TIDAL EXCHANGES OF CARBON, NITROGEN AND PHOSPHORUS BETWEEN A SARCOCORNIA SALT-MARSH AND THE KARIEGA ESTUARY, AND THE ROLE OF SALT-MARSH BRACHYURA IN THIS TRANSFER

Dissertation

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by

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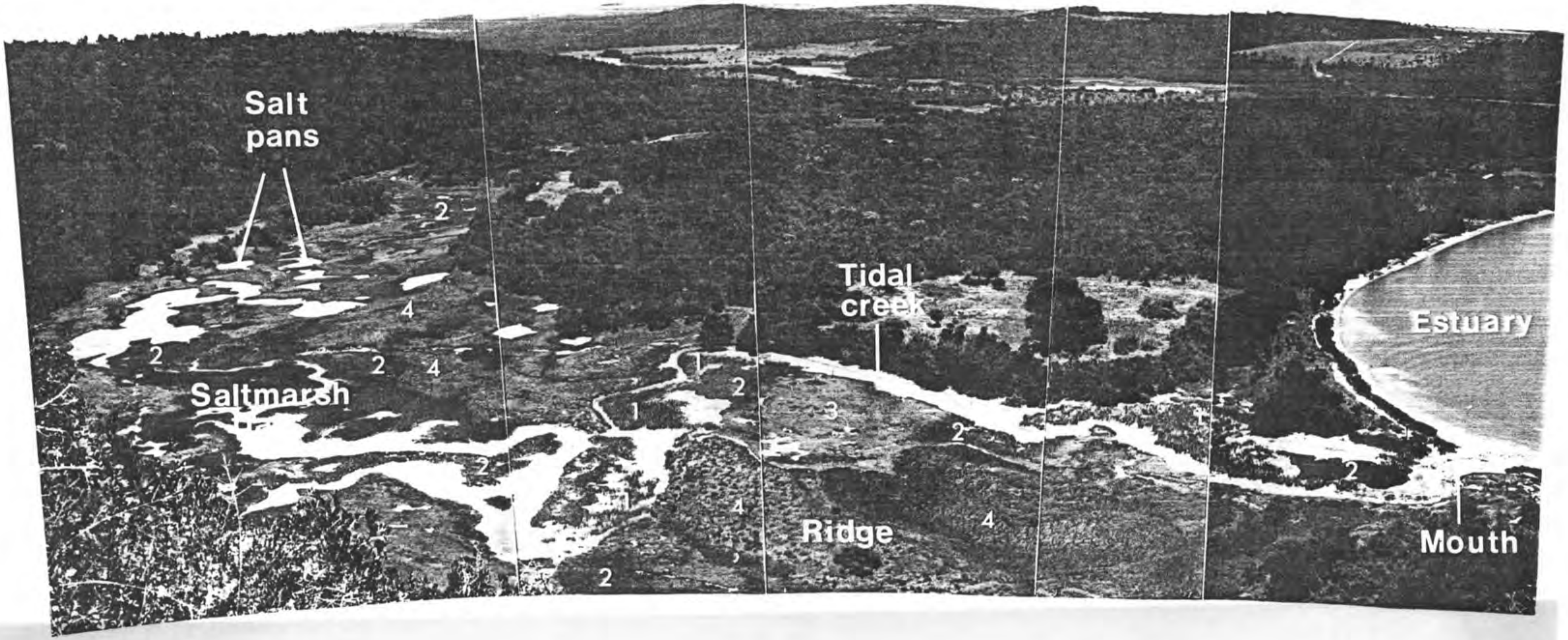
KEY TO FRONTISPIECE

1. *Spartina alterniflora*
2. *Sarcocornia perennis*
3. *Chenolea diffusa*
4. Mixed species including *Limonium scabrum*, *Disphyma crassifolium* and *Sporobolus virginicus*



Frontispiece The salt-marsh and adjacent Kariega estuary.

CONTENTS

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ABSTRACT

Tidal exchanges of organic carbon, nitrogen and phosphorus between a south temperate Sarcocornia marsh and its associated estuary are examined. Subterranean water flow was small, and the hydraulic exchange between the two systems largely surficial. The dominant tidal signal was semi-diurnal, and the extent of inundation of the marsh varied considerably as a consequence of interactions of semi-lunar tidal cycles with changes in daily mean sea level.

Annual net fluxes of organic carbon were directed from the marsh to the estuary, but amounted to less than 2% of marsh aerial net primary productivity. This indicates the incompatibility of E.P. Odum's outwelling hypothesis to this marsh-estuarine system.

The direction of net flux of organic carbon switched on a time-scale of days. These directions were largely correlated with mesoscale oceanic events, which materially altered the extent of marsh inundation, and which provided evidence of the mutual exclusivity of outwelling of DOC from the marsh and oceanic upwelling.

Laboratory mesocosm experiments using intact marsh blocks of sediment from the marsh were conducted to identify the proximate processes and interactions at the marsh-water interface responsible for the variability of marsh-estuarine exchanges. Patterns of fluxes of organic carbon, total nitrogen and phosphorus were markedly different in the structurally contrasted tidal creek and Sarcocornia Zone regions of the marsh. Both regions exported these components, but the fluxes of organic carbon and total phosphorus were significantly larger from the tidal creek than from the *Sarcocornia* zone, and the opposite applied to nitrogen. The presence of brachyuran crabs, the most numerous macrofauna on the marsh enhanced the flux of carbon, nitrogen and phosphorus from the marsh biocoenosis, largely as a result of the effect of their bioturbation. Evidence is examined which suggests that differential mobilization of nutrients in the two zones by crabs is responsible for biogeochemical coupling of these two regions, which may account for the elevated productivity of salt-marsh systems.

CHAPTER 1

INTRODUCTION

Estuarine salt-marshes are subjected to tidal inundation and drainage, and this movement of water transfers energy and matter between the marshes and adjacent estuarine systems. Although salt-marshes are among the most studied ecosystems we still do not fully understand the significance, either to the salt-marshes or to the adjacent systems, of these transfers. Fundamental to both these questions is an understanding of the magnitude and direction of transfers, and the nature of material involved.

Since the pioneering work on salt-marsh ecology by Teal (1962), considerable research effort has been directed towards examining these transfers (much of it reviewed by Nixon 1980). Early investigations suggested that tides effected large exports of particulate detritus (Odum and de la Cruz 1967) and nutrients from salt-marshes (Pomeroy _et al_. 1967). From these studies arose the widely-accepted view that tides are responsible for the large-scale export or "outwelling" (Odum 1971) of material to adjacent estuarine and coastal systems.

However, two aspects pertaining to the outwelling hypothesis have recently become increasingly evident: firstly, that tides are not responsible for large exports of material from salt-marshes, at least on an annual basis (e.g. Smith _et al_. 1983, Dankers _et al_. 1984, Kokkinn and Allanson 1985); and secondly, that the exchanges are highly variable, between marshes, for individual marshes at different times, and for different chemical fractions (e.g. Borey *et al*. 1983, Jordan *et al*. 1983, Whiting *et al*. 1985). Although a large number of studies have examined the role of specific salt-marsh components in the processing of energy and matter (e.g. macrophytes : Pierce 1983, Pakulski 1986; macrofauna : Hoffman *et al*. 1984, Chrzanowski *et al*. 1986; microbiota : Newell *et al*. 1983, Abd. Aziz and Nedwell 1986), our understanding of the factors reponsible for regulation, and hence variability, of marsh-estuarine exchanges is still poor.

Further, virtually all work on these exchanges has concerned *Spartina* salt-marshes of the east coast of North America, with little on floristically-different salt-marshes (exceptions include Jordan *et al.* 1983, Dankers *et al*. 1984, Kokkinn and Allanson 1985 and Abd. Aziz and Nedwell 1986), or those located in the southern hemisphere (exceptions include Pierce 1979, Kokkinn and Allanson 1985, and Knox 1986 p. 139).

This dissertation presents an interdisciplinary study of a south temperate *Sarcocornia perennis* (Mill.) A.J. Scott salt-marsh. The principle objectives of the study are to test the applicability or not of the outwelling hypothesis to this system, and to identify those proximate factors and interactions responsible for regulation of material exchanges between the marsh and estuary. The basis of the study is a detailed investigation of (a) the surface and subterranean hydrodynamics of the marsh, (b) the fluxes of organic carbon and of nitrogen and phosphorus effected by these water movements, and (c) the influence of the dominant macrofauna on the marsh, namely the brachyuran crabs, on these material transfers.

A number of aspects of this marsh-estuarine system make it particularly suitable for such a study. Firstly, because of its location in a semi-arid climatic region, its small catchment, and the fact it has no permanent stream inflow, means the dominant water flow on the marsh is tidal. Secondly, estuarine water enters the marsh at almost all semi-diurnal tides, and the marsh is completely drained at each low tide. Thirdly, much of the marsh surface is compact, fine-grained and impervious so that water flow on the marsh is largely surficial. Fourthly, surface water flow enters and leaves the marsh via a single narrow channel.

CHAPTER 2

DESCRIPTION OF SALTMARSH

Prior to this investigation no work had been done on this or on any other local *Sarcocornia* salt-marsh. It was therefore necessary to begin the study with a survey of the structure of the marsh, which was extended, when and where necessary, as the study progressed. The aim of the survey was not to provide an exhaustive description of as many properties of the marsh as possible, but to examine those aspects most relevent to the study *per se*. These included the location of the marsh, its topography, its macrophyte and crab communities, certain characteristics of its sediments, and its temperature environment.

2.1 Kariega estuary

The marsh is located at 33°40'37"S, 26°38'46"E in the middle reaches of the Kariega estuary, 4.9 km from the estuary mouth (Figure 1). The estuary, which is located on the south eastern seaboard of southern Africa (Figure 1, Inset), is a sinuous, elongate system, 17.4 km long from mouth to ebb-and-flow, with a mean width of only 110 m (Figures 2 and 3). Because of the small and semi-arid catchment of the Kariega River, and its impoundment at three sites, the estuary receives only small and intermittent freshwater inputs. During non-flood conditions this inflow amounts to <1% of the tidal prism (Allanson and Read 1987). Consequently, the estuary is hydrodynamically marine-dominated, and its water column largely unstratified with salinities equal to or greater than seawater. The hydrodynamics and ecology of the estuary are described more fully by Allanson and Read (1987).

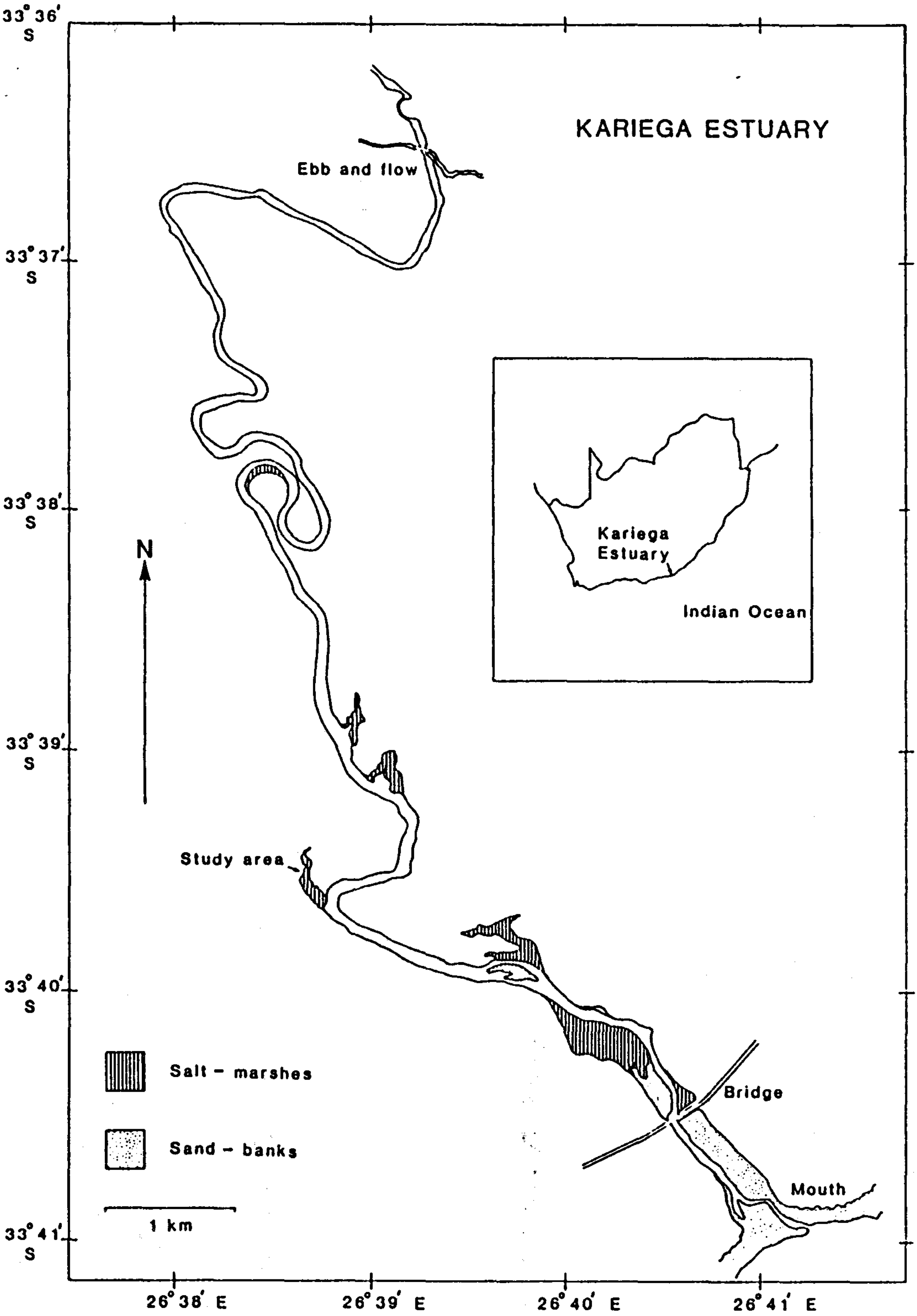


Figure 1 Map of Kariega estuary showing location of the study marsh. Inset: map of South Africa showing location of Kariega estuary.

Figure 2 South westerly view of upper reaches of Kariega estuary showing elongate, sinuous channel, and narrow intertidal areas. Arrow indicates location of study marsh.

Figure 3 Lower reaches of Kariega estuary showing non-vegetated sandbanks near estuary mouth, and salt-marshes further upstream. Study marsh lies off bottom right-hand corner of photograph.

Figure 2

Figure 3

The intertidal areas of the estuary are steep, narrow and frequently rocky, particularly in the upper reaches of the estuary, but are expanded as sand-banks and salt-marshes closer to the mouth (Figures 1 - 3). Salt-marsh vegetation also extends as a narrow intertidal ribbon along the entire length of the estuary, and is expanded locally in small areas, particularly in the middle reaches, where alluvial sediments have been deposited between hillocks juxtapositioned against the estuary channel. The salt-marshes occupy an area of 0.57 km^2, or 24% of the surface area of the estuary. The study marsh is small, with an area of only 35.5×10^{-3} km^2.

2.2 Marsh topography

The marsh was mapped from aerial photographs and its topography contoured using a Leitz Dumpy Level. Ten transects across the marsh (Figure 4), and more than 130 selected points were surveyed and fixed to a benchmark previously related to mean sea level by a qualified Surveyor. Mean sea level corresponds to the Land Levelling Datum adopted by the Director General of Surveys for the Precise Levelling of the Republic of South Africa. All elevations in the present study are reported as metres above mean sea level (m.a.m.s.l.).

The marsh is an elongate system, 750 m long and between 20 and 120 m wide, and is bound on its east and west margins by steep-sided banks, and on its northern border by a small man-made earthen wall (Figure 4). It abuts onto the estuary along its southern border, where water enters and leaves the marsh via a channel which enters the estuary at a single site.

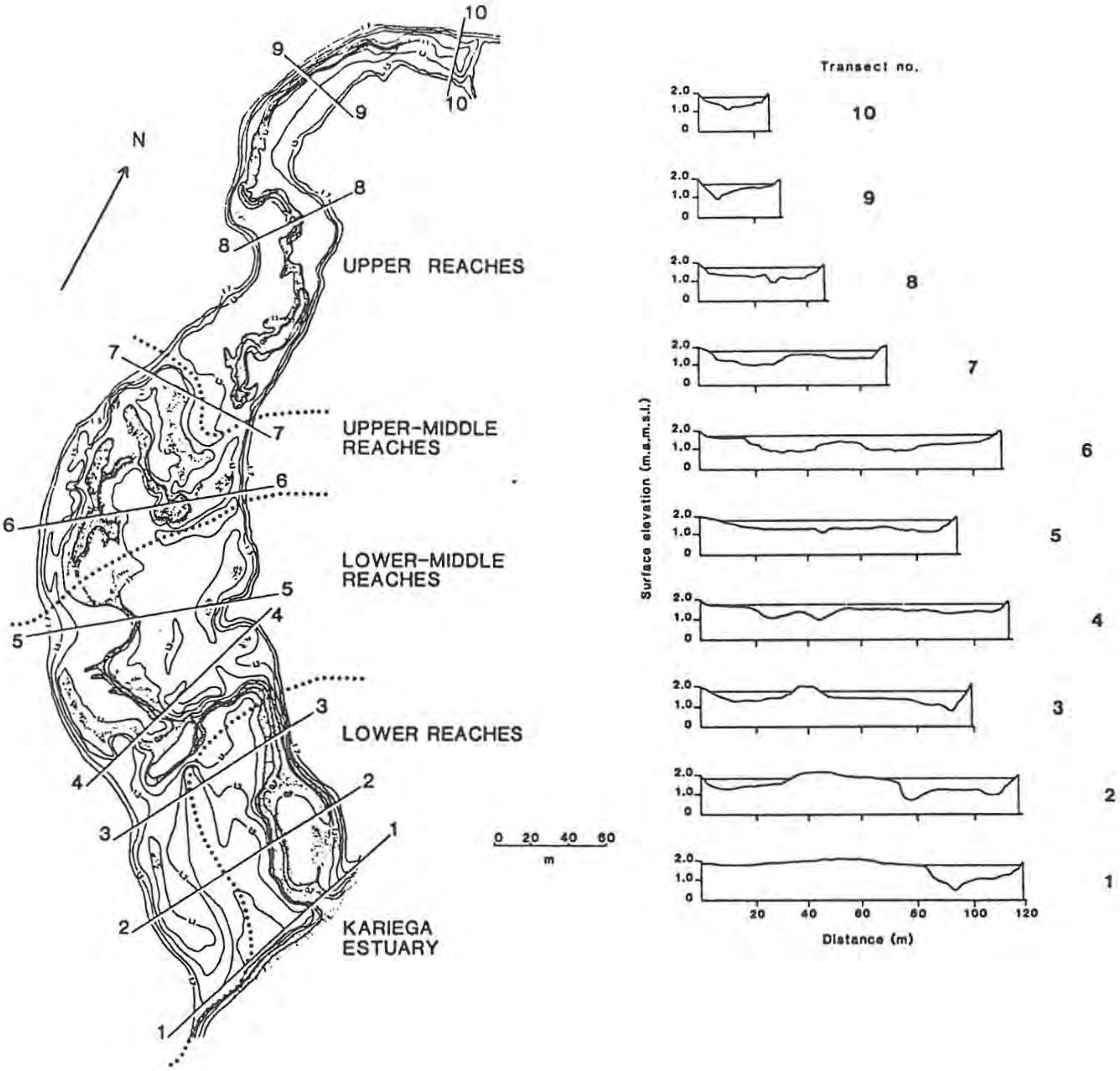


Figure 4 Topography of marsh showing cross-sectional profiles along 10 transects. Contour interval = 0.2m; elevation units = m.a.m.s.l. Stippling denotes non-vegetated areas. Horizontal lines on profiles represent maximum water level recorded during present study, namely 1.76 m.a.m.s.l. (Chapter 3).

The marsh is intertidal and located between 0.55 and 1.8 m.a.m.s.l. Although the vertical elevation of the marsh is 1.25 m, 70% of its area lies within a vertical range of only 0.4 m, namely from 1.0 to 1.4 m.a.m.s.l. (Table 1). This region is here termed the "salt-marsh flats"; terminology used to describe the marsh topography follows Long and Mason (1983). The higher regions of the marsh, with elevations >1.4 m.a.m.s.l., are confined to narrow bands along the outer margins of the marsh, and to small isolated ridges on the salt-marsh flats. The lower-lying areas, <1.0 m.a.m.s.l., are restricted to the "tidal creek" in the lower reaches of the marsh, and to a series of depressions or "salt pans" in the middle and upper reaches (Frontispiece).

Tidal water enters and leaves the marsh via the tidal creek. At low elevation tides estuarine water is confined to the tidal creek, but at higher tides the elevated, more extensive salt-marsh flats are also inundated (Figures 5 and 6).

2.3 Vegetation zonation

Thirteen macrophyte species occur on the marsh, namely: Spartina maritima (Curtis) Fernald, Sarcocornia perennis (Mill.) A.J. Scott, Sarcocornia pillansae (Moss) A.J. Scott, Triglochin bulbosum L., Chenolea diffusa Thunb., Salicornia meyerana Moss, Limonium scabrum (Thunb.) O. Kimtze, Disphyma crassifolium (L.) L. Bol., Sporobolus virginicus (L.) Kunth, Senecio rosmarinifolius L., Juncus krausii Hochst, Atriplex vestita (Thunb.) Allen, and Potamogeton pectinatus L.

Figure 5 Upper-middle reaches of marsh: low tide.

Figure 6 Upper-middle reaches of marsh: high spring-tide.

Table 1. Area occupied by different elevations of the marsh surface.

Height (m.a.m.s.l.)	Area (m2)	Percentage total area	Cumulative percentage	Regions
1.6 - 1.7	150	<1	100	Ridges and outer margins
1.5 - 1.6	2700	8	99	
1.4 - 1.5	3250	9	92	Salt-marsh flats
1.3 - 1.4	3270	9	83	
1.2 - 1.3	6190	17	74	
1.1 - 1.2	7850	22	56	
1.0 - 1.1	5990	17	34	
0.9 - 1.0	4410	12	17	Tidal creek and salt pans
0.8 - 0.9	900	3	5	
0.7 - 0.8	700	2	2	
0.6 - 0.7	80	<1	<1	
0.5 - 0.6	30	<1	<1	
Total area	35520			

Figure 7 shows the vertical zonation of the dominant macrophytes on the marsh. They are confined to the marsh flats and ridges, and are absent from the salt pans and tidal creek. *Spartina maritima* occurs immediately above the mudflats of the tidal creek, at elevations between 0.8 and 1.0 m.a.m.s.l., and it is confined to small single-species stands in the lower and lower-middle reaches of the marsh (see Frontispiece).

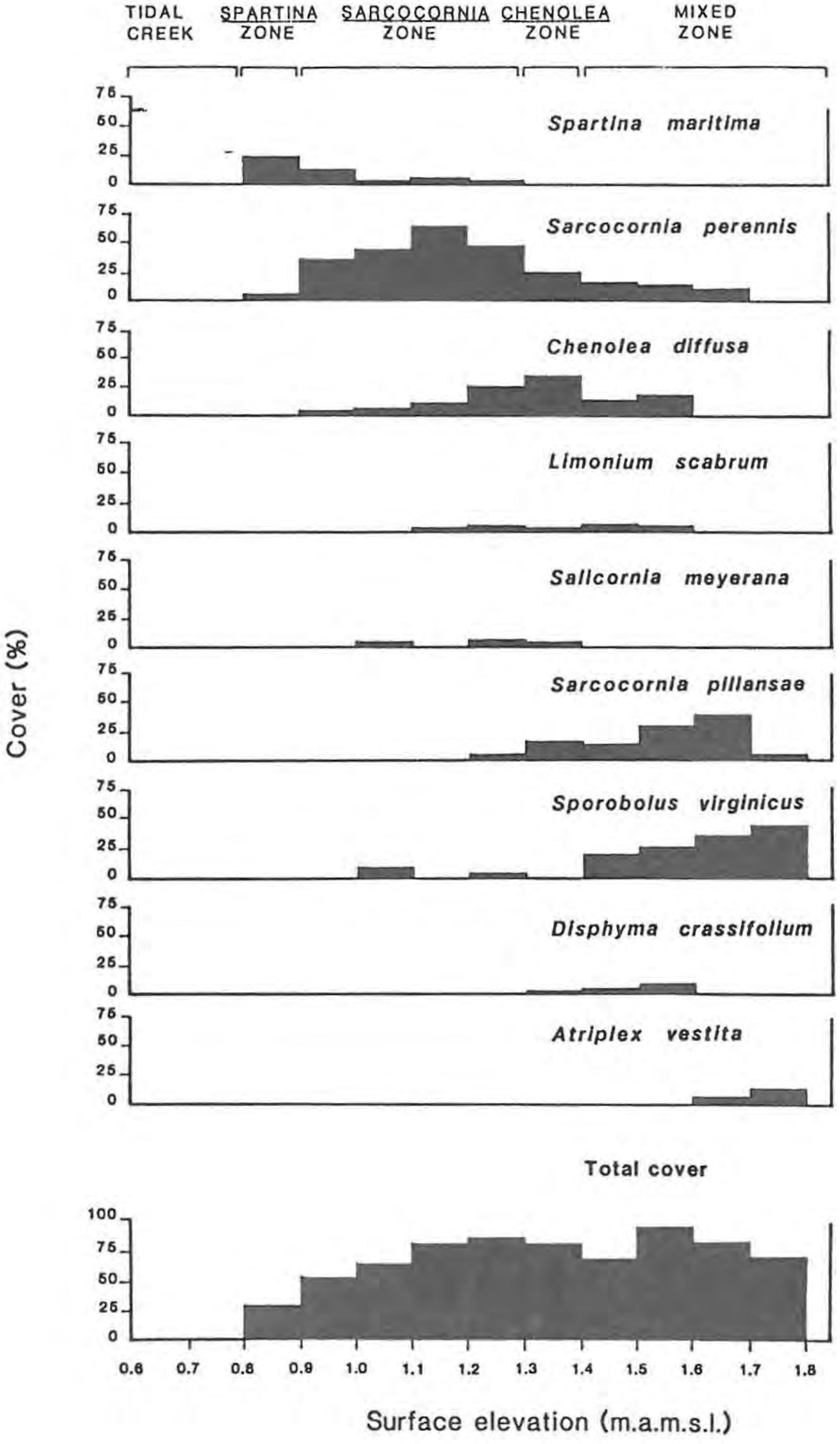


Figure 7 Percentage cover of individual macrophyte species (upper panel), and all macrophyte species combined (lower panel), in relation to marsh elevation, February 1984.

In terms of percentage area covered, *Sarcocornia perennis* (Figure 8) is the dominant macrophyte on the marsh. It occurs between 0.8 and 1.7 m.a.m.s.l., but dominates between 0.9 and 1.3 m.a.m.s.l., here termed the "*Sarcocornia* Zone". As shown in Table 1, this vertical zone accounts for 54% of the total marsh area. At 1.0 to 1.2 m.a.m.s.l. *S. perennis* forms low, very dense single-species meadows, but at higher elevations it is increasingly interspersed with *Chenolea diffusa* (Figure 9) which becomes the dominant macrophyte between 1.3 and 1.4 m.a.m.s.l., the "*Chenolea* Zone".

The *Chenolea* Zone is replaced vertically, at between 1.6 and 1.7 m.a.m.s.l., by a zone of mixed vegetation, dominated by *Sarcocornia pillansae* and the grass *Sporobolus virginicus*. *Atriplex vestita* occurs at elevations >1.6 m.a.m.s.l., and is confined to the narrow outer margins of the marsh.

The macrophyte zonation on the marsh is typical of salt-marshes of eastern Cape estuaries (Macnae 1957, MacDonald 1970, Pierce 1979). But because it is dominated by *Sarcocornia perennis*, and to contrast it with the mainly *Spartina* marshes examined in the literature, I refer to it here as a "*Sarcocornia* marsh".

2.4 Sediment characteristics

During the study it became necessary to examine certain properties of the salt-marsh sediments, namely their mud (or subsieve <63 µm) contents and redox potential (E_h) characteristics.

Figure 8 Sarcocornia perennis (Mill) A.J. Scott.

Figure 9 Chenolea diffusa Thunb.

These variables were determined at 7 stations along a transect located parallel to, and 10 m from Transect 3 shown in Figure 4. At each station subsieve contents were determined for thoroughly mixed sediment subsamples taken over 0.12 m depth intervals, to a depth of 0.96 m. Subsieve values were determined according to Buller and McManus (1979, p. 102). 50 to 100 g (wet weight) subsamples were manually wet-sieved through a 63 µm mesh sieve for 15 minutes. The dry mass of the subsieve component was determined, and expressed as mg g^{-1} (dry mass) of total sediment sieved. No dispersant was used and faecal pellets were disaggregated by gently rubbing them against the sieve side.

At each station E_h was measured at 50 mm intervals in duplicate, 0.3 m deep sediment cores. It was measured using platinum-calomel electrode half-cells and millivolt meter (Beckman Expandomatic 55-2 pH meter). Two bright platinum electrodes (wire diameter 0.48 mm, length 15 mm), constructed according to Bohn (1971), were gently inserted into each core, at each depth, through "Sellotape" sealed apertures, and allowed to stabilize for 60 minutes. These metal electrodes were cleaned after each measurement by gently rubbing them with fine emery paper; acid-cleaning techniques gave high and unstable values (as in Bohn 1971). The platinum electrodes were regularly checked in a buffered ferrocyanide/ferricyanide solution (Zobell 1946), and those which gave potentials in this solution deviating by three or more millivolts from the mean were discarded. E_h values were calculated from recorded millivolt readings by addition of 281 mV, which is the potential of 1.0 M KCl calomel electrodes measured against the standard hydrogen electrode at 20^{o} C (Selley 1977).

Figure 10 illustrates the horizontal and vertical changes in sediment subsieve (<63 μm) contents and E_h values along the transect. The salt-marsh flats were capped with fine-grained sediments with subsieve contents >900 mg g^{-1}. These overlay, at depths of ca. 0.9 m, coarser sediments with subsieve contents of 100-150 mg g^{-1}. In contrast, the sediments of the tidal creek were uniformly coarse-grained to depths of at least 1.0 m, with subsieve contents <300 mg g^{-1}.

Marsh sediments at all stations were oxidized, with positive E_h values to depths of 0.3 m. Vertical profiles of E_h in the salt-marsh flats were different from those in the tidal creek. In the salt-marsh flats (Stations 2-6) E_h values were uniformly high and exceeded +300 mV. In the tidal creek (Station 1) the surface sediments were highly oxidized, but those below the surface were more reduced with E_h values as low as +160 mV.

2.5 Distribution of dominant brachyura

Seven crab species occur on the marsh; namely, *Sesarma catenata* Ortm., *Sesarma meinerti* de Man., *Cleistostoma edwardsii* McLeay, *Cyclograpsus punctatus* M. Edw., *Uca urvillae* (M. Edw.), *Macropthalmus* sp., and *Scylla serrata* (Forskal). The community is dominated in terms of numbers by two of these, namely the grapsoid crab *Sesarma catenata*, and the ocypodoid crab *Cleistostoma edwardsii* (Figures 11 and 12). These two species are confined to the lower and lower-middle reaches of the marsh.

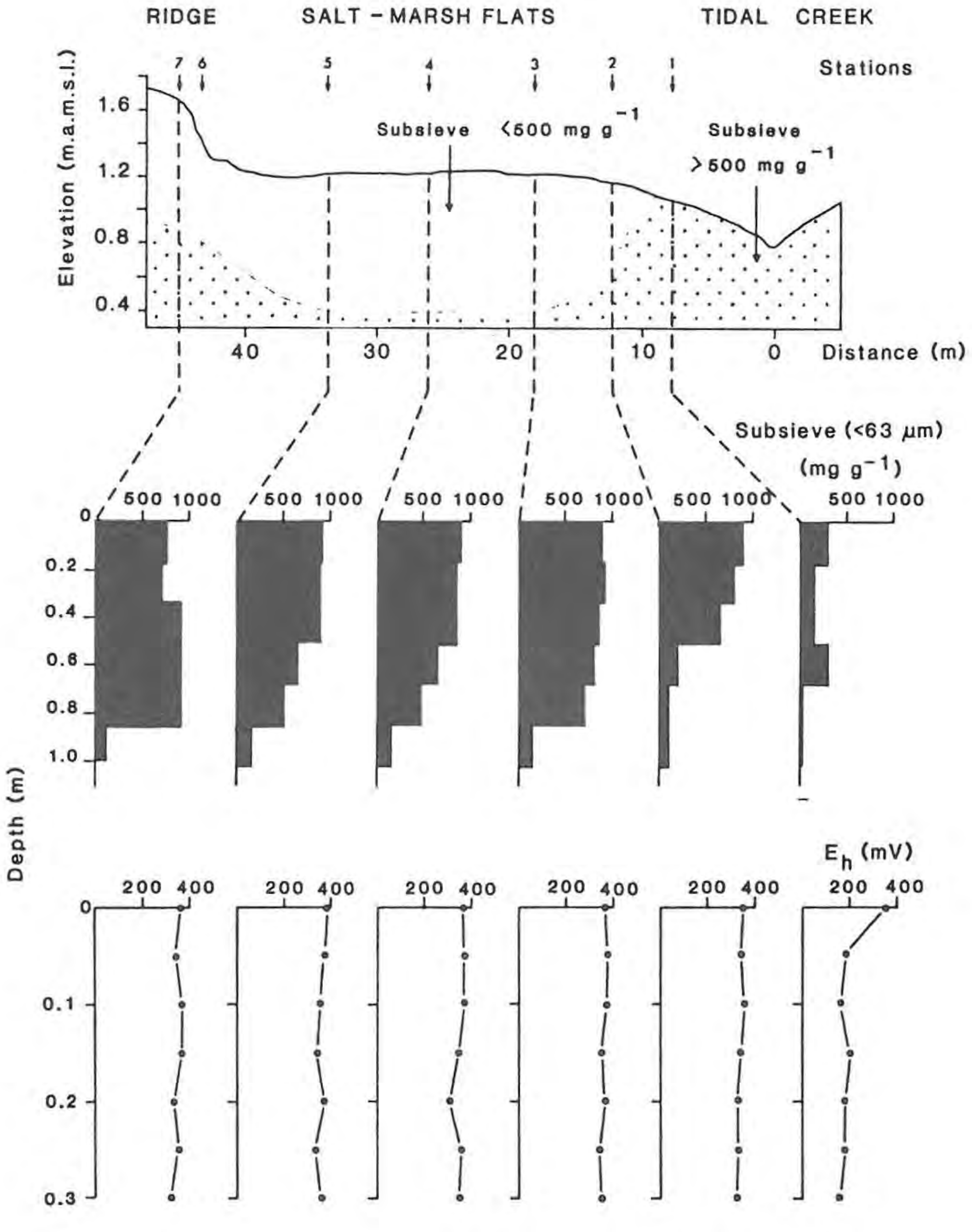


Figure 10 Sediment subsieve (<63 µm) content and E_h values at seven stations located along a transect in the loweer reaches of marsh. Stippled region denotes coarse-grained substrata (subsieve content <500 mg g^{-1}). Note: depth axes are different for subsieve and E_h panels.

Figure 11 Sesarma catenata Ortm. (x2).

Figure 12 Cleistostoma edwardsii McLeay (x3).

Their densities were determined by randomly placing (using a compass and table of random numbers) quadrats of 0.5 m x 0.5 m in the two regions. Crabs were removed from burrows within the quadrats by rapidly forcing a knife at an angle, alongside and then into each burrow. To check the efficiency of this technique eight quadrats were sampled, as above, and then immediately excavated to a depth of 0.5 m and the contents sieved to remove unsampled crabs (mesh size 1.25 mm). The mean percentage recovery(± standard deviation, S. D.) using the shortened method was as much as 78 ± 9% for S. catenata, and 95 ± 4% for C. edwardsii, which was considered adequate for the present purposes.

The organic, or ash-free dry, mass of the crabs was determined as loss of dry mass on ignition at 495 ^{o}C for 5h. Loss of inorganic crab mass due to carbonate combustion, and loss as CO_2, was checked by parallel ignition of "Analar" $CaCO_3$ samples. On no occasion was correction for this potential source of error necessary.

Table 2 summarizes the vertical distribution of C. edwardsii and S. catenata, expressed in terms of density and biomass. C. edwardsii occurred with maximum densities and biomasses between 0.7 and 0.9 m.a.m.s.l., the region broadly coincident with the base of the Spartina stands bordering the tidal creek (Figure 7). Although the distributions of the two species overlapped, S. catenata generally occurred at higher elevations than C. edwardsii, with maximum densities and biomasses in the Sarcocornia Zone at between 1.0 and 1.1 m.a.m.s.l.

Table 2. Density and ash-free dry mass of *C. edwardsii* and *S. catenata* at different marsh elevations, January 1985. 95% *C.L.* indicated.

Surface elevation (m.a.m.s.l.)	*C. edwardsii*		*S. catenata*		
	Density (no. m^{-2})	Biomass (g ash-free m^{-2})	Density (no. m^{-2})	Biomass (g ash-free m^{-2})	*n*
0.61 - 0.70	9 ± 22	1.06 ± 3.73	0	0	5
0.71 - 0.80	535 ± 43	5.16 ± 3.80	3 ± 6	0.1 ± 0.2	7
0.81 - 0.90	560 ± 22	5.41 ± 1.91	32 ± 12	7.8 ± 8.5	16
0.91 - 1.00	193 ± 33	1.67 ± 2.8	46 ± 29	8.5 ± 10.1	10
1.01 - 1.10	0	0	92 ± 27	14.1 ± 13	22
1.11 - 1.20	0	0	23 ± 14	6.3 ± 7.3	17
Mean ± 95% *C.L.*	386 ± 127	3.8 ± 0.6	47 ± 8	8.7 ± 1.0	
(*n*)	(38)	(38)	(72)	(72)	

The mean densities (± 95% confidence limits) of *C. edwardsii* were high (386 ± 127 individuals m^{-2}), and an order of magnitude higher than those of *S. catenata* (47 ± 8 individuals m^{-2}) (Table 2). However, because *S. catenata* individuals were much larger than those of *C. edwardsii*, the mean areal biomass (± 95% *C.L.*) of *S. catenata* was significantly higher than that of *C. edwardsii*; the respective values were 8.7 ± 1.0 and 3.8 ± 0.6 g ash-free dry mass m^{-2}.

2.6 Temperature

Water temperatures in the estuary were measured using a maximum-minimum thermometer, suspended 0.5 m below the water surface from a floating jetty located directly opposite the marsh. Temperatures on the marsh were measured at elevations of 0.83, 1.07, 1.35, 1.58 and 1.82 m.a.m.s.l. along a transect in the lower-middle reaches of the marsh (Transect No. 3, Figure 4) The marsh thermometers were held horizontally 50 mm above the sediment surface, below insulated wooden screens. Temperatures were measured in this manner, as opposed to using Stevenson's Screens, to provide an index of the temperature microclimate at the marsh surface at vertical levels at which the crabs live.

Figure 13 shows the weekly maximum and minimum temperatures over a 12-month period in the estuary, and at two of the five salt-marsh stations, namely those at 1.07 and 1.82 m.a.m.s.l. The maximum temperatures in the estuary ranged from 14 to 34 °C, and the minimum temperatures from 8 to 24 °C. On the marsh, the temperature range was more extreme and increased as marsh elevation increased. For instance, the mean weekly temperature range in the estuary was 7.3 ± 3.3 °C (± *S.D.*, n = 47), but on the marsh it ranged from 16.1 ± 3.7 °C (n = 46) at 0.83 m.a.m.s.l. to 32.2 ± 4.1 °C (n = 47) at 1.82 m.a.m.s.l.

2.7 Overview of marsh structure

The marsh is an intertidal system located at the interface of terrestrial and estuarine environments. However, the marsh surface is

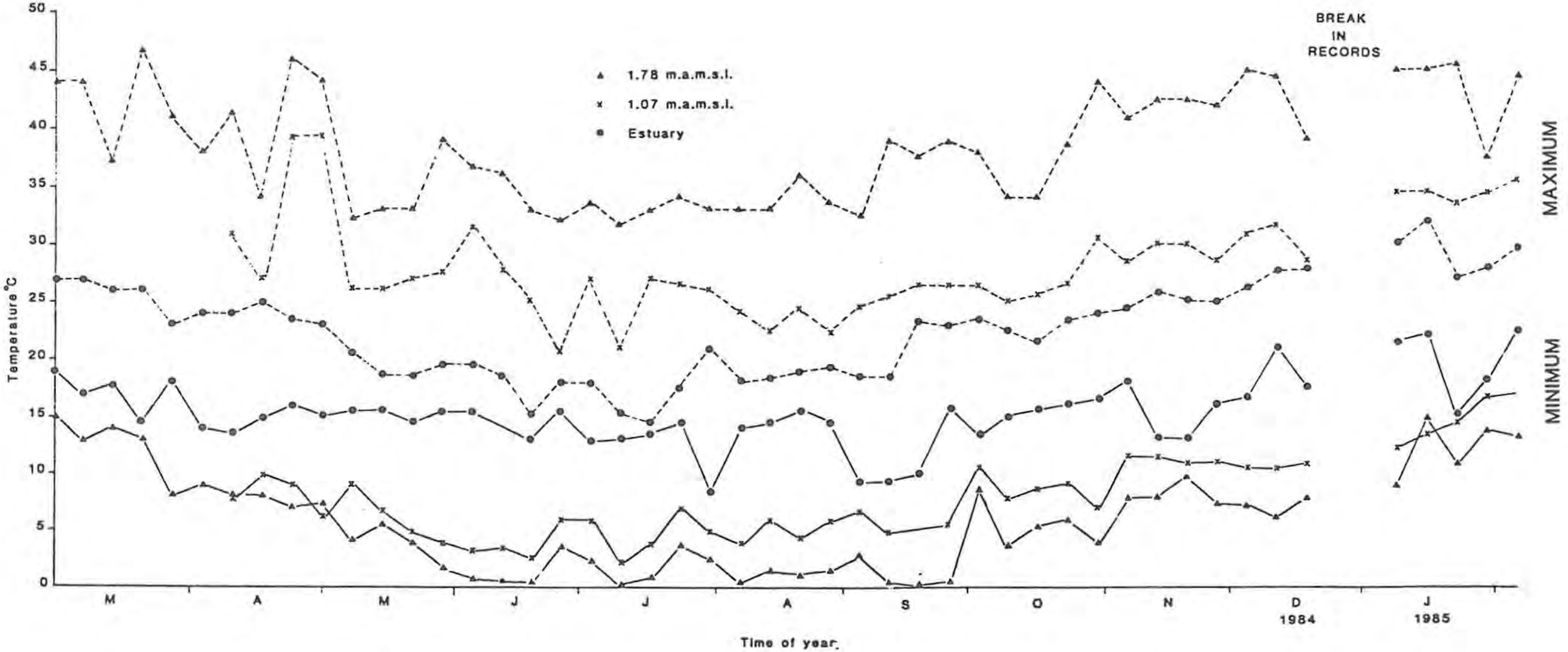


Figure 13 Weekly maximum and minimum temperatures measured during 1984 and 1985 in the estuary and at two intertidal stations in the lower-middle reaches of the marsh.

not a uniform intergrade between these two environments, and can be divided into two structural regions, namely the salt-marsh flats and the tidal creek.

The salt-marsh flats are more extensive, and occur at higher elevations than the tidal creek. The surface substrata of the salt-marsh flats are fine-grained, colonized by dense macrophyte meadows, and are inhabited by large populations of the grapsoid crab *S. catenata*. In contrast, the tidal creek is a narrow, low-lying drainage channel which connects the salt-marsh flats to the Kariega estuary. The creek is devoid of macrophytes, its substrata are coarse-grained, and it is inhabited by ocypodoid crabs of the species *C. edwardsii*.

These contrasted regions are characteristic of "high" or "mature" salt-marshes, and develop as a consequence of tidal erosion and deposition processes (Long and Mason 1983). However, they in turn influence the patterns of water flow on and off the marsh (Bayliss-Smith *et al*. 1979), and this is examined further in the next chapter.

CHAPTER 3

HYDRAULIC PROPERTIES

In this chapter I examine the hydraulic interactions between the marsh and Kariega estuary. The analysis has involved examination of the patterns of elevation of semi-diurnal tides inundating the marsh (Section 3.1), the effects of these changes on the extent and duration of marsh inundation (Section 3.2), and the patterns of water between the marsh and estuary (Section 3.3).

3.1 Patterns of elevation of semi-diurnal tides

Materials and methods

Continuous water level recordings were made over 12 months in the tidal creek at the marsh-estuarine junction, and for four weeks at a site located in the estuary directly opposite the marsh. At both sites water levels were measured using A. Ott (Model: HBe 20.110.0.1) horizontal water level recorders.

Results

Figure 14 compares water level changes in the tidal creek and estuary over the four-week period. These data confirm that the marsh is subjected to alternating, semi-diurnal periods of inundation and drainage, caused by tidal changes in water level in the estuary.

Figure 15 shows the maximum elevation of semi-diurnal tides at the marsh-estuarine junction over the 12-month period (dots), and the

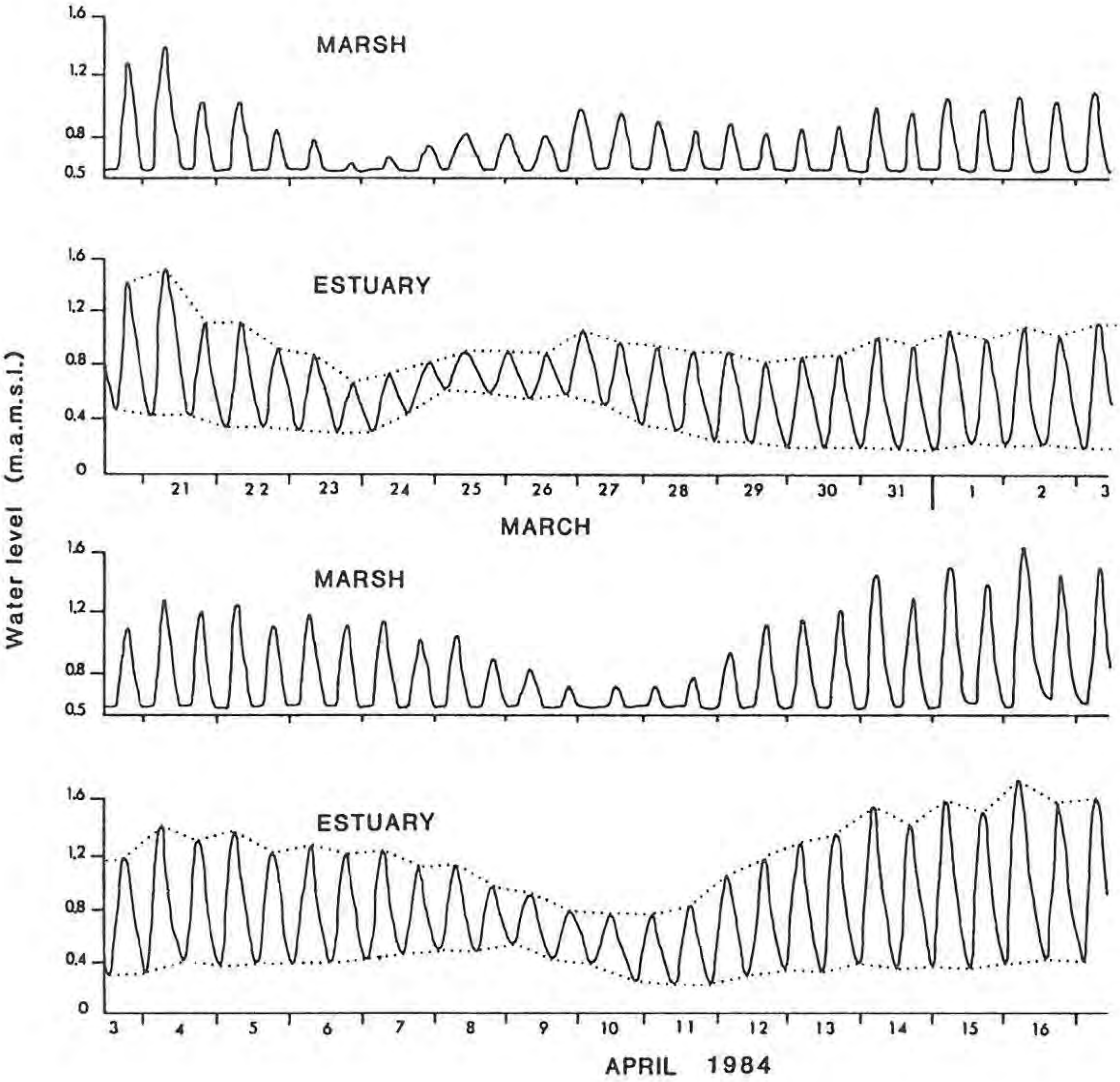


Figure 14 Simultaneous water-level changes in the tidal creek at the marsh-estuarine junction (MARSH), and at a site located directly opposite the marsh in the Kariega estuary (ESTUARY), over a four-week period.

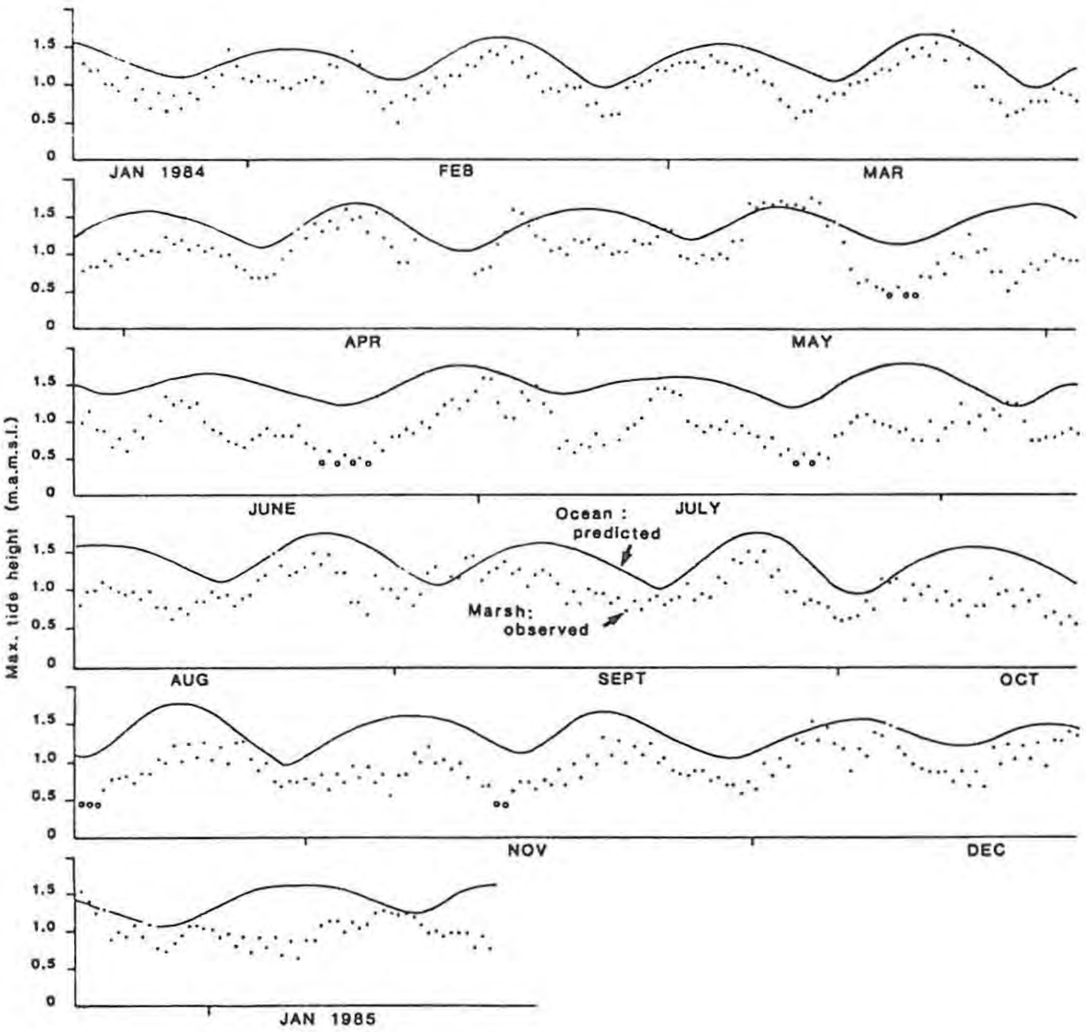


Figure 15 Comparison of maximum tide elevations at the marsh-estuarine junction (dots) with predicted maximum elevations of sea tides for the Port Elizabeth coastal area (line), 20 Jan. 1984 - 28 Jan. 1985. Clear circles represent tides at which estuarine water levels failed to enter the tidal creek.

predicted (solid lines) high-tide elevations for the ocean adjacent to the estuary (from South African Tide Tables, details in References). Although estuarine water entered the marsh at virtually all, or 98%, of the 710 tides, the elevation of tides varied considerably, from <0.55 m.a.m.s.l., when tides failed to enter the marsh, to 1.76 m.a.m.s.l., which is the upper altitudinal limit of the marsh (Chapter 2). Although the observed changes in tide elevation generally followed the sinusoidal, semi-lunar pattern predicted from Tide Tables, the tides exhibited pronounced departures from this pattern during at least 16 of the 23 semi-lunar cycles (Figure 15).

The major deviations, whether peaks or troughs, coincided consistently with long-period changes in daily mean sea level reported by de Cuevas (1986) for the open ocean near Port Elizabeth (33°59'S, 25°36'E). An example of this association is illustrated, in Figure 16. The peaks in maximum tide heights on 7, 17 and 27 May 1984 coincided with raised daily mean sea levels, while the periods of depressed tide heights on 22/23 and 29 May coincided with lowered daily mean sea levels.

These long-period (>semi-diurnal tides) daily mean sea level changes have only recently been demonstrated for this particular coast, and the processes responsible for them are not yet known. However, they are probably associated with wind-induced coastal trapped waves and/or atmospheric pressure changes (Schumann pers. comm.).

The pronounced and frequently sudden changes in tide elevation observed at the mouth of the marsh appear to be a consequence of interaction of these sea level changes with semi-lunar tidal cycles (Figure 16).

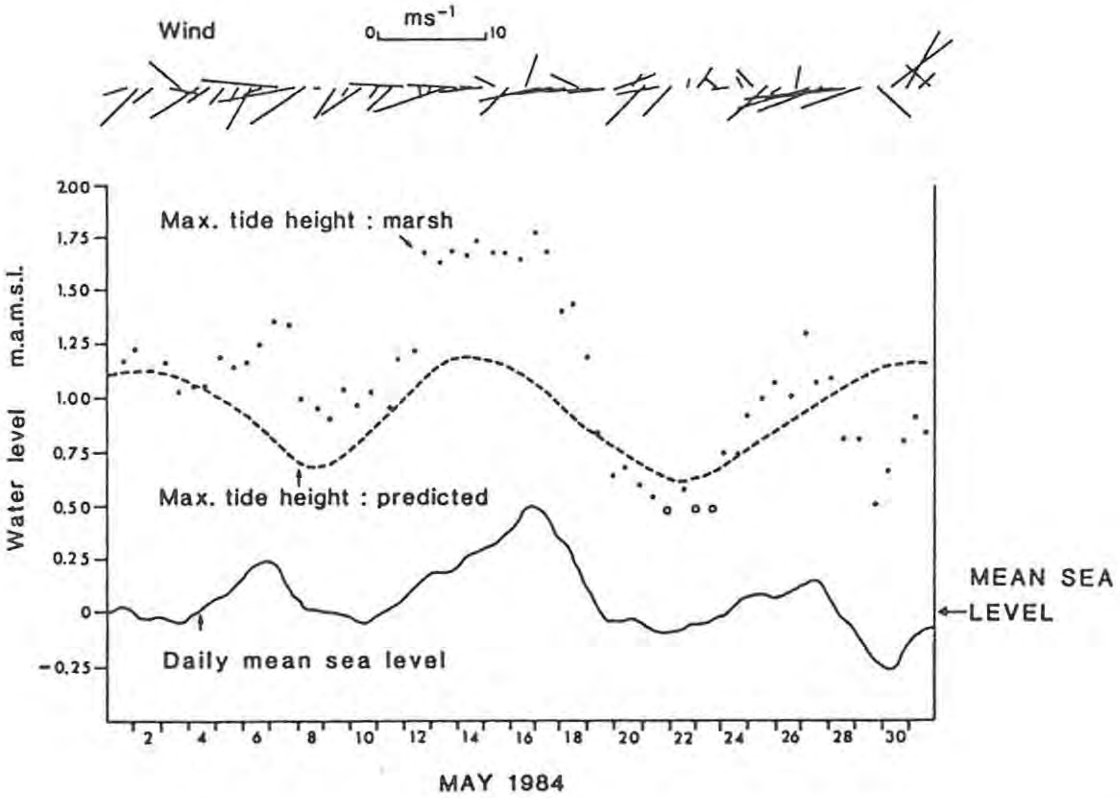


Figure 16 Comparison of maximum height of tides inundating the marsh (dots) with predicted maximum tide levels (dashed line) and daily mean sea level changes (solid lines) for the Port Elizabeth coastal area. Clear circles denote tides at which estuarine water levels were too low to inundate the marsh. Wind vectors are also presented. Daily mean sea level data are from de Cuevas (1986).

For instance, when a peak in daily mean sea level occurred during a spring-tide period, as occurred from 12 to 15 May 1984, the marsh was inundated by extremely high tides. But when depressed mean sea levels coincided with a neap-tide period, for example from 18 - 23 May, estuarine water levels dropped, and tides failed to enter the marsh.

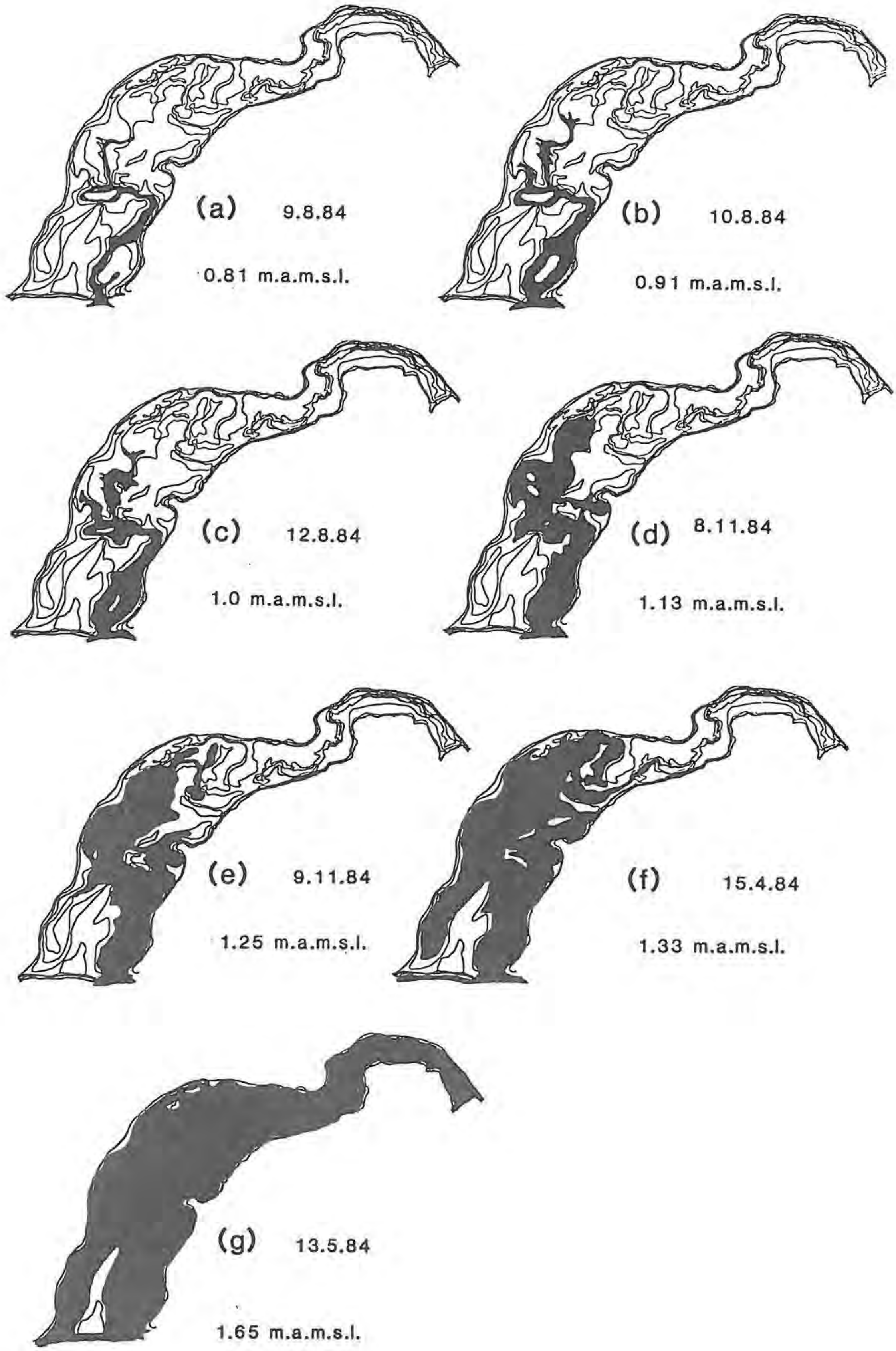
One of the consequences of these interactions is an increased tidal range. This has potentially important implications, because the vertical extent of the marsh is small, and the duration and area of inundation of the marsh is determined to a large degree by tide elevation.

3.2 Tide elevation, and area and duration of marsh inundation

Figure 17 shows the regions of the marsh inundated at high-tide for seven tides of different maximum elevations. The nature of the marsh surface inundated at each tide changed with tide elevation (Figure 18). At tides <1.0 m.a.m.s.l., the tidal creek and associated mudflats accounted for more than 70% of the marsh area inundated, but at higher tides the salt-marsh flats accounted for most of the area inundated. Because the salt-marsh flats are flatter and more extensive than the tidal creek, the area (m^2) of the marsh inundated ($\underline{I}$) at each tide increased disproportionately with increasing maximum tide elevation, m, ($\underline{H}$) (Figure 19). This relation is best described by the power equation:

$$\underline{I} = 0.965\,\underline{H}^{8.745} \qquad (1)$$

Figure 17 Pattern of inundation of the marsh. Shaded areas represent regions of the marsh inundated at high slack-tide for seven tides of increasing maximum elevations (a-g). Contour heights are as in Figure 4.



(a) 9.8.84
0.81 m.a.m.s.l.
(b) 10.8.84
0.91 m.a.m.s.l.
(c) 12.8.84
1.0 m.a.m.s.l.
(d) 8.11.84
1.13 m.a.m.s.l.
(e) 9.11.84
1.25 m.a.m.s.l.
(f) 15.4.84
1.33 m.a.m.s.l.
(g) 13.5.84
1.65 m.a.m.s.l.

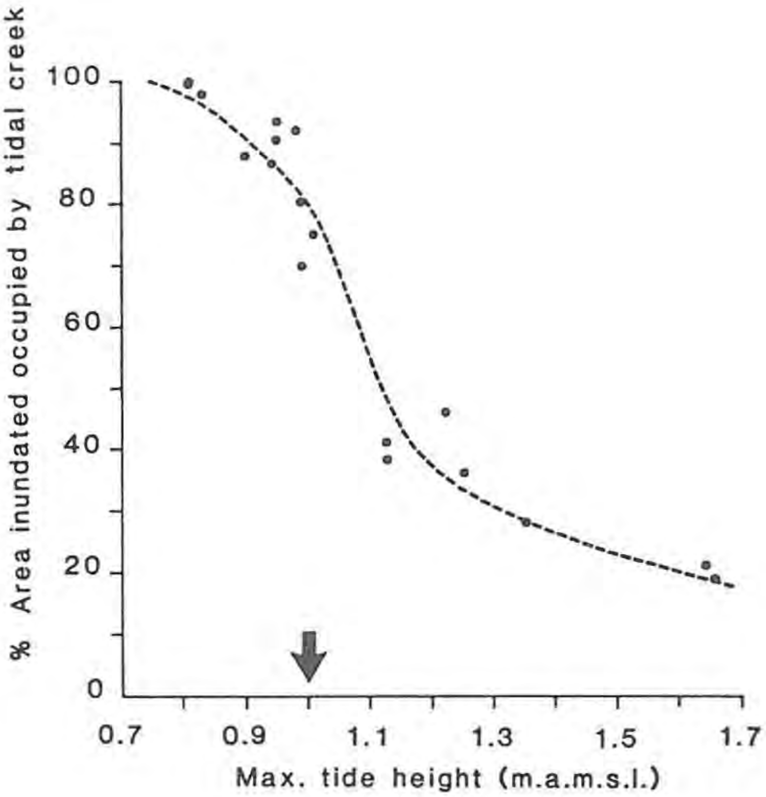


Figure 18 Changes in proportion of marsh area inundated which lacks vegetation (namely the tidal creek plus salt pans), in relation to maximum tide elevation. Arrow indicates elevation of marsh berm.

However, the marsh area inundated by particular elevation tides was less than that predicted using a hypsometric curve determined planimetrically from Figure 4 (Figure 19). This is probably a result of the hydrodynamic resistance of the marsh. Hypsometric models have frequently been used to estimate discharges on and off salt-marshes (e.g. Heinle and Flemer 1976, Woodwell et al. 1977), and this discrepancy, in accordance with Nixon (1980) and Woodroffe (1985), warns against use of these models for this purpose. The hypsometric curve for the Kariega marsh contrasts with that reported for Bly Creek basin by Eiser and Kjerfve (1986). The differences are attributable to the different developmental stages of the two marshes.

The duration of inundation of the marsh also increased with increasing tide elevation (Figure 20). The data were very variable, particularly at low elevation tides, where at certain tides the marsh was inundated for unexpectedly prolonged periods. These tides, which are differentiated by their dates in Figure 20, occurred when long-period increases in daily mean sea level coincided with neap-tides. Because the amplitudes of neap-tides are smaller than spring-tides, when the increases in daily mean sea level occurred during neap-tides the marsh was inundated longer relative to tide height than during spring-tides; see for example the tides of 24 to 28 Marh 1984 (Figure 14). These effects are important because they demonstrate that changes in daily mean sea levels influence not only the elevation of tides inundating the marsh, but also the duration of marsh inundation relative to tide height.

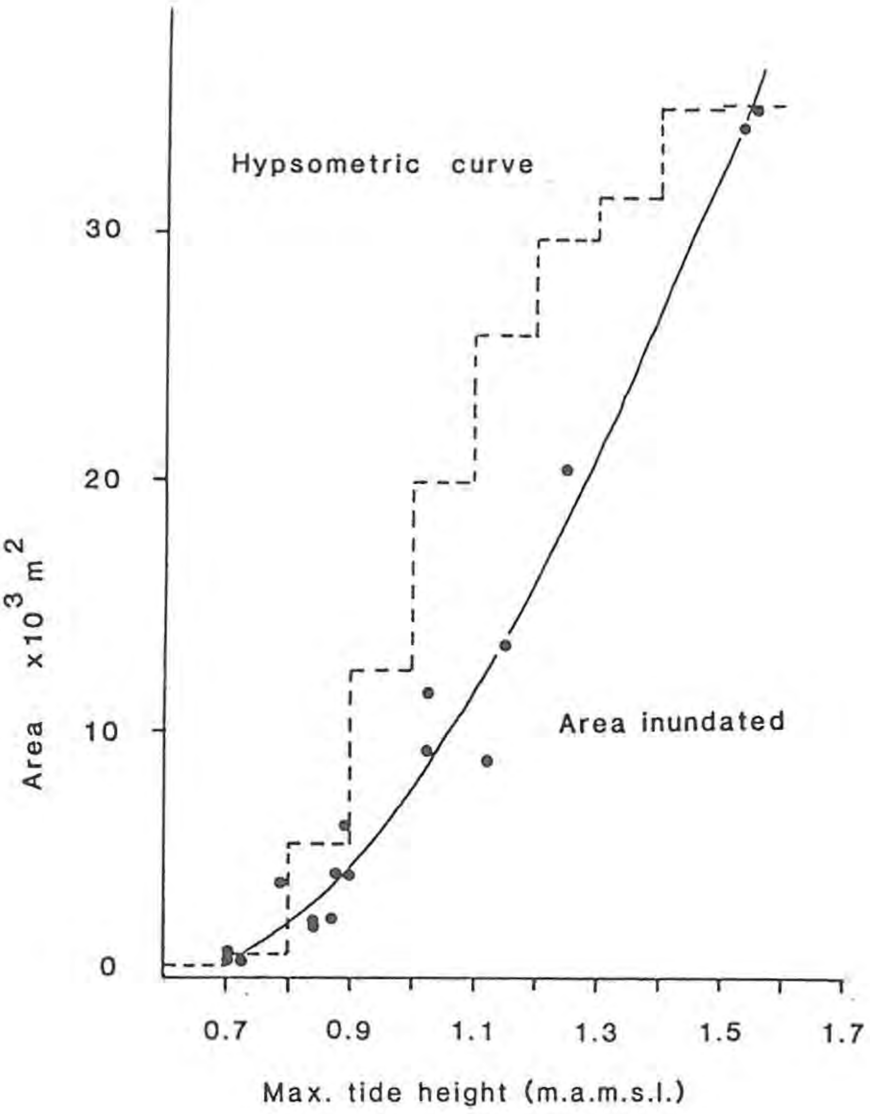


Figure 19 Comparison of the area of the marsh inundated over 18 tides (solid line) with that predicted from a hypsometric curve (dotted line) determined planimetrically from Figure 4. Arrow on horizontal axis indicates elevation of marsh berm.

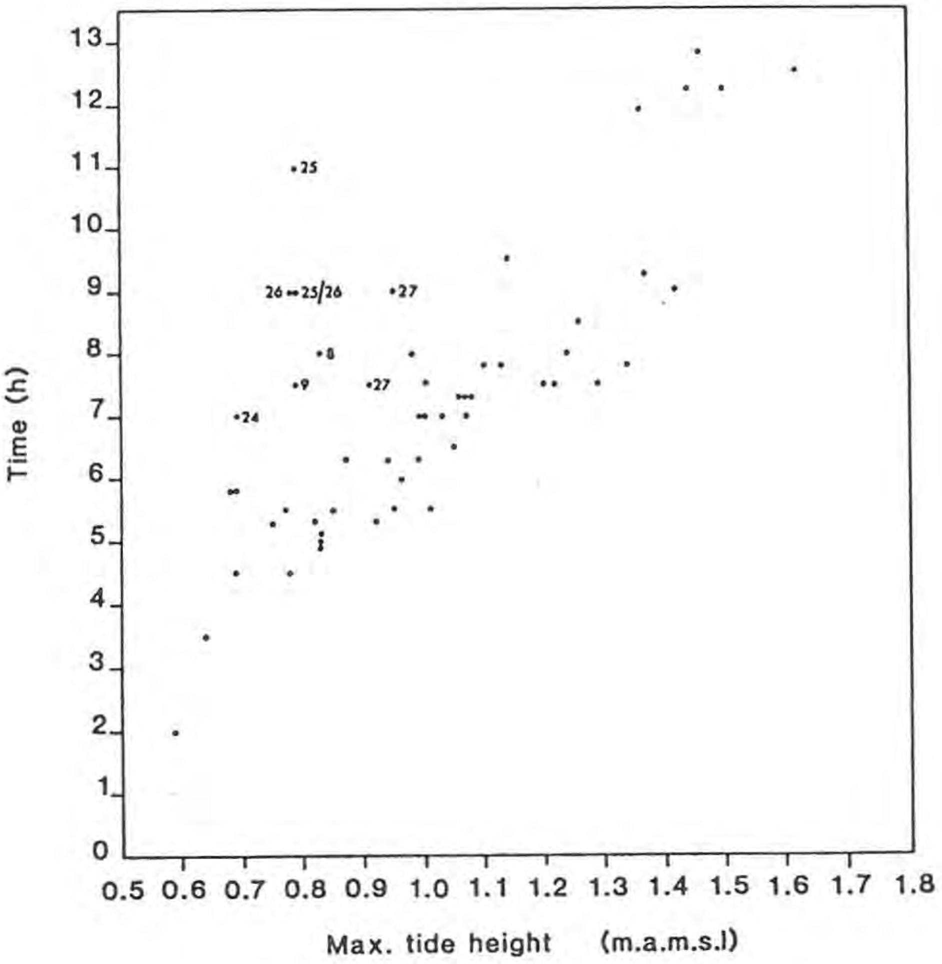


Figure 20 Duration of inundation of marsh as a function of maximum tide elevation. Dots represent same tides as in Figure 14.

3.3 Patterns of surface flow during semi-diurnal tides

The data examined in the previous section showed that the extent and duration of inundation, and the nature of the marsh surface inundated, changed with maximum tide elevation. In this section I examine the changes in flow patterns at the marsh-estuarine junction with these changes in tide elevation.

Materials and methods

Water and material exchanges between the marsh and estuary were monitored across a transect at the confluence of the two systems (Transect No. 1, Figure 4) over 47 semi-diurnal tides spanning all four seasons. The cross-sectional profile of this transect, which was surveyed at 0.20 m intervals on three occasions during the study, and did not change significantly during this period, is illustrated in Figure 21.

Current velocities were measured using a Savonius rotor, with a threshold velocity of 0.01 ms^{-1}, suspended from a manifold constructed across the creek channel (Figures 21 and 22). A pulley system attached to the manifold, and graduated horizontally and vertically at 0.10 m intervals and 0. 20 m intervals respectively, was used to place the rotor at specific positions in the creek. At the start of each tide, velocity measurements were initiated when rising water was sufficiently deep (>0.12 m) to cover the rotor placed in mid-channel on the creek bed. Velocities were then measured at 15-minute intervals for the duration of the tide. This sampling period was selected in preference to the more commonly used 60-minute interval (e.g. Roman 1984), because the marsh is located above mean sea level, and is therefore flooded for only part of each semi-diurnal tide.

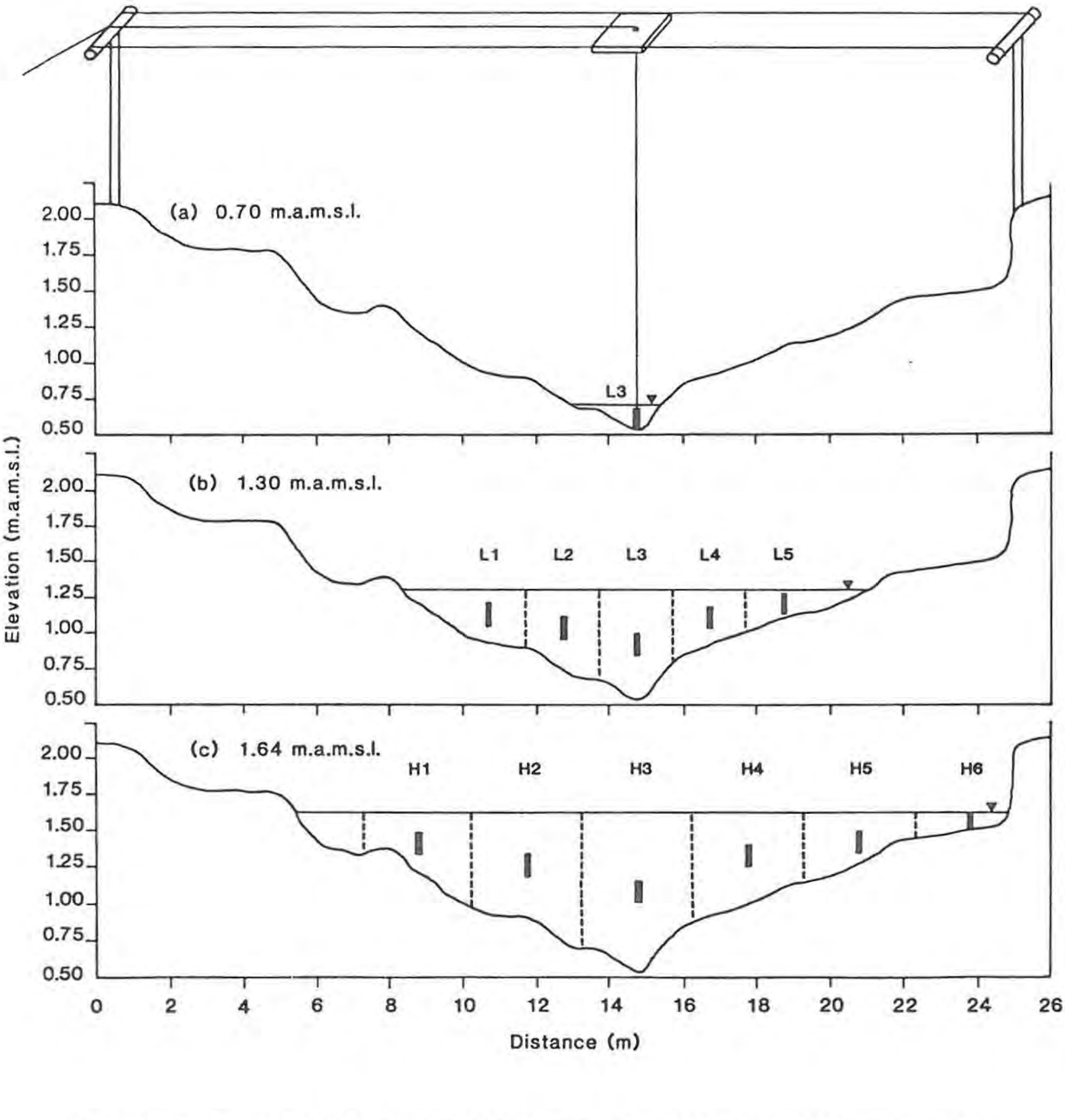


Figure 21 Cross-section of transect at the marsh-estuarine junction showing positions (solid bars, L1 - L5, H1 - H6) at which current velocities were measured at three water levels, namely 0.70 m.a.m.s.l. (a), 1.30 m.a.m.s.l. (b) and 1.64 m.a.m.s.l. (c). Vertical dashed lines represent boundaries of sectors of the cross-section.

Figure 22 Savonius rotor suspended from pulley system at marsh-estuarine junction.

Ideally, to obtain accurate estimates of discharge at any one time, current velocities should be measured simultaneously at as many vertical and horizontal positions in the creek as possible. Because equipment available did not allow for this resolution, a compromise sampling strategy was adopted. Certain studies (e.g. Bayliss-Smith et al. 1979) have measured velocities at single stations, and used these to describe velocity patterns in small tidal creeks. However, Kjerfve and Proehl (1979) and Kjerfve et al. (1981) have shown that results obtained using such procedures may not be sufficiently representative of flow in larger creeks.

Preliminary examination of velocity changes in the Kariega creek, which is much smaller than those investigated by Kjerfve and co-workers, showed that the changes in velocity across the channel were much larger than those measured vertically through the water column (Appendix 1). Consequently, a sampling procedure was employed which emphasized horizontal velocity changes at stations across the channel, rather than vertical changes at a single station. This was also necessary because of the shallow nature of the creek channel relative to the height (0.12 m) of the Savonius rotor, which precluded measurement of vertical profiles during most tides, and for considerable periods of even high tides.

At each 15-minute interval, velocities were measured at mid-depth at between 1 and 6 stations located across the channel. The number and positions of the stations employed depended on water level (Figure 21). At levels of <0.7 m.a.m.s.l. velocities were measured at only one station, L3, located in mid-channel (Figure 21a). As water levels rose velocity measurements were made at equidistant stations across the channel. At levels of 0.7 to 1.3 m.a.m.s.l. measurements were made at stations 2.0 m apart (Figure 21*b*, Stations L1 to L5), but at higher levels there was insufficient time between successive sampling intervals to measure velocities at the increased number of stations. Consequently, at water levels >1.3 m.a.m.s.l. stations 3.0 m apart were used (Stations H1 to H6, Figure 21*c*). Because these stations do not correspond with those used at lower levels (except Stations L3 and H3), I have used different notations to describe the two series.

The computations of discharge follow, with some modification, those of Kjerfve (1979). As far as possible, the terminology and notations used by this author have been maintained. Accordingly flood-tide velocities (and discharges) have been denoted negative, and ebb-tide velocities (and discharges) positive.

Instantaneous discharge per sector, $Q(t)$, ($m^3 s^{-1}$), at time t was calculated as:

$$Q(t) = V(t).A(t) \qquad (2)$$

where $V(t)$ = velocity at mid-depth at the station representative of the sector (ms^{-1}), and $A(t)$ = cross-sectional area of the sector at t, determined planimetrically (m^2).

The instantaneous cross-sectional discharge values, Q_T ($m^3 s^{-1}$) were calculated by summing the $Q(t)$ values at time t for m numbers of sectors, thus:

$$\underline{Q}_{\underline{T}} = \sum_{\underline{i}=1}^{\underline{m}} \underline{Q}(\underline{t})_{\underline{i}} \qquad (3)$$

where $\underline{i}$ is a width counter.

The values of $\underline{Q}(\underline{t})$ were used, as follows, to calculate the time-averaged instantaneous net discharge per sector $<\underline{Q}>$ ($m^3 s^{-1}$) for each tidal cycle:

$$<\underline{Q}> = \frac{1}{\underline{n}} \left\{ \frac{1}{2} \underline{Q}(\underline{t}_0) + \sum_{\underline{k}=1}^{\underline{n}-1} \underline{Q}(\underline{t}_{\underline{k}}) + \frac{1}{2} \underline{Q}(\underline{t}_{\underline{n}}) \right\} \qquad (4)$$

where $\underline{n}$ = total number of velocity readings from the start ($\underline{t}_o$) to the end of the tidal cycle ($\underline{t}_{\underline{n}}$), and $\underline{t}_k = \underline{t}_0 - \underline{k}\,\Delta\underline{t}$, where $\underline{k}$ = 1 to $\underline{n}$-1.

$<\underline{Q}_{\underline{T}}>$, the time-averaged net discharge for the entire cross-section ($m^3 s^{-1}$), as opposed to that for each sector, $<\underline{Q}>$, was computed by summing the $<\underline{Q}>$ values for all sectors, thus:

$$<\underline{Q}_{\underline{T}}> = \sum_{\underline{i}=1}^{\underline{m}} <\underline{Q}_{\underline{i}}> \qquad (5)$$

The cross-sectional net discharge per tide, Q_{TIDE}, was then calculated as follows:

$$Q_{TIDE} = \langle Q_T \rangle \, n \, \Delta t \qquad (6)$$

where Δt is the time interval between successive instantaneous discharge estimates, which in the present study was 900s.

Results

Velocity changes with tide height

Figure 23 shows the changes in velocity (averaged across the channel) with changes in water level over six tides of different maximum elevations. The contrasted velocity patterns were probably a consequence of the different extents to which the salt-marsh flats and tidal creek regions were inundated by each tide (Bayliss-Smith *et al.* 1979). During low tides (<1.0 m.a.m.s.l.) confined to the tidal creek, current velocities were low (0.01 - 0.06 ms^{-1}), and similar both at different water levels, and during flood- and ebb-tides (Figure 23*a*). Tides with these velocity characteristics may be expected not to effect large erosion and deposition processes. At higher tides the velocity differences between flood- and ebb-tides became increasingly different with increasing tide elevation. For instance, at tides between 1.0 and 1.2 m.a.m.s.l., which begin to inundate the salt-marsh flats, current velocities were more or less uniform on the flood-tide, but peaked at mid- to high-water levels on the ebb-tide (9 November 1984, Figure 23*b*). Tides such as these, with large ebb velocity pulses, probably effect net fluxes of particulate material to the estuary. At still higher tides (e.g. those of 13 May 1984 and 26 April 1986) the

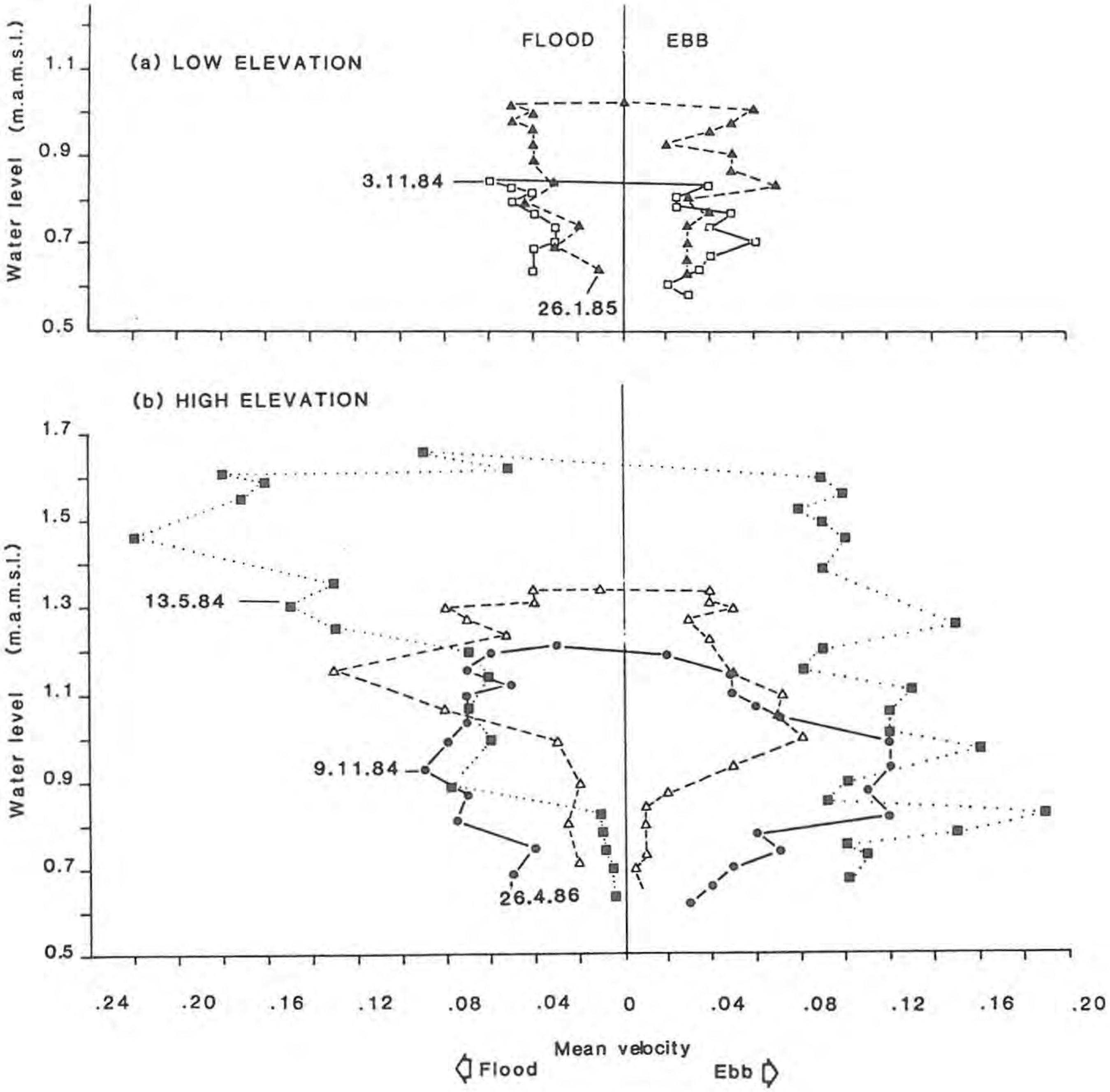


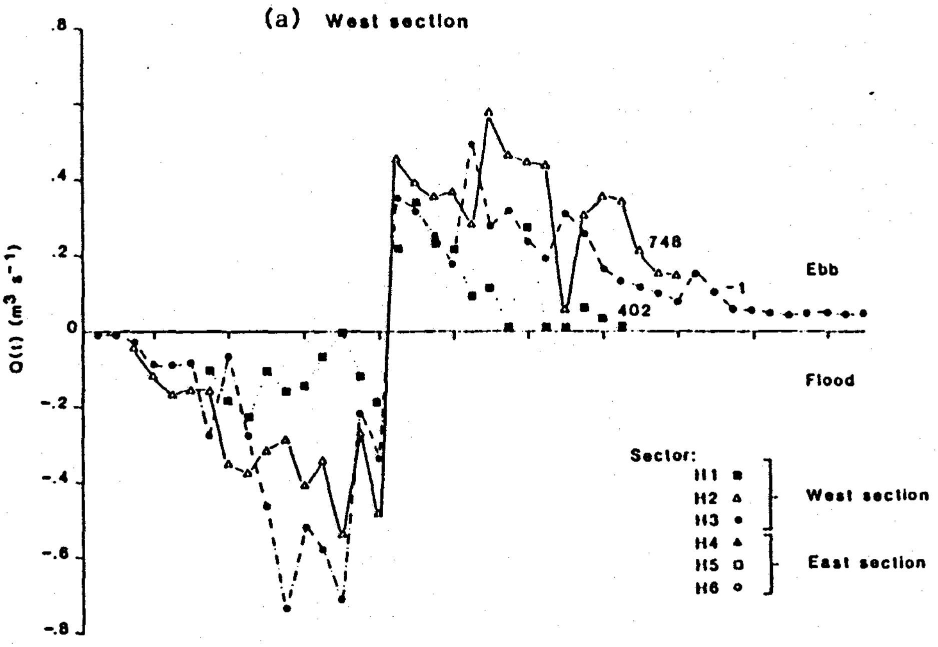
Figure 23 Relation between water level and current velocity over five semi-diurnal tides. Tides in top panel (a) are low tides of maximum elevation <1.1 m.a.m.s.l., which are confined to the tidal creek. Tides in bottom panel (b) are higher tides >1.1 m.a.m.s.l., which overtop the marsh berm and inundate to varying extents the salt-marsh flats.

velocity maximum occurred on the flood-tide at mid- to high-water levels. This velocity pattern is probably associated with large imports of particulate material from the estuary to the marsh (Chapter 4).

Changes in discharge with tide height

Discharge also varied considerably during semi-diurnal tides, and these temporal changes differed for different sectors across the creek channel. Figure 24 shows the instantaneous discharges, $Q(t)$, for sectors H1-H6 over the tide of 13 May 1984. The value indicated for each curve is the time-averaged instantaneous discharge for each sector, $\langle Q \rangle$. When these $\langle Q \rangle$ values are summed separately for western and eastern halves of the channel (*a* and *b* panels, respectively), they show the net discharge through the western half (H1 + H2 + H3) was directed from the marsh to estuary (+1149 $m^3 s^{-1}$), while that in the eastern half (H4 + H5 + H6) was directed from the estuary to marsh (-2888 $m^3 s^{-1}$). This *spatially* asymmetrical pattern of discharge accords with the hydraulic model of Fischer (1976) for non-rectangular channels. It is also important because it confirms the need, as emphasized by Kjerfve and Proehl (1979), to consider cross-channel variability when estimating discharges in creek channels.

Consequently, this precaution was taken in the present study, and Figure 25 shows the instantaneous cross-sectional discharges, Q_T, (or instantaneous discharges for all sectors combined) over five tides. Maximum discharges increased with maximum tide elevation, which would be expected since discharge was computed as a product of velocity and



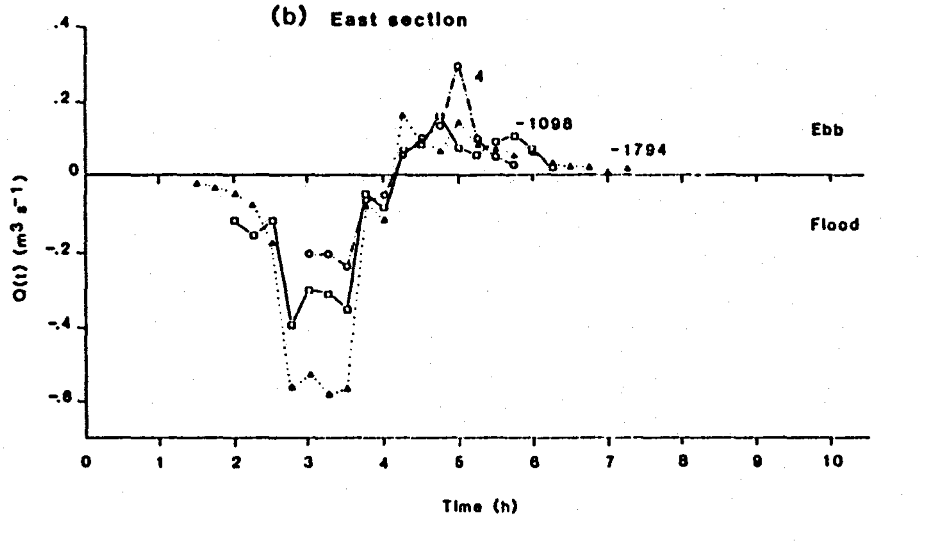
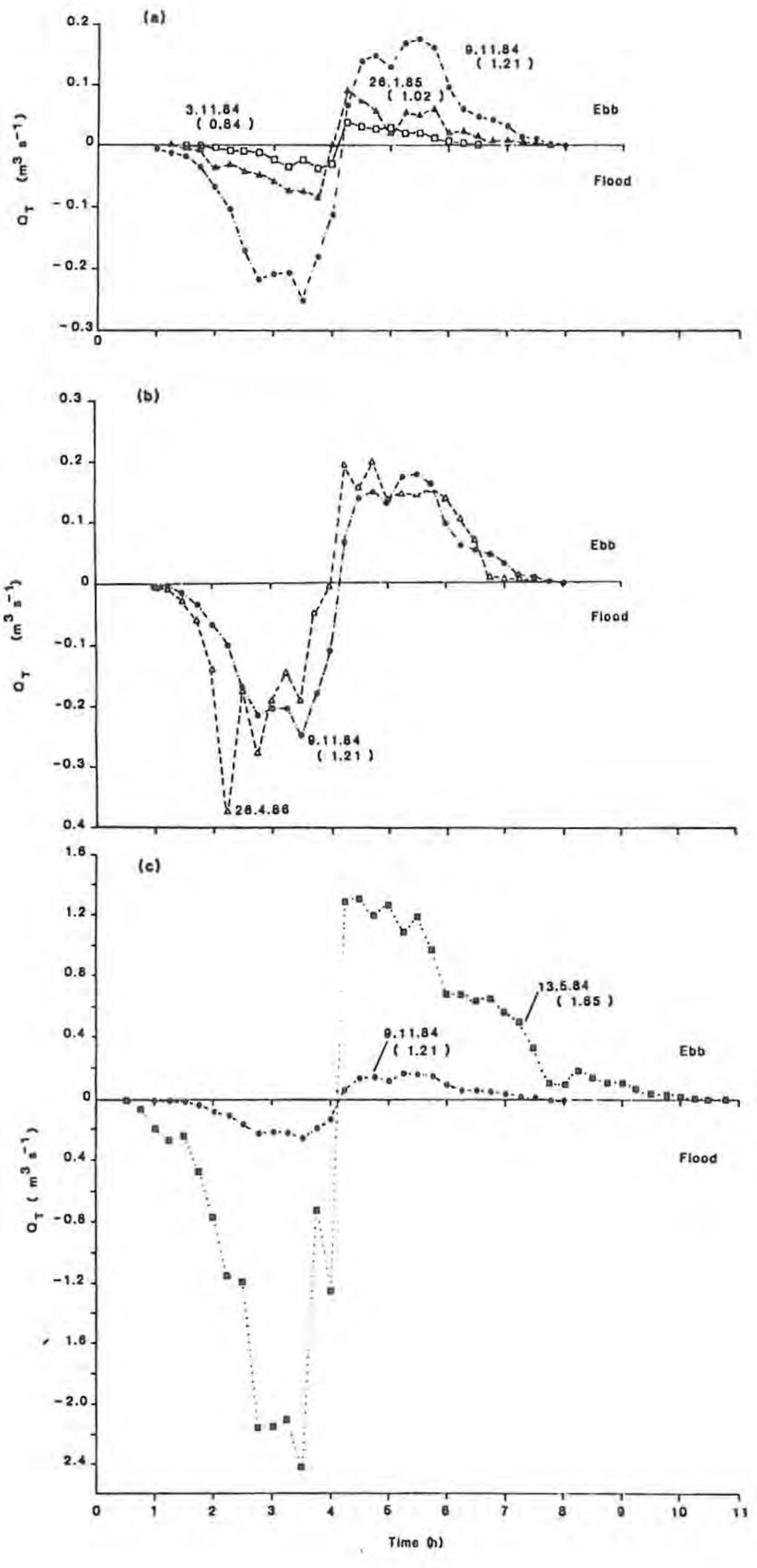


Figure 24 Instantaneous discharges per sector, *Q*(*t*), for six sectors across the tidal creek, 13 May 1984. Sectors are partitioned for purposes of explanation into those in the western (*a*) and eastern (*b*) halves of the creek channel. Numbers indicated for each curve denote time-averaged net discharge per sector, <*Q*> $(m^3\ s^{-1})$. Location and terminology of sectors are shown in Figure 21*c*.

Figure 25 Instantaneous cross-sectional discharge, Q_T, over five tides. Tides are as in Figure 23. Discharge-time curve for tide of 9 November 1984 is reproduced in each panel to assist in comparison. Note the vertical axis in panel (*c*) is not the same as in panels (*a*) and (*b*). Maximum elevations of tides are indicated in brackets (m.a.m.s.l.).


(a)
0.2
0.1
0
-0.1
-0.2
-0.3
0
9.11.84
(1.21)
26.1.85
(1.02)
3.11.84
(0.84)
Ebb
Flood
(b)
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
0.4
Ebb
Flood
9.11.84
(1.21)
26.4.86
(c)
1.6
1.2
0.8
0.4
0
0.4
-0.8
-1.2
1.6
-2.0
2.4
13.5.84
(1.65)
9.11.84
(1.21)
Ebb
Flood
0
1
2
3
4
5
6
7
8
9
10
11
Time (h)
Q_T $(m^3 s^{-1})$

cross-sectional area, and both these variables increased with tide height.

However, the patterns of discharge also varied considerably, between tides of similar elevations. The variability is probably a result of the interactions of semi-lunar tidal cycles with long-period changes in daily mean sea level (Figure 26). The tide of 2 November occurred during a neap period coincident with a period of elevated mean sea level, but the tide of 6 November occurred during a spring-tide period which coincided with a period of lowered mean sea level. Consequently, the spring-tide reached a maximum elevation of only 0.83 m.a.m.s.l., which was less than that reached by the neap-tide (0.85 m.a.m.s.l.). The marsh also took longer to flood and drain during the neap-tide, possibly because in the estuary the vertical amplitudes of neap-tides are smaller than those of spring-tides. As a consequence of these differences, discharges were greater during the early and final phases of the neap-tide, but were greater at mid- to high-water levels during the spring-tide.

For all tides,the net discharges per tide, Q_{TIDE}, ranged from +95 to -1864 m^3 $tide^{-1}$, and from <0.1 to 18% of the volume of water entering the marsh on the flood-tide (Appendix 2). At 65% of the tides Q_{TIDE} values were negative, which indicates the estuary contributed the principal source of water to the marsh. Accordingly, apart from five tides monitored after a minor river flood in April 1986, at all tides the salinity of water entering and leaving the marsh was equal to that of seawater.

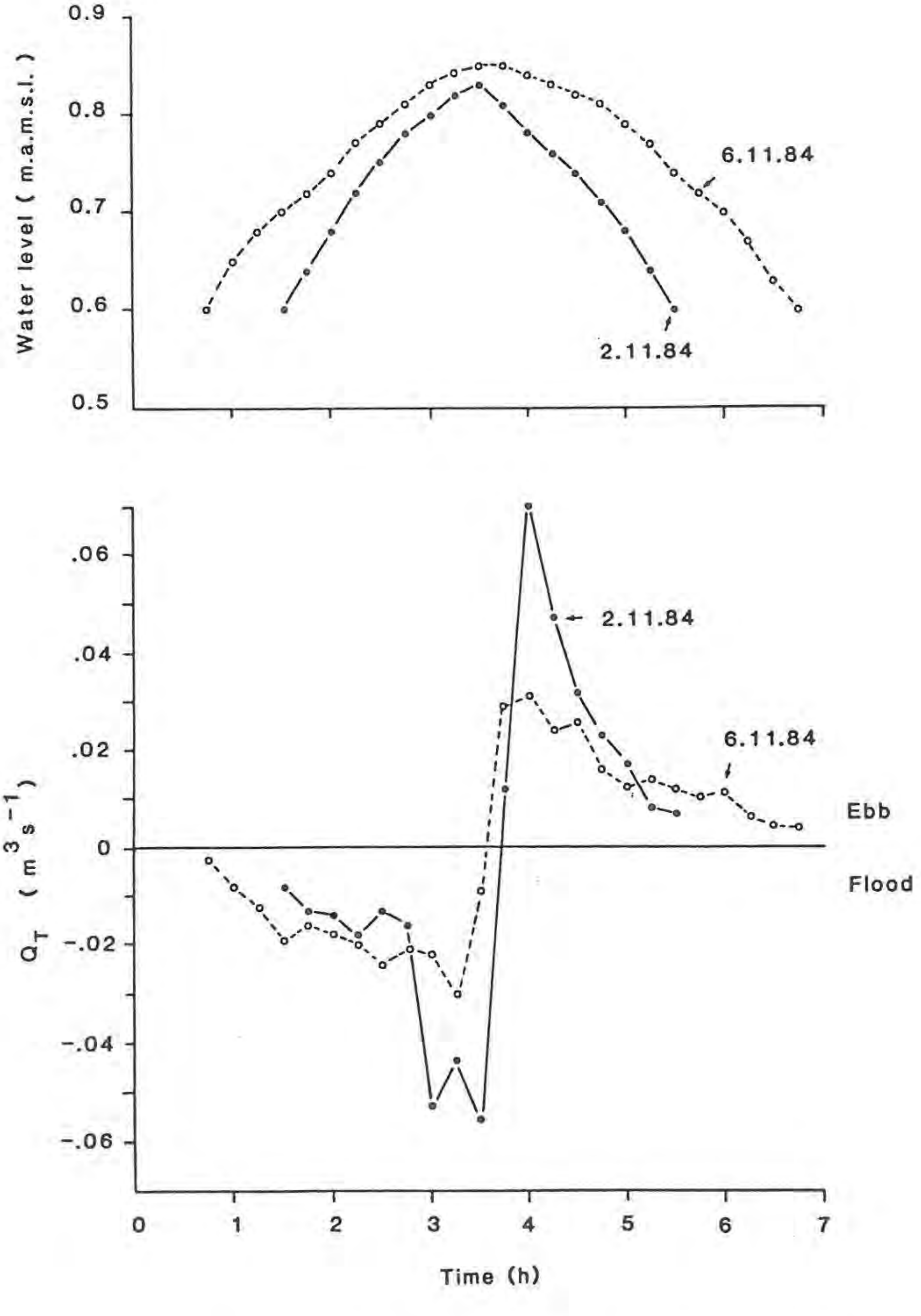


Figure 26 Contrasted patterns of water level changes (top panel) and instantaneous cross-sectional discharges, $\underline{Q}_{\underline{T}}$ (bottom panel), over a neap-tide (2 November) coincident with a period of increased daily mean sea level, and a spring-tide (6 November) which occurred during a period of decreased mean sea level.

3.4 Subterranean water flow

The data presented so far has concerned the surface flow of water between the marsh and estuary. However, several workers (e.g. Nixon 1980) have expressed the need when measuring fluxes between salt-marshes and adjacent systems to examine the nature and extent of subterranean water and material transfers. The coarse-grained sediments of the tidal creek, and those underlying the surface substrata of the salt-marsh flats, pointed to the need to investigate: (a) the vertical movement of water into the salt-marsh sediments, and (b) the horizontal flow of water below the marsh surface.

Materials and methods

Infiltration rates, water table depths, and hydraulic conductivities were measured at seven stations along a transect in the marsh lower reaches (Figure 10).

Rates of infiltration into the surface sediments were measured using a modification of the shallow-well pump-in method of Boersma (1965). Two concentric metal cylinders of height 0.30 m, and diameters 0.30 and 0.50 m, were embedded 0.10 m into the salt-marsh surface at low tide. Water levels were maintained at 0.15 m depth in both cylinders using head tanks, and rates of volume decrease in the tank feeding the central well were used as measures of infiltration rates. These estimates represent potential rates because water table fluctuations, which were pronounced in the vicinity of the tidal creek, probably influence in situ rates of infiltration.

Water table depths were determined using wells 1.0 m deep and 0.12m in diameter. Water levels in the wells were measured manually, *hourly* over two *semi-diurnal* tides, and *daily* at high-tide, over an 11-day *"semi-lunar"* period. Following inundation of a particular well, it was drained and the water level allowed to stabilize for at least one hour before the next measurement was made. This period was adequate in view of the elevated hydraulic conductivity of the sediments which underly much of the marsh surface (see below).

Hydraulic conductivity (K) was measured using the auger-hole method of Boersma (1965). Two auger wells (diameter 0.12 m and depth 1.0 m) were used at each station, and duplicate measurements of K were made for each well. These estimates of K are based on the rates of increase in water level in each hole after drainage of the hole by pumping.

The estimates of water table depths and K values were used to calculate subterranean discharge, Q_S, (x10^3 mm^3 h^{-1} m^{-1}) using the following equation (modified from Jordan and Correll 1985):

$$Q_S = \frac{K}{2L} (H_a^2 - H_b^2) \qquad (7)$$

where, K is the mean hydraulic conductivity (x10^{-2} m h^{-1}) determined for Station a and the next station towards the creek, Station b; L is the distance (m) between the two stations; and H_a and H_b are the differences in height (x10^{-2} m) between the level of the water table at the respective stations and the base of the creek.

Results

The surface sediments of the creek (Station 1) were porous with infiltration rates of 2.08 $dm^3 m^{-2} h^{-1}$ (Table 3). The finer-grained sediments of the salt-marsh flats were more impervious with infiltration rates of only 0.03 to 0.3 $dm^3 m^{-2} h^{-1}$ (Stations 2 to 6).

Table 3. Infiltration rates and mean hydraulic conductivity (*K*) values for sediments at seven stations along a 50 m transect in the marsh lower reaches.

Station	Distance from base of creek (m)	Surficial infiltration rate ($dm^3 m^{-2} h^{-1}$)	*K* ($\times 10^{-2}$ m h^{-1}) (*n* = 2)
1	7.8	2.08	8.90
2	12.3	0.30	6.70
3	18.1	0.03	5.73
4	26.0	0.02	2.60
5	33.8	0.04	1.02
6	43.2	0.06	0.94
7	45.01	0.20	0.10

Similarly, the K values for the tidal creek were higher than those for the salt-marsh flats (Table 3). The tidal creek value of 0.9×10^{-2} m h^{-1} is greater than the values reported for North American marshes, but the values for the marsh flats are similar to those reported in the literature. For instance, the K value of 2.6×10^{-2} m h^{-1} for Station 4 located near the creek is similar to the mean value of 1.1×10^{-2} m h^{-1} reported for a Spartina alterniflora marsh by Yelverton and Hackney (1986). The K values at stations further from the creek, namely Stations 6 and 7, are comparable with the value of 0.34×10^{-2} m h^{-1} reported for Great Sippewissett Marsh by Hemond and Fifield (1982).

The water table levels fluctuated markedly, and followed changes in the elevation of tides inundating the marsh over the 11-day period (Figure 27). Lower levels were recorded during the neap periods at the start and end of the sampling period, and higher levels during the spring-tide phase of 8 to 10 October. The decrease in water table level of 6 to 7 October coincided with a decrease in surface tide elevation.

Water table levels also changed on a time scale of hours (Figure 28). In agreement with the elevated K values observed in the vicinity of the tidal creek, water table fluctuations were more pronounced and more immediate in this region, and gradually attenuated, with increasing delay, as distance from the creek increased. This can be seen by comparing, for example, water table changes at Stations 2 and 6, located 12.5 and 43 m from the tidal creek, respectively.

Figures 29 and 30 show the rates and directions of subterranean water flow over a spring and neap-tide, respectively. During both tides

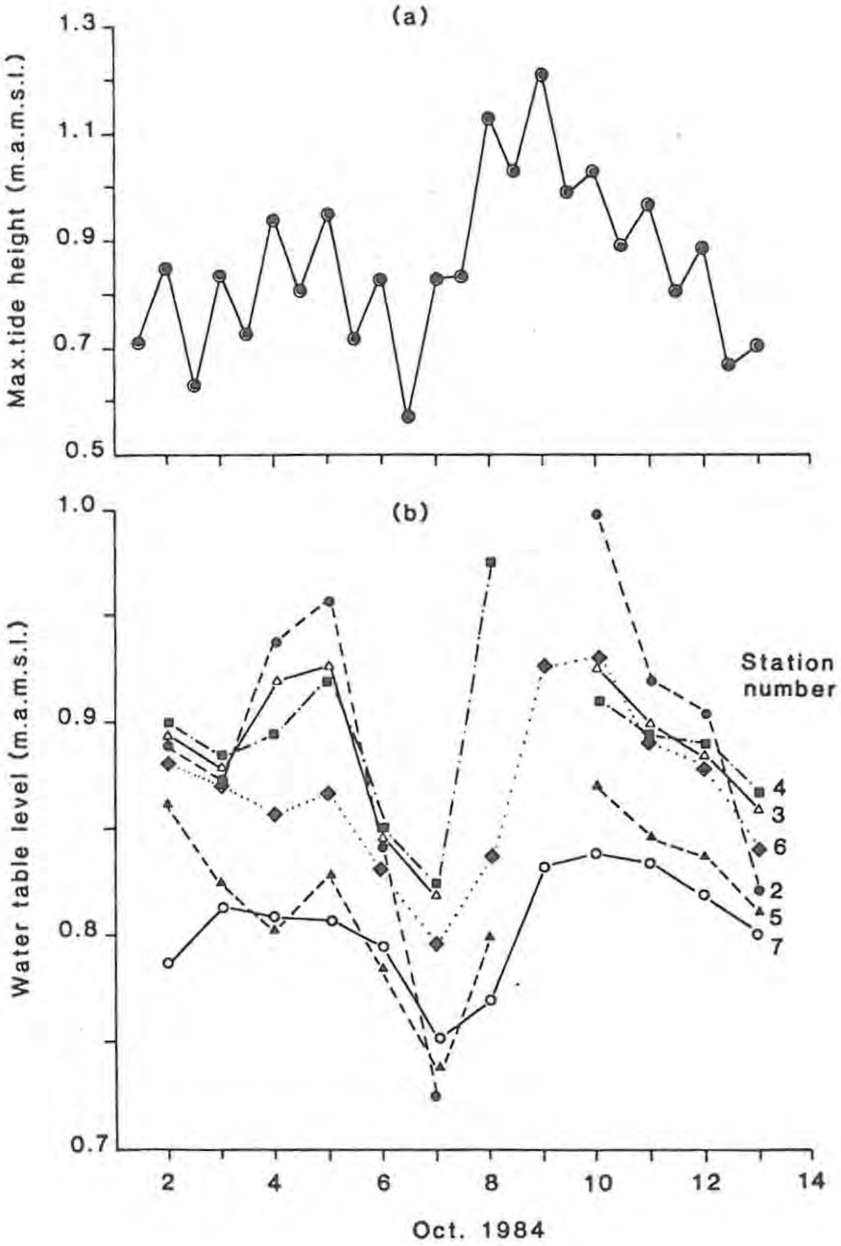


Figure 27 Relation between maximum tide height at the marsh-estuarine junction (a), and water table level (b) at seven stations (1-7) on the marsh, over an 11-day period.

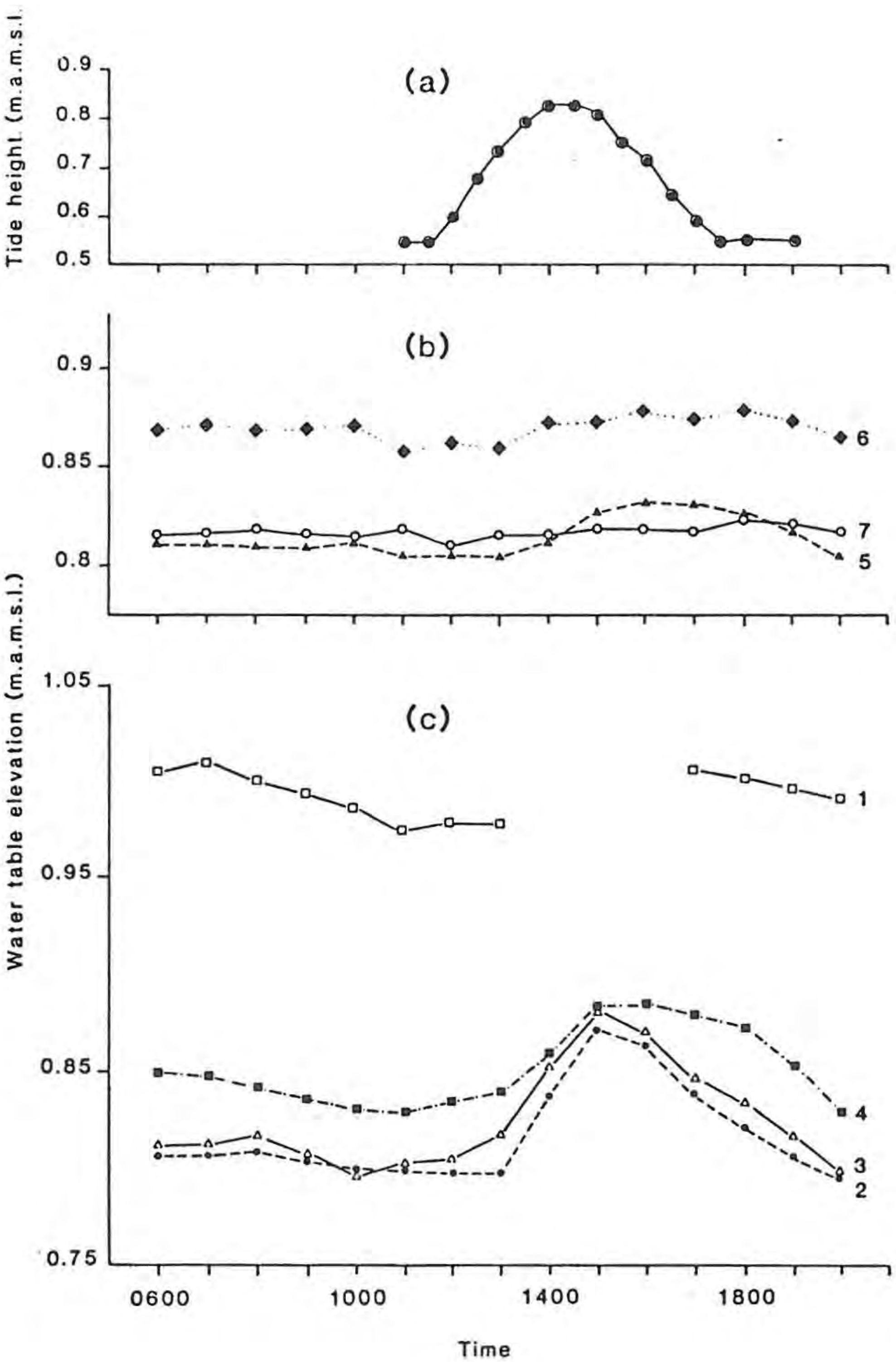


Figure 28 Changes in surface water levels at the marsh-estuarine junction (a), and water table levels (b, c) at seven stations (1-7) in the marsh lower reaches, over a 14-hour neap-tide, 3 November 1984. Station notations and positions are shown in Figure 10.

Figure 29 Changes in water table level and subterranean discharge during the spring-tide of 6 December 1984. Arrows denote directions of flow, and values below arrows indicate discharge (x 10^3 $mm^3 m^{-1} h^{-1}$).

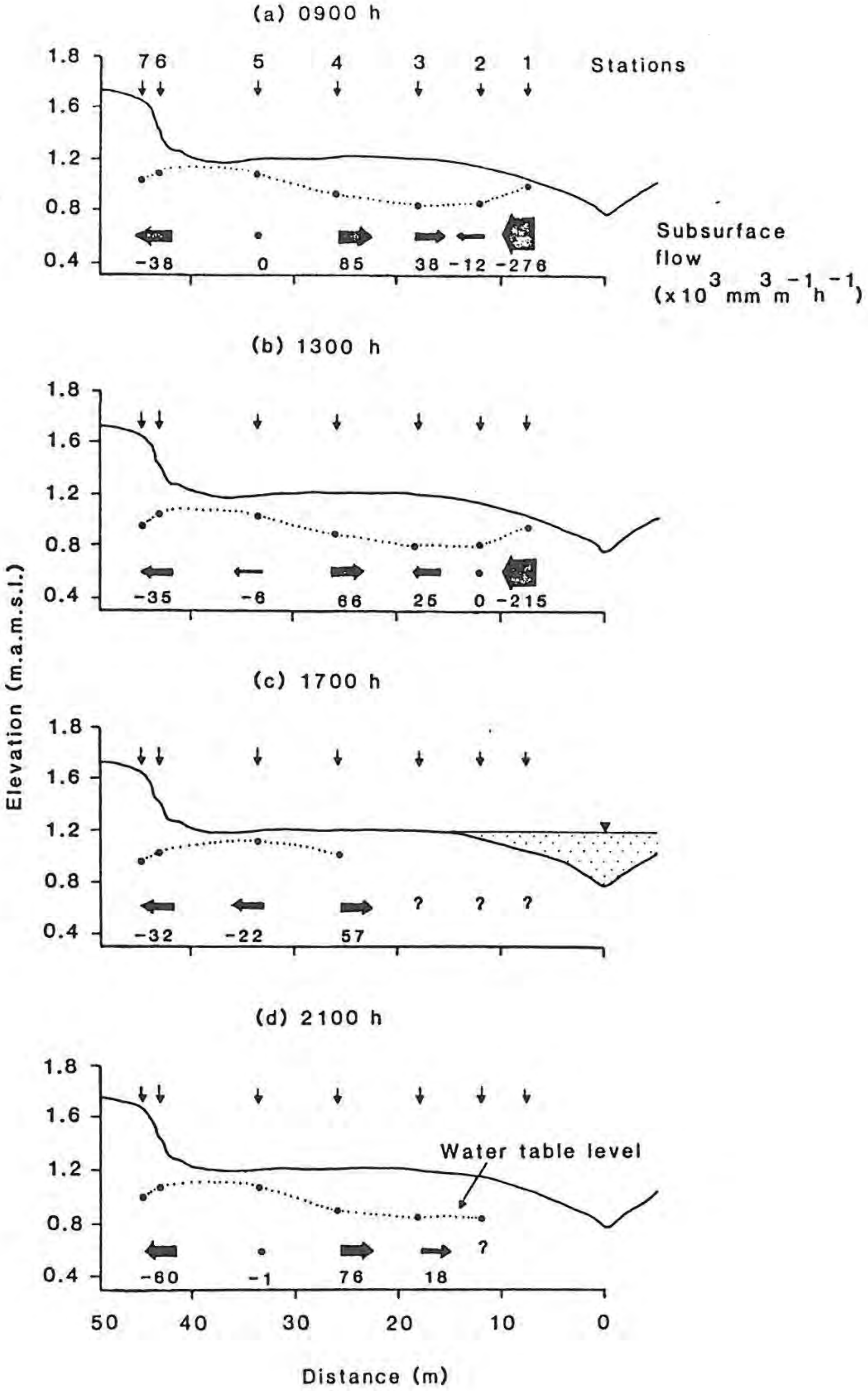
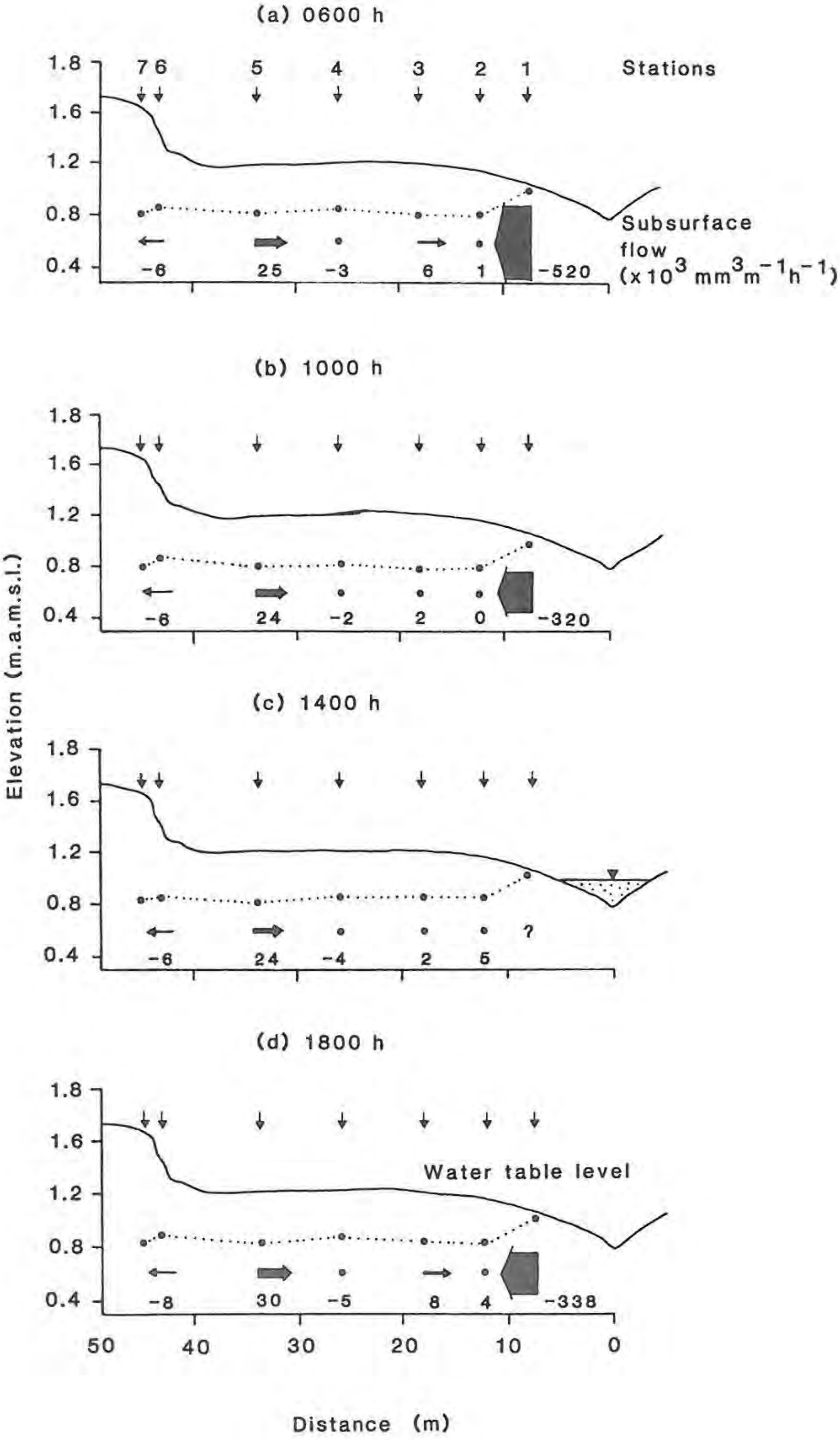

(a) 0900 h
1.8
1.6
1.2
0.8
0.4
7 6
5
4
3
2
1
Stations
Subsurface flow
($x10^3$ mm^3 m^{-1} h^{-1})
-38
0
85
38
-12
-276
(b) 1300 h
-35
-6
66
25
0
-215
Elevation (m.a.m.s.l.)
(c) 1700 h
-32
-22
57
?
?
?
(d) 2100 h
Water table level
-60
-1
76
18
?
50
40
30
20
10
0
Distance (m)

Figure 30 Changes in water table level and subterranean discharge during the neap-tide of 3 November 1984. Details as in Figure 29.


(a) 0600 h
Stations
7 6 5 4 3 2 1
Subsurface flow (x10^3 mm^{3}m^{-1}h^{-1})
-6 25 -3 6 1 -520
(b) 1000 h
-6 24 -2 2 0 -320
(c) 1400 h
-6 24 -4 2 5 ?
(d) 1800 h
Water table level
-8 30 -5 8 4 -338
1.8
1.6
1.2
0.8
0.4
Elevation (m.a.m.s.l.)
50 40 30 20 10 0
Distance (m)

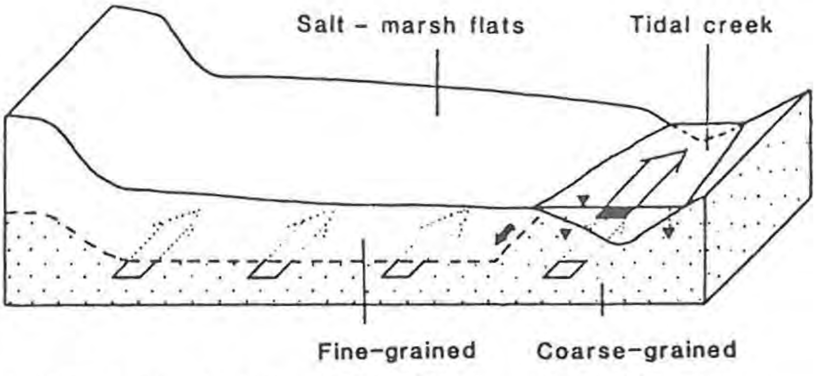
rates of subsurface flow were greatest and directed laterally into substrata of the marsh flats, in the vicinity of the tidal creek (between Stations 1 and 2). At stations located further from the creek, rates of flow were between one and two orders of magnitude lower, and the directions of flow varied locally between stations.

During the spring-tide of 6 December, the water table was slightly elevated in the vicinity of Stations 5 and 6, and subsurface water from this region drained both towards the central ridge and towards the tidal creek (Figure 30). During the neap-tide of 3 November, the water table was more uniform, and rates of lateral flow were generally lower ($<30\times 10^3$ $mm^3 m^{-1} h^{-1}$) than during the spring-tide (Figure 29). The water table below the marsh flats was also lower, which is what would be expected for a tide such as this which followed a period of prolonged neap drainage of the marsh sediments.

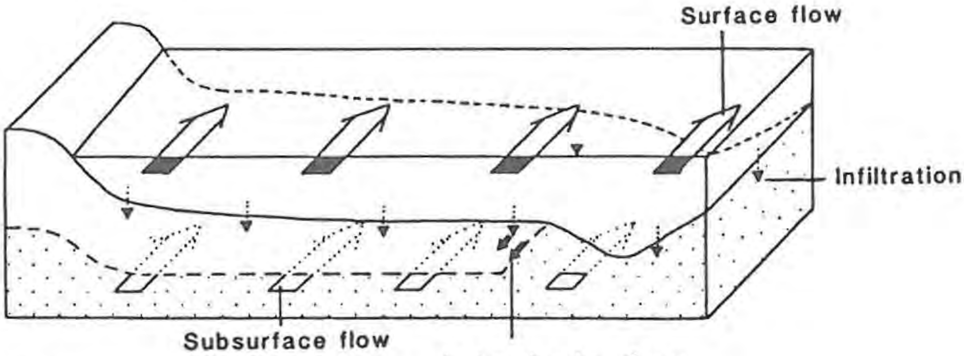
3.5 Overview of patterns of marsh inundation and drainage

Figures 31 and 32 summarize the dominant vectors of subterranean flow over semi-diurnal and semi-lunar periods, respectively. Estimates of potential rates of infiltration in the tidal creek are high (Table 3), but these are probably overestimates because subterranean water rises up through the creek sediments as surface water advances along the creek. The sediments of the salt-marsh flats are much more impervious than those of the tidal creek. These data, in combination, show that the rates of infiltration of tidal water into the surface marsh sediments are small.

(a) Low flood-tide



(b) High flood-tide



(c) Low ebb-tide

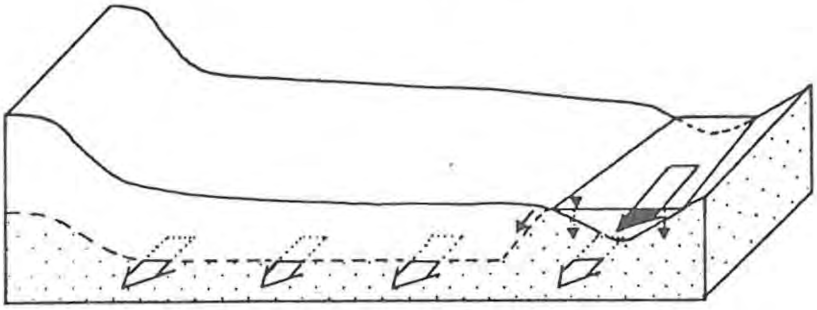
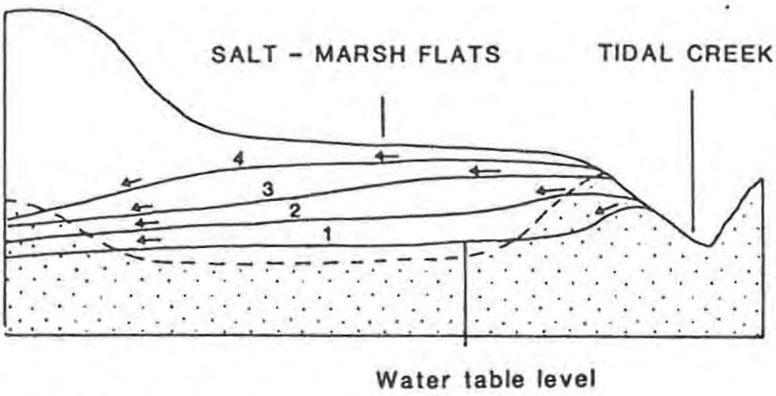


Figure 31 Pattern of semi-diurnal tidal inundation and drainage of marsh at low flood-tide (a), high flood-tide (b) and low ebb-tide (c). Directions of lateral subterranean flow below the salt-marsh flats have not been shown because flows in this region were small and their direction varied over semi-lunar tidal cycles (see Figure 32).

(a) SPRING PHASE



(b) NEAP PHASE

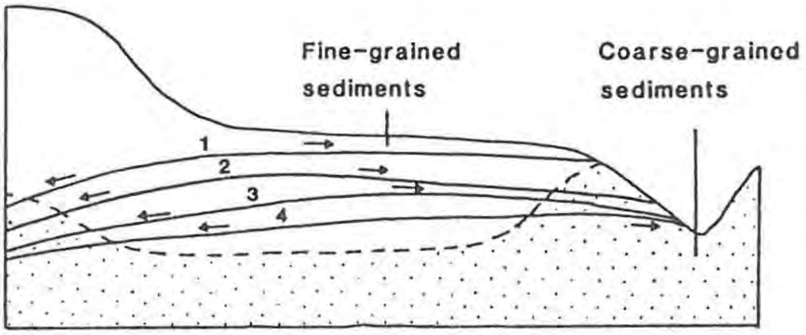


Figure 32 Water table changes over flood- (a) and ebb-phases (b) of a hypothetical semi-lunar tidal cycle. Numbers represent sequence of changes. Arrows show the dominant vectors of lateral flow.

However, lateral movement of water does occur below the marsh surface (Figures 29 and 30). It is most pronounced in the vicinity of the tidal creek, and occurs in response to the development of a subsurface hydraulic gradient, which develops between the tidal creek and marsh flats, and along which water is forced by hydrostatic pressure (Figure 32*a*). This lateral flow causes a gradual rise in the level of the water table, which occurs from the creek outwards, and which pushes up into the fine-grained sediments capping the marsh flats.

Over successive high elevation tides, for example over a spring-tidal period, the water table rises further and further from the creek (Figure 32*a*). During prolonged periods of low elevation tides, e.g. neap periods, the subterranean water gradually drains, firstly from the substrata closest to the creek, and then from regions further away (Figure 32*b*).

Although there is evidence of water flow does occur below the marsh surface, the magnitude of this flow is small in comparison to the surface flow. Assuming subterranean flow rates of 200 - 1000 $\times 10^{3}$ mm^{3} h^{-1} m^{-1} (from Figures 29 and 30), over a period of tidal inundation of 7 h, and the length of the creek banks to be 800 m (calculated for both sides of the channel), the volume of water entering the sediments of the marsh flats from the creek will be between 1 and 6 m^{3} $tide^{-1}$ for the tides of 3 November and 6 December 1984. This is <1% of the above ground volume of water which entered the marsh during these tides.

The pattern of subterranean water flow for this *Sarcocornia* marsh is similar to that described by Jordan and Correll (1985) for a *Typha* marsh in the Rhode River estuary. However, two important differences are evident: firstly, the rates of interstitial water flow are an order of magnitude lower in the *Sarcocornia* marsh than in the *Typha* marsh. Secondly, in the *Sarcocornia* marsh the lateral movement of water from the creek is larger relative to the vertical (or infiltration) component, than in the *Typha* marsh. Unfortunately, Jordan and Correll (op.cit.) do not provide detailed data on above-ground water flow, so it is not possible to compare the relative magnitudes of the above- and below-ground water transfers in the two systems.

The patterns of water flow described for these salt-marshes contrasts with that described for high energy intertidal systems, such as sandy beaches. As might be expected, the subterranean flow rates of $<650 \times 10^{3}$ $mm^{3}\ m^{-1}\ h^{-1}$ for the *Sarcocornia* marsh are much lower than those of up to 73×10^{6} $mm^{3}\ m^{-1}\ h^{-1}$ reported for sandy beaches by McLachlan *et al.* (1985). This is to be expected in view of the extremely porous sediments of sandy beaches, and the fact that percolation in these systems is driven by both tides and wave action. In the *Sarcocornia* marsh, wave action is largely filtered out because of the narrow mouth of both the estuary and salt-marsh, and the location of the marsh 4.9km from the high energy coastline. Consequently, infiltration into the marsh surface is driven mainly by tidal processes. Infiltration is reduced further by the impervious marsh surface, and by the fact that in those regions with coarse-grained sediments the water-table moves up through the sediments as surface water covers these regions. In contrast, water is flushed through largely unsaturated sediments in sandy beaches, which facilitates gravitational flow (Reidl and Machan 1972).

These contrasted hydraulic patterns suggest water flow through, and interstitial biotic and abiotic processes within, sediments play a less important role in the regulation of material exchanges in salt-marshes than in sandy beaches. Consequently, in the subsequent analysis, which examines the exchanges of material between the marsh and estuary, I have emphasized surface exchanges, and those processes which influence these transfers, which occur at the marsh-water interface.

CHAPTER 4

TIDAL FLUXES OF ORGANIC CARBON

Odum (1974) proposed that tidal inundation and drainage of salt-marshes provides an energy subsidy to these systems which promotes nutrient and food transfers within, and waste removal from them, and is responsible for their elevated productivity. This hypothesis is supported by Steever *et al.* (1976) who demonstrated a strong positive linear relation between *Spartina alterniflora* production and tidal range along the Connecticut coast of the U.S.A. Salt-marshes are highly productive ecosystems with aerial net primary production values up to 1700 gC m^{-2} y^{-1} (Gallagher *et al.* 1980). Most studies of salt-marsh production have measured aerial production, but recent evidence has shown rates of below-ground production may be as much as 50% of above-ground rates (Pomeroy *et al.* 1981).

Observations of the elevated productivity of salt-marshes has provided impetus to Odum's "outwelling" hypothesis. However, estimates of organic carbon exports from salt-marshes are very variable, and range from zero for Flax Pond, which imported organic carbon (Woodwell *et al.* 1977), to >110% for North Inlet (Chrzanowski *et al.* 1983) which showed large exports). However, in most marshes exhibit pronounced changes, in both the magnitude and direction of organic carbon fluxes, on time scales of less than a year. These may be seasonal, for instance, Great Sippewissett marsh showed a large peak in particulate organic carbon (POC) exports during spring, with smaller exports over the remainder of the year (Valiela *et al.* 1978). Gott's marsh showed largest POC losses in autumn, and actually imported this fraction in summer (Heinle and Flemer 1976). In other marshes, for example Flax Pond (Woodwell et al. 1977), the fluctuations within seasons were almost as great as those between seasons. Nixon (1980) suggested that this extreme variability was a product of the intensive sampling programme employed in the Flax Pond study and that it may be applicable to other marshes. This was confirmed by Chrzanowski et al. (1982) who sampled several series of four successive tides in North Inlet and showed that the direction of POC fluxes shifted over successive tides.

The short-term shifts observed for Flax Pond and North Inlet are important because they are of sufficient magnitude to cast serious doubt upon reported annual, and even seasonal, estimates of marsh-estuarine organic carbon fluxes. Consequently, in this chapter, in which I examine organic carbon fluxes between the Sarcocornia marsh and Kariega estuary, emphasis has been placed on elucidation of these short-term changes.

4.1 Organic carbon fluxes during periods of diminished river inflow

Material and methods

Fluxes of organic carbon were measured over 42 semi-diurnal tides. Alternate tides were monitored during four semi-lunar sampling periods, each located at approximately mid-season in autumn, winter, spring and summer. These sampling periods occurred during periods of little or no river inflow into the Kariega estuary, which is the prevailing condition in this system (Allanson and Read 1987).

During each semi-diurnal tide, water samples for organic carbon analyses were collected at mid-depth, at the mid-channel sampling station (L3 or H3) using a 75×10^3 mm^3 syringe-sampler constructed according to Liptrot (1978). Four samples were collected every 30 minutes; two were left unfiltered for total organic carbon (TOC) analysis, while the remaining two were filtered using pre-rinsed (with double-distilled water), pre-ashed (495 °C for 5 h) Whatman GF/F filter papers, and were used for estimation of dissolved organic carbon (DOC). Following filtration, the water samples were stored on ice in the dark for a maximum of one hour, before being frozen in a field laboratory. Particulate organic carbon (POC) concentrations were determined as the difference in mean ($n = 2$) concentrations between the unfiltered (TOC) and filtered (DOC) samples.

In a control experiment in which organic carbon values were compared for 10 subsamples filtered before freezing and 10 subsamples frozen unfiltered, the mean estimates of DOC concentrations were significantly ($P<0.05$) higher in the latter group. Since in the same experiment TOC values were unaffected by freezing, this difference shows the need for filtration prior to and not after freezing, if POC and DOC fractions are to be differentiated.

TOC and DOC concentrations were determined using a Beckman 915B Total Organic Carbon Analyzer, after removal of inorganic carbon by acid sparging. Because of the brackish nature of the estuarine water analyzed, difficulties were encountered in the use of this instrument. Of major concern was corrosion of the sample cell, and contamination of the oxidizing catalyst by halogen-containing reaction products of the thermal oxidation process. These problems were alleviated by frequent cleaning of the sample cell, reduction of sample volume injected into the instrument combustion tube, and regular replacement of the catalyst. Precision of the analytical techniques, as applied, and expressed as percentage coefficients of variance, were between 3 and 6% at DOC concentrations of 3-10 mgC dm^{-3} ($\underline{n}$ = 9).

Concentrations of DOC and POC were combined with estimates of discharge (determined as in Section 3.3) to calculate:

1. the instantaneous flux per sector, $\underline{F}(\underline{t})$;
2. the instantaneous cross-sectional flux, $\underline{F}_{\underline{T}}$;
3. the time-averaged instantaneous cross-sectional net flux, $<\underline{F}_{\underline{T}}>$; and
4. the cross-sectional net flux for the entire tidal cycle, $\underline{F}_{\underline{TIDE}}$.

Instantaneous flux per sector, $\underline{F}(\underline{t})$, was calculated thus:

$$\underline{F}(\underline{t}) = \underline{Q}(\underline{t})\ \underline{c}(\underline{t})\ \rho(\underline{t}) \qquad (8)$$

where $\underline{Q}(\underline{t})$ = instantaneous sector discharge ($m^3 s^{-1}$) at time $\underline{t}$, $\underline{c}(\underline{t})$ = concentration (mgC kg^{-1}) at time $\underline{t}$, and ρ = water density assumed to be 1020 kg m^{-3} (Kjerfve 1979). For each tide, $\underline{F}(\underline{t})$ values were used to derive estimates of $\underline{F}_{\underline{T}}$, $<\underline{F}_{\underline{T}}>$ and $\underline{F}_{\underline{TIDE}}$, using equations 3, 5 and 6 (Chapter 3), by substituting $\underline{F}$ for $\underline{Q}$ in these equations.

Floating wrack was sampled using a rectangular net, 0.50 m wide, 0.30 m high, and 1.0 m long from mouth to apex, anchored in mid-channel at the marsh mouth (Figure 33). The net was secured front and back to maintain its position parallel to direction of flow, and was buoyed with partially filled floats to ensure its opening remained half submerged. Its mesh size was 1.25 mm, and material retained was removed at 30 minute intervals, placed in plastic bags and returned to the laboratory where it was oven-dried to constant weight

Figure 33 Net for collection of floating wrack for determination of fluxes of coarse, floating organic carbon (FOC).

at 70^{o}C. Its organic content was determined as loss of dry mass on ignition at 495^{o}C for 5 hours. Because our laboratory does not have a CHN Analyzer, carbon content of this material was calculated assuming a carbon value of 0.45 of organic mass (Westlake 1969).

The cross-sectional flux, $\underline{F}_{(\underline{c})}$, of this fraction, here termed coarse floating organic carbon (FOC), was calculated per 30 minute interval as:

$$\underline{F}_{(\underline{c})} = \underline{M} \times 0.45 \times \underline{W}/\underline{W}_{\underline{n}} \qquad (9)$$

where $\underline{M}$ = organic dry mass of material collected over 30 minutes from $\underline{t}_0$ to $\underline{t}_1$; 0.45 is the assumed carbon content; $\underline{W}$ is the width of water in tidal creek at $\underline{t}_{0.5}$, where $\underline{t}_{0.5} = (\underline{t}_1 - \underline{t}_0)/2$; and $\underline{W}_{\underline{n}}$ is width of sample net. $\underline{F}_{\underline{c}}$ values were summed for each tide to obtain estimates of net flux of FOC per tide, $\underline{F}_{(\underline{c})\ \underline{TIDE}}$.

Results

DOC and POC fluxes during semi-diurnal tides

Before considering semi-lunar patterns of DOC and POC fluxes, it is necessary to examine their fluxes during semi-diurnal tides. To do this I have selected four tides measured on consecutive days in January 1985. These tides demonstrate the principal inter-relationships between time over tidal cycle, discharge, DOC and POC concentrations, and fluxes of these components.

These tides were also chosen because they spanned a period during which the direction of DOC fluxes switched from exports to imports, and then back again, which as discussed below, occurs frequently in this system.

The tides of 19 and 22 January 1985 exported DOC, while the intermediate tides of 20 and 21 January imported this fraction; $<F_T>$ values for the respective tides were -0.07, +0.10, +0.02, and -0.03 gC s^{-1}.

Figure 34 shows the changes in water level, and concentrations of DOC and POC over the four tides. DOC concentrations generally exceeded those of POC, but concentrations of both fractions, and particularly the concentrations of POC relative to those of DOC, were elevated at low water levels at the start and end of each tide. Observations of the release of silty material from burrows of the anomuran mudprawn, Upogebia africana (Ortm) suggested this was a consequence of bioturbation. In view of the shallowness of the creek, it may also be due to wind-induced resuspension of sediments at low water levels.

Over each tide, the changes in DOC instantaneous cross-sectional fluxes, F_T, closely followed changes in discharge, Q_T (Figure 35). These data show that the instantaneous fluxes of DOC onto and off the marsh were controlled more by changes in discharge than by DOC concentration changes in the water column. In contrast, the F_T values of POC, which were smaller than those of DOC, followed Q_T less closely. This shows that compared to DOC, the processes responsible for changes in POC concentrations exerted a more pronounced effect relative to discharge on the instantaneous fluxes of this component.

Fluxes of DOC over semi-lunar tides

Figures 36 and 37 show the net fluxes per tide of DOC and POC, expressed as $<F_t>$ and F_{TIDE}, over alternate tides during four semi-lunar sampling

Figure 34 Changes in water level (a), and concentrations of DOC (b) and POC (c) in the tidal creek over four selected tides, January 1985.

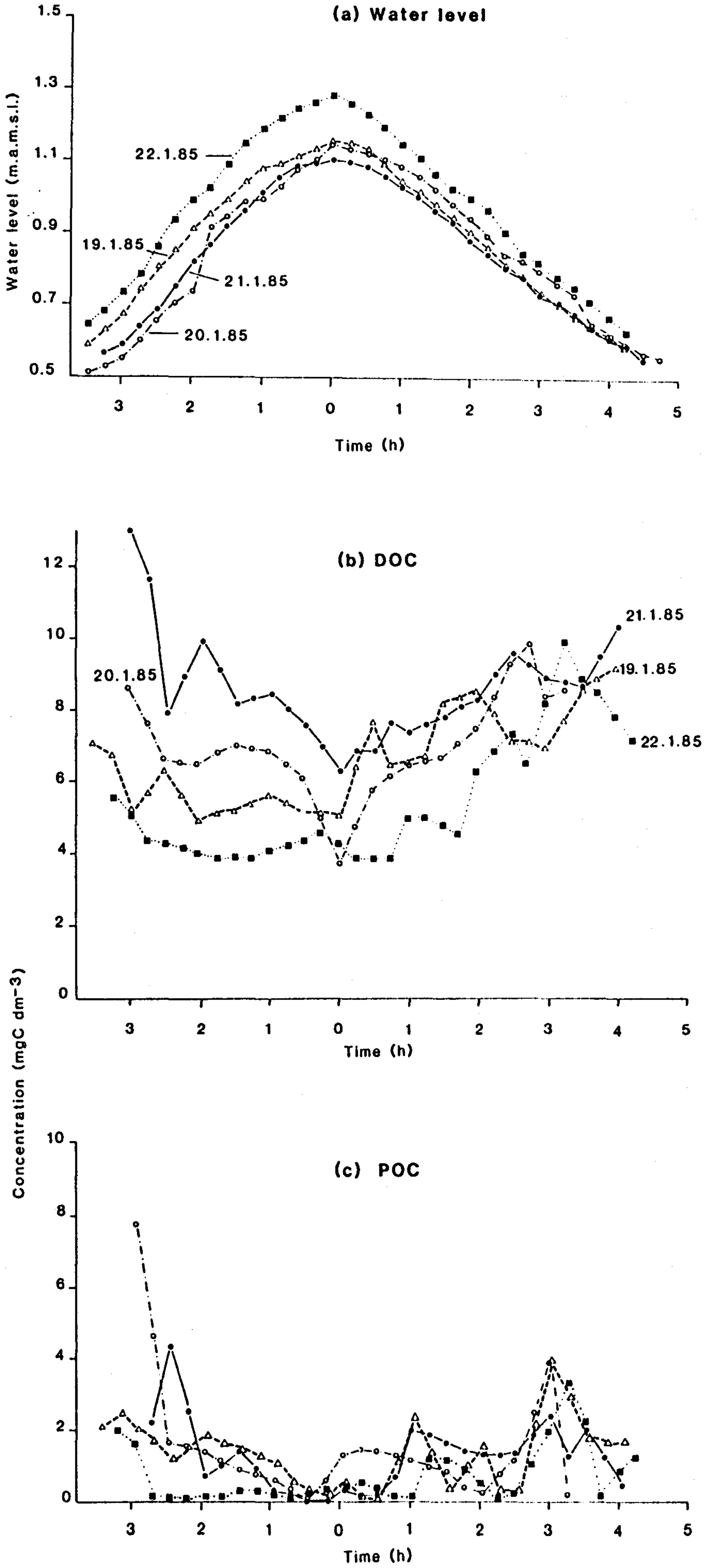

(a) Water level
Water level (m.a.m.s.l.)
1.5
1.3
1.1
0.9
0.7
0.5
22.1.85
19.1.85
21.1.85
20.1.85
3
2
1
0
1
2
3
4
5
Time (h)
(b) DOC
12
10
8
6
4
2
0
20.1.85
21.1.85
19.1.85
22.1.85
3
2
1
0
1
2
3
4
5
Time (h)
Concentration (mgC dm-3)
(c) POC
10
8
6
4
2
0
3
2
1
0
1
2
3
4
5
Time (h)

Figure 35 Instantaneous cross-sectional discharges, $\underline{Q}_{\underline{T}}$, and fluxes, $\underline{F}_{\underline{T}}$, of DOC and POC at the marsh-estuarine junction over four tides. Negative discharge and flux values denote transport onto marsh, and positive values transport from marsh to estuary. Time-averaged instantaneous cross-sectional net discharges, $<\underline{Q}_{\underline{T}}>$, and fluxes, $<\underline{F}_{\underline{T}}>$, are indicated for each tide.

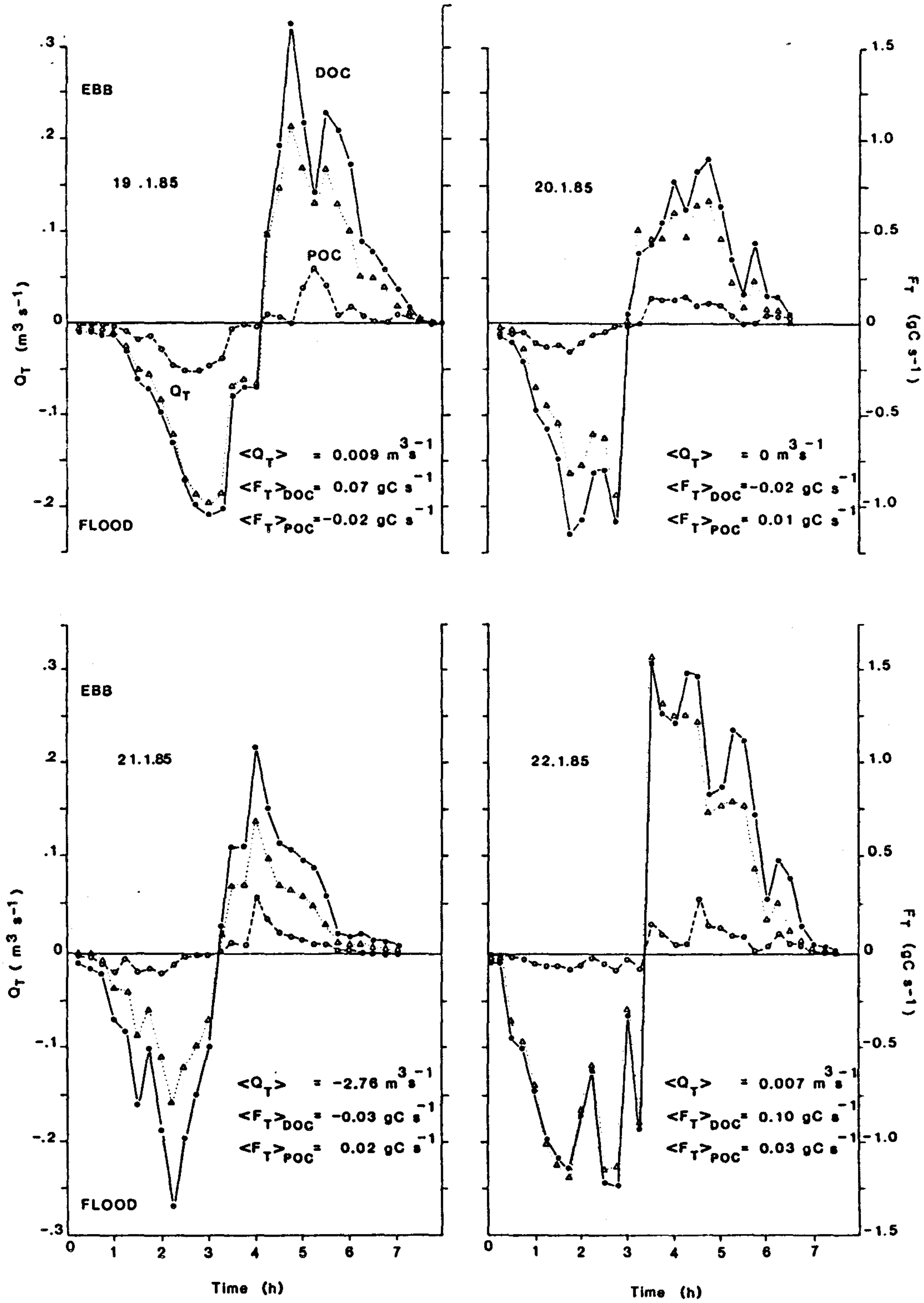

19 .1.85
EBB
FLOOD
DOC
POC
Q_T
<Q_T> = 0.009 m3 s-1
<F_T>DOC= 0.07 gC s-1
<F_T>POC=-0.02 gC s-1
20.1.85
<Q_T> = 0 m3 s-1
<F_T>DOC=-0.02 gC s-1
<F_T>POC= 0.01 gC s-1
21.1.85
EBB
FLOOD
<Q_T> = -2.76 m3 s-1
<F_T>DOC= -0.03 gC s-1
<F_T>POC= 0.02 gC s-1
22.1.85
<Q_T> = 0.007 m3 s-1
<F_T>DOC= 0.10 gC s-1
<F_T>POC= 0.03 gC s-1
Q_T (m3 s-1)
Q_T (m3 s-1)
F_T (gC s-1)
F_T (gC s-1)
.3
.2
.1
0
-.1
-.2
-.3
1.5
1.0
0.5
0
-0.5
-1.0
-1.5
0 1 2 3 4 5 6 7
Time (h)
Time (h)

Figure 36 Net fluxes of DOC and POC over alternate tides during autumn (a) and winter (b) semi-lunar sampling periods. Solid bars signify cross-sectional net fluxes per tide, $\underline{F}_{\underline{TIDE}}$; clear bars represent time-averaged instantaneous cross-sectional net fluxes per tide, $<\underline{F}_{\underline{T}}>$. Vector diagrams of mean wind direction and velocity are presented. Maximum height of tides observed at the marsh-estuarine junction, and predicted for the ocean are indicated by solid and dotted lines, respectively.

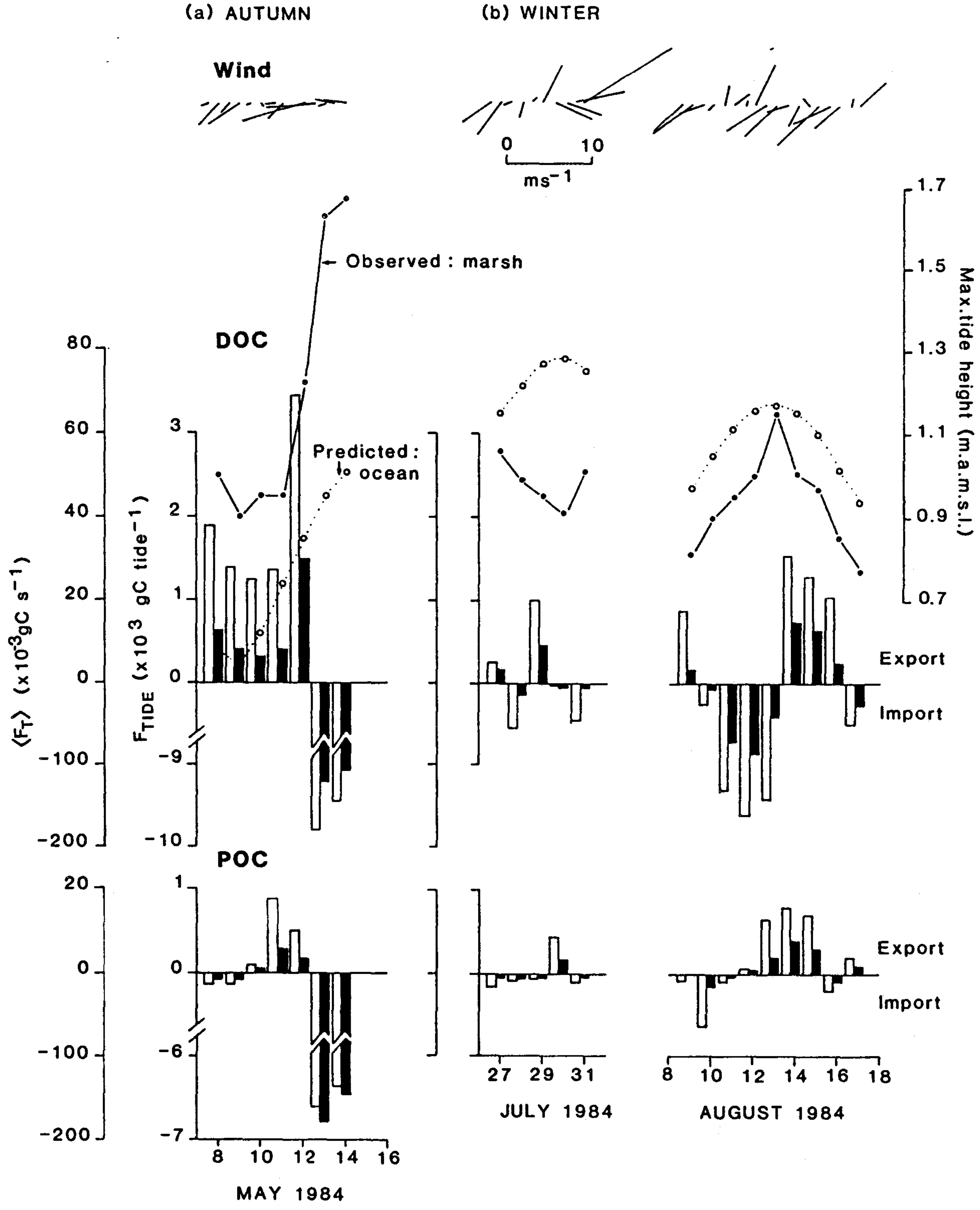
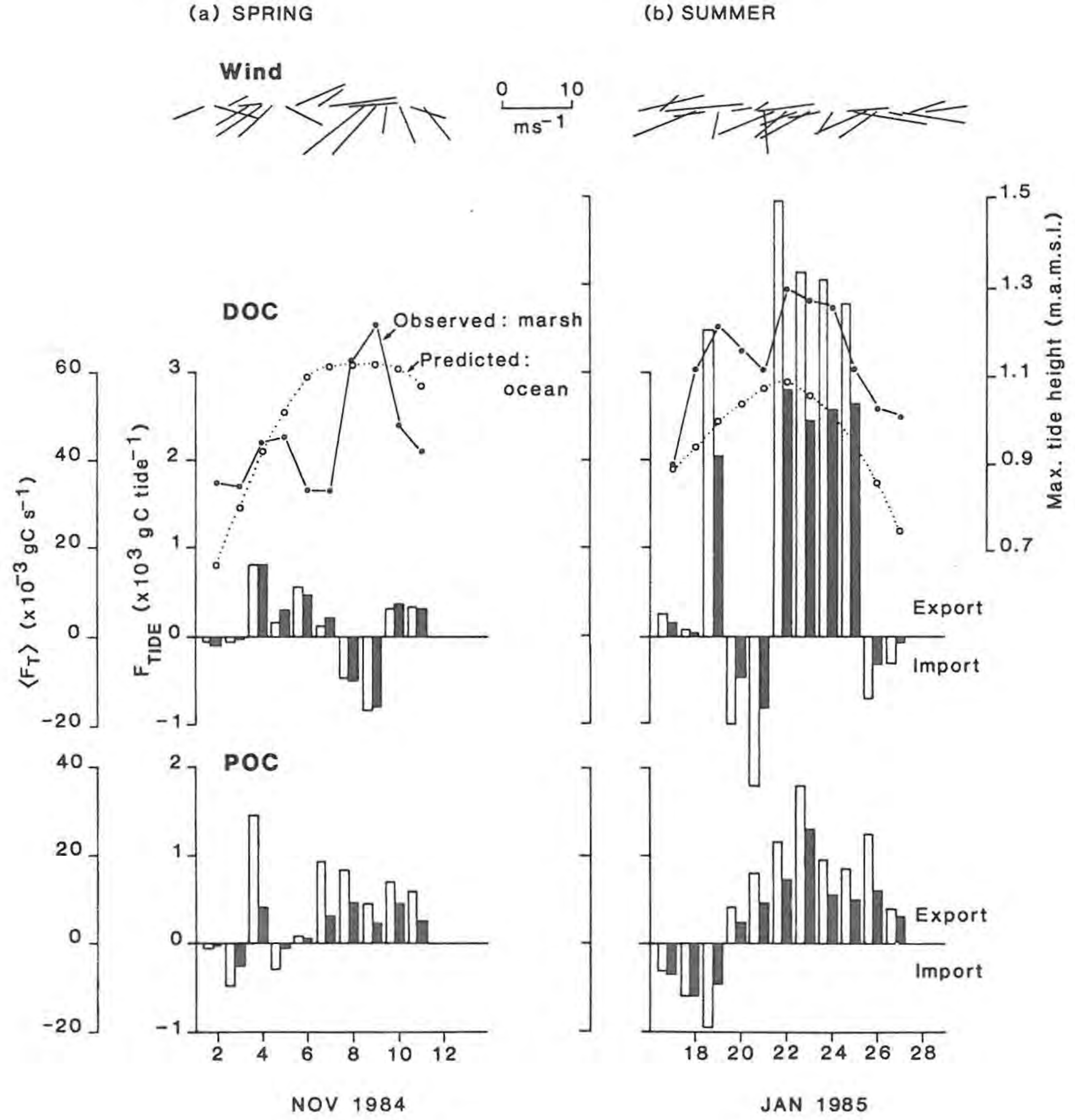

(a) AUTUMN
(b) WINTER
Wind
0
10
ms⁻¹
Observed : marsh
Predicted : ocean
DOC
POC
80
60
40
20
0
-100
-200
20
0
-100
-200
3
2
1
0
-9
-10
1
0
-6
-7
⟨F_T⟩ (x10⁻³gC s⁻¹)
F_TIDE (x10³ gC tide⁻¹)
1.7
1.5
1.3
1.1
0.9
0.7
Max.tide height (m.a.m.s.l.)
Export
Import
Export
Import
8
10
12
14
16
MAY 1984
27
29
31
JULY 1984
8
10
12
14
16
18
AUGUST 1984

Figure 37 Net fluxes of DOC and POC over alternate tides during *spring* (*a*) and *summer* (*b*) semi-lunar sampling periods. Details as in Figure 36.


(a) SPRING
(b) SUMMER
Wind
0
10
ms^{-1}
DOC
Observed: marsh
Predicted: ocean
POC
60
40
20
0
-20
3
2
1
0
-1
1.5
1.3
1.1
0.9
0.7
Max. tide height (m.a.m.s.l.)
⟨F$_T$⟩ (x10^{-3} gC s^{-1})
F$_{TIDE}$ (x10^3 g C tide^{-1})
Export
Import
2
4
6
8
10
12
NOV 1984
18
20
22
24
26
28
JAN 1985

periods. These data show that there was wide variation in both the magnitude and direction the fluxes of DOC and POC. The following analysis attempts to establish the nature and cause(s) of this variation.

The direction of DOC fluxes shifted sequentially on a time scale of days. These shifts coincided with, or followed shortly after changes in wind direction (see for example the shifts during the summer period, Figure 37*b*). Fluxes of DOC were generally directed from the marsh to estuary during periods of westerly winds, and onto the marsh during periods of easterly winds.

The coincidence of wind and direction of DOC net fluxes is probably not directly causal. The data presented in Table 4 shows that tides coincident with easterly winds, and which effected net imports of DOC, were characterized by markedly lowered water temperatures. Recent evidence has shown that winds with easterly components frequently cause upwelling of deep oceanic water on the south east Cape coast, which results in sharp decreases in surface oceanic water temperatures (Schumann *et al*. 1982). These data, in combination, show that the DOC imports onto the marsh are linked, in some way, to the tidal transfer of cold, upwelled oceanic water onto the marsh.

Changes in DOC fluxes with tide elevation

Figure 38 shows the cross-sectional net fluxes, $\underline{F}_{\underline{TIDE}}$, of DOC in relation to changes in maximum tide elevation. At tides of <1.0 m.a.m.s.l. DOC was exported at 71% of tides, and in a manner unrelated to wind direction. However, higher tides (>1.0 m.a.m.s.l.)

coincident with easterly winds exhibited imports of DOC, while those associated with westerly winds exported this fraction. These data are important because they show that the relation between wind and direction of DOC net flux as are in some way dependent on tide elevation.

Table 4. DOC F_{TIDE} estimates for summer tides of 17 to 27 January 1985, mean wind direction for 12 h prior to each tide, and temperature of water at marsh-estuary confluence at high slack-tide.

TIDE	F_{TIDE} ($\times 10^{-3}$ gC tide^{-1})	Wind direction	Temperature (^{o}C)
17 Jan	+0.16	E	21
18	+0.05	W	24
19	+2.10	W	22
20	-0.51	E	13
21	-0.83	E	15
22	+2.80	W	20
23	+2.30	W	23
24	+2.50	W	22
25	+2.60	E	22
26	-0.34	W	14
27 Jan	-0.04	E	16

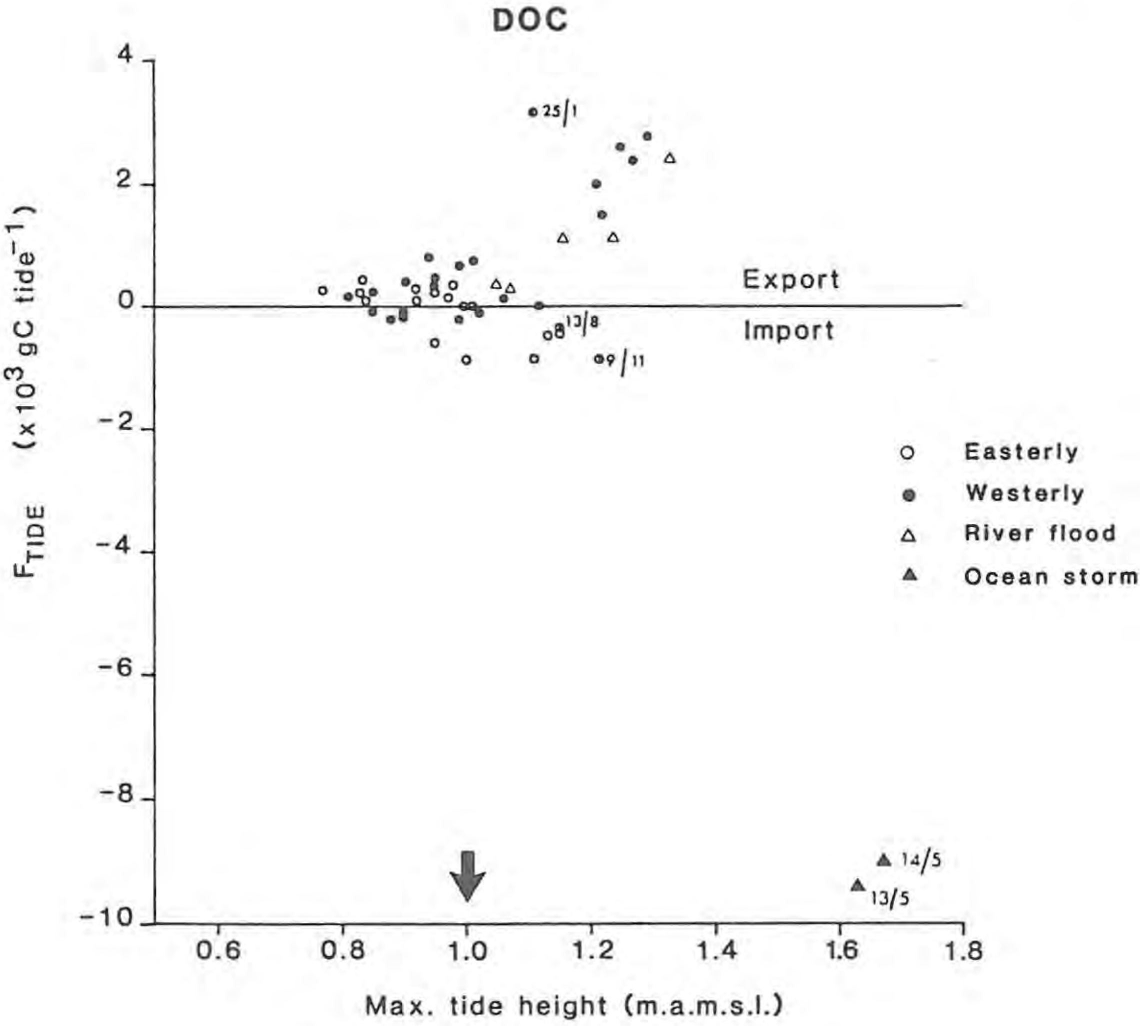


Figure 38 Cross-sectional net fluxes per tide, F_{TIDE}, of DOC in relation to maximum tide elevation. Tides are partitioned on the basis of wind direction: • westerly winds; o easterly winds. Triangles represent tides monitored after a river flood in April 1986 (Section 4.2). Numbers alongside tides are dates of tides discussed in text. Arrow indicates elevation of marsh berm.

This dependence may be a consequence of the location of the marsh in the middle reaches of the estuary, which means the sequelae of oceanic events must be propagated up the estuary before they can influence fluxes at the marsh-estuarine interface. In the absence of river inflow the tidal prism is the dominant hydrodynamic influence in the estuary (Allanson and Read 1987). Tidal amplitudes, and therefore presumably the magnitude of water movements within the estuary, are greater during spring-than neap-tides (Figure 14). Consequently, the effects of oceanic events will probably be propagated further and more rapidly up the estuary during spring-tides than during neaps. Since spring-tides usually attain higher elevations than neap-tides (Figure 14), this would account, at least in part, for the coincidence of DOC imports and easterly winds at high elevation tides but not at lower ones.

There are exceptions to this pattern, and these can be ascribed to delayed propagation of oceanic effects up the estuary. For instance, the tides of 13 August and 9 November 1984, which were associated with westerly winds but imported DOC (Figure 38), followed periods of strong easterly winds (Figures 36b and 37a respectively). Conversely, the tide of 25 January 1985, which coincided with easterly winds but exported DOC, followed a three-day period of predominantly south westerly winds (Figure 37b and Table 4).

DOC:POC fluxes onto marsh

Figure 39 compares the ratio of DOC:POC fluxes onto the marsh during tides associated with easterly and westerly winds. These data show that not only do the patterns of DOC fluxes change in response to

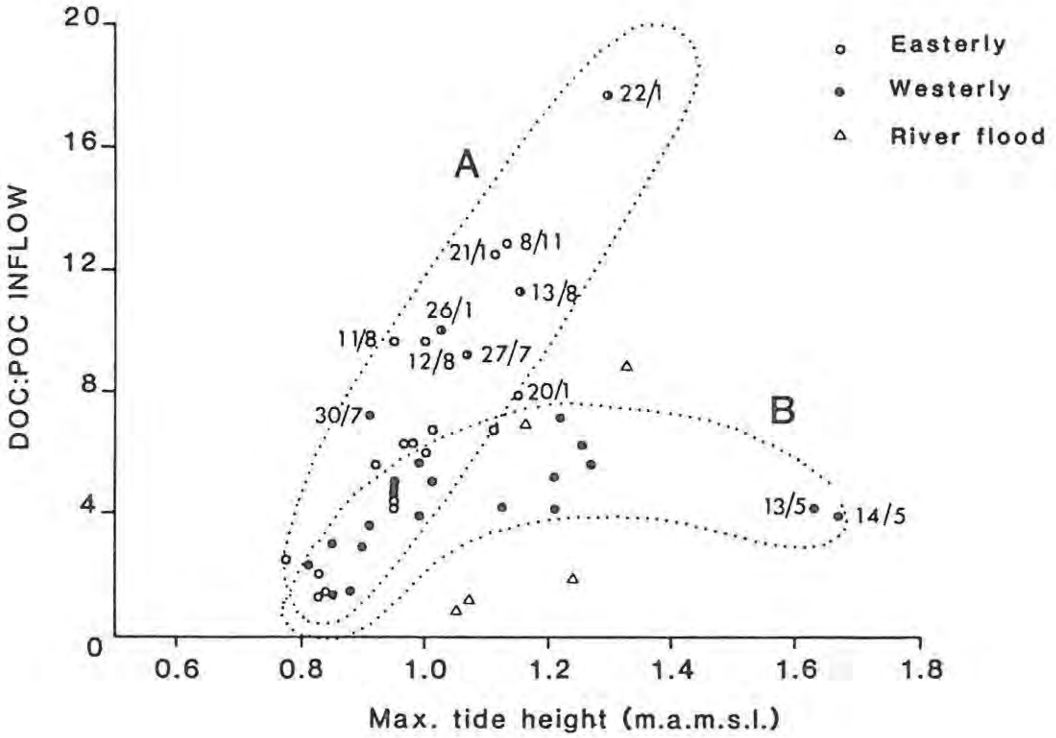


Figure 39 Ratio of DOC:POC fluxes onto marsh in relation to maximum tide elevation. Symbols as in Figure 38. Fine dotted lines differentiate tides coincident with, or immediately following, easterly winds (A) and those associated with or following westerly winds (B). Tides monitored after the river flood are represented by triangles (Section 4.2).

mesoscale atmospheric/oceanic events, but so does the nature of organic carbon transferred onto the marsh. At low elevation tides (<1.0 m.a.m.s.l.), DOC:POC flux ratios were low (ca. <3.0) and similar for tides associated with easterly and westerly winds. But at higher tides, the ratios were larger than at lower tides, and were greater for tides associated with easterly winds than westerly winds.

To check whether the imports of DOC during periods of easterly winds (Figure 38) occurred in response to elevated DOC concentrations, I have plotted DOC $\underline{F}_{\overline{TIDE}}$ values against mean flood-tide DOC concentrations for each tide (Figure 40). This is relevent because there is some evidence in the literature which suggests that marsh-estuarine fluxes of material may be dependent on concentrations of this material in tidal water inundating the marshes (e.g. Nedwell 1982, Jordan *et al.* 1983). The present data shows that this is not applicable to fluxes of DOC in this system, and that the relation between elevated DOC:POC ratios and DOC imports during easterly winds (Figure 39), is a consequence of lowered POC, rather than elevated DOC, concentrations.

POC fluxes

Figure 41 shows the changes in POC $\underline{F}_{\overline{TIDE}}$ values with maximum tide elevation. In contrast with the fluxes of DOC, fluxes of POC were directed from the marsh to estuary at most (69%) tides and in a manner not measurably dependent on wind direction. (The tides of 13 and 14 May 1984, and those which followed flooding of the Kariega River in April 1986, have been excluded from this calculation).

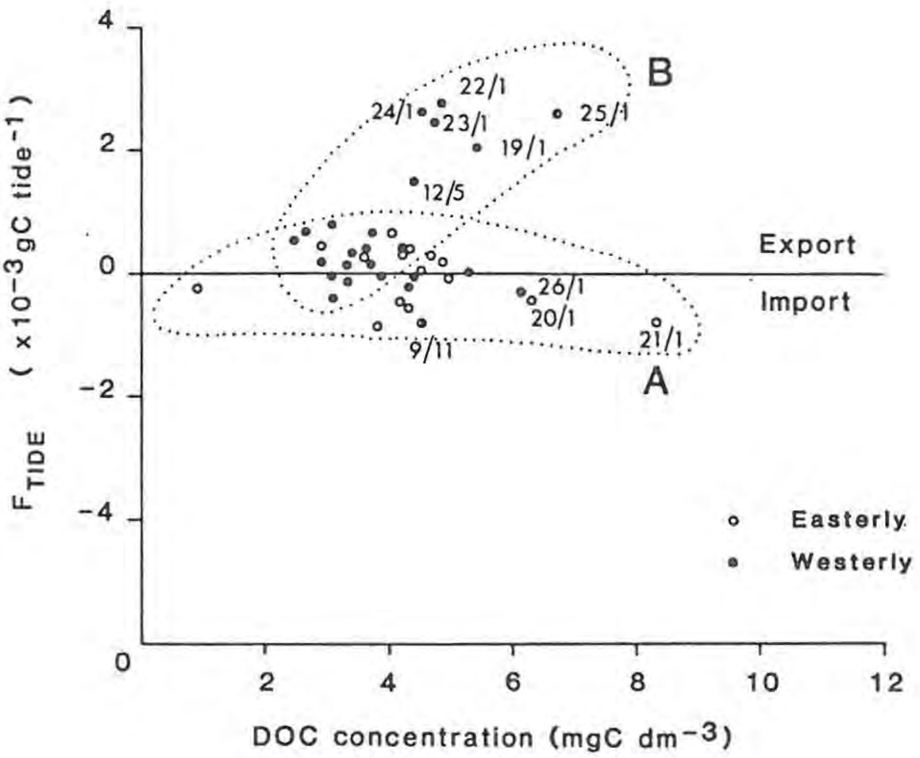


Figure 40 DOC fluxes per tide, F_{TIDE}, plotted as a function of flow-weighted mean DOC concentration in water entering the marsh. Notations as in Figure 38.

As noted earlier, the directions of POC fluxes were related to patterns of water flow at the marsh-estuary junction. For instance, most tides of between 1.0 and 1.3 m.a.m.s.l. exhibited ebb-tide velocity peaks (Section 3.3), and exported POC. Similarly, the extreme elevation tides of 13 and 14 May 1984, which showed pronounced flood-tide velocity peaks, imported this fraction.

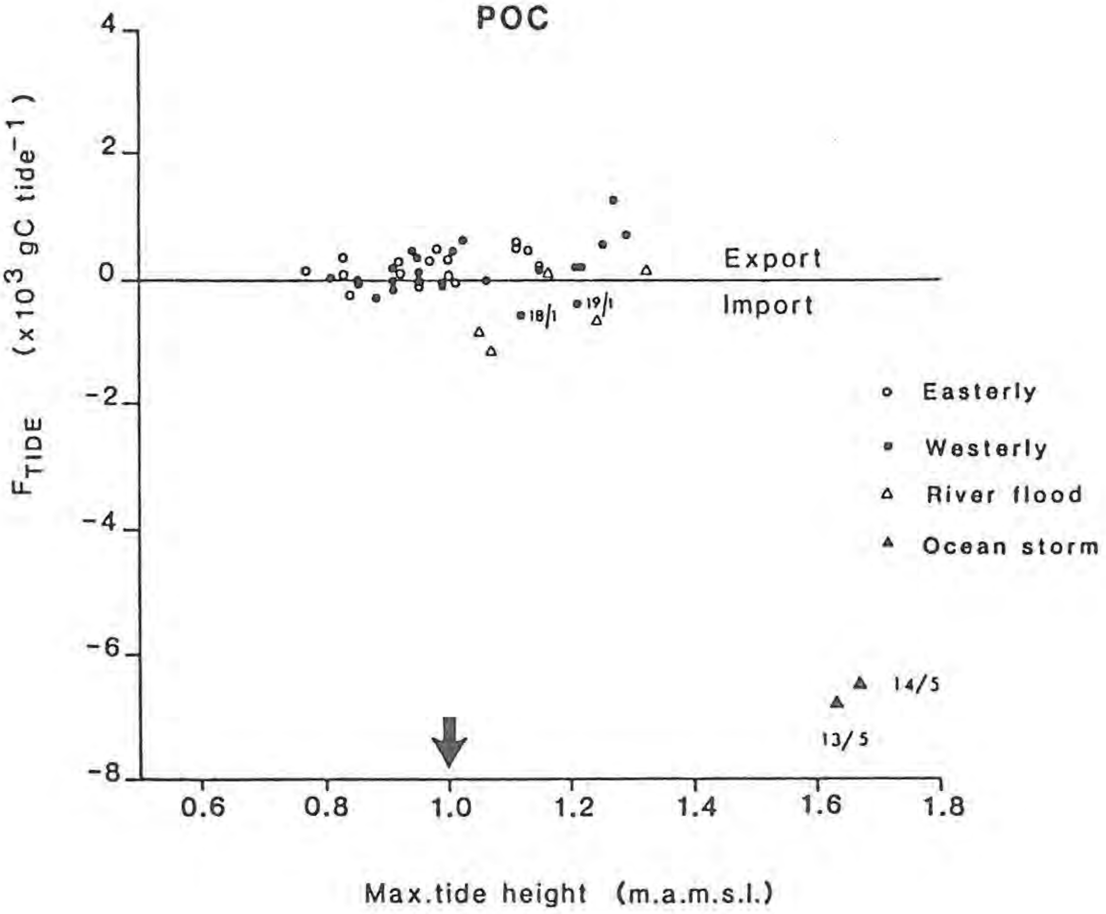


Figure 41 Cross-sectional net fluxes per tide, F_{TIDE}, of POC in relation to maximum tide elevation. Notations as in Figure 38.

Fluxes of coarse floating organic carbon (FOC)

Unlike the fluxes of DOC and POC, the fluxes of coarse floating organic carbon were directed onto the marsh at all except two of the 22 tides (Figure 42). The fluxes of FOC, which ranged from -0.5 to +0.25 kgC $tide^{-1}$ (the tides of 13 and 14 May 1984 excluded), were

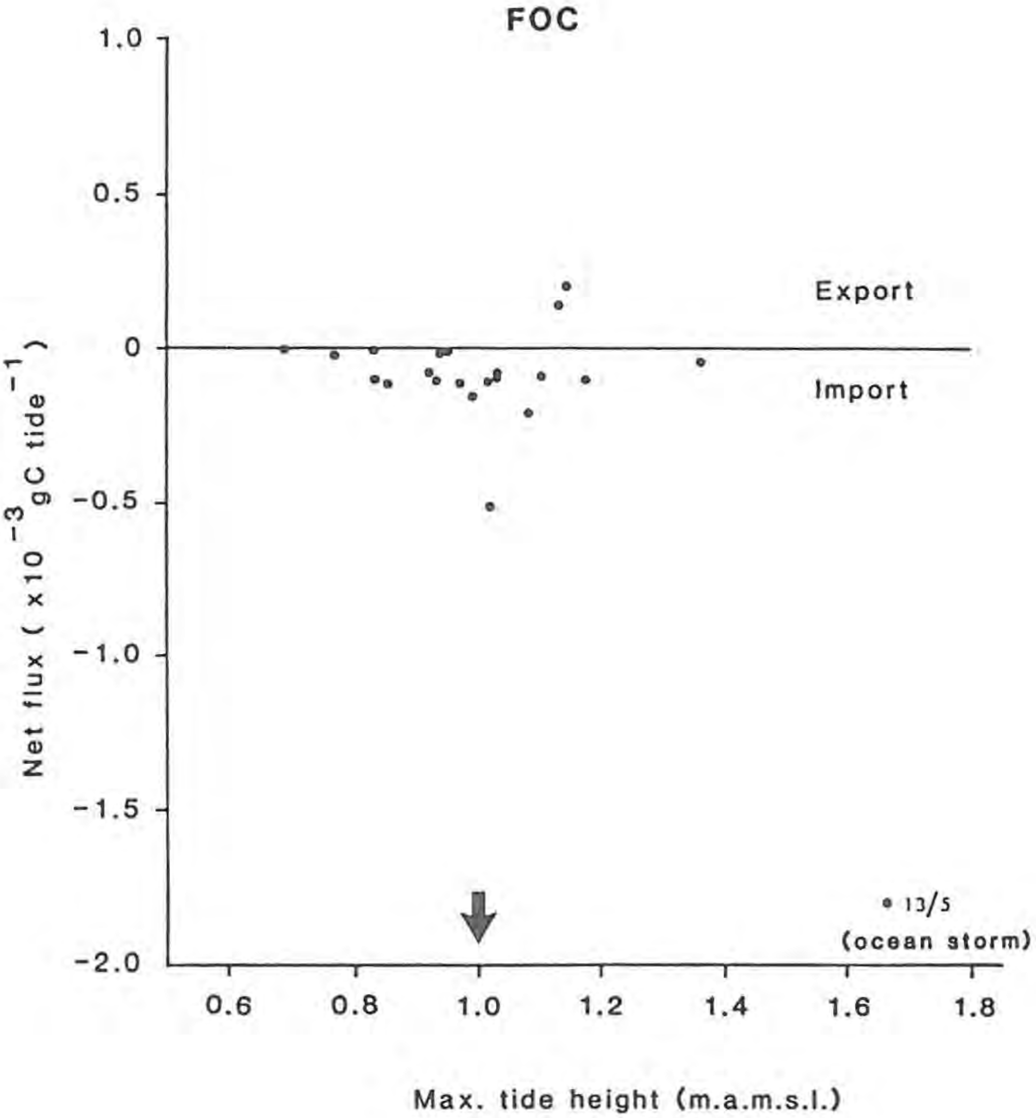


Figure 42 Net fluxes of FOC, $\underline{F}_{(\underline{c})TIDE}$, in relation to maximum tide elevation.

smaller than those of the other fractions. The comparatively small fluxes of FOC accords with evidence in the literature (Dame and Stilwell 1984, and Chalmers *et al.* 1985), which has demonstrated that although salt-marsh wrack is conspicuous little is removed from marshes by tides.

Most of the FOC transported between the marsh and Kariega estuary was of macrophyte origin, but the nature of this material varied considerably, both during and between tides (Figure 43). During the tide of 31 July 1984, 60% of FOC retained by the marsh was wrack of *Zostera capensis* Setchell. However, this component accounted for only 17% of FOC imported during the tide of 14 August 1984, when most (74%) FOC retained was derived from the macro-alga *Codium tenue* (Kuetzing) Kuetzing, which grows attached to rocks in the middle reaches of the estuary.

4.2 Effects of a minor river flood

The results examined so far apply to periods of little or no river inflow into the Kariega estuary. Although this is the prevailing condition in the estuary, it is subjected to sudden, short-lived river floods (Allanson and Read, 1987). Heavy rainfall in the river catchment during mid-April 1986 provided an opportunity to examine the effects of such an event on organic carbon fluxes between the marsh and estuary. The flood, which started on 20 April, was small-scale, with daily mean inflows of only 0.004 to 0.006 $m^3 s^{-1}$ (c.f. 0.000 to 0.003 $m^3 s^{-1}$ under non-flood conditions). DOC and POC fluxes were measured during five tides, over six days immediately following the start of the flood.

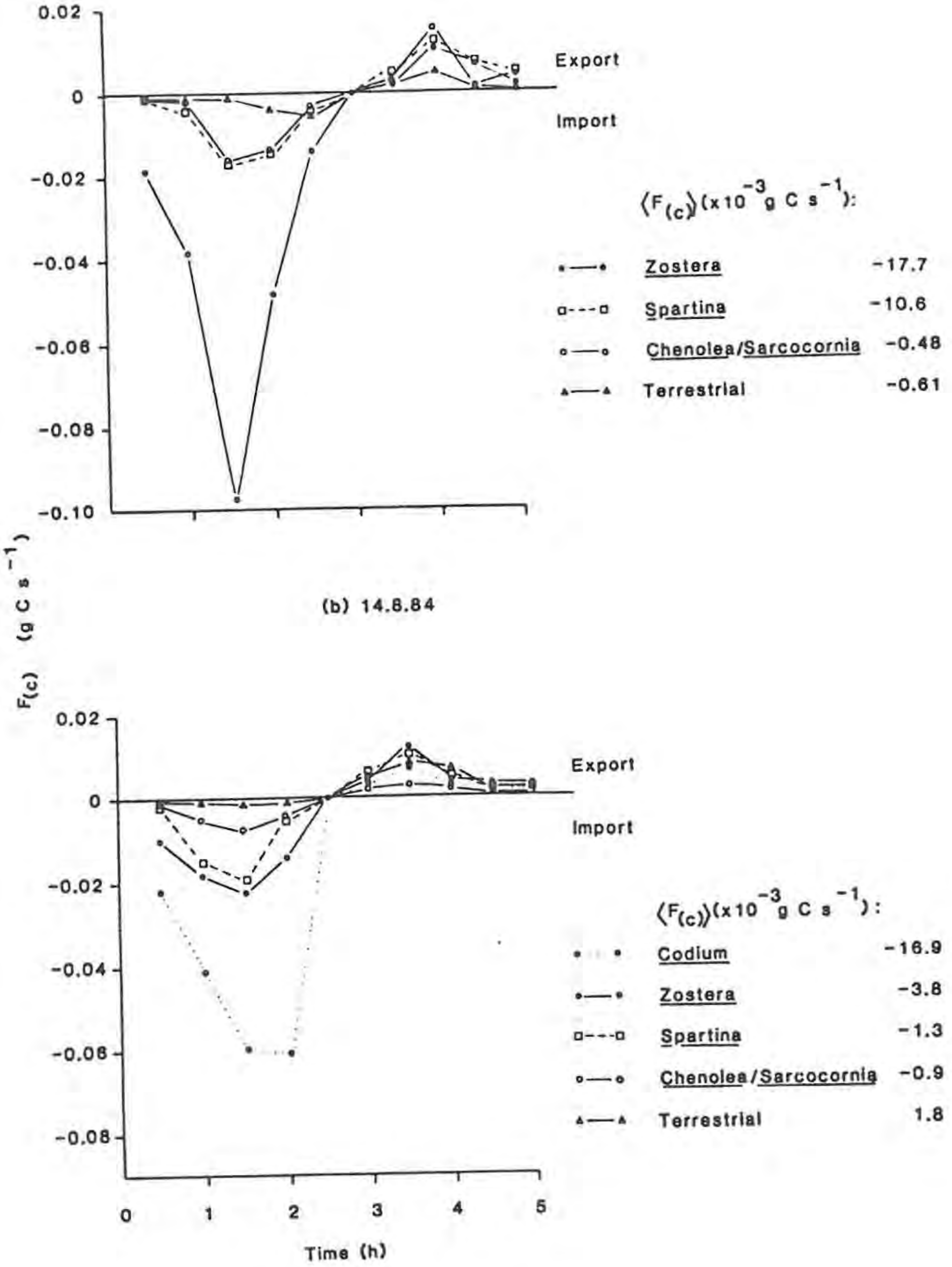


Figure 43 Instantaneous cross-sectional fluxes, $\underline{F}_{(\underline{c})}$, of different components of FOC over tides of 31 July (a) and 14 August 1984 (b). Time-averaged instantaneous cross-sectional fluxes, $\langle \underline{F}_{(\underline{c})} \rangle$, are indicated in panels adjacent to the graphs.

In agreement with the observation of Allanson and Read (1987) that the estuary is partially-mixed following river floods, the salinities of water entering the marsh early during the tides of 20 and 23 April were lower than that of sea water (Figure 44). However, because the river inflows were small, sea-water salinities were re-established at high water during these particular tides. During later tides, namely those of 25 and 26 April, the salinities were more constant and equal to that of seawater for the duration of the tides.

This post-flood recovery of the marine dominance of the estuary was accompanied by changes in the nature of organic carbon transported onto the marsh (Figure 44). At the onset of the flood concentrations of DOC and POC were elevated, and DOC:POC flux ratios low (<2.0, Figure 39). As river inflows decreased, concentrations of both components, but particularly POC decreased. Over the last two tides DOC:POC flux ratios were once again high (7.2 and 9.7, respectively), and similar to those under non-flood conditions (Figure 39).

Table 5 summarizes the net fluxes of DOC and POC, expressed as time-averaged instantaneous ($\langle \underline{F}_T \rangle$) and tidal ($\underline{F}_{TIDE}$) fluxes, over the five tides. Fluxes of DOC were directed from the marsh to estuary over all five tides, and the magnitude of fluxes were similar to those during non-flood, westerly-wind conditions (Figure 38). Unlike the fluxes of DOC, those of POC were altered by the flood (Figure 41), POC was imported onto the marsh over the first three tides but exported over the last two.

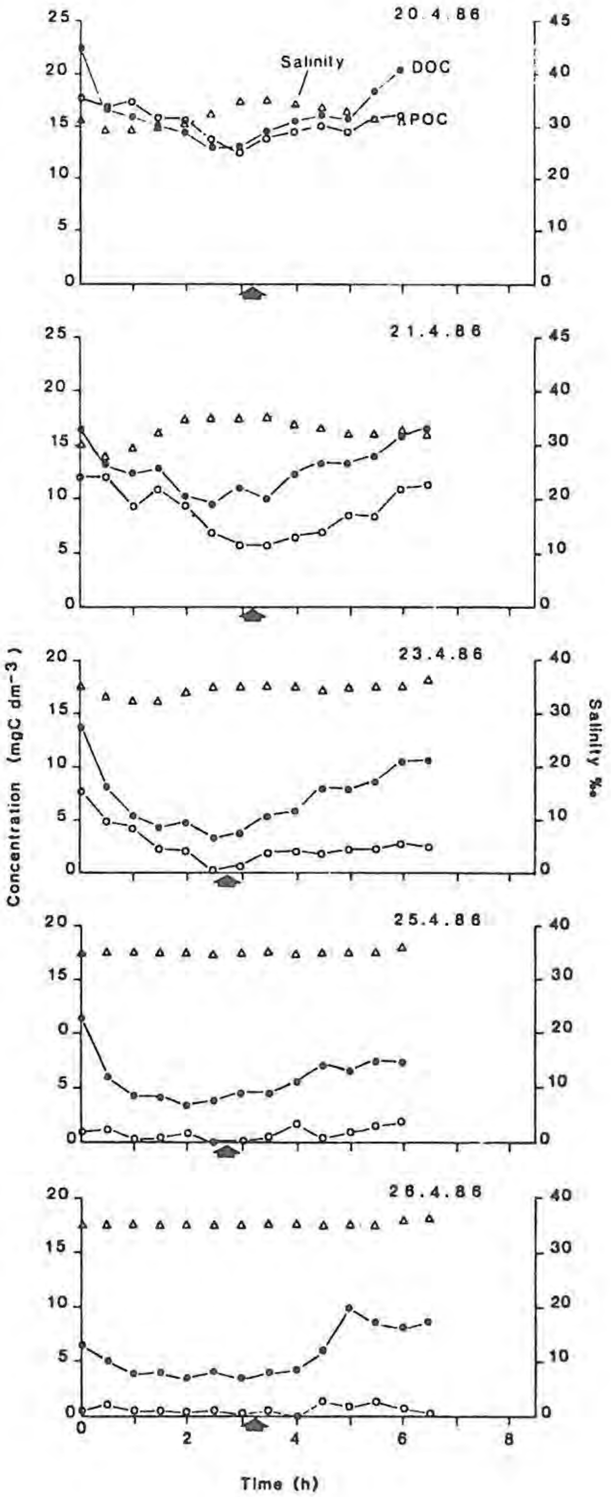


Figure 44 Changes in salinity, and DOC and POC concentrations of tidal water entering and leaving the marsh over five tides following a river flood. Arrows indicate high slack-tide.

Table 5. Net discharge, as $\underline{Q}_T$ and $\underline{Q}_{TIDE}$, and net flux of DOC and POC, as $\underline{F}_T$ and $\underline{F}_{TIDE}$, over five tides following a river flood. Negative signs denote net import to marsh; positive signs net export.

Date	Component	Maximum tide height (m.a.m.s.l.)	$\underline{Q}_T$ ($\times 10^{-3}$ m^3 s^{-1})	$\underline{Q}_{TIDE}$ (m^3 $tide^{-1}$)	$\underline{F}_T$ (gC s^{-1})	$\underline{F}_{TIDE}$ (gC $tide^{-1}$)
20.4	DOC	1.05	-0.36	-10.5	+21.5	+330.0
	POC				-25.2	-875.0
21.4	DOC	1.07	-0.42	-9.7	+19.7	+290.0
	POC				-31.7	-1190.0
23.4	DOC	1.24	-1.13	-27.5	+36.0	+1110.0
	POC				-23.2	+700.0
25.4	DOC	1.16	-8.00	-117.2	+33.8	+1100.0
	POC				+7.0	+80.0
26.4	DOC	1.33	-1.09	-24.9	+60.0	+2197.0
	POC				+7.8	+110.0

4.3 Overview of marsh-estuarine organic carbon fluxes

Figure 45 summarizes the patterns of DOC and POC fluxes between the marsh and estuary under conditions of diminished river inflow into the Kariega estuary. Under these conditions, total organic carbon is exported from the marsh in pulses. These intermittent losses occur largely as DOC and POC, and occur when high elevation tides coincide with <u>westerly</u> winds (Figure 46*a*). These exports are not continuous

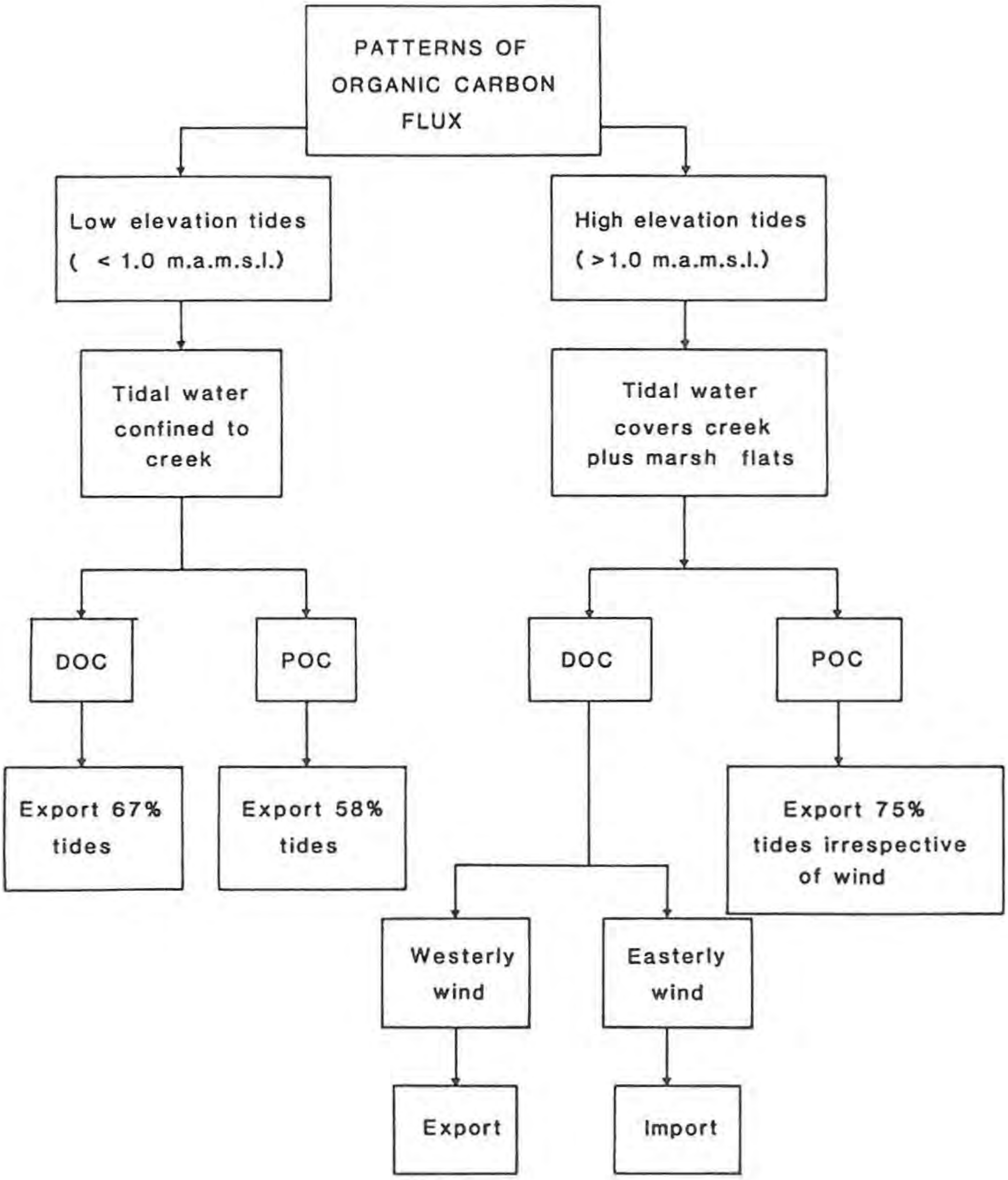
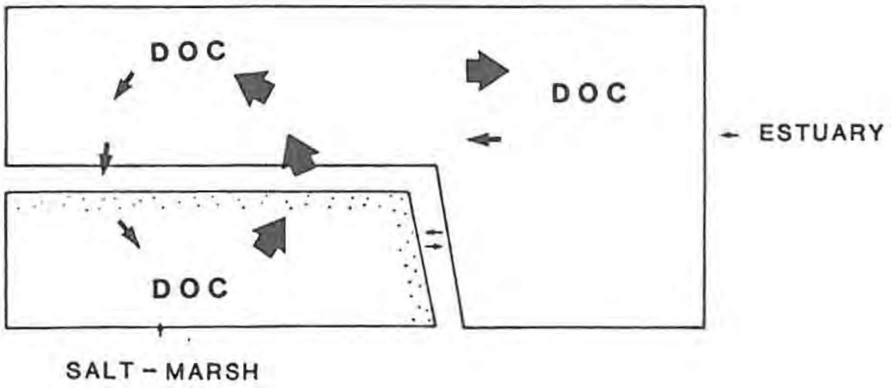


Figure 45 Summary of patterns of DOC and POC fluxes between the marsh and Kariega estuary.

(a) WESTERLY WINDS : Net export



(b) EASTERLY WINDS : Net import

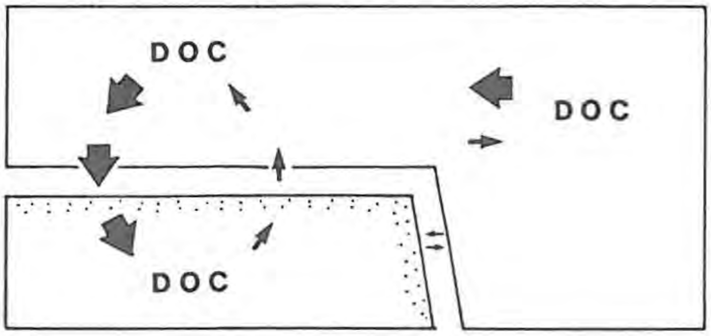


Figure 46 Schematic representation of the shift in the direction of DOC net flux from an export under conditions of westerly winds (a) to an import during periods coincident with easterly winds (b).

because, during periods when high elevation tides coincide with easterly winds, the exports of POC are compensated at least in part by DOC imports onto the marsh (Figure 46b). FOC is imported at most tides, but these fluxes are comparatively small and do not markedly alter the above pattern.

These patterns of fluxes of organice carbon are modified by storm events, which because the marsh is located in the middle reaches of the estuary, are derived from both oceanic and river sources. Data collected during this study provides information on the effects on the marsh-estuarine fluxes of organic carbon of both types of events.

The oceanic storm was a rare, 1 in 40 year event (Brundrit *et al.* in prep.), and involved a massive rise in daily mean sea level. Because it coincided with a spring-tide period, it resulted in exceptionally high tides inundating the marsh. These tides effected unusually large imports of all three organic carbon fractions onto the marsh (Figures 38, 41 and 42 respectively), largely because considerable quantities of estuarine water were retained in salt pans above the marsh (Appendix 2).

The effect of the river flood was small in comparison to that of the oceanic storm. Fluxes of DOC were not altered by the flood, but POC concentrations in the estuarine water were increased, and this provided the opportunity for tidal transport of this fraction onto the marsh.

CHAPTER 5

CARBON FLUXES AT THE MARSH-WATER INTERFACE, AND THE ROLE OF CRABS IN THESE TRANSFERS

The complexity of marsh-estuarine organic carbon fluxes, demonstrated in this study for a Sarcocornia marsh, and in the literature for Spartina marshes (reviewed by Nixon 1980), indicates the need to understand more fully the dominant processes responsible for regulation of these transfers. At each tide coastal water is brought into direct contact with the marsh biocoenosis, and the vertical exchanges across this interface, in combination with events in the water overlying the marsh, will determine material exchanges between the marsh and estuary. This chapter concerns processes at the marsh-water interface, and more specifically, the fluxes of organic carbon at this interface, and the effects of brachyuran crabs on these transfers.

5.1 DOC and POC fluxes

The contrasted structure and hydrodynamics of the tidal creek and salt-marsh flats (Chapters 2 and 3), and the different patterns of DOC fluxes effected by low and high elevation tides (Chapter 4), suggested that the patterns of organic carbon fluxes at the marsh surface were different in the two regions. This is important because tides inundate these regions to widely varying extents, and zonal differences in patterns of fluxes may therefore account, at least in part, for the marked temporal variability of the organic carbon fluxes observed at the marsh-estuarine junction (Chapter 4). These regions also constitute different proportions of the areas of salt-marshes investigated in the literature (Welsh 1980), which may provide an explanation for the frequently pronounced differences in patterns of fluxes observed between marshes. The first aim of this section was to compare the organic carbon fluxes in the tidal creek and salt-marsh flats regions of the marsh. Because the Sarcocornia Zone is the largest zone within the salt-marsh flats, I have measured fluxes within this particular zone for comparison with those in the tidal creek.

The tidal creek and salt-marsh flats are also inhabited by extremely large, and contrasted crab populations (Chapter 1). The mean density and biomass of Cleistostoma edwardsii, which inhabits the tidal creek, was 390 ± 130 individuals m^{-2} and 3.8 ± 0.6 g (ash-free) m^{-2}, respectively. For Sesarma catenata, which lives on the salt-marsh flats, the equivalent values were 50 ± 10 individuals m^{-2} and 8.7 ± 1.0 g (ash-free) m^{-2}. Although bioturbation by macrofauna is known to exert an important influence on sediment-water nutrient fluxes, most of the literature concerns benthic infauna (e.g. Yamada and Kayama 1987), and virtually no information is available on this aspect of either epifauna in general, or salt-marsh fauna in particular (whether epi- or infauna). There is also no information on the effects of macrofauna on fluxes of organic carbon from either salt-marsh or benthic sediments. Consequently, the second objective of this section was to determine the influence of the dominant crab species, namely S. catenata and C. edwardsii, on organic carbon fluxes at the marsh-water interface.

Materials and methods

Experimental design

Four experiments were conducted using laboratory mesocosms of the *Sarcocornia* and tidal creek zones of the marsh (Figure 47). A synopsis of these experiments, and the null hypotheses they were used to test, are presented in Table 6. Because of the environmental variability of intetidal regions, such as salt-marshes, a laboratory as opposed to an *in situ* experimental approach was employed.

Experiment 1 measured the net flux of organic carbon in mesocosms of the *Sarcocornia* Zone, incubated with and without *S. catenata*, under simulated *winter* temperature and photoperiod conditions. Experiment 2 was also conducted under winter conditions, but concerned exchanges in tidal creek mesocosms, incubated with and without *C. edwardsii*. Experiments 3 and 4 were equivalent to Experiments 1 and 2, but were conducted under *summer* conditions. Experiments 1 and 2 were implemented during ambient winter, and Experiments 3 and 4 during ambient summer.

The results were used to test the following null hypotheses.

H1. Net exchanges of DOC and POC are the same in the tidal creek and *Sarcocornia* zones of the marsh (ZONE).

H2. Net exchanges of DOC and POC are the same in mesocosms with and without crabs (CRABS).

H3. Net exchanges of DOC and POC are the same at successive tides over semi-lunar periods of marsh inundation (TIDE).

H4. Net exchanges of organic carbon are the same under summer and winter conditions (SEASON).

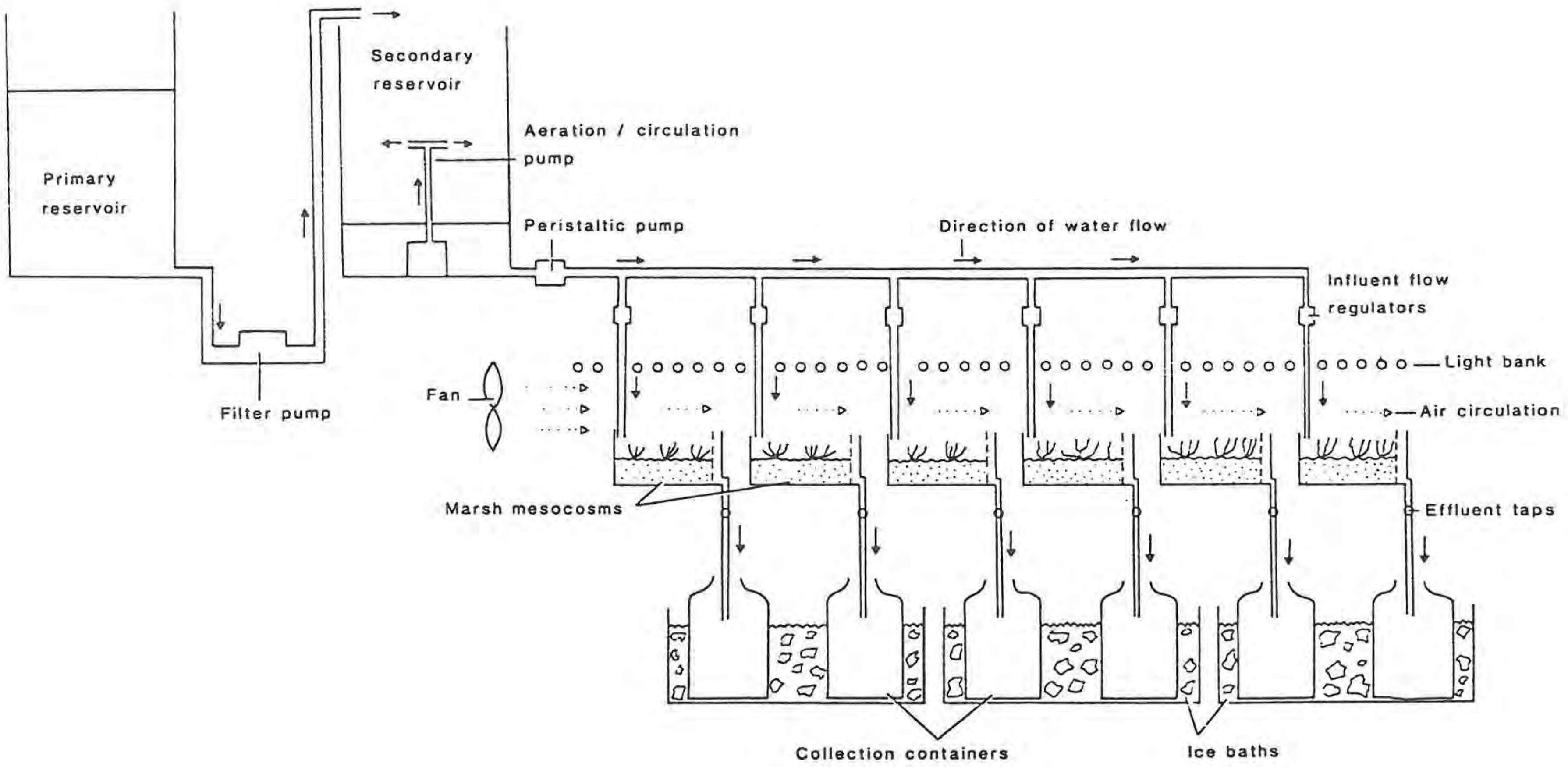


Figure 47 Laboratory mesocosms and tidal simulation system used in Experiments 1 - 4.

Table 6. Summary of mesocosm experiments used to test null hypotheses, H1-H4. Details of experiments and hypotheses are given in text.

Experiment number	Zone	Crab species	Components monitored	Temperature conditions (± S.D.)	Null Hypotheses tested			
1	*Sarcocornia* Zone	*S. catenata*	DOC, POC	Winter 16±0.7°C	H2 (CRABS) H3 (TIDE)	H1 (ZONE)	H4 (SEASON)	
2	Tidal creek	*C. edwardsii*	DOC, POC	Winter 16±0.7°C	H2 (CRABS) H3 (TIDE)			H4 (SEASON)
3	*Sarcocornia* Zone	*S. catenata*	DOC, POC	Summer 23±0.9°C	H2 (CRABS) H3 (TIDE)	H1 (ZONE)		
4	Tidal Creek	*C. edwardsii*	DOC, POC	Summer 23±0.9°C	H2 (CRABS) H3 (TIDE)			

A multifactorial analysis was used to test for the effects of zone (ZONE), presence of crabs (CRABS), tide sequence (TIDE), and season (SEASON).

Experimental procedures

In each experiment six intact sediment blocks (0.3 m wide, 0.3 m long and 0.1 m tall), with their associated macrophyte and invertebrate assemblages, were removed from the salt-marsh at low tide, and fitted into plastic baths 0.3m wide, 0.4 m long and 0.2 m high. The free margin of each block, located adjacent to the drainage or effluent port, was supported by a perforated perspex panel to prevent collapse of the sediment block.

The blocks collected from the *Sarcocornia* Zone for Experiments 1 and 3 were extracted at an elevation of 1.0 m.a.m.s.l., and those from the tidal creek for use in Experiments 2 and 4, from the marsh at 0.8 m.a.m.s.l. These sites were selected because they support mean densities and biomasses of the respective crab species (Table 2).

Sediment blocks were collected in the middle of semi-lunar spring-tidal periods to synchronize the tidal regime in the laboratory with that in the field. This synchrony was necessary because crab activity patterns are known to be coupled with tidal rhythms (e.g. Williams *et al*. 1985).

Following collection, the mesocosms were returned to the laboratory, and incubation initiated within two hours. Crabs were removed from all mesocosms on the first day of incubation, and the mesocosms flooded twice daily for the first four days. This served as an equilibration period during which a constant or base-line condition was established in the mesocosms. On Day 3, the mean number of crabs, of mean individual biomass, were introduced to the first, third and fifth mesocosms. Crabs were collected at the sites of sediment collection less than two hours before their transfer to mesocosms. The second, fourth and sixth mesocosms were incubated without crabs and served as controls.

After the four-day equilibration period the mesocosms were subjected to a "neap-tide" period of exposure, or non-flooding, followed by a "spring-tide" period during which the mesocosms were flooded twice a day. The *Sarcocornia* mesocosms, were subjected to neap and spring periods of 9 and 5 days respectively, and the tidal creek mesocosms to neap and spring phases of 6 and 8 days. These regimes were determined from 12-month water-level recordings monitored at the marsh-estuarine junction.

The mesocosms were arranged in rows (Figures 48 and 49) below two light banks fitted with sodium and halogen lamps. Incident photosynthetically active radiation, measured at the sediment surface using a Lambda Instruments LI-185 light meter, was 92 ± 4.3 (*S.D*) $\mu E\ m^{-2}\ s^{-1}$, *n* = 15. This value is only slightly lower than the levels reported to cause light saturation of photosynthesis in epibenthic algae (ca. 100 $\mu E\ m^{-2}\ s^{-1}$ Rasmussen *et al*. 1983). Air between the light banks and mesocosms was exchanged using fans to prevent overheating.

Temperatures at the marsh surface in the mesocosms were maintained at 16(±0.7) °C and 23(±0.9) °C for the winter and summer experiments,

Figure 48 Laboratory mesocosms and tidal simulation system. 1 Primary reservoir, 2 Filter pump, 3 Secondary reservoir, 4 Circulation manifold, 5 Influent flow regulators, 6 Light bank, 7 Mesocosms of the Sarcocornia Zone, 8 Effluent pipes, 9 Collection containers in ice.

Figure 49 Laboratory mesocosms of the marsh below light banks. Notations as for Figure 48.

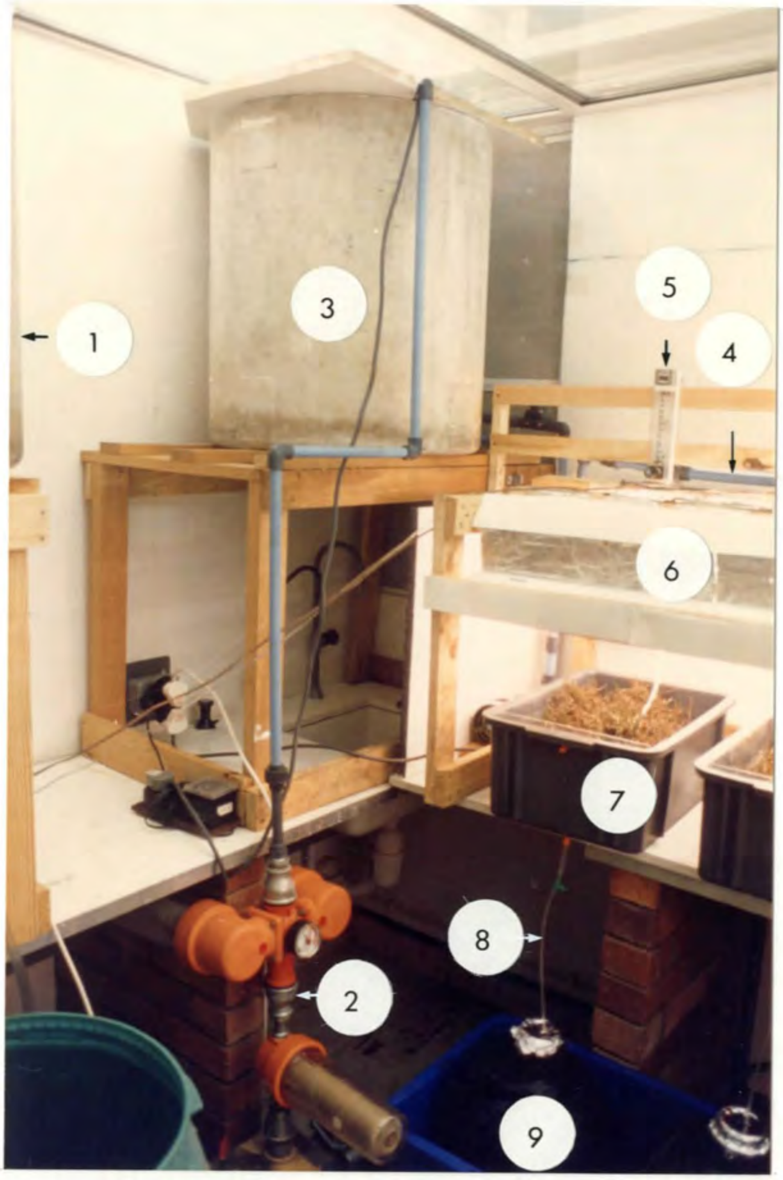
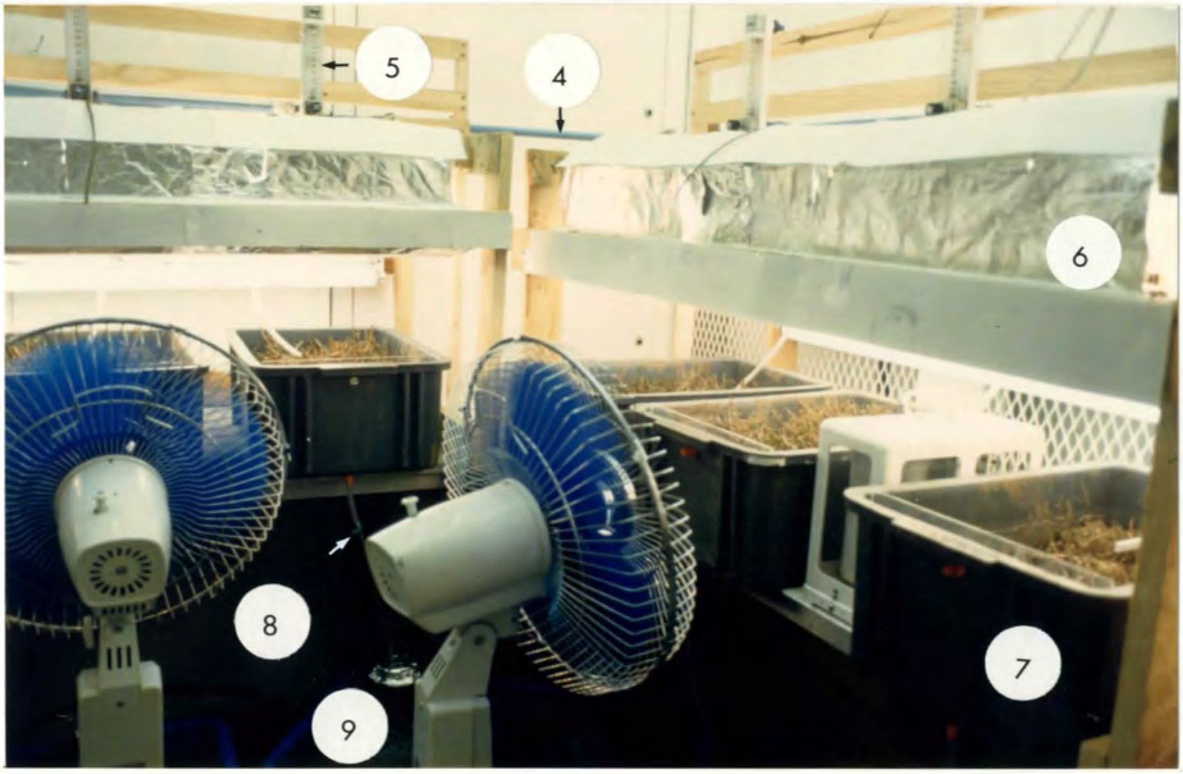


Figure 48

Figure 49



respectively. These temperatures were equal to the mean weekly temperatures recorded at an elevation of 1.07 m.a.m.s.l. (Station 1) in the lower reaches of the marsh, during the winter (May, June, July, August) and summer (November, December, January, February) months of 1984-1985 (Figure 13).

In the winter and summer experiments, mesocosms were exposed to dark:light photoperiods of 14:10h and 10:14h, respectively. These ratios are mean winter and summer values calculated from published Tables of Sunrise and Sunset (In: South African Tide Tables 1987, details in References).

Mesocosms were flooded with estuarine water collected at high-tide from the Kariega estuary at a jetty located opposite the marsh. Water was collected on alternate days, and stored in the dark at 5 °C until required, a period always less than 36h.

Eight hours before each simulated tide 60 dm^3 estuarine water was pumped into the secondary reservoir tank (Figure 47). The pump used was fitted with a 100 µm filter to remove coarse particles, and so reduce variability of estimates of material inputs into mesocosms. For two hours before inundation, water in the reservoir was thoroughly circulated using a bilge pump with attached fine-bore nozzle. Storage and treatment for this period ensured thermal equilibration and oxygen saturation of flood-water, which was then fed via a manifold into the mesocosms. Flow was regulated at 0.30 $dm^3\ min^{-1}$, using Gapmeter Type GT flow meters (Figures 47 to 49). At each tide duplicate water samples for chemical analyses were collected from the influent piping, while the mesocosms were being flooded.

Sarcocornia Zone and tidal creek mesocosms were inundated with water for 125 and 200 minutes, respectively. These periods included 30 minutes required for complete inundation of the sediment/macrophyte blocks, and 30 minutes necessary for drainage of the mesocosms. Duration of inundation was determined from the 12-month continuous water level records measured at the marsh-estuarine junction. The flood-waters were drained via narrow (2.0 mm internal diameter) plastic tubes; the bore of these tubes matched the requirements of marsh drainage.

The effluent water was collected in acid-cleaned glass bottles placed in ice-filled, black polyethylene bags. Duplicate water samples were taken from each of the collection bottles, immediately after completion of drainage. One of the duplicate influent and effluent samples were filtered through ashed, pre-rinsed Whatman GF/F filter paper and the filtrate used for determination of DOC concentrations. The filtered and unfiltered samples were stored at $-15\,^{o}C$ in the dark until analysis. The analytical techniques were as described in Chapter 3.

The areal net flux of each component, at each tide, and for each mesocosm, was computed as:

$$\underline{F}_{\underline{m}} = ([\underline{O}] - [\underline{I}])\underline{V} / \underline{A} \qquad (9)$$

where $\underline{F}_m$ = mesocosm areal net flux (µg m^{-2} $tide^{-1}$);

$[\underline{I}]$ = concentration in flood or influent water (µg dm^{-3});

$[\underline{O}]$ = concentration in ebb or effluent water (µg dm^{-3});

$\underline{V}$ = volume of water drained from mesocosm (dm^3), and

$\underline{A}$ = area of top of sediment block (m^2).

Implicit in this computation is the assumption that the volumes of water entering and leaving the mesocosm are the same. This assumption was checked, and retention of water by the marsh biocoenosis found to be between 2 and 8% of flood-water volume (P. Scott per. comm.). This was considered sufficiently small to validate the above assumption.

Statistical procedures

Analysis of Variance (ANOVA) was used to analyze the results of the mesocosm experiments. ANOVA was computed using the statistical package $SPSS^x$ (after Nie 1983). My interpretation of the ANOVA results has been based on Underwood's (1981) review of ANOVA and its application to experimental marine ecology.

To test for major deviations of the data from normality, data corrected for within-treatment means, were compared with superimposed normal distribution curves. This subjective procedure was considered adequate because only very skewed distributions affect the significance of the $\underline{F}$ - test of Analysis of Variance (Underwood 1981).

Homogeneity of variances within treatments was checked using Hartley's $\underline{F}$ - max and Cochrane's $\underline{C}$ tests (computed according to Nie (1983), and no correction for this potential source of error was necessary.

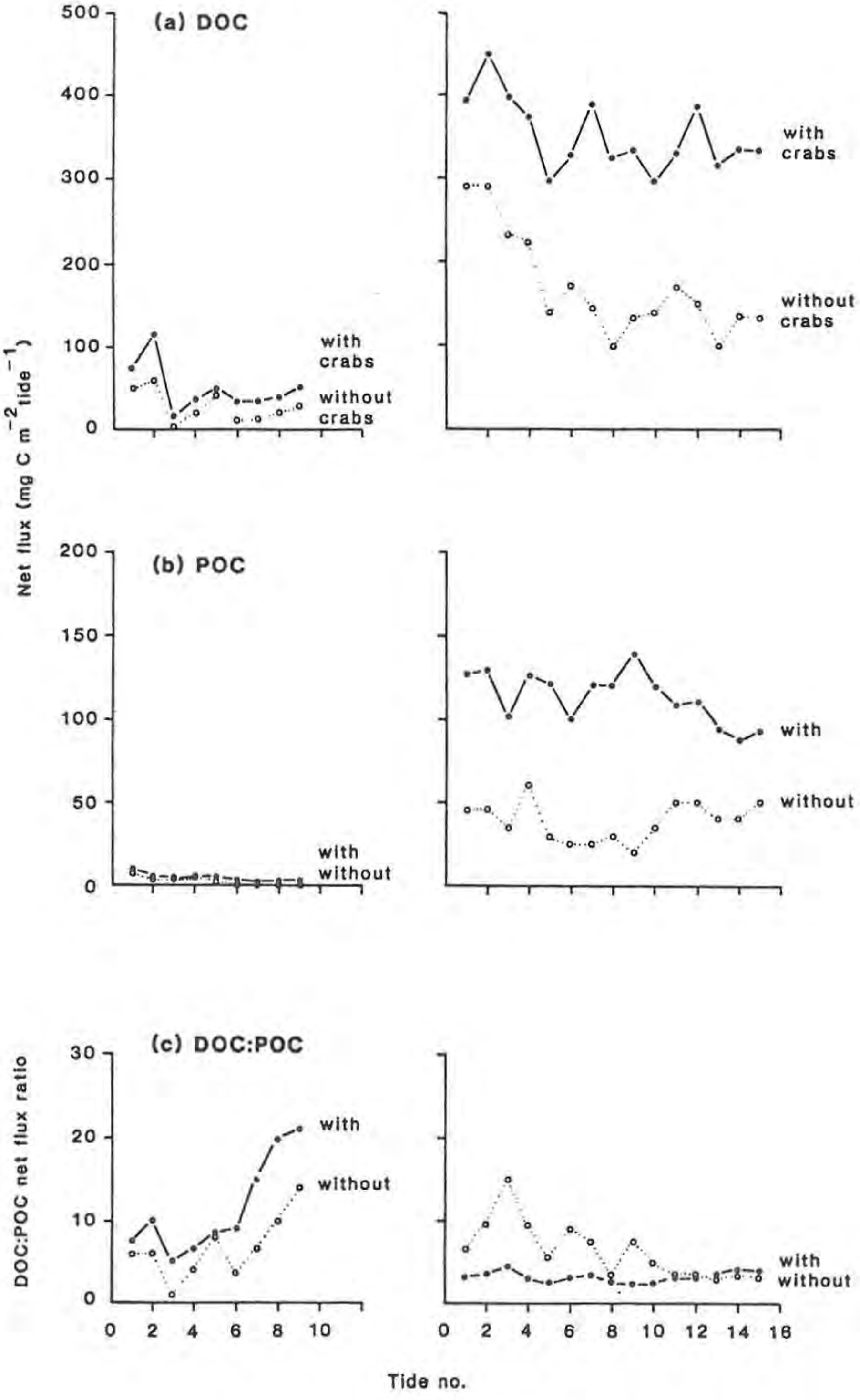
In certain isolated instances estimates of the net flux of material were not available for particular mesocosms at certain tides. For purposes of statistical testing, these missing values, of which there were 15, were replaced with "cell" means to make cell size uniform.

Results

Figures 50 and 51 compare the net fluxes (F_m) of DOC, POC and the ratio of the two, from mesocosms of the *Sarcocornia* and tidal creek zones under simulated winter (Experiments 1 and 2) and summer conditions (Experiments 3 and 4). Each panel shows the mean net flux per tide (n = 3) for mesocosms with (solid lines) and without (dotted lines) crabs, over a simulated semi-lunar period of inundation. Results of the four-way ANOVA's of these data are presented in Tables 7 and 8.

In both zones, the net fluxes of DOC and POC were directed from the marsh surface to the overlying water, at all tides, in both seasons, and whether crabs were present or not. The fluxes of both components were influenced by marsh zone (ZONE), presence of crabs (CRABS), and season (SEASON); as indicated by the highly significant *F*-tests of MAIN EFFECTS in Tables 7 and 8 ($P > 0.001$ in all cases). Fluxes of DOC also varied significantly with tide sequence (TIDE, $P > 0.001$, Table 7). Consequently, the null hypotheses H1, H2 and H4 can be rejected for both DOC and POC, and H3 for DOC. The significant *F*-tests of INTERACTION EFFECTS show that the effects of zone, crabs and season are each dependent on the other two factors (Tables 7 and 8).

Figure 50 Comparison of winter tidal net fluxes of DOC (a), POC (b) and the ratio of the two (c), in laboratory mesocosms of the *Sarcocornia* (left) and tidal creek (right) zones of the marsh. Each point represents the mean (*n*=3) net exchange per tide, for either the mesocosms with crabs (solid) or those without (dotted). Successive semi-diurnal tides were monitored over a simulated semi-lunar, spring-tidal cycle.


(a) DOC
500
400
300
200
100
0
with crabs
without crabs
with crabs
without crabs
Net flux (mg C m^{-2} tide^{-1})
(b) POC
200
150
100
50
0
with
without
with
without
(c) DOC:POC
30
20
10
0
with
without
with
without
DOC:POC net flux ratio
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2
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Tide no.

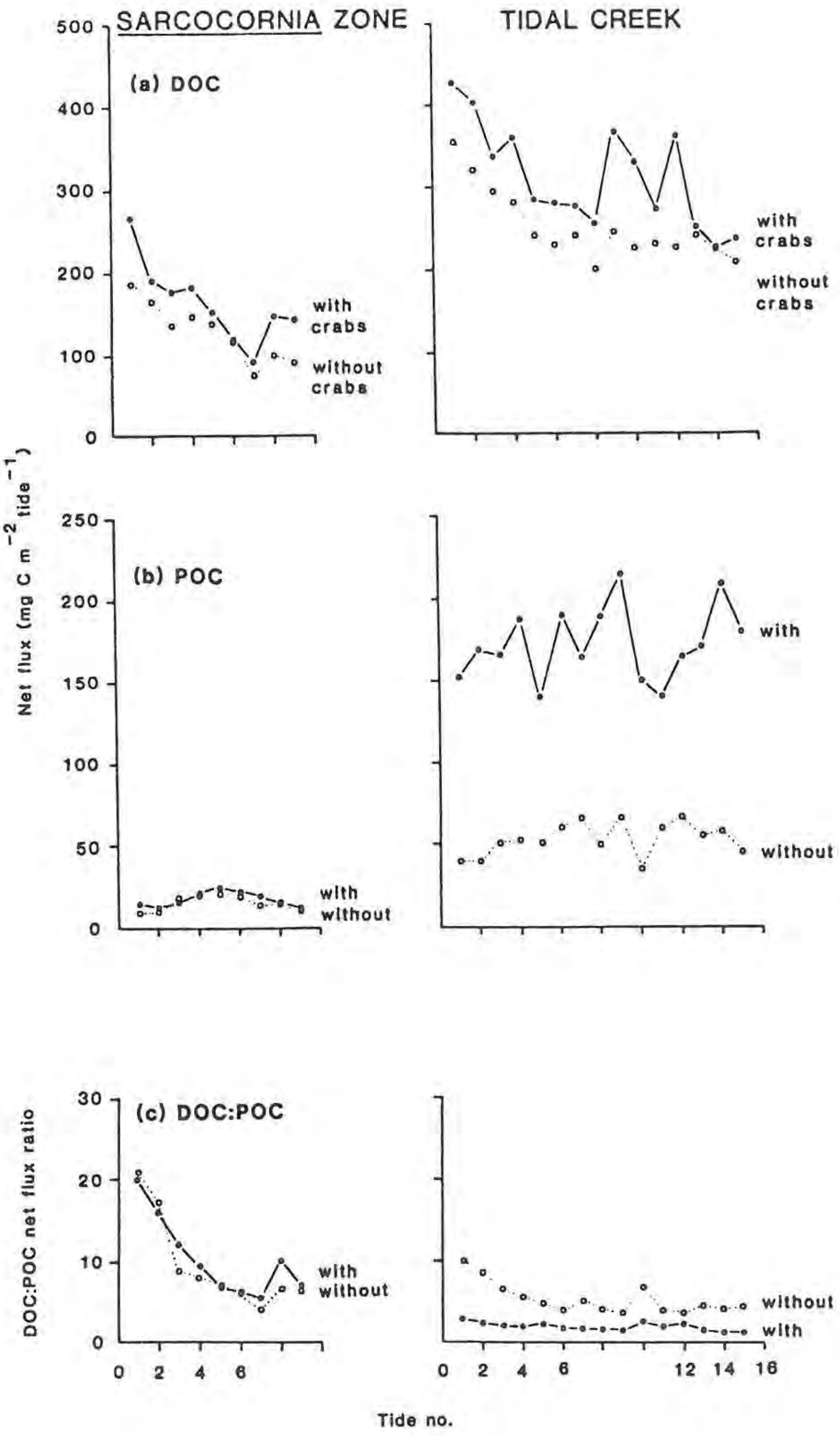


Figure 51 Comparison of summer tidal net fluxes of DOC (a), POC (b), and the ratio of the two (c), in laboratory mesocosms of the *Sarcocornia* and tidal creek zones. Details as for Figure 50.

Table 7. DOC. Four-way ANOVA table of results of Experiments 1-4, conducted to test the effects of tide sequence (TIDE), presence/absence of crabs (CRABS), season (SEASON), and marsh zone (ZONE) on DOC net fluxes at the marsh-water interface. Levels of significance of *F*-test: *** $P>0.001$, ** $P>0.01$, *$P>0.05$.

SOURCE OF VARIATION	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARE	*F*	SIGNIFICANCE OF *F*
MAIN EFFECTS					
TIDE	344246.795	8	43030.849	5.280	***
CRABS	239653.459	1	239653.459	29.406	***
SEASON	165535.260	1	165535.260	20.311	***
ZONE	2256535.142	1	2256535.142	276.881	***
2-WAY INTERACTIONS					
TIDE X CRABS	35499.277	8	4562.410	.560	
TIDE X SEASON	38427.657	8	4803.457	.589	
TIDE X ZONE	92610.667	8	11576.333	1.420	
CRABS X SEASON	17016.925	1	17016.925	2.088	
CRABS X ZONE	77907.615	1	77907.615	9.559	**
SEASON X ZONE	136534.335	1	136534.335	16.753	***
3-WAY INTERACTIONS					
TIDE X CRABS X SEASON	45850.544	8	5731.318	.703	
TIDE X CRABS X ZONE	32364.963	8	4045.620	.496	
TIDE X SEASON X ZONE	57728.107	1	7216.013	.885	
CRABS X SEASON X ZONE	27603.645	1	27603.645	3.387	*
4-WAY INTERACTIONS					
TIDE X CRABS X SEASON X ZONE	38453.800	8	4806.725	.590	
EXPLAINED	3606968.190	71	50802.369	6.234	***
RESIDUAL	1173577.107	144	8149.841		
TOTAL	4780545.297	215	22235.094		

Table 8. *POC*. Four-way ANOVA table of the results of Experiments 1-4, conducted to test effects of tide sequence (TIDE), presence of crabs (CRABS), season (SEASON), and marsh zone (ZONE) on POC net fluxes at the marsh-water interface. Levels of significance of *F*-tests: *** $P>0.001$, ** $P>0.01$, $P>0.05$.

SOURCE OF VARIATION	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARE	*F*	SIGNIFICANCE OF F
MAIN EFFECTS					
TIDE	3425.220	8	428.152	1.043	
CRABS	154505.330	1	154505.330	376.324	***
SEASON	29124.150	1	29124.150	70.937	***
ZONE	384648.780	1	384648.780	936.878	***
2-WAY INTERACTIONS					
TIDE X CRABS	2574.015	8	321.752	.784	
TIDE X SEASON	6193.839	8	774.230	1.886	
TIDE X ZONE	4458.436	8	557.305	1.357	
CRABS X SEASON	5128.988	1	5128.988	12.493	***
CRABS X ZONE	145239.635	1	145239.635	353.756	***
SEASON X ZONE	6510.371	1	6510.371	15.857	***
3-WAY INTERACTIONS					
TIDE X CRABS X SEASON	1026.829	8	128.354	.313	
TIDE X CRABS X ZONE	2193.002	8	274.125	.668	
TIDE X SEASON X ZONE	3043.709	8	380.464	.927	
CRABS X SEASON X ZONE	4315.249	1	4315.249	10.511	***
4-WAY INTERACTIONS					
TIDE X CRABS X SEASON X ZONE	1310.877	8	163.860	.399	
EXPLAINED	753698.429	71	10615.471	25.856	***
RESIDUAL	59121.268	144	410.564		
TOTAL	812819.697	215	3780.557		

Table 9 compares the mean net fluxes, calculated for all tides combined, in mesocosms of the two zones, incubated with and without crabs. The mean net fluxes of DOC and POC were greater from the tidal creek than from the *Sarcocornia* Zone, in both seasons and whether crabs were present or not (compare Δ_{ZONE} in Table 9). However, as shown by the result of the Analysis of Variance, the differences between the two zones depended on the presence of crabs, and on season (ZONE x SEASON x CRABS interaction, *P* > 0.001, in Table 7).

Table 9. Comparison of mean net fluxes of DOC and POC for all tides combined (mgC m^{-2} h^{-1}, ±95% C.L., *n* = 26 for *Sarcocornia* Zone and 44 for tidal creek). Also shown are differences in mean net fluxes between zones (Δ_{Zone}) and between mesocosms with and without crabs (Δ_{Crabs}).

	DOC			POC		
	Sarcocornia Zone	Tidal creek	Δ_{Zone}	*Sarcocornia* Zone	Tidal Creek	Δ_{Zone}
Winter:						
With crabs	25 ± 7	118 ± 6	93	3 ± 1	38 ± 3	35
Without crabs	14 ± 4	63 ± 16	49	2 ± 1	13 ± 2	11
Δ_{Crabs}	11	55		1	25	
Summer:						
With crabs	81 ± 12	104 ± 8	23	9 ± 1	57 ± 1	48
Without crabs	65 ± 8	83 ± 6	19	8 ± 1	17 ± 1	9
Δ_{Crabs}	17	21		1	40	

Both species of crabs enhanced the fluxes of organic carbon from the marsh surface (compare Δ_{CRABS} values in Table 9). However, the effects of the crabs were different in the two zones, and varied interactively with season. The enhanced losses of DOC and POC attributable to the presence of *S. catenata* (Δ_{CRABS}) were small. The differences in mean net fluxes for mesocosms with and without *S. catenata* were not significantly different from zero (Table 9).

However, comparison of means in this situation is misleading, because the variability between successive tides was large relative to the effects of the crabs. Two-way ANOVA's of fluxes from mesocosms with and without *S. catenata* over successive tides, and computed separately for the two seasons, showed that in both seasons the fluxes of DOC ($P > 0.01$), but not POC ($P < 0.05$), were significantly different in the presence of these crabs. These data in combination, show that although the enhanced fluxes of DOC attributable to *S. catenata* were small, they were significant.

The losses caused by *C. edwardsii* were larger, than those caused by *S. catenata* and were different under winter and summer conditions (c.f. *S. catenata*). The losses of DOC attributable to *C. edwardsii* were larger in winter than summer, but the opposite applied to the fluxes of POC. This seasonal effect of *C. edwardsii* on the fluxes of the two components may be a consequence of rapid microbially-mediated conversion of DOC to POC in the tidal creek sediments under summer conditions, and then resuspension of this POC by the crabs.

5.2 Biologically-mediated gaseous carbon exchanges

The larger losses of organic carbon from the tidal creek than from the Sarcocornia Zone suggested the combined rates of production and deposition of organic carbon were greater, relative to the rates of organic carbon mineralization, in the tidal creek than in the Sarcocornia Zone. This is surprising in view of the dense macrophyte meadows on the salt-marsh flats, their absence from the tidal creek, and the general view of salt-marshes as macrophyte-based ecosystems (e.g. Field 1983). It does, however, point to the importance of salt-marsh substrata, as opposed to macrophytes, in regulation of organic carbon fluxes at the interface of the marsh and water column. Velimirov (1986) has recently demonstrated that rates of organic carbon release in bell-jars, which enclosed sediments of a seagrass system, greatly exceeded (by factors of 1.5 to 30) the rates in bell-jars which enclosed sediments plus seagrass plants.

This information, in combination, led me to extend the study to examine the productivity of the surface sediments of the marsh, and to ask the following questions: (a) what are the rates of epibenthic carbon fixation and respiration on the marsh; (b) are they different in the tidal creek and Sarcocornia zones; and (c) are the ratios of the rates of epibenthic production:respiration different in the two regions?

This section also examines the influence, if any, of crabs on the rates of these metabolic process in the surface marsh sediments. As demonstrated in the previous section, crabs increase the fluxes of reduced carbon, as organic carbon, from the marsh surface. However, they may also enhance carbon losses from the marsh biocoenosis by increasing rates of organic carbon mineralization, and loss of carbon as CO_2 and HCO_3. Potentially this may occur in two ways: directly by their own respiration, and indirectly by increasing the respiration rates of the sediment micro- and meiofauna.

Crabs may also alter the rates of epibenthic carbon fixation. Several studies have documented mechanisms of positive feed-back from consumers to epibenthic algae, including nutrient excretion, increased turnover rates and mechanical disruption of the sediment surface by consumers (e.g. Hargrave 1970, Owen and Wiegert 1976). Other studies have documented no positive feed-backs (e.g. Pace *et al.* 1979), where consumers have simply reduced the biomass and productivity of the epibenthic algae.

Epibenthic *P*:*R* ratios

Materials and methods

Rates of epibenthic photosynthesis and respiration were measured using sediment samples collected at the start and end of Experiments 3 and 4. Sediments were sampled by sectioning the surface 3 mm layer from extruded sediment cores of diameter 100 mm. Prior to Experiments 3 and 4, six cores were collected in the field immediately adjacent to completion of the sites at which the mesocosm blocks were removed. After the mesocosm experiments, two cores were collected in the laboratory from each of the mesocosms. Core samples from the mesocosms with and without crabs were pooled separately. Sediment samples were stored in plastic bags at 5 °C in the dark until determination of the oxygen exchange rates, a period always less than 12h.

Sediment oxygen uptake rates were measured using a Gilson Single Valve Differential Respirometer. The techniques were based on those of Umbreit et al. (1972). 2.0 ml sediment samples were transferred using autoclaved syringe corers from each pooled sediment sample to five 18 ml "experimental" flasks. Each flask contained 2.0 ml estuarine water, which had been filtered using pre-washed Whatman GF/F filter papers, and then autoclaved. The contents of these flasks were mixed for 30s using sterile glass rods. Two "control" flasks were employed for each series of five experimental flasks, and each control flasks contained 4.0 ml pre-filtered, autoclaved estuarine water but no sediments. The central wells of both sets of flasks contained $200 mm^2$ fluted Whatman's No.1 filter paper soaked in 0.3 ml 10% KOH for removal of CO_2. Reference vessels were filled with 6.3 ml 0.01% mercuric chloride solution in distilled water, leaving a gas volume equal to that in the reaction flasks.

During incubation, flasks were shaken horizontally at a rate of 65 traverses per minute (amplitude of each shake, 275 mm). Flasks were incubated at $22 \pm 1\ ^\circ C$, which is not significantly different from the "summer" incubation temperature of 23 °C employed in Experiments 3 and 4 (Section 5.1). Incubation lasted 11 hours, with the first 15 minutes allowed for thermal equilibration prior to valve closure and isolation of the individual manometers. This was followed by a three-hour stabilization period, which was necessary because initial oxygen consumption rates decreased rapidly, and took this long to stabilize.

Readings which represent total oxygen uptake were recorded hourly for a further four hours. 0.5 ml 1% mercuric chloride was then added to each flask as a metabolic inhibitor, and after 15 minutes equilibration, volume changes equivalent to chemical consumption were noted hourly for a further four hours. Biological oxygen consumption rates were determined by difference.

Precise interpretation of "biological" and "chemical" oxygen uptake rates partitioned using metabolic inhibitors is difficult (discussed further by Dale 1978, Hargrave and Phillips 1981). For many sediments, particularly those with anaerobic substrata, measurements of aerobic respiration as biological oxygen consumption will seriously underestimate rates of organic carbon mineralization (Jones and Simon 1981). However, the surface sediments of the *Sarcocornia* marsh were oxidized with E_h values in excess of +350 mV (Chapter 1). In sediments with these redox values, aerobic respiration with oxygen as the major terminal electron acceptor is the dominant respiratory pathway (Sorensen *et al*. 1979). Therefore, biological oxygen uptake was considered a meaningful measure of community respiration for these sediments.

Rates of epibenthic net photosynthesis, NP, were determined in the same way as rates of community respiration, except that the flasks were incubated in the light (at a light intensity of 90 µE m^{-2} s^{-1}) for 8h, and the oxygen exchange values were not partitioned into biological and chemical components. Rates of epibenthic gross photosynthesis, GP, were determined by adding estimates of "dark" oxygen uptake to estimates of "light" oxygen production, which were measured in parallel treatments.

The oxygen exchange rates were converted to carbon equivalents using a factor of 0.32. Chlorophyll a, corrected for phaeophytin degradation products, and determined according to Sartory (1985), was used as an index of epibenthic algal biomass.

Results

Table 10 summarizes the mean rates of respiration and net and gross photosynthesis, and the chlorophyll a contents of the surface sediments of the Sarcocornia and tidal creek zones.

The pre-incubation values show that community respiration rates were significantly higher in the Sarcocornia Zone than in the tidal creek, and that the opposite applied to rates of epibenthic GP. The differences were such that the ratios of gross photosynthesis:respiration (P:R)were greater in the tidal creek than in the Sarcocornia Zone. The chlorophyll a contents prior to incubation were almost twice as high in the tidal creek than in the Sarcocornia Zone, and microscopic examination showed that the micro-algae in both zones were predominantly pennate diatoms.

In the Sarcocornia Zone, sediment respiration rates measured after the spring-tidal period of inundation were not significantly different from those measured before (Table 10). The rates were also similar in mesocosms with and without crabs, which shows that S. catenata had no significant effect on epibenthic rates of organic carbon mineralization in this region. In contrast, in the tidal creek the epibenthic respiration rates were significantly lower after incubation than before, and the post-incubation rates were lower in mesocosms with crabs than in

Table 10. Mean rates of respiration (*R*), and net (*NP*) and gross photosynthesis (*GP*), chlorophyll *a* contents, specific rates of *GP*, and *P*:*R* ratios of surface sediments of *Sarcocornia* and tidal creek zones, before and after laboratory incubation, with and without crabs. 95% *C*.*L*. are shown.

Species / Zone Treatment	*R*	*NP* (μgC 100mm^{-2} h^{-1})	*GP*	Chl *a* (μg 100mm^{-2})	Specific *GP* (μgC μg chl *a*$^{-1}$ h^{-1})	*P*:*R*
S. catenata / *Sarcocornia* Zone						
(a) Before incubation	4.0 ± 0.3 (*n* = 15)	1.1 ± 0.2 (*n* = 14)	5.1 ± 0.9 (*n* = 14)	9.4 ± 1.1 (*n* = 5)	0.5	1.3
(b) After incubation						
with crabs	4.5 ± 0.7 (*n* = 7)	-1.0 ± 0.6 (*n* = 7)	3.6 ± 0.8 (*n* = 7)	3.1 ± 0.4 (*n* = 5)	1.2	0.8
without crabs	4.9 ± 0.4 (*n* = 7)	1.6 ± 0.5 (*n* = 7)	6.5 ± 1.5 (*n* = 7)	8.2 ± 1.2 (*n* = 5)	0.8	1.3
C. edwardsii / tidal creek						
(a) Before incubation	2.7 ± 0.3 (*n* = 15)	8.3 ± 0.1 (*n* = 15)	11.0 ± 0.1 (*n* = 15)	18.4 ± 2.9 (*n* = 5)	0.6	4.1
(b) After incubation						
with crabs	1.4 ± 0.1 (*n* = 7)	3.0 ± 0.2 (*n* = 7)	4.5 ± 0.1 (*n* = 7)	5.4 ± 0.8 (*n* = 5)	0.8	3.2
without crabs	2.1 ± 0.1 (*n* = 6)	3.5 ± 0.1 (*n* = 6)	5.6 ± 0.1 (*n* = 6)	8.2 ± 2.5 (*n* = 6)	0.7	2.7

those without. This shows that C. edwardsii caused a significant reduction in the rates of sediment community respiration in the tidal creek.

Both crab species decreased the epibenthic rates of GP, as shown by the significantly lower post-incubation GP values in the with-crab mesocosms than in those without. The chlorophyll a concentrations were also significantly reduced, which suggests crab grazing pressure was responsible for the decline in rates of GP. Although both chloropyll a and GP were lower in mesocosms with crabs than in those without, the specific rates of GP were significantly higher in the with-crab mesocosms. Therefore, both species of crabs increased the photosynthetic efficiency of the epibenthic algae, possibly by acceleration of rates of turnover of nutrients and disruption of interstital nutrient microgradients (discussed further in Chapter 6).

Gross photosynthesis : respiration (P:R) ratios provide an index of rates of carbon fixation relative to rates of carbon mineralization, which is useful in interpretation of patterns of carbon fluxes at the marsh surface. Prior to incubation of the mesoscosms, epibenthic P:R ratios exceeded 1.0 in both zones, and were more than twice as great in the tidal creek than in the Sarcocornia Zone (Table 10). The epibenthic P:R ratios were altered by both species, but in different ways. In the Sarcocornia Zone, P:R ratios were lower in mesocosms with S. catenata than in those without, which is what might be expected as a consequence of the presence of a secondary consumer. In contrast, C. edwardsii increased the epibenthic P:R ratios in the tidal creek.

Crab respiration rates

Although epibenthic community respiration rates were not increased as a consequence of the presence of S. catenata and C. edwardsii, and were actually reduced by C. edwardsii, crabs are heterotrophic, and will therefore directly enhance rates of organic carbon mineralization at the marsh surface. The purpose of this section is to determine the respiration rates of these two crab species, and compare these rates with the rates of other pathways of carbon exchange at the marsh surface.

Materials and methods

The mass-specific respiration rates of S. catenata and C. edwardsii individuals, as oxygen uptake per unit ash-free dry mass, were determined manometrically using the Gilson Respirometer employed in the previous section. To enable meaningful comparison of estimates of carbon losses via respiration and bioturbation, crabs used to determine respiration rates were collected from mesocosms employed in Experiments 3 and 4, immediately after completion of the experiments.

Prior to the respiration measurements, crabs were equilibrated in pre-filtered (Whatman GF/F), autoclaved estuarine water at room temperature for two hours, to ensure gut clearance (Pattinson 1986). Crabs were then placed in 50 ml experimental flasks, which each contained 10 ml estuarine water treated as above. The central well of each flask contained 500 mm^2 fluted Whatman GF/C filter paper soaked in 1.5 ml 10% KOH, which served as a CO_2 trap. Control treatments were as for experimental treatments, except that they were incubated without crabs.

Experimental and control flasks were allowed to equilibrate for 15 minutes before valve closure, and changes in gas volume then monitored hourly for 3h. Flasks were incubated at 23 °C, which is the same temperature at which mesocosms were incubated in Experiments 3 and 4. Flasks were not shaken during incubation.

Rates of respiratory oxygen consumption were converted to carbon equivalents assuming respiratory quotients (*R.Q.*) of 0.71 and 1.0. Since *R.Q.* values vary depending on substrate (0.71 for lipid, 0.80 for protein, 1.0 for carbohydrate, Lampert, 1984), and the metabolic substrates of *S. catenata* and *C. edwardsii* on the marsh are unknown, it was considered necessary to compute the range of respiration rates using minimum and maximum *R.Q.* values.

Results

Table 11 compares the mean mass-specific respiration rates of *S. catenata* and *C. edwardsii*, expressed in terms of oxygen consumption, and its carbon equivalence. Assuming *R.Q.*'s of 0.71 and 1.0, the mean rates for *S. catenata* were between 514 and 731 x 10^{-3} mgC g^{-1} h^{-1}, respectively. The equivalent values for *C. edwardsii* were 229 and 325 x 10^{-3} mgC g^{-1} h^{-1}. Therefore, depending on metabolic base respired, the specific respiration rates of *S. catenata* exceeded those of *C. edwardsii* by factors of between 1.6 and 3.2.

Table 11. Mean specific respiration rates of *S. catenata* and *C. edwardsii* expressed in oxygen and carbon terms. 95% *C.L.* indicated.

Species	Mean ash-free dry mass per individual (g) ±95% *C.L.*	Oxygen consumption ($\times 10^{-3}$ mgO_2 g^{-1} h^{-1}) ±95% *C.L.*	CO_2 equivalence ($\times 10^{-3}$ mgC g^{-1} h^{-1}) ±95% *C.L.* assuming:		*n*
			R.Q. = 0.71	*R.Q.* = 1.0	
S. catenata	0.0907 ± 0.04	1372 ± 38	514 ± 14	731 ± 20	15
C. edwardsii	0.0157 ± 0.004	611 ± 27	229 ± 10	325 ± 14	19

The ash-free dry mass of S. catenata and C. edwardsii in the mesocosms of the respective zones were 6.5 and 0.6 g m^{-2}. Assuming a R.Q. of 0.71, the areal rates of organic carbon mineralization by S. catenata in the Sarcocornia mesocosms, and C. edwardsii in the mesocosms of the tidal creek were 3.3 and 0.14 mgC m^{-2} h^{-1}, respectively. Assuming a R.Q. of 1.0, the equivalent values were 4.8 and 0.2 mg C m^{-2} h^{-1}. In both cases the areal rates of carbon losses attributable to C. edwardsii respiration were less than 5% of those by S. catenata.

In both zones the crab respiratory losses of carbon were small in comparison to their effects on fluxes of organic carbon. For instance, the areal respiration rates of S. catenata and C. edwardsii amounted to only 28% and <1% of the crab-induced increases in TOC losses in the respective zones, namely 18 ± 4 and 21 ± 15 mgC m^{-2} h^{-1} (±95% C.L.) respectively.

5.3 Overview of carbon exchanges at the marsh surface

Figure 52 summarizes the transfers of carbon at the marsh-water interface in the Sarcocornia and tidal creek zones under summer conditions in the presence of crabs. In both zones, net fluxes of reduced carbon, as organic carbon, were directed from the marsh surface to the overlying water column. Mean net fluxes of TOC, for all tides combined, $\overline{F}_m$, were 360 mgC m^{-2} d^{-1} for the Sarcocornia Zone, and 966 mgC m^{-2} d^{-1} for the tidal creek. These values were calculated from data in Table 9, assuming tidal inundation twice a day, and periods of inundation of 2 and 3h per tide in the respective zones.

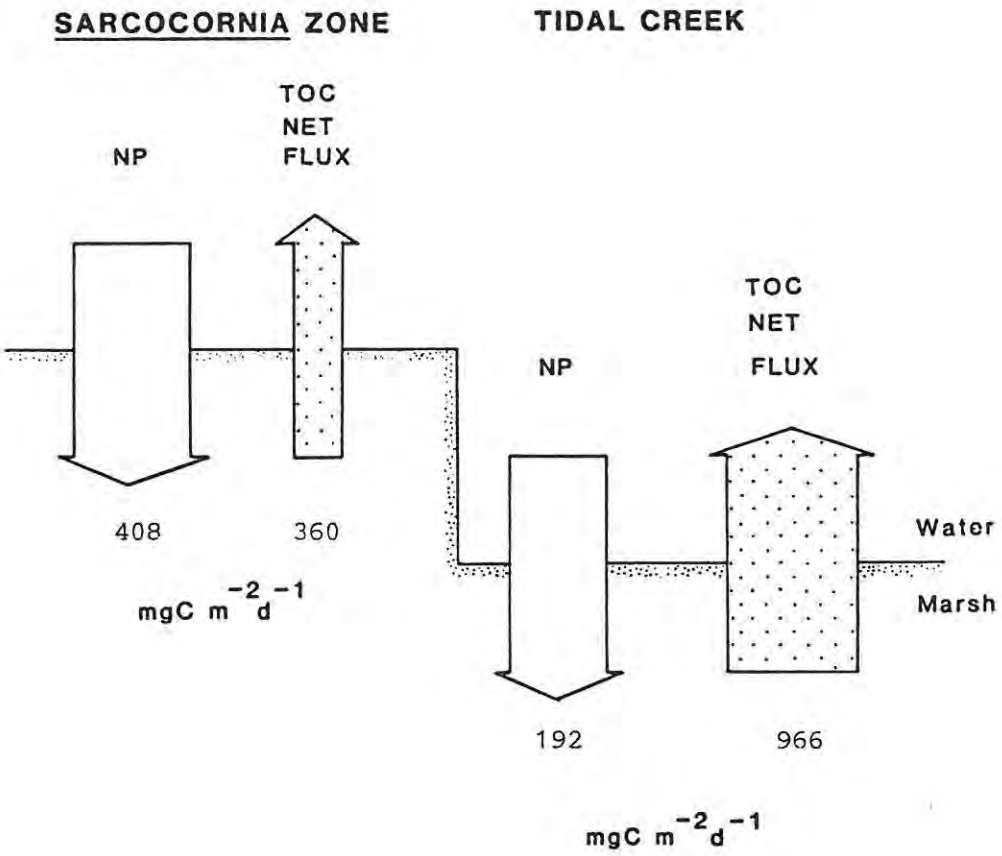


Figure 52 Summary of carbon transfers (mgC m^{-2} d^{-1}) at the marsh surface in the presence of crabs. Estimates of mean net fluxes of organic carbon, and rates of community net production were determined under summer conditions in mesocosm Experiments 3 and 4.

Both zones exhibited positive community net production values; i.e. rates of carbon fixation exceeded rates of respiratory organic carbon breakdown. In the Sarcocornia Zone, community NP (gross photosynthesis minus respiration) was 408 mgC m^{-2} d^{-1}. This was calculated by adding the NP rates of *S. perennis* (1068 mgC m^{-2} d^{-1} Christie 1981) to the epibenthis NP rates (-120 mgC m^{-2} d^{-1}), and subtracting night rates of epibenthic respiration (540 mgC m^{-2} d^{-1}). The epibenthic NP and respiration rates were calculated from the data in Table 10 assuming a 12h light:12h dark regime. In the tidal creek, community net production was 192 mgC m^{-2} d^{-1}; this was calculated by subtracting epibenthic dark respiration 168 mgC m^{-2} d^{-1} from epibenthic NP, 360 mgC m^{-2} d^{-1}

Two principal pathways of carbon net exchange can be identified at the marsh-water interface; namely transfers of gaseous carbon (methane excluded), which were directed from the water to marsh biocoenosis, and net fluxes of organic carbon, which were directed from the marsh to overlying water. Methanogenesis has been excluded from this budget because it is confined to very reduced sediments with E_h values <-150 mV (Ponnamperuma *et al*. 1966). Since the E_h values of the sediments of the Sarcocornia marsh were much higher than this (> +150 mV, Figure 10), the losses of carbon as methane were probably negligible.

In the Sarcocornia Zone the rates of community net production exceeded the TOC net fluxes but the opposite applied in the tidal creek; the net flux : NP ratios in the respective zones were 0.9 and 5.0. Therefore on a daily basis, and at least under summer conditions, the Sarcocornia Zone functioned as a carbon "sink", and the tidal creek as a carbon "source".

Reasons for the "excess carbon" in the tidal creek may include an organic carbon subsidy supplied by macrophyte below ground production in the adjacent salt-marsh flats. Agosta (1985) has recently documented lateral transfers of nutrients from sediments of the salt-marsh flats to those of the tidal creek in a Spartina marsh, and the same may apply to organic carbon in this Sarcocornia marsh. The elevated losses of organic carbon may also be a product of the experimental procedure employed. The rates of epibenthic photosynthesis were probably underestimated, as a result of the low light intensities employed during incubation (90 $\mu E\ m^{-2}\ s^{-1}$). Conversely, the organic carbon losses, from the coarse-grained sediments of the tidal creek were probably artificially high because of sediment disturbance during removal and transfer of the sediment blocks to the laboratory.

The presence of crabs exerted a marked influence on the patterns of carbon exchanges at the marsh-water interface. This occurred in two ways: by increasing the net fluxes of organic carbon, and by reducing the rates of community net production (Table 12). Both species enhanced the fluxes of TOC, probably as a consequence of bioturbation and excretion. This was particularly pronounced in the tidal creek, largely because of the increased losses of POC caused by C. edwardsii (Table 13). In contrast, S. catenata, lowered the rates of epibenthic

Table 12. Comparison of net fluxes of TOC, rates of community net production (*NP*), and the ratio of the two, in the *Sarcocornia* Zone and tidal creek in the presence and absence of crabs. Differences between mesosocms with crabs and without are denoted $\Delta_{\underline{\text{Crabs}}}$. Positive $\Delta_{\underline{\text{Crabs}}}$ values indicate increased fluxes, or ratios of fluxes, as a consequence of presence of crabs; negative values indicate decreased fluxes or ratios.

	TOC net fluxes (mgC m^{-2} d^{-1})		Community *NP* (mgC m^{-2} d^{-1})		Net flux : *NP*	
	Sarcocornia Zone	Tidal creek	*Sarcocornia* Zone	Tidal Creek	*Sarcocornia* Zone	Tidal creek
With crabs	360	966	408	192	0.9	5.0
Without crabs	288	612	672	168	0.4	3.6
$\Delta_{\underline{\text{Crabs}}}$	+72	+177	-264	+24	+0.5	+1.4

community net production at the marsh surface (Table 12). This occurred as a result of reduction of rates of epibenthic *GP*, as opposed to increased rates of epibenthic respiration (Table 13).

The present data show that both species were responsible for mobilization of carbon from the marsh surface relative to community net production. Net flux:*NP* ratios were between 1.4 and 2.2 fold larger (depending on the zone) in mesocosms with crabs than in those without (Table 12).

Table 13. Summary of the effects of *S. catenata* and *C. edwardsii* on exchanges of carbon at the marsh surface under summer conditions. 95% *C.L.* indicated. Positive values indicate enhanced losses as a consequence of presence of crabs; negative values indicate decreased losses. Note the positive and negative symbols represent the net effect of crabs and not the direction of carbon net exchange.

Species	Carbon exchanges (mgC m^{-2} h^{-1})				
	DOC flux	POC flux	Epibenthic gross photosynthesis	Epibenthic respiration	Crab respiration (*R.Q.* = 1.0)
S. catenata	+17 ± 7 (*n* = 26)	+1 ± 3 (*n* = 26)	-29 ± 8 (*n* = 7)	-4 ± 2 (*n* = 7)	+4.7 (n = 15)
C. edwardsii	+21 ± 5 (*n* = 44)	+40 ± 12 (*n* = 44)	-11 ± 3 (*n* = 6)	-6 ± 3 (*n* = 6)	+0.2 (n = 19)

CHAPTER 6

NITROGEN AND PHOSPHORUS FLUXES

During progression of the study evidence pointed increasingly towards the marked marine influence on the Sarcocornia marsh (Chapters 2 to 4) and Kariega estuary (Allanson and Read 1987). In many marine ecosystems nitrogen is known to limit rates of phytoplankton (Thayer 1974) and macrophyte (Gallagher 1975, Buresh et al. 1981) production, which in combination with the low nutrient N:P ratios (<10.0) in the water column of the Kariega estuary (Allanson and Read 1987), suggested the estuary was at least potentially nitrogen-limited.

Consequently, the study was extended at this juncture to examine the role of the marsh in nitrogen and phosphorus cycling within the estuary. Flows of carbon, nitrogen and phosphorus are only loosely coupled in aquatic ecosystems (Newell et al. 1983). This precluded extrapolation of the observed patterns of fluxes of organic carbon (Chapters 4 and 5) to those of nitrogen and phosphorus. It was therefore necessary to measure these fluxes, and this was done initially in the laboratory in mesocosms of the marsh surface (Section 6.1), and then in the field at the marsh-estuarine junction over five tides (Section 6.2)

6.1 Fluxes of nitrogen and phosphorus at the marsh-water interface

Materials and methods

The experimental procedures were described in Chapter 4, except that one of each of the duplicate filtered and unfiltered water samples, which were collected before and after each simulated tide, were analyzed as follows.

The filtered samples were analyzed for ammonium-N (Koroleff 1983), nitrate-N (Mostert 1983, after Benschneider and Robinson 1952), nitrite-N (Mostert 1983) and soluble reactive phosphorus (Mostert 1983, after Murphy and Riley 1962) using a Technicon II Autoanalyzer system. To obtain concentrations of total nitrogen (TN) and total phosphorus (TP), and total dissolved nitrogen (DN) and total dissolved phosphorus (DP), subsamples of the filtered and unfiltered samples were oxidized using the persulphate method of Koroleff (1983, p. 168), and then analyzed for nitrate and soluble reactive phosphorus (SRP). Dissolved organic nitrogen (DON) was estimated by subtracting dissolved inorganic nitrogen concentrations (ammonium-N + nitrate-N + nitrite-N) (abbreviated to DIN) from those of DN. Particulate nitrogen (PN) was determined as the difference between TN and DN estimates. Similarly, SRP concentrations were subtracted from those of TP to estimate dissolved organic phosphorus (DOP), and DP from TP to estimate particulate phosphorus (PP). Urea was determined according to Koroleff (1983).

Results

Nitrogen

The nitrogen flux data are presented in Figures 53 to 55, and their interpretation in Table 14.

The following conclusions are possible:

1. In mesocosms of both zones incubated with crabs, and which therefore simulate the field situation, mean net fluxes of nitrogen, as TN, for all tides combined, were significantly different from zero, and directed from the marsh surface to the water column (Figure 53).
2. Mean fluxes of TN were six times higher in the *Sarcocornia* Zone (43.6 ± 8.3 mgN m^{-2} $tide^{-1}$) than in the tidal creek (6.7 ± 4.8 mgN m^{-2} $tide^{-1}$) (Table 14).
3. This difference was mainly due to the larger losses of DIN, and particularly ammonium-N, from the *Sarcocornia* Zone than from the tidal creek; mean fluxes of ammonium-N in the respective zones were 27.9 and 4.3 mgN m^{-2} $tide^{-1}$.
4. The presence of crabs had a significant influence on the fluxes of TN, DIN and ammonium-N (see significant *F* - test results for main effects of CRABS, Table 14). The extent of these effects depended on the species/zone under consideration (ZONE x CRABS interaction effects Table 14). For instance, fluxes of TN were significantly increased as a consequence of the presence of *S.catenata* but were not altered by *C. edwardsii*.

Figure 53 Net fluxes of total nitrogen (TN), dissolved nitrogen (DN) and particulate nitrogen (PN) in the Sarcocornia Zone (left panel) and tidal creek mesocosms (right panel), incubated with(solid) and without crabs (dotted) over a simulated spring-tidal period. Each point represents mean net flux per tide (*n* = 3), and positive and negative values denote net exports and imports, respectively.

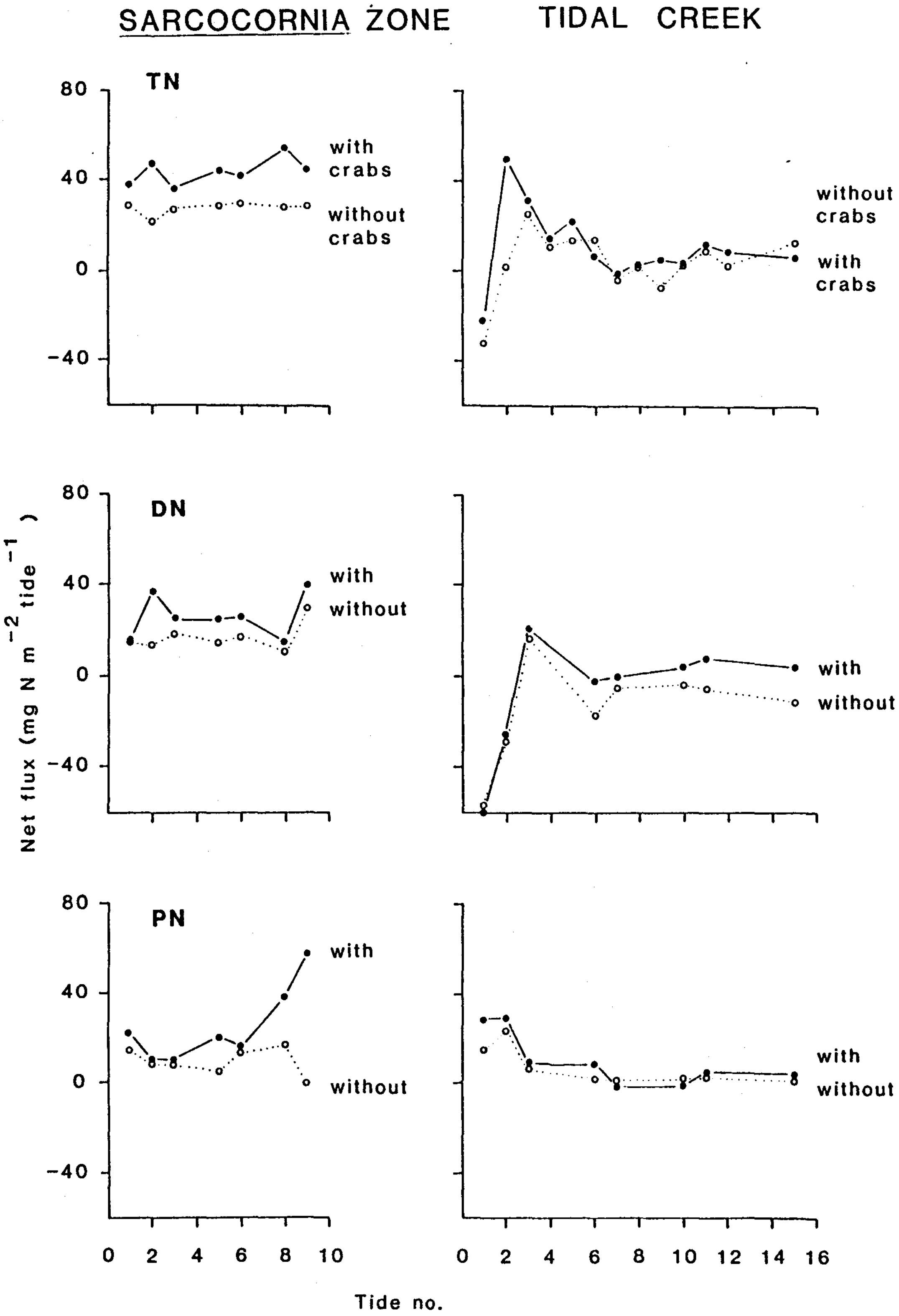
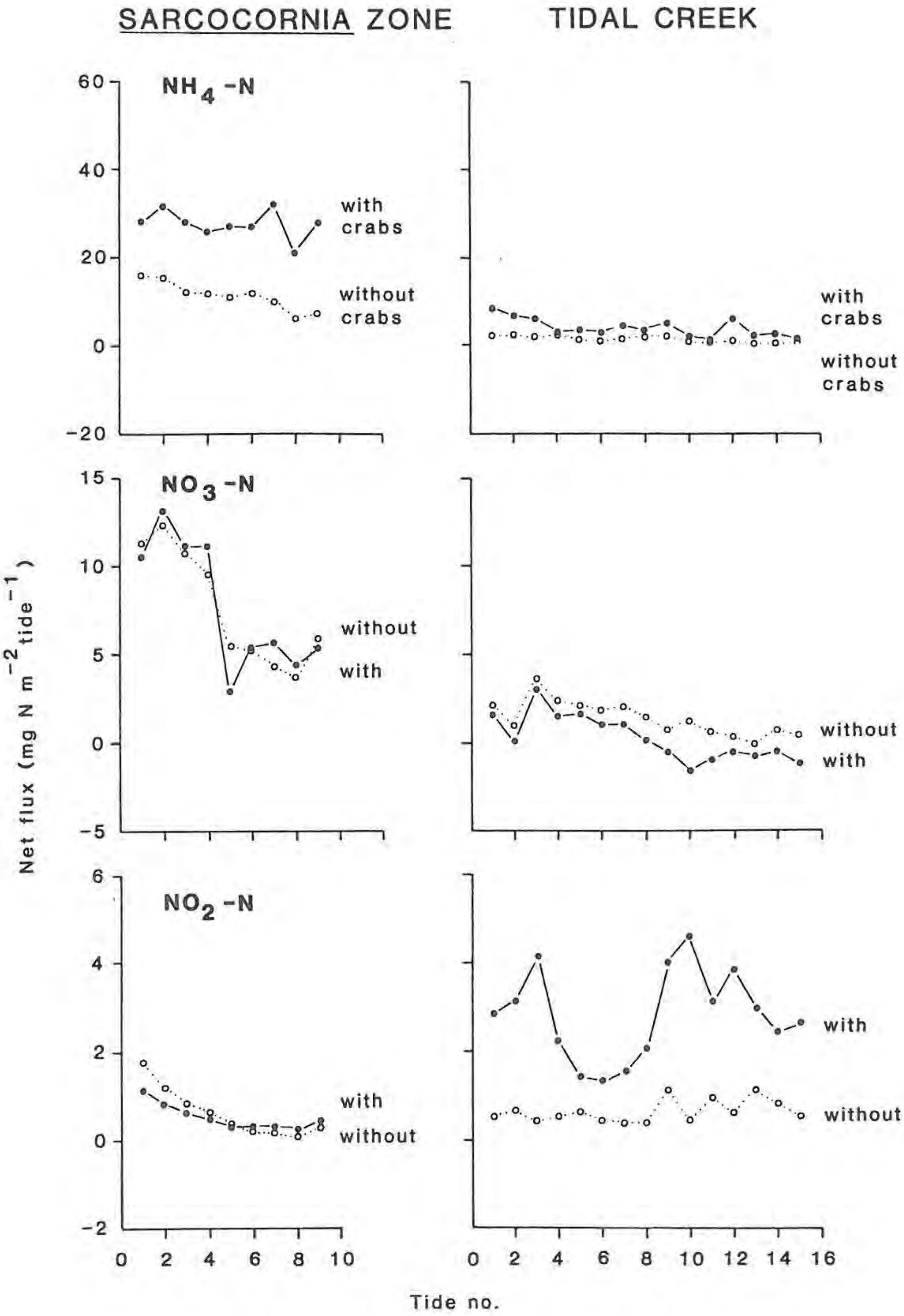

SARCOCORNIA ZONE
TIDAL CREEK
TN
DN
PN
80
40
0
-40
with crabs
without crabs
without crabs
with crabs
with
without
with
without
with
without
with
without
Net flux (mg N m^{-2} tide^{-1})
0
2
4
6
8
10
12
14
16
Tide no.

Figure 54 Net fluxes of dissolved inorganic nitrogen (DIN) components, namely ammonium-N, nitrate-N and nitrite-N, in mesocosms of tidal creek and Sarcocornia zones incubated with (solid) and without (dotted) crabs. Details as for Figure 53.


SARCOCORNIA ZONE
TIDAL CREEK
NH$_4$-N
with crabs
without crabs
with crabs
without crabs
NO$_3$-N
without
with
without
with
NO$_2$-N
with
without
with
without
60
40
20
0
-20
15
10
5
0
-5
6
4
2
0
-2
0
2
4
6
8
10
0
2
4
6
8
10
12
14
16
Net flux (mg N m^{-2} tide^{-1})
Tide no.

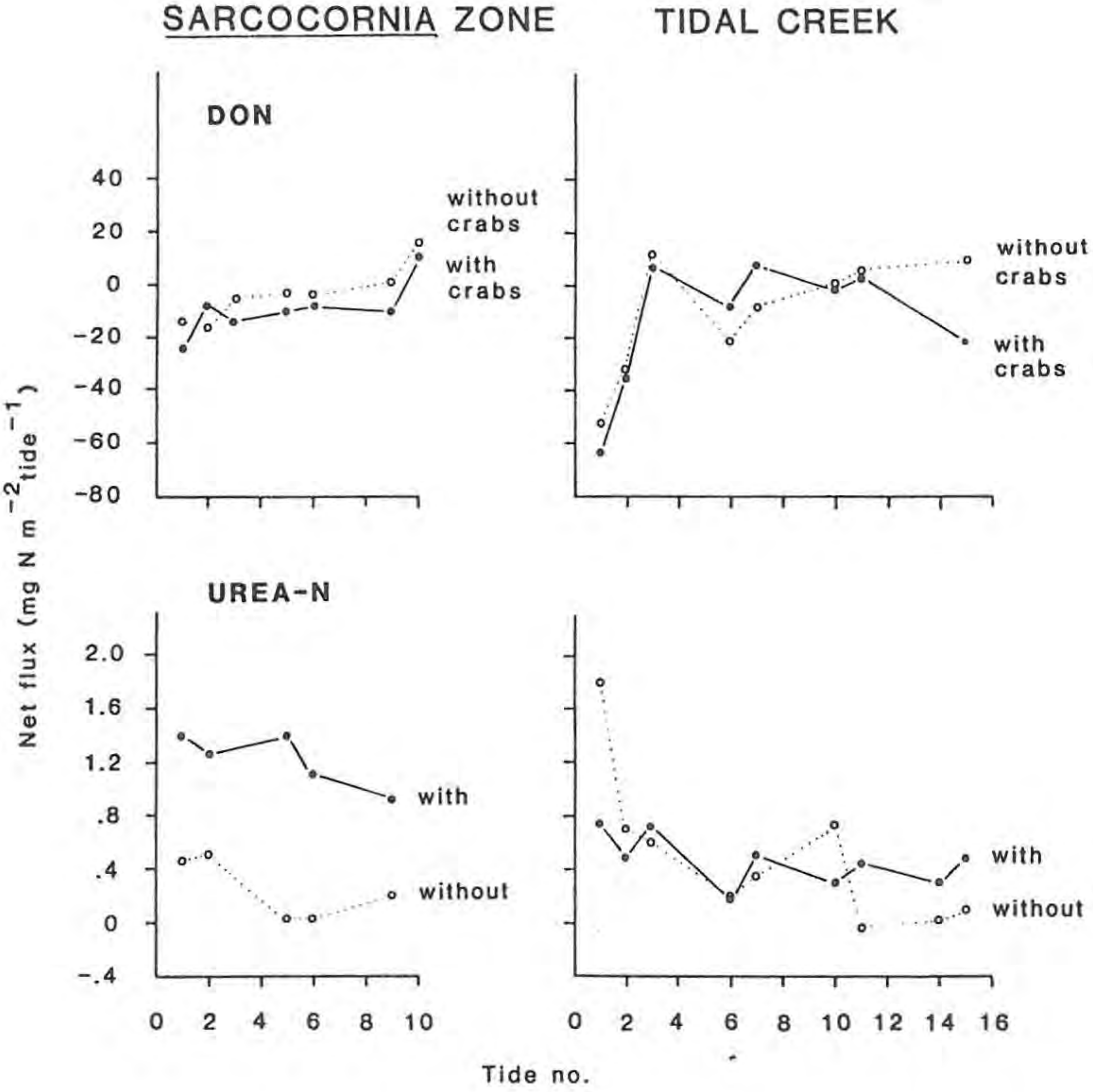


Figure 55 Net fluxes of dissolved organic nitrogen (DON) and urea in mesocosms of tidal creek and *Sarcocornia* zones incubated with (solid) and without (dotted) crabs. Details as for Figure 53.

Table 14. Mean net fluxes of nitrogen fractions in with- and without-crab mesocosms of the *Sarcocornia* and tidal creek zones. Significance levels of *F*-test results of 3-way ANOVA's: *** $P>0.001$, ** $P>0.01$, * $P>0.05$, n.s. $P<0.05$. The interaction effects not determined because of insufficient data points are denoted n.d. (+) values indicate net export from mesocosms; (-) values indicate net imports. Mean values were calculated for all tides combined.

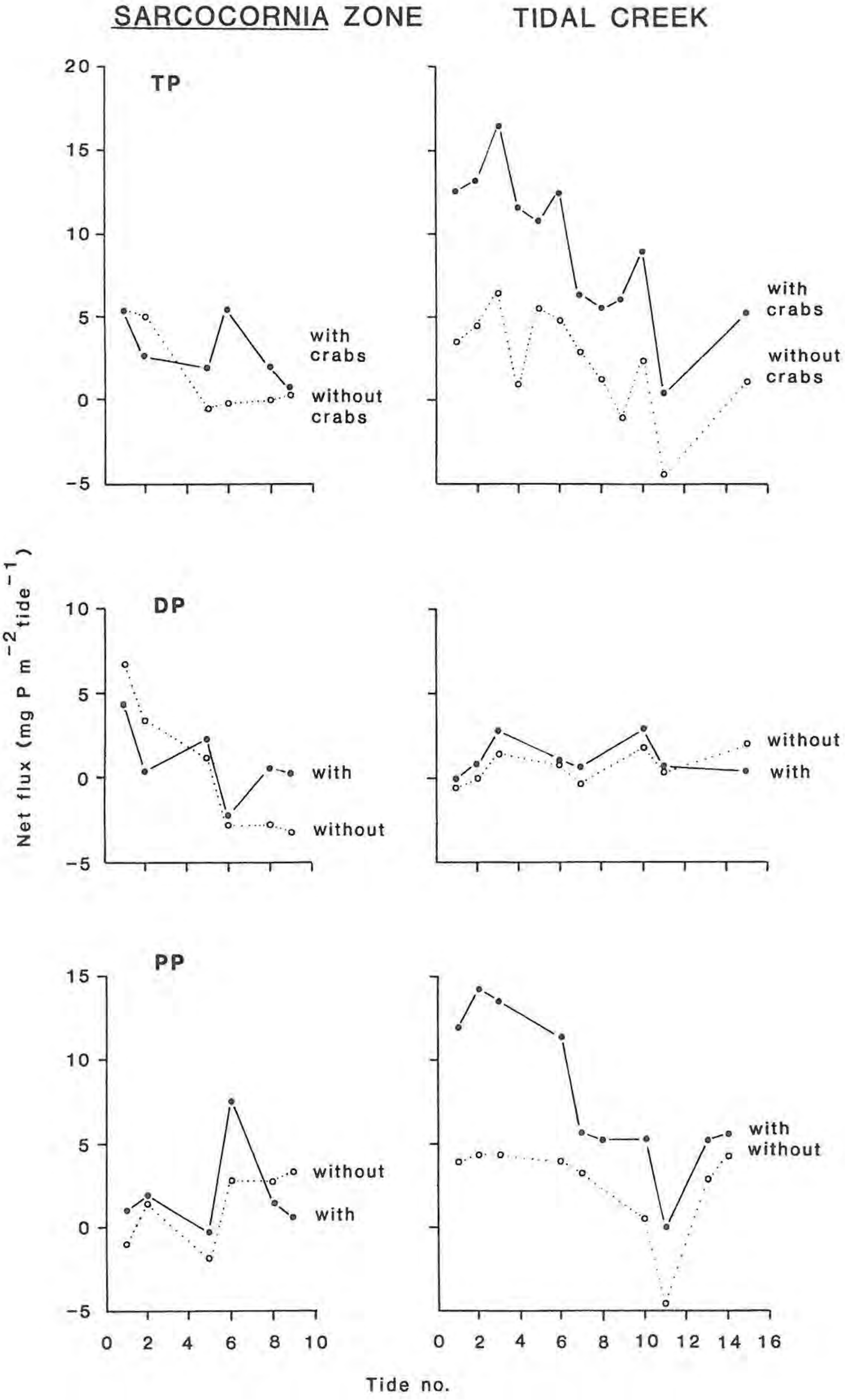
Component	Mean net flux ±95% C.L. (n) (mgN m^{-2} tide^{-1})				Significance of *F*-test results of ANOVA					
	Sarcocornia Zone		Tidal creek		MAIN EFFECTS			INTERACTION EFFECTS		
	With crabs	Without crabs	With crabs	Without crabs	ZONE (H1)	TIDE (H2)	CRABS (H3)	ZONE X TIDE	ZONE X CRABS	TIDE X CRABS
TN	+43.6 ± 8.3 (14)	+27.4 ± 4.6 (15)	+6.7 ± 4.8 (39)	+2.5 ± 5.0 (39)	***	*	***	n.d.	**	n.d.
DN	+27.1 ± 9.0 (14)	+17.3 ± 5.6 (15)	-5.3 ± 9.7 (24)	-7.5 ± 11.5 (24)	***	***	*	n.d.	n.d.	n.d.
PN	+16.5 ± 9.0	+10.1 ± 4.4 (15)	+10.6 ± 6.8 (24)	+6.9 ± 4.4 (23)	n.s	**	n.s.	n.d.	n.d.	n.d.
NH_4-N	+27.9 ± 3.4 (26)	+11.2 ± 3.2 (27)	+ 4.3 ± 0.5 (44)	+1.3 ± 0.4 (45)	***	n.s.	***	n.s.	***	n.s.
NO_3-N	+ 7.8 ± 2.7 (26)	+ 7.4 ± 2.0 (27)	+ 0.25 ± 0.5 (26)	+1.4 ± 0.4 (45)	***	*	n.s	*	n.s.	n.s.
NO_2-N	+ 0.5 ± 0.3 (26)	+0.6 ± 0.3 (27)	+ 2.9 ± 0.4 (41)	+0.6 ± 0.1 (45)	***	***	***	n.s.	***	n.s.
DIN	+36.2 ± 5.5 (26)	+19.2 ± 5.2 (27)	+ 7.4 ± 1.3 (41)	+3.3 ± 0.7 (45)	***	n.s.	***	n.s.	**	n.s.
DON	-10.4 ± 8.3 (14)	-3.6 ± 9.3 (15)	-13.4 ± 11.4 (22)	+10.9 ± 11.9 (24)	**	***	n.s.	n.d.	n.d.	n.d.
UREA-N	+ 1.2 ± 0.3 (15)	+0.3 ± 0.3 (15)	+ 0.5 ± 0.2 (26)	+0.6 ± 0.3 (27)	*	n.s.	n.s.	n.d.	n.d.	n.d.

5. This difference was largely due to the different effects of the two species on fluxes of ammonium-N. The mean increase in ammonium-N fluxes attributable to crabs, and calculated as the difference in the net fluxes in the with- and without-crab mesocosms, was 16.3 ± 3.9 mgN m^{-2} $tide^{-1}$ in the *Sarcocornia* Zone, and only 2.9 ± 0.6 mgN m^{-2} $tide^{-1}$ in the tidal creek.
6. These data, in combination, show that the pronounced zonal differences in fluxes of nitrogen, as TN, are due mainly to the differential effects of the two crab species on the fluxes of ammonium-N.

Phosphorus

1. Mesocosms of both zones incubated with crabs exhibited significant losses of phosphorus as TP (Figure 56).
2. In contrast to the fluxes of TN, the fluxes of TP were significantly higher from the tidal creek than from the *Sarcocornia* Zone; the mean TP fluxes were 9.1 ± 1.7 and 3.1 ± 1.0 mgP m^{-2} $tide^{-1}$, respectively.
3. In both zones, losses of phosphorus occurred mainly as SRP, and to a lesser extent as PP (Figure 57). These losses were offset in part by the retention of reduced phosphorus, as DOP.
4. Mean losses of SRP and PP, and uptake of DOP, were all greater in the tidal creek than in the *Sarcocornia* Zone.
5. However, comparison of the mean SRP flux values, calculated for all tides combined, is misleading because, as indicated by the significant ZONE x TIDE interaction effect in Table 15, the difference between zones was dependent on tide sequence within the

Figure 56 Net fluxes of total phosphorus (TP), dissolved phosphorus (DP) and particulate phosphorus (PP) in Sarcocornia Zone (left) and tidal creek mesocosms (right) incubated with (solid) and without crabs (dotted). Details as for Figure 53.


SARCOCORNIA ZONE
TIDAL CREEK
TP
DP
PP
Net flux (mg P m^{-2} tide^{-1})
Tide no.
20
15
10
5
0
-5
0
2
4
6
8
10
12
14
16
with crabs
without crabs
with
without

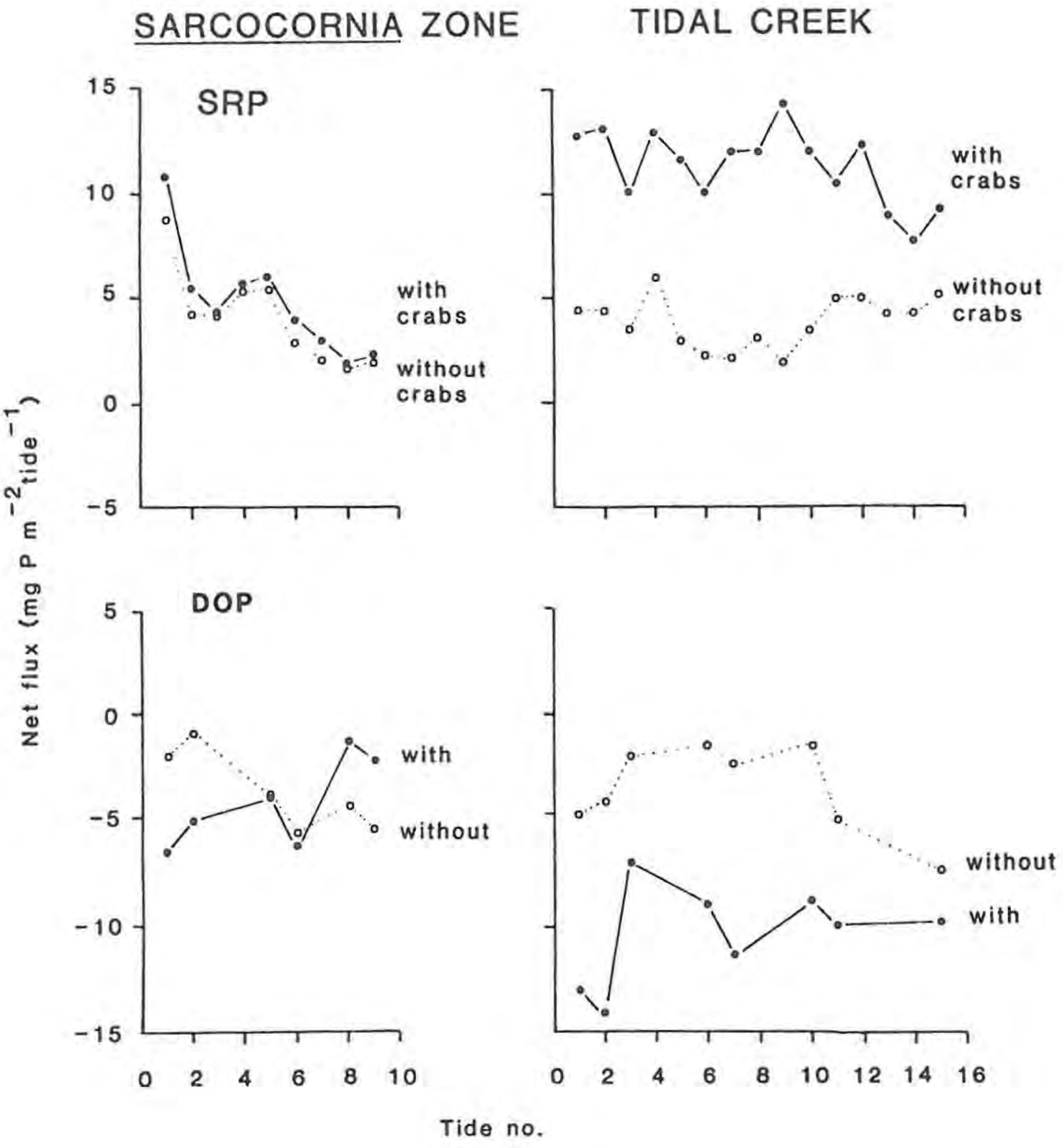


Figure 57 Net fluxes of soluble reactive phosphorus (SRP) and dissolved organic phosphorus (DOP) in mesocosms of tidal creek and Sarcocornia zones incubated with (solid) and without (dotted) crabs. Details as for Figure 53.

Table 15. Mean net fluxes of phosphorus components in with- and without-crab mesocosms of the *Sarcocornia* and tidal creek zones. Significance levels of *F*-test results of 3-way ANOVA's: *** *P*>0.001, ** *P*>0.01, **P*>0.05, n.s. *P*<0.05. (+) values denote net export from mesocosms; (-) values represent net imports. Mean values were calculated for all tides combined.

Component	Mean net fluxes ±95% *C.L.* (*n*) (mgP m^{-2} $tide^{-1}$)				Significance of *F*-test results of ANOVA					
	Sarcocornia Zone		Tidal creek		EFFECTS			INTERACTION EFFECTS		
	With crabs	Without crabs	With crabs	Without crabs	ZONE	TIDE	CRABS	ZONE X TIDE	ZONE X CRABS	TIDE X CRABS
TP	+3.1 ± 1.0 (18)	+1.6 ± 1.4 (18)	+9.1 ± 1.7 (36)	+2.4 ± 1.1 (36)	***	**	***	**	***	n.s.
DP	+0.5 ± 1.1 (24)	+0.4 ± 2.0 (18)	+0.9 ± 0.7 (18)	+0.3 ± 0.6 (24)	**	*	n.s.	***	n.s.	n.s.
PP	+2.6 ± 1.1 (26)	+1.2 ± 0.9 (18)	+8.4 ± 2.3 (38)	+2.5 ± 1.4 (24)	***	*	***	n.s.	**	n.s.
SRP	+5.0 ± 1.1 (26)	+4.2 ± 0.9 (27)	+11.4 ± 1.1 (38)	+3.9 ± 0.6 (39)	***	**	***	***	***	n.s.
DOP	-4.6 ± 1.4 (18)	-3.8 ± 1.7 (27)	-10.3 ± 1.3 (18)	-3.7 ± 1.1 (18)	***	**	***	n.s.	***	*

semi-lunar tidal cycle. For instance, in the *Sarcocornia* Zone SRP fluxes declined progessively over the semi-lunar period, but in the tidal creek SRP fluxes remained elevated.

6. Differences in fluxes of TP, PP, SRP and DOP between zones were attributable in part to the differential effects of the two crab species on the fluxes of these components (significant ZONE x CRABS interaction effects, Table 15). *C. edwardsii* in the tidal creek increased losses of TP, PP and SRP, and the retention of DOP (Figures 56 and 57). In contrast, *S. catenata* in the *Sarcocornia* Zone had little or no impact on fluxes of these components.

6.2 Preliminary observations on nitrogen and phosphorus fluxes between the marsh and estuary

Tidal fluxes of nitrogen and phosphorus were monitored over five semi-diurnal tides following the minor river flood of April 1986. The field procedures were described in Section 4.1, and the analytical techniques summarized in Section 6.1. The organic carbon flux data for the same tides were presented in Section 4.2.

Estimates of tidal, $\underline{F}_{TIDE}$, and time-averaged instantaneous, $<\underline{F}_{\overline{T}}>$, net fluxes of nitrogen and phosphorus are presented in Table 16. Fluxes of nitrate-N and nitrite-N were directed from the estuary onto the marsh over all five tides. In contrast, ammonium-N was imported over the first three tides, and exported over the last two.

Table 16. Tidal cross-sectional net fluxes, $\overline{F}_{\underline{TIDE}}$ (g tide^{-1}), and time averaged cross-sectional net fluxes, $\overline{F}_{\underline{T}}$, (μg s^{-1}) of nitrogen and phosphorus over five tides, April 1986. Maximum water level (m.a.m.s.l.) attained by each tide is indicated in brackets. If a component was not determined at a particular tide this is indicated as a horizontal dash. (+) signs denote net exports from marsh; (-) denote net imports.

Component	20.4.86		21.4.86		23.4.86		25.4.86		26.4.86	
	$\overline{F}_{\underline{TIDE}}$	$\overline{F}_{\underline{T}}$	$\overline{F}_{\underline{TIDE}}$	$\overline{F}_{\underline{T}}$	$\overline{F}_{\underline{TIDE}}$	$\overline{F}_{\underline{T}}$	$\overline{F}_{\underline{TIDE}}$	$\overline{F}_{\underline{T}}$	$\overline{F}_{\underline{TIDE}}$	$\overline{F}_{\underline{T}}$
	(1.05)		(1.07)		(1.24)		(1.16)		(1.33)	
NH_4-N	-0.6	-42.3	-0.5	-22.2	-0.7	-6.4	+1.8	+92.4	+5.2	+194.0
NO_3-N	-1.1	-48.5	-2.2	-91.8	-7.4	-319.7	-18.0	-664.2	-54.8	-2101.6
NO_2-N	-0.3	-5.5	-0.2	-4.1	-1.5	-31.1	-1.4	-55.4	-0.8	-55.5
DIN	-2.0	-86.8	-2.8	-118.2	-8.2	-343.8	-17.6	-625.9	-50.6	-1961.6
TN	+45.7	+1855.4	+67.4	+2882.4	+80.3	+3306.0	+102.8	+6755.8	+167.8	+10612.0
DN	-	-	-	-	-	-	-	-	+184.5	-
PN	-	-	-	-	-	-	-	-	-116.7	-
DON	-	-	-	-	-	-	-	-	+235.2	-
SRP	+0.9	+39.0	+1.1	+46.5	+5.0	+196.8	+4.1	+196.0	+4.6	+163.8

This shift probably occurred in response to a decline in ammonium-N concentrations in tidal water inundating the marsh (Figure 58). Wolaver et al. (1983) have noted that net fluxes of ammonium-N were directed onto a Spartina alterniflora marsh whenever concentrations of this component were high in water inundating the marsh. The present evidence indicates that ammonium-N was imported onto the Kariega marsh when concentrations exceeded a threshold level of ca. 20 μgN dm^{-3} (Figure 58).

Concentrations of nitrate-N exceeded those of ammonium-N by a factor of between 3 and 5, which may account for the consistent retention of nitrate-N by the marsh (Table 16). Boynton and Kemp (1985) have recently demonstrated a direct, positive correlation between nitrate-N concentrations in water overlying estuarine sediments and the magnitude of nitrate-N fluxes into the sediments.

Although fluxes of DIN (namely the combined fluxes of ammonium-N, nitrate-N and nitrite-N) were directed onto the marsh, nitrogen as TN, was exported to the estuary. This occurred at all tides, and data available for the tide of 26 April, suggests this export was largely as DON.

6.3 Overview of nitrogen and phosphorus fluxes

The mesocosm experiments and field observations have demonstrated that this Sarcocornia marsh exports nitrogen and phosphorus to the Kariega estuary. The marsh also functions as a processor of this material, importing certain fractions and exporting others. The field

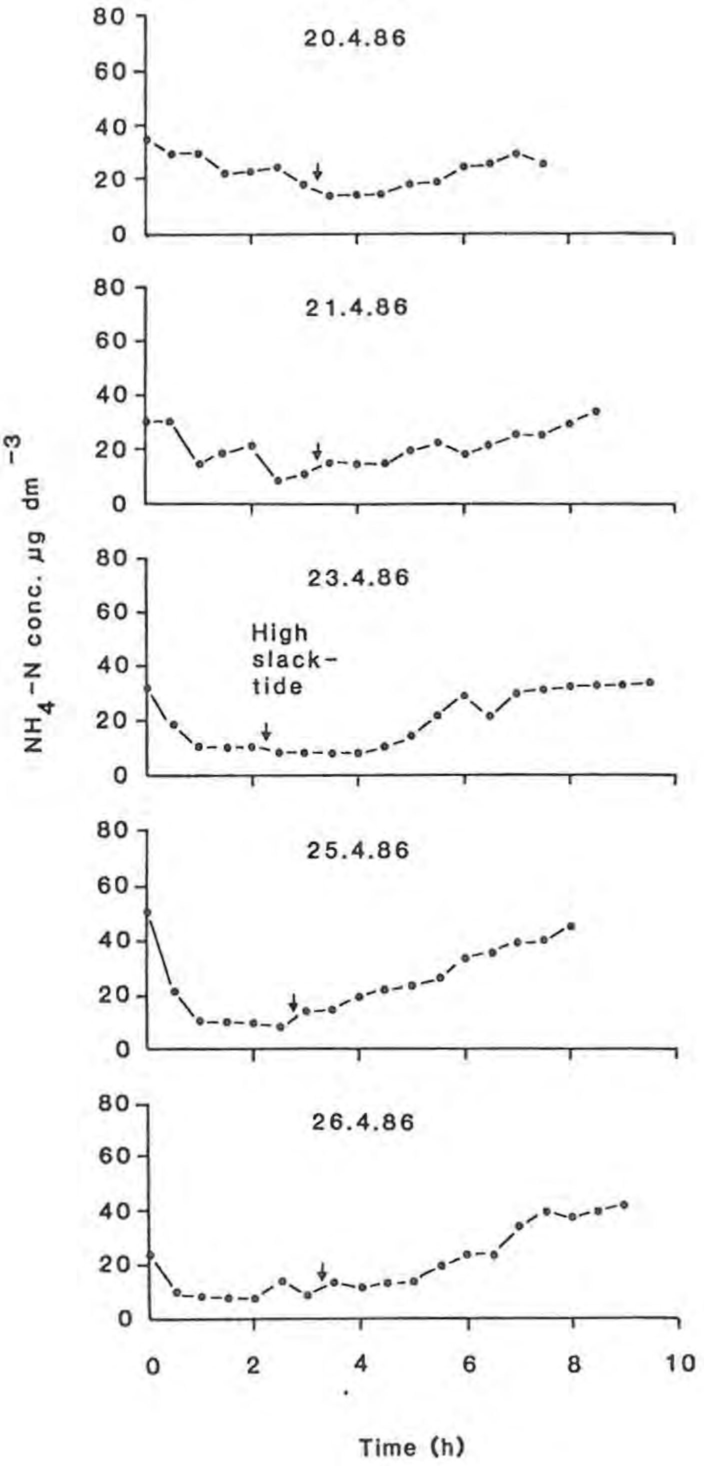


Figure 58 Ammonium-N concentrations in tidal water inundating and draining the marsh, measured at the marsh-estuarine junction over five tides. Arrows indicate high slack-tides.

observations revealed that nitrogen was imported onto the marsh largely as nitrate-N, and exported as DON. This pattern contrasts with that observed in the mesocosms, where nitrogen was imported as DON and ammonium-N, and fluxes of nitrate-N were either not significantly different from zero or were directed from the marsh surface to the water column.

These contrasted patterns may be linked to the fact that the field measurements were conducted in late autumn, and the laboratory experiments under simulated summer conditions. Yamada and Kayama (1987) have recently noted that more ammonium-N is liberated, relative to DON, from nearshore marine sediments during summer than winter. This suggests that the contrasted laboratory and field patterns of nitrogen fluxes observed for this *Sarcocornia* marsh may reflect a seasonal shift in patterns of fluxes of reduced nitrogen.

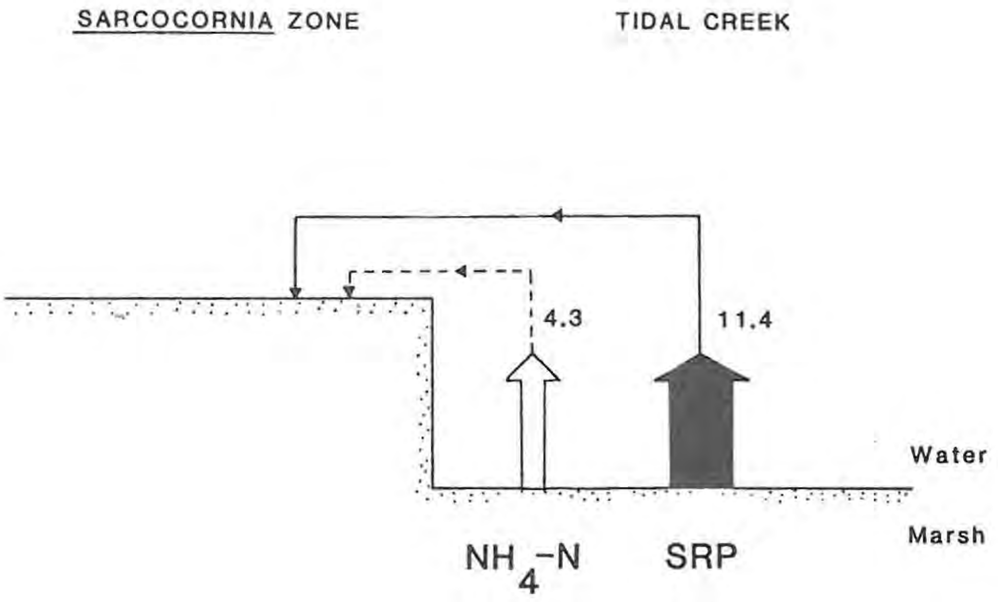
The patterns of exchange of nitrogen and phosphorus also varied spatially, within the marsh. Fluxes of TN were greater in the *Sarcocornia* Zone than in the tidal creek, but the opposite applied to fluxes of TP. Ratios of fluxes of TN : TP were 14:1 in the *Sarcocornia* Zone, and only 0.7:1 in the tidal creek, which indicates the material released from the tidal creek was, in comparison to that from the *Sarcocornia* Zone, impoverished in nitrogen relative to phosphorus.

This difference was largely attributable to the contrasted patterns of exchange in the two zones of ammonium-N and SRP. Fluxes of ammonium-N were 6 times greater in the *Sarcocornia* Zone than in the tidal creek, while fluxes of SRP were more than twice as large in the tidal creek than in the *Sarcocornia* Zone.

Nutrients released from the salt-marsh are potentially available to autotrophs in the overlying water, in adjacent regions of the marsh, and in the Kariega estuary. It is therefore worthwhile to compare the DIN:SRP flux ratios of 7:1 and 0.6:1 in the *Sarcocornia* and tidal creek zones, respectively, with the N:P atomic ratios of 16:1 predicted for marine phytoplankton (Redfield *et al*. 1963) and 30:1 for marine macrophytes (Atkinson and Smith 1983). The fact that the flux ratios are much lower than the structural ratios shows that the dissolved inorganic material released from both zones of the marsh, but particularly from the tidal creek, was impoverished in nitrogen relative to phosphorus. However, both regions *do* function as sources of nitrogen and phosphorus.

Several workers have provided evidence of concentration-dependent patterns of ammonium-N (Wolaver *et al*. 1983) and SRP fluxes (Jordan *et al*. 1983) between salt-marshes and adjacent systems (discussed further in Chapter 7). These findings, in combination with the contrasted patterns of ammonium-N and SRP fluxes in the *Sarcocornia* and tidal creek zones, and the bi-directional flow of water on and off the marsh, suggests that these two zones may be biogeochemically coupled. A hypothetical model of this coupling is presented in Figure 59. During tidal inundation the elevated quantities of SRP released from the tidal creek will be transported onto, and probably retained to some extent by,

(a) Flood - tide



(b) Ebb - tide

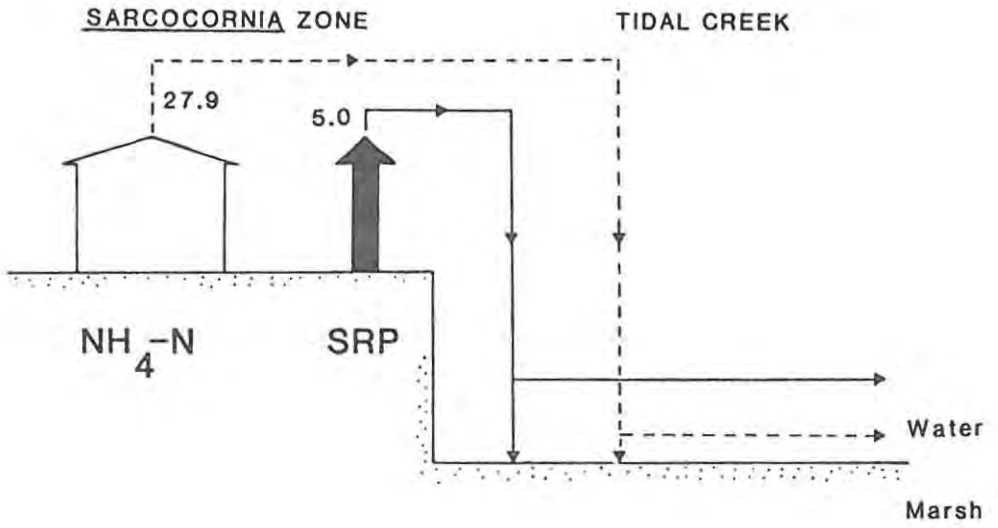


Figure 59 Hypothetical model of biogeochemical coupling of the tidal creek and *Sarcocornia* zones of the marsh. Arrows indicate hydraulically-mediated transfers of ammonium-N (dashed) and SRP (solid) during flood- (*a*) and ebb-phases (*b*) of a semi-diurnal tide. Values are net fluxes in mg m^{-2} tide^{-1}.

the salt-marsh flats. Conversely, on the ebb-tide the ammonium-N released from the Sarcocornia Zone will be retained by the substrata of the tidal creek as the tidal water drains back to the estuary.

Of particular significance is the fact that the crabs on the marsh are to a large extent responsible for the differences in fluxes of these components in the two zones. These data, in combination, suggest that the crabs on the marsh play a key role, not only in increasing the losses of nitrogen and phosphorus from the marsh surface, but also in coupling the major zones of the marsh. Such coupling would tend to conserve nitrogen and phosphorus in salt-marshes, and may account at least in part for the elevated productivity (e.g. Westlake 1963) of these ecosystems.

CHAPTER 7

DISCUSSION

The size and complexity of ecosystems has necessitated research approaches which tend to treat ecosystems, and parts thereof, as discrete units. But evidence in the literature points increasingly towards the importance of interactions, both between (e.g. Wulff and Field 1983) and within ecosystems (e.g. Jansson et al. 1982, Nixon 1986) to their functioning.

The nature of these interactions varies considerably, and in a review of material and energy flow in coastal ecosystems, Field (1983) differentiated between "open" and "closed" systems. Although no ecosystem is entirely closed or entirely open, his classification does reflect the hypothetical extremes of an ecological continuum. At one end this includes ecosystems virtually dependent on internal biogeochemical cycling of "old" material, and at the other, systems dependent on continuous inputs of "new" material from sources external to the system. He considers high energy systems such as rocky shores and sandy beaches as "open" systems, and salt-marshes and estuaries as more "closed". Other systems, for example the Benguela kelp bed system, are "open" under certain hydrodynamic conditions, and "closed" under others (Field 1982).

Two aspects are implicit in this concept of "open" and "closed" ecosystems, the rate of material transfer between ecosystems, and the rate of cycling within them. The present dissertation has been concerned with first of these, namely the tidal transfer of material and particularly of organic carbon, between a Sarcocornia salt-marsh and the Kariega estuary.

7.1 Comparison with other salt-marsh systems

The mean net flux of TOC (DOC plus POC) for the Sarcocornia marsh, for all tides combined was 5.1 ± 7.7 gC m^{-2} y^{-1} (±95 % C.L., n = 40 tides, excluding post river-flood tides). Insight into the magnitude of this loss can be gained by comparing it with an estimate of the rate of community net production of the marsh. The export of TOC amounted to only 2 % of the rate of marsh community net production of 260gC m^{-2} y^{-1}. This shows that the rate of "consumption" (sedimentation plus respiration) of organic carbon on the marsh approximates the rate of carbon "production" (carbon fixation), and that there is no large export of organic carbon. It also shows the incompatibility of Odum's outwelling hypothesis to this particular system, at least with regards annual fluxes of organic carbon.

Table 17 compares the fluxes of organic carbon from the Sarcocornia with values reported in the literature. Apart from the value for Flax Pond, where the flux of TOC was directed onto the marsh, the value of 2 % for the Kariega marsh is the lowest reported estimate. It is similar to that of 3 to 5 % noted by Borey et al. (1983) for a Texas marsh, but considerably lower than the values of 84 to 117 % reported for Town Creek (Chrzanowski et al. 1983), and 93% for a marsh in the Ems-Dollard estuary (Dankers et al. 1984).

Table 17 Summary of annual fluxes of organic carbon between salt-marshes and coastal systems, and comparison of TOC fluxes with marsh net aerial primary production. Because patterns of DOC and POC fluxes are frequently different, only data for those salt-marshes for which flux estimates for both fractions are available have been included. (+) values denote net exports from marshes, (-) values net imports. (n.d.) indicates not determined.

System	Carbon flux (gC m^{-2} y^{-1})			Net aerial primary production (gC m^{-2} y^{-1})	TOC flux % primary production	Reference
	DOC	POC	TOC			
Ware Creek, Virginia	+80	+35	+115	599	19	Axelrad et al. 1976
Carter Creek, Virginia	+25	+116	+142	599	24	Axelrad et al. 1976
Flax Pond, New York	+8	-61	-53	372	0	Woodwell et al. 1977
Canary Creek, Delaware	+38	+62	+100	252	40	Lotrich et al. 1979
Coon Creek, Texas	+21	+4	+25	550-900	3-5	Borey et al. 1983
Town Creek, South Carolina	+317 - +416	+66 - + 117	+383 - +533	455	84-117	Chrzanowski et al. 1983
Low Marsh, Rhode River	+21	-32	-11	n.d.	n.d.	Jordan et al. 1983
High marsh, Rhode River	+43	+14	+57	n.d.	n.d.	Jordan et al. 1983
EMS-Dollard marsh, The Netherlands	+511	-47	+464	500	93	Dankers et al. 1984
Kariega marsh, South Africa	+7	+3	+10	260*	2	This study

* The estimate of community net production for the Sarcocornia marsh is an area-weighted value calculated using the areas of the salt-marsh flats and tidal creek in Table 1, the epibenthic production and respiration rates in Table 10, and the net aerial productivity estimate for Sarcocornia perennis of 390gC m^{-2} y^{-1} (Christie 1981). A 12 h light:dark regime was used, and the rates of epibenthic community respiration in the light assumed to be equal to those measured in the dark (Table 10).

Insufficient data are available to compute meaningful long-term estimates of fluxes of nitrogen and phosphorus between the marsh and estuary. Therefore it is not possible to evaluate the applicability or not of the outwelling hypothesis in this situation. However, the results of the mesocosm experiments and field measurements, do allow conclusions to be drawn regarding the general directions of nitrogen and phosphorus fluxes. The marsh exported reduced forms of nitrogen (ammonium-N and DON) and imported oxidized forms (nitrate-N and nitrite-N). This accords with the results observed in several other studies (Axelrad 1974, Valiela and Teal 1979, Woodwell et al. 1979, Jordan et al. 1983 and Abd. Aziz and Nedwell 1986).

Virtually all marshes import nitrate-N (see also Wolaver and Zieman 1983, 1984), although significant exports of this component have been documented for certain marshes (e.g. Valiela et al. 1978, Jordan and Correll 1983, and Whiting et al. 1987) These exports are unusual, and have been attributed to ground-water inputs of nitrate-N (Valiela et al. 1978), and nitrification of ammonium-N to nitrate in water draining from the marsh (Whiting et al. 1987).

The magnitude and direction of net fluxes of ammonium are generally more variable than those of nitrate-N (Nixon 1980). Although most studies have measured annual exports of ammonium-N, others, for example Axelrad et al. (1976), Daly and Mathieson (1981), Jordan et al. (1983), and Wolaver and Zieman (1984) have reported annual imports. However, in most studies the directions of fluxes of ammonium-N varied considerably between tides (Nixon 1980 Figure 13). The exports of soluble reactive phosphorus (SRP) from the marsh (Figure 57, Table 16) accord with the results of most studies (e.g. Nixon 1980 Table 15, Welsh 1980, Jordan *et al*. 1983, Dankers *et al*. 1984), but contrast with the annual imports of SRP reported by Wolaver and Zieman (1984).

There is increasing evidence that the variability of marsh-estuarine fluxes is attributable, at least in part, to concentration-dependent patterns of uptake and release by the marshes. Certain salt-marshes, at least at certain times, import nutrients when nutrient concentrations in water overlying the marsh are high, but export these components when concentrations are low. For instance, nitrate-N concentrations in water overlying salt-marsh (Nedwell 1982) and sub-tidal estuarine sediments (Boynton and Kemp 1985) are known to exert a significant effect on nitrate-N fluxes to and from these biocoenoses. Similarly, Kristensen (1985) noted that nitrate-N and phosphate-P fluxes between polychaete burrows and the overlying water column, were very sensitive to changes in water column concentrations of these components. At concentrations of below 10-15 µm for nitrate-N, and 3 µm for phosphate-P, these components were released from the sediment/burrow biocoenosis, but at higher concentrations both fractions were retained. In Kristensen's study the fluxes of ammonium-N were independent of overlying concentrations. This contrasts with the present study where the switch in direction of ammonium-N fluxes coincided with a decline in ammonium-N concentrations in the tidal water inundating the marsh (Section 6.2).

During the past 25 years two parallel views of salt-marsh functioning have developed (Nixon 1980): firstly, their role as sources of organic material and nutrients, which is exemplified by Odum's outwelling hypothesis, and secondly, their role as nutrient "buffers" or modulators, which was proposed by Kalber (1959). Although evidence in the literature, and in this dissertation, points to the validity of the second view, I think it would be unwise to view salt-marshes as performing only a "buffering" role.

Johannes et al. (1983) have recently identified three patterns of nutrient fluxes in a coral reef community: a concentration-dependent pattern (Type 1), a diel or metabolically controlled pattern (Type 2), and a pattern not measurably related to either light or changing nutrient concentrations (Type 3). They postulated that as dissolved nutrient concentrations in the water column increased relative to nutrient demand, nutrient uptake patterns by the reef community shifted from Type 1 to Type 2, and then to Type 3. Although this relationship still needs to be tested, it does suggest that whether salt-marshes exhibit concentration-dependent patterns of nutrient fluxes or not also depends on the nutrient demand of the marsh biocoenosis. Because both variables are controlled by a nexus of interacting environmental factors, this would also offer an explanation for the pronounced temporal and spatial variability of marsh-estuarine fluxes.

7.2 Temporal variability of marsh-estuarine organic carbon fluxes

Most studies have measured fluxes over isolated semi-diurnal tides monitored at weekly, two-weekly or monthly intervals, and these have then been used to calculate annual estimates for comparison with other marshes (e.g. Borey et al. 1983, Jordan et al. 1983). Although these studies have shown that fluxes between marshes and estuaries are variable (see for example Woodwell et al. 1977), this variablity has been largely ignored in subsequent analyses. This is perhaps a consequence of the controversy associated with the outwelling hypothesis, and the need to describe the role of salt-marshes in strong terms, such as "sources" or "sinks", "exporters" or "importers", and "transformers" of material. However, as noted by Cloern and Nichols (1985), in their overview of the temporal dynamics of San Francisco Bay, the significance of annual and seasonal estimates of ecosystem processes cannot be assessed without comparing them to the variability on shorter time scales, or to variability caused by single events such as storms. These short-term changes will be particularly pronounced in estuarine intertidal regions, such as salt-marshes, which form the interface between four environments: land, ocean, rivers and atmosphere.

The semi-lunar sampling strategy employed in this study has demonstrated the occurrence of sequential shifts in the direction of net fluxes of organic carbon (Section 4.1). The magnitude and frequency of these shifts questions the validity of seasonal trends and annual estimates reported in the literature (e.g. Borey et al. 1983, Jordan et al. 1983), and indicates the need restructure sampling programmes to time scales which will incorporate these shifts.

The study has also demonstrated the dominant influence of mesoscale atmospheric/oceanic processes in regulating organic carbon, and particularly DOC, fluxes between the marsh and estuary. The manner in which this regulation is thought to occur is summarized in Figure 60.

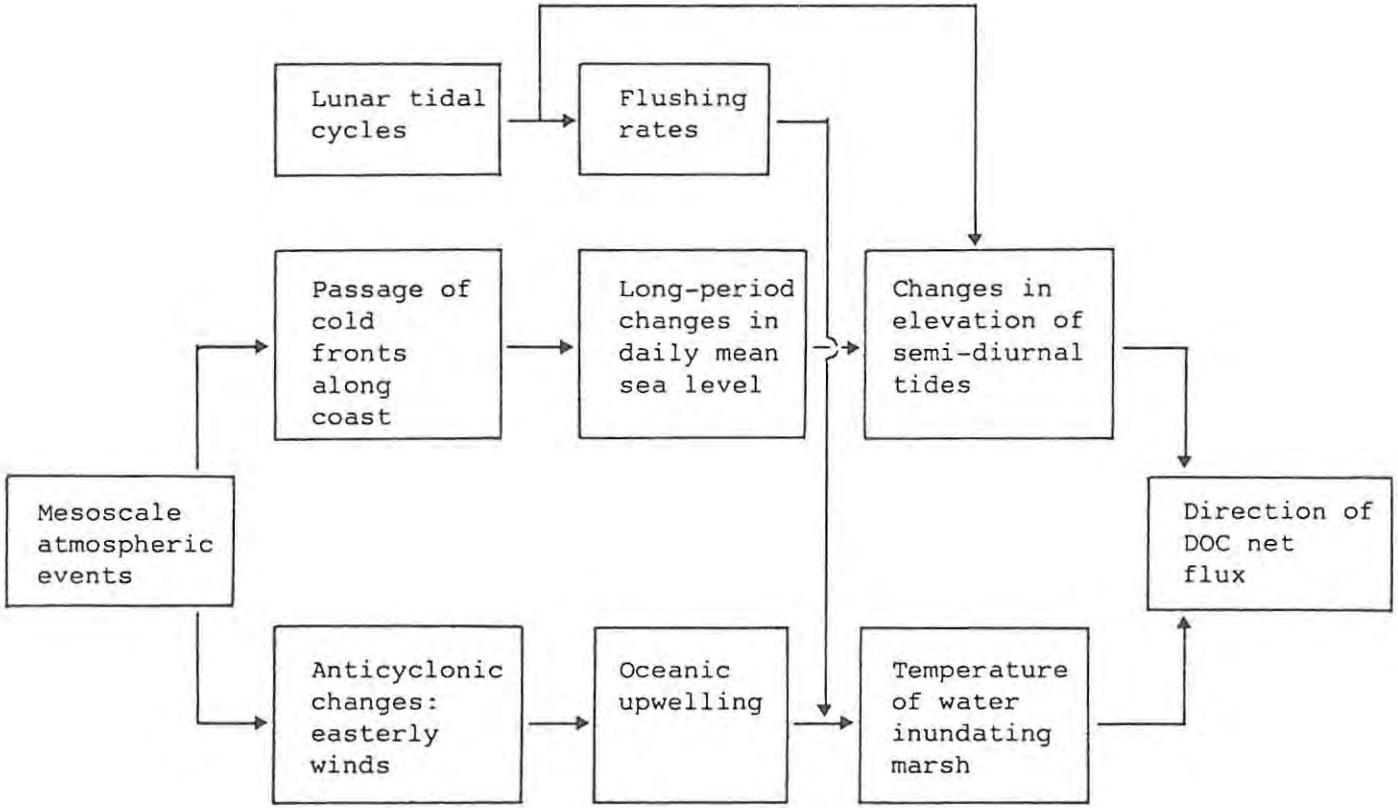


Figure 60 Proposed control of marsh-estuarine fluxes of DOC in a marine-dominated estuary.

This conceptual model has been constructed for a salt-marsh in a marine-dominated estuary, and will probably differ, in estuaries, or parts of estuaries, receiving large freshwater inflows.

Apart from the effect of tides, the principal oceanic influences on the fluxes of DOC were long-period changes in daily mean sea level, and oceanic upwelling. Evidence in the literature has shown the marked effects of changes in daily mean sea level on circulation patterns in estuarine and bay systems (e.g. Walters and Gartner 1985, Wong 1985, Olson 1986). Several authors (e.g. Kjerfve et al. 1978) have suggested that these changes may be important influences on material fluxes between salt-marshes and estuaries, but apart from this study, investigations of these effects have not been carried out. As noted earlier, the interaction of changes in daily mean sea level with lunar tidal cycles are responsible for pronounced changes in elevation of tides inundating the Kariega marsh. Because net fluxes of DOC, whether imports or exports, are frequently larger at high than low elevation tides (Figure 38), this interaction will have a marked effect on long-term transfers between the marsh and estuary.

Another important aspect arising from this study is the fact that oceanic upwelling and marsh outwelling appear to be mutually exclusive, at least with regard to fluxes of DOC. Odum (1968) noted : "Most fertile zones in coastal waters capable of supporting expanded fisheries result either from the upwelling of nutrients from deep-water, or from outwelling of nutrients or organic detritus from shallow-water nutrient traps such as reefs, banks, seaweed or seagrass beds, algal mats and salt marshes." Implicit in this statement is the separateness of the two processes. In contrast to this, the present study shows that, at least for this marsh-estuarine system, transfers of cold, upwelled oceanic water onto the marsh inhibits marsh outwelling of DOC.

It is not possible to separate the effects of changes in daily mean sea level and the effects of upwelling, because the two processes are probably interdependent. For instance, south easterly winds which frequently cause upwelling on this coast (Schumann et al. 1982), will probably also cause decreases in daily mean sea level (Brundrit pers. comm.). The influence of these events, and their interaction, will probably also vary seasonally. On the south east Cape coast, south easterly winds (Heydorn and Tinley 1980), and therefore probably also upwelling, occur most frequently during summer. Conversely, the atmospheric events responsible for the passage of cold fronts along the coast, which appear to be related to marked daily mean sea level changes, are most frequent during winter (Heydorn and Tinley 1980). Consequently, exports of DOC from the marsh may be expected to be larger during winter than summer.

7.3 Effects of crabs on material fluxes at the marsh-water interface

Salt-marshes are regions of elevated rates of carbon (Westlake 1963) and nitrogen fixation (Nixon 1980). They are also regions of deposition of suspended particulate material, which is facilitated by basin shape and topography (Odum et al. 1979), the presence of macrophytes (Chrzanowski and Zingmark 1986, Gleason et al. 1979) and the bi-directional nature of water flow (Bayliss-Smith et al. 1979). As noted earlier, marshes may also retain dissolved nutrients in response to increased nutrient concentrations in the water inundating them (Nedwell 1982). As a consequence of these processes, concentrations of organic carbon and nutrients within salt-marshes are orders of magnitude higher than in the water which intermittently overlies them (McCaffrey et al. 1980). Consequently, processes responsible for the mobilization of this material will probably be important in determining the role of these marshes in the functioning of coastal systems.

Several authors have noted that fluxes of nutrients from coastal sediments are larger when interstitial nutrient concentrations are elevated in the sediments (McCaffrey et al. 1980, Hopkinson and Wetzel 1982, Yamada and Kayama 1987). Nutrient fluxes from sediments are frequently greater than the diffusion rates predicted from one-dimensional models of diffusion derived from concentration profiles in sediments (e.g. Rutgers van der Loeff et al. 1984), and this has been attributed to faunal activity within the sediments (Yamada and Kayama 1987). The present study has shown that the presence on salt-marshes of crabs, one of the most common and abundant macrofaunal components in these ecosystems (Montague 1980), have this effect (Chapters 5 and 6).

There is some evidence that the effect of water temperature changes on crab activity may be responsible, at least in part, for the shifts in direction of DOC fluxes observed between the marsh and estuary. A hypothetical model of the way in which this may occur is presented in Figure 61. Field observations have shown that when the marsh is inundated with cold water, probably following oceanic upwelling, S. catenata individuals remain in their burrows, but when the marsh is

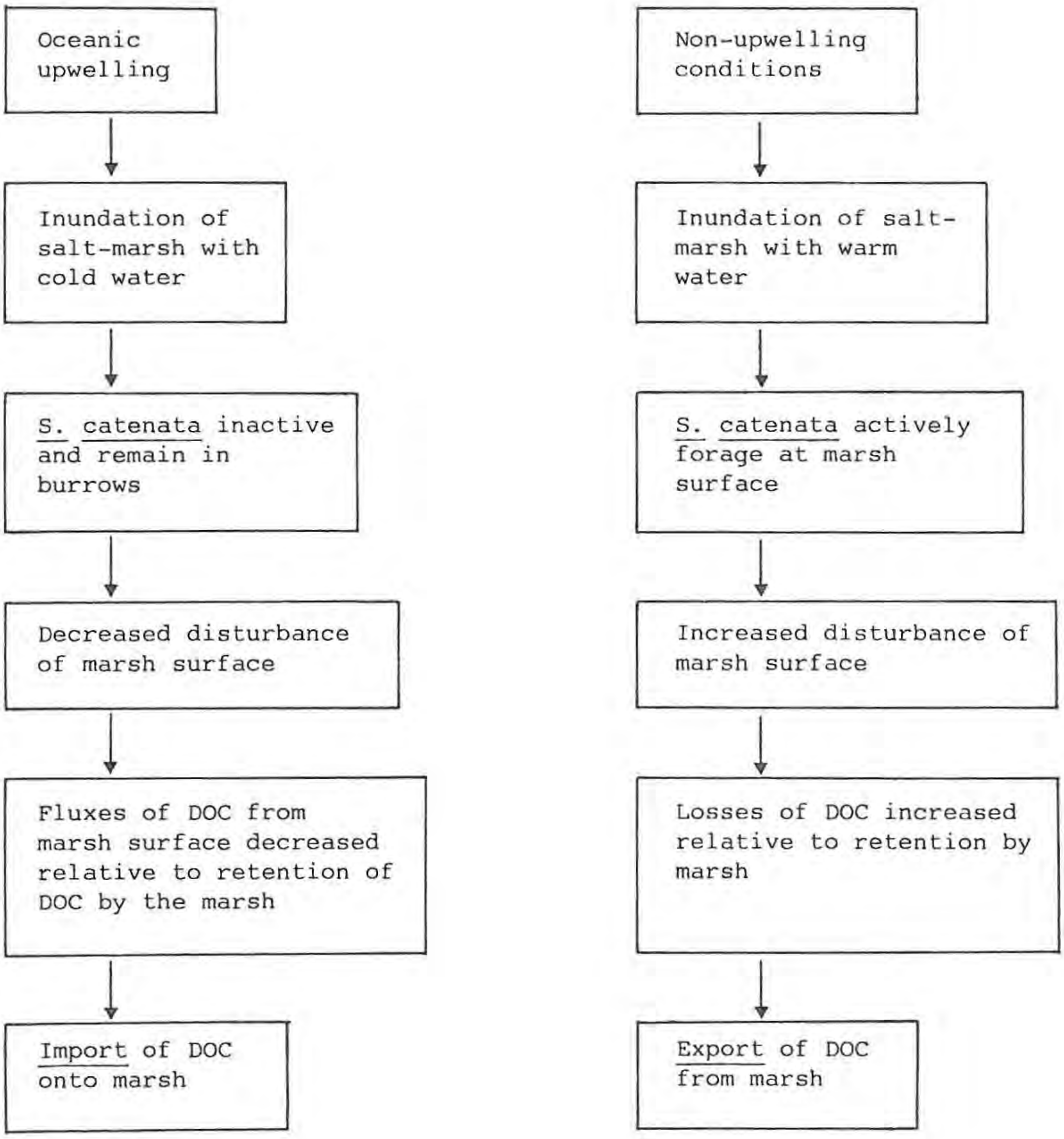


Figure 61 Hypothetical model of the way in which *S. catenata* effects switches in the direction of DOC fluxes between the marsh and estuary in response to mesoscale oceanic events.

inundated by warmer tides the crabs move to the marsh surface and actively forage. Although these behavioural patterns still need to be quantified, they suggest, in combination with the marked influence of crabs on DOC fluxes, that the behavioural responses of crabs to water temperature changes, may be the key factor responsible for the observed DOC shifts.

Data are not available on rates of organic carbon excretion by these, or any other crab species. However, the limited data available for other marine macrofauna suggests that rates of excretory organic carbon losses are smaller than those due to respiration. For example, Field (1972) noted that organic carbon losses from a sea-urchin, Strongylocentrotus droebachiensis, amounted to 60 % of its respiratory carbon losses. The respiratory losses at the marsh surface attributable to crabs were small in comparison to the increased organic carbon losses they effected (Section 5.2). This information suggests that the crab-induced losses of organic carbon from the marsh surface occurred largely as a consequence of bioturbation. These bioturbation effects are important not only because of their magnitude but also because, unlike the carbon losses as CO_2, they involve a transfer of reduced carbon to the water column, where it is potentially available for export to, and use in the adjacent estuary.

As noted earlier, the increased losses of nitrogen from the marsh surface, particularly in the Sarcocornia Zone, occurred mainly as ammonium-N. This component is known to be the major nitrogen-containing excretory product of Crustacea (Needham 1957, Corner and Newell 1967, Snow and Williams 1971), although Spaargaren (1985) has recently noted that nitrate-N may account for up to 63 % of the total inorganic nitrogen excreted by the crab *Carcinus maenas*. Pattinson (1985) reports the following relation between mass-specific rates of excretion ($\underline{S}$) (μmol NH_4-N g^{-1} h^{-1}) and ash-free dry mass g, ($\underline{W}$), for *S. catenata* individuals sampled from this marsh: $\underline{S} = 9.263\ \underline{W}^{-0.696}$. The losses of ammonium-N in the mesocosms attributable to excretion by *S. catenata* were calculated using this equation, the mean number (10) and mean ash-free dry mass (0.65 g) of crabs in the mesocosms, and an inundation period of 2 h per tide. The calculated excretory losses (ca. 3.5 mgN m^{-2} tide^{-1}) were small (21%) in comparison to the enhanced ammonium-N losses in the mesocosms (16.7 mgN m^{-2} tide^{-1}), which points to the importance of bioturbation, as opposed to excretion losses by these crabs. In contrast, the burrowing bivalve, *Theora lata*, increased the fluxes of ammonium-N from subtidal estuarine sediments, but over 80% of the increased losses were due to bivalve excretion (Yamada and Kayama 1987).

Figure 62 summarizes the hypothetical effects of four functional groups of macrofauna on the fluxes of dissolved and particulate material at sediment-water interfaces. Apart from the present study no quantitative data are available on the effects of motile deposit-feeding epifauna (Group 1). Because most information concerns sessile suspension-feeding bivalves (Group 2), and these probably have the opposite effects to crabs, the following analysis compares the bioturbation and biodeposition effects of these two groups. The filter-feeding (Group 3) and deposit-feeding infaunal groups (Group 4) probably perform intermediate functions, and most work done on these groups has been

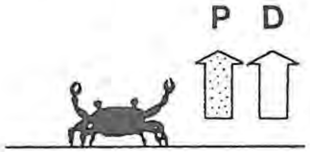
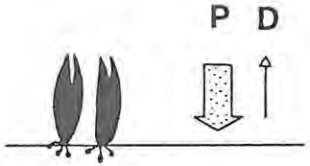
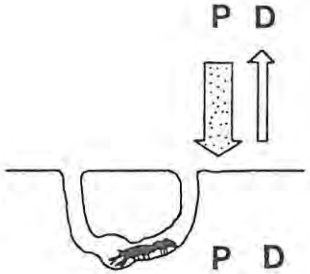
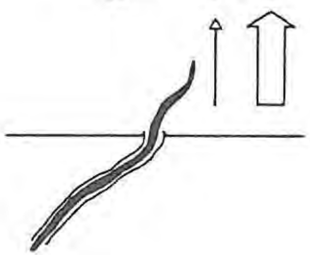
	Functional Group	Effects	Silhouette	References
1.	Motile epifauna (deposit feeders) e.g. *S. catenata* and *C. edwardsii*	*Bioturbation* effect. Increased fluxes of both dissolved and particulate components from sediment surface		This study
2.	Sessile epifauna (suspension feeders) e.g. oyster reefs (*Crassostrea virginica*) mussel beds (*Mytilus edulis*)	*Biodeposition* role. Increased sedimentation of particulate material, greater than increased release of dissolved material		Dame *et al*. 1984 Chrzanowski *et al*. 1986 Kautsky and Evans 1987
3.	Infauna (suspension feeders) e.g. chronomid larvae (*Chironomus plumosus*)	*Bioturbation* plus *biodeposition* role. Increased sedimentation plus increased resuspension and remineralization		Granéli 1979 Matisoff *et al*. 1985
4.	Infauna (deposit feeders) e.g. tubificids (*Limnodrilus* sp.) bivalve (*Theora lata*)	*Bioturbation* role. Increased losses of both dissolved and particulate material.		Matisoff *et al*. 1985 Yamada and Kayama 1987

Figure 62 Effects of different functional groups of macrofauna on fluxes of dissolved (D) and particulate (P) material at sediment-water interfaces.

either theoretical in nature (Aller 1982) or has concerned their effects on sediment structure (e.g. Rhoades 1974).

Chrzanowski *et al.* (1986) have recently demonstrated large transfers of POC from the water column to the sediments of a tidal basin by *Crassostrea virginica* oyster beds. The transfer into the oyster beds was 20 tims greater than the estimate of POC flux from the basin. Conversely, *S. catenata* and *C. edwardsii* increased the fluxes of POC from the marsh surface by factors of 0.1 to 2.4 (Table 9).

Jordan and Valiela (1982) have noted that the ribbed mussel, *Guekensia demissa*, filtered 1.8 times the quantity of PN exported from a *Spartina* marsh by tidal flushing. Half of the PN filtered by the mussels was deposited, while the other half was absorbed. Of the nitrogen absorbed approximately 50% was excreted and returned to the water column as ammonium-N. Kuenzler (1961) noted that 94 % of the particulate phosphorous filtered by *G. demissa* was deposited at the marsh surface and only 6 % was absorbed. Most of the phosphorus absorbed (83%) was excreted to the water column as phosphate - P. In both studies the overall effect was a net transfer of material to the sediments; i.e. biodeposition exceeded mineralization (excretion). Conversely, *S. catenata* and *C. edwardsii* were responsible for the mobilization of these components from the marsh surface mainly through their bioturbation effects.

These results point to the need to reconsider the way in which the role and importance of macrofauna in aquatic ecosystems are assessed. While this is conventionally done by quantifying the rates of passage of energy and matter through the organisms, the present evidence shows that their "indirect" effects, such as bioturbation, may also be important. Similarly, Kuenzler (1961) and Kautsky (1981) have suggested that mussels are more important as agents of sedimentation and nutrient cycling than as agents of energy flow.

7.4 Significance of salt-marshes in the Kariega estuary

Two aspects are implicit in the outwelling hypothesis; firstly, that energy and nutrients are exported in large quantities from salt-marshes, and secondly, that these exports are responsible for "elevated fisheries" in adjacent aquatic systems. Although this dissertation has been primarily concerned with the first of these, certain general conclusions can be drawn regarding the role of salt-marshes in the Kariega estuary. These conclusions are rather tentative, but before the influence of salt-marshes in this system can be quantified more precisely, further data are required on nitrogen and phosphorus fluxes between the marsh and estuary, and particularly on the influence of mesoscale oceanic events on these transfers. Detailed information is also required on the hydrodynamics of the estuary, and especially on the retention times of water in different regions of the system.

Smith (1984) has provided evidence which suggests that whether nutrient limitation occurs in coastal systems or not depends on the retention time of water, relative to the turnover rate of nutrients, in the systems. Therefore in estuaries, or parts thereof, with large advective through-flows of water, other factors such as biomass wash-out may be expected to limit net production. Consequently, in these systems the importance of nutrient inputs from salt-marshes will depend on the hydrodynamic characteristics of the estuary, and on the location of salt-marshes within it.

In view of the attenuated river inflows into the Kariega estuary, the allochthonous river inputs of organic carbon, nitrogen and phosphorus will probably also be attenuated. This would make the estuary, and particularly its upper reaches more dependent on internal biogeochemical cycling (i.e. more "closed") than estuaries receiving large freshwater inflows. Therefore in estuaries, which receive attenuated river inflows, exports of material from salt-marshes will play a disproportionately elevated role in the functioning of the estuarine ecosystem. This contrasts with the situation observed for many north temperate estuaries (e.g. Haines 1977), but the nature of the estuaries in the two regions are different. The southern African sub-continent is semi-arid, and consequently its estuaries receive small freshwater inflows, which are also seasonal. The estuaries in the eastern Cape region of South Africa are deeply incised river valleys inundated after the previous glaciation (Heydorn and Tinley 1980), and are therefore narrow, elongate systems with large intertidal to pelagic ratios. This suggests that although the salt-marshes in these estuaries are not as expansive as those on the east coast of North America they probably play a more important role in the functioning of these estuaries than their size would indicate.

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Appendix 1 Vertical (a) and horizontal (b) variability of velocity readings (m/s) at the marsh-estuarine junction. Vertical readings were taken at 0.1m depth intervals at Station L3, and horizontal readings at mid-depth at Stations L1-L5. Readings made at mid- and high-tide during flood and ebb phases of the tide of 12 June 1984. Velocity differences across the channel (b) were consistently greater than vertical changes through the water column in midchannel (a). Consequently, the sampling programme designed to measure discharge between the marsh and estuary emphasized horizontal rather than vertical velocity variability (see Section 3.3).

(a) VERTICAL VARIABILITY:

Tide Level (m.a.m.s.l.)	Depth interval from surface (m) 0 - 0.10	0.11 - 0.20	0.21 - 0.30	0.31 - 0.40	0.41 - 0.50	0.51 - 0.60
0.89 (flood)	.02	.02	.03	.04	.05	.02
1.01 (flood)	.03	.03	.03	.03	.04	.06
1.09 (flood)	.03	.04	.04	.03	.04	.04
1.07 (ebb)	.03	.03	.03	.04	.04	.03
1.02 (ebb)	.03	.03	.04	.04	.03	.02

(b) HORIZONTAL VARIABILITY:

Tide level (m.a.m.s.l.)	Station L1	L2	L3	L4	L5
0.92 (flood	.05	.04	.03	.02	0
1.04 (flood)	.10	.05	.035	0	0
1.11 (flood)	.09	.07	.03	.025	0
1.05 (ebb)	.05	.03	.07	0	0
1.00 (ebb)	.05	.03	.06	0	0

Appendix 2. Surface flood-, ebb-, and net discharges over 47 semi-diurnal tides. Negative signs denote discharge onto marsh, positive values indicate discharge to estuary.

Date	Maximum tide height (m.a.m.s.l.)	Flood discharge (m^3)	Ebb discharge (m^3)	Net discharge (m^3 $tide^{-1}$)	Net discharge/ inflow (%)
8.5.84	0.99	-338	+305	-33	10
9.5.84	0.90	-222	+198	-24	11
10.5.84	0.95	-279	+253	-26	9
11.5.84	0.95	-252	+248	-4	2
12.5.84	1.22	-1083	+1159	+76	7
13.5.84	1.63	-13721	+11980	-1760	13
14.5.84	1.67	-14454	+12590	-1864	13
27.7.84	1.06	-906	+910	+4	2
28.7.84	0.99	-356	+366	+10	3
29.7.84	0.95	-295	+318	+23	7
30.7.84	0.91	-283	+316	+33	10
31.7.84	1.01	-425	+400	-25	6
9.8.84	0.81	-115	+127	+12	9
10.8.84	0.91	-260	+252	-8	3
11.8.84	0.95	-295	+310	+15	5
12.8.84	1.00	-411	+394	-17	4
13.8.84	1.15	-1159	+1108	-51	4
14.8.84	1.01	-601	+636	+35	6
15.8.84	0.97	-309	+282	-27	9
16.8.84	0.85	-182	+174	-8	4
17.8.84	0.77	-135	+125	-10	7
2.11.84	0.85	-172	+141	-31	18
3.11.84	0.84	-172	+176	+4	2
4.11.84	0.94	-369	+372	+3	0
5.11.84	0.95	-310	+319	+9	3
6.11.84	0.83	-217	+204	-13	6
7.11.84	0.83	-134	+116	-18	13
8.11.84	1.13	-988	+910	-78	8
9.11.84	1.21	-1440	+1315	-125	9
10.11.84	0.98	-363	+365	+2	0
11.11.84	0.92	-302	+289	-13	4
17.1.85	0.88	-201	+186	-15	8
18.1.85	1.12	-920	+866	-54	6
19.1.85	1.21	-1193	+1220	+27	2
20.1.85	1.15	-1016	+1111	+95	9
21.1.85	1.11	-739	+665	-74	10
22.1.85	1.29	-1918	+1977	+59	3
23.1.85	1.27	-1410	+1367	-43	3
24.1.85	1.25	-1738	+1574	-164	9
25.1.85	1.11	-705	+697	-8	1
26.1.85	1.02	-432	+428	-4	0
27.1.85	1.0	-457	+433	-24	5
20.4.86	1.05	-525	+555	+30	5
21.4.86	1.07	-444	+424	-20	4
23.4.86	1.24	-1106	+1052	-54	5
25.4.86	1.16	-1009	+936	-73	7
26.4.86	1.33	-2756	+2708	-48	2