Exchange of water between the macrophyte beds and the adjacent channel would tend to modify any diurnal variations that may occur in dissolved phosphorus in either of the two compartments.

An enclosure, made from P.V.C. tubing and black polythene sheeting described in Appendix 2), was therefore used to minimise water movement within the macrophyte beds. It was designed to rise and fall with fluctuating water level, and to have a minimum shading effect on the enclosed community. It was hoped that the size of the enclosure (1,5m I.D., depth 1-2 m) would be large enough to circumvent problems associated with the enclosure of macrophytes. These are discussed in Part 4 (p.80).

c. Sampling procedure

The enclosure was first rinsed in the main channel, and then placed at Station 3 at 08h00. Surface samples were collected at approximately 3 h intervals until 07h00-08h00 the following day. On one occasion water

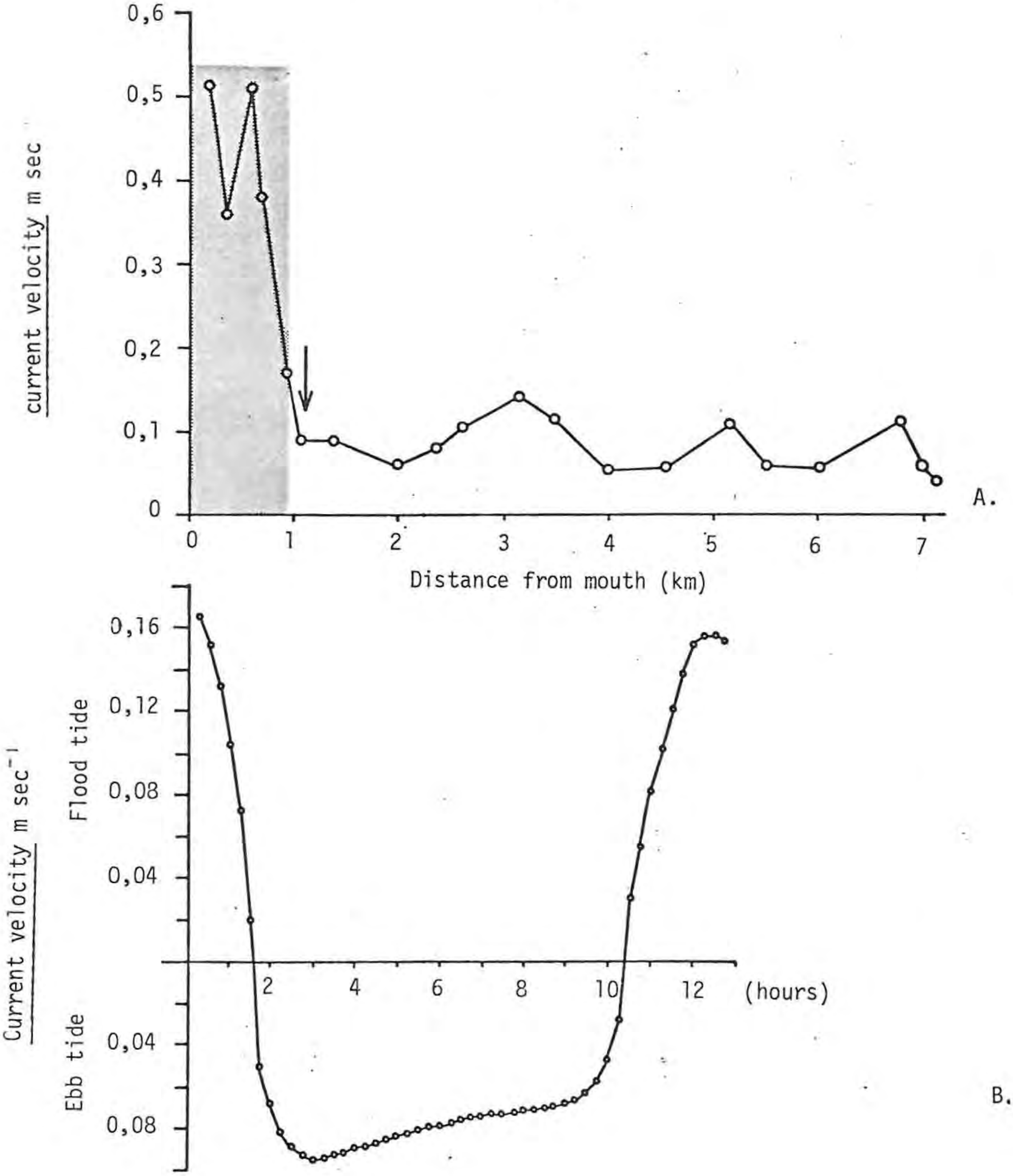

Fig. 23: A. Mean current velocities along the Swartvlei estuary over a spring tidal cycle. Shading indicates narrow mouth region. B. Current velocities over ebb and flood of a spring tide at the site indicated by arrow in 23A, where samples for the calculation of phosphorus flux were collected. Data supplied by N.R.I.O.

was also collected at the bottom of the water column 1,4 m below an Enteromorpha mat. Samples were analysed for SRP, TDP or TP, as described on p. 54 . A total of 9 series of diurnal samples were collected.

RESULTS

1. Phosphorus flux due to tidal exchange

Tidal volumes, and concentrations of TP and TDP measured during the ebb and flow of three tidal cycles are shown in Table 11a. The amounts of phosphorus entering and leaving the estuary were calculated from these data (Table 11b).

Over the neap tide, when tidal penetration was minimal, there was a small net loss of phosphorus from the estuary (1,9 kg). TDP values of inflowing water were almost identical to those of outflowing water. Over mean tides, however, there was a net import of TP (12,5-17,4 kg). A possible reason for this import is suggested by examination of current velocities along the estuary and at the sampling site. Fig. 23 shows:

a. a marked decrease in mean current speed from the narrow mouth region to the main body of the estuary;

b. lower current velocities over the ebb tide than the flood tide, at the sampling site.

Suspended particles tend to settle out with a decrease in current velocity. It is not unreasonable to suggest, therefore, that sedimentation of particulate phosphorus occurs upstream of the mouth region, during ebb tides.

Table 11a. Water levels, tidal volumes and concentrations of total and total dissolved phosphorus 1,1 km upstream of the mouth over three tidal cycles. Tidal volumes were calculated from data supplied by N.R.I.O.

Date	24 February 1977	15 March 1977	29 March 1977
Tidal cycle	Mean	Mean	Neap
Water level at high water (m) (+G.M.S.L.)^{o}	0,71	0,60	0,51
Water level at low water (m) (-G.M.S.L.)	0,11	0,33	0,11
Tidal amplitude (m)	0,82	0,93	0,62
Volume of water in estuary at high water ($\times 10^6 m^3$)	1,01	0,90	0,85
Volume of water in estuary at low water ($\times 10^6 m^3$)	0,23	0,19	0,23
Volume of water entering during flood ($\times 10^6 m^3$)	0,78	0,79	0,62
TDP* concentration of water entering estuary ($\mu g \ \ell^{-1}$)	21	-	20
TDP concentration of water leaving estuary ($\mu g \ \ell^{-1}$)	20	-	20
TP** concentration of water entering estuary ($\mu g \ \ell^{-1}$)	37	74	24
TP concentration of water leaving estuary ($\mu g \ \ell^{-1}$)	21	52	24

-	not determined
^{o}G.M.S.L.	Geodetic Mean Sea Level
*TDP	Total Dissolved Phosphorus
**TP	Total Phosphorus

Table 11b. Comparison of amounts of phosphorus entering and leaving the estuary during three tidal cycles (in kg).

Date	24 February 1977	15 March 1977	29 March 1977
Tidal cycle	Mean	Mean	Neap
TDP entering the estuary	16,4	-	12,40
TDP leaving the estuary	15,6	-	12,40
TP entering the estuary	28,9	58,5	13,0
TP leaving the estuary	16,4	41,1	14,9
Net import	12,5	17,4	
Net export			1,9

\- not determined

In general, phosphorus concentrations in the mouth region increased with increasing salinity (Fig. 24).

2. Export of Zostera from the estuary

The composition (by dry mass) of floating vegetation was as follows: Zostera leaves, 96%; Ruppia leaves, 3%; all other (algae, and Acacia, Juncus, Salicornia fragments), 1%. Therefore, Zostera was by far the most abundant drifting vegetation type in the water column. A comparison of the amounts of eelgrass collected over four tidal cycles (Table 12) shows that the largest export occurred over the spring tide. The net gain measured on 15 March 1977 was probably because the tides were rising from neaps to springs, and eelgrass that had previously been stranded above high water level was washed into the main channel.

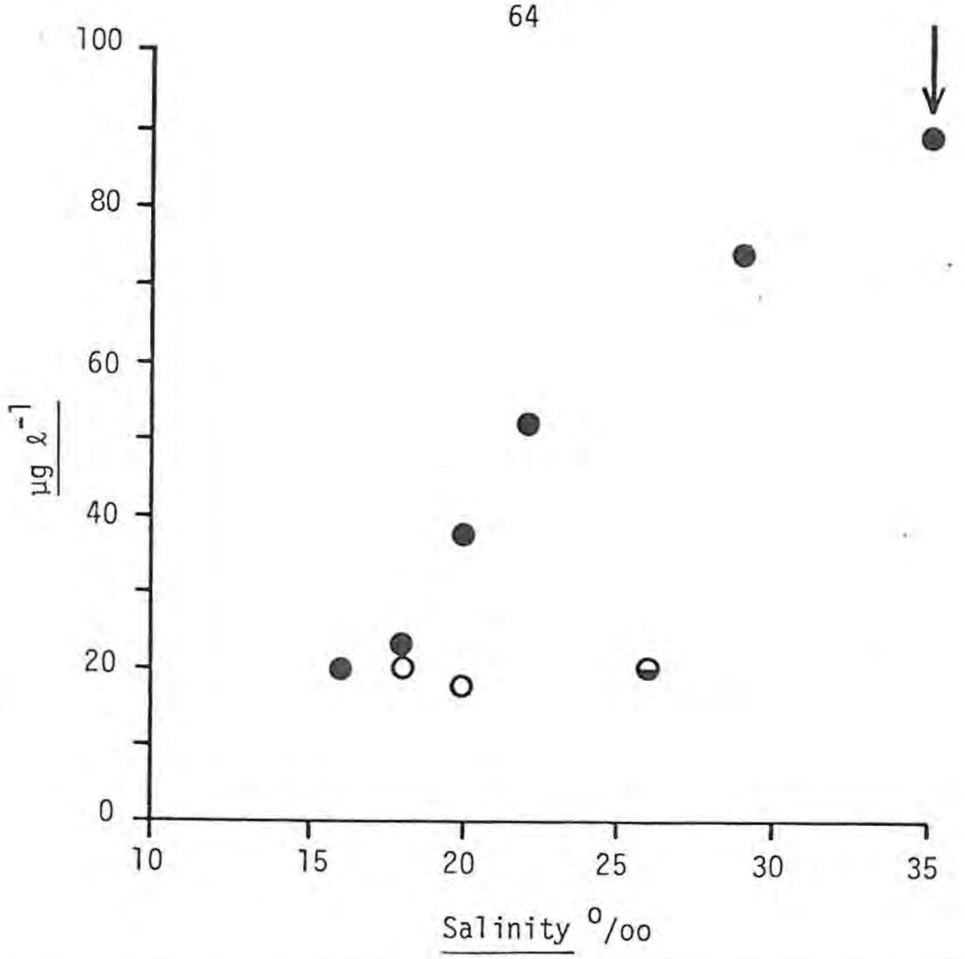

Fig. 24. Total phosphorus (●) and total dissolved phosphorus (o) values of water samples collected in the mouth region February-March 1977, plotted against salinity. Arrow indicates value from seawater next to mouth.

Table 12. Amounts of _Zostera_ leaves collected over four tidal cycles, showing the quantities exported as phosphorus (all units in kg.).

Date Tidal cycle	24 February 1977 Mean	7 March 1977 Spring	15 March 1977 Mean	29 March 1977 Neap
Zostera collected over ebb	33	554	35	33
Zostera collected over flood	4	32	43	16
Net gain (+) or loss (-)	-29	-522	+8	-17
Net export of phosphorus*	0,06	0,99		0,32

* Assuming that _Zostera_ contains 0,19% of its dry mass as phosphorus (see text for explanation).

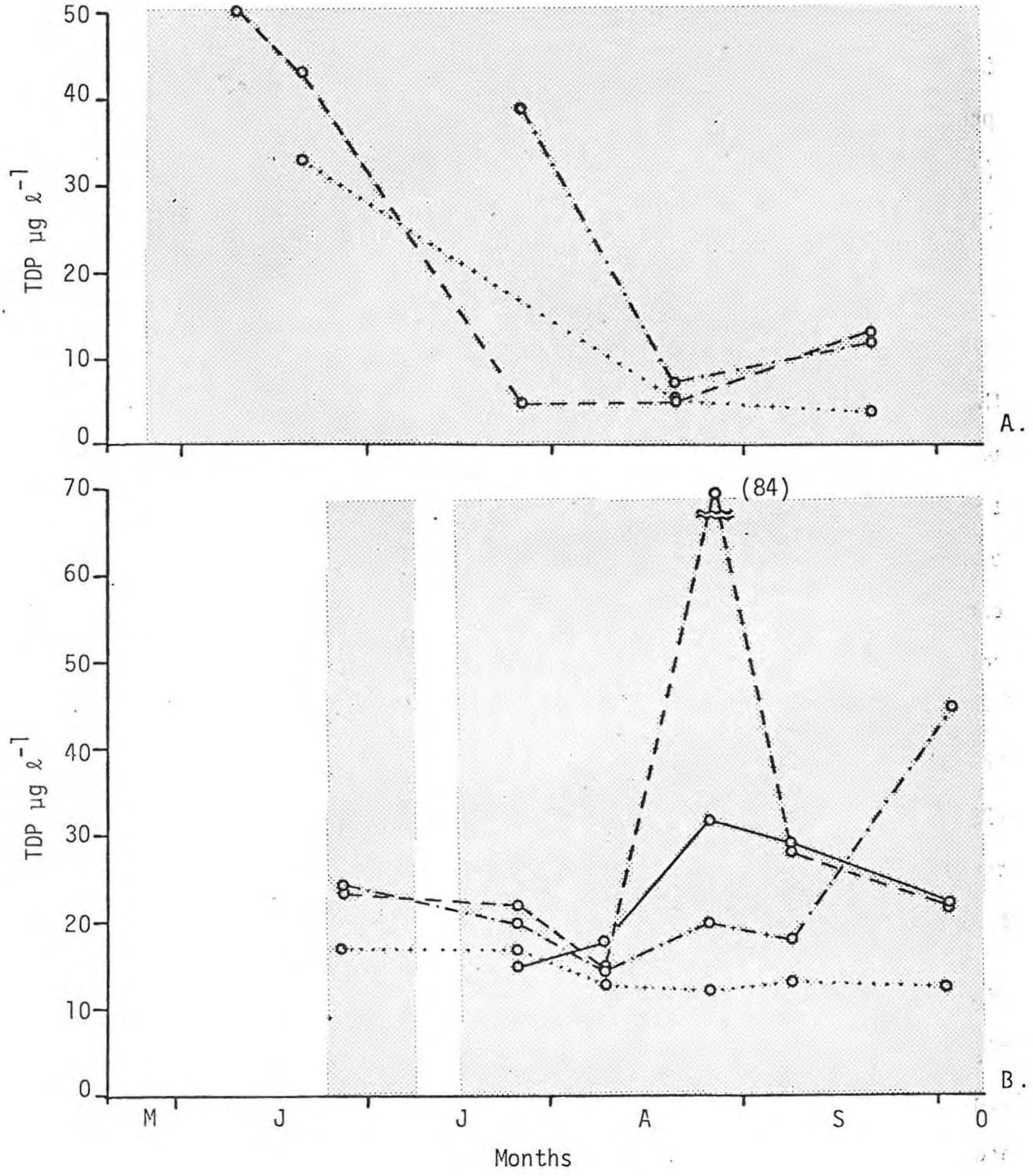

Fig. 25. Mid-day total dissolved phosphorus (TDP) values in the 1976 (A) and 1977 (B) lagoon phases. The samples were collected at a depth of 1 m. o——o Station 1; o---o Station 2; o-·-·o Station 4; o···o Station 7. Shading indicates when the mouth was closed.

The amount of phosphorus in the eelgrass leaves was found to be 0,19%, S.D. ± 0,03% of the dry mass. Calculation of the total amount of phosphorus lost as eelgrass leaves (Table 12) showed that it was small (< 1 kg) when compared to net tidal exchange of phosphorus (1,9-17,4 kg, Table 11b p.63).

3. Changes in TDP of the water column after mouth closure

Mid-day TDP values showed different trends in the 1976 and 1977 lagoon phases (Fig. 25). In 1976, there was a drop in TDP to below 10 $\mu g\ \ell^{-1}$, and a minimum value of about 5 $\mu g\ \ell^{-1}$ was recorded throughout the estuary 13 weeks after closure. In the second 1977 lagoon phase, a considerable fluctuation in values was evident, although TDP levels did not fall below 12 $\mu g\ \ell^{-1}$. The greatest range of values was found in the lower reaches, in the region of dense Zostera beds (Fig. 26). The mean values obtained at each station were approximately the same (22-26 $\mu g\ \ell^{-1}$) with the exception of Station 7, where the mean was considerably lower (12 $\mu g\ \ell^{-1}$) possibly because of dilution with phosphorus-poor Swartvlei water.

Fig. 27 shows TDP concentrations in the water column at Station 4. The highest values recorded in the study were found here, in the anaerobic regions at the sides of the channel and below the halocline (110 $\mu g\ \ell^{-1}$ and 259 $\mu g\ \ell^{-1}$ respectively). Subsequent mixing of the water column, as indicated by salinity data, was associated with an increase in TDP above, and a decrease below the halocline (Fig. 27b).

The quantities of dissolved phosphorus in the water column at the start of Enteromorpha mat formation (20 June 1976), and the time of maximum cover (19 August 1976) were calculated from mean TDP values along the

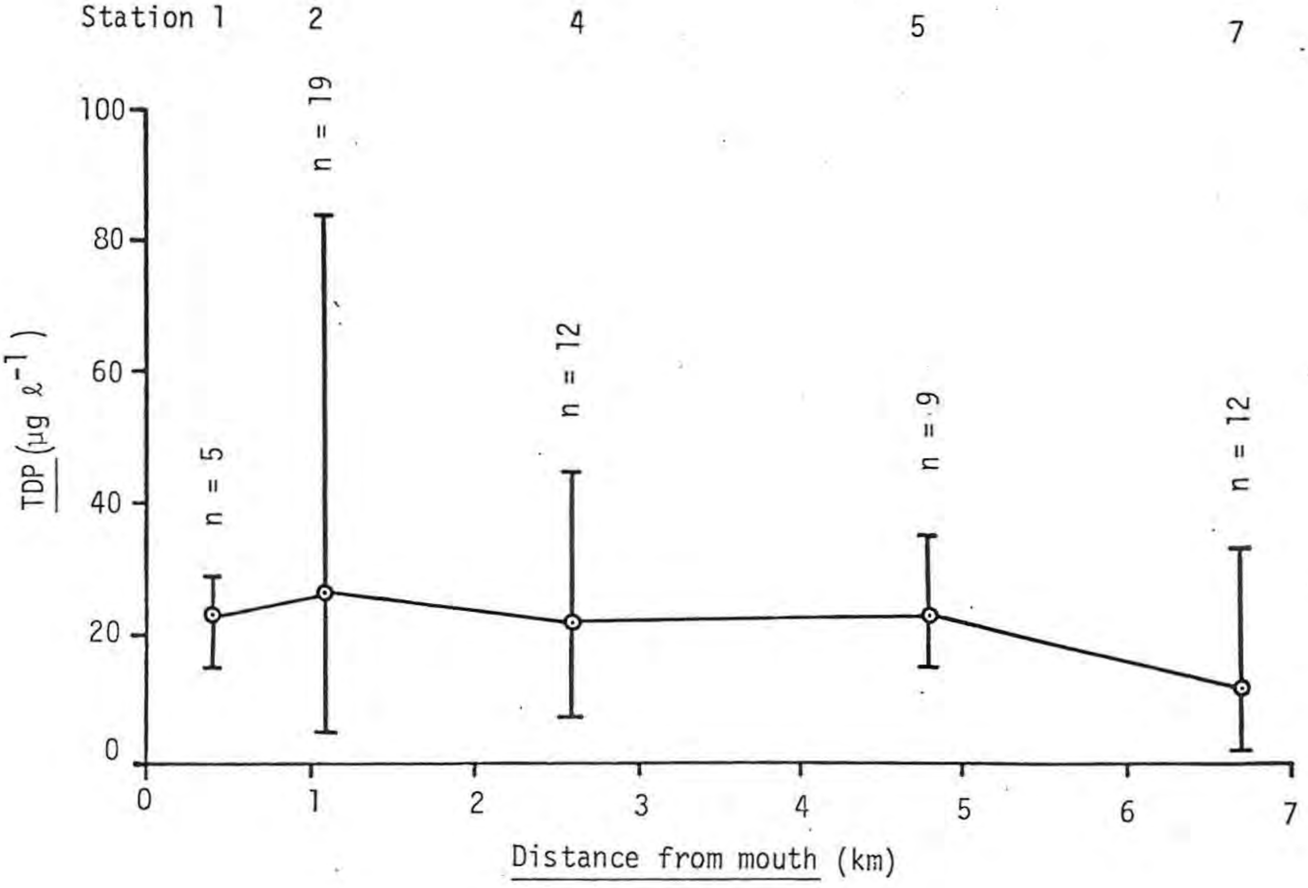

Fig. 26. Mean concentrations (⊙) and ranges (I) of total dissolved phosphorus (TDP) values at each main channel station in the lagoon phases. The samples were collected at mid-day. The number of determinations (n) is also shown.

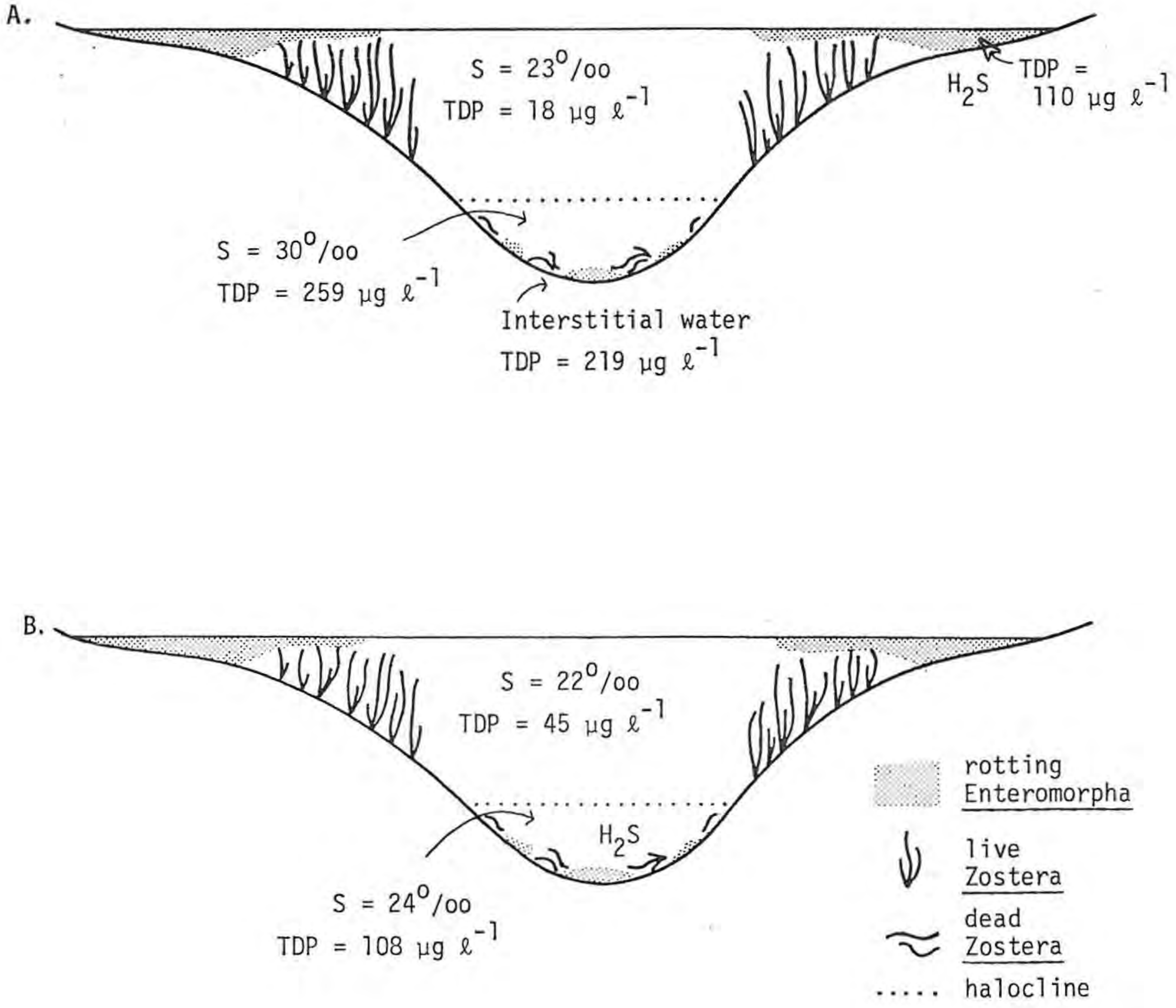

Fig. 27. Total dissolved phosphorus (TDP) values at Station 4 in the anaerobic regions, water column and sediment on 6 September 1977 (A), and in the water column above and below the halocline on 2 October 1977 (B), after some mixing had occurred. H_2S was present in the anaerobic regions.

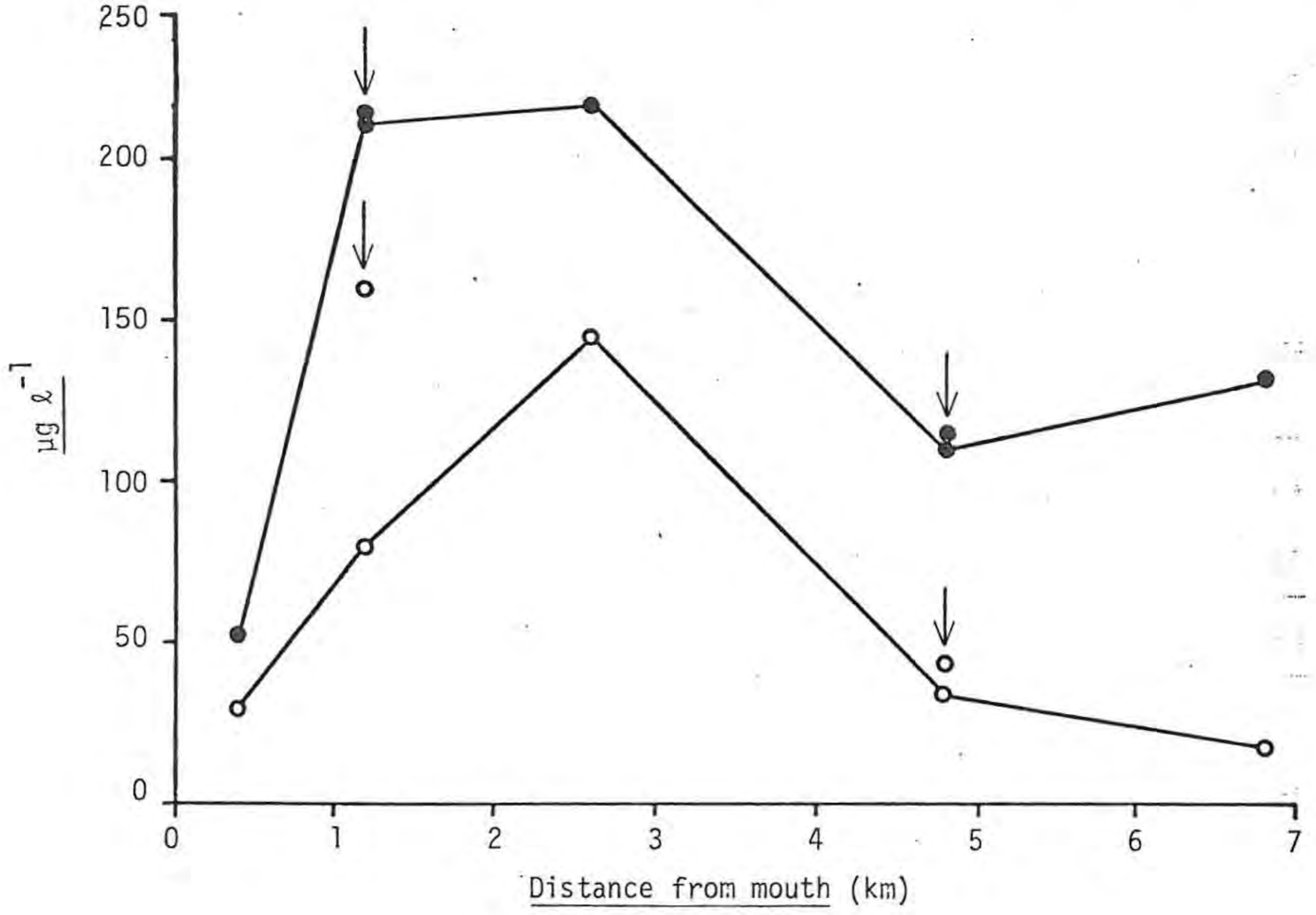

Fig. 28. Total dissolved phosphorus (●—●) and orthophosphate (○—○) concentrations in interstitial water from sediments along the Swartvlei estuary on 19 September 1977. The samples were taken from the main channel (Stations 1, 2, 4, 5 and 7) except for arrowed values, which were taken from macrophyte beds at Stations 3 and 6.

estuary and volume data provided by N.R.I.O. (Table 13). The data indicated a depletion of 43 kg of phosphorus from the water column over this period.

Table 13. Quantities of total dissolved phosphorus in the water column on 20 June 1976 and 19 August 1976. Volume of water calculated from water levels, using data provided by N.R.I.O.

Date	Water level*	Volume of water	TDP** ($\mu g\ \ell^{-1}$)	Mass of TDP (kg)
20 June 1976	+0,9	$1{,}40 \times 10^6\ m^3$	40	56
19 August 1976	+1,25	$2{,}09 \times 10^6\ m^3$	6	13
Mass of phosphorus depleted				43

* metres above geodetic mean sea level

** total dissolved phosphorus

4. Phosphorus concentrations in the sediments and Enteromorpha

a. the sediments

Fig. 28 shows TDP values of the top 120 mm of the sediments. The values, which ranged from 46 $\mu g\ \ell^{-1}$ at Station 1 to 219 $\mu g\ \ell^{-1}$ at Station 4, were highest in the lower reaches of the estuary. SRP values, although lower than those of TDP, showed a similar trend (Fig. 28).

b. Enteromorpha

The amount of phosphorus in Enteromorpha was found to be 0,14% S.D. ± 0,02% of the dry mass of the alga. The total dry mass of Enteromorpha in the estuary at the end of the 1976 lagoon phase was estimated to be 52 tonnes S.D. ± 21 tonnes. Therefore, the quantity of phosphorus present

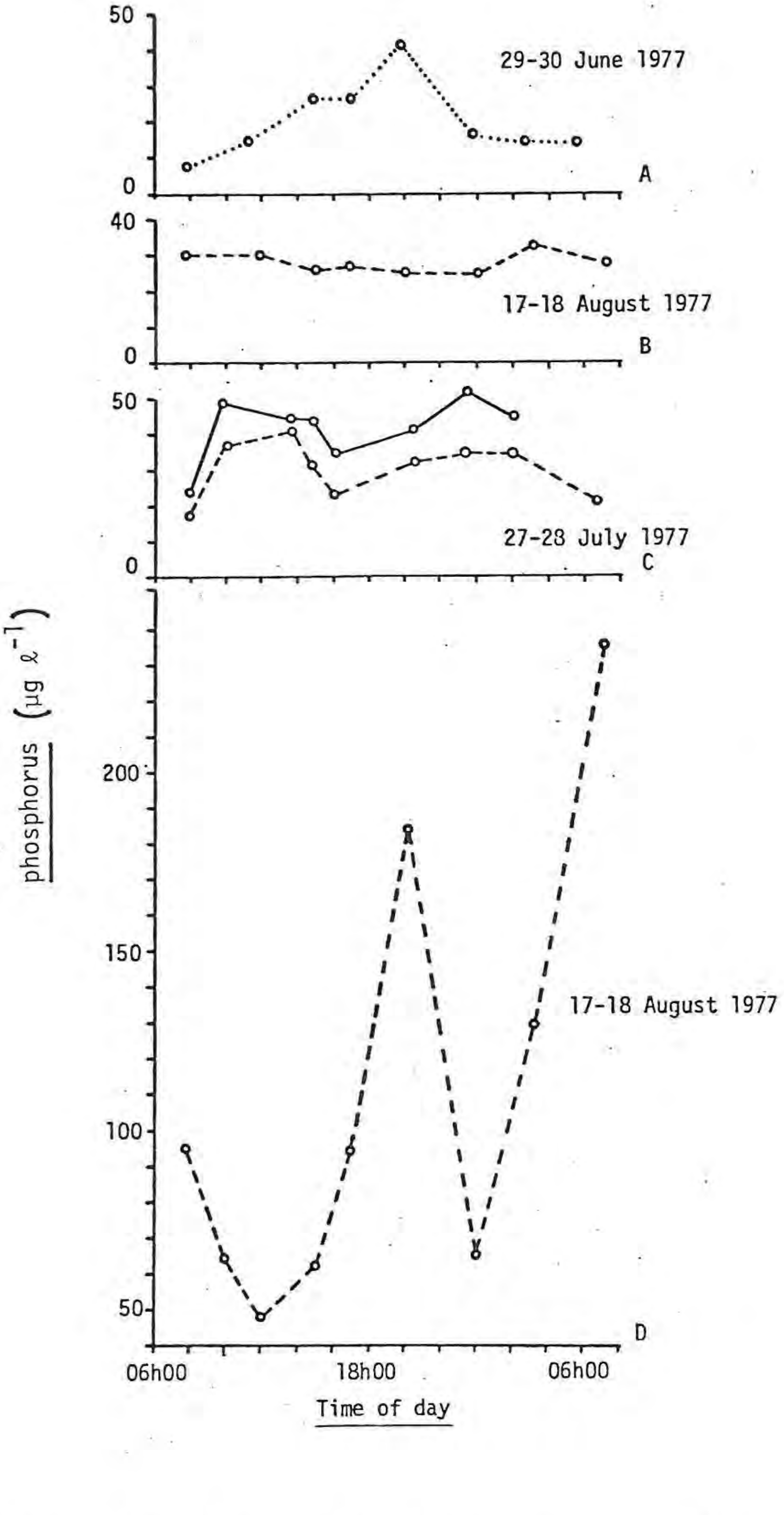

Fig. 29: Diurnal fluctuations of total phosphorus (——), total dissolved phosphorus (---) and soluble reactive phosphorus (....) in surface water at a dense *Zostera* bed at Station 3 (A, C, D) and in the adjacent main channel (B). All results were obtained between June-August, when the mouth was closed. Curve D was obtained from samples extracted from an *Enteromorpha* mat.

in Enteromorpha at the time of the biomass estimate was 73 kg S.D. ± 28 kg.

5. Diurnal phosphorus variations in the water column inside the macrophyte communities

The results of the diurnal studies are as follows:

i. TDP and SRP concentrations of water amongst Zostera fronds rose during the day and fell at night;

ii. TDP values of water inside an Enteromorpha mat decreased from dawn to mid-day, and then rose towards the evening;

iii. two peaks in TDP values, in both the day and night, were recorded in water from amongst Zostera fronds that had a dense covering of Enteromorpha.

Diurnal differences in the Zostera bed were most marked at the start of the first lagoon phase of 1977, when a five-fold difference between minimum (8 $\mu g\ \ell^{-1}$) and maximum (42 $\mu g\ \ell^{-1}$) SRP values was recorded (Fig. 29a). Maximum values were always recorded in the daylight between 12h00 and 19h00. No distinct trends were measured in a diurnal series of samples taken from the adjacent main channel (Fig. 29b).

The results shown in Fig. 29a were recorded amongst Zostera with a poorly developed Enteromorpha component. A diurnal curve from inside a patch of Zostera that had a dense covering of Enteromorpha around the eelgrass fronds (although not forming mats on the surface) indicated peak values during the day and also at night (Fig. 29c).

By far the greatest diurnal phosphorus fluctuations were recorded in the dense Enteromorpha mats. On 17-18 August 1977, a diurnal range in TDP

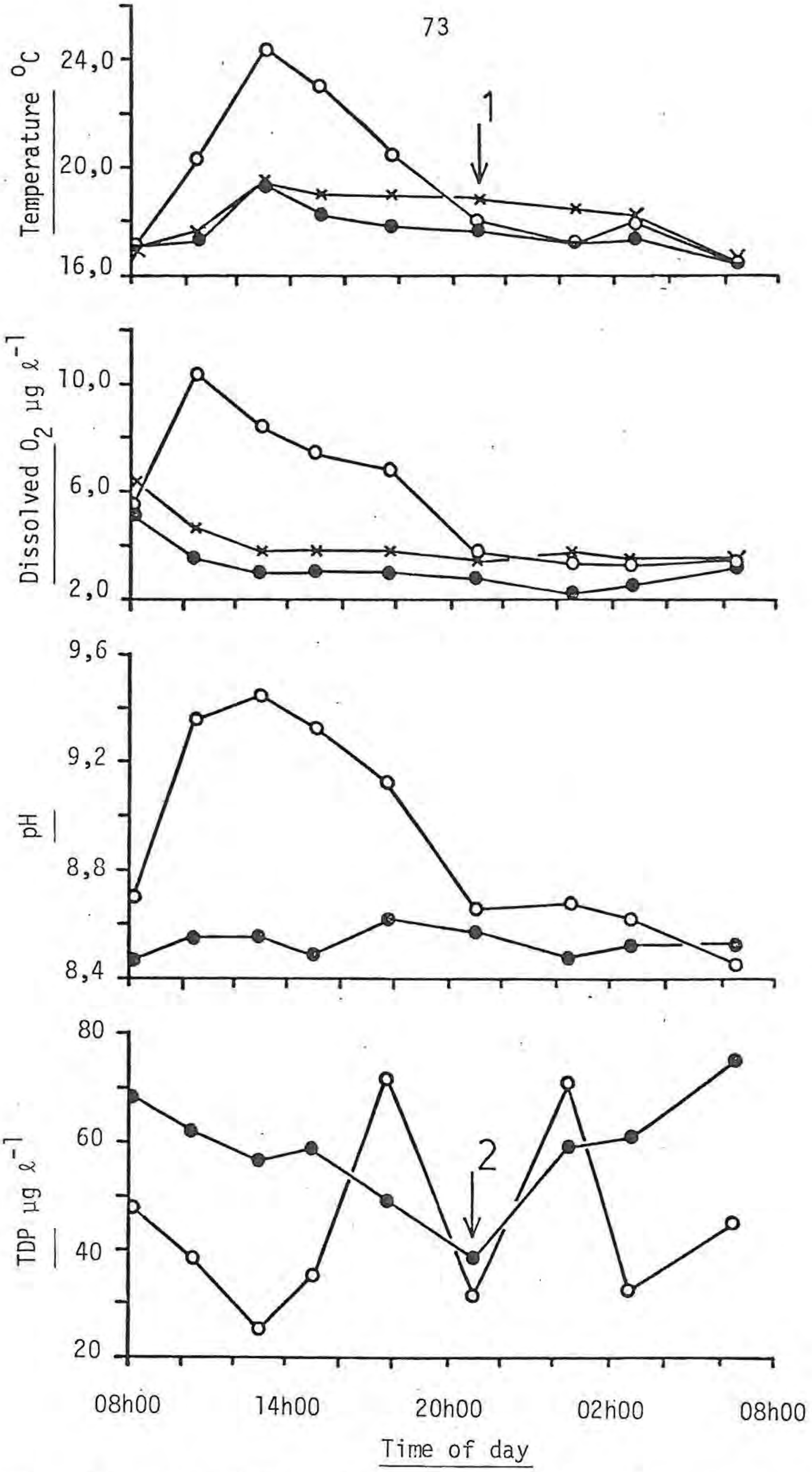

Figure 30. Diurnal variations in temperature, dissolved oxygen, pH and total dissolved phosphorus (TDP) of water inside an Enteromorpha mat (o——o) and at the bottom of the water column 1,4 m below the mat (●——●) at Station 3 on 14-15 September 1977. Mid-water temperature and dissolved oxygen values are also shown (x——x). Salinity = 25^0/oo; depth = 1,51 m. Arrow 1 indicates when water column became thermally unstable; Arrow 2 indicates nocturnal drop in surface TDP values.

between 48 and 235 $\mu g\ \ell^{-1}$ was obtained (Fig. 29d). Although the highest TDP values were measured at night, the concentration at one point at night fell to a value similar to the minimum value recorded at mid-day.

Due to these impressive fluctuations, the water inside and outside an Enteromorpha mat was examined in more detail. Temperature, salinity, pH and TDP were measured inside the mat and at the bottom of the water column 1,4 m beneath the mat. In addition temperature, salinity and dissolved oxygen values were obtained at midwater. The results are shown in Fig. 30. The pattern of TDP variation was identical to the previous Enteromorpha curve (Fig. 29d): a drop in TDP towards mid-day, and then an increase towards dusk. There was an erratic fluctuation of values at night.

Examination of the other physico-chemical data revealed a possible explanation for the large differences in TDP recorded in the mat at night. In daylight, the water column remained thermally stable, and temperatures decreased from the surface to the bottom of the water column (Fig. 30a). At night, temperatures on the surface fell below those measured at midwater. As there was no salinity stratification in the water column, there would be a tendency for the cooler surface water in the Enteromorpha mat to be replaced by warmer underlying water, due to density differences of the two water masses. This exchange of water could explain the erratic nocturnal fluctuations of TDP values inside the Enteromorpha mat.

DISCUSSION

The importance of seawater as a source of phosphorus for the estuary is shown by Fig. 27, which indicates that the TP content of water in the mouth region increases with an increase in salinity. The net import of this nutrient over mean tides suggests that the sediments become progressively richer in phosphorus during the tidal phase. Evidence for phosphorus accumulation can be seen in the distribution of phosphorus in the sediments of the estuary, where the highest concentrations are found in the lower reaches, upstream of the mouth region (Fig. 28).

The sedimentation of suspended material in the lower reaches would be enhanced by the decrease in current speeds, and also by the Zostera beds. The ability of macrophytes to trap seston is frequently reported (e.g. Wood et al. 1969; Gaudet, 1974; Howard-Williams and Lenton, 1975). Analysis of sediments from the lower reaches* in April, 1976 (tidal phase) showed that the percentage of particles less than 62 µm in diameter was higher in the Zostera beds (8,5% S.D. ± 3,2%) than in the main channel (1,0% S.D. ± 1,0%). Therefore, the Zostera beds could be major sites for sedimentation of particulate phosphorus in the tidal phase.

Accumulation of phosphorus may not be a feature of all estuaries. For example, Leach (1971) estimated that there was a net loss of phosphorus from the sediments of the Ythan estuary. In this system, which is similar in size to the Swartvlei estuary, river discharge is substantial, and larger volumes of water leave with the ebb tide than penetrate with the flood. Consequently, current velocities are higher over the ebb than the flood, an exact reversal of the situation in the Swartvlei estuary. This would favour particle suspension during ebb tides, and may explain the net loss of phosphorus from the Ythan estuary. A net loss of phosphorus from the sediments was also reported from the Izembek lagoon by McRoy et al., (1972).

If seawater is so important in providing the estuary with phosphorus, what happens to the phosphorus regime when the mouth closes? In the 1976 lagoon phase, TDP values of the water column became progressively less.

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* By dry sieving the upper 11 cm of the sediments.

Calculations of the quantity of phosphorus (43 kg) depleted from the water in this period showed it was within the lower limits of that present in Enteromorpha (45 kg) at the end of the lagoon phase. Phosphorus depletion in the 1976 lagoon phase could, therefore, have been due to uptake by Enteromorpha. This depletion did not occur in the 1977 lagoon phase, when extensive algal mats were present prior to mouth closure.

Apart from the upper reaches, the mean TDP values in the water column in the lagoon phases (22-26 $\mu g\ l^{-1}$) are strikingly similar to concentrations found in the Tamar Estuary and the Doboy Sound:

Estuary	Reference	Dissolved phosphorus range
Doboy Sound, Georgia	Pomeroy et al., 1965	22-28 $\mu g\ \ell^{-1}$
Tamar Estuary	Butler & Tibbitts, 1972	21-29 $\mu g\ \ell^{-1}$
Swartvlei Estuary	This study	22-26 $\mu g\ \ell^{-1}$

A buffering process in which phosphate concentrations are maintained at a constant level, despite changes in salinity, is postulated by some authors (e.g. Stéfansson and Richards, 1963; Butler and Tibbits, 1972). This level, within the range of 21-37 $\mu g\ l^{-1}$ (Liss, 1976) is probably due to phosphate exchange between the sediments and the overlying water. A high phosphate concentration, low salinity and low pH promote movement of phosphate from the water to the sediments; and vice versa for a low phosphate concentration, high salinity and high pH (Liss, 1976). Pomeroy et al. (1965) made the important point that this exchange is mostly a physico-chemical process, and could occur even when the sediments were poisoned with formalin. A sediment-water buffer mechanism could well be occurring in the Swartvlei estuary, as mean phosphorus values in the water column are similar to those recorded in other estuaries.

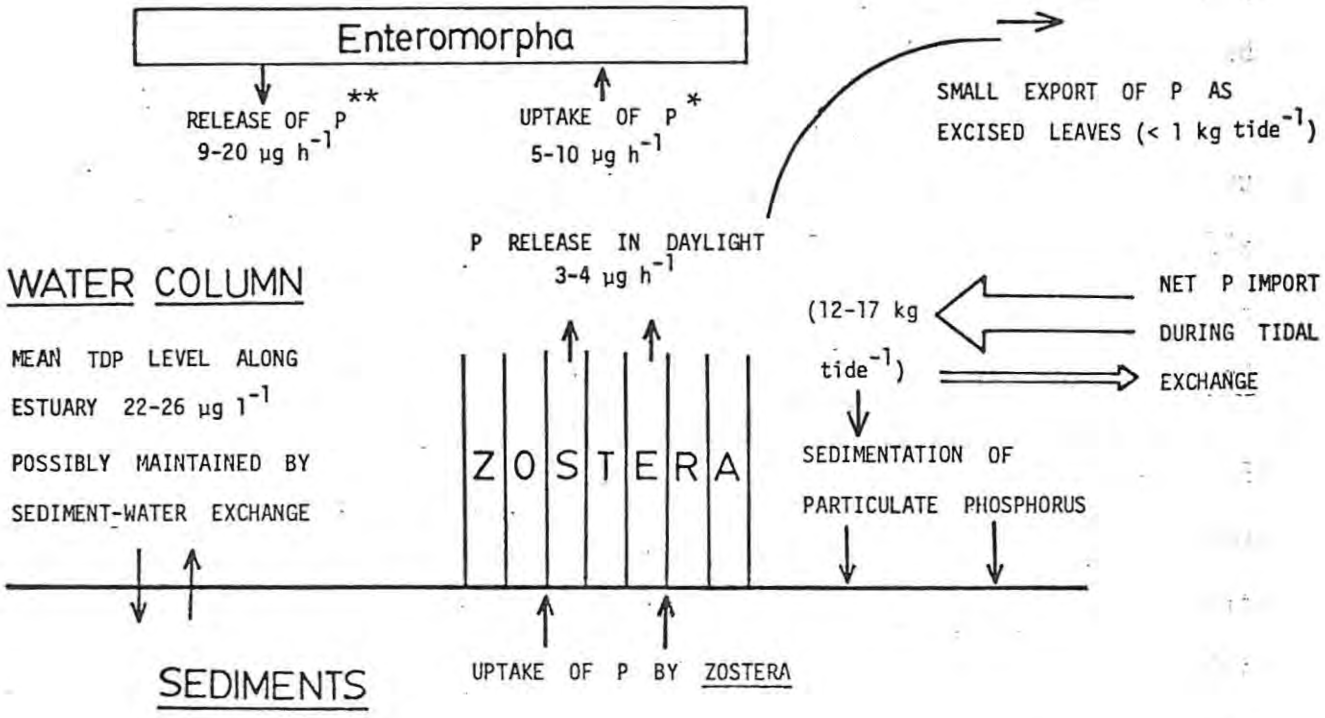


Fig. 31: Dynamics of phosphorus flux and cycling in the Swartvlei estuary. * uptake of phosphorus from dawn to mid-day; ** release of phosphorus from mid-day to the following dawn.

Sediment-water exchange can be controlled by rooted macrophytes which act as nutrient pumps. The diurnal phosphorus fluctuations inside macrophyte beds suggest that Zostera releases phosphate into the surrounding water, at least in daylight (Fig. 29a). There is also some evidence to suggest uptake of phosphate by Enteromorpha. TDP values of water from inside the algal mat decrease from dawn to mid-day (Figs 29d, 30d). Phosphorus released by Zostera in daylight, therefore, could well be taken up by Enteromorpha.

For most of the day, however, there was an increase in TDP values of water inside the algal mat. This could be due to release of phosphorus from the algal cells, or from particulate phosphorus trapped amongst the filaments. Baas Becking and Mackay (1956) showed that Entermorpha produces highly reducing acidic compounds, mostly in the dark, that dissolve any particulate phosphorus trapped amongst the algal filaments. Hence, phosphate is released into the water. The net phosphate increase in water inside mats in August-September could reflect onset of senescence of Enteromorpha. It would be interesting to repeat the studies in June when algal growth is rapid, to see if there is a net uptake of phosphorus.

The diurnal curves obtained in this study do not agree with curves reported by other workers. For example, Bruce and Hood (1959) showed that in Texas bays, phosphate concentrations in the water column decreased during the day and increased at night. They demonstrated that this diel pattern was due to uptake and subsequent release of phosphate by phytoplankton. Phosphate variations similar to those in Texas bays have been shown to occur in the Sargasso Sea (Ryther et al., 1961).

The dynamics of flux and cycling of phosphorus in seawater inflows, the macrophytes and sediments in the Swartvlei estuary are shown in Fig. 31.

PART 4 - COMMUNITY METABOLISM

The final section of the thesis describes community metabolism in the estuary. This was measured in an attempt to understand the patterns of energy fixation and utilization along the estuary, both in the tidal and lagoon phases.

The community metabolism of a system is a measurement of the rate of gross production of oxygen (GP) by the primary producers, and the rate of oxygen consumption (R) by the whole community (Odum and Hoskin, 1958). In photosynthesis, plants use inorganic materials to build up organic matter, with sunlight providing the energy for the reaction. Oxygen is released as a by-product:

$$1{,}3 \times 10^6 \text{ kcal radiant energy} + 106\ CO_2 + 90\ H_2O + 16\ NO_3 + 1PO_4 + \text{mineral elements} = 3258 \text{ g protoplasm} + 154\ O_2 + 1{,}287 \text{ kcal heat energy dispersed} \quad (2)$$

(modified from Odum, 1971)

Measurement of oxygen production is thus an indirect method of calculating the production of organic matter (Vollenweider, 1969).

Metabolic rates of aquatic communities have been estimated by measuring the rate of change of dissolved oxygen in the water column over a 24 h day. They have been calculated in ponds (Welch, 1968; Goulder, 1970), rivers (Hoskin, 1959; Fisher and Carpenter, 1976), estuaries (Nixon and Oviatt, 1972), lagoons (Nichols, 1966) marine embayments (Odum and Hoskin, 1958; Odum and Wilson, 1962) and coral reefs (Odum and Odum, 1955; Odum et al., 1959).

The main advantage of this technique over other methods for measuring primary production is that it allows measurement of metabolic rates in a completely natural environment, and thus the errors associated with the enclosure of communities are avoided (Westlake, 1969). These errors include 1) nutrient depletion by the enclosed community; 2) growth of bacterial populations on the sides of the enclosure; 3) a possible lengthy equilibration period for the community to adapt to the enclosure (Wetzel, 1969). In addition, isolation reduces turbulence. Turbulence is reported to stimulate metabolic rates both in macrophytes (Odum and Hoskin, 1958; Conover, 1968) and phytoplankton (Mann _et al._, 1972).

The calculation of community metabolism by freewater oxygen changes has several disadvantages:

1. The method is unsuitable for production studies of oligotrophic waters, where diurnal oxygen variations are small (Talling, 1969).

2. Allowance has to be made for atmospheric exchange of oxygen with the water column, when the water becomes super- or under-saturated with oxygen. This diffusion correction is usually calculated from the diurnal oxygen curve (Odum and Hoskin, 1958). Night-time respiration rates are assumed to be constant, and any variation in the nocturnal oxygen rate-of-change curve is attributed to diffusion. A diffusion constant is then applied to the whole curve. Hall and Moll (1975) point out that this correction method "appears to give erroneously high values because night-time respiration is not constant, but higher in the evening". Owens (1965) found that application of extreme diffusion constants to diurnal curves could lead to errors of up to 25% in the estimation of community metabolism.

3. When oxygen changes are measured at a fixed station in the community, results will be in error if water moving into the station has a different oxygen content to that simultaneously leaving the station (Odum and Hoskin, 1958). Errors would be particularly large if the chosen station is unrepresentative of the area, e.g. when monitoring

changes inside a macrophyte bed adjacent to a channel with no macrophyte cover.

4. When the water is super-saturated with oxygen, bubbles of gas may be evolved from the submerged plants. Collection of these bubbles, using plastic bags (Odum and Odum, 1955) or inverted glass funnels (Owens, 1965) revealed that loss of gas from the community could be as high as 1 ℓ m^{-2} day^{-1}. If this is assumed to be oxygen, up to 6,5% of the total oxygen production may be lost to the atmosphere without dissolving in the water (Owens, op.cit.).

5. Respiration rates in daylight are either assumed to be equal to respiration rates at night (Odum and Hoskin, 1958), or to vary with the dissolved oxygen concentration (Odum and Wilson, 1962). In the latter instance, daylight respiration rates are always considered to be less than those measured in the early evening, when oxygen concentrations are at a maximum.

There is a growing body of evidence, however, which suggests that in a large number of both terrestrial and aquatic plants, these assumptions are invalid. Respiration rates in the light far exceed those measured in the dark (e.g. Jackson and Volk, 1970; Hatch *et al*., 1971; Zelitch, 1971; Black *et al*., 1976; Downton *et al*., 1976). Elevated day-time respiration, termed photorespiration, is defined by Zelitch (1971) as "the respiration... that differs biochemically from normal dark respiration and is specifically associated with substrates produced during photosynthesis." Oxidation of these substrates lowers net photosynthesis substantially, and therefore reduces plant growth (Zelitch, *op.cit*.).

Preliminary measurements of large diurnal oxygen variations demonstrated that the technique of diurnal curve analysis could be used to calculate community metabolism in the Swartvlei estuary. However, Odum and Hoskin (1958) stated that the irregular flow systems of some estuaries made them unsuitable for diurnal curve studies: water movement makes a particular water mass difficult to follow, and increases the diffusion rate of oxygen between the atmosphere and water.

In this study, the standard diurnal curve technique was adapted to conditions found in the Swartvlei estuary, with the following modifications:

i. a method was devised to follow water masses as they moved along the estuary;

ii. an enclosure was used to minimise advection through a Zostera bed and to estimate day-time respiration rates;

iii. bubbles evolved by Zostera were collected to prevent underestimation of gross production.

In addition, estimates of epipsammic community metabolism in the extensive sandflats were made in the 1977 lagoon phase. These were measured using the light/dark bottle technique as high diffusion rates, caused by wind-induced turbulence of a shallow water column, precluded the use of the freewater method.

MATERIALS AND METHODS

1. Diurnal oxygen curve analysis

This method was developed by H.T. Odum and co-workers in the 1950's. It is explained in detail by Odum and Hoskin (1958) and in a slightly revised form by Odum and Wilson (1962). Analysis of a typical diurnal curve is described in Appendix 1 (p126). A total of 75 diurnal curves were analysed: these were obtained on 15 different days between June, 1976 and September, 1977.

ii. Sampling stations

In the 1976 lagoon phase, diurnal readings were obtained at monthly intervals at Stations 2-8 (Fig. 1). These diurnal curves did not always show a typical trend with oxygen minima just after dawn and maxima in the late afternoon. Irregularities were frequent, e.g. oxygen maxima at midnight. Salinity data indicated that these variations were due to transfer of water into, and out of the stations.

Measurements of the extent of seawater penetration along the estuary (Part 2, p.28), indicated that a substantial volume of water was neither flushed out to sea with the ebb, nor pushed into Swartvlei with the flood (Fig. 12). It was found that water masses could be followed along the estuary using data on their salinities and, to a lesser extent, temperatures. It was decided to employ this technique in both the tidal and lagoon phases of 1977, in an effort to minimise errors associated with diurnal measurements at a fixed station.

Water masses were not followed in situ : instead, 11 stations were established at 0,5 km intervals along the main channel (Fig. 32). Diurnal data collected at each station were used to determine the movement of the water masses along the estuary (Fig. 33), and diurnal curves for each water mass (or, mobile station) were then plotted.

3. Calculation of the mean depth of the mobile stations

Results of the regular sampling programme (Part 2, p.32) indicated that macrophytes considerably modified the dissolved oxygen content of the water column. Light/dark bottle experiments showed that the metabolic

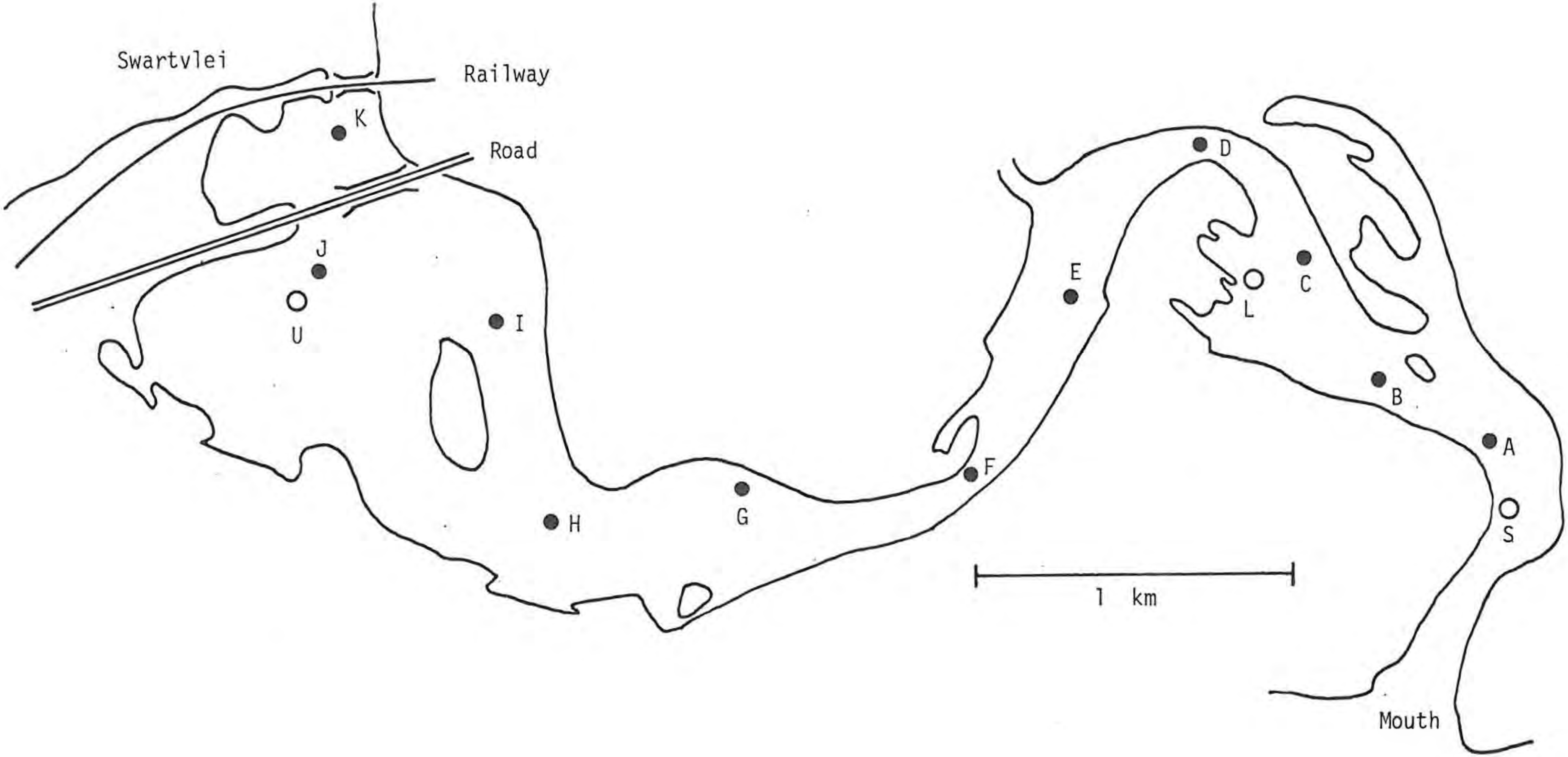


Fig. 32. Map of the Swartvlei estuary, showing sampling stations for freewater community metabolism studies (● A-K) and for epipsammic production studies (O S, L, U) in 1977.

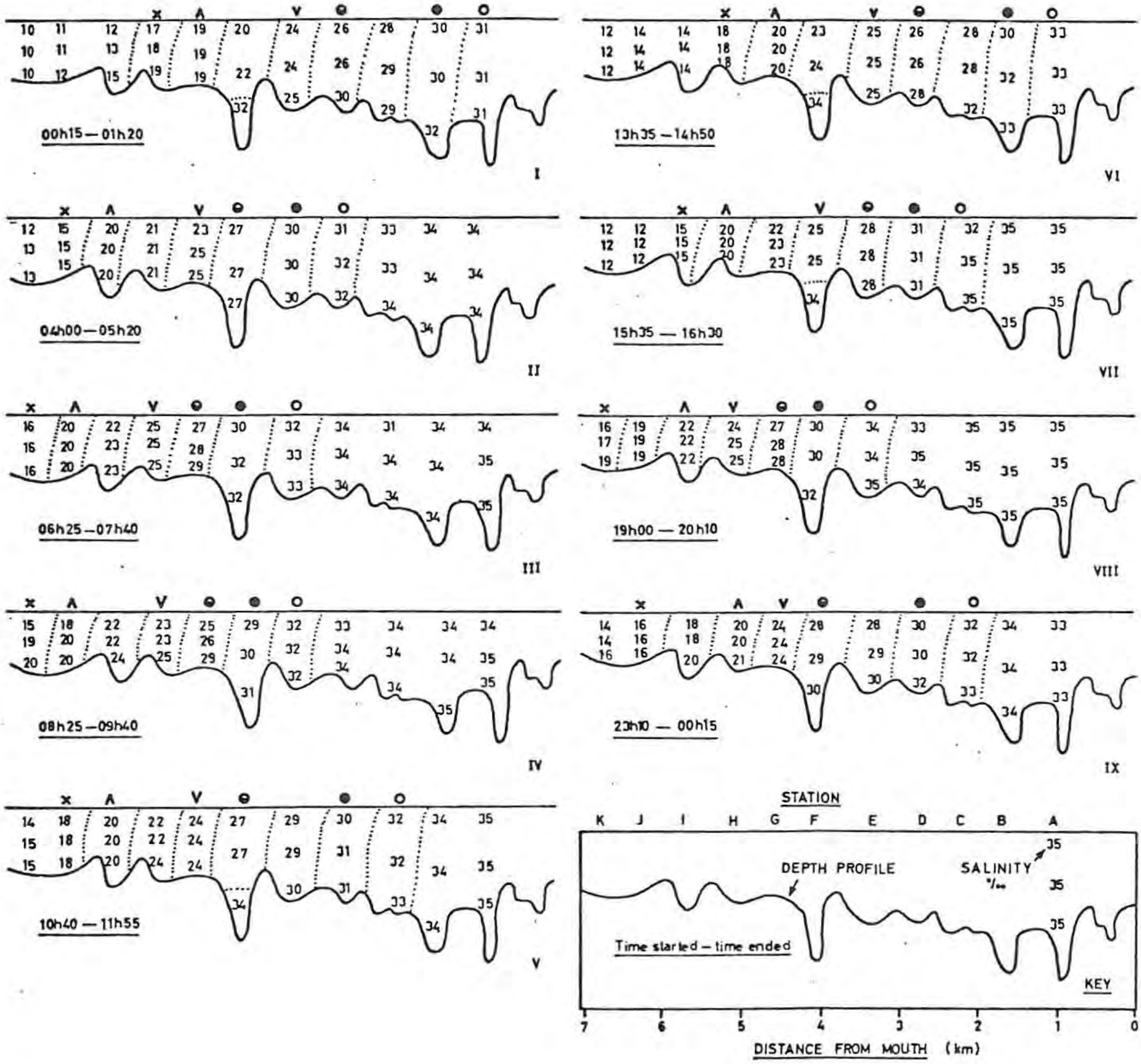


Figure 33. Diurnal salinity profiles of the Swartvlei estuary on 20 January 1977, to show how the mobile stations were followed by means of their salinities. Mobile stations 1 - 6 are indicated by the symbols o, ●, ⊖, v, ʌ, x; the depth scale has been omitted.

activity of phytoplankton in the main channel was negligible (Allanson, pers.comm.). Thus, oxygen fluctuations measured in the main channel were probably induced by metabolic activity in the adjacent macrophyte beds.

To convert gross production values from a volume to an areal basis, the GP data were multiplied by the depth of the station in metres (see Appendix 1). Two factors are important here:

i. the depth of the main channel is inevitably the maximum depth of that particular section of the estuary;

ii. The bulk of the macrophyte beds, and hence the highest metabolic activity, occurs at depths far shallower than the maximum depth of the section.

Therefore, use of the depth of the main channel in the conversion of metabolic rates would tend to give erroneously high values. Comparisons of the maximum depths with the mean depths of sections along the estuary showed that the mean depths were in the order of 30% less than the maximum depths. Tests were then performed, in which the mean depth and oxygen content of a section were compared to the depth and oxygen content of the main channel:

a. depth of main channel - 2,2 m
b. O_2 content of channel - 17,8 g m^{-2}
c. mean depth of section - 1,5 m
d. Mean O_2 content of section - 13,5 g m^{-2}
e. estimation of mean O_2 content using mean depth and channel data - 12,2 g m^{-2}

Whereas use of the maximum depth (b) over-estimated the O_2 content by 32%, calculation of the mean O_2 content from mean depth and O_2 concentration in the channel (e) under-estimated the O_2 content by only 10%. This

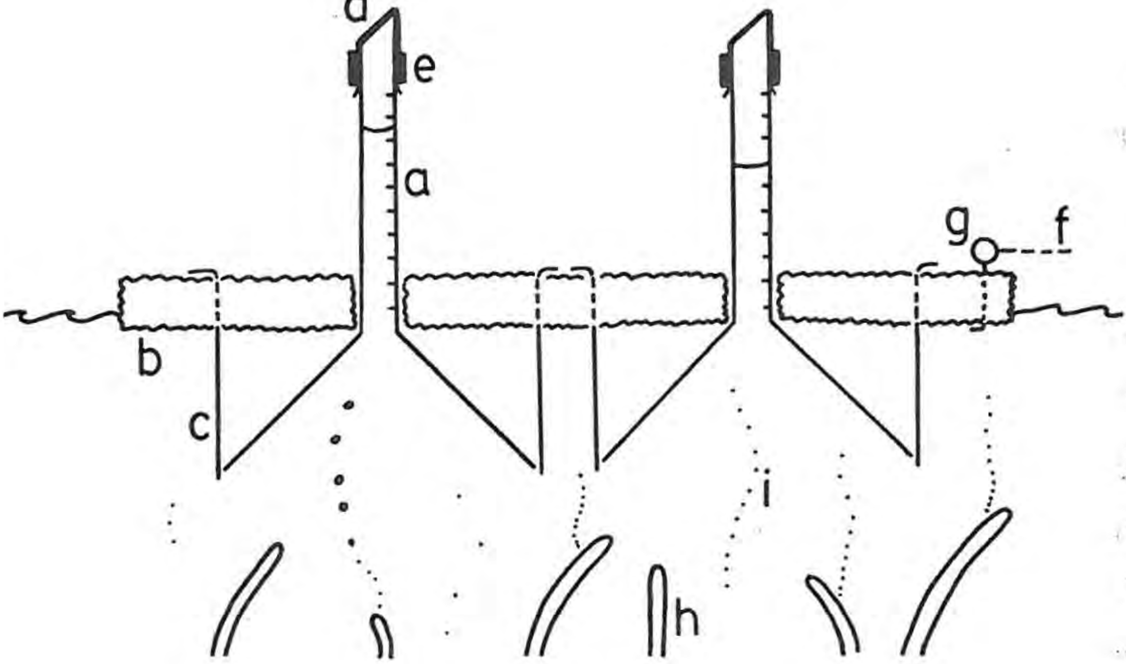


Fig. 34. The collection of bubbles over a Zostera bed. Two 150 mm diameter Pyrex funnels (a) were fixed to a polystyrene raft (b) by wire stays (c). The graduated stems of the funnels were sealed with rubber sheeting (d) held in position by a tight rubber collar (e). The funnels, which were filled with water when first put in position, were tethered inside the enclosure shown in Appendix 2 by a line (f) attached to a loop (g) at the end of the raft. The tips of the Zostera blades (h) and streams of released bubbles (i) are also shown.

under-estimation was considered preferable to the higher over-estimation; therefore, the mean depth of the section was used in productivity calculations.

These mean values were computed from data on the morphometry of the sections (Anon, 1975) and the actual water depth in the main channel.

4. Measurements of metabolism using an enclosure

Besides following a mobile station as a means to reduce errors associated with advection of water, an attempt was made to minimise advection through a Zostera bed using an enclosure. This apparatus, described in Appendix 2 and illustrated in Fig. 41, was placed in the Zostera bed at Station 3 at the start of each diurnal sampling programme between February and September 1977. Readings for diurnal curve analysis were taken both inside and outside of the enclosure.

5. Collection of bubbles

Gas bubbles evolved from Zostera leaves in the light were collected under inverted 150 mm diameter, graduated Pyrex funnels. These were supported over the leaves using a polystyrene raft, tethered inside the tidal enclosure (Fig. 34). The apparatus was placed in the enclosure in the early morning, and the volume of gas was measured at sunset.

The bubbles were assumed to be pure oxygen, although it is realised that other gases in the water could diffuse into the bubbles. The volume of oxygen m^{-2} at normal temperature was first determined using Charles' Law:

$$\frac{V_1}{T_1} = \frac{V_2}{T_2} \qquad (3)$$

where V_1 = volume of gas m^{-2} at ambient temperature (ℓ)

T_1 = temperature at which volume of gas was read (^{O}K)

V_2 = volume of gas m^{-2} at $273^{O}K$ (ℓ)

T_2 = normal temperature ($273^{O}K$)

The small fluctuations in barometric pressure from normal pressure, and the relative crudeness of the collection technique, precluded the use of any volume corrections for pressure in this calculation. Knowledge of the density of oxygen at normal temperature and pressure (N.T.P.) enabled the calculation of the mass of oxygen from the volume of oxygen at N.T.P.:

$$W = D \times V \qquad (4)$$

where W = mass of oxygen at N.T.P. (g)

D = density of oxygen at N.T.P. (1,4290 g ℓ^{-1} loc.cit. Sears and Zemansky, 1964)

V = volume of oxygen at $273^{O}K$ (ℓ)

This mass was added to the GP value obtained from diurnal oxygen curve analysis of data measured in the enclosure.

6. Measurement of day-time respiration rates

The basic assumption behind this technique is that if an illuminated plant is suddenly darkened, it continues to respire oxygen at the same rate as during illumination. This principle has been employed by plant physiologists to detect post-illumination bursts of oxygen uptake, a feature of plants that exhibit photorespiration (Downton et al., 1976).

Two of the tidal enclosures shown in Fig. 41 were placed in the dense Zostera bed at Station 3. Measurements of temperature, salinity and oxygen were made at the surface, midwater and bottom of the water column in both enclosures. After an equilibration period of 0,5h, a black polythene cover designed to exclude light was placed over one of the enclosures. This cover was painted white on the upper surface to reflect sunlight, and hence minimise heat absorption. A hole 0,1 m in diameter in the middle of the cover enabled the oxygen probe to be lowered inside the enclosure. This hole was plugged with a weighted polystyrene disc. Readings inside the enclosure were made 1 h after it was darkened.

This procedure was repeated at different times of the day (09h45 - 14h35), water temperatures (11,3 - 20,5^{0}C), salinities (22 - 35^{0}/oo) and oxygen saturation values (60 - 180%). A total of nine values of respiration rates during daylight was thus obtained.

7. Measurement of epipsammic community metabolism

Three extensive areas of submerged, bare sand were chosen (Fig. 32). Microscopic examination of the sand at each station showed that fragments of macrophytes, unidentified brown organic aggregates and unicellular algae were present. The latter consisted mainly of diatoms of the genus Navicula.

Ambient water was carefully siphoned into 2 light and 2 dark bottles (volume = 125 mℓ) at each station, at approximately 10h00. Care was taken to exclude air bubbles, and the bottles were flushed out by at least 3x their volume. An additional bottle was fixed with Winkler reagents for the determination of the initial dissolved oxygen concentration. About 5 mℓ of sand, collected from the top 1 cm of the sandflat, were placed in each of the light and dark bottles. α-chlorophyll concentrations obtained by grinding freshly-collected sand with 90% acetone in a mortar and then analysing for pigments (SCOR UNESCO method, cited in Strickland and Parsons, 1968) showed that most of the α-chlorophyll was contained in this upper 1 cm of sand (Fig. 35). It is therefore likely that most of the primary production occurs in this upper layer.

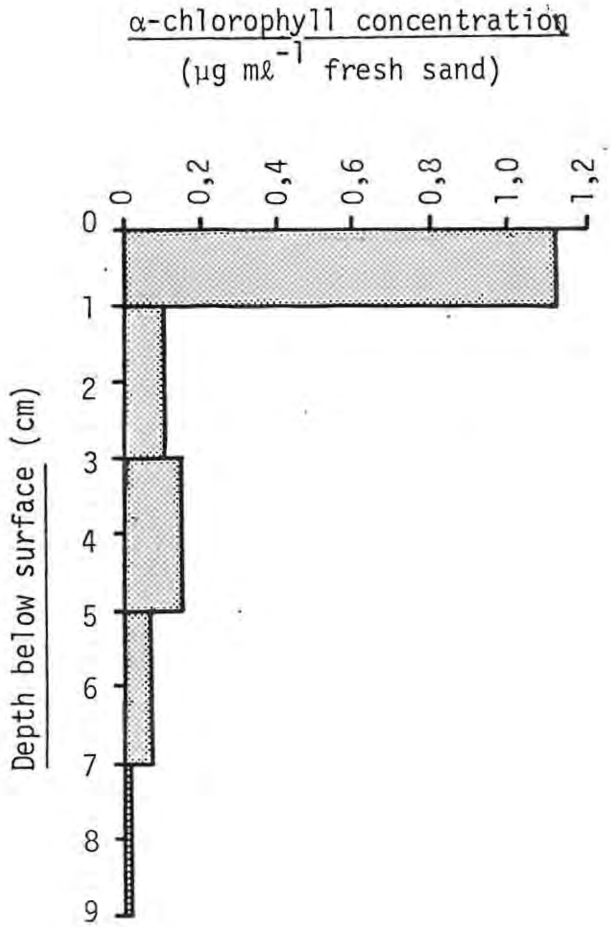


Fig. 35: The concentration of α-chlorophyll at different depths below the surface of the sandbank, 1,1 km from the mouth (Station S, Fig. 32). Time: 10h00.

The bottles were then stoppered, placed horizontally on the sand, and left for 4 h.

At the end of the incubation period, Winkler reagents were added to the bottles and the oxygen content of each bottle was determined. The settled volume of sand in each bottle was measured with a measuring cylinder, and the concentration of α-chlorophyll determined after acetone extraction with a Pye Unicam 6000 spectrophotometer. The mass of α-chlorophyll m^{-2} was calculated from the volume of sand and the concentration of α-chlorophyll in that volume.

The results of the 4 h incubation periods were converted to daily rates of community metabolism as follows:

$$\text{Gross production mg } O_2\ m^{-2}\ \text{day}^{-1} = \text{Gross production in incubation period} \times \frac{\text{Daily R}}{\text{R falling in incubation period}} \tag{5}$$

$$\text{Respiration mg } O_2\ m^{-2}\ \text{day}^{-1} = \text{Day-time respiration} \times 12 + \text{Night-time respiration} \times 12 \tag{6}$$

where R - solar radiation (MJ m^{-2});

Day-time respiration - respiration rate recorded in incubation period (mg O_2 m^{-2} h^{-1});

Night-time respiration - day-time respiration compensated for a lower temperature ($-3C^{o}$) assuming a Q_{10} of 2,0 (mg O_2 m^{-2} h^{-1}).

8. Measurement of environmental variables

The total number of environmental variables measured was as follows:

i. diurnal oxygen metabolism - tidal phase: salinity, temperature, percentage macrophyte cover, solar radiation;

ii. diurnal oxygen metabolism - lagoon phase: salinity, temperature, percentage macrophyte cover, solar radiation, α-chlorophyll, total dissolved phosphorus;

iii. epipsammic production: salinity, temperature, solar radiation, α-chlorophyll in the sand.

The 'percentage macrophyte cover', which is defined as the percentage area covered by macrophytes in the section containing the station, is shown for each section of the estuary in Fig. 5b. In the tidal phase, the percentage was taken as the mean percentage cover over which the mobile station flowed. It is meant to represent biomass of macrophytes; the latter was not directly determined, as the sampling programme was not initially designed to correlate metabolic rates with plant biomass.

Solar radiation on each diurnal sampling day, and over the incubation period of the light/dark bottles, was measured with a Lambda Instruments Corp. LI-500 integrator. The collection and analysis of water for TDP was described earlier (p.54) ; 1 ℓ water samples for α-chlorophyll analysis were collected simultaneously as these samples, from Stations 2, 4, 5 and 7 at a depth of 1 m. These were analysed as described on p.91 .

Correlation coefficients of the metabolic rates with environmental variables were calculated using a standard multiple regression programme run on an I.C.L. 1903 T computer.

RESULTS

1. Freewater oxygen curve analysis

The method of following 'mobile stations' along the estuary in both tidal and lagoon phases, gave a far lower diffusion constant ($\bar{x}$ = 0,68 g O_2 m^{-3} h^{-1}) as compared to using 'fixed stations' ($\bar{x}$ = 1,58 g O_2 m^{-3} h^{-1}). This suggests that a large part of k (diffusion constant) is due to lateral advection of water through the station, rather than exchange of oxygen with the atmosphere. Diurnal curves with k values > 2,0, which were common with fixed stations but not recorded when mobile stations were used, were therefore rejected.

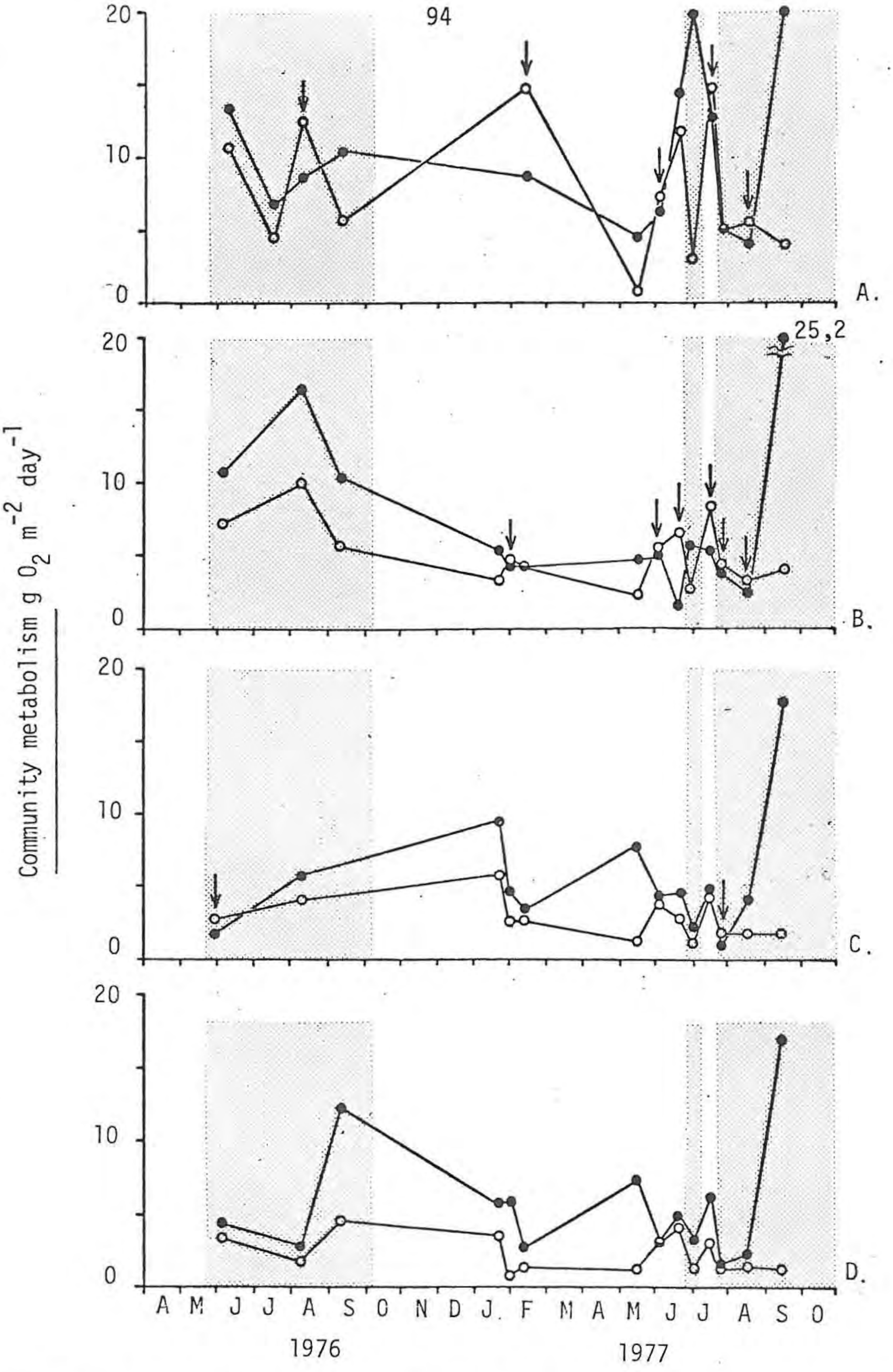


Figure 36. Community metabolism in the Swartvlei estuary in 1976-1977. A. Zostera bed 1,1 km from the mouth (Station 3); B. in the region from 1,1 km to 3,0 km from the mouth (Stations A-E); C. in the region 3,1 to 5,0 km from the mouth (Stations E-G); D. in the region 5,1 to 7,0 km from the mouth (Stations G-I). The positions of the stations are shown in Fig. 32. The days on which gross production exceeded respiration are indicated by arrows. Shading indicates when mouth was closed.

Values for GP and R ranged from 0,7 - 14,9 g O_2 m^{-2} day^{-1} and 0,9 - 25,2 g O_2 m^{-2} day^{-1} respectively. On most days R exceeded GP, which indicated that more oxygen (and hence, organic matter)was respired than produced by the communities along the estuary. Net production (GP > R) was most frequently found in the lower 3 km of the estuary (Fig. 36), and was not recorded in the upper reaches, 5,0 - 7,0 km from the mouth. Metabolic rates were generally higher in the lower reaches, especially in the dense Zostera beds (Fig. 37), and decreased upstream of this region. The highest respiration rates, up to 25,2 g O_2 m^{-2} day^{-1}, were recorded in September, when the Enteromorpha mats were rapidly decomposing along the estuary. Fisher-Behrens test indicated that there were no significant differences ($P < 0,05$) between mean GP or R values recorded in the tidal and lagoon phases.

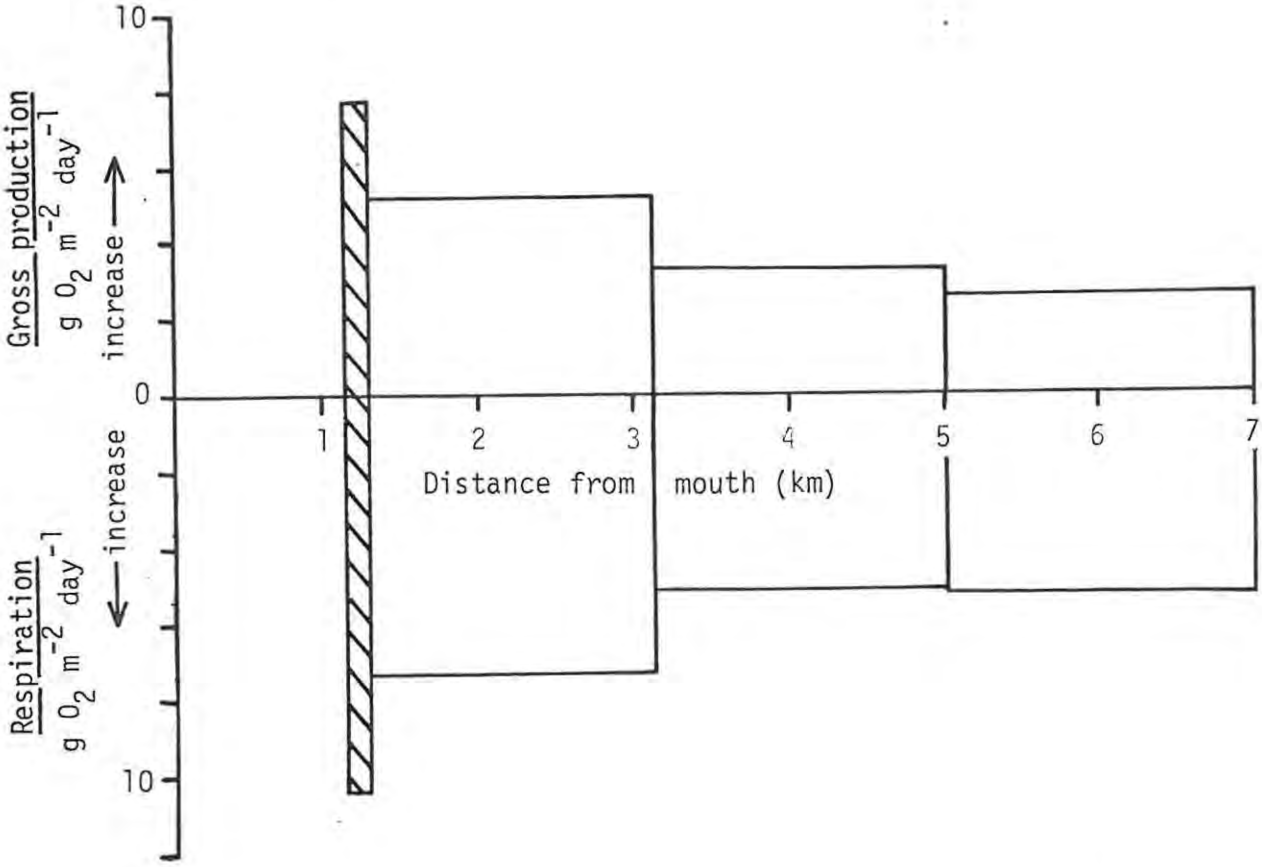


Fig. 37: Mean values of gross production and respiration of oxygen in the Swartvlei estuary in 1976 and 1977. The striped bars represent metabolism in a Zostera community. Note decrease in metabolic rates away from the mouth.

To estimate the annual amount of oxygen produced and respired in the estuary, the curves in Fig. 37 b, c and d were integrated to obtain g O_2 m^{-2} yr^{-1}. These data were then multiplied by the areas (m^2) covered by each section. The results are shown in Table 14. Apparently the amount of oxygen respired exceeded the amount produced by 2 710 tonnes.

Table 14. The total budget of oxygen produced and respired by the estuary between September 1976 and September 1977 (tonnes), in sections 1,1 - 3,0 km, 3,1 - 5,0 km and 5,1 - 7,0 km from the sea.

Section (km)	Gross production	Respiration
1,1 - 3,0	1 090	1 470
3,0 - 5,0	740	1 340
5,0 - 7,0	1 130	2 860
TOTAL	2 960	5 670
		- 2 960
NET		2 710

Table 15 shows the correlation coefficients (r) of metabolic rates with the known environmental variables. It indicates that, at the 95% level of probability:

i. metabolic rates showed significant positive correlations to percentage macrophyte cover;

ii. GP showed a significant positive correlation ($r = +0,50$) to salinity in the tidal phase, but not in the lagoon phase. R was not significantly correlated to salinity in either phase;

Table 16. A comparison of rates of community metabolism at Station 3 (a *Zostera* bed), both inside and outside a polythene enclosure (g O_2 m^{-2} day^{-1}).

Date (1977)	Tidal or lagoon phase	Gross Production Inside	Gross Production Outside	% Deviation from mean	Respiration Inside	Respiration Outside	% Deviation from mean
10-11 February	Tidal	8,3	8,1	1,2	8,5	8,9	2,3
22-23 June	Tidal	10,1	11,9	8,2	11,0	14,1	12,4
29-30 June	Lagoon	3,1	3,4	4,6	22,5	20,6	4,4
27-28 July	Lagoon	4,5	4,2	3,5	4,8	3,6	14,3
17-18 August	Lagoon	5,1	5,8	6,4	4,0	4,0	0
13-14 September	Lagoon	4,5	3,9	7,1	26,2	20,8	11,5
Mean % deviation of values inside and outside of enclosure				5,2%			7,5%
Standard error of mean % deviation				1,1%			2,5%

iii. metabolic rates showed significant positive correlations to phytoplankton α-chlorophyll concentration in the lagoon phase;

iv. R was significantly correlated to temperature ($r = +0,44$) in the lagoon phase, but not in the tidal phase. GP was not correlated to temperature in either phase;

v. metabolic rates were poorly correlated to solar radiation, and TDP of the water column.

Table 15. Correlation coefficients (r) of metabolic rates with known environmental variables. Dash (–) indicates that the variable was not measured. The significant values ($P < 0,05$) are underlined.

	Lagoon phase		Tidal phase	
	Gross production	Respiration	Gross production	Respiration
Salinity	-0,18	-0,14	-0,50	+0,11
Temperature	-0,19	+0,44	-0,09	+0,01
Solar radiation	+0,05	-0,33	-0,04	+0,01
% Macrophyte cover	+0,59	+0,48	+0,58	+0,38
Phytoplankton α-chlorophyll concentration	+0,34	+0,54	-	-
Total dissolved phosphorus concentration	+0,06	+0,08	-	-

2. Community metabolism measurements using an enclosure

Wincoxon's signed rank test indicated that there was no significant difference ($P < 0,05$) between metabolic rates measured inside and outside of the polythene enclosure (Table 16). The enclosure, therefore, had no apparent effect on the metabolic rates of the enclosed community.

3. Collection of bubbles

The amount of gas collected over the *Zostera* community varied from 0 to 6,6 g m^{-2} day^{-1} (Table 17). Virtually no bubbles were evolved when the water column was under-saturated with dissolved oxygen.

Examination of the *Zostera* beds with SCUBA showed that streams of minute bubbles were released from *Zostera* leaves in the late morning and afternoon, when the water was super-saturated with oxygen. Gas was also seen to collect inside the hollow *Enteromorpha* filaments.

Table 17. Gross production, and bubble production of a *Zostera* community in the Swartvlei estuary, 1,1 km from its mouth.

Date (1977)	Gross production (g O_2 m^{-2} day^{-1})	Bubble production[1] (g m^{-2} day^{-1})	% bubble production is of total production
10 February	8,3	6,6	44
17 May	0,7	0,0*	0
2 June	6,1	1,1	15
22 June	10,1	0,5	5
29 June	3,1	<0,1*	<3
13 July	6,6	0,2	3
27 July	4,5	0,5	11
13 September	4,5	0,0*	0
			$\bar{x}$ = 10%

[1] assuming bubbles to be oxygen.

* days on which the water column remained under-saturated with oxygen.

4. Measurement of day-time respiration rates

Day-time respiration rates obtained from experiments using the darkened enclosure were fairly constant under the different physico-chemical conditions. The mean value obtained was 1,0 g O_2 m^{-2} h^{-1} (Table 18).

Table 18. Day-time respiration rates of a Zostera community, 1,1 km upstream of the mouth of the Swartvlei estuary. These were calculated by measuring the oxygen depletion of water inside a darkened enclosure.

Date (1977)	Time of day	Depth (m)	Initial temperature (^oC)	Salinity ($^o/oo$)	Initial % saturation of O_2	Respiration rate g O_2 m^{-2} h^{-1}
29 June	11h00	1,30	16,7	35	82	0,9
13 July	10h55	0,85	11,3	22	115	0,5
13 July	12h00	0,85	11,8	22	95	1,2
25 July	09h45	1,00	15,7	35	116	1,3
27 July	13h35	1,00	17,5	33	138	0,9
2 September	10h30	1,25	17,9	26	65	1,0
2 September	12h30	1,25	18,5	26	69	0,9
2 September	14h35	1,25	20,5	26	125	1,0
13 September	10h24	1,50	18,4	24	60	1,0
						$\bar{x}$ = 1,0
						s = 0,2

Application of Wilcoxon's signed rank test indicated that these values were significantly higher ($P < 0,01$) than dark respiration values ($\bar{x}$ = 0,54 g O_2 m^{-2} h^{-1}) recorded in the same period. Dark respiration values were corrected for higher temperatures (+3^oC) in daylight, and a

Q_{10} of 2,0 was assumed. After an initial high oxygen uptake in the darkened enclosure (Fig. 38), uptake rates decreased to levels recorded at night (0,41 S.D. ± 0,24 g O_2 m^{-2} h^{-1}).

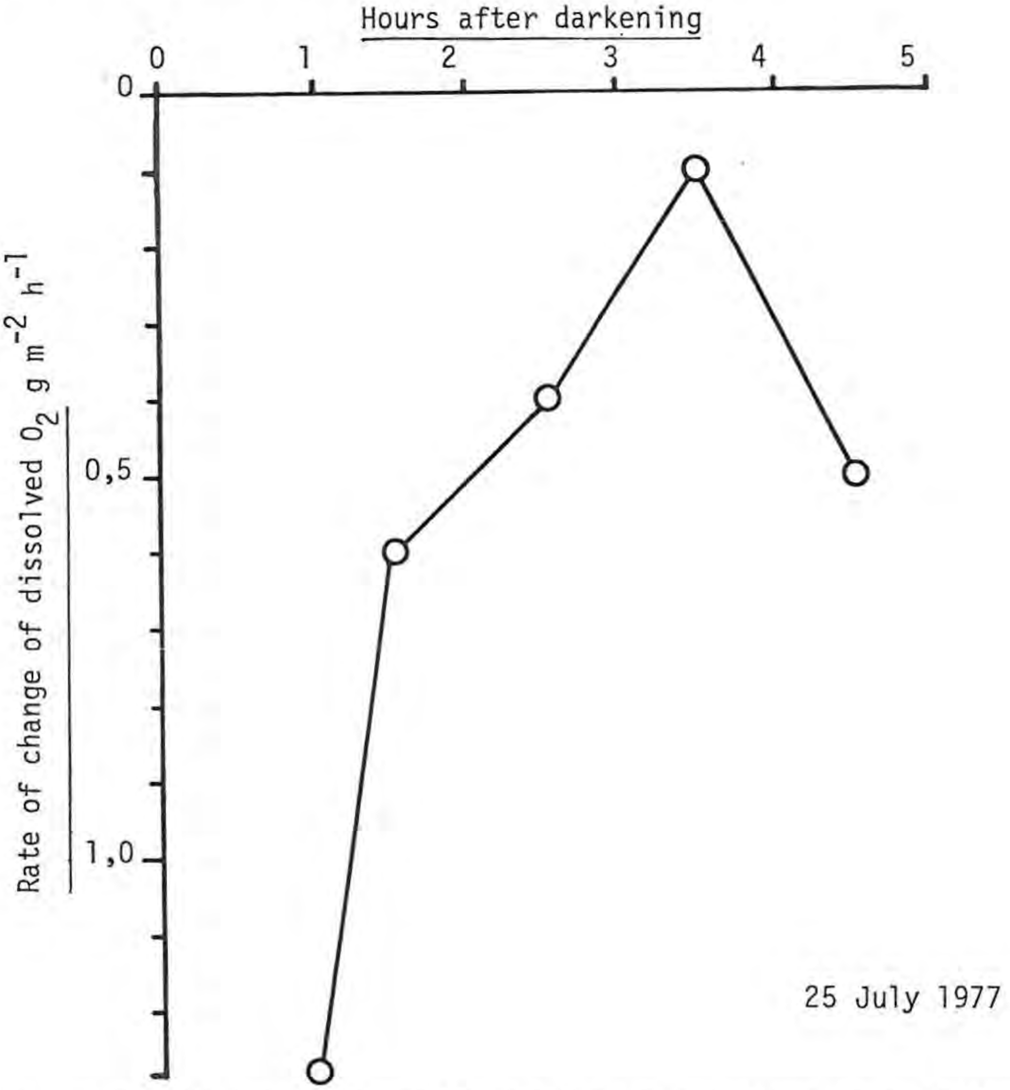


Fig. 38. Rates of oxygen depletion of the water column in a Zostera bed, inside a darkened enclosure. Note the initial high oxygen depletion. Time of darkening: 09h45; temperature: 15,7°C; salinity = 35 ^{o}/oo; initial O_2 concentration: 9,4 ppm, 116% saturation.

5. Epipsammic production

Metabolic rates of the epipsammic community and concurrent values of salinity, temperature, solar radiation and α-chlorophyll concentration of the sand are shown in Fig. 39. Oxygen production and respiration

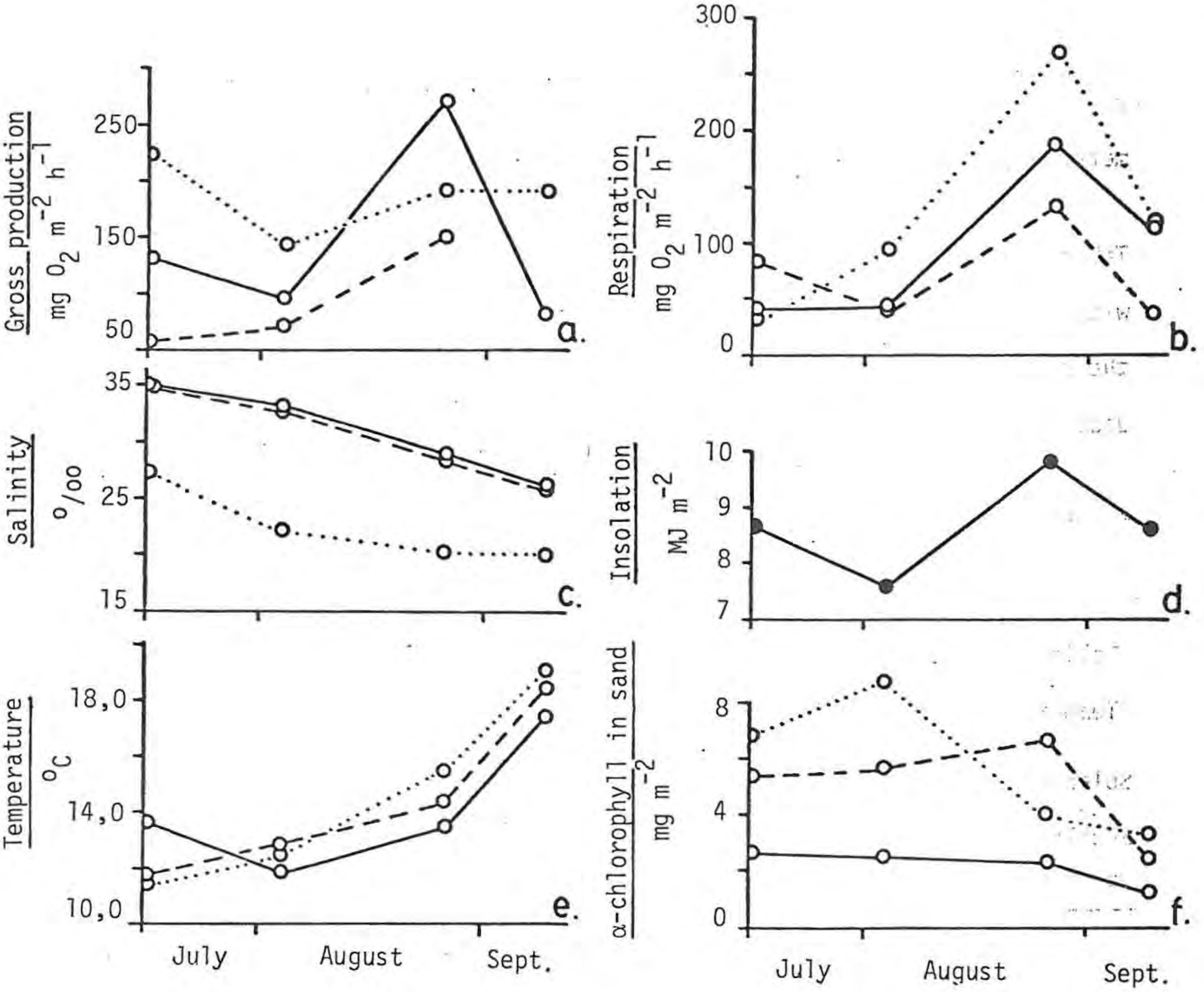


Fig. 39. Gross production (a) and Respiration (b) rates of the epipsammic community at Stations S (——), L (----) and U (....) in the Swartvlei estuary in the 1977 lagoon phase. Concurrent values for salinity (c), insolation (d), water temperature (e) and α-chlorophyll concentration in the sand (f) are also shown. The positions of the stations can be seen in Fig. 32.

values ranged from 55 to 270 mg O_2 m^{-2} h^{-1}, and from 35 to 270 mg O_2 m^{-2} h^{-1}, respectively. Table 19 shows correlation coefficients between the metabolic rates and the known environmental parameters.

Table 19. Correlation coefficients (r) of epipsammic metabolic rates with environmental variables over sandflats in the Swartvlei estuary in the second lagoon phase of 1977. The significant values ($P < 0{,}05$)are underlined.

	Gross production	Respiration
Salinity	-0,50	-0,63
Temperature	+0,09	+0,43
Solar radiation	+0,56	+0,76
α-chlorophyll concentration in sand	+0,11	-0,23

There was a high positive correlation between solar radiation and metabolic rates, and a high negative correlation between salinity and metabolic rates. The correlations were significant at the 95% probability level.

Extrapolation of epipsammic community metabolism from hourly to daily rates, indicated that mean daily values for GP and R were 17% of mean values recorded in the *Zostera* bed in the same period (Table 20).

Table 20. Mean daily values of gross production (GP) and respiration (R) over sandflats in the Swartvlei estuary in the second lagoon phase of 1977. Mean values for a Zostera community are also shown. Units in g O_2 m^{-2} day^{-1}.

Date (1977)	Mean GP	Mean R
18 July	0,7	1,0
5 August	0,7	1,2
24 August	1,4	4,0
6 September	0,5	1,8
Mean	0,8	2,0
Mean for Zostera community	4,5	12,6

DISCUSSION

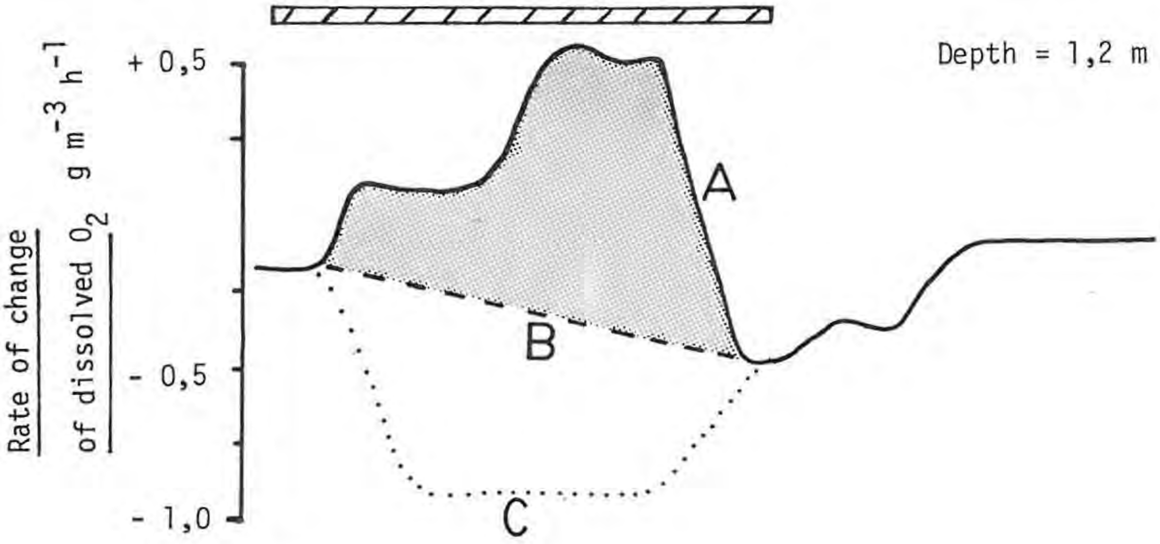
Tidal penetration, which provides a source of phosphorus for an estuary, also generates currents which aid nutrient cycling and prevent an accumulation of waste products. These factors are considered by Odum (1971) to be instrumental in maintaining the high productivity of an estuary. The importance of current velocity as a growth factor was demonstrated by Conover (1968). He found that growth of *Zostera marina* L. was stimulated by an increase in current speeds up to ± 0,5 m s^{-1}, above which the plants were uprooted from the sediments. Currents are thought to stimulate growth by enhancing transfer of nutrients between the plant and water, and hence increase metabolic rates (Odum and Hoskin, 1958; Conover, 1968).

It is therefore surprising that closure of the mouth of the Swartvlei estuary, with a subsequent reduction in current speeds, should have no significant effect on community metabolism. Also, the lagoon phases generally occur in winter, when solar radiation is reduced. As has been shown by seasonal growth studies of Zostera marina (Sand-Jensen, 1975) and Ruppia communities (Nixon and Oviatt, 1973), productivity of these seagrasses is highest in summer, when both temperatures and solar radiation reach maxima. In a system dominated by Zostera and Ruppia, one would expect the highest productivity to occur in the summer months.

Epipsammic production rates, however, showed a positive correlation with solar radiation (r = +0,56). This result is in agreement with findings by Pomeroy (1959) in a study of submersed salt marsh algae in Georgia. In general, metabolic rates were higher in the areas with submersed macrophytes, and increased with percent cover of Zostera and Ruppia. Salinity was shown to be an important factor governing production rates in the tidal phase, but not in the lagoon phase. This suggests that it is not salinity per se that is important, but an associated factor. For example, high salinity in the tidal phase is associated with spring tides (Fig. 12) when current speeds are high, with high inorganic carbon content (Fig. 17) and with high phosphorus content (Fig. 24).

Multiple regression analysis showed that between 32 and 55% of the variation in GP, and between 14 and 74% of the variation in R could be attributed to the known parameters. This suggests that community metabolism is also strongly influenced by factors that were not measured e.g. nitrate, inorganic carbon content, biomass of macryphytes and current velocities.

The covered enclosure experiments indicated that day-time respiration rates were significantly higher than dark respiration rates. This implies that a considerable error is introduced to the calculation of community metabolism if night-time respiration rates are extrapolated throughout the day, as illustrated in Fig. 42. Almost half of the total organic material produced is immediately required. The high respiration rates were measured when Enteromorpha mats were present, and when Zostera had only a light cover of epiphytes. It is likely, therefore, that photorespiration occurs in Zostera. Although it has been demonstrated in Enteromorpha sp. (Tolbert and Garey, 1976), Najas flexis (Hough, 1974), Cymodocea rotundata and Halophila ovata (Hough, 1976), this is the first report to suggest that photorespiration also occurs in Zostera.



1. Gross production - 5,9 g O_2 m^{-2} day^{-1}
   Respiration - 7,0 g O_2 m^{-2} day^{-1}
2. Gross production - 12,9 g O_2 m^{-2} day^{-1}
   Respiration - 12,7 g O_2 m^{-2} day^{-1}

Fig. 42: Calculation of community metabolism from the rate of change curve of dissolved oxygen, corrected for diffusion (curve A) using 1. day-time respiration rates extrapolated between night-time values (curve B); 2. respiration rates obtained from darkened enclosure values (curve C). Zostera community 1,1 km from the mouth of the Swartvlei estuary, in the lagoon phase, 27-28 July 1977. Dashed bar indicates daylight.

Table 20. Gross production, measured using the Odum and Hoskin (1958) technique, in ecosystems with a similar flora to that of the Swartvlei estuary. The values are annual variations except where stated otherwise.

Ecosystem	Dominant plants	Reference	Gross Production
Sonoran lagoons, Mexico	*Zostera*, *Enteromorpha*	Nichols, 1966	1,7 - 5,0
Estuarine impoundment, Oregon, U.S.A.	*Zostera*, *Ruppia*, *Enteromorpha*	Lyford and Phinney, 1968	0,3 - 11,7 mean = 2,6
Baltic rockpools, Denmark	*Enteromorpha*	Ganning and Wulff, 1970	2,7 - 21,8 (summer)
Estuary and coastal pond, New England, U.S.A.	*Zostera*	Nixon and Oviatt, 1972	2,9 - 3,6 (summer)
Estuarine embayment, New England, U.S.A.	*Ruppia*, *Ulva*	Nixon and Oviatt, 1973	< 0,2 - 5,2
Swartvlei estuary	*Zostera*, *Ruppia* *Enteromorpha*	This study	2,6 - 7,8 (means)*
Estuaries in general		Odum, 1971	7,9 - 19,5** (means)

* Range of mean values from each section of the estuary.

** Converted from 10 - 25 x 10^3 kcal m^{-2} yr^{-1} assuming g $O_2 \equiv 3,5$ kcal (Brody, *loc.cit.* Hall and Moll, 1975).

The large excess of the amount of oxygen required over the amount of oxygen produced per year is remarkable in a system that apparently maintains a high biomass of macrophytes (up to 1,5 kg dry mass m^{-2}), and exports up to 0,5 tonne dry mass of Zostera leaves per tidal cycle. One would expect the estuary to be autotrophic ($GP > R$) rather than heterotrophic ($GP < R$). The rates of GP are, however, similar to those in other ecosystems with a similar flora, and measured by the Odum and Hoskin diurnal oxygen curve technique (Table 20). Mean values along the Swartvlei estuary (2,6 - 7,8 g O_2 m^{-2} day^{-1}) are lower than the mean values (7,9 - 19,5 g O_2 m^{-2} day^{-1})* cited for estuaries by Odum (1971). The latter values are apparently from estuaries that contain large expanses of Spartina alterniflora or Thalassia testudinum. Data from Westlake (1963), Mann (1972) and Zieman (1975) suggest that these are two of the most productive plants in the world. Odum's values could either: 1) represent the upper limits to estuarine primary production rather than the mean, or: 2) reflect the inadequacy of diurnal curve analysis as a way of measuring gross production in estuaries.

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* Converted from kcal assuming 1 g $O_2 \equiv 3{,}5$ kcal (Brody, loc.cit. Hall and Moll, 1975).

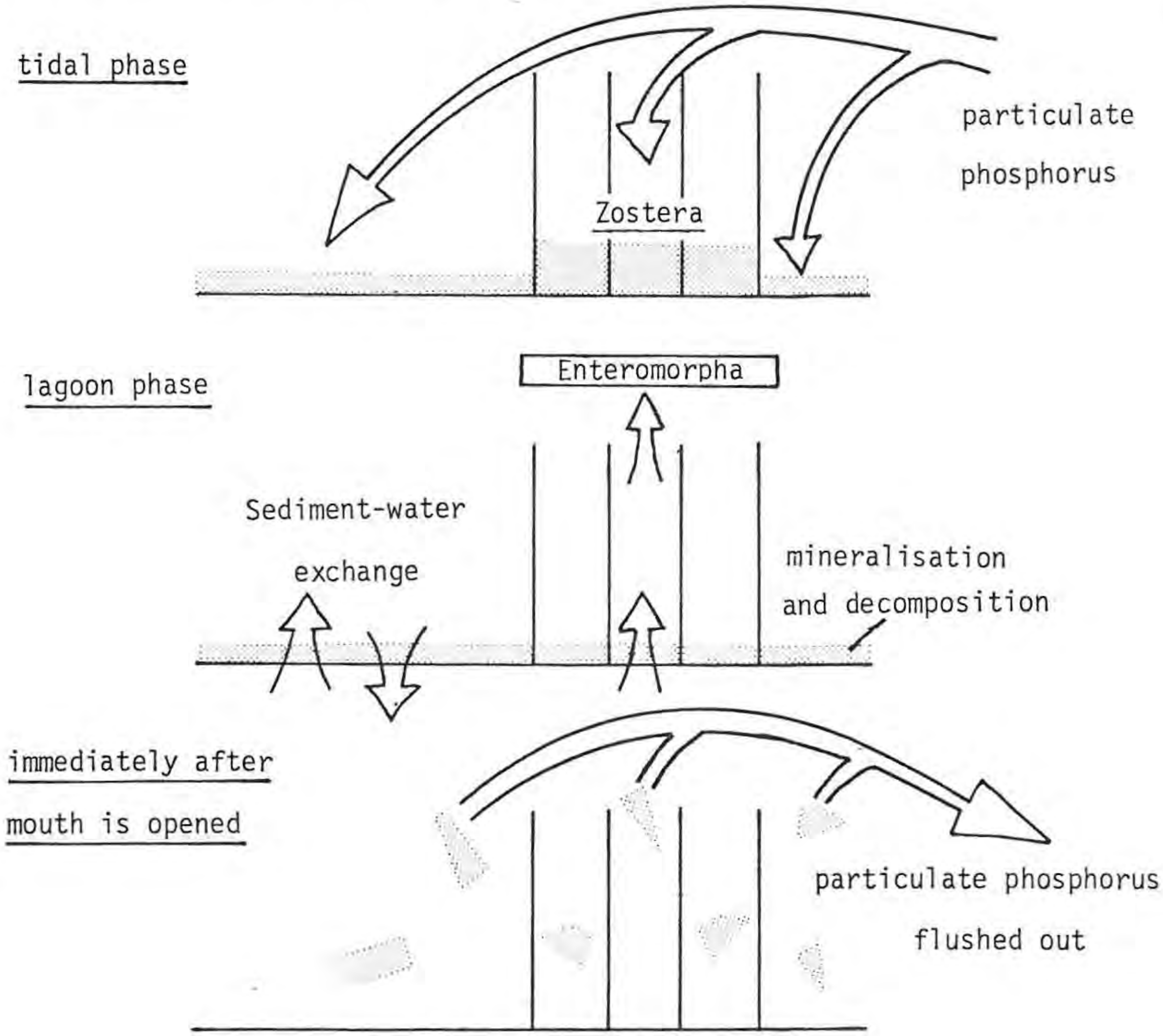
FINAL COMMENTS

Changes in phosphorus content and production of both phytoplankton and Zostera have recently been studied in another closed estuary, the Grevelingen estuary in the Netherlands (Nienhuis and de Bree, 1977; Vegter, 1977). At Grevelingen, primary production of phytoplankton was not markedly affected by mouth closure. Growth of Zostera, however, increased by a factor of between 25 - 250, probably because of an increase in the transparency of the water (Nienhuis and de Bree op.cit.). Phosphate vlaues of the water also increased after closure from 20 - 60 $\mu g\ \ell^{-1}$ to 300 $\mu g\ \ell^{-1}$ four months later (Vegter op.cit.). Vegter attributed this rise to phosphate release from the sediments via wave action or bioturbation. It is tempting to speculate that phosphate release was also enhanced by Zostera, as has been demonstrated by McRoy et al. (1972) and this study.

Phosphate release by Zostera could also explain the abundant growth of Enteromorpha over the eelgrass beds. As Harlin (1975) noted, any nutrients that leaked out of eelgrass leaves would be available to the surrounding algae before the open water; also, nutrients around the leaves would be present in higher concentrations than in the open water, and may thus tend to stimulate algal growth. Simultaneous release of P by Zostera and uptake by Enteromorpha indicates that phosphorus is cycled between these two macrophytes.

Enteromorpha also proliferates over the tidal flats and the sides of the main channel where there is no Zostera. These are areas where the sand-prawn, Callianassa kraussi is extremely common. Forbes (1974) showed that this species enhances transfer of water between the sediments and the overlying water column. It would be interesting to investigate this phenomenon as a further means of phosphorus transfer.

The net import of particulate phosphorus in the tidal phase indicates that the sediments become progressively richer in phosphorus. Mineralisation of inorganic phosphorus particles, and decomposition of organic particles in the sediments would make this phosphorus available to plants. The phosphorus could be lost from the sediments by three processes. Firstly, there could be a direct sediment-water exchange. Secondly, in the lagoon phase a substantial amount could be taken up by *Enteromorpha* via *Zostera*. Thirdly, when the mouth is opened, current speeds along the estuary exceed 0,5 m sec^{-1} (measured by timing floats), which are far higher than those recorded over spring tides (Fig. 23). These velocities are maintained for up to 2 days. A considerable amount of sediment must be flushed out of the estuary over this period, including the particulate phosphorus that had been deposited in the previous tidal phase, as well as the *Enteromorpha* mats. These possible relationships are summarised below:

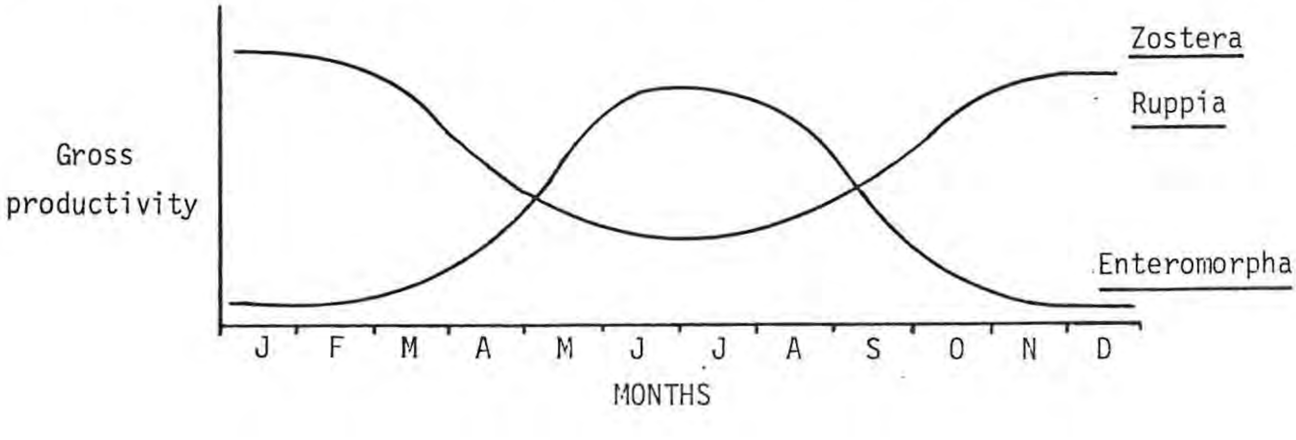


A more detailed study on the phosphorus flux between seawater, the water column and sediments in the estuary would prove highly valuable to test this hypothesis.

Evidence from the community metabolism rates in the Swartvlei estuary supports the result of the Grevelingen studies: mouth closure is not detrimental to primary production. This is surprising as besides reducing current speeds, mouth closure usually occurs in winter when there is a 50% reduction in insolation over summer values (Fig. 3).

Lack of a seasonal change in productivity could be due to two reasons. Firstly, unlike Zostera species in Europe and North America, Z.capensis remains apparently healthy throughout winter except for those plants covered by Enteromorpha mats. Dry weights of eelgrass at Station 3 in July 1977 (winter) ranged from 390 to 1 090 g m^{-2}, compared with 200 to 1 480 g m^{-2} in late summer. Winter biomass values in the Netherlands were < 5 g m^{-2}, a twenty-fold decrease from summer values (Nienhuis and de Bree, 1977).

Secondly, lower solar radiation and cooler winter temperatures (< 16°C) apparently favour growth of Enteromorpha in the estuary. Studies elsewhere (Phillips, 1960; Nixon and Oviatt, 1973; Sand-Jensen, 1975) indicate that optimum growth of Zostera and Ruppia occurs in summer. Growth of high-insolation favouring plants in summer (Zostera and Ruppia) and low-isolation favouring plants in winter (Enteromorpha) would tend to maintain gross productivity at a relatively constant level for most of the year:



A similar growth overlap of high- and low-light favouring plants has been shown by Pomeroy and Stockner (1976) to occur in the Squamish River Estuary, British Columbia.

The large deficit of oxygen respired over oxygen produced in the estuary could be explained by two possibilities:

1. the diurnal curve technique does not adequately measure gross production;

2. there is a substantial import of organic matter into the estuary.

The results of gas collection over Zostera showed that up to 44% of the total gross production of oxygen was lost as bubbles. As the highest loss occurred in summer, it is likely that summer values for gross production at the mobile stations were underestimated. In winter, the Enteromorpha mats float on the surface because of bubbles of gas trapped in the lumina of the filaments. The mats tended to sink at night, when this gas became depleted and made the filaments less buoyant. This was also noticed when Enteromorpha was darkened in the measurement of day-time respiration rates. In the day-time, the bubbles were replenished and the mats once again resurfaced. As the mats were in direct contact with the atmosphere during the day, there would be direct loss of oxygen to the atmosphere, which would result in underestimation of gross productivity. Presumably both GP and R would also be underestimated when the Zostera leaves float on the surface at low water, for the same reason.

Another pathway for oxygen loss has recently been demonstrated. Oremland and Taylor (1977) showed that an appreciable amount of photosynthetically evolved oxygen in Thalassia testudinum is not released into the water, but is transferred to the sediments via the vascular system. This could be a characteristic of submersed aquatic plants, and would lead to an underestimation of gross production when the diurnal oxygen curve technique is used to measure productivity. These extra disadvantages of the oxygen curve method call for its re-appraisal as a means to accurately measure primary productivity in submersed hydrophytic communities.

The second possibility for the excess of oxygen respired is that there is an import of organic material into the estuary. This could have three sources:

1. the sea;
2. terrestrial vegetation;
3. river inflows and detritus from Swartvlei.

Measurements of the amount of marine algae and other allochthonous vegetation netted at flood tide, and the high light transmittance of seawater at 430 nm, suggest that the marine contribution to the pool of organic detritus is small. Leaf-fall from the banks of the estuary was also small, estimating from the amount netted at ebb tide (< 1% of the total vegetation exported) and observations with SCUBA along the channel in the lagoon phase. No plant detritus from Swartvlei was seen in appreciable quantities in the estuary, except after floods.

A major source of organic material, however, is present in river inflows (p. 48) which could annually provide the Swartvlei system with 3 400 tonnes of dissolved and particulate organic matter. Humic material is precipitated when mixed with seawater and the pH is raised. Incorporation of this precipitate into the pool of particulate organic matter, and its subsequent respiration by the microflora and microphagous animals, could account for at least part of the estimated large respiration deficit in the Swartvlei estuary.

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APPENDIX I

Diurnal oxygen curve analysis

a. Stations representative of the different communities studied were established;

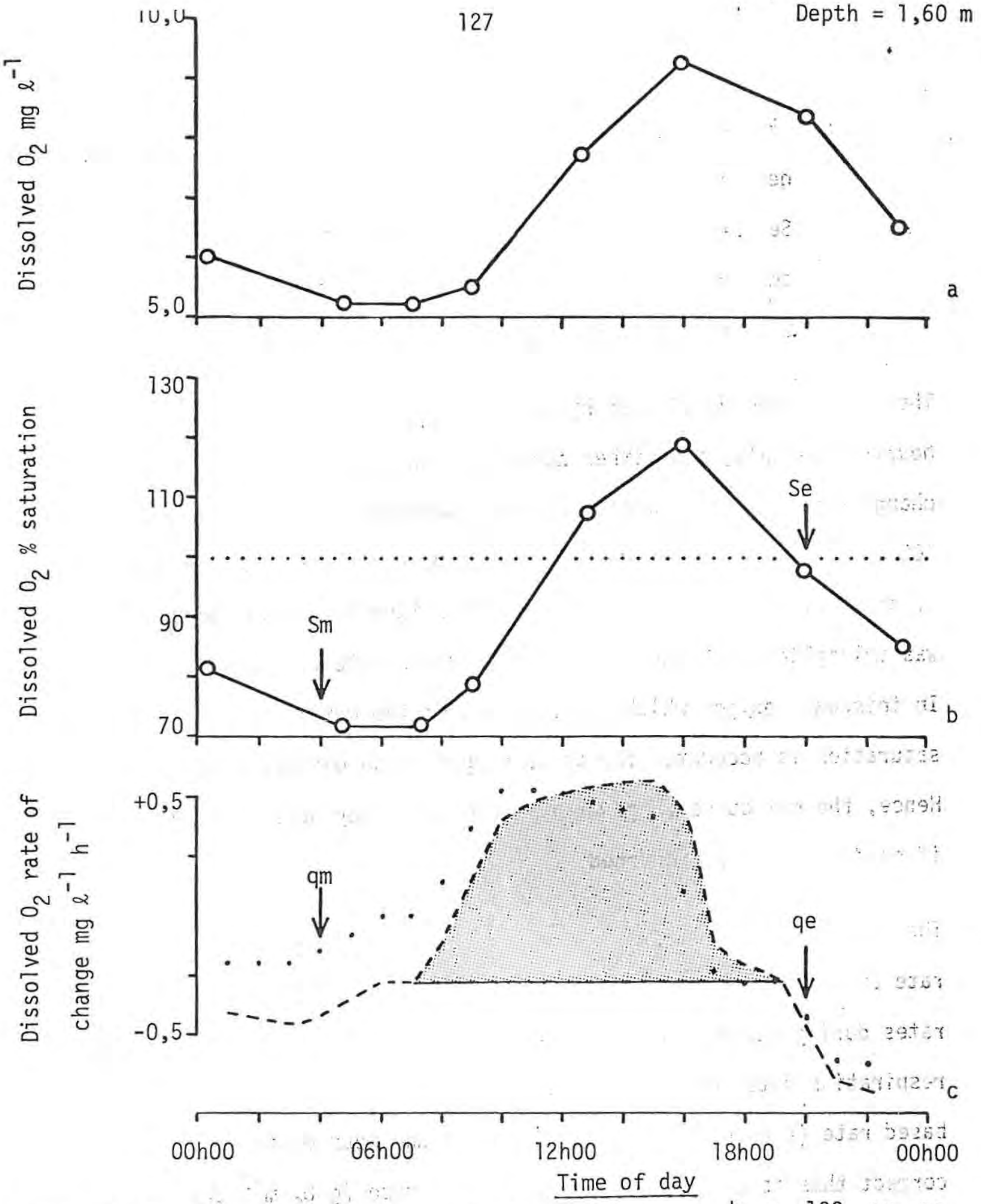
b. the salinity ($^{o}/oo$), temperature (^{o}C) and dissolved oxygen (mg ℓ^{-1}) were measured at each station, as previously described (p. 19). Measurements were taken at the surface, midwater and bottom of the water column, at approximately 3 h intervals over a total period of 24 h. Sampling began at either 00h00 or 08h00. The depth of each station was also determined;

c. diurnal changes in the percentage oxygen saturation of the water column were calculated from data on salinity, temperature and dissolved oxygen, using saturation values contained in Strickland and Parsons (1968). Diurnal curves from the mean values of dissolved oxygen and percentage saturation obtained at each station on each sampling run, were then plotted (Fig. 40a and b);

d. the rate of change of dissolved oxygen in mg ℓ^{-1} h^{-1} ($\equiv$ g m^{-3} h^{-1}) every successive hour was calculated from the oxygen curve, using a 2 h interval (dotted line in Fig. 40 c);

e. this rate of change curve was then corrected for diffusion using the equation:

$$k = 100 \frac{qe - qm}{Se - Sm} \qquad (7)$$



Gross production = Shaded area x depth

= $6{,}43\ g\ O_2\ m^{-3} \times 1{,}60\ m$

= $10{,}28\ g\ O_2\ m^{-2}$

Respiration = Mean hourly respiration rate x 24 x depth

= $0{,}4\ g\ O_2\ m^{-3}\ h^{-1} \times 24 \times 1{,}60\ m$

= $15{,}36\ g\ O_2\ m^{2}$

$$k = 100\ \frac{qm \sim qe}{Sm \sim Se}$$

$$= 100\ \frac{0{,}15 \sim 0{,}40}{73 \sim 98}$$

$$= 100\ \frac{0{,}25}{25}$$

$$= 1{,}0$$

Fig. 40. Diurnal oxygen curve analysis. For explanation, please refer to text.

where k = volume based diffusion constant

qe = rate of O_2 change at a time after sunset ($gm^{-3}\ h^{-1}$)

Se = the oxygen saturation value at this time (%)

qm = rate of O_2 change at a time before dawn ($g\ m^{-3}\ h^{-1}$)

Sm = the oxygen saturation value at this time (1%)

The k value was multiplied by the saturation deficit or surplus at hourly intervals, and either added to or subtracted from the rate of change curve. For example, if the % saturation value exceeded 100%, the surplus value was multiplied by k and added to the rate of change curve. If the value was less than 100%, the deficit was multiplied by k and subtracted from the rate of change curve. In this way, oxygen which diffused out of the water during supersaturation is accounted for as is oxygen which diffused in. Hence, the new curve (Fig. 40 c) is one which may have resulted if no diffusion had occurred.

f. The dawn rate of change line was then extrapolated to the post-sunset rate of change line, to obtain theoretical values for respiration rates during the day (Fig. 40 c). The mean of all the hourly respiration rates was multiplied firstly by 24 to obtain a volume-based rate ($g\ O_2\ m^{-3}\ day^{-1}$), and then by the mean depth (m) to correct this to an area-based respiration rate ($g\ O_2\ m^{-2}\ day^{-1}$).

g. The area between the day-time 'hump' of the corrected rate of change curve and the estimated respiration line was then integrated. This gave the gross production in $g\ O_2\ m^{-3}\ day^{-1}$; it was then multiplied by the mean depth (m) to obtain an area-based production rate ($g\ O_2\ m^{-2}\ day^{-1}$).

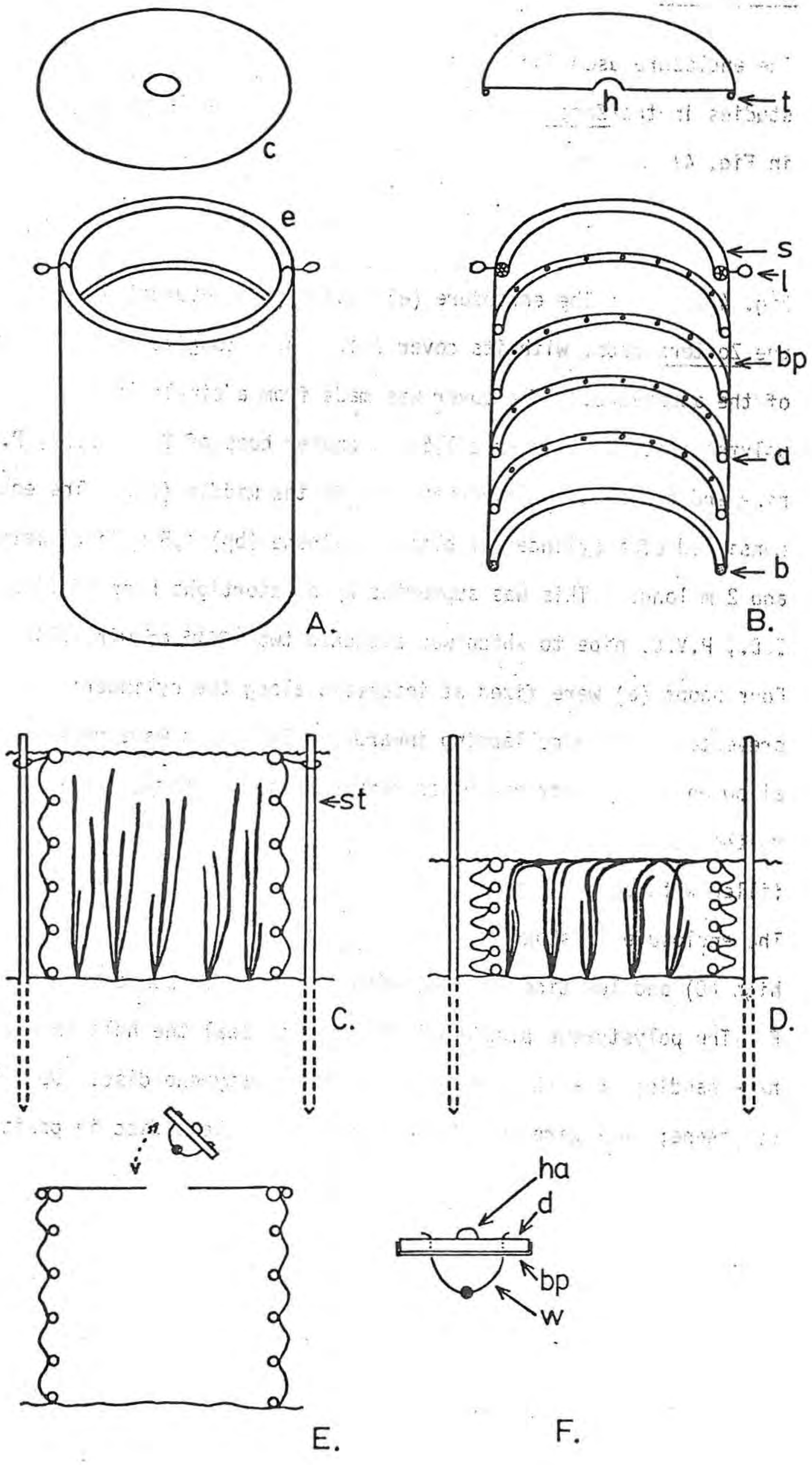


Fig. 41. See opposite for caption.

APPENDIX 2

The enclosure used for community metabolism and diurnal phosphorus studies in the *Zostera* bed and *Enteromorpha* mats at Station 3 is shown in Fig. 41.

Fig. 41. A. The enclosure (e) used for the diurnal studies in the *Zostera* beds, with its cover (c). B. Longitudinal section of the apparatus. The cover was made from a circle of black polythene stretched over a 1,6 m diameter hoop of 20 mm I.D., P.V.C. pipe and had a 0,10 m diameter hole in the middle (h). The enclosure consisted of a cylinder of black polythene (bp) 1,5 m in diameter and 2 m long. This was supported by a watertight hoop of 50 mm I.D., P.V.C. pipe to which was attached two loops of wire (l). Four hoops (a) were fixed at intervals along the cylinder: these prevented it from collapsing inwards. The hoops were perforated to allow entry of water and hence reduce their buoyancy. Attached to the bottom of the enclosure was a hoop of 25 mm I.D. tubing filled with sand (b) to prevent water from seeping underneath. The enclosure is shown fixed in a *Zostera* bed with stakes (st) at high (C) and low tide (D), and with its cover in position (E). F. The polystyrene plug which was used to seal the hole in the cover. ha - handle; d - 20 cm diameter white polystyrene disc; bp - black polythene; w - wire loop with weight, which kept disc in position.