An analysis of factors controlling the distribution of zooplankton in the Knysna estuary, South Africa.

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Thesis submitted for the Degree of Master of Science in the
Zoology Department, Faculty of Science,
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September 1987.

CONTENTS

APPENDICES

ABSTRACT

The Knysna estuary system, on the south coast of South Africa, was sampled for zooplankton over period of one year. All species were recorded and an attempt was made at relating the distribution of populations to physical factors within the estuary. Over 50 species were identified. *Pseudodiaptomus hessei, Acartia(Paracartia) longipatella* and *A.(Acartiella) natalensis* were the dominant copepods in the upper estuary. *Paracalanus* spp. were dominant near the mouth. Zooplankton distribution was found to be related to tidal exchange. The zooplankton displayed a seasonal cycle of abundance, with maximum numbers occuring during summer. *P. hessei* displayed no pronounced seasonal cycle in abundance. Its abundance was strongly related to freshwater inflow. Seasonal succession was evident between *A. natalensis,* the summer dominant, and *A. longipatella,* the winter dominant. The controlling factors for this cyclical dominance were not clear. Diel vertical migration behaviour was shown to various degrees by virtually all zooplankton populations. The stimulus for this behaviour could not be definitely identified.

INTRODUCTION

BACKGROUND

In South Africa there is a rapidly increasing demand for fresh water from the agricultural, industrial and urban sectors. Because of the arid nature of this country it is becoming increasingly important to examine critically water requirements for other uses. One such requirement is for the proper functioning of estuaries.

In 1984 a 3-year project was launched to investigate the freshwater requirements for the Knysna estuary. This system was chosen for a pilot study since it is one of South Africa's richest estuaries, and is of considerable importance from a recreational point of view. The hydrology and biology of the system was thoroughly investigated with emphasis on salinity. The zooplankton populations were studied to determine possible short-term and immediate responses to salinity fluctuations.

The first detailed account of the ecology of this system was published by Day, Millard and Harrison (1952). In comparison with other estuaries, Knysna was found to have the richest fauna amongst South African estuaries, comprising 357 species excluding fish, birds and plankton. Day (1967) published a further account of the biology of Knysna estuary. Here attention was drawn to the role of detritus. Genade (1973) and Korringa (1956) published accounts on oyster culture. Other publications covered topics such as siltation problems (Chunnett 1965), trace-metal studies (Watling & Watling 1975) and ecological impact and conservation managemant reports (Grindley 1976, Grindley & Snow 1983).

Plankton studies in the estuary have usually formed part of impact analyses and sampling has been restricted to either specific areas in the estuary, or to single occasions. No studies have been undertaken to investigate possible long-term changes and adaptations in the zooplankton.

This thesis is the result of one year of sampling the zooplankton population in the Knysna estuary. The aim of the study was dual purpose in firstly attempting to detect any short-term and immediate responses to changes in salinity, and secondly, to provide a comprehensive record of the zooplankton and the factors controlling its distribution in this particular system.

REFERENCES

Chunnett, E.P. 1965. Siltation problems in the Knysna lagoon. *CSIR Report MEG 353*, Pretoria. 25pp.

Day, J.H. 1967. The biology of Knysna estuary, South Africa. In: *Estuaries*. Lauff, G.H. (ed.) Washington, DC. American Association for the Advancement of Science Publication No. 83 : 397-407.

Day, J.H., Millard, N.A.H. & Harrison, A.D. 1952. The ecology of South African estuaries. Part III Knysna: A clear open estuary. *Trans. Roy. Soc. S. Afr.* 33(3) : 367-413.

Genade, A.B. 1973. A general account of certain aspects of oyster culture in the Knysna estuary. *S. Afr. Nat. Oceanogr. Symposium. Cape Town.* Abstracts : 26-28.

Grindley, J.R. 1976. *Report on the ecology of Knysna estuary and proposed Braamekraal marina.* School of Environmental Studies, Univ. of Cape Town. 123 pp.

Grindley, J.R. & Snow, C.S. 1983. *Environmental effects of the discharge of sewage effluent into Knysna lagoon.* School of Environmental Studies, Univ. of Cape Town. 55 pp.

Korringa, P. 1956. Oyster culture in South Africa. Hydrological, biological and ostreological observations in the Knysna lagoon, with notes on conditions in other South African waters. *Invest. Rep. Div. Sea Fish. S. Afr.* **20**. 85 pp.

Watling, R.J. & Watling, H.R. 1975. Trace metal studies in Knysna estuary. *Omgewing - Environment RSA* 2(10) : 5-7.

PART I

The distribution of zooplankton in the Knysna estuary system, South Africa.

1.1 ABSTRACT

Zooplankton distribution in the Knysna estuary system was investigated. More than 50 zooplankton species were identified, and the average annual dry biomass was calculated at 186mg.m^{-3}. Through most of the estuary the dominant copepods were *Pseudodiaptomus hessei, Acartiella natalensis* and *Paracartia longipatella*. Due to the permanently open mouth, ocean water penetrates as far as Thesen's Island on each high tide. Neritic copepods such as *Calanoides carinatus* and *Centropages brachiatus* thus were recorded some distance up the estuary. The Ashmead Channel east of Thesen's Island was inhabited by a truly estuarine zooplankton community.

No relationship was found between copepod distribution and temperature or dissolved oxygen. The copepods were distributed along a salinity gradient from truly estuarine species at the head of the estuary to neritic forms near the mouth. Tidal exchange was found to be the most important factor determining the distribution of copepods in this system. The role of zooplankton in estuaries is discussed briefly.

1.2 INTRODUCTION

The Knysna estuary is situated on the south coast of South Africa, 501 km east of Cape Town (34°04'35"S 23°03'40"E). It is one of South Africa's richest estuaries, probably because of its permanently open rocky mouth and the clarity of the water (Day *et al* 1952). It is also of considerable recreational and economical importance.

For these reasons Knysna estuary has been the focal point of many studies and a substantial body of both published and unpublished information on the system are available. Knowledge on the zooplankton is, however, limited to single sampling observations, usually during summer. This paper is the first of three discussing distribution of the zooplankton in Knysna estuary with respect to physical controlling factors in both the short and longer term, biological factors and behavioural adaptations.

This first paper is aimed at relating the distribution of various zooplankton species to physical conditions within the estuary.

1.3 PHYSIOGRAPHY

The Knysna River arises in the Outeniqua mountains and the catchment area of 526km^2 receives an average rainfall of 922mm spread relatively evenly through the year. As a result there is a steady flow of water into the estuary. The river runs through a steep, wooded gorge where slope erosion is minimal, so that the river is clear, though peat-stained. The riverflow is usually not strong. Once in ten or twelve years the river is said to come down in flood, staining the whole estuary brown and killing off much of the benthic fauna (Day *et al* 1952). This may be very significant in maintaining an estuarine rather than a marine fauna in the lagoon.

The estuary is an S-shaped stretch of water with a channel about 19km long, broadening to form a lagoon over 3km wide and up to 6m deep (Fig. 1.1). At the head of the estuary the river has cut deeply into the flood plain, but thereafter the banks become flatter and there are many intertidal salt marshes between the Red Bridge and Leisure Isle near the heads.

The estuary opens between two rocky headlands which prevents a sandbar forming and closing the mouth. Marine sediments do not enter the estuary. This makes Knysna estuary unusual among South African estuaries. The tidal reach is about 10km and the tidal range and fall at the mouth at spring-tide is 1.8m, which is maintained right up to the Red Bridge (Grindley 1985). Ocean water penetrates on each high tide. During spring tides the ocean water penetrates to well beyond the railway bridge, mixing with the more turbid green water in the shallows (Grindley 1985). This facilitates the

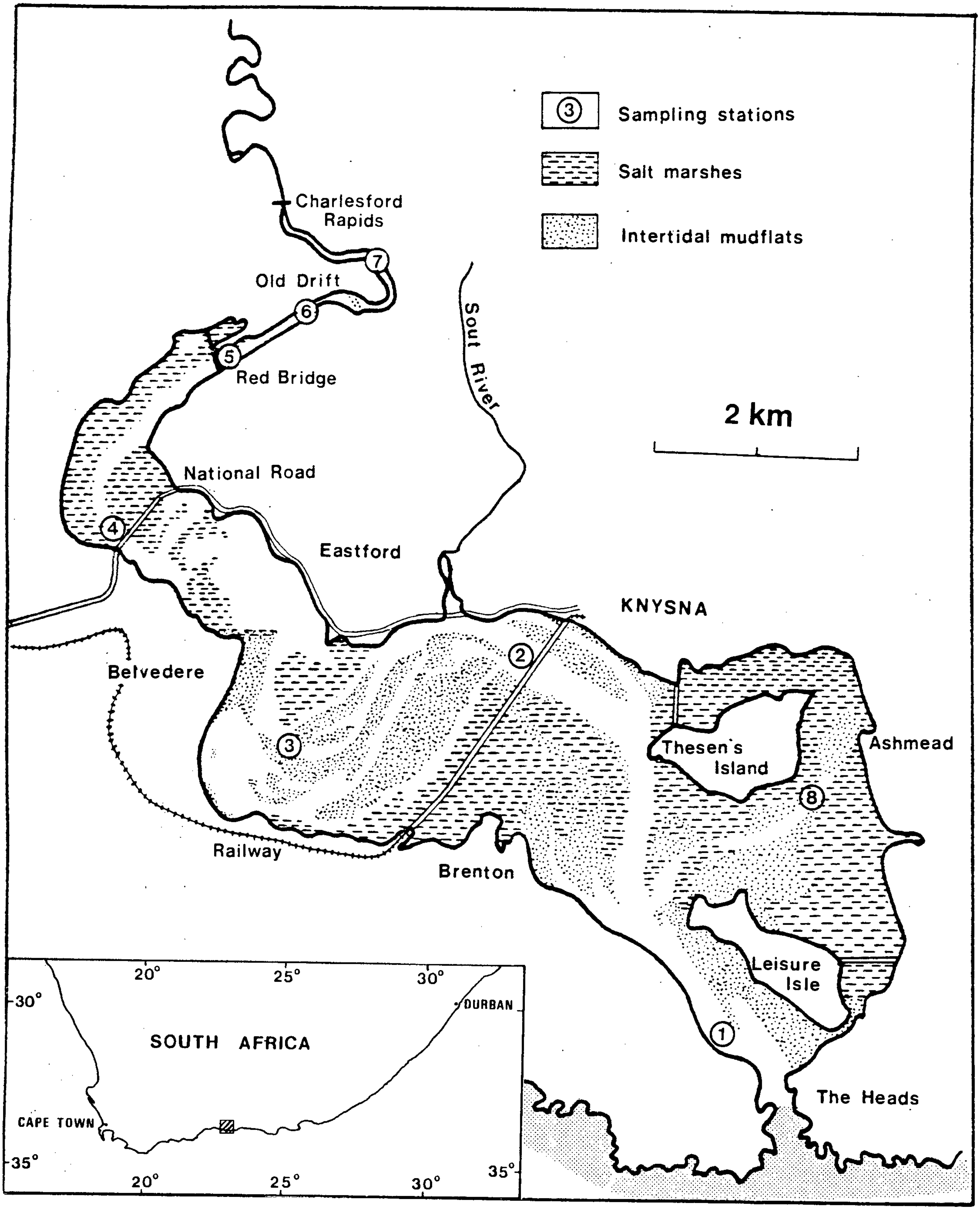

FIG. 1.1 : Map of Knysna estuary and location of the sampling stations.

penetration of neritic marine species and limits the survival of purely estuarine species.

1.4 METHODS

Sampling was undertaken at a series of 7 stations spread up the length of the estuary from the mouth to the head, as well as an eighth station in the Ashmead Channel (Fig. 1.1). Samples were taken once in summer (December) and once in winter (June). Both surface and bottom samples were taken at each station, at night and during daylight hours. By sampling in different seasons and times of day, as well as taking both surface and bottom samples, it was hoped to include as many of the species present as possible.

Surface measurements of salinity, temperature and dissolved oxygen were made at all stations immediately prior to zooplankton collection. Temperature and dissolved oxygen were measured with a YSI Model 57 dissolved oxygen meter, and salinity with an AOC Model 10419 automatic temperature compensated hand refractometer. Sampling commenced at mid-day to mid-afternoon at station 1 and proceeded up the estuary to station 7. After darkness, and while the tide was high, sampling proceeded from station 7 down towards the mouth. This sampling technique combined with the tidal lag in the estuary, resulted in all samples being taken at around mid-tide with slow tidal currents.

The zooplankton samples were taken with a 36cm diameter plankton net with 124um aperture nylon mesh. A D-shaped net of the same aperture size and also with a 124um nylon mesh was used for the bottom samples. This net was weighted and fitted on to a simple sledge to allow it to sample the water just above the bottom, without collecting the sediment. Both nets were hauled simultaneously for 2 minutes at approximately 2 knots from a 15hp motor boat. The bottom net was closed before it was hauled to the surface to prevent sampling the upper water column.

After every haul the nets were carefully rinsed to prevent contamination of the next sample. The samples were immediately preserved with 5% formalin and analysed in the laboratory.

Each sample was made up to a standard volume (500ml), from which 25ml subsamples were taken after agitation. The subsamples were counted and the animals identified to species, where possible. Relative abundance of species was then expressed in symbols from + = present to ++++ = very abundant.

1.5 RESULTS

The hydrological data are presented graphically in Fig. 1.2. Values are averaged for day and night observations. Station 8 was only sampled in summer.

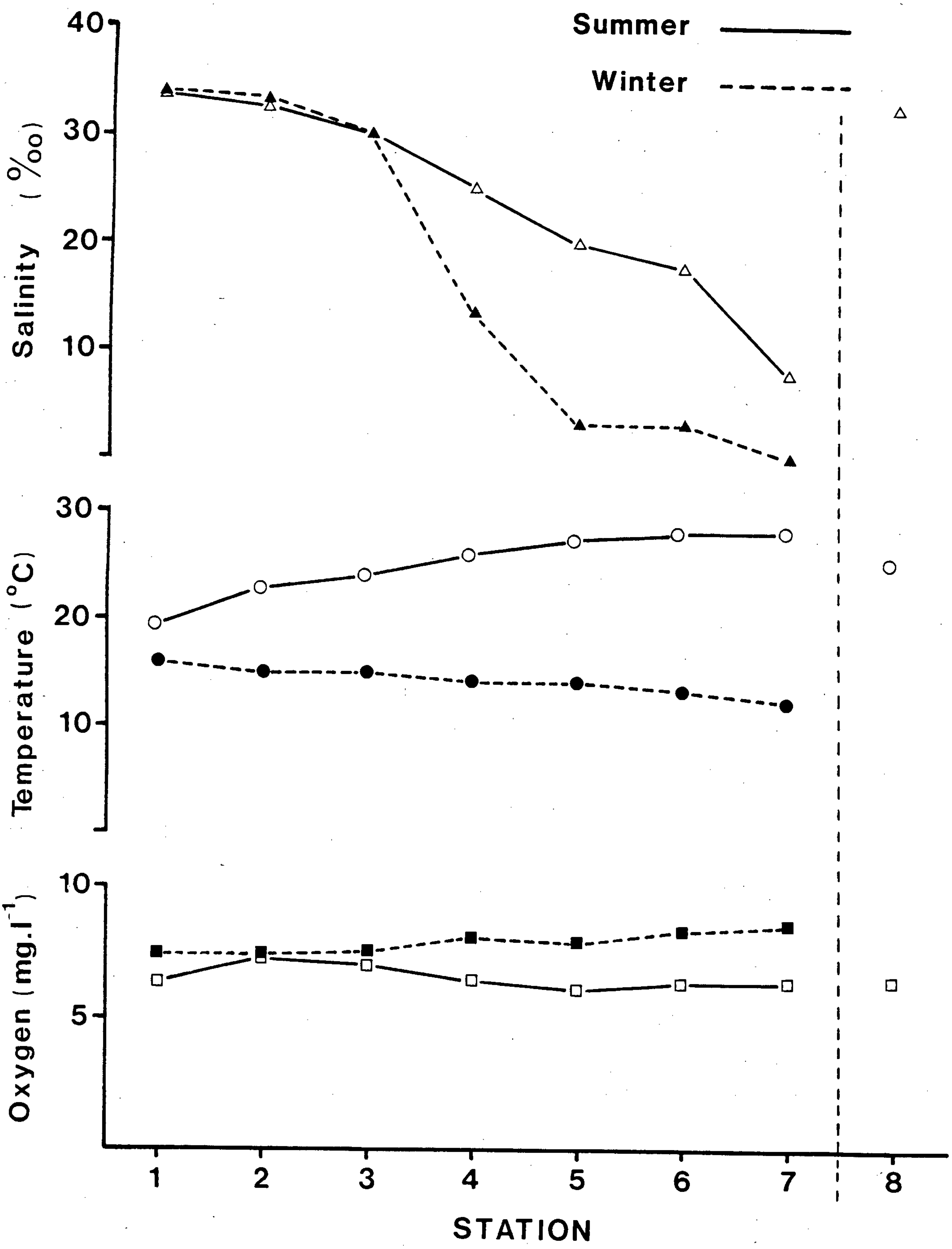

FIG. 1.2 : Recorded surface salinity (°/oo), temperature (°C) and dissolved oxygen (mg.l^{-1}) for different sampling stations on 26 June 1985 (winter) and 1 December 1985 (summer).

The salinity decreased from 34°/oo at the mouth (station 1) to 0°/oo at the head, with the greatest salinity change occurring between stations 3 and 5. The dissolved oxygen content of the water increased from 7,5 $mg.l^{-1}$ at station 1 to 9 $mg.l^{-1}$ at station 7 in winter. This pattern was reversed in summer with a slight decline in oxygen content from 6.5 $mg.l^{-1}$ at the mouth to 6.1 $mg.l^{-1}$ at the head. The surface water temperature also showed a reversed pattern between summer and winter. In summer temperatures increased from 19.5°C to 28.0°C from mouth to head, and in winter they declined from 16.5°C to 12.5°C. During the winter months the estuary is thus cooler than the sea, and in summer it is warmer.

At station 8, the Ashmead Channel, high salinities, similar to those in the adjacent main channel (33°/oo) were measured. Measured surface temperatures were, however, higher than in the adjacent main channel, and the dissolved oxygen content was lower. The higher temperature and lower oxygen reflect the shallowness of the channel.

An average annual biomass of 186$mg.m^{-3}$ was calculated from samples collected throughout the year (see Part II).

All zooplankton species collected and identified are presented in Table 1.1. Over 50 species were identified. The zooplankton was dominated by Copepoda. Amphipoda and Mysidacea contributed several species, but their numeric abundance was always relatively low. Isopoda, Annelida,

TABLE 1.1 : Zooplankton species recorded in the Knysna estuary and their relative abundance. (+ = present, ++ = common, +++ = abundant, ++++ = very abundant)

SPECIES	St.1	St.2	St.3	St.4	St.5	St.6	St.7	St.8
PROTOZOA								
Foraminifera	+	+	+	+	-	-	-	-
Noctiluca millaris	++	++	+	-	-	-	-	
CTENOPHORA	+	-	-	-	-	-	-	-
POLYCHAETA								
Polychaete larvae	-	+	+	+	++	++	+	+
Prionospio sexoculata	-	-	-	+	+	-	-	-
ACARINA								
mite	-	-	-	-	+	-	++	-
CRUSTACEA								
Ostracoda	-	-	+	-	-	-	-	+
Copepoda								
Acartia(Paracartia) africana	+++	++	++	++	-	-	-	+++
Acartia(Paracartia) longipatella	++	++	++	+++	++	++	++	-
Acartia(Acartiella) natalensis	-	+	++	+++	+++	+++	++	-
Acartia spp. immature	+++	+++	+++	+++	+++	+++	+	+++
Calanoides carinatus	++	++	-	-	-	-	-	-
Centropages brachiatus	+	-	+	-	-	-	-	-
Coryceus spp.	+	+	-	-	-	-	-	-
Cyclops spp.	-	-	-	-	+	++	+++	+++
Harpacticoid copepods	++	++	++	+++	+++	+++	++++	++++
Halicyclops spp.	-	-	-	++	+	++	++	-
Nauplii stages	+++	++++	++++	++++	++++	+++	++	++++
Oithona brevicornis/nana	+++	+++	+++	++	+	++	++	-
Oithona similis	+++	++	?	-	-	-	-	-
Oncaea subtilis	+++	++++	+	-	-	-	++?	-
Oncaea mediterranea?	+	+	-	-	-	-	-	-

Paracalanus aculeatus	+	-	-	-	-	-	-	-
Paracalanus crassirostris	++	++	+	-	-	-	-	-
Paracalanus parvus	+++	+++	+	-	-	-	-	-
Paracalanus spp. immature	+	+	-	-	-	-	-	-
Pseudodiaptomus hessei	-	+++	+++	++++	++++	++++	++++	++++
Pseudodiaptomus nudus	+	-	-	-	-	-	-	-
Pseudodiaptomus spp. immature	++++	++++	++++	++++	++++	++++	++++	++++
Saphirella stages	-	++	++	++	-	-	-	-
Cirripedia								
Cirripede nauplii	+	++	+	+	++	++	+	-
Decapoda								
Zoea and mysis larvae	+	++	++	++	++	++	++	++++
Mysidacea								
Gastrosaccus brevifissura	++	-	+	++	+	-	-	+
Mesopodopsis similis	-	-	-	+	+	-	-	-
Mysidopsis similis	-	-	+	-	-	-	-	-
Rhopalophthalamus terranatalis	-	-	-	-	+	-	-	-
Cumacea								
Iphinoe truncata	+	+	+	-	+	+	-	+
Tanaidacea								
Tanaid sp.	+	+	+	+	-	-	-	-
Isopoda								
Exosphaeroma immature	-	+	+	-	-	-	+	
Eurydice immature	+	-	-	-	-	-	-	-
Parasitic isopod	-	+	+	+	+	-	+	+
Amphipoda								
Afrochiltonia subtenuis	-	++	+	+	-	+	+	+
Corophium triaenonyx	-	-	-	+	++	++	++	-
Cymadusa filosa	-	-	+	+	-	-	-	-
Hyale maroubrae	-	-	-	-	-	+	-	-
Melita zeylanica	-	-	-	+	+	+	+	-
Paramoera capensis	-	+	+	+	-	-	-	-
Perioculodes longimanus	+	+	+	-	-	-	-	-
Urothoe sp.	-	-	-	-	-	-	+	-

INSECTA								
Chironomid larvae	-	-	-	-	+	++	++	-
MOLLUSCA								
Gastropod larvae	+	++	+++	++	+++	+++	++	
Lamelibranch larvae	+	+		+	+	++	+	
CHAETOGNATHA								
Sagitta sp.	+	+	+	+	+	-	+	-

Mollusca, Insecta and other organisms were present in lesser numbers.

Ctenophora were only collected once at station 1 during the day. Generally only the larval stages of the Polychaeta were collected in the plankton, but occasionally adult *Prionospio sexoculata* were recorded. The larvae were most abundant in summer, in the upper estuary.

Ostracoda were only collected occasionally, once at station 3 and once in the Ashmead Channel.

The distribution range of each species is largely a function of the range of salinities it can tolerate. The salinity tolerance ranges of various Copepoda are shown in Fig. 1.3. The Copepoda in Knysna estuary can broadly be divided into three groups on this basis of salinity: 1) a stenohaline community at stations 1 and 2, where the salinity is high and relatively stable, 2) a euryhaline community at stations 2 and 3, and 3) true estuarine communities from station 3 to 7, the regions with low and variable salinity regimes.

The first category include species such as *Oncaea subtilis*, *Calanoides carinatus*, *Centropages brachiatus*, *Oithona similis*, and *Corycaeus* spp. These are stenohaline neritic marine forms (Grindley 1985) that can penetrate into the estuary due to the fact that the salinity up to station 2 is close to that of seawater. On the high tide full salinity sea water penetrates as far as Thesen's Island.

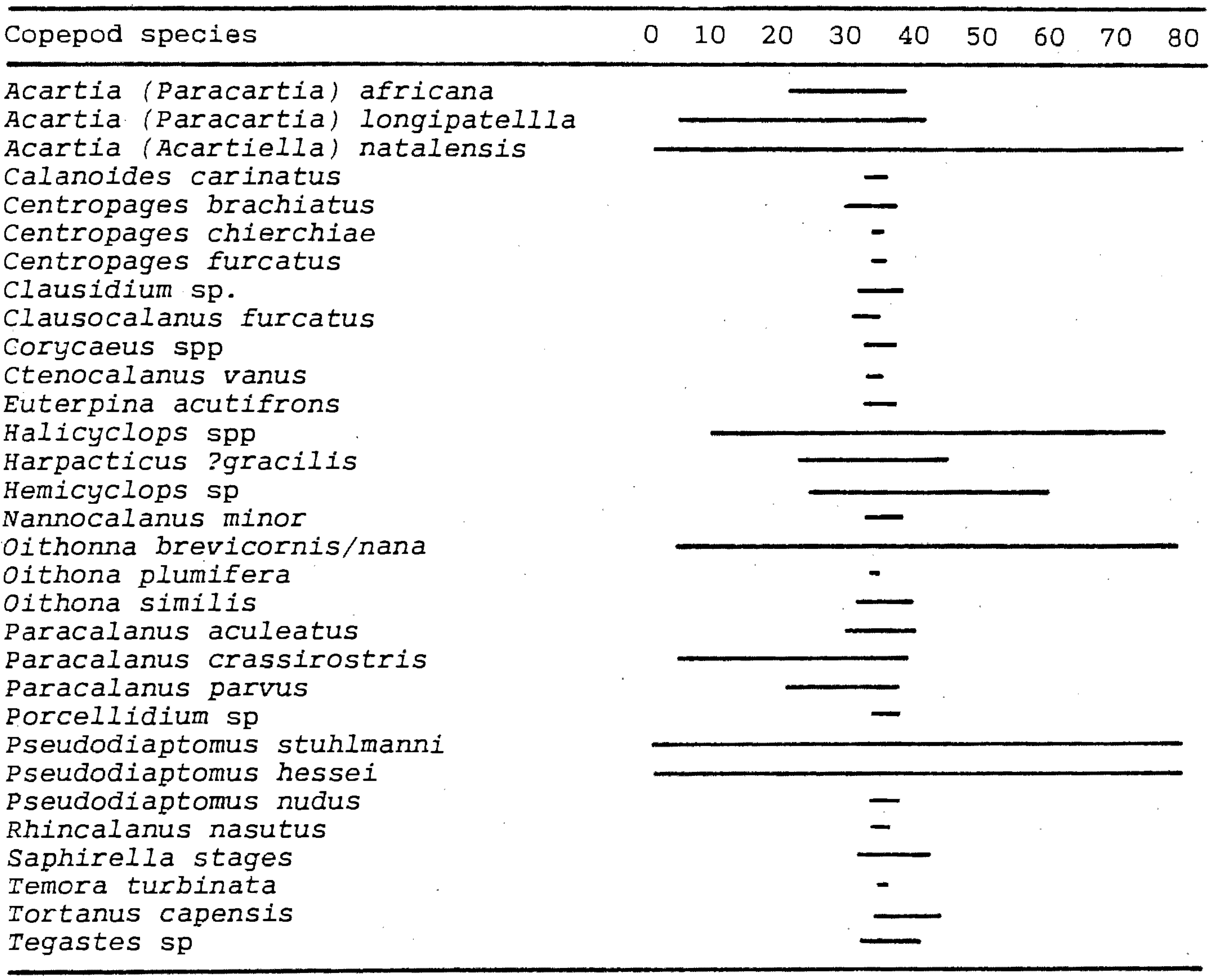

FIG. 1.3 : Recorded salinity range of Copepoda (from Grindley 1981).

Paracalanus crassirostris and *P. parvus* were relatively common at station 2, and occasionally present at station 3, and fall into the second category. These are euryhaline species, tolerable of a wider range of salinities, and can thus penetrate up to station 3. These two species occur in most estuaries on the south and east coast of South Africa (Grindley 1985). Korringa (1956) recorded *Paracalanus parvus* as one of the common species at the Heads and 2.5 miles off-shore. According to Fig. 1.3 *Paracalanus crassirostris* has a recorded salinity range of 5 - $40^{o}/_{oo}$. It could thus tolerate, and theoretically extend its range into, the less saline water of the upper estuary. By contrast *P. parvus* is restricted to the lower reaches of the estuary by its narrow range of salinity tolerance.

The third category, the true estuarine forms, includes species such as *Acartia (Paracartia) africana*, *Acartia (Paracartia) longipatella*, *Acartia (Acartiella) natalensis*, *Pseudodiaptomus hessei* and *Oithona nana/brevicornis*. These species are tolerant of a wide range of salinities (Fig. 1.3). *Acartiella natalensis*, *Paracartia longipatella* and *Pseudodiaptomus hessei* are the dominant copepods in the upper reaches of the estuary.

Harpacticoid copepods were difficult to identify and were therefore not separated into species. They were more common in the upper estuary. Quantitative counts indicated approximately 2-3 times as many species occurring in the upper estuary above station 4 compared to the lower estuary.

The Mysidacea are represented by *Gastrosaccus brevifissura*, *Mesopodopsis africana*, *Rhopalophthalamus egregius* and *Mysidopsis similis*. *Gastrosaccus* occurs in the lower estuary, while *Rhopalophthalamus* and *Mesopodopsis* are more common in the upper estuary. Net avoidance by mysids probably affects the relative abundance as indicated in Table 1.1. The Cumacea include *Iphinoe truncata*.

Tanaidacea were only recorded in the lower estuary. *Apseudes digitalis*, a common estuarine tanaid, was identified.

The Isopoda were only represented by immature forms, of which *Exosphaeroma* and *Eurydice* were identified. A parasitic isopod was often recorded throughout the estuary.

The Amphipoda include *Corophium triaenonyx* and *Melita zeylanica* in the upper estuary and *Paramoera capensis*, *Perioculodes longimanus*, and *Cymadusa filosa* lower down in the estuary. *Afrochiltonia subtenuis* occurred throughout the estuary. Immature *Corophium triaenonyx* were exceptionally abundant in the upper reaches of the estuary in winter.

Chironomid larvae were only present from stations 4 - 7, when salinities were below $10^{\circ}/_{\circ\circ}$.

Larvae of lamellibranchs and gastropods, crab zoea mysis larvae and cirripede nauplii were generally more abundant during summer. Zoea larvae occurred throughout the estuary, but were exceptionally abundant at station 8 in summer. Gastropod and lamellibranch larvae were concentrated in the upper and middle estuary.

The Chaetognatha were represented by a species of *Sagitta*.

The Ashmead channel (st. 8) has a high salinity (35°/oo at the time of sampling), yet has an estuarine component of zooplankton. *Pseudodiaptomus hessei* was by far the numerically dominant copepod. *Paracartia africana* was the only species af *Acartia* present, and more abundant than elsewhere in the estuary. *Acartiella natalensis* and *Paracartia longipatella* were present in significant numbers in the rest of the estuary, but did not seem to occur in the Ashmead channel. Grindley (1978) recorded *Acartiella natalensis* from this area in summer (January). *Paracartia longipatella* could possibly be present in the Ashmead channel during the colder winter months, since it usually replaces *A. natalensis* in winter in the rest of the estuary, and also in other systems (Wooldridge & Melville-Smith 1979).

No relationship between temperature and oxygen and the distribution of zooplankton species were evident. Temperature appears to be of importance only on the longer term, affecting seasonal differences in zooplankton numbers and composition.

1.6 DISCUSSION

The mouth of Knysna estuary is inhabited by neritic species, while further up estuarine species dominate the zooplankton. *Paracalanus* spp. are numerically most abundant in the lower reaches, while *Pseudodiaptomus hessei* and *Acartia* spp. are the dominant copepods in the upper estuary.

Day (1967) described the zooplankton of Knysna estuary as rather poor and suggested that plankton is not a major food source in the estuary, since there are relatively few plankton feeders. An analysis of Table 1.2 shows that, compared with other South African estuaries, Knysna estuary is in fact relatively rich in both zooplankton biomass and species diversity. West coast estuaries have very low zooplankton species diversity and biomass. Not all of these are true estuaries all year round, which partly explains their poor planktonic fauna. The Orange River is in fact a river mouth rather than an estuary. The Berg and the Olifants run fresh to the sea during winter, which results in a seasonally fresh or neritic zooplankton community. Milnerton is cut off from the sea and hypersaline in summer, with a resulting impoverished fauna. Many of the south coast estuaries are seasonally closed off from the sea by a sandbar, such as for example the Bot River and Swartvlei estuaries, or siltation and turbidity are high. Extreme salinity fluctuations and turbidity have been associated with an impoverished fauna. East coast estuaries generally display a richer species diversity, probably due their subtropical nature. Knysna can be compared to east coast estuaries in species diversity evidently due to its permanently open mouth and clear water.

Biomass is not a very reliable source for comparison, since it is a temporally extremely variable entity. Only long-term

TABLE 1.2 : Biomass and diversity of zooplankton in South African estuaries

	Dry Biomass ($mg.m^{-3}$)	Diversity (No. of spp)
Orange river estuary*	55.6	17
Groen river estuary*	8.5	6
Olifants river estuary*	26.5	32
Berg river estuary*	16.2	25
Rietvlei*	<3.0	13
Milnerton estuary*	23.7	28
Klaasjagers estuary*	5.6	17
Bot river estuary (Coetzee 1985)	83.1	44
Swartvlei (Grindley 1981)	116.0	45
Knysna	**186.1**	**>50**
Keurbooms (Day, 1981)	56.0	-
Swartkops (Grindley 1981)	50.0	-
Sundays (Wooldridge & Bailey 1982)	730.0	-
Keiskamma estuary (Read & Allanson 1983)	2562.0	32
Msikaba estuary (Wooldridge 1976)	15.5	67
Richards Bay (Grindley & Wooldridge 1974)	175.0	<80
St. Lucia (Grindley, 1976)	52.5	93

* Grindley (1979)

monitoring over several years would give a truer reflection of the standing stock. Most biomass records rely on a few irregular samples taken over a one year period. Nevertheless, the biomass in Knysna estuary appears to be among the higher values estimated for South African estuaries (Table 1.2). The biomass data for the Keiskamma estuary is probably somewhat biased in that the data was collected during drought conditions. Biomass increased with increasing salinity in the upper estuary.

1.6.1 Salinity

Salinity is a controlling factor determining the distribution of zooplankton in the estuary in that each species has a salinity range within which it survives and can optimally thrive.

Thus, for example, copepod zooplankton in the Bristol Channel and Severn Estuary have been divided into four distinct assemblages along a salinity gradient (Collins & Williams 1981). *Eurytemora affinis* was the dominant true estuarine copepod in water at salinities less than 28°/oo. *Acartia bifilosa* occurred in salinities of 27 to 33.5°/oo and is considered estuarine and marine. *Centropages hamatus* is the most abundant of the euryhaline assemblages (31 - 35°/oo) and the stenohaline species *Calanus helgolandicus* occurs at salinities > 33°/oo.

Similarly, the zooplankton species in Knysna estuary have a preferred salinity range in which they predominate. *Pseudodiaptomus hessei* and *Acartiella natalensis* are the dominant true estuarine copepods. *Paracartia africana* can be considered estuarine and marine, since it occurred predominantly in the lower estuary, in salinities ranging from 18°/oo to 34°/oo, but is known to occur in marine waters off Namibia (Unteruberbacher 1964). *Paracalanus parvus* is a euryhaline species occurring at stations 1 to 3, at salinities between 30 and 35°/oo. *Calanoides carinatus* is a stenohaline species occurring only at salinities >32°/oo.

1.6.2 Tidal exchange

The presence of an estuarine population in the Ashmead channel, where salinities are high, is somewhat of an anomaly if one considers salinity as the prime factor determining the distribution of zooplankton in estuaries. Grindley & Wooldridge (1974) suggested that the distribution of zooplankton in estuaries is affected by the extent of tidal exchange. They found tidal exchange to be the single most important factor controlling the distribution of copepods in Richards Bay.

The distribution of zooplankton in estuaries will be determined by the circulation of fresh and salt water and by the exchanges between various parts of the estuary. These exchanges are regulated by tidal oscillation in the short term, and fluctuations in river flow over the longer periods of time. In addition to the tidal movements there is a net seaward movement of water. Since the works of Ketchum (1951a,b) and Pritchard (1952) on the process of mixing and estuarine circulation patterns, much attention has been given to quantifying such aspects as residence times, which play an important role in the distribution of planktonic populations.

Ketchum (1954) and Barlow (1955) have described the relation between the circulation and planktonic populations in estuaries. If a planktonic organism is to maintain itself in a position in the estuary, it is neccessary that the biological processes that maintain it balance the processes that disperse it. In other words, the rate at which a planktonic population must reproduce in order to maintain itself in the estuary is determined by the vigour of the circulation. An estuarine population could thus only exist where the rate of tidal exchange does not exceed its reproductive rate. The effect of a rapid circulation can be inferred from the population at the mouth of the Knysna estuary, where the water is replaced with every tidal cycle. This requires the estuarine planktonic forms to multiply at enormous rates to offset losses to maintain the population. They can thus never establish dominance and the planktonic population is similar to that of the adjacent ocean (Korringa 1956). Typically, estuarine species such as *Pseudodiaptomus* and *Acartia* are found in areas of the estuary where tidal exchange is low (i.e. a high residence time).

The Knysna hydraulic model at the National Research Institute for Oceanology at Stellenbosch was used to determine the residence time of water in certain areas of the estuary. The results have been described by Grindley (1976) and are represented in Fig. 1.4 which shows the testing localities and results. The zooplankton sampling stations for the present study are shown in comparison. Truly estuarine copepods were collected in largest numbers where the residence times were longest. Highest densities of *Pseudodiaptomus hessei* and *Acartia* spp. were observed between Belvedere and Charlesford Rapids. The residence time at station 8, in the Ashmead Channel is not known, but is expected to be between that measured at point A and that at point B. This would give a residence time similar to that of the middle estuary. The zooplankton community found here is typically estuarine, with few, if any of the species found in the adjacent main channel. The residence times in this area is similar to those in the upper estuary above the National Road Bridge (Fig 1.4). No correllation with other physical factors such as surface salinity and temperature were found.

1.6.3 Importance of zooplankton in the estuary

Estuaries are highly productive systems. No estimates exist for the Knysna system in particular, but productivity in

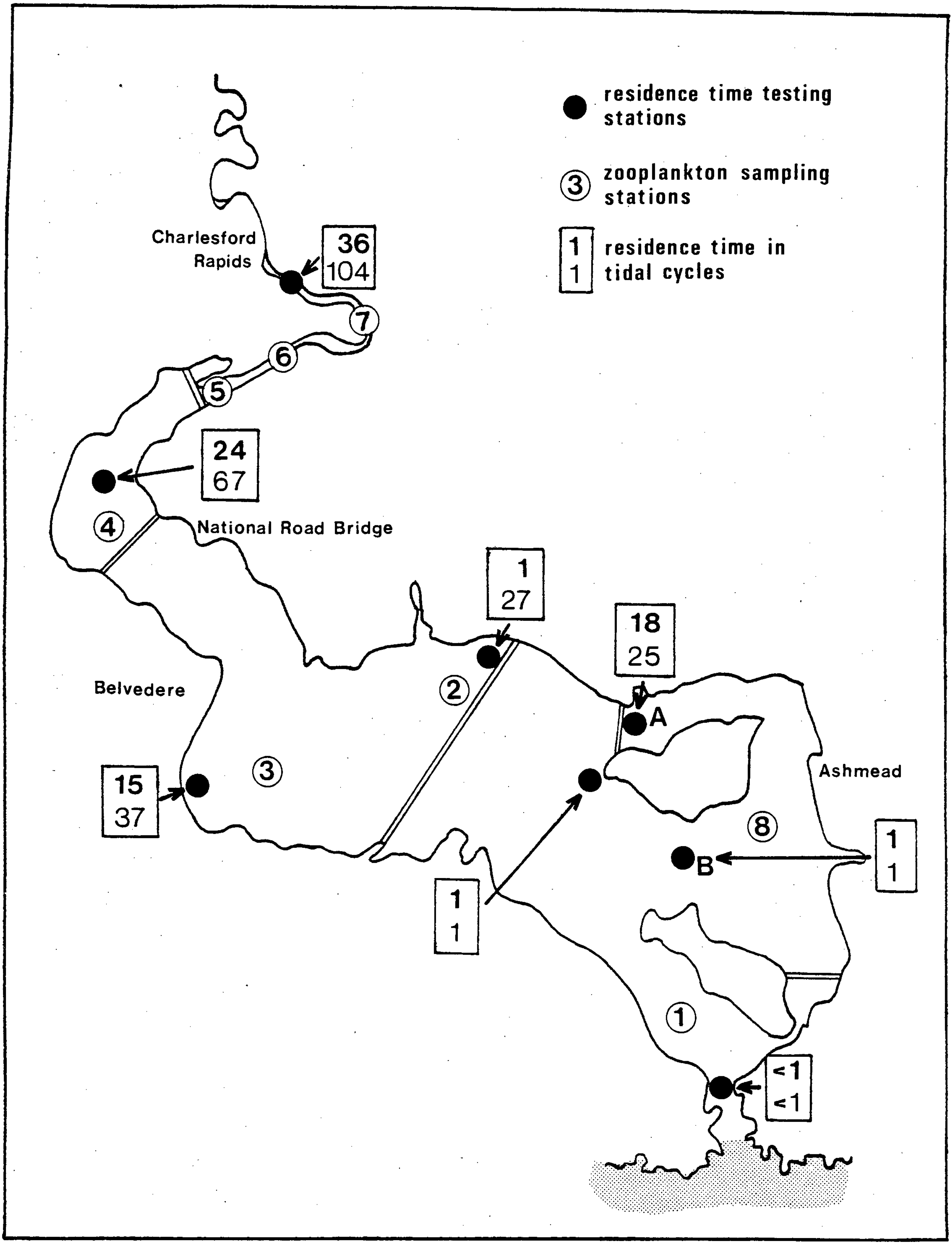

FIG. 1.4 : Residence times in tidal cycles (**bold** = spring tide, normal = neap tide) and sampling stations as obtained from the Knysna Lagoon model investigation report. Zooplankton sampling stations are given in comparison.

clear, deep estuaries ranges from 100-500 $gC.m^{-2}.yr^{-1}$ for phytoplankton, 100$gC.m^{-2}.yr^{-1}$ for benthic microalgae, about 500$gC.m^{-2}.yr^{-1}$ for seagrasses, and 500-1000$gC.m^{-2}.y^{-1}$ for saltmarsh macrophytes (Day & Grindley 1981).

Phytoplankton is consumed by the zooplankton and other suspension feeders such as barnacles, oysters and mussels. More important, especially in the Knysna estuary where phytoplankton biomass is low, is the organic detritus with its community of micro-organisms which is a better source of food (Odum & De la Cruz 1967). The most abundant zooplankton species in Knysna, *Pseudodiaptomus hessei,* feeds partly on detritus (Grindley 1976).

Pseudodiaptomus hessei and *Acartia* spp. form an important part of the diet of mysids such as *Rhopalophthalamus terranatalis* and *Mesopodopsis slabberi* (Wooldridge & Bailey 1982). These mysids and copepods are actively preyed upon by the round herring *Gilchristella aestuarius,* as well as other estuarine dependent fish such as mullet, *Lithognathus lithognathus, Rhabdosargus holubi* and *Monodactylis falciformis* (Wooldridge & Bailey 1982). The latter species was on occasion collected in the plankton net at station 4 . *Hyporamphus capensis* were also occasionally caught. *Gilchristella aestuarius, Hepsetia breviceps* and mullet are plentiful in Knysna (Grindley 1985).

Juvenile fish are abundant especially between the Red Bridge and the Old Drift (Haw, unpublished thesis). *Gilchristella* seems to prefer the middle reaches of an estuary (Jerling &

Wooldridge 1987). This mixed salinity, saltwedge zone is the area of highest zooplankton biomass. Grange & Allanson (1987) also found that zooplankton community grazing rates were highest in the saltwedge zone.

Gilchristella aestuarius and several other zooplankton feeding fish are important prey items in the diet of birds and larger predatory fish (Wallace *et al* 1983).

All evidence at present seem to point to the importance of zooplankton in the transfer of energy to the higher trophic levels. This contribution to secondary productivity is emphasized by the abundance and high productivity of common species such as *Pseudodiaptomus hessei.*

1.7 REFERENCES

Barlow, J.P. 1955. Physical and biological processes determining the distribution of zooplankton in a tidal estuary. *Biol. Bull.* **109**(2) : 211-225.

Collins, N.R. & Williams, R. 1981. Zooplankton of the Bristol Channel and Severn Estuary. The distribution of four copepods in relation to salinity. *Mar. Biol.* **64** : 273-283.

Day, J.H. 1967. The biology of Knysna estuary, South Africa. In: Lauff, G.H. (ed.) *Estuaries.* Horn-Schafer, Baltimore. pp. 397-407.

Day, J.H. 1981. Summaries of current knowledge of 43 estuaries in southern Africa. In: Day, J.H. (ed.) *Estuarine ecology with particular reference to southern Africa.* A.A. Balkema, Cape Town. pp. 251-330.

Day, J.H., Blaber, S.J.M. & Wallace, J.H. 1981. Estuarine fishes. In: Day, J.H. (ed.) *Estuarine ecology with particular reference to southern Africa.* A.A. Balkema, Cape Town. pp. 197-221.

Day, J.H. & Grindley, J.R. 1981. The estuarine ecosystem and environmental constraints. In: Day, J.H. (ed.) *Estuarine ecology with particular reference to southern Africa.* A.A. Balkema, Cape Town. pp. 345-372.

Day, J.H., Millard, N.A.H. and Harrison, A.D. 1952. The ecology of South African estuaries. Part III. Knysna: A clear open estuary. *Trans. Roy. Soc. S. Afr.* 33(3) : 367-413.

Grange, N. and Allanson, B.R. 1987. Comparative feeding ecology of zooplankton communities from two contrasting East Cape estuaries. *6th National Oceanographic Symposium, Stellenbosch, 6-10 July 1987.*

Grindley, J.R. 1976. Residence time tests. In: *Knysna lagoon model investigation part I.* CSIR report C/SEA 7609. pp. 28-38 and figs 75-91.

Grindley, J.R. 1978. *Environmental effects of the discharge of sewage effluent into Knysna Estuary.* School of Environmental Studies, University of Cape Town. 62 pp.

Grindley, J.R. 1985. Knysna (CMS 13). In: *Estuaries of the Cape, Part II: Synopsis of available information on individual systems.* CSIR Report 429.

Grindley, J.R. & Wooldridge, T. 1974. The plankton of Richards Bay. *Hydrobiol. Bull.* **8**(1/2) : 201-212.

Haw, P.M. 1984. *Freshwater requirements of Knysna Estuary.* School of Environmental Studies Report No. 55, Univ. of Cape Town. 136 pp. (unpubl. M.Sc. thesis)

Jerling, H.L. and Wooldridge, T. 1987. Aspects of the ecology of an estuarine copepod *Pseudodiaptomus hessei* (Calanoida) in the Sundays River estuary. *6th National Oceanographic Symposium, Stellenbosch, 6-10 July 1987*

Ketchum, B.H. 1951a. The exchanges of fresh and salt waters in tidal estuaries. *J. Mar. Res.* **10** : 18-38.

Ketchum, B.H. 1951b. The flushing of tidal estuaries. *Sewage and Industrial Wastes* **23**(2) : 198-200.

Ketchum, B.H. 1954. Relation between circulation and planktonic populations in estuaries. *Ecology* 35(2) : 191-200.

Korringa, P. 1956. Oyster culture in South Africa. Hydrographical, biological and ostreological observations in the Knysna lagoon, with notes on conditions in other South African waters. *Invest. Rep. Div. Sea Fish. S. Afr.* **20**. 85 pp.

Odum, E.P. & De la Cruz, A.A. 1967. Particulate organic detritus in a Georgia salt marsh - estuarine ecosystem. In: Lauff, G. (ed.) *Estuaries*. Am. Ass. Adv. Sci., Washington. pp. 383-388.

Perkins, E.J. 1974. *The biology of estuaries and coastal waters*. Academic Press, London. 678 pp.

Pritchard, D.W. 1952. Salinity distribution and circulation in the Chesapeake Bay estuarine system. *J. Mar. Res.* **11** : 106-123.

Read, G.H.P. & Allanson, B.R. 1983. Community structure and distribution of the estuarine dependent biota of the Keiskamma River estuary with particular reference to the influence of cyclical and episodic variation in salinity gradients in maintaining this community. *Progress Report to SANCOR, December 1983*.

Unteruberbacher, H.K. 1964. The pilchard of South West Africa (*Sardinops ocellata*). Zooplankton studies in the waters of off Walvis Bay with special reference to the copepoda. *Administration of South West Africa Marine Research Laboratory, Investigational Report No.11*

Wallace, J.H., Kok, H.M., Beckley, L.E., Bennett, B., Blaber, S.J.M. & Whitfield, A.K. 1984. South African estuaries and their importance to fishes. *S. Afr. J. Sci.* **80** : 203-207.

Wooldridge, T. & Bailey, C. 1982. Euryhaline zooplankton of the Sundays estuary and notes on trophic relationships. *S. Afr. J. Zool.* **17**(4) : 151-163.

Wooldridge, T. & Melville-Smith, R. 1979. Copepod succession in two South African estuaries. *J. Plankton Res.* **1**(4) : 329-341.

PART II

Seasonality and copepod succession in the zooplankton of Knysna Estuary, South Africa.

2.1 ABSTRACT

The zooplankton of the Knysna estuary displays seasonal cycles in abundance, with maximum numbers occuring during the summer months. *Pseudodiaptomus hessei* is present throughout the year and is numerically the dominant copepod in the upper reaches. *Acartia* spp. were also observed throughout the year, and are present in similar numbers to *P. hessei* in the middle and lower estuary. Together these species constitute about 90% of the zooplankton.

P. hessei displays no pronounced seasonal cycle of abundance, but its abundance is strongly related to freshwater inflow. The species appears to breed throughout the year, but during periods of low salinity, *P. hessei* utilises the "new resources" and breeding increases to a maximum.

Acartia natalensis and *A. longipatella* show clear seasonal cycles in dominance and abundance. *A. natalensis* occurs in summer, while *A. longipatella* is the winter dominant. Temperature appears to play a major role in their succession. Other controlling factors involved were not clear. Selective predation could, however, not be excluded on the basis of the available data.

2.2 INTRODUCTION

Estuarine zooplankton is adapted to a highly variable environment, large seasonal differences in physical factors such as temperature being characteristic of estuaries. Subsequently, the zooplankton displays a highly variable seasonal cycle in abundance, with high summer densities being a characteristic (Riley 1967). Distribution has often been correlated to temperature (Barlow 1955, Faber 1966, Olsson & Ohlund 1974, Watson & Carpenter 1974, Coetzee 1985). Many observations also imply involvement of biological factors such as predator-prey interactions (Grahame 1976, Jeffries 1962, Fulton 1983).

Relative species abundance changes seasonally with species being abundant successively. Patterns of seasonal succession between zooplankton copepods have been observed and well documented in western Atlantic estuaries (Conover 1956, Sage & Herman 1972, Knatz 1978) and in South Africa by Wooldridge & Melville-Smith (1979).

During an investigation of zooplankton in the Knysna estuary in 1985 and 1986, seasonal variations in abundance and community structure were observed. *Acartia(Paracartia) longipatella, A.(Acartiella) natalensis* and *Pseudodiaptomus hessei* were numerically the most important copepods encountered. This investigation therefore concentrates on interactions between these three species.

2.3 METHODS

Sampling took place over a period of twelve months at seven sampling stations on the Knysna estuary (Fig. 2.1). These stations had already been established as temperature and salinity monitoring stations for the first phase of the project and were maintained for this analyses, which was part of the second and biological sampling phase. The sampling programme began in early autumn (March) 1985 and was continued quarterly until early spring (September), after which samples were taken monthly until February 1986.

The zooplankton samples were taken at night with a 36cm diameter plankton net using nylon mesh of 124um aperture. A 12,5cm diameter Clarke Bumpus plankton sampler without the sampler was towed simultaneously to measure the volume of water sampled. The nets were towed at approximately two knots from a 15 or 35hp motor boat. As the upper reaches of the estuary were only navigable during high tide, sampling was begun at high water in the upper reaches and proceeded down towards the mouth. Sampling could therefore only take place on days when high tide in the upper reaches of the estuary coincided with sunset. Despite this fairly standard sampling procedere, tidal effects could not be totally excluded. Two minute samples were taken from just below the water surface at each station. Surface temperature, salinity and dissolved oxygen content of the water were also recorded at the same time. Temperature and oxygen were recorded with

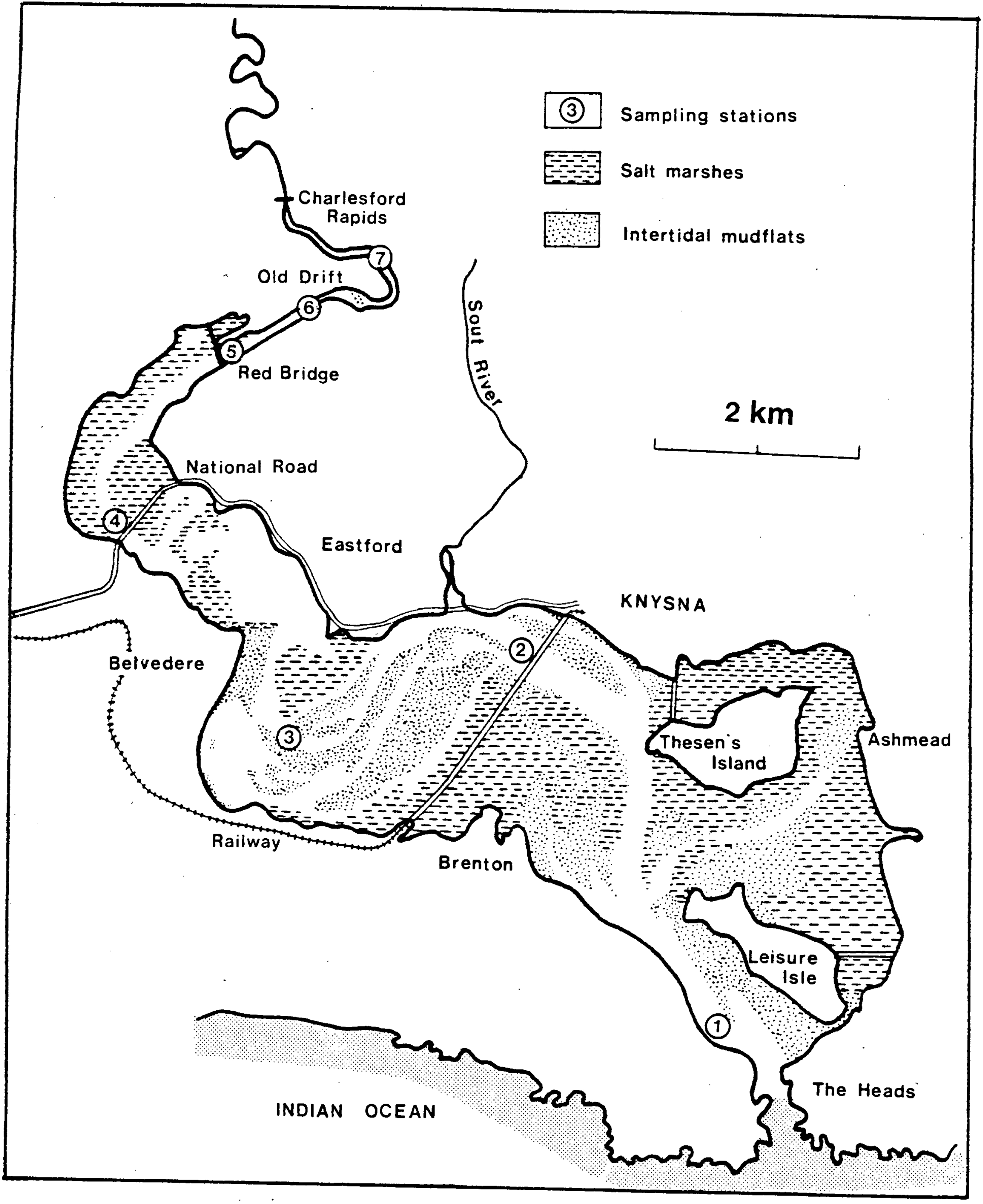

FIG. 2.1 : Map of Knysna estuary showing the sampling stations.

a YSI Model 57 dissolved oxygen meter, and salinity with an AOC Model 10419 automatic temperature compensated hand refractometer.

After every haul the nets were thoroughly rinsed to ensure that plankton did not adhere to the gear to contaminate the following sample. The plankton samples were immediately preserved in 5% formalin.

In the laboratory the plankton samples were made up to a standard volume (500ml) from which 10 or 25ml subsamples were taken with a wide-mouth pipette after agitation, depending on the number of organisms in the sample. All the organisms were then identified and counted and the results expressed as the number of organisms.m^{-3} of water.

Biomass was calculated from settled volumes of zooplankton. Whereas settled volume is generally considered a somewhat unreliable measure of biomass, the relative uniformity in size of the pankton of lagoons and estuaries gives a constant packing density. It has been shown that the correlation between settled volume and biomass (dry weight) is significant at the 1% level (Biomass(mg) = 18.6 x settled volume(ml)) (Grindley & Wooldridge 1974).

The species of *Acartia* found in Knysna estuary belong to two subgenera, i.e. *Acartiella* and *Paracartia* (Connell & Grindley 1974). For simplicity these subgenera have been neglected and the species are merely referred to by the genus *Acartia*.

2.4 RESULTS

Details of the salinity, temperature and oxygen readings recorded are presented in Table 2.1. The seasonal trends in monthly temperature, salinity and zooplankton numbers and biomass, averaged for the whole estuary, are presented in Fig. 2.2. The temperature reflected normal seasonal trends, maximum temperatures being recorded from December to March (summer) and lowest temperatures in June/July.

Monthly salinity variations were small from March to September, which is probably a result of irregular sampling. Sampling initially occured every three months, with monthly samples only taken as from September. Significant fluctuations in monthly average salinity were only observed from September. These fluctuations are mainly due to variations in freshwater inflow. Sampling at different states of the tide also affected the readings. Increased riverflow caused the very low salinities, especially at the head of the estuary, in November, and to a lesser extent in January. In both these cases salinities had recovered a month later. Modelling of a $302m^3.s^{-1}$ flood in Knysna estuary has shown that salinities return to normal after about 15 days (Huizinga & Haw 1986). Floods of $40m^3.s^{-1}$ occur every

TABLE 2.1 : Physical data for Knysna estuary at the time of zooplankton sampling from March 1985 to February

DATE	MEASUREMENT	STATION 1	2	3	4	5	6	7
23.3.1985	Salinity (°/oo)	34.5	31.8	30.0	24.8	21.0	15.8	10.5
	Temperature (°C)	20.5	22.0	22.3	22.8	22.7	23.0	22.2
	Oxygen (mg.1^{-1})	9.2	8.7	8.6	8.5	6.7	5.9	6.9
3.7.1985	Salinity	34.0	33.0	30.0	30.0	23.0	14.5	5.5
	Temperature	16.6	16.1	15.3	15.2	15.2	15.2	15.1
	Oxygen	8.2	7.8	8.5	7.9	7.4	7.7	7.7
14.9.1985	Salinity	36.0	32.0	30.0	23.0	20.0	13.0	8.0
	Temperature	16.3	16.2	17.0	18.0	17.8	17.6	17.5
	Oxygen	10.0	9.2	9.7	8.8	9.0	9.6	9.5
5.10.1985	Salinity	37.0	31.0	33.0	32.0	27.0	24.0	13.0
	Temperature	18.2	18.9	19.0	19.4	20.2	20.2	21.2
	Oxygen	7.2	7.2	7.2	5.8	6.5	6.9	7.0
3.11.1985	Salinity	32.0	22.0	9.5	0.0	0.0	0.0	0.0
	Temperature	15.2	17.1	19.7	19.5	18.5	17.7	17.6
	Oxygen	10.2	11.0	10.3	10.5	11.2	11.6	11.7
1.12.1985	Salinity	32.0	30.0	29.0	22.0	18.0	17.0	7.5
	Temperature	22.1	23.7	24.0	25.9	26.2	26.6	27.2
	Oxygen	7.0	7.4	7.0	6.6	6.4	6.0	6.5
8.1.1986	Salinity	34.0	25.0	20.0	4.0	2.0	0.0	0.0
	Temperature	21.7	25.0	25.8	24.0	23.0	22.8	22.5
	Oxygen	8.6	8.4	7.6	5.9	7.6	8.1	9.0
8.2.1986	Salinity	38.0	30.0	29.0	24.0	10.0	8.5	5.5
	Temperature	19.4	22.8	32.2	24.2	24.0	24.0	23.6
	Oxygen	10.4	7.5	7.4	8.2	6.8	6.8	8.8

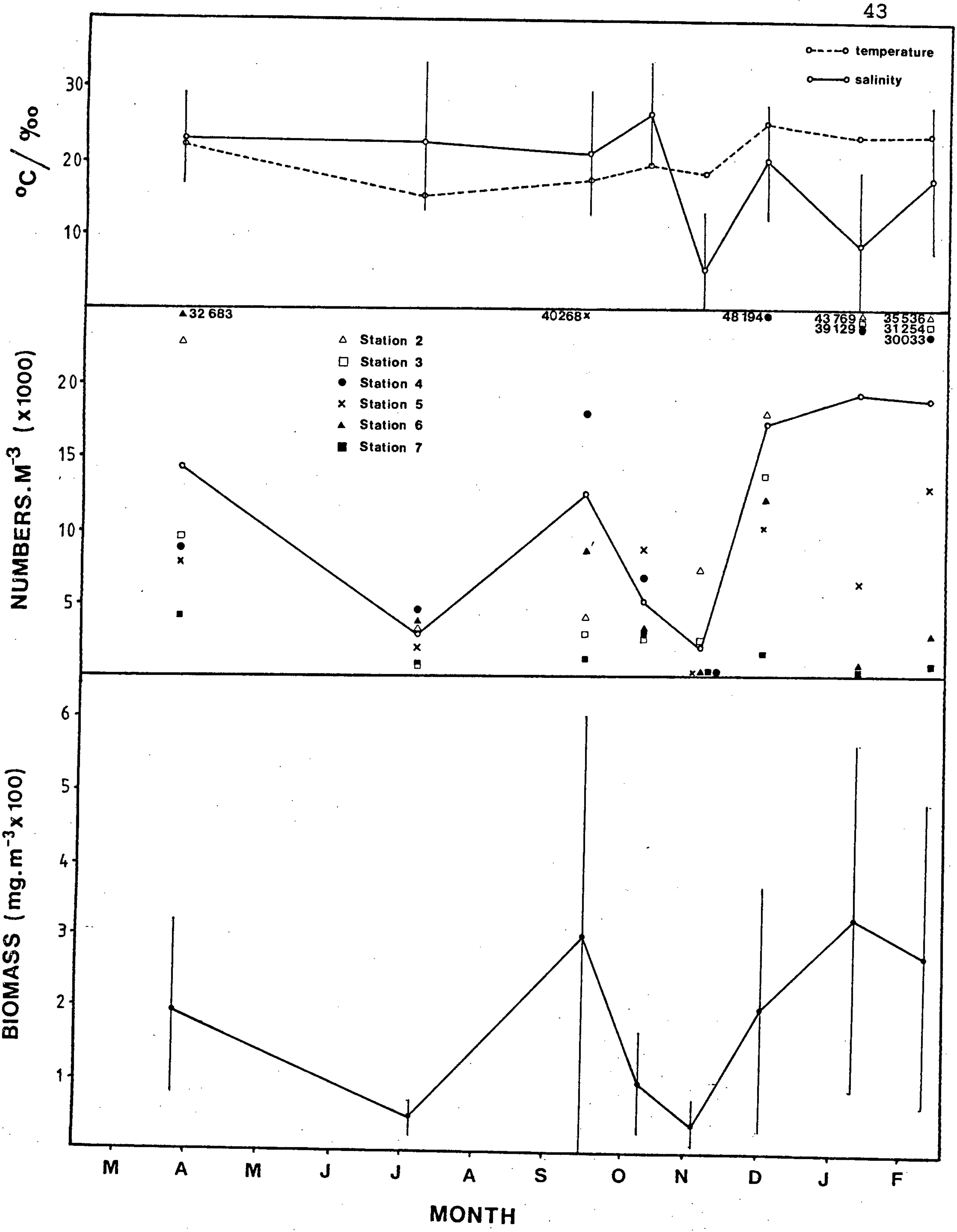

FIG. 2.2 : Average monthly surface salinity and temperature and zooplankton numbers.m^{-3} and biomass (g.m^{-3}). Bars represent standard deviation.

two years in Knysna. Data obtained from modelling $40m^3.s^{-1}$ and $302m^3.s^{-1}$ floods (Haw, unpubl. thesis) indicate that the salinities recorded in November in this study may have been due to a flood of greater magnitude than $40m^3.s^{-1}$.

Zooplankton biomass and numbers were highest during the summer months with a peak in mid-summer (Fig. 2.2). There was a secondary smaller peak in early spring (September). Maximum biomass and numbers were thus reached when surface water temperatures were highest. Using Spearman's rank correlation coefficient, a significant correlation was found between zooplankton numbers and temperature (r_s = 0.81, $p<0.05$), but no relationship was found between salinity and zooplankton numbers (r_s = -0.21, $p>>0.05$). Seasonal changes in numbers (converted to $\log_{10}$) of *Pseudodiaptomus hessei* and *Acartia* spp. are represented in Fig. 2.3. It was found that station 1 represented a marine zooplankton population as opposed to an estuarine one. This study was aimed at the dominant truly estuarine plankton populations and therefore stations 2 - 6 only are considered. The estuary was divided into upper (stations 5 - 7), middle (stations 3 - 4) and lower (station 2) regions to show both spatial and temporal distribution. Both genera were present throughout the year with no complete dominance shown by either genus at any particular time. Both genera were also always present in all samples taken. *Acartia* were present in larger numbers during the summer months (January - March) when surface water temperatures were highest. Numbers peaked in January

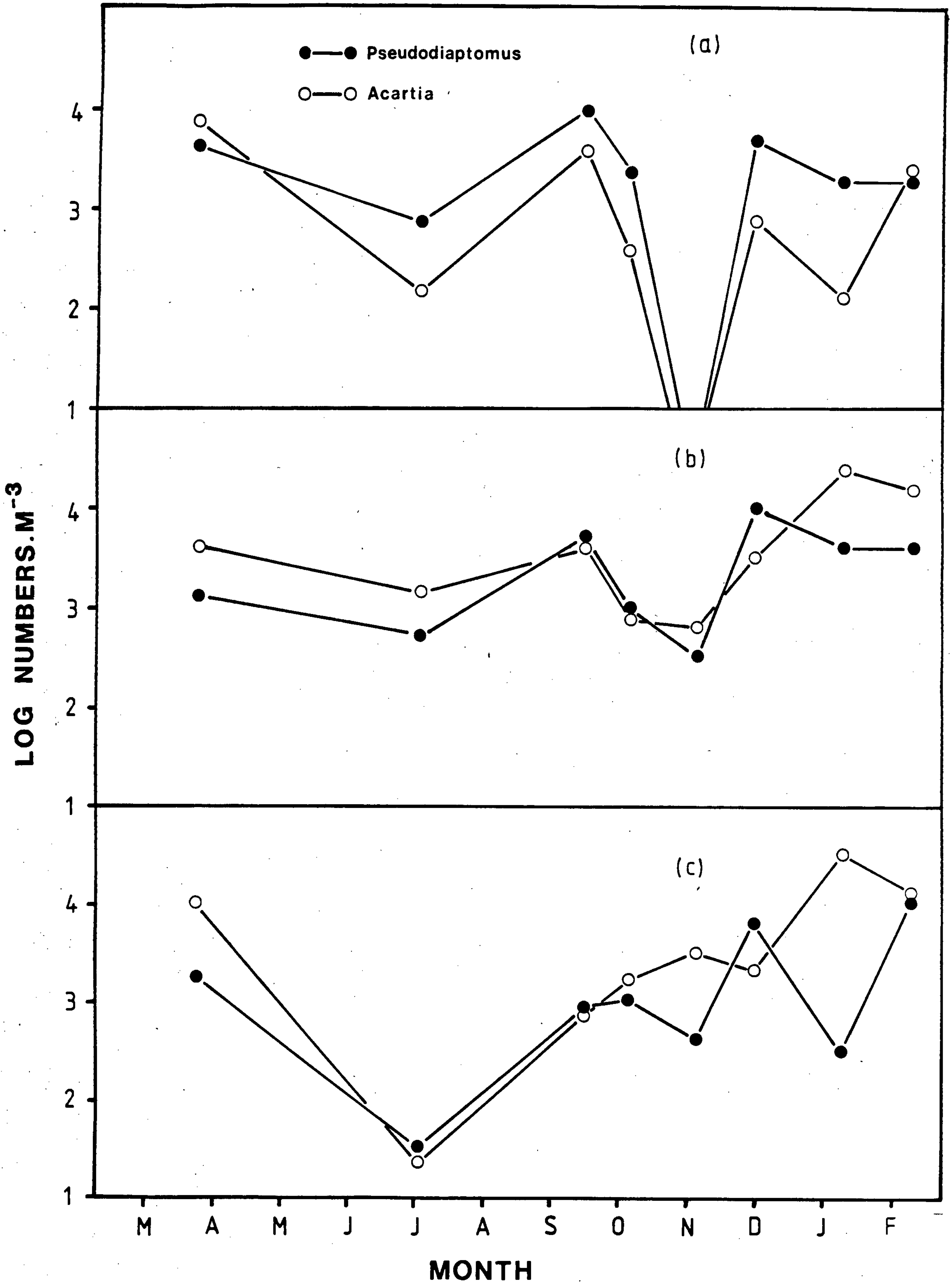

FIG. 2.3 : Temporal distribution of *Pseudodiaptomus hessei* and *Acartia* spp. in the upper (a), middle (b) and lower (c) Knysna estuary.

(14 103.m^{-3}) and were lowest in July (561.m^{-3}). *Pseudodiaptomus* was the numerically more abundant genus during winter and spring, when surface water temperatures were lowest, with a peak in numbers in September (6 780.m^{-3}) and December (7 172.m^{-3}). *Pseudodiaptomus* was found to be more abundant than *Acartia* virtually throughout the year in the upper estuary. In the lower reaches *Acartia* was more abundant, especially during the warmer summer months. Increased riverflow in November resulted in a decrease in numbers of especially *Pseudodiaptomus hessei*.

Acartia species show a clear temporal and spatial distribution between *A. natalensis* and *A. longipatella* (Fig. 2.4). *A. africana* is present throughout the year in relatively low numbers in the lower and middle estuary, but it was observed in the upper estuary in March only. *A. natalensis* was present in March in the lower estuary and only reappeared in December, with peak numbers in January (15 940.m^{-3}). It was still present in late June in the middle and upper reaches. When the species reappeared in these regions in December, it was present in larger numbers than in the lower estuary. Numbers peaked in January in the middle estuary (20 560.m^{-3}) and in March in the upper estuary (2 280.m^{-3}). *Acartia longipatella* was present in the lower estuary from September to December, with a peak in numbers in October (260.m^{-3}). In the middle and upper reaches it was present from late June until December, with maximum numbers in September. *A. longipatella* adults were

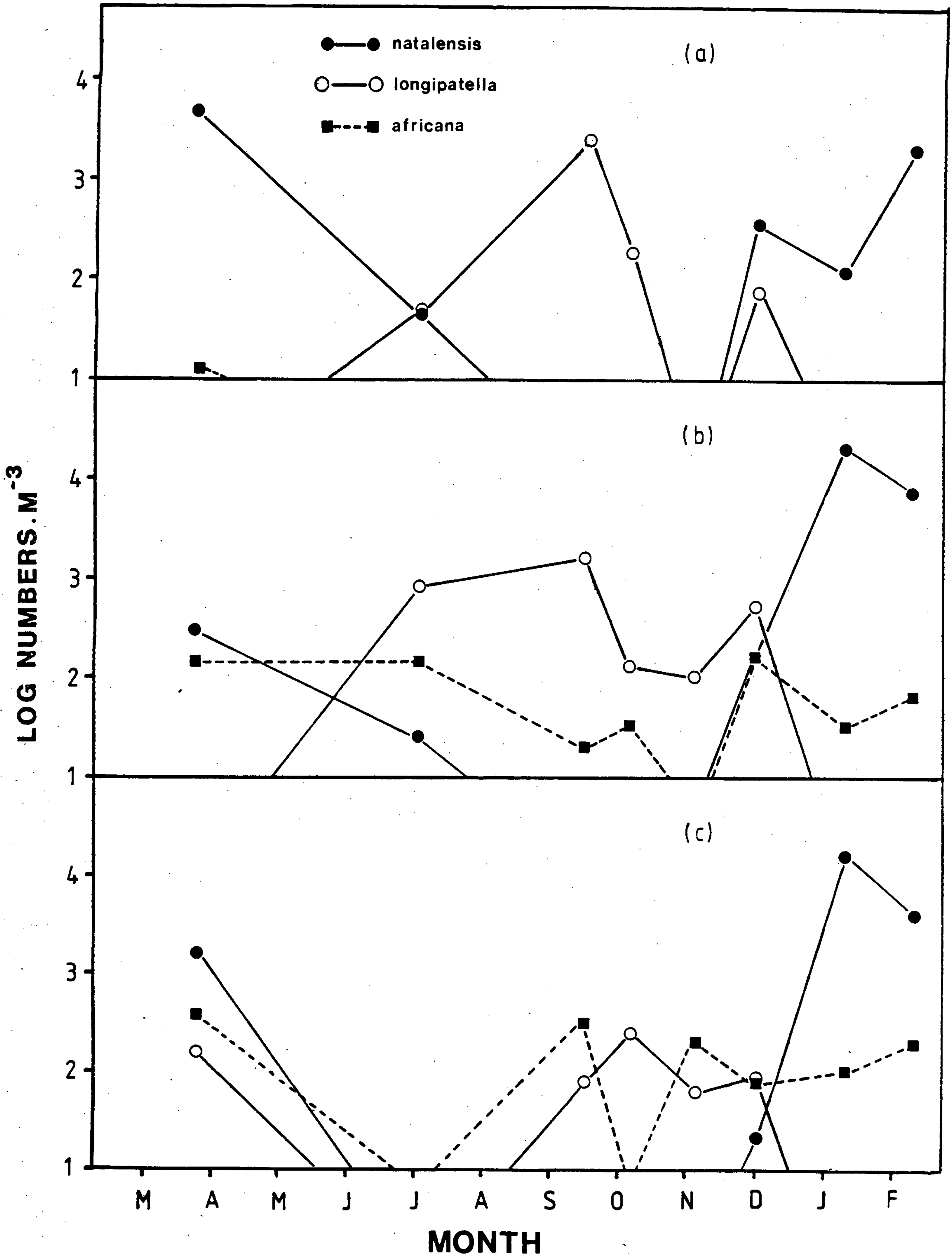

FIG. 2.4 : Seasonal succession and temporal distribution of *Acartia natalensis*, *A. longipatella* and *A. africana* in the upper (a), middle (b) and lower (c) Knysna estuary.

absent from the upper reaches in November, when salinities were low, but had reappeared by December ($75.m^{-3}$).

A. longipatella was collected at salinities ranging from 7.5 to 32°/oo and at temperatures of 15.1 to 27.2°C, although 60% of specimens were collected between 15 and 21°C. *A. natalensis* was collected at salinities ranging from 2 to 32°/oo, and temperatures of 15.1 to 27.2°C. In this temperature range 85% of occurences were above 21°C. It was difficult to distinguish between the two *Acartia* species in the immature stages, and these are therefore not included.

A three-dimensional plot of adult *Acartia* numbers against salinity and temperature (Fig 2.5a), obtained using the SACLANT program, clearly shows the seperation of the two species along a temperature gradient. Fig 2.5b shows the points for which data was collected. *A. natalensis* generally occurs at higher temperatures than *A. longipatella*. The species overlap at the extreme low and high temperatures. A correlation coefficient of 0.485 ($p < 0.02$) was obtained between *A. natalensis* distribution and temperature. *A. longipatella* showed a negative correlation of -0.219 to temperature, which was not significant. Factors other than temperature appear to influence the distribution of *A. longipatella* to a greater extent than *A. natalensis*.

No clearcut relationship could be found between salinity and the distribution of *Acartia*. Both species occur over a wide salinity range and overlap quite considerably. A

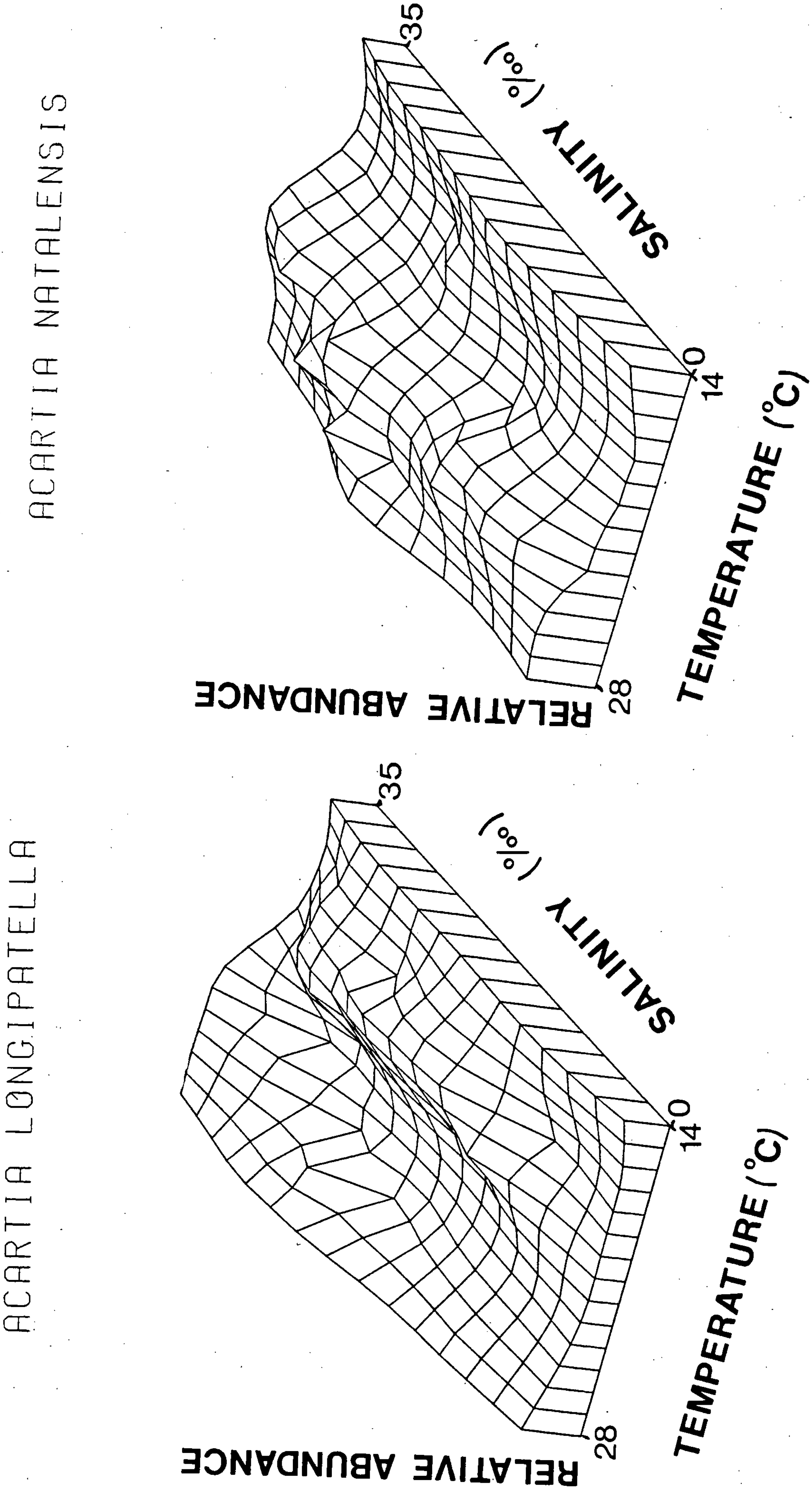

FIG. 2.5a : Abundance of adult *Acartia natalensis* and adult *A. longiptella* as a function of temperature and salinity.

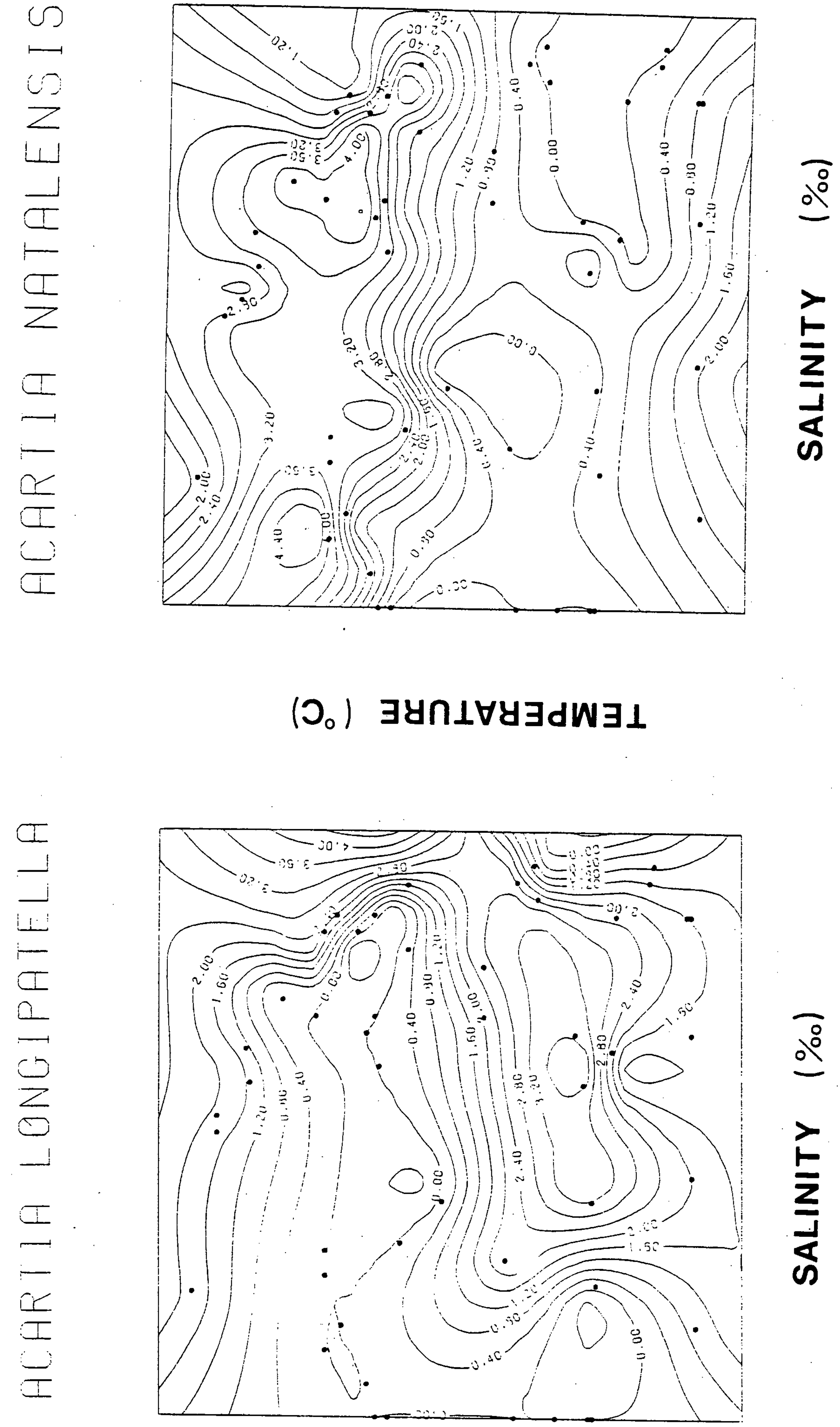

FIG. 2.5b : SACLANT plot showing the distribution of *A. natalensis* and *A. longipatella* with temperature and salinity, giving data points.

longipatella is somewhat more abundant at higher salinities. At a combination of high salinity and high temperature, *A. longipatella* appears more abundant than *A. natalensis*, but this could be a function of the plotting program since no actual data was collected for these conditions (Fig 2.5b).

Pseudodiaptomus hessei was most abundant in September (6 780.m^{-3}) and December (7 172.m^{-3}). Numbers declined throughout the summer and winter with minimum abundance in June (534.m^{-3}). In November during heavy river discharge and low salinities, abundance was also low (187.m^{-3}). The population had recovered within a month to maximum recorded abundance in December.

Significant changes in the population structure of *P. hessei* only seem to occur in the juvenile to adult ratio (nauplii excluded) (Fig. 2.6). The male to female ratio was 1:1 from February to September, increasing to 1:1.5 during the summer months. A maximum of 1:2 was reached during periods of low salinity. The adult to juvenile ratio ranged from 2:1 to 1:4 with the highest percentage of juveniles in the population during periods of low salinity, and the lowest in the middle of summer (January). Gravid females were determined by presence of both attached and free egg sacs. They generally accounted for 45-65% of the female population, with a peak of 81% in January.

The immature stages (stage I - V) comprised over 50% of the population throughout the year, except in January, when they

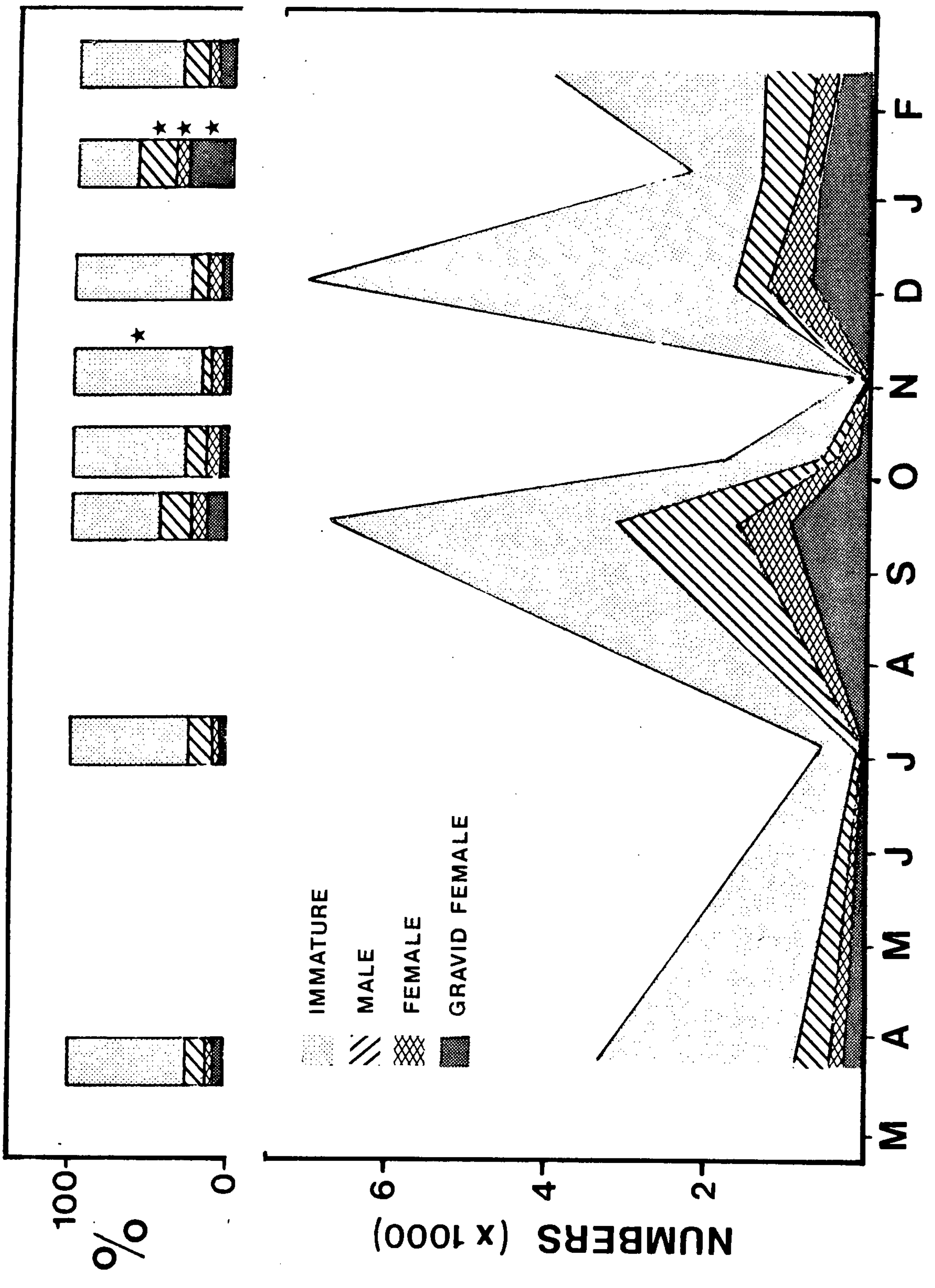

FIG. 2.6 : Seasonal changes in the numeric and % abundance of male, female, gravid female and juvenile stages of *Pseudodiaptomus hessei* (* indicates highest % abundance over the whole period).

only made up 37% of the population. The percentage of immature stages in the population peaked in December, one month after very low salinities. Adult stages peaked in January, with a second smaller peak in September. The percentage of adults in the population was lowest in November, when salinities were lowest. Adults were then only recorded in the lower reaches of the estuary and only in small numbers.

Figure 2.7 shows the percentage of nauplii in the zooplankton population, together with the average surface salinity and temperature. The abundance of nauplii seemed to be related to temperature ($r_s = -0.684$, $p < 0.05$). The percentage nauplii decreased with decreasing temperatures from March, increasing again in October, peaking in December when surface water temperatures were highest.

2.5 DISCUSSION

The seasonal cycle of estuarine zooplankton is extremely variable and can change drastically from one year to the next, as was indicated in a study of Delaware Bay by Deevey (1960). In Kungsbacka Fjord (Olsson & Ohlundh 1974) copepod abundance fluctuated significantly over the two year study period. Similar changes in annual abundance were recorded by Wooldridge & Bailey (1982) in the Sundays estuary over a two year period. The present study was only conducted over

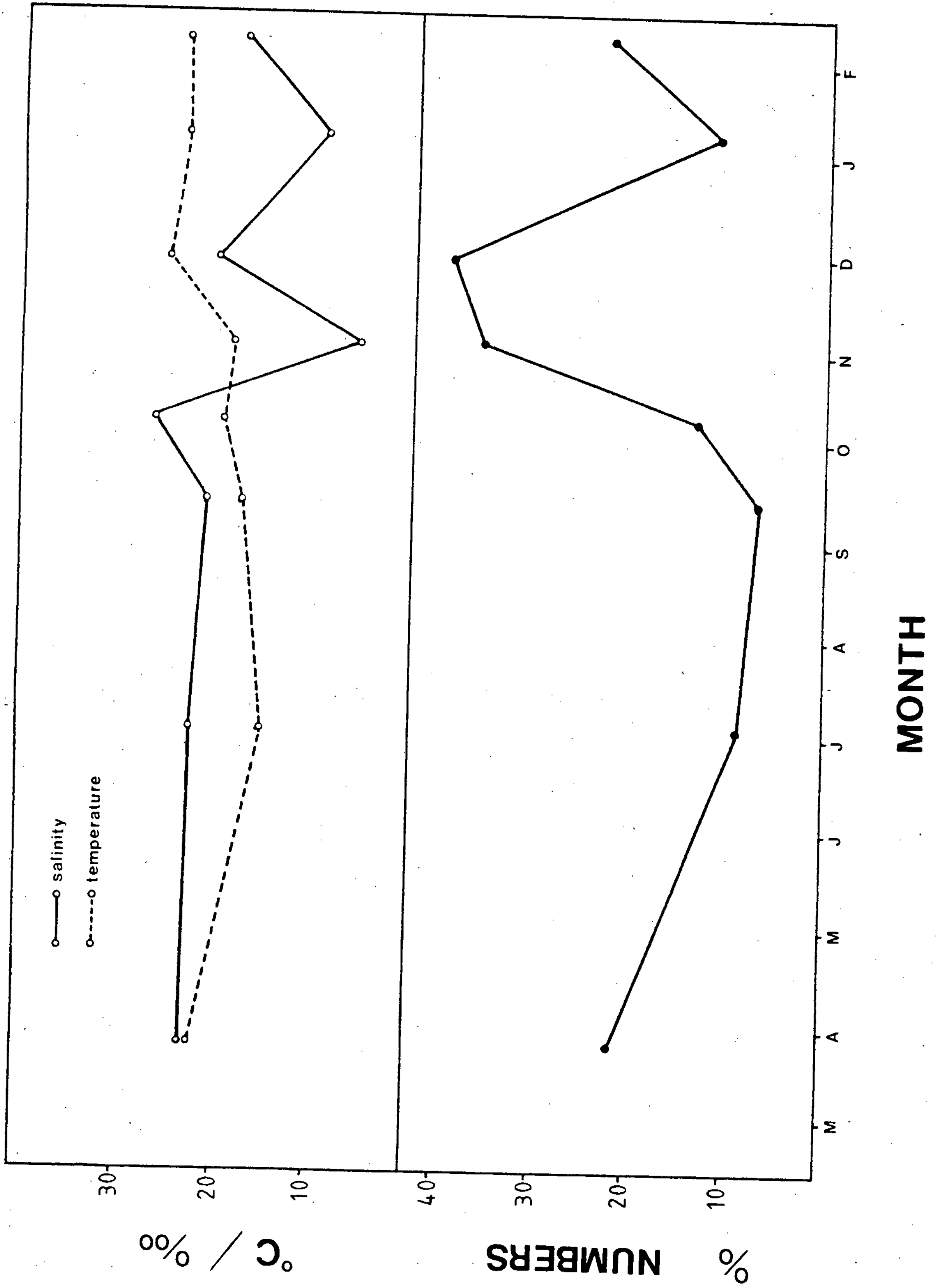

FIG. 2.7 : Average monthly surface salinity and temperature and percent of nauplii in the total zooplankton.

a period of one year and hence no record has been made of the extent of annual fluctuations in the zooplankton standing crop. Seasonal trends in species composition will, however, still persist and follow a general trend appparently without great annual variation (Grindley 1981).

2.5.1 Biomass

A high summer biomass is characteristic of estuarine zooplankton (Riley 1967, Grindley 1981). In Knysna zooplankton biomass and reproduction (as abundance of nauplii) were significantly correlated to temperature. Both production and biomass were highest in spring- summer.

The very low surface salinities recorded in November indicate increased freshwater discharge. This flushed the zooplankton seaward, resulting in a low zooplankton biomass for November. Most of this biomass was recorded in the lower estuary, with station 6 having a strong freshwater component and very few estuarine copepods. Zooplankton numbers had however recovered a month later to 48 200.m^{-3} at station 4 (average of 17 298.m^{-3} for the whole estuary), with the copepod *Pseudodiaptomus hessei* dominating the community. Increased river flow thus seems to have a beneficial effect on the zooplankton, probably in providing more nutrients and detritus to the system which allows a rapid growth in the zooplankton community. Similar results have been recorded for the Swartkops estuary (Wooldridge & Melville-Smith 1979), Richards Bay (Grindley & Wooldridge 1974), Sundays estuary (Wooldridge & Bailey 1982) and in Lake St. Lucia following the great floods of May 1971 (Grindley 1983).

High levels of primary production generally occur during spring, which commonly result in high zooplankton densities in summer . While this may hold true for oceanic plankton, this is not neccessarily the case in estuaries. In Lake St. Lucia summer flood waters dilute the plankton, but introduce detritus and nutrients. This allows peak plankton biomass to develop in the autumn months, instead of in the warmer summer months (Grindley 1983). Primary production is related to both temperature and nutrient availability. High temperatures and high nutrient availability do not, however, always coincide in estuaries.

The phytoplankton biomass in the Knysna estuary has not been determined, but the clarity of the water suggest it to be low (Day 1981). For many copepods phytoplankton is not, however, always the primary food source. Food particle size probably plays an important role in the feeding of filter feeding copepods such as *Acartia* and *Pseudodiaptomus*, as has been demonstrated for *Euterpina acutifrons* (Nassogne 1970) and *Pseudocalanus minutus* (Poulet 1970). *P. hessei*, which is the numerically most abundant copepod, appears to feed mainly on nanoplankton, detritus and bacteria. (Grindley 1976b).

Grindley (1970) states that *P. hessei* normally attains maximum abundance in early spring. The data from Knysna agree with this in that a peak in abundance was observed in September. The data also indicate that low salinities (i.e. increased river flow) induce population growth. This can occur in any season and in this study occured in November, with a subsequent peak in biomass one month later. A similar situation occured in the Swartkops estuary, where a peak in biomass was observed in November (Grindley 1976a).

Pseudodiaptomus hessei is considered a pioneer species (Wooldridge & Melville-Smith 1979). Relatively dense populations of this species are rapidly established after flooding. *P. hessei* is able to flourish in water of low salinity and exploit the resources of the "new water". *Acartia* was numerically dominated by *Pseudodiaptomus* within about three weeks of recorded low salinities, even though juvenile *Acartia* species were present in larger numbers during the initial period of low salinity. This rapid regeneration of *P. hessei* at low salinity and when the water temperature was high, has been established in laboratory experiments. Unpublished work by Rob Rippingdale and Shirley Grindley show that *P. hessei* matures faster and exhibits increased fecundity at high temperatures and low salinities. Preliminary studies by Jerling & Wooldridge (1987) found that the development of *P. hessei* from egg to adult varied from 16 days at 25°C to 45 days at 16°C, but could find no difference in the development at different salinities.

P. hessei seems adapted to establishing itself rapidly after flooding, especially at higher temperatures. *Acartia*, on the other hand does not seem to increase its reproductive rate at low salinities. It would appear that it cannot successfully compete with *P. hessei* in establishing itself after flooding.

A pattern of elimination of the pioneer species does not develop in the Knysna estuary, nor other South African estuaries such as the Eastern Cape estuaries (Wooldridge & Melville-Smith 1979), Richards Bay (Grindley & Wooldridge 1974) and Botriver (Coetzee 1985).

2.5.2 Succession

A clear pattern of seasonal succession was evident between *Acartia longipatella* and *A. natalensis*. *A. natalensis* is present during the warmer summer months and is replaced by *A. longipatella* in winter. Wooldridge & Melville-Smith (1979) recorded this succession between *A. longipatella* and *A. natalensis* in the Swartkops and Sundays estuaries.

In New England and western Atlantic estuaries the replacement of *Acartia tonsa* by *A. clausi* in winter-spring has been well documented (Jeffries 1962, Conover 1961, Sage & Herman 1972). In the Navesink River estuary (western Atlantic) the occurence of *A. clausi* is rare and here *A.*

tonsa is replaced by the more brackish-water calanoids *Pseudodiaptomus coronatus* and *Eurytemora afinis* (Knatz 1978). In Beaufort, North Carolina *A. tonsa* is replaced by *Centropages* spp. in winter (Fulton 1983).

Fulton (1982, 1983) has shown with predation experiments that the replacement of *A. tonsa* by *Centropages* is not directly due to temperature changes, even though a positive correlation exists. Decreases in water temperature resulted in increases in abundance of predatory mysids, which selectively preyed on *A. tonsa*. After *Centropages* became dominant, predation by mysids had no effect on copepod species composition. Rising temperatures in spring again favoured recruitment of *A. tonsa* and inhibited *Centropages* recruitment.

Both species of *Acartia* were collected within their recorded salinity range (Fig. 2.5a,b) (Connell & Grindley 1974). *A. longipatella* was recorded at temperatures as high as 27°C and *A. natalensis* at a low 15°C. Temperature and salinity are thus not the only regulating factors. Other factors are, however, not clearly evident in the data. Wooldridge & Melville-Smith (1979) found some evidence of competition in the elimination of *A. longipatella*. In the absence of *A. natalensis*, *A. longipatella* was present during all seasons with maximum abundance during winter. They also suggested that other factors probably operate in that *A. natalensis* is present only in low numbers in the Sundays estuary, even though it occurs in comparable salinity and temperature ranges to those in the Swartkops, where it is abundant. A similar situation occurs in the Navesink where *A. clausi* is excluded (Knatz 1978). The reasons for these two situations are not entirely clear. In Knysna *A. longipatella* occurs in greater abundance than *A. natalensis* when both temperature and salinity are high. This could further point to competition in that these conditions may inhibit the productivity of *A. natalensis* and give *A. longipatella* the competitive edge again.

The very low abundance of *A. natalensis* in the Sundays estuary could possibly be associated with the high abundance of mysids (Wooldridge & Bailey 1982). However, it is not known whether mysids do in fact prey selectively on *A. natalensis*, or if a low abundance of *A. natalensis* is normally associated with a high abundance of mysids. Gut content analyses of mysids in the Sundays estuary did show that both *A. natalensis* and *A. longipatella* are preyed upon (Wooldridge & Bailey 1982). Standard zooplankton sampling methods do not adequately sample the mysid population in an estuary. For this reason few reliable records of estuarine mysid populations exist.

In this study the mysid population was not purposefully sampled. Therefore it cannot be assumed that mysid abundance is low on the evidence of the collected data. The occurence of selective predator-prey interactions in the control of copepod abundance thus cannot be excluded on the basis of the present data.

Knowledge of the tolerance of the nauplii of these two species to different salinity and temperature regimes, as well as each species' breeding success at different salinities and temperatures would throw further light on their successional behaviour and competitive abilities.

2.6 REFERENCES

Barlow, J.P. 1955. Physical and biological processes determining the distribution of zooplankton in a tidal estuary. *Biol. Bull.* **109** : 211-225.

Bayly, I.A.E. 1965. Ecological studies on the planktonic copepoda of the Brisbane River Estuary with special reference to *Gladioferens pectinatus* (Brady) (Calanoida). *Aust. J. Mar. Freshwat. Res.* **16** : 315-350.

Coetzee, D.J. 1985. Zooplankton and some environmental conditions in the Bot River Estuary. *Trans. Roy. Soc. S. Afr.* **45**(3/4) : 363-377.

Connell, A.D. and Grindley, J.R. 1974. Two new species of *Acartia* (Copepoda, Calanoida) from South African estuaries. *Ann. S. Afr. Mus.* **65**(3) : 89-97.

Conover, R.J. 1956. Oceanography of Long Island Sound 1952-1954. VI. Biology of *Acartia clausi* and *A. tonsa*. *Bull. Bingham Oceanogr. Coll.* **15** : 156-233.

Conover, R.J. 1961. A study of Charlestown and Green Hill ponds, Rhode Island. *Ecology* **42**(1) : 119-140.

Day, J.H. (ed.) 1981. *Estuarine Ecology with particular reference to southern Africa.* Cape Town, A.A. Balkema, 441 pp.

Deevey, G.B. 1960. The zooplankton of the surface waters of the Delaware Bay region. *Bull. Bingham Oceanogr. Coll.* 17(2) : 5-53.

Faber, D.J. 1966. Seasonal occurrence and abundance of free- swimming copepod nauplii in Narragansett Bay. *J. Fish. Res. Bd Can.* 23(3) : 415-422.

Fulton III, R.S. 1982. Preliminary results of an experimental study of the effects of mysid predation on estuarine zooplankton community structure. *Hydrobiologia* 93 : 79-84.

Fulton III, R.S. 1983. Interactive effects of temperature and predation on an estuarine zooplankton community. *J. Exp. Mar. Biol. Ecol.* 72 : 67-81.

Grahame, J. 1976. Zooplankton of a tropical harbour: the numbers, composition and response to physical factors of zooplankton in Kingston Harbour, Jamaica. *J. Exp. Mar. Biol. Ecol.* 25 : 219-237.

Grindley, J.R. 1970. The role of freshwater in the conservation of South African estuaries. *Republic of South Africa Water Year 1970 Convention: Water for the future.* 5 pp.

Grindley, J.R. 1976a. Plankton of the Swartkops Estuary. In: *Proceedings of the First Interdisciplinary Conference on marine and freshwater research in southern Africa.* Port Elizabeth. Council for Scientific and Industrial Research S122.

Grindley, J.R. 1976b. *Report on the ecology of Knysna Estuary and proposed Braamekraal Marina.* School of Environmental Studies, University of Cape Town.

Grindley, J.R. 1981. Estuarine plankton. In: *Estuarine ecology with particular reference to southern Africa.* J.H. Day (ed.) Balkema, Cape Town, pp. 117-146.

Grindley, J.R. 1983. The role of zooplankton in the St. Lucia estuary system. In: *St. Lucia Research Review, Proceedings of the symposium held at Queen Elizabeth Park, Pietermaritzburg, 16 February 1982.* Pietermaritzburg, Natal Parks Board pp. 88-107.

Grindley, J.R. and Wooldridge, T. 1974. The plankton of Richards Bay. *Hydrobiol. Bull.* 8 : 201-212.

Huizinga, P. and Haw. P.M. 1986. A mathematical transport-dispersion model of the Knysna estuary. *The Civil Engineer in South Africa*, July 1986.

Jeffries, H.P. 1962. Succession of two *Acartia* species in estuaries. *Limnol. Oceanogr.* **7** : 354-364.

Jerling, H.L. and Wooldridge, T. 1987. Aspects of the ecology of an estuarine copepod *Pseudodiaptomus hessei* (Calanoida) in the Sundays River estuary. *6th National Oceanographic Symposium, Stellenbosch, 6-10 July 1987.*

Knatz, G. 1978. Succession of copepod species in a middle Atlantic estuary. *Estuaries* 1(1) : 68-71.

Nassogne, A. 1970. Influence of food organisms on the development and culture of pelagic copepods. *Helgolander wiss. Meeresunters.* **20** : 333-345.

Olsson, I. and Olundh, E. 1974. On plankton production in Kungsbacka Fjord, an estuary on the Swedish west coast. *Mar. Biol.* **24** : 17-28.

Poulet, S.A. 1973. Grazing of *Pseudocalanus minutus* an naturally occuring particle matter. *Limnol. Oceanogr.* **18** : 564-573.

Riley, A. 1967. The plankton of estuaries. In G.H. Lauff (ed.) *Estuaries* pp.316-326. Am. Ass. Adv. Sci., Washington.

Rippingale, R.J. and Hodgkin, E.P. 1974. Predation effects on the distribution of a copepod. *Austr. J. Mar. Freshwat. Res.* **25** : 81-91.

Sage, L.E. and Herman, S.S. 1972. Zooplankton of the Sandy Hook Bay area, N.J. *Chesapeake Sci.* **13** : 29-39.

Watson, N.H.F. and Carpenter, G.F. 1974. Seasonal abundance of crustacean zooplankton and net plankton biomass of Lakes Huron, Erie and Ontario. *J. Fish. Res. Bd Can.* **31**(3) : 309-317.

Wooldridge, T. and Bailey, C. 1982. Euryhaline zooplankton of the Sundays estuary and notes on trophic relationships. *S. Afr. J. Zool.* **17**(4) : 151-163.

Wooldridge, T. and Melville-Smith, R. 1979. Copepod succession in two South African estuaries. *J. Plankt. Res.* 1(4) : 329-431.

PART III

Vertical distribution of zooplankton in the Knysna estuary, South Africa.

3.1 ABSTRACT

The vertical distribution and migration behaviour of the dominant zooplankton species in Knysna estuary is described. Samples were taken over one 24-h period at one station in the estuary. Only *Oithona* spp. did not show diel vertical migration behaviour.

Adult *Acartia* spp. were present in surface waters only in very small numbers and did not display strong vertical migratory behaviour. Most of the *Acartia* population was found in bottom waters, where the two species *A. longipatella* and *A. natalensis* showed a spatial distribution related to the tide. These two species apparently utilized different tidal currents to maintain their position in the estuary.

All stages of *Pseudodiaptomus hessei* showed a very pronounced diel vertical migration. The stimulus for the migration was not definitely identified. Changes in light intensity and/or endogenous activity changes have been proposed. Tidal movement also plays a large role in the vertical distribution of *P. hessei* and other zooplankton.

3.2 INTRODUCTION

Accounts of the vertical migration of planktonic animals date from the time of Cuvier (1817, in Cushing 1952), who wrote that in the morning and evening, and even on cloudy days, the Daphniae generally stationed themselves on the surface, but that in the heat of the day, they sought the depths of the water. Subsequently this behaviour has been shown to occur in almost all groups of zooplankton, and it is particularly well-marked in the plankton of estuaries. Some of the patterns observed vary somewhat from those found in the sea or lakes. If plankton samples are taken during the hours of daylight in a South African estuary, very little zooplankton is obtained, whereas at night, much greater numbers are obtained and the composition is found to differ markedly from that found during the day. Species which dominate the plankton during the day appear in small numbers in relation to other species at night and many species appear at night which do not occur at all during the day (Grindley, 1970).

In this study the vertical migration behaviour of the dominant zooplankton species in the Knysna estuary is investigated as part of a one-year study on the zooplankton of this system.

3.3 METHODS

Samples were taken at one station (Fig. 3.1) on 28.6.1985 during an average tide and quarter moon over a 24h period employing standard procedures. The station was chosen because pronounced vertical salinity differences only occur above the National Road Bridge (Haw, unpubl. thesis). Zooplankton density is relatively high at station 4, and the estuary is also fairly deep at this point. Surface and bottom samples were taken every hour. Qualitative samples were taken with a 36cm diameter net with nylon mesh of 124um aperture for the surface samples, and a D-shaped net with the same sampling area and of the same mesh aperture on a sledge for bottom sampling. Both nets were simultaneously hauled horizontally for two minutes at approximately 2 knots. The surface net was hauled immediately below the surface. The D-net was maintained just above the bottom by being weighed down and mounted on a simple sledge. A 12.5cm diameter Clarke Bumpus Plankton Sampler without the sampler was towed at the same time to provide a measure of the volume of water sampled and to provide some quantifying measure for the 36cm net.

After every haul the nets were carefully washed to ensure that no plankton adhered to the gear to contaminate the next sample. The plankton samples were preserved immmediately with formalin made up to approximately 5%

Zooplankton numbers were too high to allow counting of whole samples. Subsamples (25ml) were taken by means of a wide-

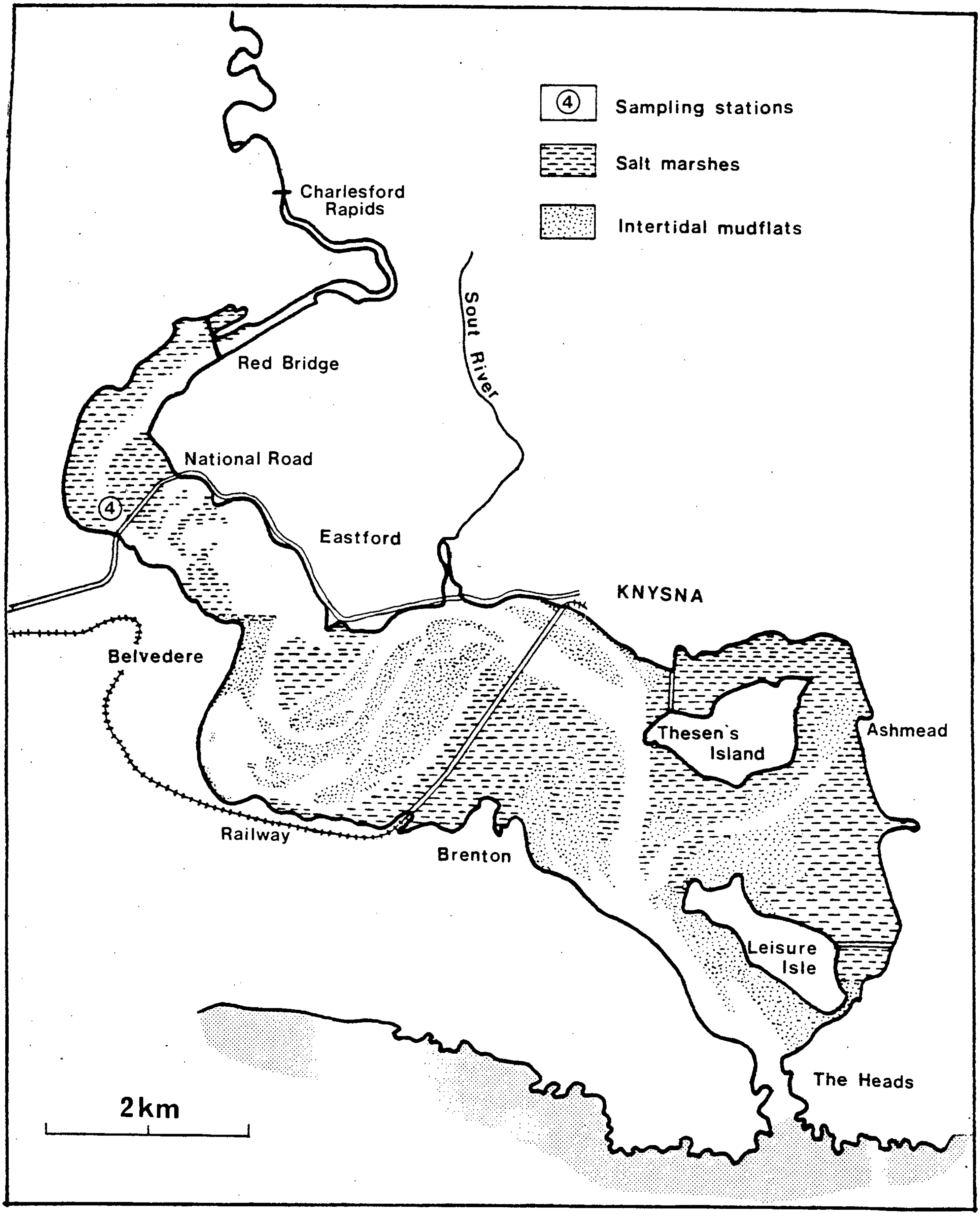

FIG. 3.1 : Map of the Knysna estuary showing the position of the 24-h sampling station.

mouthed pipette from a well-mixed suspension made up to a standard volume of 500ml. The samples were analysed and counted in a Perspex counting tray under a dissecting microscope. Where possible, identification was made down to species. Copepodite stages were noted for *Pseudodiaptomus hessei*.

Biomass was calculated from settled volumes of zooplankton. The relative uniformity of size of the plankton of lagoons and estuaries gives a constant packing density, and it has been shown that a significant correlation exists between settled volume and biomass (dry weight) with a correlation coefficient significant at the 1% level. The regression line was calculated and found to be biomass(mg dry weight) = 18,6 x settled volume(ml) (Grindley & Wooldridge, 1974).

The salinity, temperature and oxygen content of the water was taken with every plankton sample. Temperatures were taken at the surface using the temperature option on the oxygen meter (accurate to 0.5°C). Oxygen was recorded at the surface using a YSI model 57 dissolved oxygen meter with a YSI 5739 dissolved oxygen probe, accurate to 0,01mg.l^{-1}). Salinity was determined at the surface with a automatic temperature compensated hand refractometer, AOC model 10419 (1% accuracy).

3.4 RESULTS

The state of the tide is represented diagrammatically in Fig. 3.2. The surface salinity varied with the tides, reaching 26°/oo at high tide and dropping to 6-8°/oo at low tide. The surface temperature showed a diurnal trend reaching a peak of 15,8°C in the late afternoon, and cooling continuously during the night to 12°C at 07h00. A tidal cycle was superimposed on the diurnal cycle. The period of darkness is indicated by a black band above the graph of zooplankton biomass in Fig. 3.2. It was a clear night with a quarter moon.

The plankton biomass obtained in each sample is represented by the histograms at the bottom of Fig. 3.2. A very small biomass was obtained at the surface during the day (mean biomass 0,65mg.m^{-3}), but at night the biomass increased significantly (mean biomass 1,80mg.m^{-3})(Mann-Whitney U test; $n_1 = 10$, $n_2 = 15$; $U = 3,207$; $p < 0.01$). Peaks were observed at 23h00 and 06h00, with a smaller peak at 18h00. These peaks could be related to tidal changes. Since the low tides coincided with dawn and dusk, and the high tide with full darkness, it is difficult to distinguish tidal and light effects.

Fig. 3.2 also indicates the actual numbers of plankton at the surface as numbers.m^{-3}. The numbers of zooplankton at the surface was also significantly lower during the day (average number of 164.m^{-3}) than during the night (average number of 873.m^{-3})(Mann Whitney U test; $n_1 = 10$, $n_2 = 15$; $U =$

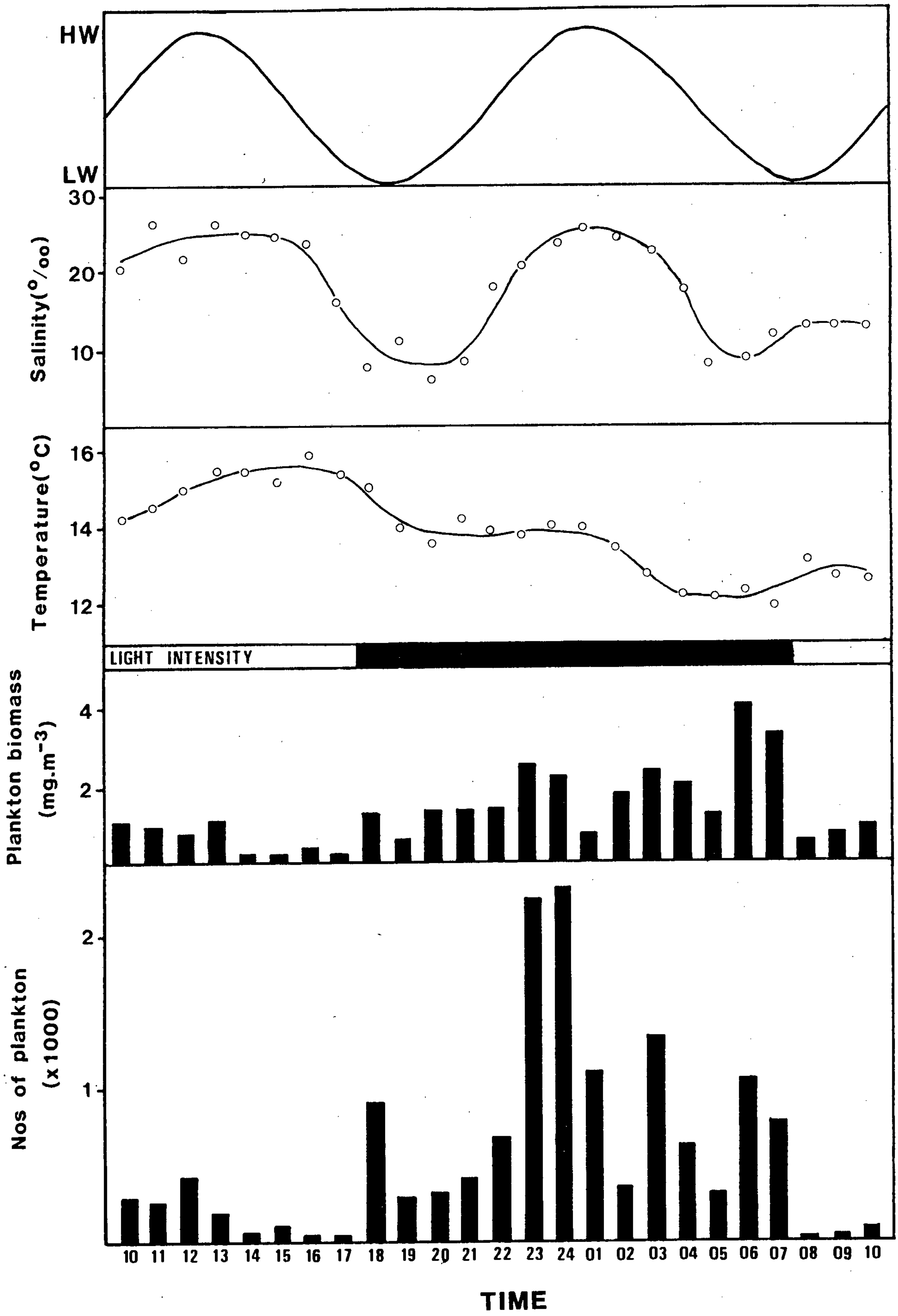

FIG. 3.2 : Changes in the state of the tide, surface salinity (°/oo), surface temperature (°C), light intensity and biomass (mg.m^{-3}) and total numbers of zooplankton at the surface over a 24h period.

3,633; *p* < 0,001). Two peaks can be observed in the actual numbers at 01h00 and 06h00, and a smaller peak at 18h00. Only the peak at 06h00 and the smaller peak just after sunset coincide with the peaks in biomass. The very large peak in numbers only at around midnight is due to large numbers of immature copepods and nauplii. These peaks also could be related to tidal change, with the high numbers of plankton occuring at the surface near high and low tide.

The majority of plankton collected consisted of *Pseudodiaptomus hessei*, *Acartia* spp and harpacticoid copepods. These species all appear to exhibit vertical migration behaviour (Fig. 3.3). *Pseudodiaptomus hessei* was only collected in the surface waters between sunset and sunrise. *Acartia* spp and the harpacticoid copepods were present in low numbers at the surface during the day, but increasing numbers appeared at the surface at night. The presence of copepod nauplii at the surface (which consisted mainly of *P. hessei* nauplii) could be more related to the high tide than light intensity.

The harpacticoids showed a clear vertical migration pattern with no distinct peaks in numbers, nor a distributional relationship to the tides. Harpacticoid copepods seem to be evenly distributed in the water masses, resulting in even sampling and no concentration of species in water masses of certain temperature and salinity.

The distribution of copepod nauplii show the strongest relationship to the tides, with peaks in numbers coinciding

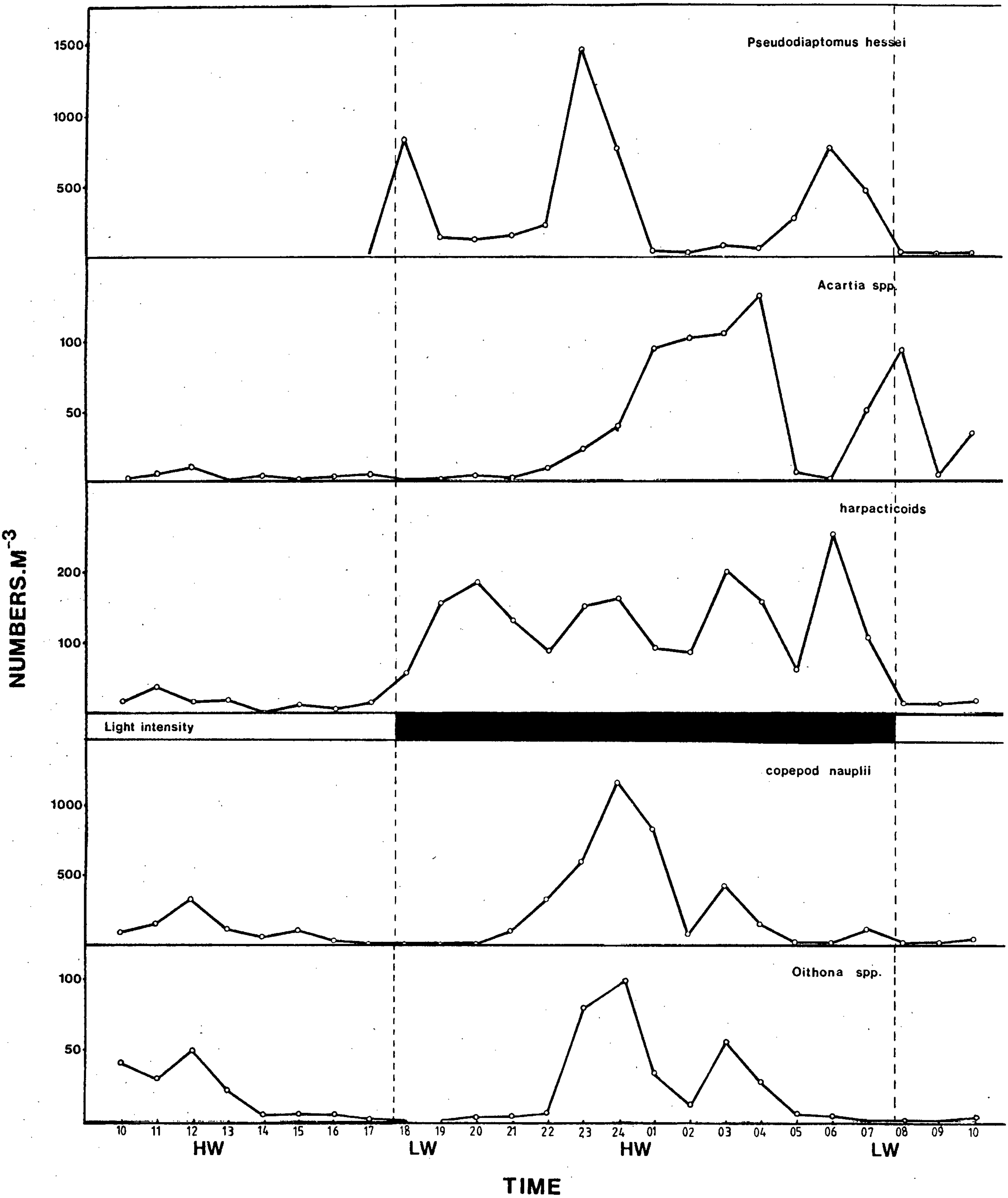

FIG. 3.3 : Changes in the numbers of *Pseudodiaptomus hessei*, *Acartia* spp., harpacticoid copepods, copepod nauplii and *Oithona* spp. at the surface and over a 24h period.

with high tide. Vertical migration does seem to take place, as the numbers of nauplii around high tide were three times as high at night (full darkness) than during the day (n=3; x_{night} = 855,3 ± 228,1; x_{day} = 196,7 ± 88,5).

The distribution of *Oithona* spp. at the surface seem to be related to the tide. Significant numbers were only recorded at the surface at high tide which indicates that this species is more abundant lower down the estuary. There is no clear evidence for vertical migration in this species as the average numbers at night were not significantly higher than during the day.

The *Acartia* species consisted mostly of immature stages (which could not be identified to species). Adult *Acartia longipatella*, *Acartia africana* and *A. natalensis* were present in much lower numbers. They only appeared at the surface in significant numbers from midnight with a peak at 04h00, a sudden drop in numbers and a second peak after sunrise at 08h00. Looking at the distribution of adult stages of *A. natalensis* and *A. longipatella* separately (Fig. 3.4) a spatial distribution related to tide is observed. The adult *Acartia* spp. generally tend to be found in larger numbers near the bottom, showing only a slight migration towards the surface between midnight and sunrise. *Acartia natalensis* is present in larger numbers in the bottom waters around low tide, while *A. longipatella* is more abundant at high tide. This indicates that *A. natalensis* is more abundant in the higher reaches of the estuary, while *A. longipatella* has a greater population density towards the

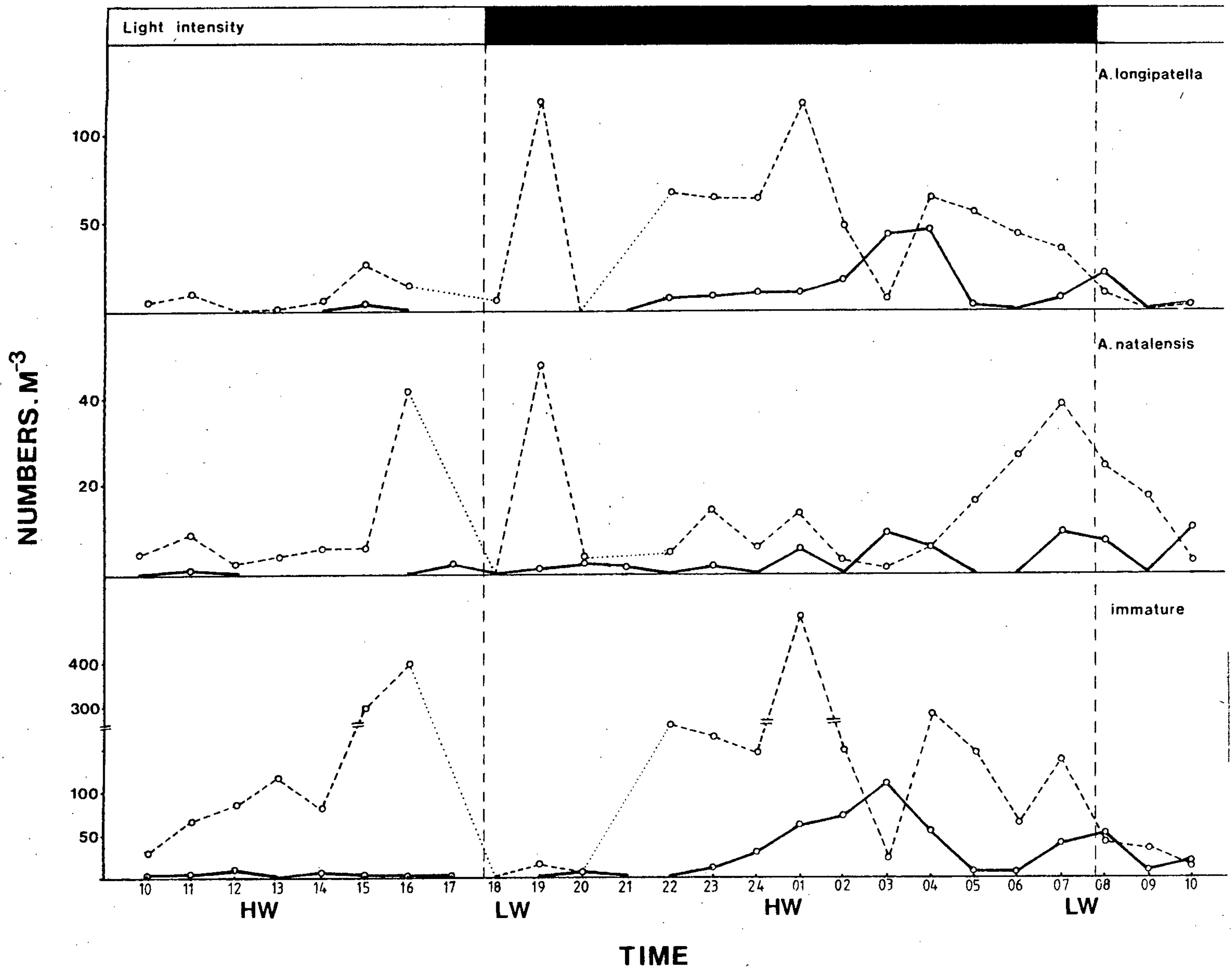

FIG. 3.4 : Changes in the numbers of two species of *Acartia* (*A. natalensis* and *A. longipatella*) and their immature stages in the surface (o———o) and bottom (o-------o) waters.

mouth. This agrees with the findings of Wooldridge and Erasmus (1980) in the Sundays river estuary. *A. natalensis* was found in faster flowing currents and so moved higher up the estuary. The immature *Acartia,* which probably consisted mostly of *A. longipatella,* showed a similar distribution pattern in both bottom and surface water as the adult *A. longipatella.* This suggests that the immature stages of *Acartia* spp exhibit the same behavioural responses as the adults.

Fig. 3.5 shows the numbers of male, female, stage V and immature stages of *P. hessei* at the surface.. The ratio of stages and sexes varied from one sample to another, presumably as a result of sampling different water masses in the tidal current. In all except the female stages there was a sudden increase and peak in numbers after sunset. All except the males showed a peak around midnight and all stages showed a peak in numbers 2 hours before sunrise. The latter peak was more pronounced in the late and mature stages. The immature stages showed the most pronounced peak around midnight, with the incoming tide. Immature stages are thus present in larger numbers lower down the estuary and their distribution is more closely related to the tide than the adult stages. The increase in numbers just after sunset and just before sunrise coincided with low tide. Larger populations of *P. hessei* are found higher up the estuary, in water of lower salinities. With the outgoing tide these populations are moved downstream and could thus explain the higher numbers around low tide. The population structure is

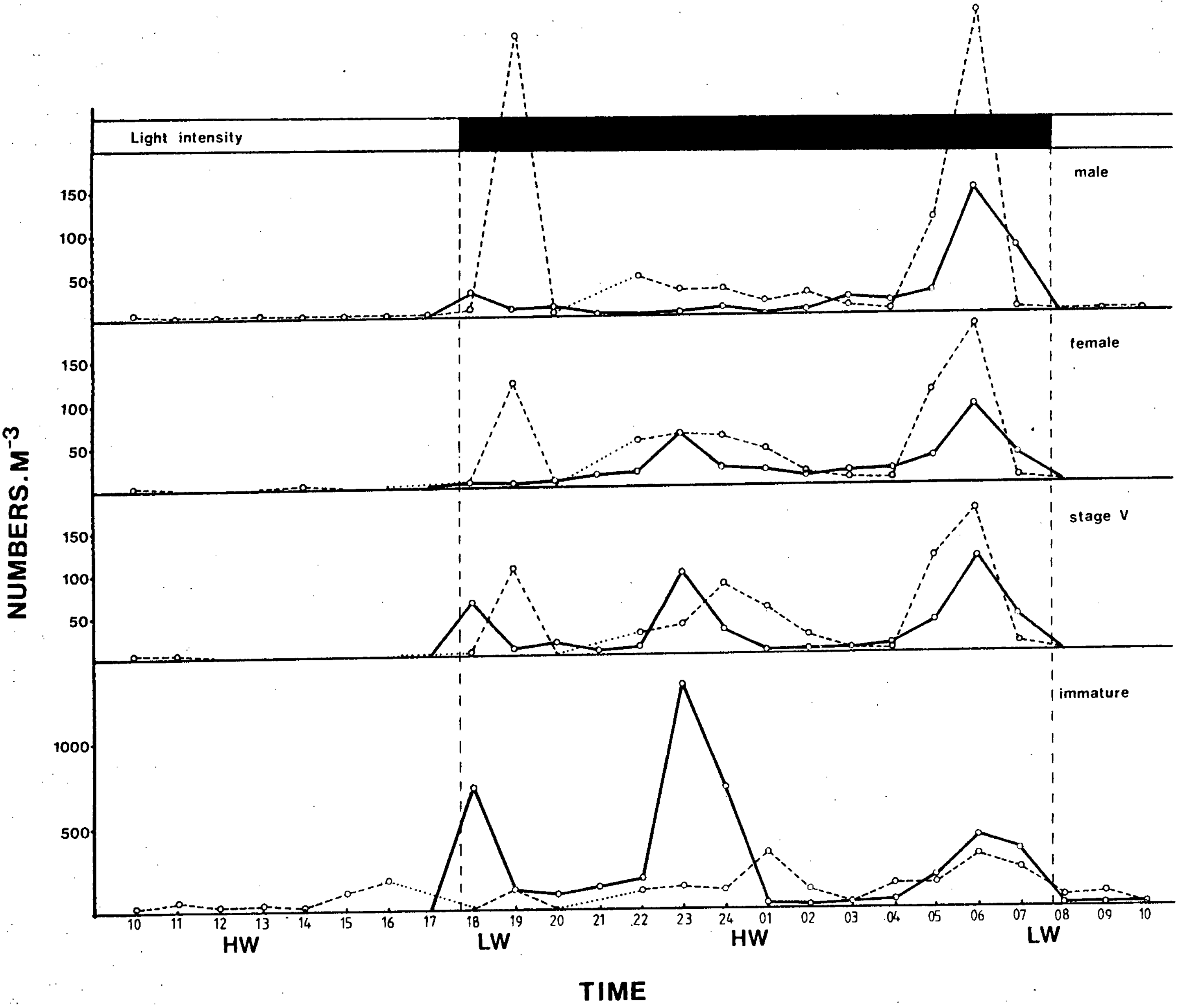

FIG. 3.5 : Changes in the numbers of adult male and female, stage V and immature stages of *Pseudodiaptomus hessei* in the surface (o———o) and bottom (o--------o) waters in the Knysna estuary.

roughly the same in both cases, except for the higher numbers found later in the night. This can be explained by a 'pre-dawn rise', as observed by other authors in marine and lake zooplankton (Cushing 1951).

The peaks in numbers at the bottom generally coincide with the peaks in numbers at the surface, thus also showing a tidal relationship. The bottom peaks were however much larger, especially in the adult males where the bottom peaks were more than twice as large. This simultaneous increase in numbers of *P. hessei* in both surface and bottom waters suggests that there must be a contribution to the population in the water from the bottom mud. The presence of a population of *P. hessei* in close association with the bottom mud on the bed of estuaries has been established for South African estuaries using a sledge sampler and in laboratory observations (Grindley 1972).

3.5 DISCUSSION

The results of the 24h sampling series in Knysna estuary indicate that nearly all of the species of zooplankton that were sampled do undertake vertical migration. This migration must be of great significance to have developed in so many groups of planktonic animals. Its survival value to estuarine zooplankton could be in maintaining their position in the estuary. By performing vertical migration the animals move between inflowing saline water along the bottom of the estuary and outflowing low salinity surface water. They thus drift alternately upstream and downstream, tending to maintain their position in the estuary. The fact that migration is inhibited by a strong salinity discontinuity (Lance 1962, Grindley 1964) supports this hypothesis in that it would prevent planktonic animals from migrating into strongly outflowing freshwater during a river flood, and thus would prevent them being swept out to sea.

In a well stratified estuary such as Msikaba estuary indigenous zooplankton are able to survive close to the mouth in relatively high numbers with little loss to the sea (Wooldridge 1976). In well mixed estuaries with a strong tidal flow, such as Richards Bay, the distribution of zooplankton appears to relate to distance from the mouth. Indigenous zooplankton only survived in areas of the estuary subject to limited tidal exchange (Grindley & Wooldridge 1974). In cases where an estuary is completely flushed with the low tide, no permanent plankton will develop (Rogers 1940). In the Sundays river estuary strong tidal currents occur, yet the zooplankton biomass is characteristically high. Wooldridge & Erasmus (1980) showed that the endemic zooplankton populations maintained themselves within the estuary by avoiding or utilizing currents in both a vertical and a lateral plane.

In Knysna estuary populations of different species of *Acartia* could be utilizing the tidal currents to maintain a spatial distribution. *A. natalensis* is more abundant in bottom waters at low tide, whereas *A. longipatella* migrates into the bottom waters during high tide. *A. natalensis* thus maintains its position higher up in the estuary than *A. longipatella*. *A. natalensis* was seldom collected near the mouth (St. 1), while *A. longipatella* was fairly common (see Part I).

Pseudodiaptomus hessei avoids the stronger current by remaining near the bottom, the adult stages only migrating to the surface in significant numbers at the turn of the tide, when current velocities at the surface are lowest. This would reduce the possibility of being flushed from the system on the low tide. The immature stages are present in larger numbers than the adults in surface waters at all times. They thus do not seem to actively avoid faster currents as is the case for the adult stages. This would explain their presence in larger numbers lower down the estuary.

Some function of light, either directly or indirectly, seems to be responsible for the vertical movements in *Pseudodiaptomus hessei*. No adult stages and only very few stage V copepodites were recorded in surface waters during the day. Numbers were also very low at the bottom during the day. With a decrease in light intensity *P. hessei* became abundant in both surface and bottom waters, and a second movement was observed at dawn. *Acartia* species did not show such a strong relationship to light in their vertical migration behaviour, and adult stages were sometimes present in the surface waters during the day. The overriding controlling factor in their observed distribution pattern seemed to be tidal rather than light induced.

The works of Ringelberg (1961, 1964) and McNaught & Hassler (1964) argue strongly in favour of the rate of change in light intensity providing the causal stimulus at dusk, and probably also at dawn. Once the rate of change reaches a threshold level, migration is initiated. Hart & Allanson (1976) in their study on diel vertical migration of *P. hessei* in Lake Sibaya found the dusk ascent of this copepod consistent with this interpretation. In Knysna the rate of change of light was not measured, but both the dusk rise and the dawn ascent were noticably performed at low light intensities, supporting the findings of Hart & Allanson. The role of endogenous rhythmicity in vertical migration has been considered in detail by Rudjakov (1970). His hypothesis generally accounts for aspects of vertical migration either inconsistent with the classical concepts of causal factors or else for which no adequate explaination had been advanced. The typical dusk rise is considered to result from increased locomotor activity, induced endogenously. Nocturnal sinking is considered to result from a decrease in endogenous activity. The dawn rise is a simple manifestation of a secondary peak in endogenous activity at dawn, and ascent to day depth is accomplished by passive sinking. The migration of *P. hessei* in the Knysna estuary shows features consistent with theories of endogenous rhythms. The dawn rise before any actual increase in light , suggests the presence of an intrinsic rhythm (Harris 1963). It thus seems that a interaction of light intensity changes and endogenous activity changes, together with sampling of different water masses at different states of the tide would result in the observed vertical migration patterns in *P. hessei*.

The adaptive significance of vertical migration towards the surface at night in *P. hessei* and other planktonic animals is as yet not clear. *P. hessei* feeds by night throughout the water column, and rests on and in the bottom sediments during daylight hours (Hart & Allanson 1976, Grindley 1972). By resting on the bottom sediments, energy conserving opportunities may arise analogous to those suggested by McLaren (1963) to arise from alternate occupation of warm and cooler waters. Little support has, however, been found for this hypothesis in the case of *P. hessei* (Hart & Allanson 1976)

3.6 REFERENCES

Cushing, D.H. 1951. The vertical migration of planktonic Crustacea. *Biol.Rev.* **26** : 158-192.

Grindley, J.R. 1964. Effect of low-salinity water on the vertical migration of estuarine plankton. *Nature* **203** : 781-782.

Grindley, J.R. 1970. The plankton of South African estuaries. *Oceanography in South Africa Contribution H.1* : 1-16.

Grindley, J.R. 1972. The vertical migration behaviour of estuarine plankton. *Zool. Afr.* 7(1) : 13-20.

Grindley, J.R. 1977. The zooplankton of Langebaan Lagoon and Saldanha Bay. *Trans. Roy. Soc. S. Afr.* **42**(3 & 4) : 341-370.

Grindley, J.R. and Wooldridge, T. 1974. The plankton of Richards Bay. *Hydrobiol. Bull.* **8**(1/2) : 201-212.

Hart, R.C. and Allanson,B.R. 1976. The distribution and diel vertical migration of *Pseudodiaptomus hessei* (Mrazek) (Calanoida, Copepoda) in a subtropical lake in southern Africa. *Freshwater Biol.* **6** : 183-198.

Lance, J. 1962. Effects of water of reduced salinity on the vertical migration of zooplankton. *J. Mar. Biol. Assoc. U.K.* **42** : 131-154.

McLaren, I.A. 1963. Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. *J. Fish. Res. Board Can.* **20** : 685-727.

McNaught, D.C. and Hassler, A.D. 1964. Rate of movement of populations of *Daphnia* in relation to changes in light intensity. *J. Fish. Res. Board Can.* **21** : 291-318.

Ringelberg, J. 1961. A physiological approach to an understanding of vertical migration. *Proc. K. Ned. Akad. Wet. Ser. C.* **64** : 489-500.

Ringelberg, J. 1964. The positively phototactic reaction of *Daphnia magna* Straus: a contribution to the understanding of diurnal vertical migration. *Neth. J. Sea Res.* **2** : 319-406.

Rudjakov, J.A. 1970. The possible causes of diel vertical migrations of planktonic animals. *Mar. Biol.* **6** : 98-105.

Wooldridge, T. 1976. The zooplankton of Msikaba estuary. *Zool. Afr.*11(1) : 23-44.

Wooldridge, T. and Erasmus, T. 1980. Utilization of tidal currents by estuarine zooplankton. *Estuarine Coastal. Mar. Sci.* **11** : 341-370.

CONCLUSIONS

The important factors found to control the distribution of zooplankton in the Knysna estuary are salinity and river discharge, temperature, biological factors and tidal exchange. Vertical migration acts together with these factors in maintaining position in the estuary.

Salinity

Salinity determines the broad distribution of zooplankton. Truly estuarine euryhaline species occur in the main estuary, where salinities are low and variable. The dominant estuarine copepods were *Pseudodiaptomus hessei, Acartiella natalensis* and *Paracartia longipatella*. Neritic species occur near the mouth of the estuary and penetrate the estuary on the high tide. These include *Calanoides carinatus, Oithona similis* and *Centropages brachiatus*. Ocean water penetrates up to 5 km up the estuary, due to the permanently open mouth. This allows the penetration of neritic zooplankton populations as far as Thesen's Island, and results in a large section of the estuary having high salinities and a strong marine faunal component.

The zooplankton in higher salinity areas is characteristically more diverse. Ninety percent of copepod species identified occurred in the lower estuary, but only 30% of the copepod biomass was represented. Productivity and biomass are higher at lower salinities.

The zooplankton can be compared to east coast estuaries in species diversity and richness. More than 50 species were identified, and the average annual dry biomass is 186mg.m^{-3}.

River discharge

Changes in the salinity regime of this estuary will affect the zooplankton distribution. In the open Knysna system salinity changes are primarily the result of changes in the freshwater discharge into the estuary. River discharge plays an important role in the distribution and abundance of the numerically dominant copepod *Pseudodiaptomus hessei*. This pioneer species attains maximum abundance after periods of strong river discharge, utilizing the nutrients entering the estuary with the river water. The species also reproduces more rapidly at lower salinities. The zooplankton biomass will thus increase with increased river flow and decreased salinity. A decrease in riverflow will increase the range of tidal influence and allow neritic species to enter higher up the estuary. Zooplankon species diversity will then increase, but biomass will decrease.

Studies during drought conditions in the Keiskamma estuary by Read & Allanson (1983) have in fact indicted that in the upper estuary zooplankton biomass increased significantly and community structure changed when the salinity increased from 1 to 29°/oo. Diversity was not affected. Short term effects of lack of freshwater input thus appeared to be beneficial in expanding the utilizable area of the estuary. A similar situation could arise in Knysna estuary. In the longer term lack of freshwater input may result in hypersalinity. Hypersaline conditions such as those that occurred in the St Lucia system will result in the disappearance of much of the zooplankton (Grindley 1981). Studies on the Knysna sytem have shown, however, that it is very unlikely that the salinity in the upper reaches of the estuary will ever exceed 40°/₀₀ (Haw, unpublished thesis).

An important factor to consider in discussing the effect of river discharge on the zooplankton in estuaries, is to what extent, if at all, a high zooplankton biomass at short-term elevated salinities is dependant on previous energy inputs by freshwater.

Temperature

Temperature plays a role in seasonal variations in the zooplankton community. Biomass is generaly higher during the warmer summer months. It also indirectly plays a role in the cyclical dominance of the two *Acartia* species, *Acartiella natalensis* (the summer dominant) and *Paracartia longipatella* (the winter dominant).

Biological factors

Predation and competition were not directly investigated. The available data on the seasonal succession of *Acartiella natalensis* and *Paracartia longipatella* does however not preclude it. It would be usefull to sample the estuary for possible predators such as the Mysidaceae, and to determine the breeding success and tolerances of the nauplii of the *Acartia* species at different salinity and temperature regimes. This would throw further light on their respective competitive abilities, and would hopefully determine whether predation is of importance in controlling zooplankton in the Knysna system.

Tidal exchange

The most important factor controlling the distribution of zooplankton is tidal exchange. *Pseudodiaptomus hessei* can only successfully maintain itself where the tidal residence time is long enough to allow the population to replace itself before being flushed out of the estuary. The highest concentrations of *P. hessei* correspond to the areas of longest residence times (ie. between Belvedere and Charlesford Rapids). *P. hessei* also occurs in abundance in the Ashmead Channel, in the lower half of the estuary. It is able to survive there due to the long tidal residence time. The salinity in this area is high, since the only water entering this channel originates from the mouth of the estuary.

Vertical migration

Diel vertical migration was observed in almost all the zooplankton, but was most pronounced in *Pseudodiaptomus hessei*. The importance of this probably endogeous rhythmic behaviour is not totally clear. It could be important in maintaining a position in the estuary, by the organism alternately migrating into the outflowing freshwater layer and the inflowing saline water.

Tidal currents appear to be effectivly utilized or avoided by vertical movements as an aid to maintaining a position in the estuary. The two species of *Acartia*, *A. natalensis* and *A. longipatella*, utilise the tidal currents to maintain a spatial distribution in the estuary. In this way *A. natalensis* maintains a position higher up in the estuary. *P. hessei* also avoid the stronger flowing currents by remaining on the bottom until the change of the tide, thus preventing it from being washed out of the estaury.

Further 24h studies at different tidal cycles would be needed to clarify to what extent tidal currents affect the diel vertical migration pattern.

REFERENCES

Grindley, J.R. 1981. Estuarine plankton. In: *Estuarine ecology with particular reference to southern Africa.* J.H. Day (ed.) Balkema, Cape Town, pp. 117-146.

Haw, P.M. 1984. *Freshwater requirements of Knysna estuary.* School of Environmental Studies Report No. 55, Univ. of Cape Town. 136 pp. (unpubl. M.Sc. thesis).

Read, G.H.P. & Allanson, B.R. 1983. Community structure and distribution of the estuarine dependent biota of the Keiskamma River estuary with particular reference to the influence of cyclical and episodic variation in salinity gradients in maintaining this community. *Progress Report to SANCOR, December 1983.*

ACKNOWLEDGEMENTS

I would like to thank the following people for their assistance with this thesis:

My field assistants, for spending nights collecting samples in all weather.

Lagoon Charter Cruises in Knysna, for their helpfulness, advice and hire of boats at exceptional hours.

My supervisor, Dr C. L. Griffiths, for comment on the manuscript and also for identification of Amphipoda.

My co-supervisor, Prof. J. R. Grindley, for help with the fieldwork and plankton identification, as well as for comment on the manuscript.

My husband, Hilton Davies, for his continual support and encouragement.

Funding for this project was provided by the South African National Committee on Oceanographic Research (SANCOR).

APPENDIX 1

Total numbers.m^{-3} of zooplankton sampled at six stations in the Knysna estuary over a period of one year.

Date	St.2	St.3	St.4	St.5	St.6	St.7	Mean
23.3.1985	22 757	9 466	8 702	7 832	32 683	4 115	14 259
3.7.1985	2 943	708	4 381	1 735	3 743	1 869	2 563
14.9.1985	4 060	2 736	17 860	40 268	8 396	931	12 375
5.10.1985	-	2 734	6 797	8 508	3 315	3 110	4893
3.11.1985	7 296	2 407	93	123	262	126	1 718
1.12.1985	18 051	13 635	48 194	10 219	12 264	1 427	17 298
8.1.1986	39 129	43 769	23 974	6 513	1 061	280	18 121
8.2.1986	35 536	31 254	30 033	12 815	2 782	837	18 876

APPENDIX 2

Total numbers.m^{-3} of *Acartia* spp. collected over a period of one year at six sampling stations in the Knysna estuary.

Date	St.2	St.3	St.4	St.5	St.6	St.7	Mean
23.3.1985	9 450	3 999	4 120	2 386	18 219	1 579	6 626
3.7.1985	24	96	2 746	123	303	72	561
14.9.1985	703	868	6 799	8 872	3 666	10	3 486
5.10.1985	1 665	298	1 247	897	230	0	723
3.11.1985	3 116	1 179	0	0	0	0	716
1.12.1985	1 847	1 663	4 541	705	1 753	124	1 772
8.1.1986	32 505	33 082	18 639	383	8	0	14 103
8.2.1986	13 337	11 962	19 430	5 587	1 640	281	8 706

APPENDIX 3

Numbers.m^{-3} of adult *Acartia natalensis, A. longipatella* and *A. africana* sampled over 1 year at 6 stations in the Knysna estuary.

I. *Acartia (Acartiella) natalensis*:

Date	St.2	St.3	St.4	St.5	St.6	St.7	Mean
23.3.1985	1468	282	1121	1544	12032	1510	2993
3.7.1985	0	1	53	11	90	35	32
14.9.1985	0	0	0	11	2	4	3
5.10.1985	0	0	0	6	4	0	2
3.11.1985	0	0	0	0	0	0	0
1.12.1985	21	163	171	231	862	48	249
8.1.1986	15 936	22 486	18 639	367	8	0	9 573
8.2.1986	3 983	2 930	11 507	5 252	1 348	248	4 211

II. *Acartia (Paracartia) longipatella*

Date	St.2	St.3	St.4	St.5	St.6	St.7	Mean
23.3.1985	171	0	0	0	0	0	29
3.7.1985	0	0	1 487	29	100	9	271
14.9.1985	76	221	3 211	6 239	1 752	0	1 916
5.10.1985	259	6	260	460	93	0	180
3.11.1985	58	197	0	0	0	0	43
1.12.1985	85	122	930	89	59	75	227
8.1.1986	0	0	0	0	0	0	0
8.2.1986	0	0	0	0	0	0	0

III. *Acartia (Paracartia) africana*

Date	St.2	St.3	St.4	St.5	St.6	St.7	Mean
23.3.1985	383	251	32	35	0	0	117
3.7.1985	6	8	276	0	0	0	48
14.9.1985	291	19	18	0	0	0	55
5.10.1985	8	27	34	7	1	0	13
3.11.1985	209	8	0	0	0	0	36
1.12.1985	84	40	281	0	0	0	68
8.1.1986	105	60	0	0	0	0	28
8.2.1986	206	60	66	0	0	0	55

APPENDIX 4

Numbers.m^{-3} of male, female, gravid female and immature stages and total numbers and of *Pseudodiaptomus hessei* sampled over a period of one year at six sampling stations in the Knysna estuary.

Date	St.2	St.3	St.4	St.5	St.6	St.7	Mean
23.3.1985							
male	200	211	213	145	1 561	97	405
female	189	124	201	421	1 263	277	412
gravid female	86	110	154	230	759	162	250
immature	1 412	288	1 394	4 088	7 021	1 236	2 573
total	1 801	623	1 808	4 654	9 845	1 610	3 390
3.7.1985							
male	14	13	233	32	113	19	71
female	6	14	128	59	112	23	57
gravid female	0	8	83	32	64	4	32
immature	10	66	464	132	1 503	263	406
total	30	93	825	223	1 728	305	534
14.9.1985							
male	107	105	2 842	5 357	736	190	1 556
female	265	109	2 236	6 451	717	145	1 653
gravid female	210	74	1 710	3 348	488	139	993
immature	384	244	3 720	14 397	2 581	97	3 570
total	756	458	8 798	26 205	4 034	432	6 780
5.10.1987							
male	89	66	165	785	93	3	200
female	179	82	267	1 386	138	3	342
gravid female	114	60	144	474	32	1	138
immature	731	335	919	3 806	1 415	407	1269
total	999	483	1 351	5 710	1 648	410	1 773
3.11.1985							
male	17	39	7	1	0	0	11
female	41	98	13	0	0	0	25
gravid female	35	37	0	0	0	0	12

immature	370	538	20	0	0	0	155
total	428	655	40	1	0	0	187
1.12.1985							
male	1 170	162	3 233	664	399	15	940
female	959	257	4 936	925	1 243	78	1 340
gravid female	464	135	2 707	368	657	48	730
immature	4 230	662	12 247	4 970	6 522	267	4 816
total	6 449	1 081	20 416	6 559	8 164	360	7 172
8.1.1986							
male	26	1 144	1 276	983	79	0	585
female	0	542	2 264	2 103	65	0	829
gravid female	0	211	2 032	1 752	57	0	674
immature	290	1 174	1 241	2 078	192	11	831
total	316	2 860	4 781	5 164	336	11	2 245
8.2.1986							
male	700	891	837	1 942	21	0	732
female	1 002	559	1 808	901	11	0	713
gravid female	247	393	1 384	740	5	0	462
immature	7 376	1 329	3 080	3 351	297	0	2 572
total	9 078	2 779	5 725	6 194	329	0	4 018

APPENDIX 5

Numbers and biomass of zooplankton collected at hourly intervals over a 24-h period at the National Road Bridge in Knysna estuary.

Sample no.	Time	Surface		Bottom	
		biomass (mg.m^{-3})	numbers (per m^3)	*biomass (mg.m^{-3})	numbers (per m^3)
1	10h35	1.12	288		209
2	11h30	0.93	259		243
3	12h30	0.74	456		134
4	13h25	1.12	200		183
5	14h25	0.19	72		139
6	15h25	0.19	122		509
7	16h20	0.37	42		706
8	17h45	0.19	49		-
9	18h20	1.30	917		103
10	19h15	0.56	310		2476
11	20h15	1.30	334		34
12	21h15	1.30	424		-
13	22h10	1.30	689		765
14	23h10	2.60	2257		1252
15	00h10	2.23	2325		1086
16	01h05	0.74	1119		2072
17	02h05	1.86	345		503
18	03h05	2.42	1353		154
19	04h00	2.05	643		495
20	05h40	1.30	336		1453
21	06h20	4.09	1073		2631
22	06h55	3.35	780		772
23	07h55	0.56	185		197
24	08h55	0.74	50		160
25	09h50	0.93	105		92

* Biomass of the bottom samples was not calculated due to the presence of sediment in most of the samples which affected the settled volumes.

APPENDIX 6

Physical data collected hourly over 24 hrs at the National Road Bridge in Knysna estuary.

Sample	Salinity (°/oo)	Temperature (°C)		Dissolved oxygen ($mg.l^{-1}$)	
	surface	surface	bottom	surface	bottom
1	20.5	14.2	14.6	10.0	9.7
2	25.9	14.6	14.8	9.2	8.6
3	22.0	15.0	14.8	8.6	8.3
4	26.0	15.5	15.0	9.2	9.1
5	25.0	15.5	15.0	8.7	8.9
6	24.5	15.2	14.9	8.9	9.1
7	24.0	15.8	15.1	9.6	9.2
8	16.0	15.4	15.2	8.9	7.6
9	7.9	15.0	15.2	9.9	7.8
10	11.0	14.0	15.0	8.5	8.4
11	6.0	13.6	14.9	8.5	8.6
12	8.0	14.2	14.9	8.9	9.7
13	18.0	13.9	14.8	9.4	9.8
14	21.0	13.8	14.4	9.4	9.8
15	24.0	14.1	14.5	9.4	9.2
16	26.0	14.0	14.4	8.6	8.6
17	24.5	13.5	14.3	8.9	8.8
18	23.0	12.8	14.2	8.8	8.9
19	18.0	12.3	14.0	9.0	9.0
20	8.0	12.2	14.0	9.0	8.0
21	9.0	12.3	13.3	8.6	8.7
22	12.0	12.0	14.2	8.2	8.4
23	13.0	13.2	14.5	8.2	8.1
24	14.0	12.8	14.5	7.7	8.9
25	14.0	12.5	14.6	8.0	8.6