THE INFLUENCE OF CONTRASTING FRESHWATER INFLOWS ON THE FEEDING ECOLOGY AND FOOD RESOURCES OF ZOOPLANKTON IN TWO EASTERN CAPE ESTUARIES, SOUTH AFRICA

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by

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"Natura nusquam magis est tota quam in minimis"

Pliny

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DECLARATION

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ABSTRACT

The trophodynamic implications of reduced freshwater inflow on the zooplankton of eastern Cape estuaries was investigated by a comparison of the community composition and standing stocks, grazing rates and food resources of zooplankton in two systems, the Kariega and the Great Fish estuaries, which are subject to contrasting freshwater inflow.

The climate of South Africa is semi-arid, and the low rainfall, coupled with high evaporative loss, result in the region having one of the lowest conversions of rainfall to run-off in the world. In addition, many of the major rivers are extensively impounded, consequently, estuaries often experience prolonged periods of zero or reduced freshwater inflow. The amount of freshwater available for estuarine management in the future is expected to decline as the demand for domestic, agricultural and industrial use increases. The influence of climate, tidal amplitude and wave action are essentially constant, consequently, the individual characteristics of an estuary are determined largely by the indirect influences of catchment size and regulation. Estuaries along the eastern Cape coast range from negative hypersaline systems, to positive systems in which a salinity gradient is well established. The Kariega estuary is a homogeneous marine estuary as a result of minimal freshwater inflow, whereas the Great Fish estuary receives sustained freshwater inflow and is partially-stratified.

The quality and quantity of particulate food resources for suspension-feeders depended to a large extent on the allochthonous import of material associated with freshwater inflow. Nutrients, rather than light penetration of the watercolumn are the major factor limiting phytoplankton standing stocks. In the Kariega estuary, phytoplankton standing stocks were

low (up to 1.0 μg l^{-1}) and the estuary is classified as oligotrophic. Correlation analyses indicated that lower quality detritus, originating from fringing macrophytes, may contribute substantially to suspended particulate organic material. Phytoplankton food resources were considerably higher in the Great Fish estuary (up to 21.8 μg l^{-1}) which is classified as mesotrophic/eutrophic, and correlation analyses indicated that phytoplankton comprised the dominant fraction of the particulate organic material. Although this suggested that the organic material was of a higher quality, the seston was "masked" by a higher suspended inorganic load. Consequently, the organic fraction comprised between 13 and 22 % of total particulate material in the Great Fish estuary, compared with between 20 and 39 % in the Kariega estuary.

Food resources demonstrated a fairly uniform distribution along the length of the Kariega estuary and exhibited a slight seasonal increase during warmer months. By contrast, the point source influence of freshwater inflow resulted in a spatial gradient of food resources in the Great Fish estuary with higher values recorded towards the upper reaches. There was evidence that higher concentrations of particulate material in the upper reaches are also a consequence of hydrodynamic trapping. There was no marked seasonal pattern in the availability of food resources which were generally elevated in response to sporadic pulses of freshwater inflow. Tidal currents were responsible for elevating suspended food resources by re-suspension of material from the sediments. This effect was probably of greater importance in the Kariega estuary where food resources were generally limiting.

In the Kariega estuary, the zooplankton community was dominated by calanoid copepods of the genera *Acartia* and *Pseudodiaptomus*. However, in the Great Fish estuary, the community was dominated by the mysid *Mesopodopsis slabberi*, and the calanoid *P. hessei*. Community biomass generally reflected the trophic status of the estuary. The mean seasonal biomass recorded in the Kariega estuary was 38 mg m^{-3} compared with 1597 mg m^{-3} in the Great Fish estuary. Greater spatial variability in community biomass was evident in the Great Fish estuary, partly in response to the food resource gradient, but also due to the inability of the mysid shrimps, which dominated the community biomass, to penetrate the lower salinity water of the upper reaches. Zooplankton in the Kariega

estuary demonstrated a seasonal pattern of abundance whereas in the Great Fish estuary, community biomass was elevated in response to sporadic pulses of freshwater inflow.

Grazing rates, measured *in situ* using a modified Gliwicz-Haney chamber, indicated that the zooplankton communities were capable of "clearing" substantial proportions of the watercolumn at certain times of the year. The pattern of grazing pressure over a diel cycle was examined in relation to the diel vertical migration movements of the zooplankton. Higher nighttime grazing rates were generally associated with the greater abundance of zooplankton resulting from the movement of zooplankton into the watercolumn after dusk, and their return to the sediments at dawn. Seasonal estimates of diel grazing pressure, extrapolated from daytime and nighttime feeding rates, indicated that the zooplankton "cleared" up to 40 % of the watercolumn in a day in the Kariega estuary, and up to 120 % d^{-1} in the Great Fish estuary. However, values of around 25 % d^{-1} in the Kariega estuary, and 50 to 80 % d^{-1} in the Great Fish estuary, were not uncommon.

Multiple regression analyses were used in an attempt to explain the influence of environmental factors on the variation in *in situ* grazing rates. These attempts were largely unsuccessful and the possible reasons, as well as recommended improvements to the methods used, are discussed. Seston concentration in the estuaries was highly variable as a result of the effects of tidal re-suspension and freshwater inflow. Consequently, further laboratory-based experiments were carried out to examine the influence of seston concentration on the filtration rates of the dominant calanoid copepods. Results indicated that some of the unexplained variability in the community filtration rates may be attributed to differences in species-specific response to changes in seston concentration.

CHAPTER ONE

GENERAL INTRODUCTION

As the transition zone between freshwater and seawater, estuaries are highly dynamic and respond rapidly to changes in environmental conditions (Ketchum, 1983). This variation results in pronounced environmental stresses and consequently a reduced species diversity (Kennish, 1986). Despite this, the unique combination of physical, chemical and biological factors, characteristic of estuaries, place them among the most productive ecosystems on earth (Odum, 1971).

From a human perspective, estuaries have both an historical and functional importance (Ketchum, 1983). The shelter they provide has been exploited for the development of harbours, while their aesthetic appeal has resulted in the development of large residential and recreational centres (Kennedy, 1980). However, as ecosystems, their special features and relatively small size make them highly vulnerable to disturbance (Knox, 1986). Estuarine structure and function are strongly influenced by human activities within the estuary, as well as the river catchments (Knox, 1986). An inadequate understanding of estuarine sensitivity combined with mismanagement has, consequently, led to their degradation (Jackson & Lipschitz, 1984).

Due to the semi-arid climate of South Africa, estuaries of the eastern Cape region are characterized by low freshwater inflow, although this varies with individual catchment characteristics (Allanson & Read, 1987; Reddering & Rust, 1990). The ever increasing abstraction of freshwater to meet growing agricultural, industrial and domestic demands (Wallace *et al.*, 1984; Allanson & Read, 1987) has adversely affected many estuaries. Where freshwater inflow is insufficient to balance evaporative loss, estuaries have become hypersaline and experience a loss of biological functioning (Whitfield & Bruton, 1989). Further, increased sedimentation in the estuary mouth, caused by a decrease in flood scour, has resulted in many estuaries becoming periodically, or permanently closed to the sea (Reddering, 1988a). Jezewski & Roberts (1986) calculated that approximately 8 % of the mean annual run-off is required for the maintenance of South Africa's estuaries. This figure was based on the total volume required to compensate for evaporative loss, as well as a flooding requirement to control the opening of estuary mouths (Whitfield & Bruton, 1989). Much attention has recently been focussed on modelling and predicting the physical regime of South African estuaries (e.g. Huizinga, 1985; Reddering, 1988a; 1988b; Reddering & Rust, 1990). However, notwithstanding the importance of the physical environment, very few studies have considered the effects of reduced freshwater inflow on the biotic component (e.g. Allanson & Read, 1987; Whitfield & Bruton, 1989), although the importance of such research has become increasingly recognized.

Zooplankton are an important component of many aquatic ecosystems. They provide an important pathway for the trophic transfer of energy from primary production and detrital pools to secondary production (Rigler, 1971; Haney, 1973; Conover, 1978; Frost, 1980; Raymont, 1980; Peters, 1984). Studies of South African estuaries have shown that zooplankton are a dominant food resource for many fish types (e.g. Whitfield, 1980; 1985; Coetzee, 1981; Talbot & Baird, 1985; Harrison & Whitfield, 1990).

Early work on zooplankton in South African estuaries was largely descriptive (e.g. Grindley, 1963; 1977; Grindley & Wooldridge, 1974; Wooldridge, 1976; 1977) but included some behavioural studies (e.g. Grindley, 1972). Towards the end of the 1970's, studies began to focus on the factors influencing the distribution of zooplankton in estuaries and highlighted, for example, the role of tidal currents on the distribution of zooplankton (Wooldridge & Erasmus, 1980), and the influence of temperature and salinity gradients on successionary trends (Wooldridge & Melville-Smith, 1979; Wooldridge & Bailey, 1982). More recently, research has been directed towards studies of population dynamics and production estimates (Wooldridge, 1986; Jerling & Wooldridge, 1991). These and other studies (e.g. Allanson & Read, 1987) have indicated that increased zooplankton standing stocks and higher productivity may be linked to elevated freshwater inflow. However, the precise mechanisms responsible are not clear.

The research in this dissertation investigates aspects of the feeding ecology of estuarine zooplankton communities in an attempt to elucidate the influence of freshwater inflow in determining zooplankton standing stocks. A largely holistic approach was adopted involving a comparison of two contrasting eastern Cape systems, the Kariega estuary which has minimal freshwater inflow, and the Great Fish estuary which has sustained freshwater inflow. Most of the subsequent Chapters comprise an introduction, methods and results sections, and a discussion. Additional information, where appropriate, is given as appendices.

Chapter 2 provides an overview of eastern Cape estuaries and emphasizes the prevailing environmental conditions and concludes with a summary of current knowledge of the study sites. A general review of factors influencing zooplankton feeding is presented in Chapter 3. The origin, nature and distribution of particulate food resources are examined in Chapter 4, and the influence of freshwater inflow on the sources, quality and quantity of seston in estuaries is discussed. Chapter 5 investigates the distribution, composition and abundance of zooplankton communities and community grazing pressure. In Chapter 6, the effect of diel vertical migration in determining short term variability in grazing pressure is investigated. In Chapter 7, the feeding appendages and functional feeding of the dominant zooplankton are compared. The potential influence of differences in feeding behaviour on community structure and *in situ* community filtration rates is discussed. A general discussion is presented in Chapter 8.

CHAPTER TWO

THE CHARACTERISTICS OF EASTERN CAPE ESTUARIES WITH EMPHASIS ON THE INFLUENCE OF RIVER INFLOW - A DESCRIPTION OF THE STUDY SITES

2.0 OVERVIEW OF THE MAIN FACTORS INFLUENCING EASTERN CAPE ESTUARIES

Introduction.

The definition of an estuary, proposed by Pritchard (1967a) at the First International Conference on Estuaries held in 1964, stated that an estuary was a "semi enclosed coastal body of water which has a free connection with the open sea and within which seawater is measurably diluted with freshwater from land drainage". In the context of South African estuaries, this definition causes some problems since it does not include estuaries whose tidal inlets are closed by sandbars during the dry season or those in which evaporative loss of water in the upper reaches leads to hypersalinity. Accordingly, Day (1980) modified the definition to the following: "An estuary is a partially enclosed coastal body of water which is either permanently or periodically open to the sea, and within which there is a measureable variation of salinity due to the mixing of seawater with freshwater derived from land drainage."

Along the eastern Cape coast of South Africa, a distance of some 450 kilometres, there are approximately 65 estuaries, from the Kromme river estuary in the west, to the Great Kei river estuary in the east (Figure 1). Of these, only 15 are tidal throughout the year, thus few eastern Cape systems are true estuaries. The conditions in blind estuaries are fundamentally different, primarily because the free exchange between the estuary and the sea is prevented. Therefore, a clear distinction between blind, and true estuaries should be made (Reddering, 1988a).

Origins of eastern Cape estuaries.

The majority of eastern Cape estuaries are classified as mature Ria-type, formed by the drowning of steep-sided river valleys by rises in sea level. The mature state is reached when the valley is filled to capacity with sediment (Reddering & Rust, 1990). By comparison with those of the northern Hemisphere, estuaries of the eastern Cape are small and generally have a tidal prism volume of less than 10^6 m^3 (Reddering, 1988a). The channel of a mature estuary is generally narrow and is maintained by the scouring action of periodic river flooding. In addition, characteristic features of eastern Cape estuaries are; i) constricted tidal inlets, and ii) well-developed flood tide deltas. Tidal flats are present in some estuaries (Reddering, 1988b).

The characteristics of eastern Cape estuaries arise from the particular conditions which prevail in the area and involve the interaction of factors such as river discharge, catchment characteristics and tidal action (Read, 1983). These are discussed in the following Sections.

Influence of climatic conditions.

River inflow is responsible for the allochthonous import of materials into an estuary as well as influencing the patterns of circulation and mixing (Read, 1983; and references cited therein). Thus, the influence of climate on the pattern of rainfall and run-off plays an important role in the development and functioning of estuarine ecosystems. In addition, estuaries with large drainage basins generally receive greater run-off (Reddering, 1988a), although this also depends upon the extent of catchment impoundment.

The interior plateau of South Africa is semi-arid and few estuaries receive freshwater inflows of equivalent magnitude to their northern Hemisphere counterparts (MacKay & Schumann, 1990). In the eastern Cape, mean annual precipitation (MAP) increases from 300 mm in the dry north-west to over 1000 mm in the south-east whereas evaporation increases in the opposite direction (Whitfield & Bruton, 1989). Catchment rainfall (MAP) for the major estuaries is shown in Table 1. South Africa has one of the lowest conversions of rainfall to run-off relationships of any country in the world (Alexander, 1985), and in the eastern Cape varies from less than 3 % of MAP in the northwest to more than 12 % in the south-east (Whitfield & Bruton, 1989). In addition, Tyson (1986) has described cyclical phenomena which give rise to wet and dry climatic conditions of between 12 and 20 years duration. During dry spells, estuaries commonly experience prolonged periods of reduced or zero flow which may be punctuated by major floods (MacKay & Schumann, 1990).

Table 1. Major estuaries: Catchment, river inflow and rainfall.

ESTUARY	CATCHMENT AREA (km^2)	MEAN ANNUAL DISCHARGE ($m^3 \times 10^6$)	MEAN ANNUAL RAINFALL (mm)	MAP REFERENCE
Kromme	1125	105	600	1
Gamtoos	34438	485	500-1500	2
Swartkops	1438	84	460-755	3
Sundays	22063	29	550	4
Bushmans	2688	38	600	5
Kariega	688	15	550	6
Kowie	625	23	638	7
Great Fish	29937	479	400	8
Keiskamma	2500	133	500	9
Buffalo	1313	82	800	10
Nahoon	625	-	700	11
Gonubie	500	35	750	12
Kwelera	375	32	800	13
Great Kei	20559	1001	500	14

Data from Heydorn and Tinley (1980) and Day (1981); after Marker (1988).

The generally arid climate of most of South Africa has required the construction of dams on most of the major rivers to supply freshwater for domestic, industrial and agricultural use (Reddering & Rust, 1990), and due to the increasing demand for new supplies, the degree of catchment impoundment and abstraction of freshwater is growing (Whitfield & Bruton, 1989). The retention of freshwater by impoundments causes a distinct effect on the flood events encountered by estuaries. In general, the number of floods and the volume of water per flood is reduced and the period of time in between floods is increased (Reddering, 1988b).

In some areas, natural run-off has been augmented by the artificial transfer of water from one geographically distinct river basin to another (Inter Basin Transfer, IBT)(Petitjean & Davies, 1988). There are currently two schemes in operation and one of these, the Orange river project, is responsible for the mass transfer of part of the net run-off from the Orange river, and its tributary the Caledon river, to two eastern Cape systems, the Great Fish and Sundays rivers (Dept. of Water Affairs, 1987).

Influence of the coastal environment.

The eastern Cape coast is characterized by predominantly semi-diurnal tides with a small diurnal inequality (MacKay & Schumann, 1990). The mean spring tidal range is 1.61 metres (Hydrographer, 1987) and eastern Cape estuaries are thus classified as microtidal. Actual water levels may be influenced significantly by coastal trapped waves which are reported to occur along the coast (Schumann & Brink, 1990).

The open, exposed shores of the eastern Cape coast are subject to high wave action which deposit large amounts of sand into tidal inlets and cause the easterly migration of estuarine tidal inlets due to the net direction of sediment transport by the dominant south-westerly swell. The extent of the resulting constriction of the tidal inlet is determined by the opposing effects of tidal currents and wave action. Generally, the scouring capacity of the tidal currents is greater in estuaries with a larger tidal prism (Reddering, 1988b).

The constriction of the tidal inlet causes an asymmetry in the tidal flow by limiting the extent of the ebb tide to a greater extent than the flood tide. Since the flood tide is characterized by higher current velocities, more sediment enters the estuary and is deposited on the incoming tide than leaves the estuary during the ebb tide, resulting in extensive shoaling in the lower reaches. The frequency and magnitude of river flooding has an important bearing on tidal inlet morphology since floods erode sand deposits which are flushed out to sea (Reddering, 1988b).

Conclusions.

Along the eastern Cape coast where the influence of climate, tidal amplitude and wave action are essentially constant, the individual characteristics of an estuary are determined largely by the indirect influence of catchment size and regulation, since these are the major factors controlling the amount of freshwater inflow (Reddering, 1988a). The relationship between catchment size and run-off into eastern Cape estuaries is shown in Figure 2.

Only about 23 % of eastern Cape estuaries receive sufficient freshwater inflow at frequent enough intervals for flood scouring to maintain an open tidal inlet throughout the year. Due to the generally poor run-off in the region, these "true" estuaries range along a continuum from negative systems in which hypersaline conditions have developed in the upper reaches due to evaporative losses exceeding inflow, to positive systems in which a salinity gradient is well established (Day, 1981).

Due to the highly dynamic nature of estuaries, the position occupied along the continuum by individual systems may constantly change as a result of episodic events which cause wide-scale shifts in the characteristics of the estuary (Whitfield & Bruton, 1989).

Selection of hydrodynamically contrasting systems.

In their study entitled, "The response of estuaries along the south eastern coast of southern Africa to marked variation in freshwater inflow", Allanson & Read (1987) selected the Kariega estuary and the Great Fish estuary as study sites due to their differing inputs of freshwater (Table 1). The Kariega receives a reduced input of freshwater as a result of a small, highly regulated catchment. By contrast, river inflow into the Great Fish estuary is sustained due to the comparatively large catchment area and the translocation of water from the Orange river. Since this study represents an extension of the work reported in their study, and due to the extensive data base which was consequently available, the choice of study sites was retained. The following Section provides an overview of the characteristics of each estuary relevant to this study. A more detailed account is given by Allanson & Read (1987).

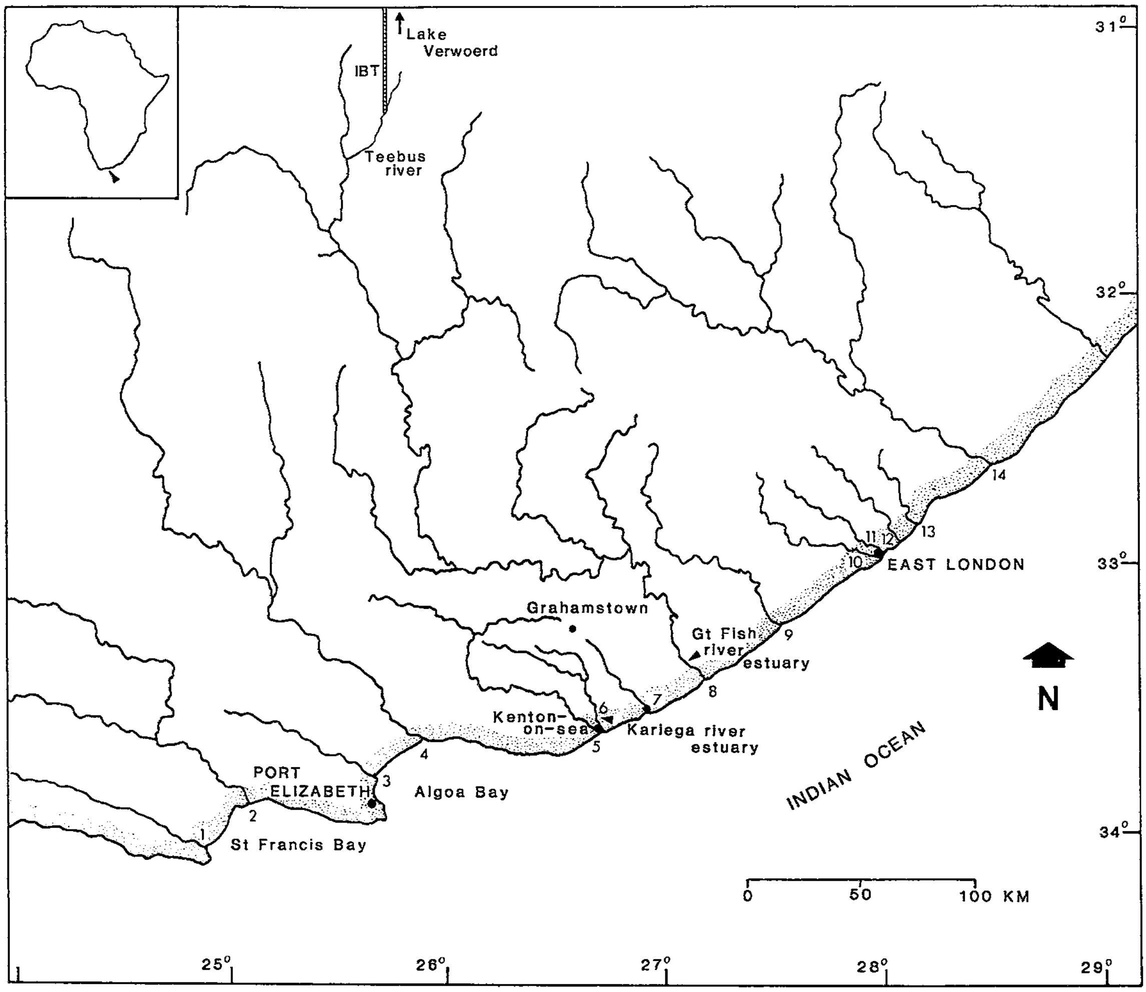


Figure 1. The eastern Cape coastline showing the major river systems and estuaries. The numbered estuaries are listed in Table 1.

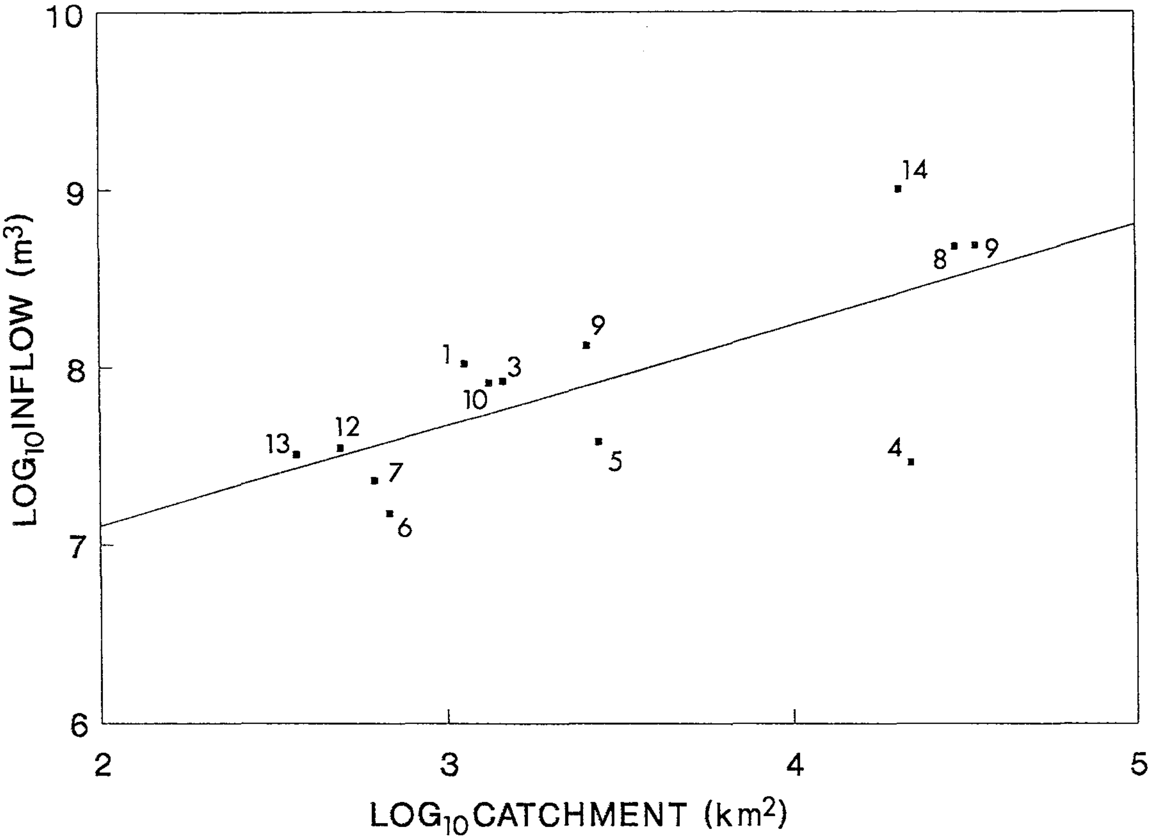


Figure 2. The relationship between river inflow and catchment size for the major estuaries occurring along the eastern Cape coast. Numbered estuaries are listed in Table 1.

2.1 RESEARCH SITES

Kariega estuary.

The Kariega estuary is situated 110 km north-east of Port Elizabeth, adjacent to the town of Kenton-on-sea (33° 41'S/26° 42'E) (Figure 1). The estuary is approximately 18 km in length and the furthest extent of ebb and flow is marked by a causeway. A series of brackish water pools occupy the river course immediately above the causeway for the majority of the year. The catchment area is comparatively small (688 km^2) (Table 1) and is impounded by a series of three dams (Settlers', Howiesons poort and Moss dams) in the vicinity of Grahamstown. The volume of river inflow was measured at gauging weir P3H001 (33° 33¼'S/26° 36¼'E) (Dept. of Water Affairs), situated just above the causeway. Inflow for the ten year period October 1979 to October 1989 is shown in Figure 3a. Other than during episodic flood events, which require the overflow of Settlers' Dam and occur approximately every 3 to 5 years, river inflow is negligible for extended periods of time and hypersaline conditions in the upper reaches have been reported (Hodgson, 1987). Due to the reduced freshwater inflow, the high turbidity levels associated with rivers in the region do not influence the Kariega estuary to any great extent under normal conditions and consequently light penetration of the watercolumn is high. Despite this, a turbidity maximum is evident between 6.4 and 10.5 km from the mouth, arising principally from tidal shear and wind-induced turbulence (Allanson & Read, 1987).

In the upper and middle reaches, the estuary takes the form of a narrow, meandering channel of between 40 and 60 metres wide, which increases to a maximum of about 100 metres in the lower reaches, which are dominated by saltmarshes and sandflats (Figure 4, 6). Average depth in midstream is between 2.5 to 3.5 metres with occasional deep scour holes of up to 5 metres depth. The cross-sectional dimensions of the channel at selected Stations are shown in Figure 4. The tidal inlet is constricted and the mouth displaced in an easterly direction by the deposition of sand from longshore currents and wave action (Figure 8), however, scouring by tidal currents is sufficient to maintain a permanently opened connection with the sea. Extensive sand shoals in the extreme lower reaches and the deposition of sandy sediments up to 3.5 km inland are evidence of flood tide domination.

The tidal prism volume of 2.062 x 10^6 m^3 (Allanson & Read, 1987) is larger than the majority of estuaries in the eastern Cape and this provides a possible explanation of the ability of the mouth to remain permanently open in view of the infrequent flood scour events (Reddering, 1988a). In addition, a rocky promontory on the eastern side of the tidal inlet prevents further displacement of the mouth of the estuary. The flow ratio (river discharge volume: prism volume) of 8.6 x 10^{-3} indicates that the system is well mixed. The time required to replace the existing freshwater in the estuary with river discharge is relatively long at about 45 days (Allanson & Read, 1987). A summary of the hydrodynamic features is given in Table 2.

Table 2. Hydrodynamic characteristics of the Kariega, and Great Fish estuaries. Standard deviation given in brackets.

	KARIEGA ESTUARY	GREAT FISH ESTUARY
Volume (m^3)	3.590 x 10^6	2.253 x 10^6
Average Tidal Cycle (h)	12.25 (± 0.33)	12.35 (± 0.31)
River flow per tidal cycle (m^3)	17 739	274 505
Ratio $\frac{\text{Prism volume}}{\text{River flow}}$	116	6
Flow ratio $\frac{\text{Discharge volume}}{\text{Tidal prism volume}}$	8.6 x 10^{-3}	0.17
Flushing time (d)	45	0.80

After Allanson & Read (1987).

Great Fish river estuary.

The Great Fish estuary, which forms a natural border between the Republic of South Africa and the independent homeland of the Ciskei, is situated about 160 km north-east of Port Elizabeth (Figure 1). According to Day (1981), the estuary extends some 20 km inland during late autumn but is certainly shorter during the rainy seasons. In this study, ebb and flow was evident 10 km inland (Station O, Figure 5) although the water remained fresh at all times.

The catchment area of the Great Fish river is large (29 937 km^2) (Table 1), but extensively impounded. Natural run-off is augmented by Inter-Basin Transfer (Orange river project) of water from the Oviston Intake Tower at Lake Verwoerd to the Teebus river via the 82.8 km long Orange river tunnel (Figure 1). Although this has lead to a dramatic increase in the flow rate in the upper catchment (between 500 and 800 %), the most significant effect on the lower reaches has been a decrease in seasonal variation of the flow regime, and the river is now perennial rather than seasonal.

Freshwater inflow to the upper reaches of the Great Fish estuary, measured at gauging weir Q9H018 (33° 14¼'S/26° 59¼'E) (Dept. of Water Affairs) for the ten year period ending October 1989 is shown in Figure 3b. The magnitude of inflow during episodic floods, and the sustained flow during periods in between these events, is apparent. The high turbidity associated with the Great Fish estuary is as a result of extremely high levels of suspended sediment carried by catchment run-off, particularly in times of flood. Black (1901) confirms that this characteristic was fundamentally similar in the 1850's before the soils and vegetation were altered by farming and prior to the implementation of Inter-Basin Transfer.

Flocculation, which occurs at the interface of freshwater with higher-salinity water, results in a decrease in the amount of suspended particulate material in the middle reaches of the estuary. An increase in salinity of 8 ‰ above freshwater was observed to cause a marked decrease in the amount of suspended sediment (Allanson & Read, 1987). Due to the deposition of large quantities of silt, the estuary is comparatively shallow and, on average, between 1.5 and 2.5 metres deep. The channel ranges from 70 metres wide in the upper and middle reaches to about 150 metres in the lower reaches (Figure 7a). Channel morphology and cross-sectional dimensions at selected Stations are shown in Figure 5. The tidal inlet of the Great Fish estuary shows a similar displacement to the eastern shore as evidenced in the Kariega system. Further drift is prevented by the rocky outcrop on the eastern bank, shown in Figure 9. Constriction of the tidal inlet by sand deposition has similarly resulted in a flood-dominated tidal system, however, due to the scouring activity of flood waters and the net migration of terrestrially-derived sediments, sandy substrata is restricted almost entirely to the mouth of the estuary. During ebb tides, large quantities of terrestrially-derived suspended material are washed out to sea and cause high turbidity in the adjacent coastal zone (Figure 7b).

The tidal prism volume estimated for the Great Fish estuary is 1.624×10^6 m^3 and the flow ratio is 0.17, thus classifying the Great Fish estuary as a partially-stratified system. The rapid exchange of water demonstrated by the short flushing time of 0.8 days is a direct consequence of the magnitude of freshwater discharge into the system (Allanson & Read, 1987). A summary of the hydrodynamic features of the estuary appears in Table 2.

Sampling Stations.

During 1987 and 1988, a sampling survey was carried out to investigate aspects of the food resources and feeding ecology of the zooplankton communities of the Kariega, and Great Fish estuaries. Based on the hydrodynamic characteristics of these estuaries reported in this Chapter, each system was divided into three regions for the purposes of investigating the variation along the length of the estuaries. In the Great Fish estuary, these corresponded to the regions of i) freshwater, ii) partially-mixed water, and iii) full seawater salinity, and in the Kariega estuary to i) the region of the turbidity maximum, and ii) upstream and, iii) downstream of it. The sampling Stations, corresponding to these regions are shown in Figures 4 and 5. The results of this survey are reported in Chapters 4 and 5.

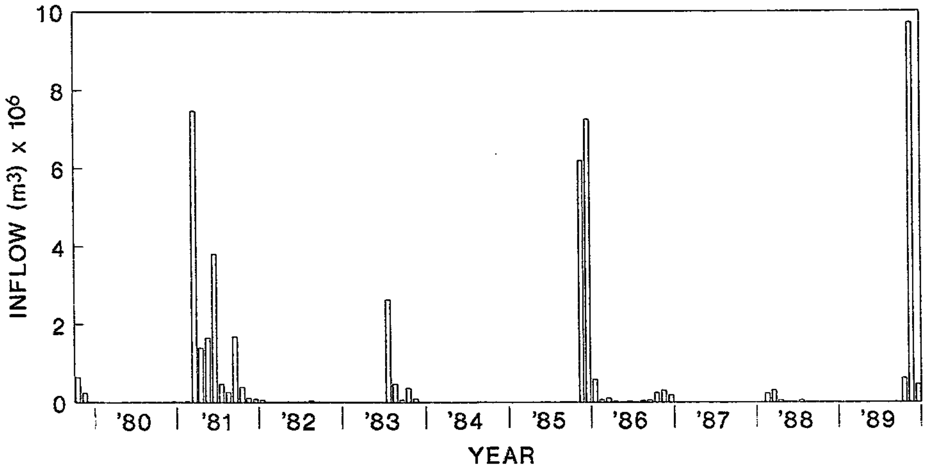


Figure 3a. Monthly river inflow into the Kariega estuary measured at gauging weir P3H001 (Dept. of Water Affairs) for the ten year period October 1979 to October 1989.

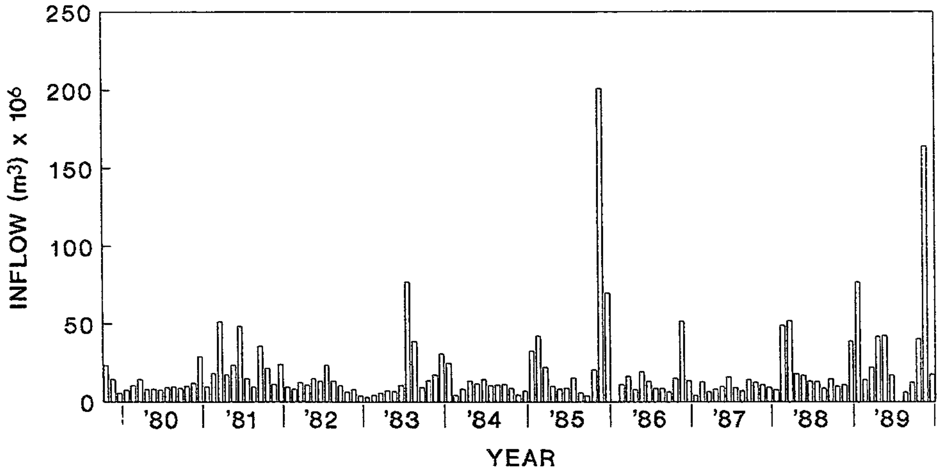


Figure 3b. Monthly river inflow into the Great Fish estuary measured at gauging weir Q9H018 (Dept. of Water Affairs) for the ten year period October 1979 to October 1989.

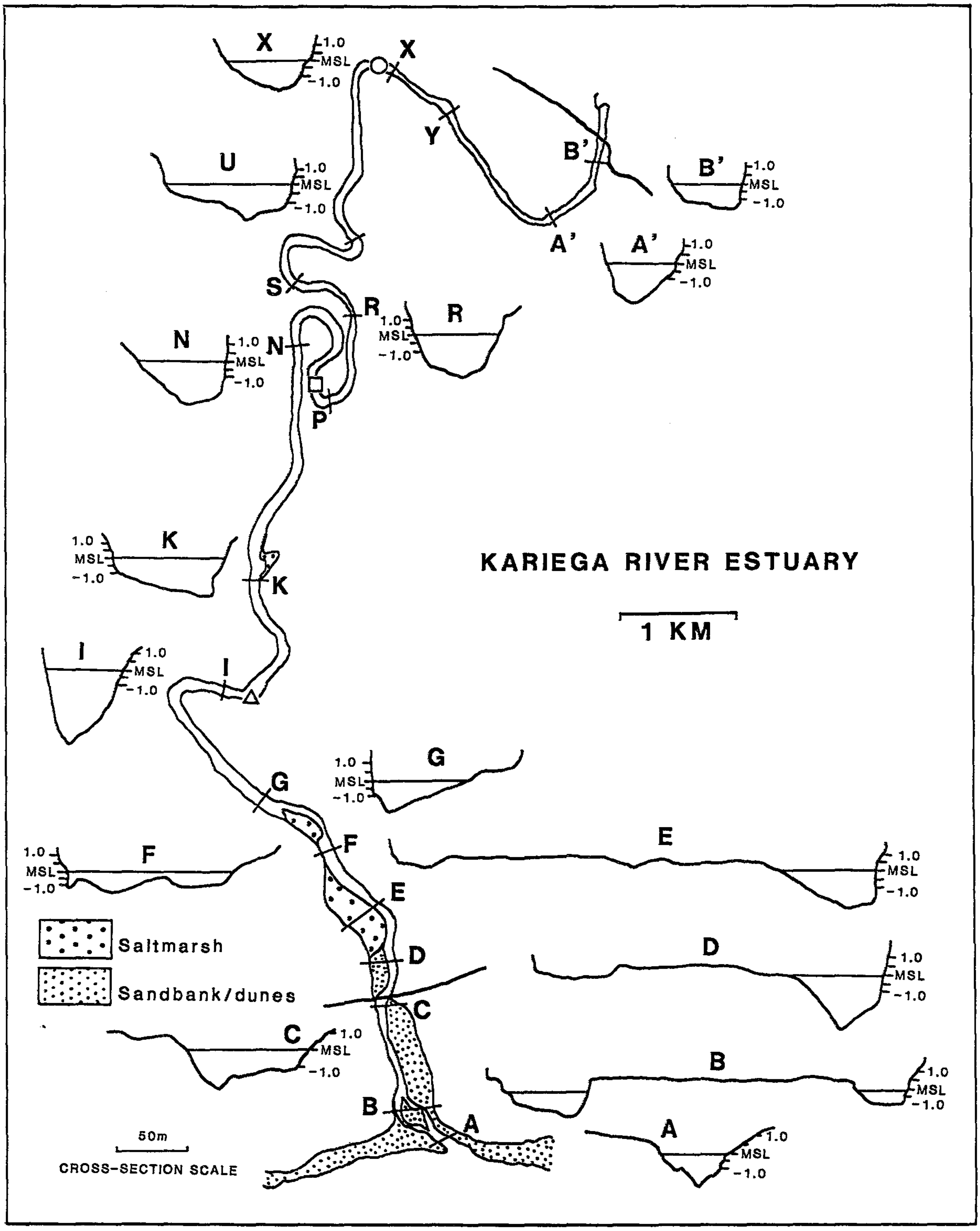


Figure 4. Map of the Kariega estuary showing cross-sectional dimensions of the channel at selected localities (A to B'). The causeway, which marks the furthest extent of ebb-and-flow is situated just above Station B'. The positions of the three sampling Stations used during routine sampling work carried out during 1987/1988 and corresponding to the upper-, middle-, and lower reaches of the estuary are given by the symbols ○, □ and △, respectively. (Re-drawn from Allanson & Read, 1987).

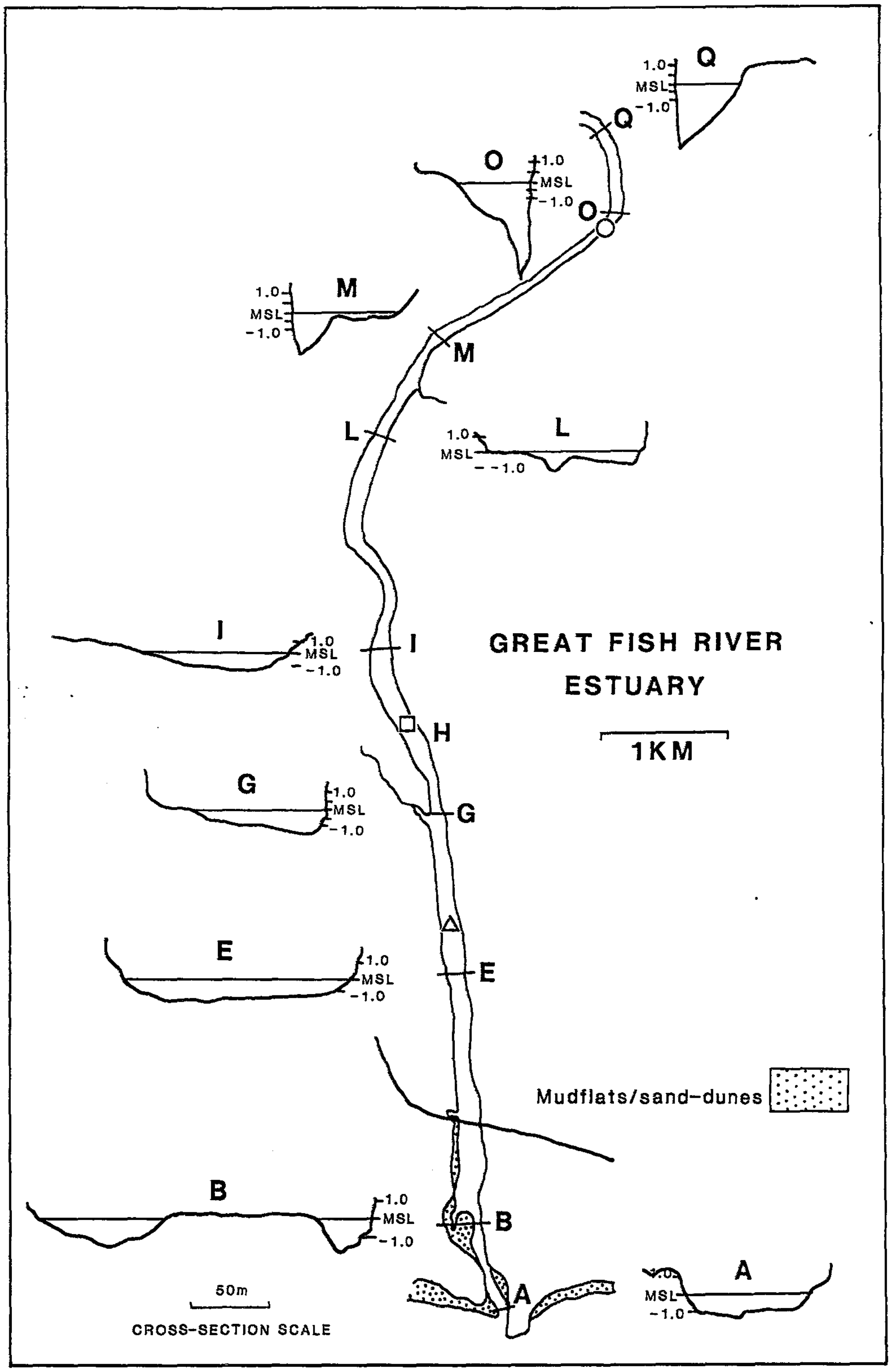


Figure 5. Map of the Great Fish estuary showing cross-sectional dimensions at selected localities. Tidal influence extends at least as far as Station Q, although freshwater was recorded at Station O throughout the sampling period during 1987/88. The positions of the three sampling Stations used during 1987/88 and corresponding to the upper- (freshwater), middle- (mixed), and lower reaches (seawater) are given by the symbols ○ , □ and △ , respectively. (Re-drawn from Allanson & Read, 1987).

Figure 6. Aerial photograph of the Kariega estuary illustrating the narrow, channel-like nature of the middle and upper reaches.

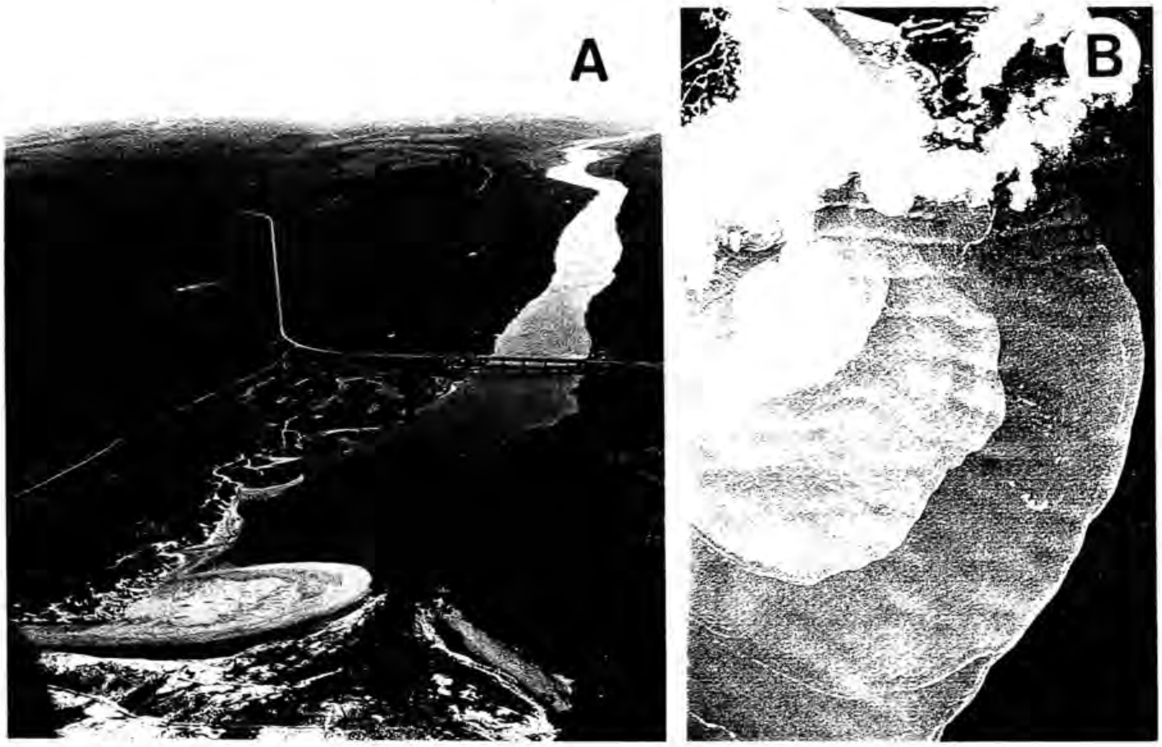


Figure 7. Aerial view of the Great Fish estuary showing the middle and lower reaches during flood tide (A); and (B), turbid plumes extending into the coastal zone as a result of the discharge of large quantities of suspended material (mainly silt) from the estuary during an ebb tide (Photograph (B) courtesy of A.K. Whitfield).

Figure 8. The mouth of the Kariega estuary illustrating the constriction and migration of the tidal inlet as a result of the deposition of sandy sediments by wave action and longshore drift. The rocky promontory at the mouth (see text) was obscured by the tide at the time the photograph was taken.

Figure 9. The mouth of the Great Fish estuary showing similar displacement of the tidal inlet. The rocky headland on the eastern (Ciskei) coast which prevents further migration of the tidal inlet is clearly visible.

CHAPTER THREE

FACTORS INFLUENCING PARTICLE CAPTURE BY SUSPENSION-FEEDING CALANOID COPEPODS - A REVIEW

INTRODUCTION.

An understanding of zooplankton feeding biology is a necessary step in evaluating the functional role of zooplankton communities in aquatic food webs. In the past, zooplankton feeding studies have been limited by a lack of suitable techniques and equipment, however, in the last decade or so, significant developments have taken place which have contributed greatly to our understanding of zooplankton feeding. This review is concerned primarily with recent advances rather than with providing an in-depth, historical perspective.

FUNCTIONAL RESPONSE.

Food resources for pelagic zooplankton are often limiting as a result of low phytoplankton productivity, patchiness, vertical migration and community grazing (Lampert, 1978). The response of zooplankton to changes in food concentration is important to aspects of plankton ecology, such as, i) feeding strategy and energy budgets (Mullin *et al.*, 1975; Lehman, 1976) and ii) ecosystem modelling (Steele, 1974; Jφrgensen, 1976; Sjöberg, 1977).

Feeding rate is usually expressed by a pair of equations, which describe the filtration, or "clearance" rate and also the ingestion rate of the animal (Frost, 1972; McClatchie & Lewis, 1986; Price & Paffenhöfer, 1986a; Paffenhöfer, 1988). Holling (1959) described three forms of the functional response of predators to varying concentrations of prey, derivations of which have subsequently appeared in the literature. Three mathematical expressions are commonly used to describe the relationship between predator and the prey concentration. These are, i) the Ivlev equation, ii) the rectilinear model, and iii) the

Michaelis-Menten equation (Figure 1). Ingestion rate is proportional to food concentration at low values, but with increasing concentration, either approaches asymptotically, or reaches, a maximum value at some high food concentration (Mullin, 1963; Parsons *et al.*, 1967; Frost, 1972; Sjöberg, 1980), termed the "incipient limiting level" (Muck & Lampert, 1980). Combinations of physical, physiological and behavioural factors contribute to the form of the curve (Leonard, 1989). Differences in the functional response between the two most commonly used equations, the Ivlev and rectilinear models, can be attributed to different behavioural responses in feeding (Mullin *et al.*, 1975). Ivlev's (1961) curvilinear response assumes decreased handling efficiency with increasing concentration, while the rectilinear model implies constancy of feeding response below the level of satiation (Parsons *et al.*, 1967). In a statistical analysis, however, Mullin *et al.* (1975) were unable to select a particular form of functional response curve which would most adequately fit their data.

In most mathematical models of functional response, the predator is assumed to respond in a constant manner to prey encountered across a range of prey concentration values (Leonard, 1989). This assumption has been questioned by several authors (e.g. Mayzaud & Poulet, 1978; Huntley, 1988) who have recognized the importance of behavioural mediation in the determination of feeding rates as a possible explanation for the high variability of experimental results and lack of replicability.

Foraging theory.

Optimal foraging models predict that the filter-feeder will adjust its filtration rate in such a way as to maximize its net energy intake (Price & Paffenhöfer, 1986a). Since the energetic costs of filtration are high, and described by a power function of the filtration rate, it seems reasonable to expect that filtration activity should be variable (Lam & Frost, 1976; Lehman, 1976). The models proposed by these authors derive their formulation from different aspects of the process of energy intake, however, the relationship between filtration rate and food concentration is similar (Muck & Lampert, 1980). Figure 2 shows that at low concentrations (1), the filtration rate increases until an ingestion rate is reached at which the gut is completely full (2). Under these conditions, the filtration rate is at a maximum and subsequently declines as the food concentration increases further. Thus, the filtration behaviour is controlled by the relative amount of food in the gut, while the filtration rate is assumed to be controlled by the rate of feeding appendage movement. More recent work (Price & Paffenhöfer, 1986a) has suggested that changes in time allocation to feeding (intermittent feeding) may be an important factor influencing filtration rate.

Threshold feeding concentration.

"Threshold feeding concentration" is defined as the food concentration below which feeding ceases or its rate is significantly lowered (Sjöberg, 1980). Evidence for a threshold feeding response has been reported by various authors (e.g. Parsons *et al.*, 1967; 1969; Frost, 1975; Mullin, *et al.*, 1975; Reeve & Walter, 1977) and several researchers have incorporated this response into functional feeding curves (e.g. Mullin *et al.*, 1975). Different theoretical reasons have been put forward to explain the occurrence of a threshold concentration in feeding studies (Muck & Lampert, 1980). Threshold feeding may provide a refuge density for phytoplankton (McAllister, 1970), but may also represent a concentration at which energy expended on filter-feeding is disproportionate to that gained from the digestion and assimilation of the food obtained (Muck & Lampert, 1980). The "threshold feeding hypothesis" of Lampert (1977) and Lampert & Schober (1980) states that the superior species is the one with the lowest food requirement needed to maintain a population under given circumstances.

MECHANISTIC VERSUS BEHAVIOURAL FEEDING.

Particle size selection.

Frost (1972) significantly advanced our understanding of the filter-feeding process through a mathematical description of his grazing rate measurements of *Calanus*. The underlying assumption of Frost's equations (discussed by Williams, 1982; McClatchie & Lewis, 1986) is that particles are retained with 100 % efficiency. Feeding experiments in which copepods were exposed to mixtures of different sized particles, however, have shown greater retention efficiencies for larger sized particles (Mullin, 1963; Richman & Rogers, 1969; Paffenhöfer, 1971; Poulet, 1973; Frost, 1977; Runge, 1980). This has generally been attributed to passive size retention efficiency (Boyd, 1976; Frost, 1977; Steele &

Frost, 1977), however, Wilson (1973), provided evidence from research on *Acartia tonsa* that indicated a behavioural component, a view that led to widespread disagreement.

The mechanistic viewpoint.

The view that copepod feeding is a passive filtration process can be traced back to early feeding studies. Cannon (1928) described how particulate material brought to the feeding appendages in the feeding current was retained by the setae and setules on the second maxillae. The mechanistic viewpoint stems from attempts (e.g. Nival & Nival, 1976) to relate the structure of the feeding appendage to the retention efficiency of different sized particles by calculating the cumulative frequency distribution of setular spacing. This implies that particle size selection can be expressed by selectivity coefficients, which are mathematically equivalent to filtering efficiencies (Vanderploeg & Scavia, 1979; Vanderploeg, 1981). The second maxillae of copepods were thought to function purely as passive sieves (Boyd, 1976; Nival & Nival, 1976; Frost, 1977). Boyd (1976) modified this theory further into the "leaky-sieve" hypothesis which adds a factor of 25 % to the mean intersetular spacing to account for distensibility. Thus, the higher efficiency with which particles too large to pass through the sieve-structure were retained, provided an adequate explanation for observations of the apparent "selection" of these particles. Mechanistic theory allows models to be developed in which the feeding rate can be predicted from size-frequency data of the food resource encountered (Lam & Frost, 1976; Wroblewski & O'Brien, 1976; Conover & Huntley, 1980).

Behavioural mediation of filter-feeding.

The mechanistic argument implies no behavioural basis for food selection (Légier-Visser *et al.*, 1986). Although the "leaky-sieve" model appears to describe the particle retention capabilities of some copepods adequately (e.g. Nival & Nival, 1976; Frost, 1977), the results of other studies cannot be explained in this manner (Wilson, 1973; Poulet, 1973; 1974; Richman *et al.*, 1977; Glasser, 1978; Poulet & Marsot, 1978; Donaghay & Small, 1979; Donaghay, 1980; Richman *et al.*, 1980; Poulet & Marsot, 1980). The behavioural hypothesis stems from Wilson's (1973) observations that *Acartia*, feeding on latex beads, appeared to "set" the spacing of the feeding appendages to selectively capture particles just larger than the size class most abundant. Richman & Rogers (1969) demonstrated that

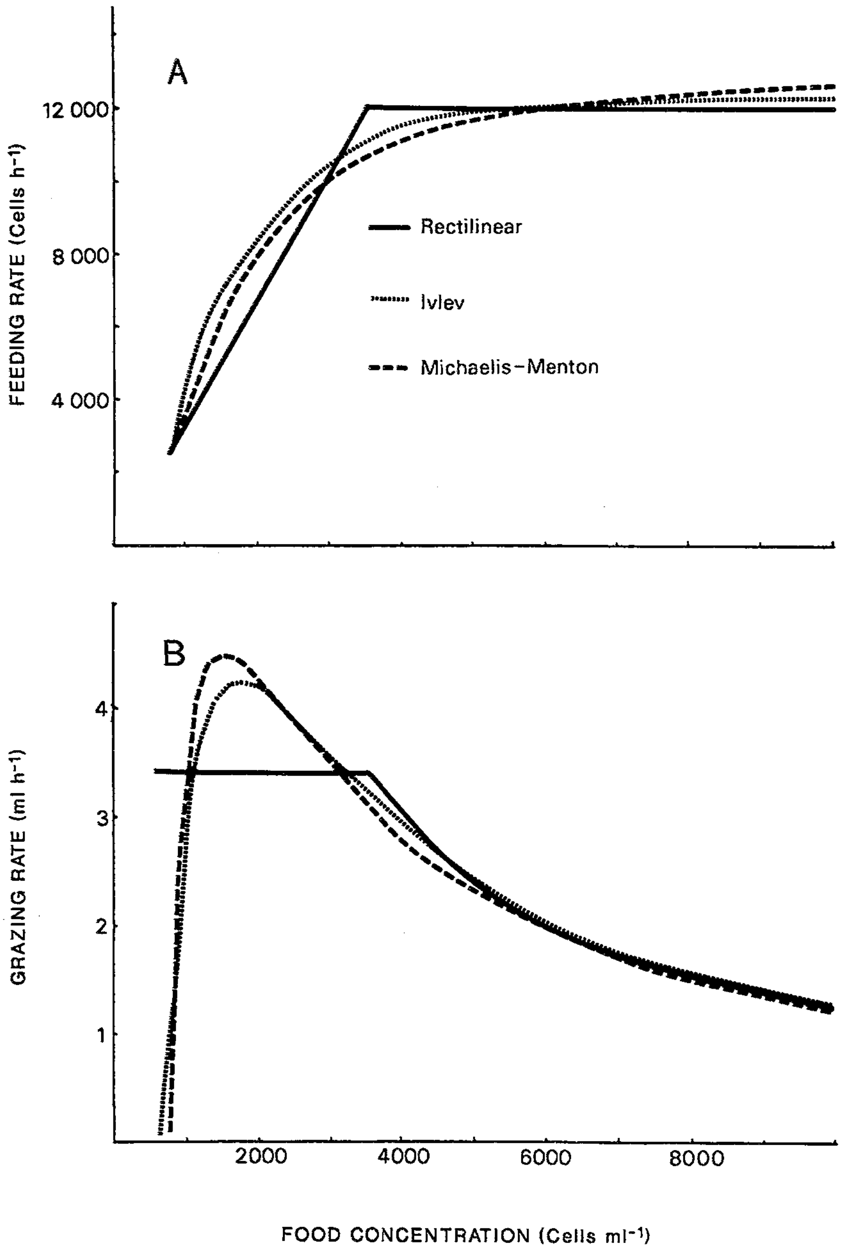


Figure 1. Three expressions (the (i) Ivlev, (ii) rectilinear and (iii) Michaelis-Menten equations) describing the relationship between food concentration, and a) ingestion, and b) filtration.

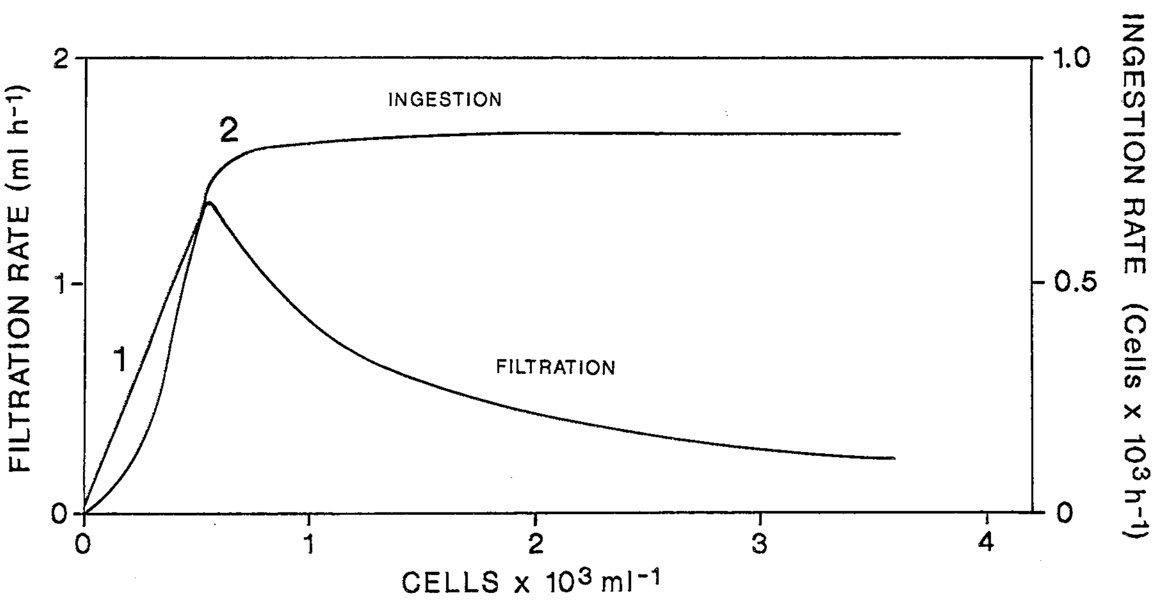


Figure 2. The relationship between filtration rate and ingestion rate with changing food concentration.

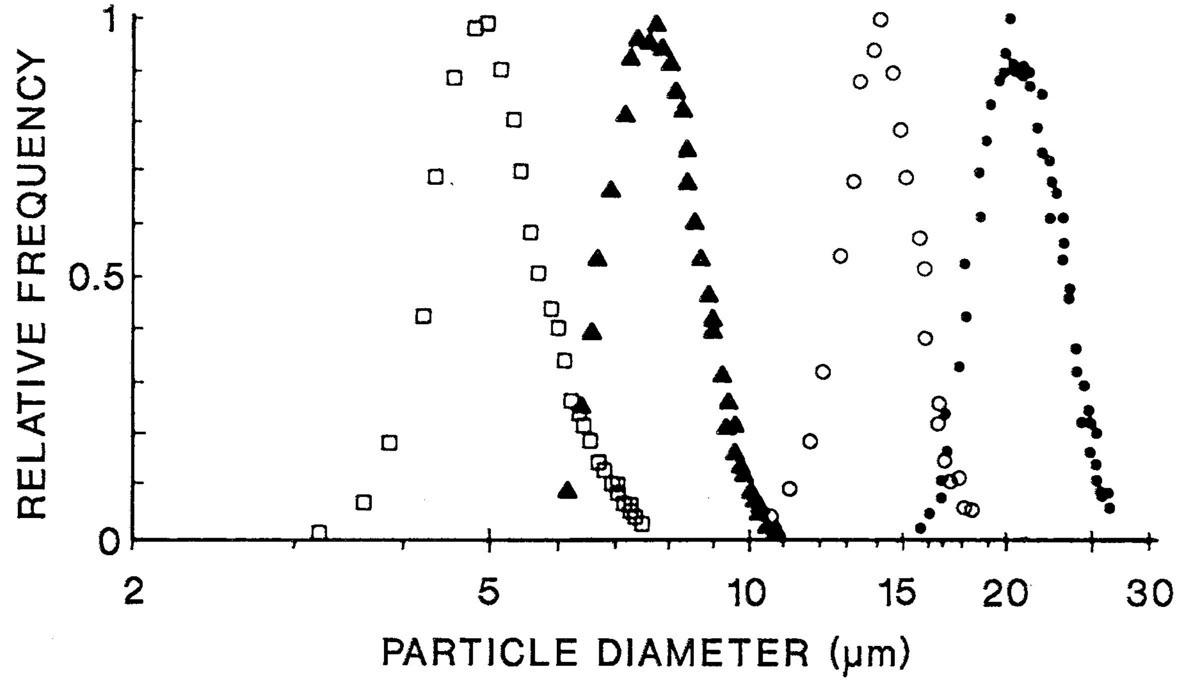


Figure 3. Mixture of phytoplankton and latex beads designed to test selective feeding capabilities of calanoid copepods (Donaghay & Small, 1979). Relative volume distributions of *Thalassiosira pseudonona* (squares), nominally 8 μm diameter latex spheres (triangles), *T. fluviatilis* (open circles), and nominally 20 μm diameter latex spheres (filled circles) showing the positions of the distributional peaks.

Calanus, in a synchronously growing population of single and paired diatom cells, could switch to feed preferentially on the population of greater abundance. Donaghay & Small (1979) studied the feeding response of *Acartia* in a mixture of equal concentrations of latex beads and two species of diatoms, in which one species was larger, and one smaller, than the latex beads (see Figure 3). They found selection for diatoms over latex beads and attributed their observations to post-capture rejection of the non-food particles. This work has subsequently been confirmed for *Calanus* by Huntley *et al.* (1983). Poulet & Marsot (1978; 1980) manufactured microcapsules, some containing phytoplankton homogenate and others without. Mixtures of both types of microcapsule were offered to *Acartia*, *Eurytemora*, and *Calanus* and all showed a positive selection for the particles releasing stimulatory compounds, suggesting a chemically-mediated response. In natural particle assemblages, copepods appear to show a "peak-tracking" response in which particles in size classes constituting biomass peaks are selectively removed (Poulet, 1973; 1974; Richman *et al.*, 1977; Cowles, 1979; Richman *et al.*, 1980). Authors vary in their interpretation of this response; Poulet (1973; 1974) considered it to be "opportunistic" feeding as opposed to the selective feeding mechanism proposed by Richman *et al.* (1977). These studies provided evidence that copepods exhibit complex behavioural plasticity and that future models would need to incorporate factors such as feeding history, food quality and chemosensory abilities into their formulation (Huntley, 1988).

In recent years, the two main sources of evidence challenging the passive-mechanical hypothesis have been; a) improved understanding of hydrodynamic principles governing copepod feeding (reviewed by Jϕrgensen, 1983), and b) direct visual evidence of the feeding process from cinematographic studies (e.g. Alcaraz, *et al.*, 1980).

HYDRODYNAMIC ASPECTS: FEEDING AT LOW REYNOLDS NUMBERS.

It has only recently been recognized that zooplankton filter-feeding occurs at low Reynolds numbers (e.g. Koehl & Strickler, 1981; Gerritsen & Porter, 1982; Porter *et al.*, 1983; and reviewed in detail by Jφrgensen, 1983). The Reynolds number expresses the ratio between inertial and viscous forces and is given by the function:

$$\mathrm{Re} = p\nu L/\mu$$

where, p = density of the medium
L = linear dimension of the object
ν = relative velocity of the fluid across a solid body
μ = dynamic viscosity of the medium

(after Koehl & Strickler, 1981)

Since copepods are generally small (usually no more than a few millimetres in length), the feeding environment is characterized by Reynolds numbers < 1 which are dominated by viscous forces and laminar flow (Koehl & Strickler, 1981; Légier-Visser *et al.*, 1986).

There are several important consequences of feeding at low Reynolds numbers. The feeding medium is not stirred by the movement of the feeding appendages, consequently the direction of chemical stimuli is not confused (Koehl & Strickler, 1981). Food particles follow streamlines and can be moved towards the mouthparts without touching the appendage (McClatchie & Boyd, 1983). The setae and setules of the second maxillae are surrounded by a region of reduced fluid flow termed the boundary layer. At low Reynolds numbers, the layer is thick, relative to the structural dimensions (Koehl & Strickler, 1981), and in most cases reported, is greater than half the distance between the setae and setules respectively (Koehl & Strickler, 1981; Vanderploeg & Paffenhöfer, 1985; Price & Paffenhöfer, 1986b). Since the boundary layers of adjacent setae and setules overlap, water flows over the feeding appendage as opposed to through it (Gerritsen & Porter, 1982).

Price & Paffenhöfer (1986b) calculated the boundary layer for the tip-, mid- and base-region of the second maxillae of *Eucalanus elongatus*. They found that due to the smaller diameter of the setae at their tip region and the greater velocity at which they move, the boundary layer is at a minimum, and less than half, the intersetal distance suggesting that in that region, fluid flow would be unrestricted. Observations of passively retained particles, however, showed no statistical difference between the number of particles that passed through the basal or distal regions. The discrepancy between the calculated and observed movement of particles was thought to be due to the complexity of applying boundary layer calculations to an appendage that oscillates at variable velocity as well as the complex fluid flow near the maxillae caused by adjacent appendages.

VISUAL OBSERVATIONS OF FEEDING APPENDAGE MOVEMENT DURING FOOD CAPTURE.

Since the debate over the precise mechanism by which copepods feed was started over 80 years ago, attempts have been made to observe the process directly, with the naked eye, using a microscope, or with cinematographic techniques (Cannon, 1928; Lowndes, 1935; Marshall & Orr, 1955; Gauld, 1964; 1966; Conover, 1966; Koehl & Strickler, 1981). Until recently, the techniques and equipment available were not sufficiently sophisticated (Paffenhöfer *et al.*, 1982) and additionally, the principles of fluid mechanics had been overlooked (Rubenstein & Koehl, 1977). Early studies based on microscope studies of animals in small volumes, described the feeding current vortices and eddies surrrounding the animal. Modern interpretations of these results argue that this would result in the wasteful re-filtering of water (Alcaraz *et al.*, 1980) and they are now considered to be artifacts of the small volume of water in which the experiments were conducted. The interpretations of these studies, and the mechanistic concept of copepod feeding led to the development of a generally accepted paradigm of filter-feeding which is only now being re-examined.

Cinematographic evidence of feeding behaviour.

A major breakthrough was made with the work of Alcaraz *et al.* (1980), presented at a meeting on "Ecology and Evolution of Zooplankton Communities" (in Kerfoot, 1980), which visually demonstrated the feeding behaviour of *Eucalanus crassus*. Most significantly, their evidence showed clearly that viscous forces dominate the feeding process of copepods and consequently the feeding appendages act as paddles rather than as sieves. During the last decade, this pioneering work has been developed by other researchers to examine differences between taxa, as well as the influence of different food conditions.

Mode of particle capture based on cinematographic evidence.

Generalized accounts of the mode of particle capture used by calanoid copepods, based on cinematographic evidence, are provided by Koehl & Strickler (1981) and Paffenhöfer *et al.* (1982) from observations of *Eucalanus pileatus* and *Eucalanus crassus*, respectively.

The following description synthesizes their accounts: The feeding current, which drives the particles and water toward the animal in a postero-lateral direction, is generated by the beating of the second antennae and the maxillipeds. The feeding current passes through the tips of the setae of the second maxillae. If a particle is detected, the co-ordinated movement of all the mouthparts re-directs it into the median plane of the animal. If the animal was untethered, this asymmetric movement would re-orientate the animal in the direction of the particle. Re-positioning the particle separates it from the large volume of feeding current. The second maxillae, which until this point remain motionless, fling open as the particle nears the space between the endtips of the setae. This rapid movement results in an inrush of water that fills the low pressure area created by the sudden outward movement. Copepods capture "parcels" of water, squeeze the water through the setae and retain the particles (Strickler, 1982). Contact between the feeding appendages and particles occurs only when the water is compressed by the movement of the second maxillae closing (McClatchie & Boyd, 1983). Although maxillary setules are hidden in the boundary layer, it is likely that the setule length and spacing should determine which particles are retained (Koehl & Strickler, 1981). The continuous action of the second antennae and the first maxillae, generating the feeding current, prevents the anteriorly-directed escape of water. Particles trapped on the second maxillae are combed off by the endites of the first maxillae and transported to the mouth where they are sucked in by a rapid movement of the mandibles.

Variations among taxa.

Although the general features of this description hold true for other copepods, studies by other authors have revealed variations of this behaviour, which can be attributed to two factors, namely i) behavioural differences between taxa and, ii) different feeding conditions.

Yule & Crisp (1983) caution against the assumption that all copepods exhibit similar feeding behaviour. Although the number of comparable studies published are limited to observations of less than ten other species, variations of this mechanism have been described. For example, Cowles & Strickler (1983) demonstrated that the maxillipeds of *Centropages hamatus* oscillate in a figure-of-eight motion during feeding current production, and Price & Paffenhöfer (1986b) have shown the direction of water flow to be from the outside to the inside of the second maxillae of *Eucalanus elongatus*. Probably the most significant behavioural difference has been noted in *Acartia*. The characteristic "scoop-net" movement of the second maxillae of *Acartia clausi* was first observed in microscopic studies by Gauld (1964). During feeding, these appendages are flexed, spreading the setae ventrally and laterally. Particles are strained from the water as the setae close up (Rosenberg, 1980). In addition, he described how the thoracic legs, together with the second antennae, "suck" unfiltered water into the space between the legs and the mouthparts, and assist in the feeding process by moving forward during the capture stroke to counter the backward movement of the mouthparts.

ENCOUNTER RATES AND FEEDING.

The feeding process begins with i) an encounter event (Marrasé *et al.*, 1990), which is followed by ii) recognition and attack of the prey item, iii) prey capture and iv) successful ingestion (Gerritsen & Strickler, 1977). The rate of encounter directly affects the following steps and is therefore important with respect to the response of calanoid copepods to changes in the concentration of the food source (Gerritsen & Strickler, 1977).

Cushing (1959) first attempted to model encounter rates and derived the following formula:

$$\text{encounter rate} = v \times A \times C$$

where,
v = velocity of the copepod
A = contact surface (dimensions of the 1st antennae)
C = food particle concentration

This model, however, neglects the role of feeding currents and the hydrodynamic properties of the feeding medium. Due to the dominance of viscous forces at low Reynolds numbers, shear deformation decreases with distance away from an object (Koehl & Strickler, 1981). Consequently, the motion of the feeding appendages draws a "cone" of water towards the copepod. Due to shear characteristics, particles in the feeding current are accelerated by the feeding current as they approach the feeding appendages. Marrasé *et al.* (1990) incorporated particle velocity into Cushing's original expression by combining it with copepod velocity and derived estimates of encounter rate greater than that of the original model. In addition, the feeding current allows remote sensing of particles (Koehl & Strickler, 1981; Andrews, 1983; Strickler, 1985; Légier-Visser *et al.*, 1986) as well as re-orientation of particles as they approach the copepod (Paffenhöfer *et al.*, 1982; Vanderploeg & Paffenhöfer, 1985).

Recently, Rothschild & Osborn (1988), and modified by Evans (1989), proposed a theoretical model of the influence of small-scale turbulence on encounter rates. They proposed that kinetic energy associated with small-scale turbulence would increase encounter rates by increasing the velocity of copepods and their algal prey. Microcosm experiments (Oviatt, 1981; Alcaraz, *et al.*, 1988), have demonstrated that copepods may not respond favourably to turbulent environments. This has been ascribed to disruption of the feeding currents (Oviatt, 1981), or to changes in feeding behaviour resulting in decreased feeding efficiency (Alcaraz *et al.*, 1988). In observations of *Centropages hamatus* at different levels of turbulence, Marrasé *et al.* (1990) found that although small-scale turbulence increased encounter rates, the potential benefit was negated by the behavioural responses induced which resulted in more frequent switching to a non-feeding mode. These results were combined with those of Costello *et al.* (1990) to calculate what they termed the effective encounter rate which examined the rate of encounter during the feeding mode. They calculated increased effective encounter rates during turbulent as opposed to non-turbulent conditions, dependent however, on food concentration. In order to predict encounter rates accurately, it is essential that future models incorporate flow conditions as well as animal behaviour (Marrasé *et al.*, 1990).

THE ROLE OF MECHANO-, AND CHEMORECEPTION IN FEEDING.

With a more complete understanding of the fluid-dynamical aspects of copepod feeding, it has been recognized that energy costs associated with feeding in a viscous medium were previously greatly underestimated. The ability to detect and respond only to "suitable" particles is of great benefit to organisms feeding in an often nutritionally dilute environment (Cowles & Strickler, 1983). Paffenhöfer *et al.* (1982) and Koehl & Strickler (1981) suggested that particles large enough to be handled individually are detected by chemosensory reception while several other authors (e.g. Strickler & Bal, 1973; Zaret, 1980) have proposed that mechanoreception is involved in food capture. By contrast, copepod feeding models based on a passive-mechanical process, imply no basis for selection of food by complex behavioural processes (DeMott, 1988a).

Several morphological studies have been conducted (e.g. Strickler & Bal, 1973; Friedman & Strickler, 1975; Friedman, 1980) which describe structures believed to function in chemo-, and mechanoreception. These receptors are found primarily on i) the antennae, which detect chemical signals and fluid distortion from approaching particles (Strickler & Bal, 1973; Friedman, 1980) and ii) the mouthparts, which determine the "suitability" of particles trapped from the feeding current (Friedman & Strickler, 1975).

Experimental studies have demonstrated that copepods will select for live algal cells in the presence of senescent or heat-killed cells (Starkweather & Bogdan, 1980; Bartram, 1981; Paffenhöfer & Van Sant, 1985; Cowles *et al.*, 1988). Copepods are able to differentiate and selectively ingest algal cells in mixtures containing similarly sized beads. (Fernández, 1979; Donaghay & Small, 1979; Huntley *et al.*, 1983; DeMott, 1988b). Poulet & Marsot (1978) used a microencapsulation technique and demonstrated that the calanoid copepods *Eurytemora herdmanni* and *Acartia clausi* fed preferentially on capsules containing phytoplankton homogenate as opposed to capsules containing seawater. Huntley (1982) and Huntley *et al.* (1986) have demonstrated the ability of some copepods to reject particular species of dinoflagellate.

Remote sensing provides the copepod with initial information of the dimensions and quality of particles approaching in the feeding current at between hundreds of microns to a millimetre away (Strickler, 1982; Price *et al.*, 1983). Mechanoreceptors on the first antennae detect the pressure disturbance caused by the presence of particles in the feeding current (Légier-Visser *et al.*, 1986). Motile prey such as ciliates and rotifers provide a strong mechanical stimulus (Williamson & Butler, 1986; Jonnson & Tiselius, 1990). Thus, hydrodynamic conspicuousness may provide the basis for selection by mechanosensory means (Kirk, 1985).

Extracellular dissolved compounds may be released by food and non-food organisms (Poulet & Marsot, 1978; 1980). These exudates are trapped in the boundary layer surrounding a particle, forming an area of "active space" (Andrews, 1983), and provide the stimulus for capture (Buskey, 1984). Due to viscous forces associated with feeding, the active space is sheared by the feeding current and elongated along the path of flow towards the chemoreceptors of the first antennae, facilitating early detection (Légier-Visser *et al.*, 1986). The source direction of the chemical stimulus is unlikely to be disrupted by the action of the feeding appendages because of laminar flow at low Reynolds numbers (Koehl & Strickler, 1981).

Copepods capture suitable particles detected in the feeding current by mechanoreceptors and chemoreceptors on the first antennae. Following capture, particles are transferred to the mouth, and tested by short-range chemoreceptors on the mouthparts and either ingested or rejected (Poulet & Marsot, 1980; Koehl & Strickler, 1981; Paffenhöfer *et al.*, 1982). Little is known about precisely which chemicals provide chemosensory stimuli for copepods, however several authors (Poulet & Marsot, 1978; 1980; Poulet & Oullet, 1982; Poulet & Gill, 1988) have demonstrated that copepods are particularly sensitive to amino-acids. Cowles *et al.* (1988) have demonstrated that *Acartia tonsa* responds to chemical cues associated with the protein content of the food since they appear to maximize protein intake during selection.

Remote detection enables copepods to assess the feeding current and elicit a capture response only when suitable food items are present. Thus, copepods increase the chance of obtaining food by scanning a far larger volume of water (Cowles & Strickler, 1983). Further research is required to provide quantitative data to determine i) the sensitivity of discrimination between natural particles, ii) the influence of food abundance on selection behaviour, and iii) the influence of foraging strategies on the dietary overlap of co-existing species (DeMott, 1988a).

ACTIVE AND PASSIVE FEEDING MODES.

Copepods feeding in mixtures of large and small particles remove larger particles at a greater rate than the small particles relative to their frequency in the feeding suspension (Yule & Crisp, 1983). The advent of microcinematographical techniques (e.g. Price *et al.*, 1983; Vanderploeg & Paffenhöfer, 1985; Price & Paffenhöfer, 1986b) have enabled first hand observations of copepod feeding which have demonstrated two feeding modes. These are i) an active feeding mode in which large particles are detected in the feeding current and elicit an oriented capture response, and ii) a passive feeding mode, whereby particles which are too small to be handled individually are collectively handled and ingested.

Active and Passive modes.

During active capture, as a particle of sufficient size approaches in the feeding current, it is detected by distant mechanoreception, following which the copepod re-orients itself to facilitate the capture process (Price *et al.*, 1983). The co-ordinated movement of the mouthparts drag the particle in a "parcel" of water towards the second maxillae. The proximity of the particle to the animal elicits a capture response of the second maxillae which up until this time remain motionless. Rapid flapping actions of the second maxillae capture the particle which is then passed to the mouth by the mandibles (Price *et al.*, 1983). The copepod may adjust its handling to accommodate the perceived dimensions of the particle (Paffenhöfer *et al.*, 1982; Price & Paffenhöfer, 1984). Following the capture process, undesirable particles may be rejected at the mouth (Paffenhöfer *et al.*, 1982).

In contrast to active capture, the passive collection of small particles generally involves low amplitude oscillations of the second maxillae. This may serve to reduce the boundary layer around the setules (Price *et al.*, 1983) and is usually maintained despite the presence or absence of particles (Vanderploeg & Paffenhöfer, 1985). Since the second maxillae move at a much slower velocity during passive capture, the boundary layer is considerably thicker compared with feeding in the active mode (Vanderploeg & Paffenhöfer, 1985). During feeding on small particles, periodic breaks in maxillary movement occur, presumably to allow the copepod to comb accumulated particles from the maxillary surface and pass them to the mouth (Price *et al.*, 1983). Since passive collection does not involve prior detection or re-orientation, only particles passing close to the medial plane of the copepod are likely to be captured (Vanderploeg & Paffenhöfer, 1985). Particles accumulated in this manner are funnelled to the mouth for ingestion (Price & Paffenhöfer, 1986b).

Transition between Active and Passive feeding.

A number of attempts have been made to determine the size threshold at which particles switch from being passively, to actively captured. From a cinematographic study, Price *et al.* (1983) determined the size threshold for the copepods *Eucalanus pileatus* and *Paracalanus parvus* to lie between 6 and 12 μm particle diameter. The threshold size, taken to be the size above which a sharp increase in the clearance rate was measured, was determined to occur at 12 μm particle diameter for *Diaptomus sicilis* (Richman, *et al.*, 1980), and between 13 to 15 μm diameter for *Calanus pacificus* (Frost, 1977). Other studies (e.g. Vanderploeg, 1981; Bartram, 1981), however, have reported gradual increases in selectivity with increasing particle size. In a cinematographic study of *Diaptomus sicilis* feeding on different sized algae (Vanderploeg & Paffenhöfer, 1985), the intermediately-sized alga was captured actively with a probability higher than the small alga but lower than the larger alga, suggesting a gradual transition from active to passive feeding mode with decreasing particle size. The difference in filtration rates between small and large-sized particles in copepod feeding is attributed to inefficiency of passive accumulation of small particles relative to raptorial feeding on larger particles (Price & Paffenhöfer, 1984).

Effects of size and concentration of algae in monocultures and in mixtures.

Studies have been conducted to test the effects of algal size and concentration on the capture mode of various species of copepod. Vanderploeg & Paffenhöfer (1985) observed the feeding of *Diaptomus sicilis* in monocultures of algae (*Chlamydomonas* sp.) of three different sizes and at three different concentrations. They found that the percentage of active captures (of total captures observed) decreased with decreasing algal size. Algae $\leq 4\ \mu m$ diameter were only captured by the passive mode but algae $\geq 6\ \mu m$ were captured by both active and passive mode. He concluded that algal size is the primary factor determining the mode of capture but that concentration may play a secondary role. Price & Paffenhöfer (1986a) extended the complexity of their study to observe *Eucalanus elongatus* feeding in monocultures as well as mixtures of different-sized cells at different concentrations and different volumetric ratios. Experiments were conducted using a small cylindrical diatom (*Thalassiosira weissflogii*, 13 μm diameter) and a large elongated diatom (*Rhizosolenia alata*, 450 x 20 μm). In monocultures, cell capture was found to be primarily by the passive and the active feeding modes respectively. They found at all mixture ratios, that *E. elongatus* was able to switch rapidly from one feeding mode to another and, in addition, to capture cells passively while handling cells captured by the active mode.

Taxa differences - passive versus active: continuous versus switching.

Observations on a number of copepod genera and species have demonstrated variations in the behavioural response of small and large particle capture mode. Cowles & Strickler (1983) have shown that *Centropages typicus* holds the second maxillae stationary and movement occurs only in response to active capture of individually detected particles. Preliminary observations of other copepods e.g. *Eucalanus* sp., *Paracalanus* sp., *Neocalanus* sp. and *Temora* sp. (Price *et al.*, 1983) demonstrated that during passive capture the second maxillae flap at a low amplitude, but that the animal will switch to a rapid flapping of the second maxillae following detection of a particle large enough for individual capture. The feeding current maintains a flow across the maxillae even though they are stationary but is "enhanced" by low amplitude flapping of the second maxillae. The freshwater copepod *Diaptomus sicilis* differs behaviourally in that the active and passive modes operate simultaneously under all feeding conditions. Thus, the enhanced passive flow through the feeding appendages is continuous (Vanderploeg & Paffenhöfer, 1985). According to Price & Paffenhöfer (1986b) interspecific behavioural differences of maxillary movement may provide information on the relative dependence of the animal on continual feeding on small particles or individual detection of large particles.

LABORATORY VERSUS *IN SITU* FEEDING STUDIES.

The current understanding of zooplankton functional feeding has been derived mainly from laboratory studies, however, problems associated with extrapolating these results to field conditions have been recognized (e.g. Boyd *et al.*, 1980; Dagg & Grill, 1980; Frost, 1980; Kiφrboe *et al.*, 1982; Dagg, 1983; Dagg & Wyman, 1983; Nicolajsen *et al.*, 1983). Laboratory studies often result in stressed conditions through excessive handling or overcrowding which lead to misinterpretation of both grazing rates and selective feeding (e.g. Roman & Rublee, 1981; Dagg, 1983). The feeding response of zooplankton to the size, concentration and quality of suspended particles has been most widely studied, however, the phytoplankton and latex beads commonly used in laboratory feeding studies do not adequately simulate the complex mixture of phytoplankton, bacteria, detritus and inorganic particles which comprise the natural seston (Roman & Rublee, 1981). This problem has been avoided in several studies which used zooplankton and particle assemblages collected from the natural environment, however, laboratory conditions do not reflect ambient temperature and light (Roman & Rublee, 1981). Perhaps more importantly, controlled laboratory experiments do not take into account the extreme heterogeneity of the natural feeding environment (e.g. Kiφrboe *et al.*, 1982).

Consequently, the need for greater emphasis on *in situ* grazing measurements was recognized (e.g. Wang & Conover, 1986). A number of methods have been developed for this purpose, the most common of which are, i) the incubation technique, normally involving radio-active tracers (e.g. Haney, 1971; 1973; Haney & Hall, 1975; Gulati *et al.*, 1982; Hart, 1984; 1986; Jarvis, 1987; Mourelatos *et al.*, 1989), and ii) the gut fluorescence method (e.g. Mackas & Bohrer, 1976; Boyd *et al.*, 1980; Dagg & Wyman, 1983; Nicolajsen *et al.*, 1983). The advantages and disadvantages of these methods are discussed in several papers which compare the available techniques (Kiφrboe *et al.*, 1985; Peterson *et al.*, 1990). *In situ* techniques overcome to a large extent the artficiality inherent in laboratory studies which have so far precluded the development of effective predictive models of the natural environment, however, at the present time, there have been comparatively few applications of these techniques. In view of the problems associated with extrapolating the results of laboratory studies to environments such as estuaries, which exhibit high short term variability in environmental conditions, an *in situ* approach was adopted in this study (Haney, 1971; 1973), in an attempt to derive realistic zooplankton community grazing rates.

CHAPTER FOUR

THE INFLUENCE OF FRESHWATER INFLOW ON THE NATURE, AMOUNT AND DISTRIBUTION OF ESTUARINE SESTON

4.0 INTRODUCTION

An evaluation of the nature, concentration and distribution of potential food resources is central to studies of trophodynamics in aquatic ecosystems (e.g. Boyd & Goodyear, 1971; Mayzaud & Poulet, 1978; Laane, 1980; Runge & Ohman, 1982). In the natural environment, suspended particulate material (seston) is composed of a complex mixture of phytoplankton, detritus, bacteria and inorganic particles (e.g. Roman & Rublee, 1981), although in the estuarine environment, detritus is generally the most abundant food resource (Mann, 1988). Seston may vary considerably with respect to size distribution, composition and nutritional potential, both temporally and spatially (Riley, 1970; Tenore, 1977; Roman & Rublee, 1981; Nicolajsen *et al.*, 1983; Mayzaud *et al.*, 1984b).

Estuaries are allochthonous-dominated systems, and the nature and availability of particulate food resources is strongly dependent on biotic and abiotic inputs, notably riverine inflow and oceanic influences. Variability in river discharge may alter the influx of nutrients markedly and play an important role in determining phytoplankton standing stocks (Joint & Pomroy, 1981; Cloern *et al.*, 1983; Peterson & Festa, 1984; Bennett *et al.*, 1986; Stearns *et al.*, 1987; Garcia-Soto *et al.*, 1990; Jordan *et al.*, 1991). Elevated turbidity, due to suspended inorganic material associated with river run-off, may be an important factor limiting phytoplankton production in estuaries (Heinle & Flemer, 1975; Joint & Pomroy, 1981; Pennock, 1985). In addition, large quantities of detritus are often associated with freshwater inflow (Sutcliffe, 1972; Tenore, 1977; Naimen & Sibert, 1978; Chervin *et al.*, 1981; Findlay *et al.*, 1991).

Patterns of circulation and distribution in estuaries are dependent largely upon tidal characteristics and freshwater inflow (Pritchard, 1967b; Dyer, 1973; Day, 1981). The seaward movement of less dense freshwater from river run-off over denser water of marine origin results in stratification of the watercolumn, the extent of which depends upon the amount of freshwater inflow and the velocity of tidal currents (e.g. Dyer, 1973). In stratified, or partially-stratified estuaries, a turbidity maximum, caused by an accumulation of particles which include phytoplankton, occurs in the upper estuary by a process known as hydrodynamic trapping (Festa & Hansen, 1978; Moon & Dunstan, 1990). Reduced currents and flocculation at the interface of fresh, and saline water cause the sedimentation of suspended particles into the denser seawater layer which are then re-circulated in the estuary (Postma, 1967). Tidal currents cause turbulent mixing which break down stratification in the watercolumn and resuspend bottom sediments, providing nutrients for phytoplankton growth as well as organic matter for filter-feeders (e.g. Fanning *et al.*, 1982; Tiselius, 1988; Wainright, 1990). As a result of the oscillatory nature of tidal currents associated with the spring-neap cycle, the intensity of mixing is extremely variable (Auclair *et al.*, 1982; Ducklow, 1982).

Due to the semi-arid nature of the climate and variable catchment size and regulation, estuaries in the eastern Cape of South Africa range from those in which freshwater inflow is sustained, to those in which inflow is negligible for long periods of time (see Chapter 2). In general, the increase in salinity in estuaries subject to reduced freshwater inflow results in a decrease in stratification and turbidity (Lucas, 1986; Hilmer & Bate, 1990). Under these circumstances nutrients may be a limiting factor for phytoplankton growth and greater emphasis may be placed on autochthonous processes (Allanson & Read, 1987; Hilmer & Bate, 1990). Consequently, there is likely to be a switch from a phytoplankton-dominated system to one dominated by submerged macrophytes (Hilmer & Bate, 1990).

In this Chapter, the influence of freshwater inflow on the temporal and spatial distributions of potential food resources for suspension-feeders is compared in two estuaries, the Kariega and Great Fish estuary, which exhibit contrasting hydrodynamic characteristics as a result of marked differences in freshwater inflow.

4.1 METHODS

4.1.1 SAMPLING.

Temperature, salinity and current speed contours.

To assist in determining the potential for stratification, depth profiles (0.5 metre intervals) of temperature, salinity and current speed were made at half hourly intervals over a tidal cycle at one Station in both estuaries (Stn P, Kariega; Stn F, Great Fish).

Seasonal and spatial patterns of seston distribution.

Measurements of seston characteristics and physical parameters were made at monthly intervals on spring tides for a period of a year in the Kariega and Great Fish estuaries. Sampling was undertaken at three sampling Stations (1, 2 and 3), corresponding to the upper, middle and lower reaches of each estuary in order to examine the spatial variability (see Site descriptions, Chapter 2). Measurements of total particulate material (TPM), total particulate organic material (TPOM), particulate protein and carbohydrate, and chlorophyll *a* were made from water samples collected from mid-depth in midstream, and sieved through a 35 μm nytex mesh screen to exclude crustacean zooplankton. Attempts to measure particulate lipid were made using two separate methods described in Strickland & Parsons (1968) and Parsons *et al.* (1984). Both were largely unsuccessful and attributed to problems associated with the high inorganic content of the seston. Consequently, further attempts were discontinued. Temperature and salinity were measured *in situ*. Particle size distributions were obtained from Coulter Counter analyses when the apparatus was operational.

Diel distribution of seston.

Seston characteristics were measured at approximately half hourly intervals at one Station in both estuaries over a diel cycle (Stn P, Kariega; Stn H, Great Fish). Sampling was undertaken according to the methods described in the Section above ("Seasonal and spatial patterns..."), although measurements of TPM, TPOM and chlorophyll *a* only, were made.

Seston size fractionation.

Determinations of the size distribution of seston were made from water samples fractionated through nytex mesh screens. Water samples were screened through 80, 35, 20, 10, and 5 μm pore diameter nytex mesh and filtered onto Whatman GF/F glass fibre filters. Determinations of TPM, TPOM and chlorophyll *a* were made from the seston retained by the filters. An analysis of the particle size distribution of the sample was made using the Coulter Counter.

4.1.2 MEASUREMENT OF SESTON.

i) Total particulate material (TPM) was measured by filtering water samples onto pre-ashed and weighed Whatman GF/F glass fibre filters. Filters were dried at 55 °C to constant mass, and the total suspended material expressed as mg l^{-1}.

ii) Total particulate organic material (TPOM) was measured as the change in mass of TPM (above), after ashing for 5 hours at 490 °C. TPOM was expressed as mg l^{1}.

iii) Chlorophyll *a* was measured from water samples which had been filtered onto Whatman GF/F glass fibre filters in the field and subsequently air-dried and stored in the dark on ice. On return to the laboratory, chlorophyll pigments were extracted in 90 % acetone in the dark at 4 °C for 24 hours. Chlorophyll *a* was calculated from the absorbance of light at 750, 664, 647 and 630 nm measured on a Shimadzu U.V.-150-02 double-beam spectrophotometer using the equations given in Parsons *et al.* (1984). Chlorophyll *a* was expressed as μg l^{-1}.

iv) Particulate protein was measured from water samples filtered onto a 0.45 μm membrane filter to which an inert powder had been added to facilitate the subsequent removal of the seston sample. Protein was extracted from the powder/seston mixture in a 0.1 M NaOH solution and precipitated by the addition of trichloroacetic acid (TCA) using the methods of Kaushik & Hynes (1968) and Eze & Dumbroff (1982). Photometric assay of protein was carried out using the Folin-Ciocalteau method and protein values were obtained by comparison with a standard curve (Appendix A) derived from bovine serum albumin (Clarke & Switzer, 1977), and expressed as μg l^{-1}.

v) Particulate carbohydrate was measured from seston retained on inert powder as described above for protein. Carbohydrate content was determined from the powder/seston mixture using the photometric assay method of Raymont *et al.* (1964). Values were obtained by comparison with a standard curve derived from glucose (Appendix A), and expressed as μg l^{-1}.

vi) Particle size distributions were determined using a Model Z_B Coulter Counter (fitted with a 100 μm aperture) using the method of Sheldon & Parsons (1967).
vii) Current speed measurements were made with a Savonius rotor and expressed as m sec^{-1}.
viii) Temperature (°C) was recorded using a standard mercury-in-glass thermometer.
ix) Salinity (‰) was recorded with an Atago S-10 refractometer.
x) River inflow (m^3 x 10^6 $month^{-1}$) was recorded from gauging weirs situated just above the extent of tidal influence in both estuaries (see Chapter 2).

4.1.3 ANALYSIS OF DATA.

The distribution of most water quality data tends to be non-normal (Sanders *et al.*, 1987), and often follows a log-normal distribution. Consequently, statistical procedures used were non-parametric tests based on ranks of data rather than absolute values, since parametric tests are invalid for non-normal data. Thus, for seasonal and diel seston measurements, medians of the three replicate sample measurements were plotted in order to be consistent with the decision to use non-parametric statistics. Seasonal time-series measurements were further analysed as follows:

i) Spearman-Rho correlation coefficients were calculated for the following matrices:

a) for each estuary, the medians of each variable from the three sampling Stations were grouped to test for correlation between variables within the estuary.

b) for each sampling Station (ie Kariega Stations 1, 2 and 3; Great Fish Stations 1, 2 and 3) correlation between variables was tested (12 data points for each variable).

c) for each variable, correlation between Stations 1 to 3 in both the Kariega and Great Fish estuaries was tested using the 12 monthly median values at each sampling Station.

Spearman correlation coefficients range between -1.0 and +1.0 and were interpreted as follows:

0 < coeff. < 0.3 -0.3 < coeff. < 0	Correlation not significant.
0.3 < coeff. < 0.6 -0.3 < coeff. < -0.6	Indicates possible relationship, but may not be statistically significant.
coeff. > 0.6 coeff. < 0.6	Indicates significant correlation.

The results are shown in Appendix B.

ii) The Kruskal-Wallis test was used to check for significant differences between the medians at Stations 1, 2 and 3 in the Kariega estuary and accordingly between Stations 1, 2 and 3 in the Great Fish estuary.

The results are shown in Appendix C.

4.2 RESULTS

Stratification and mixing.

Depth profiles of temperature, salinity and current speed were plotted as two-dimensional contours and are shown in Figures 1 (Kariega) and 2 (Great Fish). In the Kariega estuary, sampling began at 1330 h (5/5/85) and the current speed plot shows that the tide turned to flood at approximately the same time, some two and a half hours after low water at sea (SA Navy Tide Tables). A slight residual stratification is evident in the temperature contours, probably due to surface warming by solar radiation. There was a slight decrease in the salinity as the tide came in, indicating that the salinity in the upper reaches was elevated due to evaporation, low river inflow and poor tidal exchange. In general, little stratification is evident throughout the tidal cycle with respect to temperature, salinity and current speed.

A marked contrast is observed in data obtained from the Great Fish estuary (Figure 2). Sampling commenced at 0900 h (17/5/85) at which time the tide was ebbing. A halocline was evident on the ebb tide and is matched by a strong thermocline and more intense seaward flow in the upper layers. The tide turned at 1200 h, some three hours after low

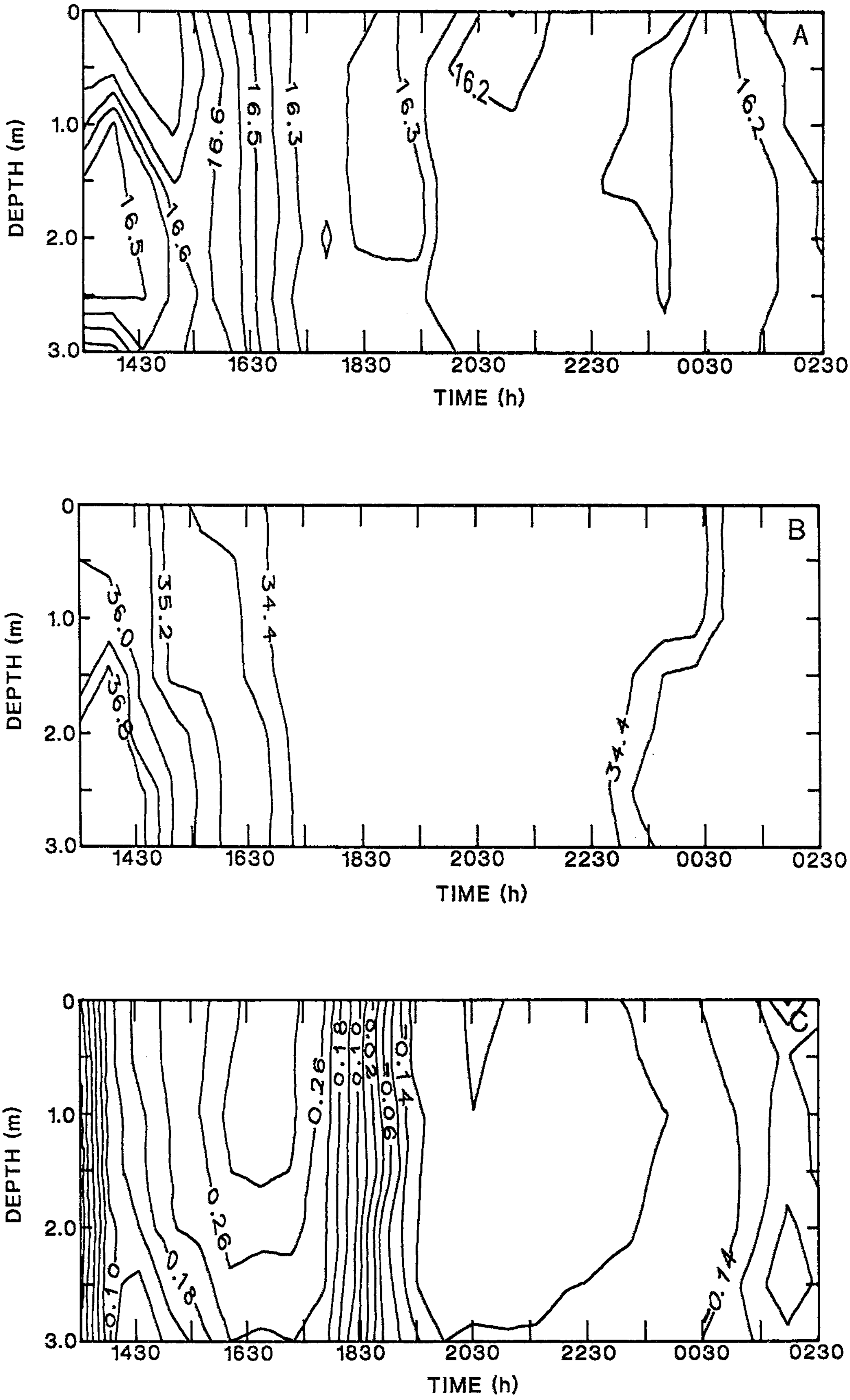


Figure 1. Time series depth-profiles of a) Temperature, b) Salinity, and c) Current speed, measured over a spring tidal cycle at Station P in the Kariega estuary on 5/5/85. In c), ebb currents are shown as negative values.

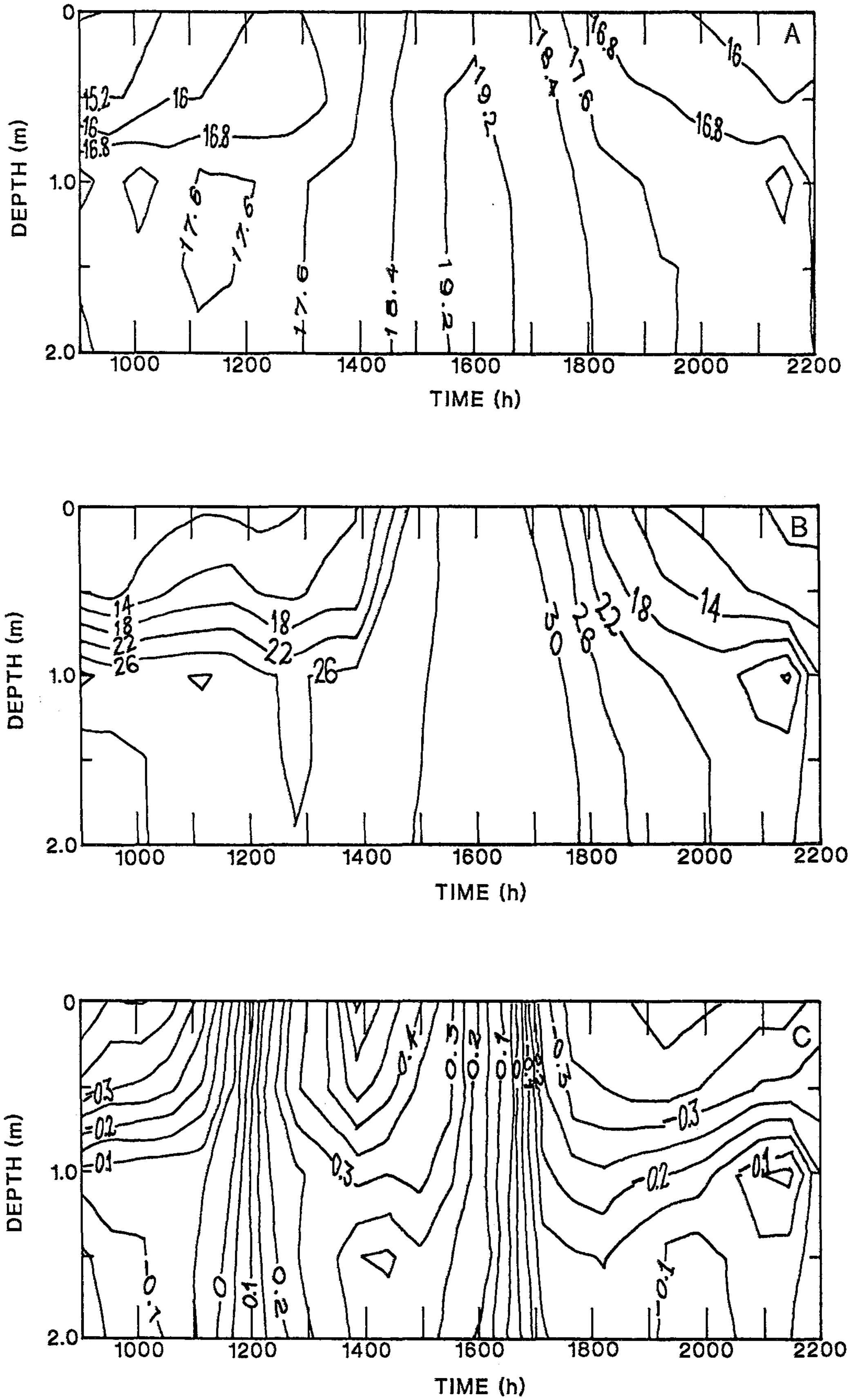


Figure 2. Time series depth-profiles of a) Temperature, b) Salinity, and c) Current speed, measured over a spring tidal cycle at Station F in the Great Fish estuary on 17/5/85. In c), ebb currents are shown as negative values.

tide at sea. Immediately afterwards, the salinity and thermal stratification began to break down as the denser saline water pushed upstream in the lower layer, leading to turbulent mixing across the pycnocline and later at the estuary bed due to bottom friction, subsequently extending into the watercolumn. Slack high water occurred at 1630 h, 75 minutes after highwater at sea. After the onset of the ebb tide, thermal and salinity stratification were set up within 3 hours.

Seasonal patterns.

a) Kariega estuary.

Time series plots of river inflow, salinity, temperature, TPM, TPOM, chlorophyll *a*, particulate protein and carbohydrate are shown in Figure 3. Box-and-whisker plots are shown in Appendix D. Freshwater inflow occurred at a rate of less than 10^4 m^3 $month^{-1}$ throughout the sampling period. This was consistent with measurements obtained over the long term for this estuary (cf Figure 3a, Chapter 2). Just prior to sampling, however, a minor pulse of freshwater occurred during the three month period October 1986 to December 1986. This had the effect of a slight reduction in the salinity in the upper reaches to between 30 and 32 ‰ during the first five months of sampling. In general, however, the salinity was uniformly marine at around 35 ‰ at all Stations throughout the year. Differences in the seasonal median salinity between Stations were tested and indicated significant differences in absolute values between all Stations (Appendix C). Box-and-whisker plots, however, show that these differences were small (Appendix D). Correlation coefficients demonstrated that the salinity response was similar at all Stations (Appendix B). A marked seasonal temperature pattern was evident, ranging from a maximum of ≈ 29 °C in January/February to a minimum of 15 °C in June/July. Temperature responded similarly at all three Stations and median testing demonstrated that there were no significant differences between absolute values (Appendix C).

Although no clear seasonal trends in TPM and TPOM were apparent, chlorophyll *a*, particulate protein and particulate carbohydrate concentrations were generally at a minimum during the colder months between June and August (Figure 3). A total of 28 particle size distributions were determined from water samples collected at all three Stations during the sampling survey. In all cases, the majority of particle volume (≈ 75

%) occurred in the < 20 μm diameter (ESD) size classes. In general, two types of particle size distribution were found. These were, a) those in which the peak in particle volume occurred in the smallest size class, and b) those in which a peak occurred between the 2 and 20 μm particle diameter size class. Representative particle size distributions are shown in Figure 4.

The summer phytoplankton bloom during 1987, which began in August, was short-lived and already in decline during November, although during the previous summer, higher values were maintained until at least February (Figure 3f). Nutrients may have been limiting during the latter part of the study due to the virtual cessation of freshwater inflow during 1987. As a result of the longitudinal and vertical homogeneity of the Kariega estuary, differences in seston characteristics along the length of the estuary were small. Correlation coefficients demonstrated that in general, variables responded similarly at each of the three Stations. A Kruskal-Wallis test of seasonal medians demonstrated significant differences in the absolute values of TPM and chlorophyll *a* between Stations, however, box-and-whisker plots indicate that these differences were small (Appendix D). Correlation analyses highlighted few significant relationships between variables either at individual Stations or for the estuary as a whole, however, significant correlations of TPM and carbohydrate with temperature, and a possible correlation of protein with temperature, were observed (Appendix B). Correlation analyses indicated that freshwater inflow was not an important influence in the Kariega estuary (Table 1). Chlorophyll *a* was not significantly correlated with other seston variables, however, this may be explained in part by the fact that chlorophyll *a* concentrations were consistently very low during the study period.

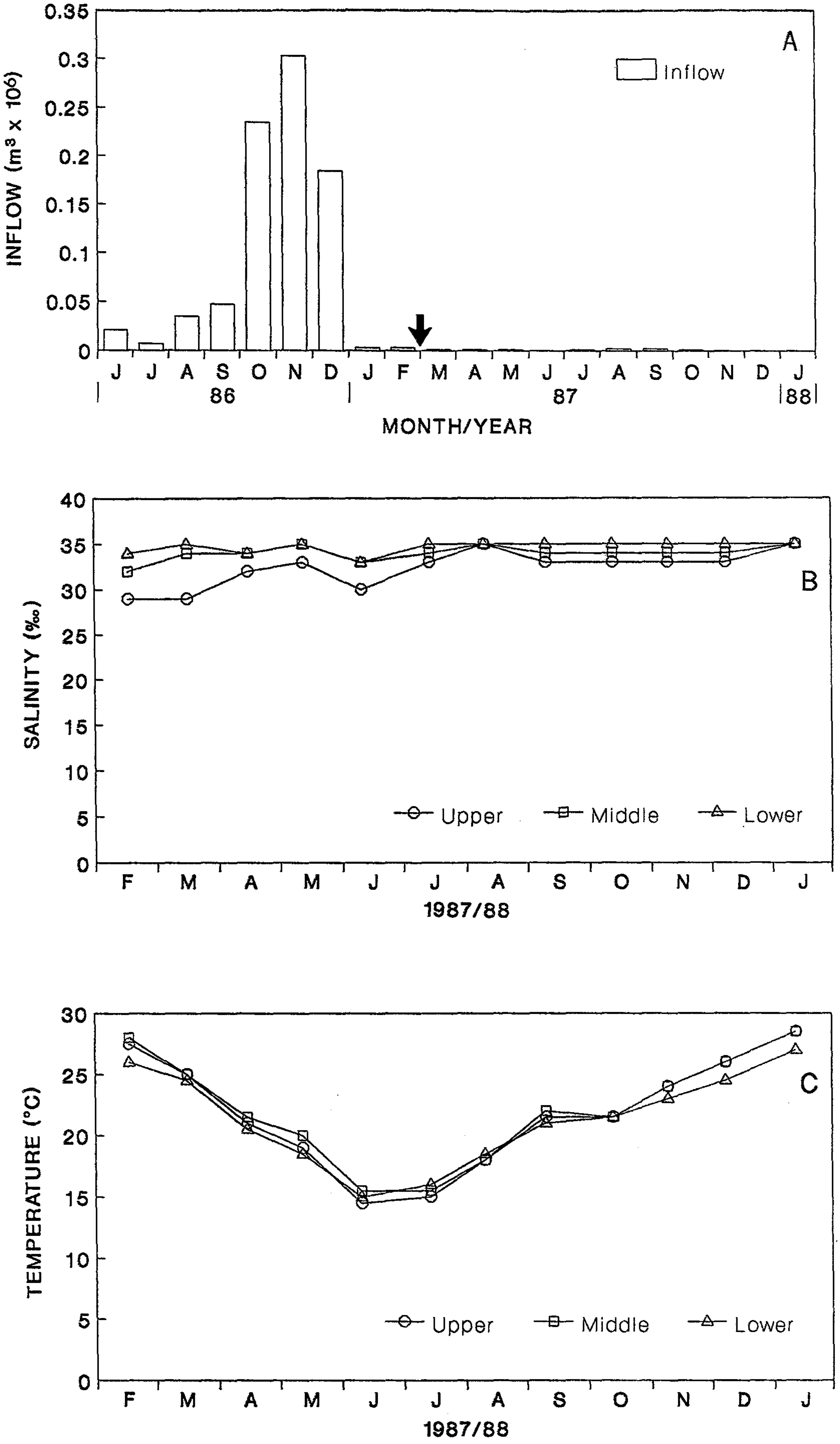
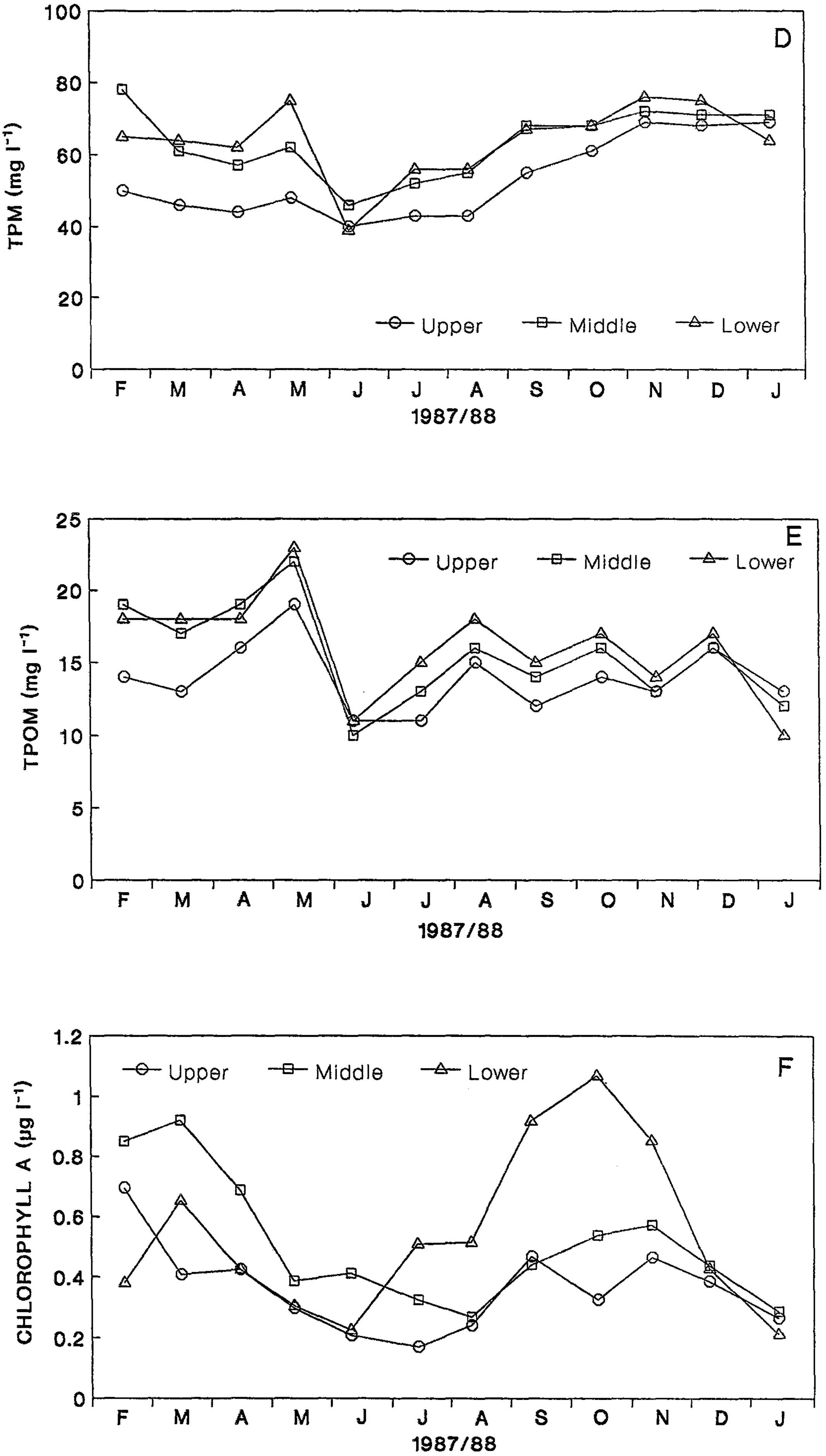


Figure 3. Time series plots of a) River inflow, b) Salinity, c) Temperature, d) TPM, e) TPOM, f) Chlorophyll *a*, g) Protein, and h) Carbohydrate, measured over a seasonal cycle in the Kariega estuary during 1987/88. Note: in (a), start of the sampling programme indicated by arrow; in (b) to (e), measurements taken at three sampling Stations.



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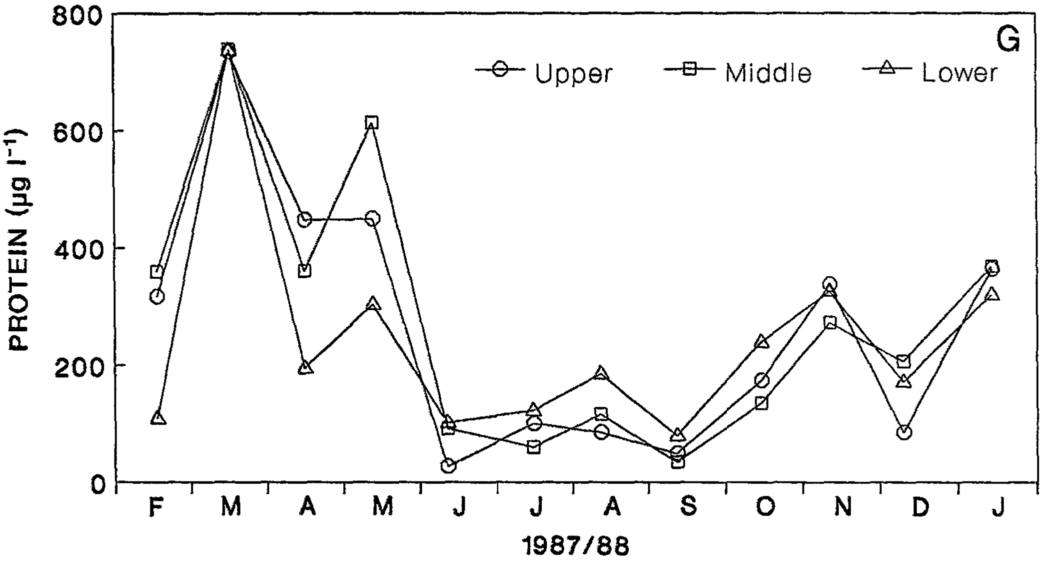

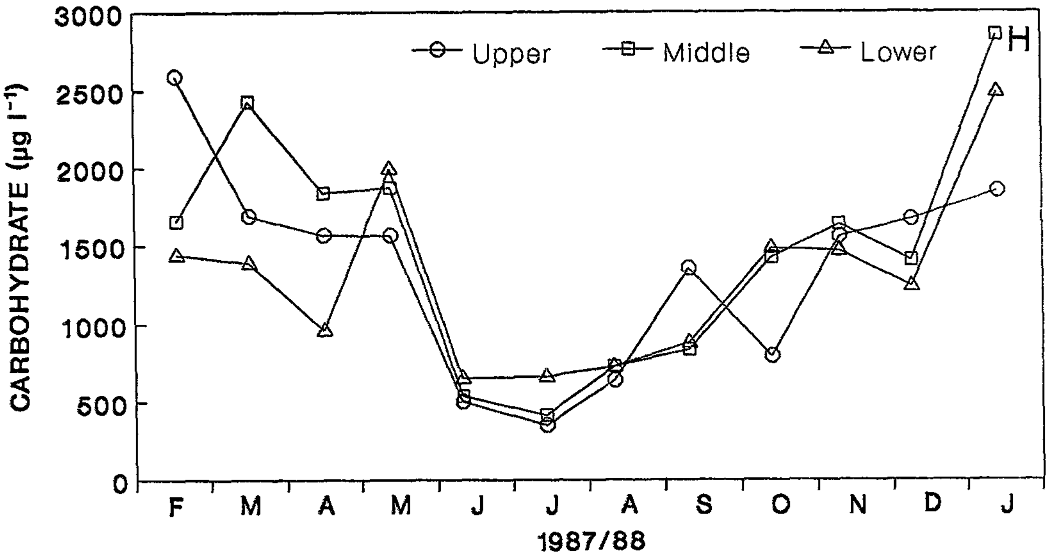

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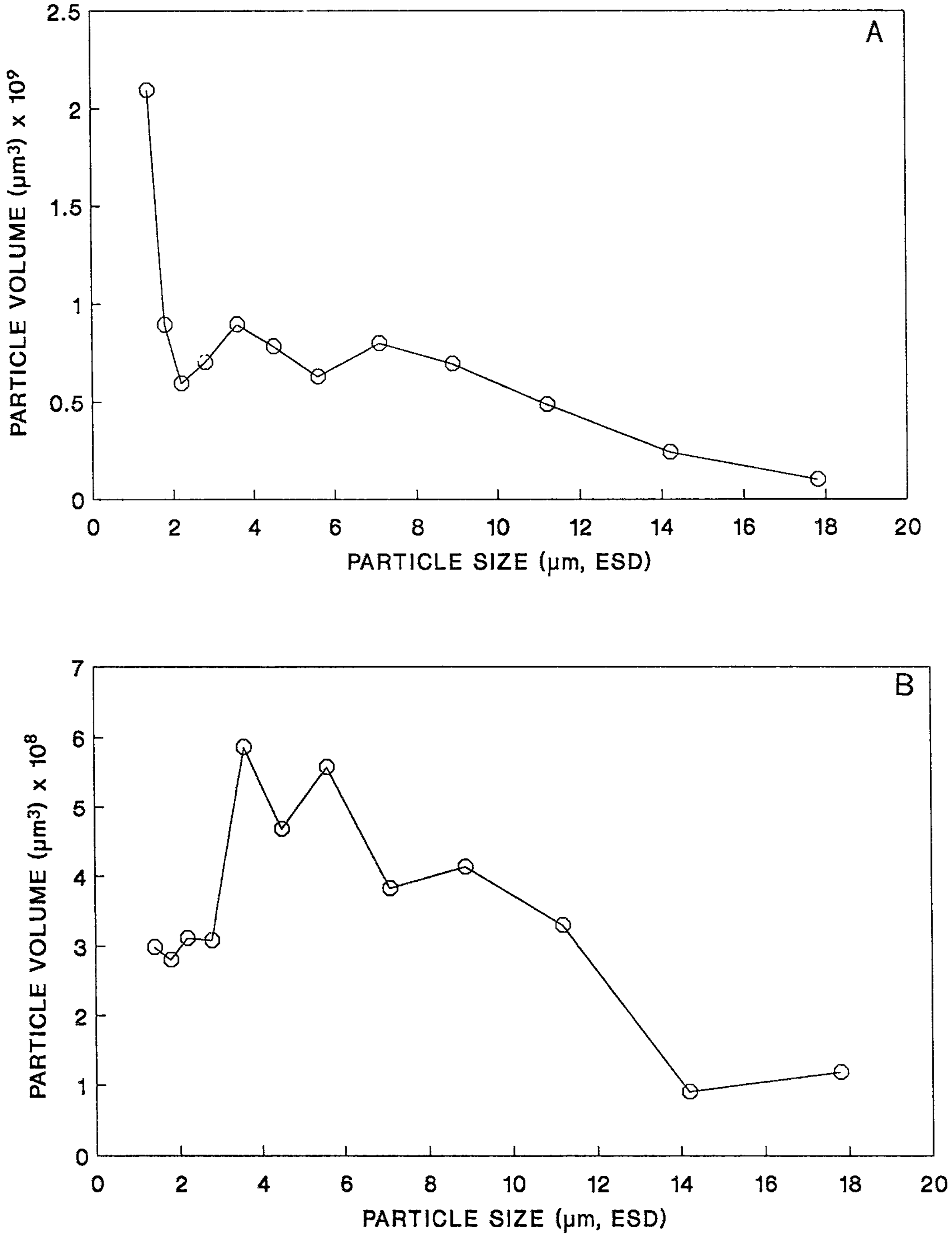


Figure 4. Examples of the two typically occurring particle size spectrums obtained from the Kariega estuary (see text for details), measured using a Coulter Counter. Examples: a) Station P (11/6/87), b) Station J (16/4/87).

Table 1. Selected Spearman Correlation Coefficients for Stations 1 to 3 in the Kariega estuary (n.s. = not significant, * = possibly significant, ** = significant).

		KARIEGA	
CORRELATION WITH RIVER FLOW	STATION 1	STATION 2	STATION 3
TPM	-0.18 n.s	0.09 n.s.	0.03 n.s.
TPOM	0.08 n.s.	0.55 *	0.58 *
Chlorophyll *a*	0.48 *	0.15 n.s.	0.39 *
Protein	0.11 n.s.	0.00 n.s.	-0.15 *
Carbohydrate	0.11 n.s.	0.07 n.s.	-0.02 n.s.
CORRELATION WITH CHLOROPHYLL *a*			
TPM	0.04 n.s.	0.48 *	0.02 n.s.
TPOM	0.09 n.s.	0.42 *	-0.07 n.s.
Protein	0.04 n.s.	0.39 *	0.14 n.s.
Carbohydrate	0.48 *	0.34 *	-0.19 n.s.

b) Great Fish estuary.

Time series plots of river flow, salinity, temperature, TPM, TPOM, chlorophyll *a*, particulate protein and carbohydrate are shown in Figure 5. Box-and-whisker plots are shown in Appendix D. During the sampling period, freshwater inflow was sustained at between 5 x 10^6, and 15 x 10^6 m^3 month^{-1}. Monthly inflow was comparable with values obtained in the long term for the estuary (see Figure 3b, Chapter 2). Although no flood events occurred for the duration of the sampling period, a brief pulse of elevated inflow occurred during November 1986, just prior to sampling. Box-and-whisker plots and time series plots clearly show the salinity gradient which exists between the head and the mouth of the estuary. The salinity regimes at each Station are clearly very different, with Station 1 under permanent upper-estuary freshwater conditions, Station 2 at between 10 to 14 ‰, and Station 3 under marine influence. Salinity demonstrated a negative correlation with river flow as expected, however, the correlation was not significant. This was probably due to the fact that eastern Cape estuaries show a rapid response to rainfall and high variability in river flow rates, and that the river inflow recorded was for the entire month prior to sampling. Time series plots show minor differences in temperature between Stations, superimposed upon the marked seasonal pattern. Maximum temperature (≈ 30 °C) occurred in February/March and the minimum temperature (≈ 13 °C) was recorded during June/July. Station 3 remains slightly cooler than upstream stations due to efficient flushing of the lower estuary by seawater.

Time series, and box-and-whisker plots demonstrate that the seston variables measured were markedly higher compared with the Kariega estuary and not subject to clear seasonal patterns. The ratio TPOM/TPM was generally lower which suggests a greater dominance of inorganic suspended particles in this estuary compared with the Kariega estuary. A total of 27 particle size distributions from all three Stations were measured and the particle size spectrums were similar to those obtained from the Kariega estuary, except that the total particle volume was invariably much higher. Representative size spectrums are shown in Figure 6. Due to the influence of freshwater inflow in the upper reaches, there were considerable differences between sampling Stations (difference of medians testing, Appendix C). The concentrations of TPM, TPOM, chlorophyll *a* and carbohydrate were significantly higher at Station 1 than at downstream Stations (Appendix C). In general, a gradient existed from the upper to the lower reaches. Spearman rank correlation matrices demonstrated that, with the exception of protein, seston variables at Stations 1 and 2 were better correlated than either Stations 2 and 3, or Stations 1 and 3, indicating a somewhat different regime in the lower reaches of the estuary. River inflow appears to be an important factor influencing seston characteristics, and is most apparent in the upper reaches. TPM, and chlorophyll *a*, in particular, responded positively to freshwater inflow. Time series plots show clear peaks of these variables in June, and again in September, and these coincide with small elevations in the amount of freshwater discharge into the estuary. Correlation analyses indicated that TPM, TPOM and chlorophyll *a*, particularly, were positively correlated with freshwater inflow, however, correlations were more significant in the upper region of the estuary (Table 2, Appendix B). The ratio TPOM/TPM was negatively correlated with river inflow which suggests that high concentrations of suspended inorganic material are associated with elevated freshwater inflow. The significant correlation between chlorophyll *a* and TPOM, protein and carbohydrate seems to indicate that phytoplankton is a dominant food resource for suspension-feeders, particularly at Stations 1 and 2.

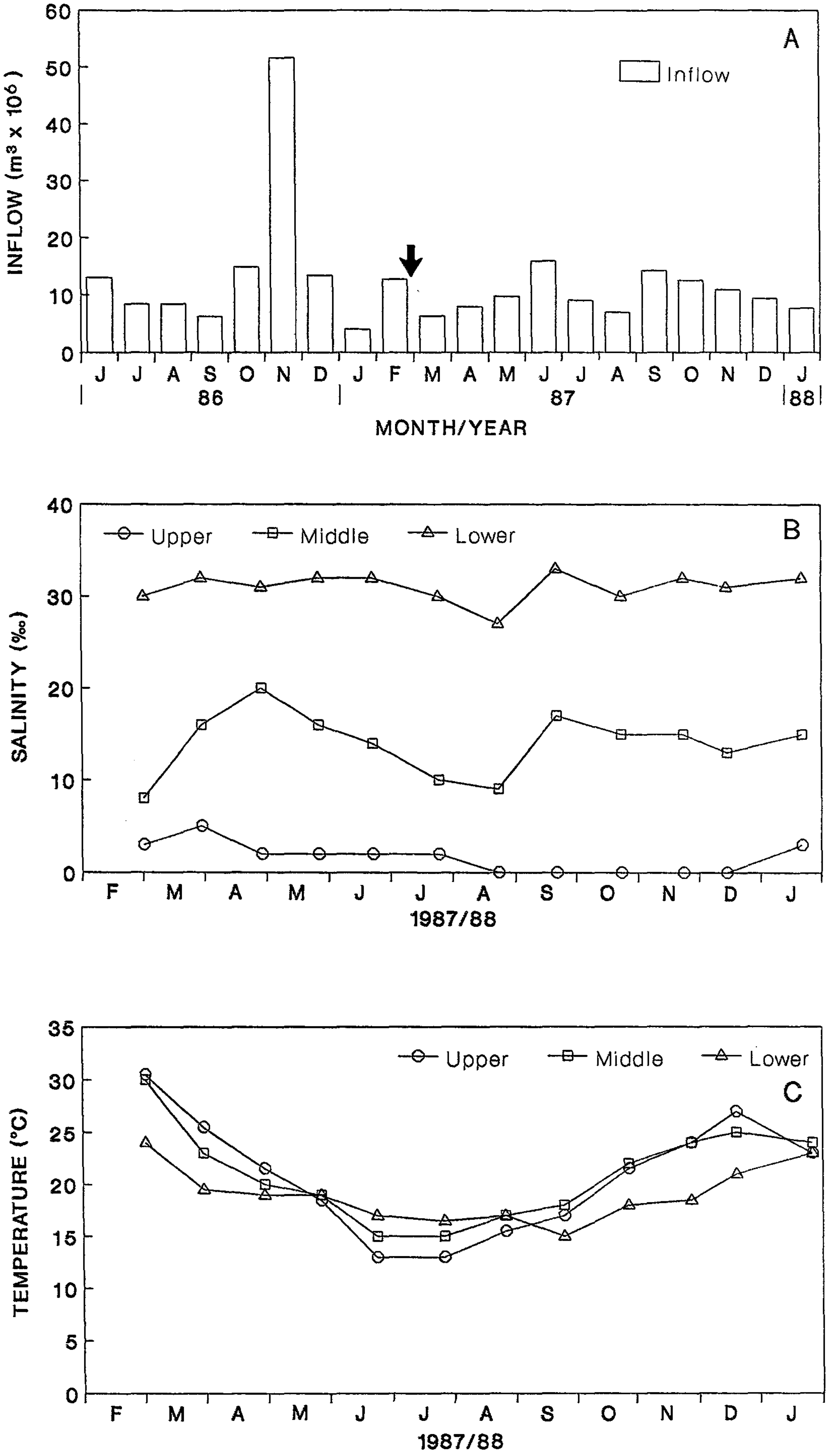


Figure 5. Time series plots of a) River inflow, b) Salinity, c) Temperature, d) TPM, e) TPOM, f) Chlorophyll *a*, g) Protein, and h) Carbohydrate, measured over a seasonal cycle in the Great Fish estuary during 1987/88. Note: in (a), start of the sampling programme indicated by arrow; in (b) to (e), measurements taken at three sampling Stations.

Figure 5. Results of five (a to e) size-selection feeding experiments with *P. hessei* and *Acartia* spp. In each experiment, the top panel illustrates particle-size distribution (TPV) at experiment end in the i) the control bottle, and ii) replicate_1 bottle (of six) for *P. hessei*. The middle panel illustrates particle size distribution (TPV) at experiment end in i) the control bottle, and ii) replicate_1 bottle (of six) for *Acartia* spp. Ambient water temperature and the date of the experiment are shown. The mean selectivity coefficients of (W') of six replicates with 95 % confidence limits for both *P. hessei* and *Acartia* spp. are shown in the bottom panel.

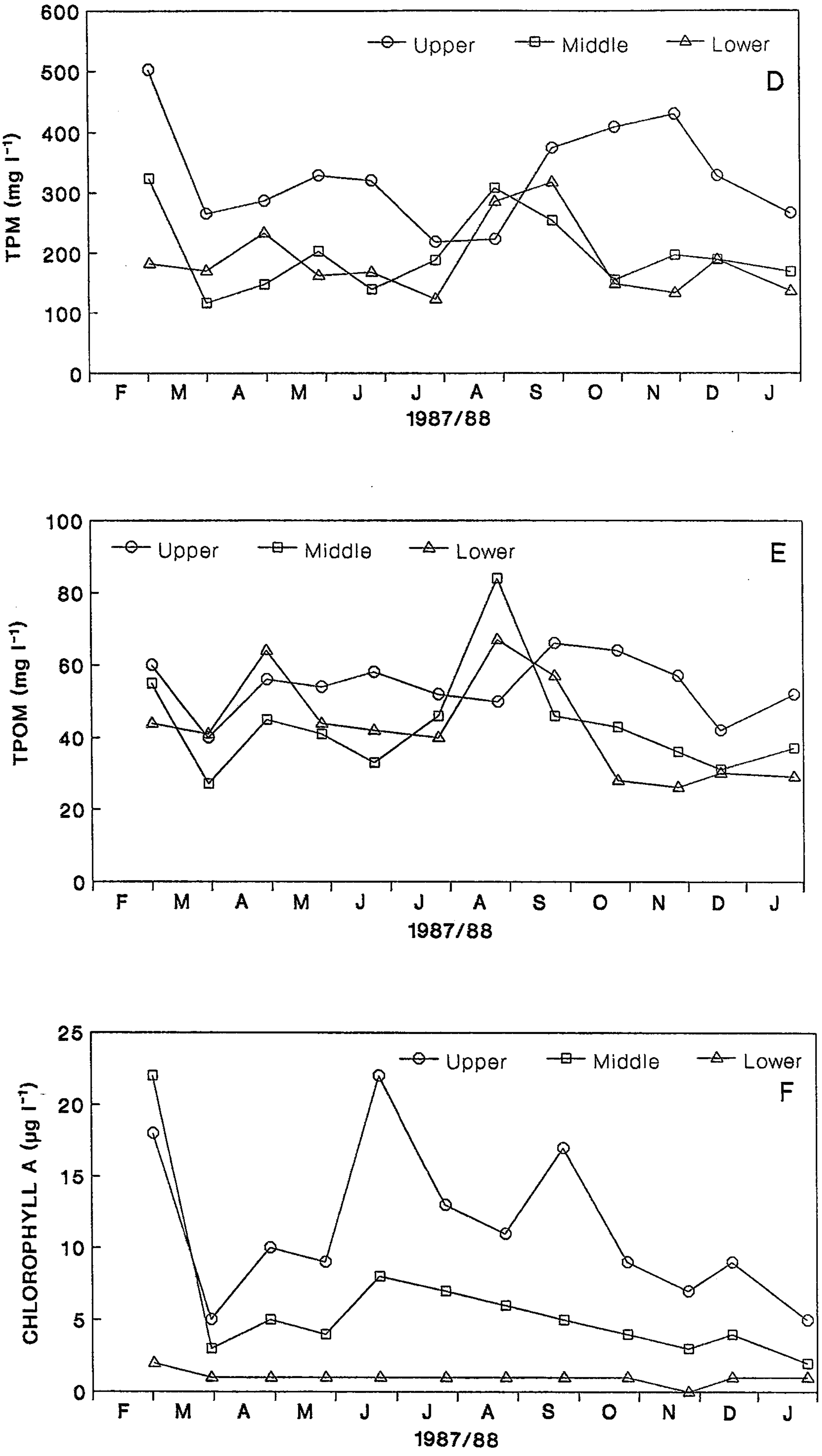


Figure 5 (continued).

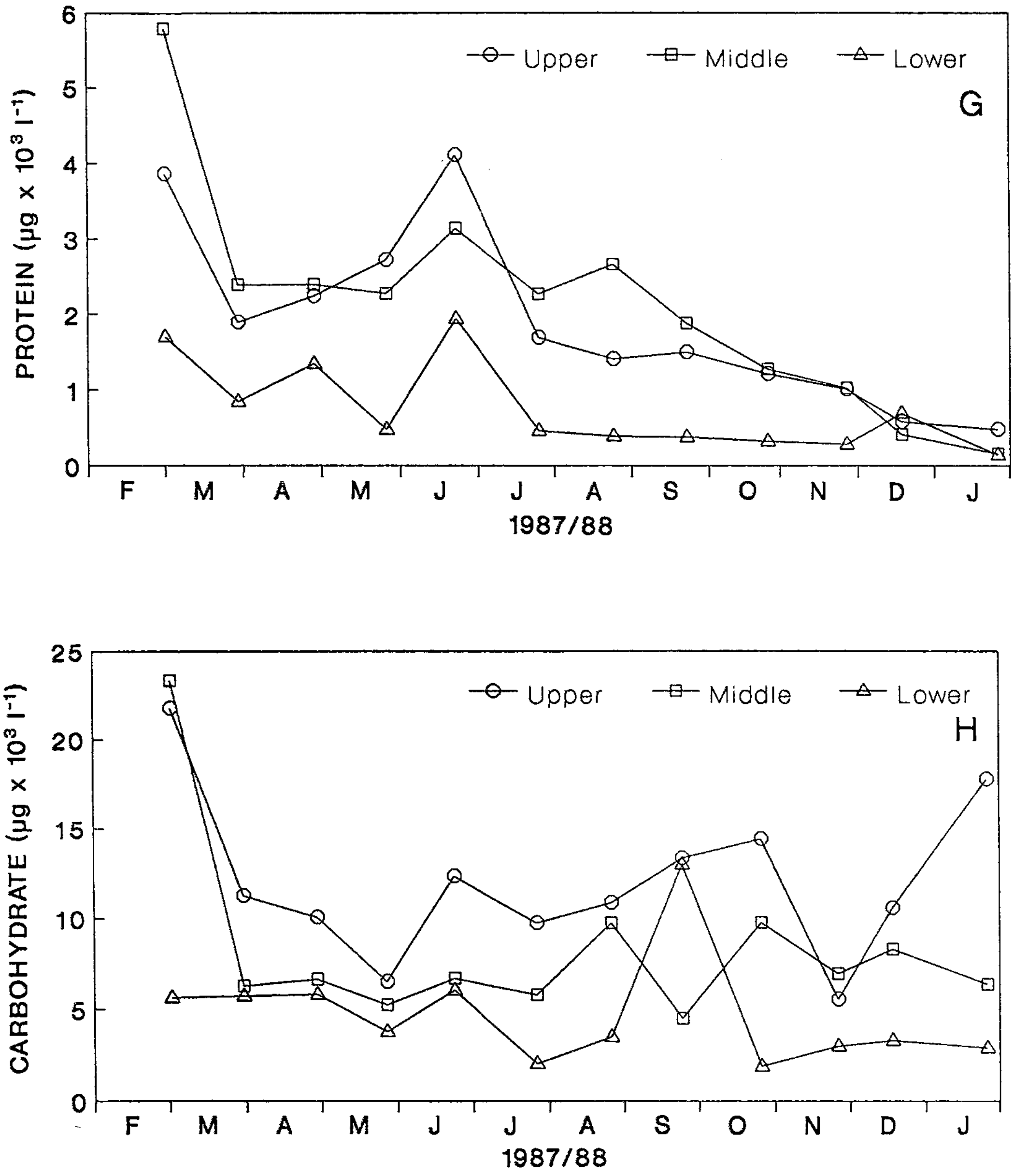


Figure 5 (continued).

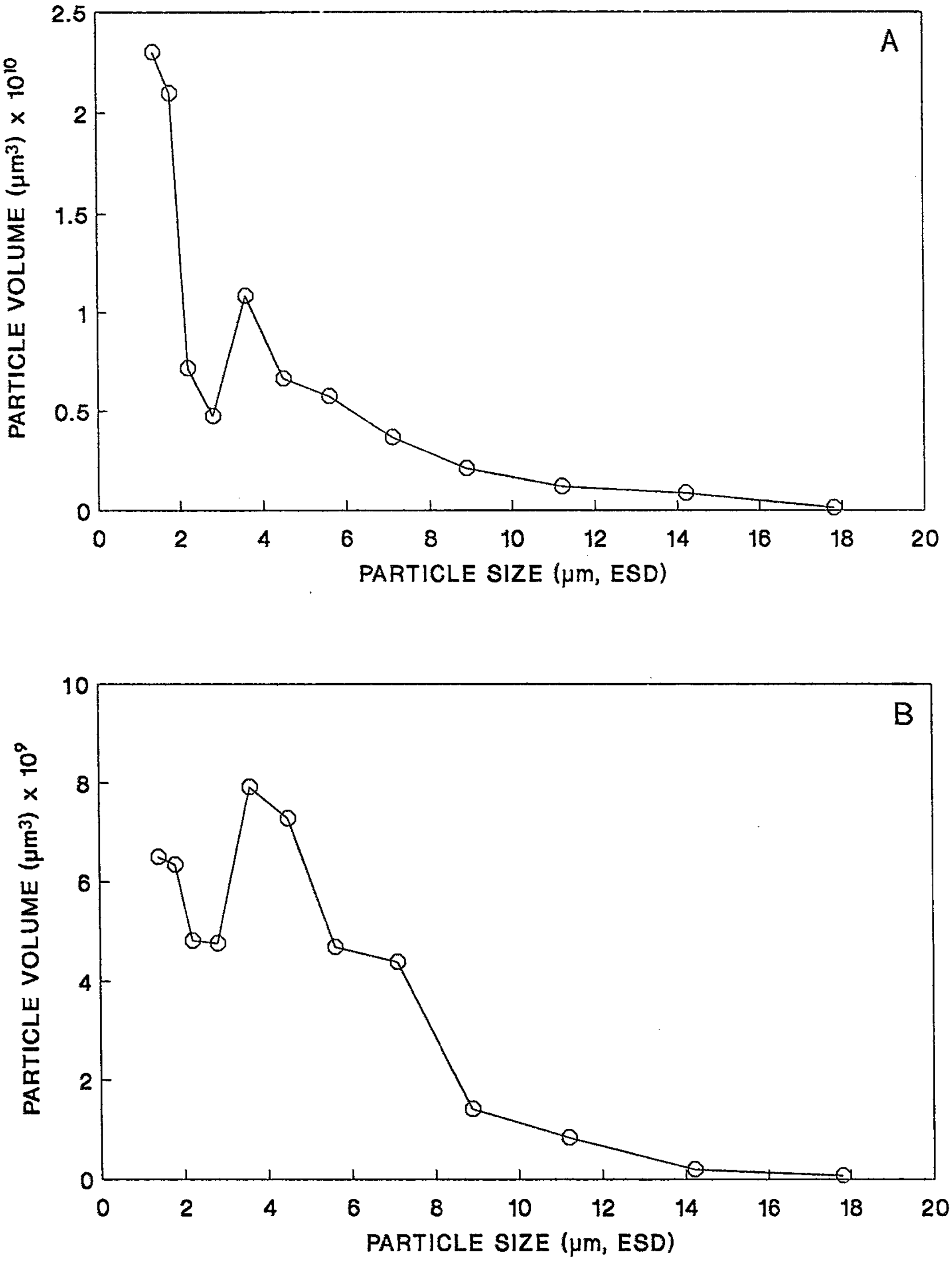


Figure 6. Examples of the two typically occurring particle size spectrums obtained from the Great Fish estuary (see text for details), measured using a Coulter Counter. Examples: a) Station F (28/5/87), b) Station O (30/4/87).

Table 2. Selected Spearman Rank Correlation Coefficients for Stations 1 to 3 in the Great Fish estuary (n.s. = not significant, * = possibly significant, ** = significant).

		GREAT FISH	
CORRELATION WITH RIVER FLOW	STATION 1	STATION 2	STATION 3
TPM	0.70 **	0.07 n.s.	-0.31 *
TPOM	0.63 **	-0.07 n.s.	-0.40 *
Chlorophyll *a*	0.36 *	0.30 *	0.06 n.s.
Protein	0.17 n.s.	0.01 n.s.	0.14 n.s.
Carbohydrate	0.10 n.s.	0.46 *	-0.19 n.s.
CORRELATION WITH CHLOROPHYLL *a*			
TPM	0.11 n.s.	0.30 *	0.35 *
TPOM	0.51 *	0.60 **	0.44 *
Protein	0.61 **	0.75 **	0.53 *
Carbohydrate	0.20 n.s.	0.22 n.s.	0.24 n.s.

Diel patterns.

The variation in seston concentration over two diel cycles in the Kariega estuary (a and b), and one diel cycle in the Great Fish estuary (c) is shown in Figure 7. In all cases, considerable variation in the seston variables was recorded. Although the alternating re-suspension and sedimentation of suspended material into, and out of, the watercolumn is likely to be a major factor responsible for the variation observed, it is not possible to separate this effect from the variability caused by the movement of different water masses, with different seston loads, past a fixed sampling point. This influence was probably of greater significance in the Great Fish estuary where a greater upstream-downstream variation in the seston was evident. Although seston variability was presumably linked to the pattern of tidal currents, there is no obvious correlation with the state of the tide apparent in this study.

Fractionation.

The results of seston size fractionation experiments are shown in Table 3 (Kariega and Great Fish). The particle size distributions of the water samples prior to fractionation are

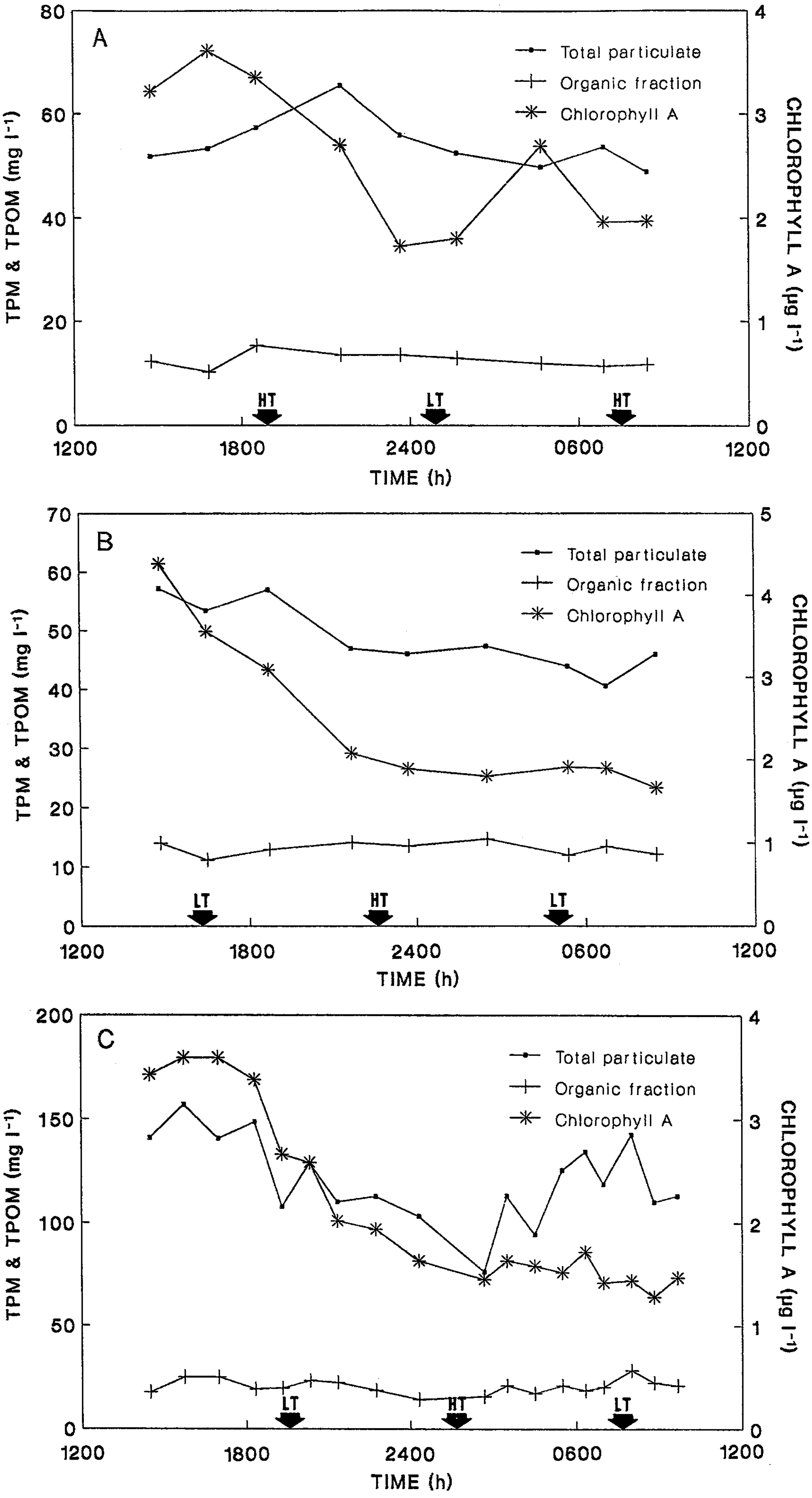


Figure 7. Variation in seston concentration over nearly an entire diel cycle at Station P in the Kariega estuary (a and b), and at Station H in the Great Fish estuary in (c). State of the tide indicated along the X-axis.

shown in Figure 8. Particle size distributions were characteristic of those measured routinely in the estuaries (see Section above, "Seasonal patterns"). In all cases, the vast majority (≈ 75 % by mass) of suspended material (TPM, TPOM and chlorophyll *a*) occurred in the < 20 μm particle diameter size classes. The largest contribution to the suspended particulate material was the fraction which passed through a 5 μm mesh.

Table 3. Fractionation of water samples from the Kariega and Great Fish estuaries.

a) Size fractionation of seston sampled from Station L, Kariega estuary (12/1/90).

SIZE FRACTION (μm)	TPM	TPOM	CHLOROPHYLL *a*
	CUMULATIVE % RECOVERED		
80 <	13.1	9.9	4.3
35 - 80	14.3	11.1	4.5
20 - 35	15.2	13.1	6.8
10 - 20	15.9	17.8	7.4
5 - 10	18.6	19.8	21.0
0.2 - 5	100.0	100.0	99.9
TOTAL	0.111 mg l^{-1}	0.025 mg l^{-1}	1.23 μg l^{-1}

b) Size fractionation of seston sampled from Station P, Kariega estuary (18/1/90).

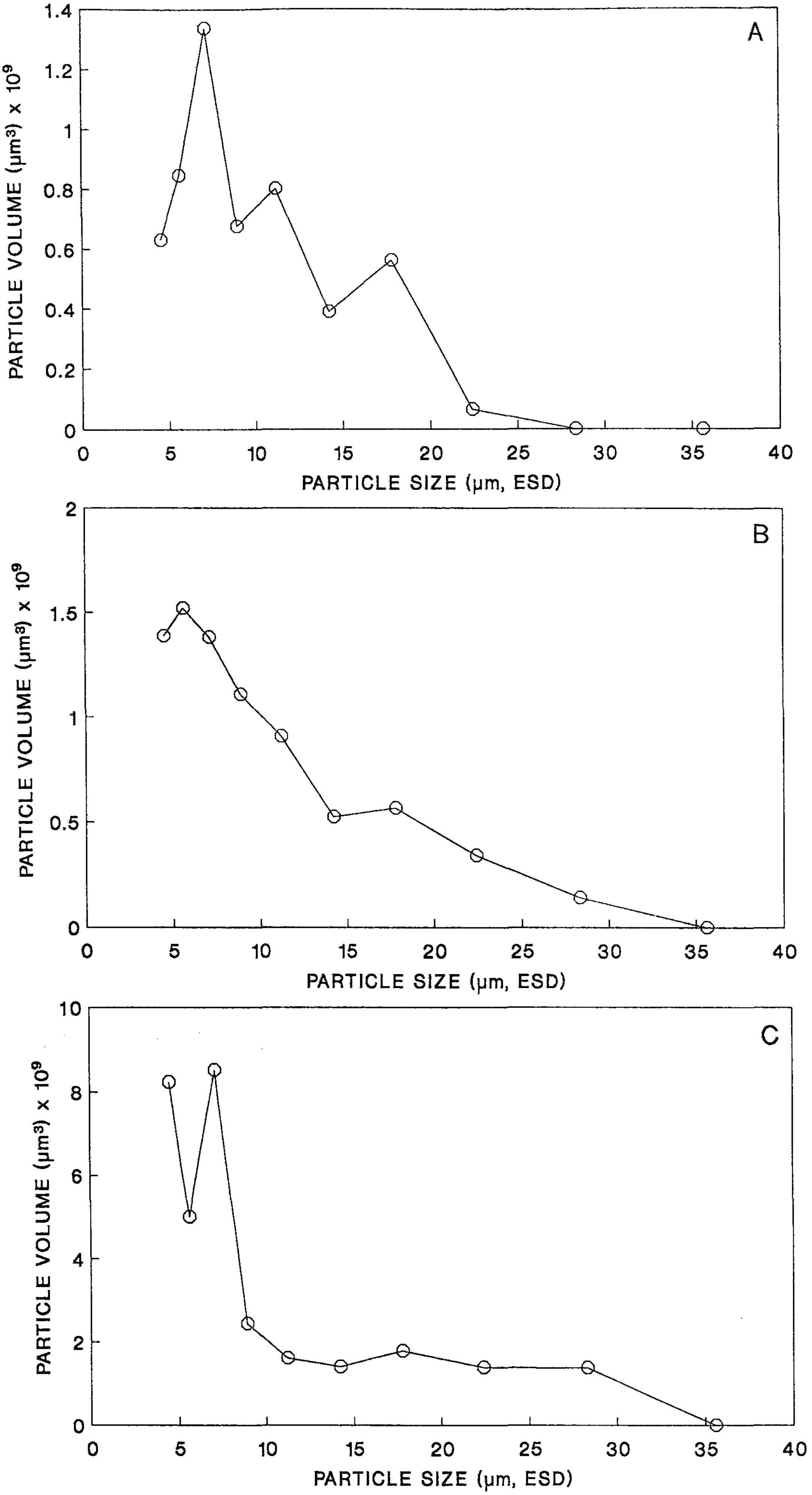
SIZE FRACTION (μm)	TPM	TPOM	CHLOROPHYLL *a*
	CUMULATIVE % RECOVERED		
80 <	2.4	1.8	1.7
35 - 80	3.4	2.5	4.0
20 - 35	5.9	8.6	22.9
10 - 20	7.0	9.0	31.4
5 - 10	7.3	9.7	51.5
0.2 - 5	100.1	100.1	99.9
TOTAL	0.143 mg l^{-1}	0.028 mg l^{-1}	1.72 μg l^{-1}

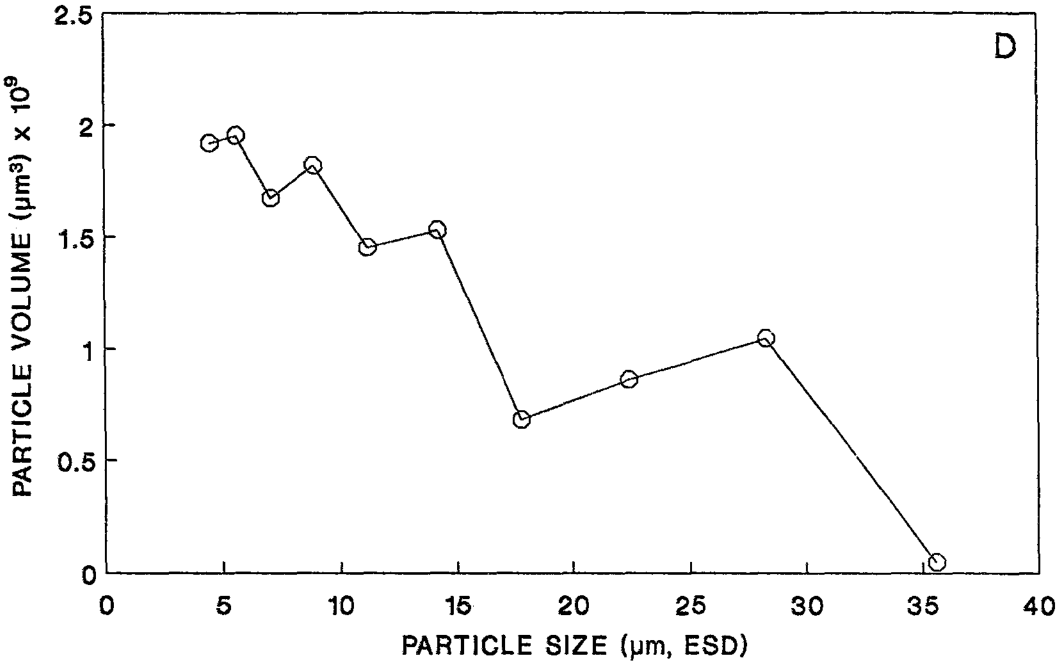
c) Size fractionation of seston sampled from Station P, Kariega estuary (26/1/90).

SIZE FRACTION (μm)	TPM	TPOM	CHLOROPHYLL *a*
		CUMULATIVE % RECOVERED	
80 <	8.8	8.9	7.4
35 - 80	12.8	13.0	8.5
20 - 35	15.3	15.6	22.9
10 - 20	16.9	17.1	44.8
5 - 10	18.5	18.6	54.1
0.2 - 5	100.0	100.0	100.1
TOTAL	0.161 mg l^{-1}	0.027 mg l^{-1}	0.31 μg l^{-1}

d) Size fractionation of seston sampled from Station H, Great Fish estuary (31/1/90).

SIZE FRACTION (μm)	TPM	TPOM	CHLOROPHYLL *a*
		CUMULATIVE % RECOVERED	
80 <	9.0	9.9	7.5
35 - 80	13.1	14.4	14.6
20 - 35	15.0	16.9	14.9
10 - 20	17.5	19.4	26.7
5 - 10	19.0	21.0	39.1
0.2 - 5	99.9	100.0	100.1
TOTAL	0.150 mg l^{-1}	0.024 mg l^{-1}	1.30 μg l^{-1}


A
PARTICLE VOLUME (µm³) x 10⁹
0
0.2
0.4
0.6
0.8
1
1.2
1.4
PARTICLE SIZE (µm, ESD)
0
5
10
15
20
25
30
35
40
B
PARTICLE VOLUME (µm³) x 10⁹
0
0.5
1
1.5
2
PARTICLE SIZE (µm, ESD)
0
5
10
15
20
25
30
35
40
C
PARTICLE VOLUME (µm³) x 10⁹
0
2
4
6
8
10
PARTICLE SIZE (µm, ESD)
0
5
10
15
20
25
30
35
40



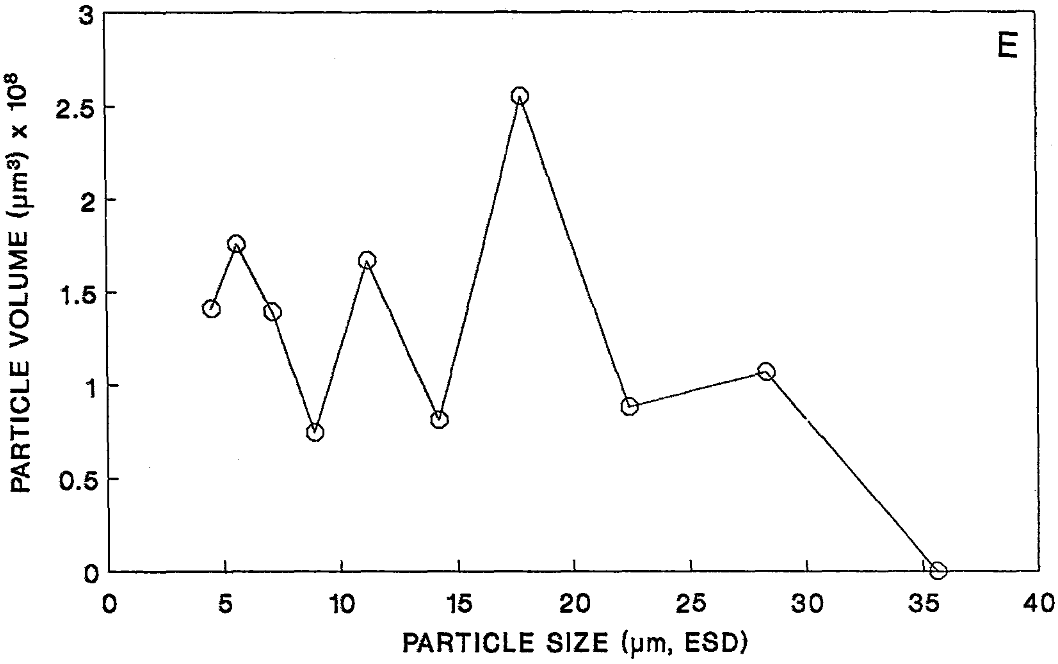


Figure 8 (continued).

e) Size fractionation of seston sampled from Station H, Great Fish estuary (4/2/90).

SIZE FRACTION (μm)	TPM	TPOM	CHLOROPHYLL *a*
		CUMULATIVE % RECOVERED	
80 <	1.5	10.9	0.4
35 - 80	3.9	13.7	2.4
20 - 35	5.3	14.9	3.0
10 - 20	7.4	14.9	3.3
5 - 10	10.1	18.9	3.8
0.2 - 5	100.0	99.9	100.1
TOTAL	0.112 mg l^{-1}	0.025 mg l^{-1}	4.82 μg l^{-1}

4.3 DISCUSSION

A comparison of the seasonal and spatial variability in the nature of the seston of the Kariega and Great Fish estuaries emphasizes the importance of freshwater inflow in determining food resources for suspension-feeders. A reduction in freshwater inflow results in a general increase in salinity and a decrease in turbidity and the stratification event (Allanson & Read, 1987; Hilmer & Bate, 1990; this Chapter). Phytoplankton standing stocks in the Kariega estuary, indicated by chlorophyll *a*, were extremely low and the estuary may be described as predominantly oligotrophic. Although the low turbidity favoured high phytoplankton production, Allanson & Read (1987) have demonstrated that nutrients are limiting, and under conditions of low flow, the estuary may rely almost entirely on nutrient input from the adjacent ocean. The importance of freshwater inflow is illustrated in the time series plot of chlorophyll *a*. Negligible freshwater inflow occurred throughout 1987 and was characteristic of normal flow. The summer phytoplankton bloom (1987/88) was short-lived and of low magnitude, presumably as a result of severe nutrient limitation under the low inflow conditions (Allanson & Read, 1987). By contrast, during the previous summer (1986/87), the phytoplankton peak was of greater magnitude and was maintained well into the autumn. This was probably in response to a higher nutrient status in the watercolumn which would have resulted from the small pulse of freshwater inflow that occurred in early spring. Although the freshwater pulse occurred before the onset of the spring phytoplankton bloom, the nutrient status of the watercolumn is thought to have remained elevated due to the extremely low flushing rate of the system. Since freshwater inflow is normally negligible ($< 5 \times 10^4$ m^3 $month^{-1}$), summer phytoplankton blooms of low magnitude and short duration are likely to be common in the Kariega estuary.

The situation in the Great Fish estuary contrasted markedly with the Kariega estuary. Phytoplankton standing stocks were considerably higher and the system may be classified as mesotrophic/eutrophic. Elevated phytoplankton standing stocks were generally restricted to the middle and upper reaches of the estuary. During periods of sustained inflow, nutrients have been demonstrated to be considerably higher (between 3 and 12 times greater) than in the Kariega estuary and negatively correlated with salinity (Allanson & Read, 1987), indicating the importance of freshwater in determining the nutrient status of the estuary. Phytoplankton standing stocks increased rapidly following freshwater pulses, a response previously described by Allanson & Read (1987). Using data from Middleton *et al.* (1981), O'Keeffe (1990) has shown that over a period of 19 years, highest monthly rainfall in a year occurred in every month except April, November and December. Thus, phytoplankton blooms may occur fairly randomly throughout the year in response to rainfall events, consequently clear seasonal patterns are unlikely. Poor light penetration, particularly towards the upper reaches of estuaries, and due to high inorganic turbidity associated with freshwater inflow, is considered to be a major factor limiting phytoplankton production in some northern Hemisphere estuaries (Heinle & Flemer, 1975; Joint & Pomroy, 1981; Pennock, 1985). Due to the shallow nature of eastern Cape estuaries, turbulence results in cyclical re-suspension of sedimented phytoplankton into the euphotic layer which is thought to enable the phytoplankton to remain viable and productive despite high turbidity (Lucas, 1986).

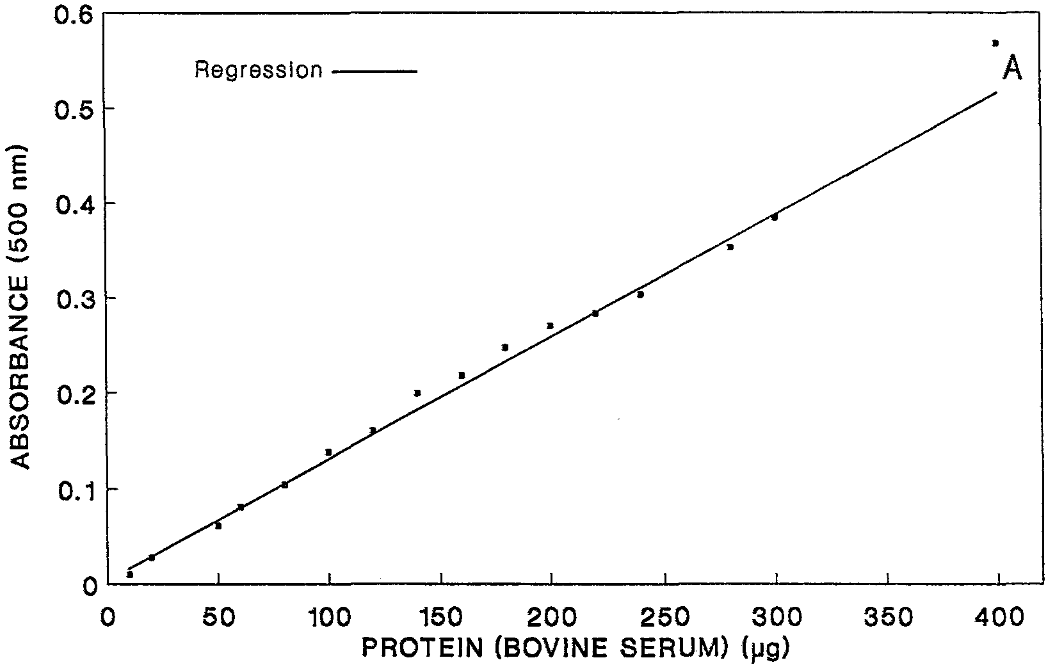
Although the high chlorophyll *a* concentrations observed in the upper and middle reaches of some eastern Cape estuaries may be derived both from autochthonous production and riverine input (Lucas, 1986; Hilmer & Bate, 1990), Lucas (1986) has suggested that the majority of chlorophyll *a* in the Great Fish estuary is as a result of the accumulation of phytoplankton of riverine origin by hydrodynamic trapping, the same process by which sediments are retained in the estuary (Moon & Dunstan, 1990). By contrast, autochthonous processes are likely to dominate in the Kariega estuary.

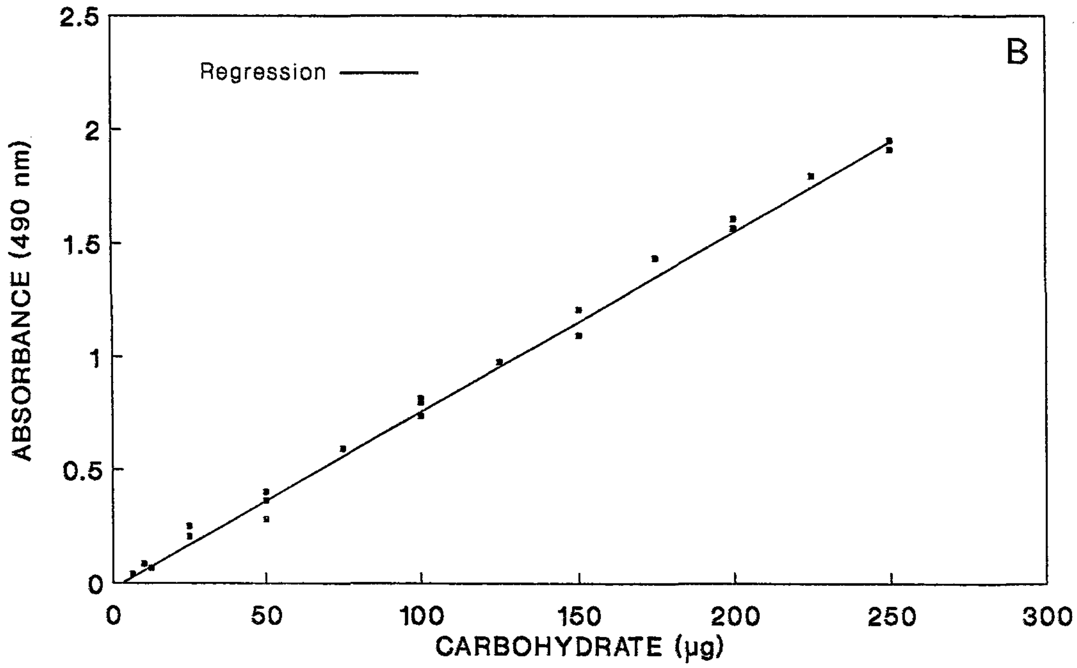
The considerable variation in seston concentration measured over a tidal cycle indicates the importance of tidal re-suspension in these estuaries. Estuaries of the eastern Cape are flood-tide dominated as a result of shallow constricted mouths (Reddering, 1988b). Tidal currents during the flood tide generate turbulent mixing which cause re-suspension of benthic material which, due to the shallow nature of the estuaries, may extend to the water surface (H. MacKay, pers. comm.). In the Great Fish estuary, turbulent mixing causes the breakdown of stratification and the seston has been demonstrated to be evenly distributed throughout the watercolumn (Lucas, 1986). The subsequent re-establishment of salinity stratification indicates that the resuspended material could be removed rapidly from the upper layers during the ebb phase. Changes in the pattern of re-suspension occur in the spring-neap cycle. Less vertical mixing on the flood tide and more intense stratification on the ebb tide occurs during neap tides (Haas, 1977; Largier, 1986; MacKay & Schumann, 1990). The slightly greater depth of the Kariega estuary probably results in reduced current speeds and generally less bed-generated turbulence. In the absence of allochthonous inputs, however, re-suspension may represent a more important source of organic material to the watercolumn.

Long term reductions in river flow result in a decrease in phytoplankton biomass and a switch to a system dominated by submerged macrophytes (Hilmer & Bate, 1990). Measurements in the Kariega estuary demonstrated that macroalgae production may account for approximately 25 % of total primary production whereas, in the Great Fish estuary, nearly the entire primary production is of phytoplankton origin (Allanson & Read, 1987). Since macrophytes are generally not consumed directly, much of the macrophyte production enters the food chain as detritus (Mann, 1988). In the Kariega estuary, chlorophyll *a* was not significantly correlated with TPM, carbohydrate or protein which suggests a greater contribution of resuspended benthic detrital material to the seston pool. This is in general agreement with the results of Allanson & Read (1987) which demonstrated that only about 35 % of the variation in total organic carbon (TOC) was accounted for by changes in chlorophyll *a*, indicating that other sources of carbon were important. In the Great Fish estuary, results suggested that phytoplankton was the primary source of organic material since chlorophyll *a* was significantly correlated with TPM, protein and carbohydrate. The results of Allanson & Read (1987) similarly emphasized the importance of phytoplankton carbon sources in the seston.

Allanson & Read (1987) recorded bacterial densities from three eastern Cape estuaries which included the Kariega and the Great Fish. Bacterial counts were similar in all three, although the highest population (0.98×10^6 ml^{-1}) was recorded in the Kariega estuary. Compared with northern Hemisphere estuaries, these densities are low, and it is unlikely that bacteria constitute an important food source for suspension-feeders (de Villiers & Allanson, 1988).

Detrital material of potentially inferior quality may comprise a substantial proportion of the available food resources for suspension feeders in marine-dominated systems such as the Kariega, however, in estuaries subject to sustained freshwater inflow, such as the Great Fish, despite the majority of the organic material being of high quality phytoplankton, riverine influx of fine silt may mask potential food resources. Despite the differences in the source and nature of seston in the Kariega and Great Fish estuaries, similarities exist in the size distribution of particles. The distribution of seston into mainly the nanoplanktonic size class may have important consequences in the feeding of groups such as the zooplankton since the ability of zooplankton to feed selectively depends on the mode of feeding employed which is determined by the size of the food particles (e.g. Price *et al.*, 1983; Vanderploeg & Paffenhöfer, 1985; Price & Paffenhöfer, 1986b). This is further compounded by the fact that inorganic and organic particles exhibit a remarkably similar size distribution which may preclude selective feeding based on size-selection.





Appendix A. Standard curves used in the photometric assay of a) Protein, and b) Carbohydrate.

Appendix B. Spearman-Rho correlation coefficients for four matrices ((a) - (d), see text for details) using seston data collected in the Kariega and Great Fish estuaries over a seasonal cycle during 1987/88.

a) for each estuary, the medians of each variable from the three sampling Stations were grouped to test for correlation between variables within each estuary.

i) Kariega estuary

	SALIN	TEMP	TPM	TPOM	RATIO	PROT	CARB	CHL A	FLOW
SALIN	1.00								
TEMP	0.02	1.00							
TPM	0.42	0.63	1.00						
TPOM	0.27	0.08	0.30	1.00					
RATIO	-0.10	-0.45	-0.54	0.59	1.00				
PROTEIN	0.08	0.48	0.24	0.37	0.20	1.00			
CARBO	0.04	0.73	0.45	0.27	-0.07	0.74	1.00		
CHL A	0.19	0.22	0.31	0.31	-0.05	0.24	0.15	1.00	
RIVER FLOW	-0.12	0.04	-0.12	0.39	0.36	0.03	0.02	0.28	1.00

ii) Great Fish estuary

	SALIN	TEMP	TPM	TPOM	RATIO	PROT	CARB	CHL A	FLOW
SALINITY	1.00								
TEMP	-0.13	1.00							
TPM	-0.66	0.14	1.00						
TPOM	-0.45	-0.21	0.78	1.00					
RATIO	0.46	-0.43	-0.64	-0.07	1.00				
PROTEIN	-0.40	-0.08	0.28	0.35	0.01	1.00			
CARBO	-0.65	0.19	0.62	0.50	-0.37	0.42	1.00		
CHLORO	-0.90	0.04	0.64	0.51	-0.38	0.66	0.73	1.00	
RIVERFLOW	-0.08	0.05	0.06	-0.07	-0.23	0.12	0.04	0.14	1.00

Appendix B (cont.).

b) for each sampling Station (i.e. Kariega Stations 1,2 & 3; Great Fish Stations 1,2 & 3) correlation between variables was tested (12 data points for each variable).

i) Kariega estuary

Station 1

	SALIN	TEMP	TPM	TPOM	RATIO	PROT	CARB	CHL A	FLOW
SALINITY	1.00								
TEMP	-0.03	1.00							
TPM	0.33	0.79	1.00						
TPOM	0.12	0.18	0.17	1.00					
RATIO	-0.36	-0.42	-0.69	0.52	1.00				
PROTEIN	-0.19	0.37	0.22	0.40	0.31	1.00			
CARBO	-0.26	0.87	0.52	0.40	0.02	0.59	1.00		
CHLORO	-0.47	0.39	0.04	0.09	0.13	0.04	0.48	1.00	
RIVERFLOW	-0.35	0.03	-0.18	0.08	0.34	0.11	0.11	0.48	1.00

Station 2

	SALIN	TEMP	TPM	TPOM	RATIO	PROT	CARB	CHL A	FLOW
SALINITY	1.00								
TEMP	-0.04	1.00							
TPM	-0.08	0.85	1.00						
TPOM	0.08	0.13	0.15	1.00					
RATIO	0.20	-0.42	-0.46	0.78	1.00				
PROTEIN	0.27	0.51	0.31	0.54	0.30	1.00			
CARBO	0.30	0.66	0.47	0.44	0.08	0.93	1.00		
CHLORO	-0.43	0.48	0.48	0.42	0.05	0.39	0.34	1.00	
RIVERFLOW	-0.19	0.03	0.09	0.55	0.38	0.00	0.07	0.15	1.00

Station 3

	SALIN	TEMP	TPM	TPOM	RATIO	PROT	CARB	CHL A	FLOW
SALINITY	1.00								
TEMP	0.20	1.00							
TPM	0.46	0.47	1.00						
TPOM	-0.01	-0.06	0.12	1.00					
RATIO	-0.36	-0.59	-0.45	0.71	1.00				
PROTEIN	0.44	0.39	0.34	0.15	-0.08	1.00			
CARBO	0.35	0.66	0.67	0.11	-0.36	0.67	1.00		
CHLORO	0.57	-0.15	0.02	-0.07	-0.14	0.14	-0.19	1.00	
RIVERFLOW	-0.03	0.06	0.03	0.58	0.32	-0.15	-0.02	0.39	1.00

Appendix B (cont.).

ii) Great Fish estuary

Station 1

	SALIN	TEMP	TPM	TPOM	RATIO	PROT	CARB	CHL A	FLOW
SALINITY	1.00								
TEMP	0.24	1.00							
TPM	-0.28	0.48	1.00						
TPOM	-0.27	-0.16	0.70	1.00					
RATIO	0.00	-0.81	-0.76	-0.14	1.00				
PROTEIN	0.44	-0.25	0.03	0.26	0.04	1.00			
CARBO	0.29	0.21	0.21	0.34	-0.17	0.01	1.00		
CHLORO	-0.13	-0.48	0.11	0.51	0.21	0.61	0.20	1.00	
RIVERFLOW	0.30	0.05	0.70	0.63	-0.30	0.17	0.10	0.36	1.00

Station 2

	SALIN	TEMP	TPM	TPOM	RATIO	PROT	CARB	CHL A	FLOW
SALINITY	1.00								
TEMP	-0.08	1.00							
TPM	-0.40	0.15	1.00						
TPOM	-0.29	-0.28	0.65	1.00					
RATIO	0.17	-0.56	-0.51	0.21	1.00				
PROTEIN	-0.23	-0.33	0.08	0.37	0.26	1.00			
CARBO	-0.61	0.44	0.17	0.14	0.04	0.20	1.00		
CHLORO	-0.49	-0.43	0.30	0.60	0.11	0.75	0.22	1.00	
RIVERFLOW	-0.29	0.12	0.07	-0.07	-0.29	0.01	0.46	0.30	1.00

Station 3

	SALIN	TEMP	TPM	TPOM	RATIO	PROT	CARB	CHL A	FLOW
SALINITY	1.00								
TEMP	-0.04	1.00							
TPM	-0.01	0.05	1.00						
TPOM	-0.12	-0.21	0.77	1.00					
RATIO	-0.20	-0.06	-0.24	0.37	1.00				
PROTEIN	-0.12	0.19	0.36	0.47	0.50	1.00			
CARBO	0.47	-0.11	0.69	0.69	0.15	0.61	1.00		
CHLORO	-0.37	0.36	0.35	0.44	0.24	0.53	0.24	1.00	
RIVERFLOW	-0.12	-0.04	-0.31	-0.40	-0.12	0.14	-0.19	0.06	1.00

Appendix B (cont.).

c) for each variable, correlation between Stations 1 to 3 in both the Kariega and Great Fish estuaries was tested using the 12 monthly median values at each sampling Station.

i) Kariega estuary

		Stations	
SALIN	1	2	3
1	1.00	0.79	0.65
2	0.79	1.00	0.67
3	0.65	0.67	1.00

		Stations	
TPOM	1	2	3
1	1.00	0.78	0.73
2	0.78	1.00	0.95
3	0.73	0.95	1.00

		Stations	
TEMP	1	2	3
1	1.00	0.99	0.99
2	0.99	1.00	0.98
3	0.99	0.98	1.00

		Stations	
PROTEIN	1	2	3
1	1.00	0.91	0.81
2	0.91	1.00	0.76
3	0.81	0.76	1.00

		Stations	
TPM	1	2	3
1	1.00	0.89	0.80
2	0.89	1.00	0.77
3	0.80	0.77	1.00

		Stations	
CARBO	1	2	3
1	1.00	0.83	0.62
2	0.83	1.00	0.80
3	0.62	0.80	1.00

		Stations	
CHL	1	2	3
1	1.00	0.30	-0.30
2	0.30	1.00	0.00
3	-0.30	0.00	1.00

		Stations	
RATIO	1	2	3
1	1.00	0.94	0.95
2	0.94	1.00	0.87
3	0.95	0.87	1.00

ii) Great Fish estuary

		Stations	
SALIN	1	2	3
1	1.00	0.04	0.13
2	0.04	1.00	0.66
3	0.13	0.66	1.00

		Stations	
TPOM	1	2	3
1	1.00	0.36	0.04
2	0.36	1.00	0.56
3	0.04	0.56	1.00

		Stations	
TEMP	1	2	3
1	1.00	0.98	0.85
2	0.98	1.00	0.85
3	0.85	0.85	1.00

		Stations	
PROTEIN	1	2	3
1	1.00	0.87	0.81
2	0.87	1.00	0.76
3	0.81	0.76	1.00

Appendix B (cont.).

TPM	Stations 1	 2	 3
1	1.00	0.37	0.04
2	0.37	1.00	0.28
3	0.04	0.28	1.00

CARBO	Stations 1	 2	 3
1	1.00	0.31	0.11
2	0.31	1.00	-0.30
3	0.11	-0.30	1.00

CHL	Stations 1	 2	 3
1	1.00	0.96	0.48
2	0.96	1.00	0.57
3	0.48	0.57	1.00

RATIO	Stations 1	 2	 3
1	1.00	0.69	0.48
2	0.69	1.00	0.46
3	0.48	0.46	1.00

Appendix C. Kruskal-Wallis testing for difference of medians among sampling Stations, per variable.

NSD = No significant difference in medians.

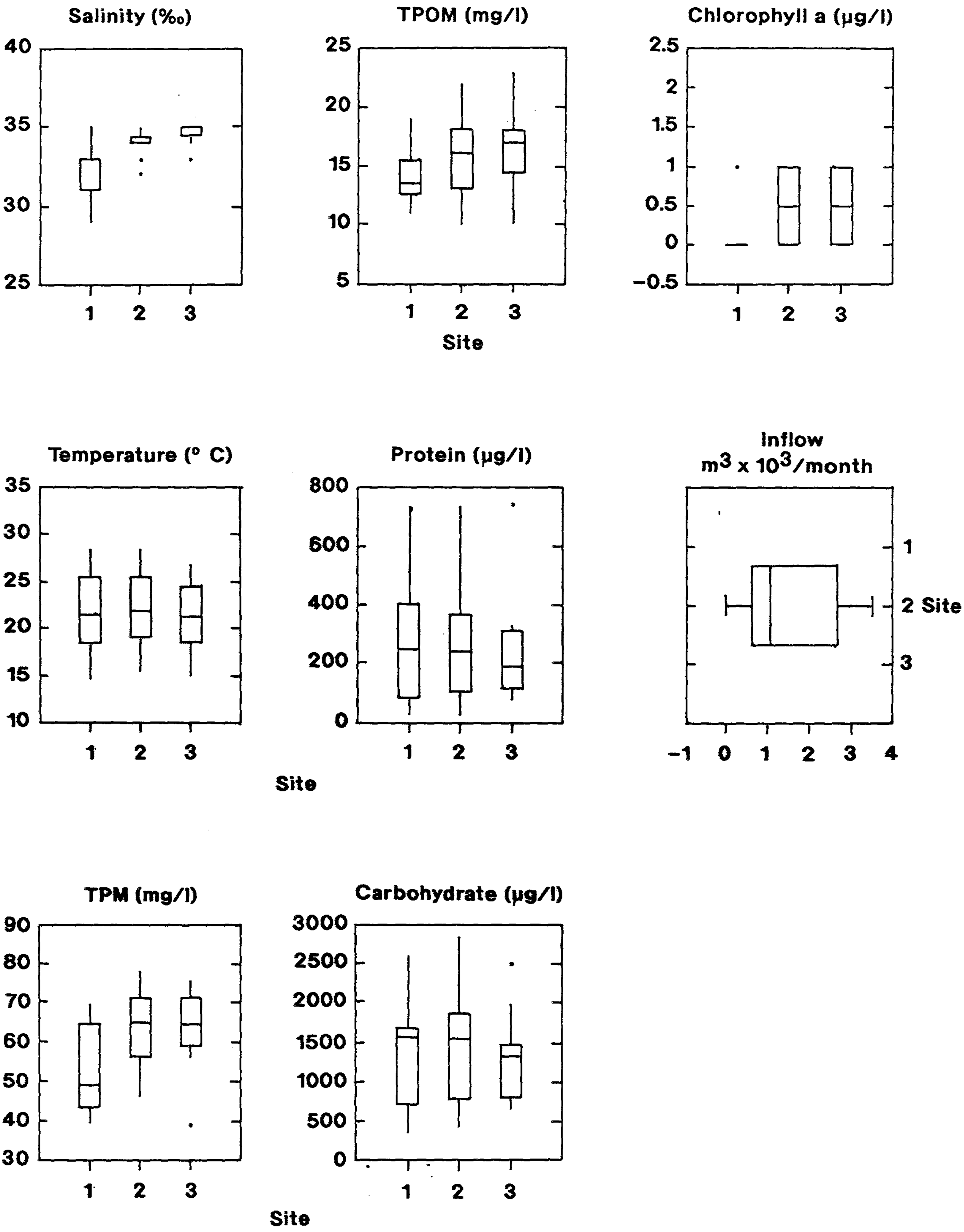
KARIEGA ESTUARY

Variable	Level of confidence	Station medians different
Salinity	95 %	K1 ≠ K2 K2 ≠ K3 K1 ≠ K3
Temperature	NSD	
TPM	95 %	K1 ≠ K2 K1 ≠ K3
TPOM	NSD	
Protein	NSD	
Carbohydrate	NSD	
Chlorophyll a	90 %	K1 ≠ K2 K1 ≠ K3

GREAT FISH ESTUARY

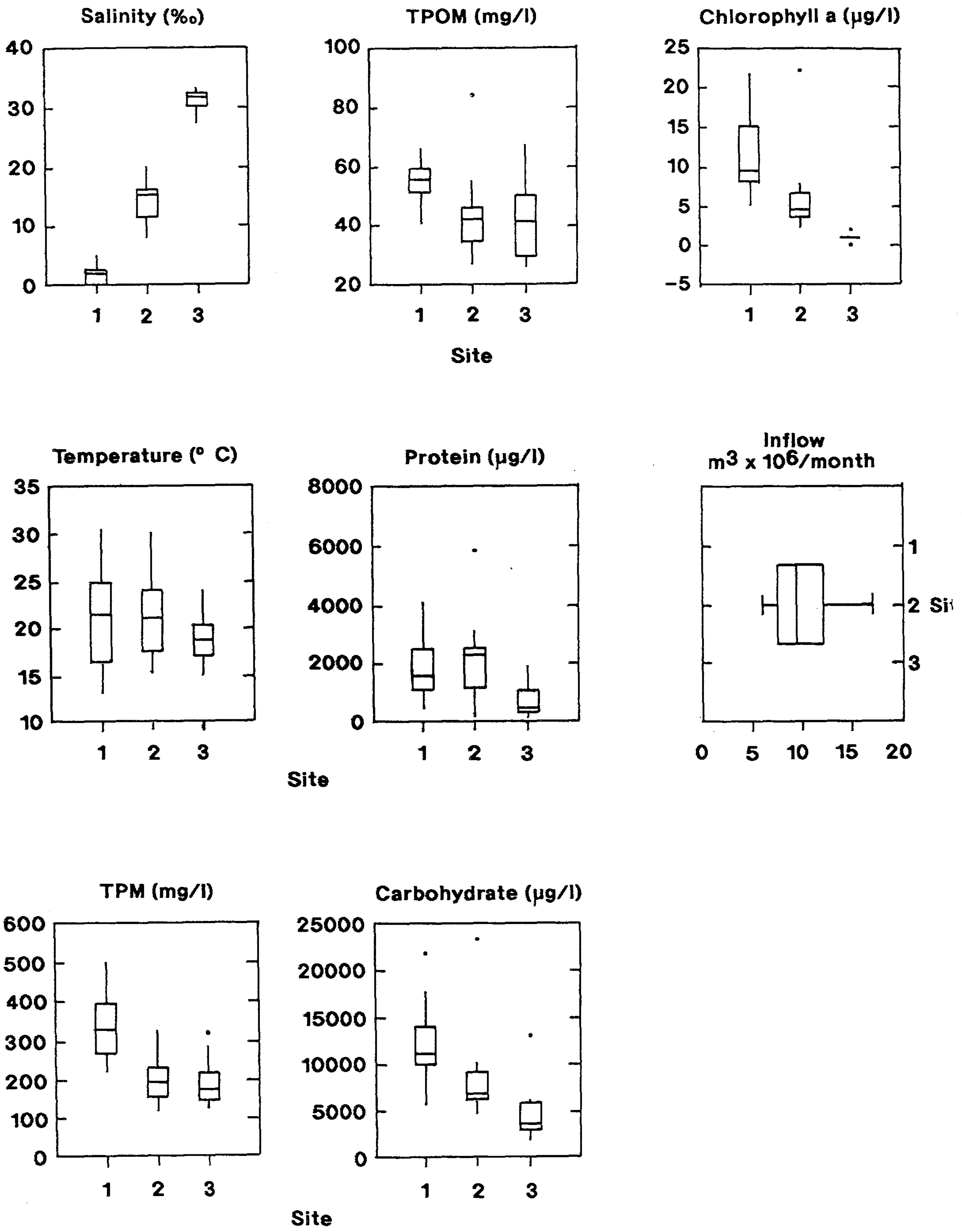
Variable	Level of confidence	Station medians different
Salinity	95 %	F1 ≠ F2 F2 ≠ F3 F1 ≠ F3
Temperature	NSD	
TPM	95 %	F1 ≠ F2 F1 ≠ F3
TPOM	95 %	F1 ≠ F2 F1 ≠ F3
Protein	95 %	F1 ≠ F3 F2 ≠ F3
Carbohydrate	95 %	F1 ≠ F2 F2 ≠ F3 F1 ≠ F3
Chlorophyll a	95 %	F1 ≠ F2 F1 ≠ F3 F2 ≠ F3

a) Kariega estuary.



Appendix D. Box-and-whisker plots of environmental and seston variables measured over a seasonal cycle in a) the Kariega estuary, and b) the Great Fish estuary.

b) Great Fish estuary.



Appendix D (continued).

CHAPTER FIVE

FACTORS INFLUENCING TEMPORAL AND SPATIAL PATTERNS OF ZOOPLANKTON COMMUNITY BIOMASS, COMPOSITION AND FEEDING ACTIVITY

5.0 INTRODUCTION

The feeding activity of zooplankton communities plays an important role in the trophic transfer of energy, nutrient recycling and productivity in the pelagial of many aquatic ecosystems (e.g. reviews by Rigler, 1971; Haney, 1973; Conover, 1978; Raymont 1980; Frost, 1980; Peters, 1984).

The results of many laboratory studies have demonstrated that the functional feeding of zooplankton may vary in response to several factors which include the size and dimensions of food particles (Muck & Lampert, 1980), their concentration (e.g. Frost, 1972; Nicolajsen *et al.*, 1983), chemical composition (e.g. Richman & Dodson, 1983), past feeding history (e.g. Runge, 1980; Huntley, 1988) and environmental factors, notably temperature (Deason, 1980; Kiφrboe *et al.*, 1982; Dagg & Wyman, 1983). In addition, diel feeding activity rhythms have been described which may be associated with diel vertical migration (e.g. Gauld, 1953; Boyd *et al.*, 1980; Baars & Oosterhuis, 1984; Huntley *et al.*, 1987).

Due to the extreme variability of the natural environment there are problems associated with extrapolating laboratory results to field conditions and these have been discussed in some detail (e.g. Boyd *et al.*, 1980; Dagg & Grill, 1980; Frost, 1980; Kiφrboe *et al.*, 1982; Dagg, 1983; Dagg & Wyman, 1983). In recent years, greater emphasis has been placed on *in situ* studies (e.g. Wang & Conover, 1986; Stearns *et al.*, 1987). Several techniques (e.g. Haney, 1971) have been used which derive estimates of zooplankton community filtration rates (CFR's) from *in situ* incubations of short time interval duration. Filtration, or grazing rates are usually expressed as the proportion of the watercolumn filtered by the resident zooplankton community per unit time.

The majority of *in situ* studies of zooplankton feeding have been conducted in freshwater lakes. The high community filtration rates (CFR's) that are often demonstrated, occasionally in excess of 100 % d^{-1}, are attributed to the high densities of grazers occurring in these systems (e.g. Haney, 1973; Haney & Hall, 1975; Gulati *et al.*, 1982; Hart, 1984; 1986; Jarvis, 1987; Mourelatos *et al.*, 1989). By contrast, the frequency of grazers encountered in coastal and oceanic environments is generally insufficient for significant grazing pressure to be detected (Napp & Long, 1989).

At the present time there are no quantitative studies of the feeding activity of zooplankton in South African estuaries. The seasonally high abundance of zooplankton in some systems (e.g. Grindley, 1981; Wooldridge & Bailey, 1982; Allanson & Read, 1987), however, indicates that the impact of zooplankton grazing may be considerable, and comparable to situations described in some freshwater lakes. The zooplankton grazers in eastern Cape estuaries typically exhibit low species diversity, and are comprised predominantly of calanoid copepods of the genera *Acartia* and *Pseudodiaptomus*, although mysids of the genus *Mesopodopsis* and *Rhopalophthalmus* may also be important (e.g. Wooldridge & Bailey, 1982). Distinct temporal and spatial patterns of distribution and abundance in response to salinity and temperature are described by Wooldridge and Melville-Smith (1979). In addition, marked differences in species composition and biomass between estuaries subject to differing freshwater inflow have been shown (Wooldridge & Melville-Smith, 1979; Wooldridge & Bailey, 1982) and are thought to be linked to the resulting trophic conditions of an estuary (Allanson & Read, 1987).

Freshwater inflow into an estuary is an important factor in determining the quality and quantity of food resources available to the zooplankton community and is described in detail in Chapter 4. In general, estuaries subject to elevated freshwater inflow are generally of a higher trophic status although the high suspended silt loads, characteristic of rivers in the region, may have adverse effects for zooplankton filter-feeders (e.g.

Arruda *et al.*, 1983; McCabe & O'Brien, 1983; Hart, 1986). The availability of food resources is further complicated by the role of tidal currents in the re-suspension of bottom sediments and, in addition, complex patterns of distribution and circulation arise from the mixing of freshwater with seawater.

In this Chapter, the temporal and spatial patterns of zooplankton community structure, biomass and feeding activity from two estuaries of contrasting trophic status are described. Further, attempts are made to determine the influence and relative importance of food quality and quantity as well as environmental factors (ie temperature) on zooplankton filtration rates.

5.1 METHODS

Zooplankton community composition and biomass, and community grazing activity were sampled in the Great Fish and Kariega estuaries during regular monthly sampling trips in 1987 and the early part of 1988. For the purposes of examining the spatial variability, sampling was carried out at three Stations along each estuary, corresponding to the upper, middle and lower reaches (see Chapter 2). In addition, sampling was carried out during daylight, and again after dark, in order to assess diel variation which might arise through diel vertical migration movements, and/or feeding activity rhythms. All sampling was carried out from a boat in the midstream.

5.1.1 ZOOPLANKTON COMMUNITY COMPOSITION AND BIOMASS.

Sampling procedure.

Zooplankton community samples were collected with a Kahl Scientific Instrument Corporation No. 012WA300 12.5 cm diameter Clarke-Bumpus plankton sampler equipped with a flowmeter and fitted with an 80 μm nytex mesh net, and net cod-end. Three replicate samples were collected at each Station by towing the sampler for 30 seconds at a depth of $\approx$ 1.0 metre below the surface. The volume filtered (m^3) was calculated from flowmeter units using a conversion constant derived from routine calibration tests made over a measured distance in a swimming pool.

Samples were rinsed into bottles and preserved in a 4 % formalin solution. Calanoid species and life-history stages (naupliar/copepodite) and mysids were identified, measured and enumerated under a low power binocular microscope (Wild) from subsamples taken according to the method of Allanson & Kerrich (1961). Normally, a minimum of 100 individual nauplii, copepodites and mysids of each species were counted. Conversions to biomass were made using pre-determined length-biomass relationships.

Length-biomass relationships.

Length-biomass relationships of the dominant zooplankton forms were derived according to the method of Hart & Allanson (1975). Length measurements were made using an ocular micrometer calibrated against a slide graticule. The length of the cephalothorax was measured on all calanoid copepodite stages, the total length to the base of the spine (if present) was measured on the nauplii, and carapace length (distance along the dorsal midline from the tip of the rostrum to the posterior margin of the carapace) was measured on all mysids.

Dry biomass determinations were made using a Cahn model G2 microbalance. Measurements of calanoids were made from batches of 50 individual nauplii and 30 individual copepodites in pre-sorted size classes. Measurements of between 1 and 5 mysids were made depending upon individual size. All samples were dried for 24 hours at 60 °C on pre-weighed aluminium foil discs. Samples were subsequently re-weighed and individual biomass taken as the difference, divided by the number in the sample.

5.1.2 ZOOPLANKTON GRAZING RATES.

***In situ* experimental approach.**

Community filtration rates (CFR's) were measured using the *in situ* technique of Haney (1971; 1973) which has been reviewed by several authors (e.g. Peters, 1984; Kiφrboe *et al.*, 1985; Jarvis, 1987; Napp & Long, 1989). The grazing chamber employed was modified from Haney's original design (Hart & Christmas, 1984). The procedure involves the capture of a natural zooplankton population, exposure to radio-labelled algae over a short time interval, retrieval and sieving to retain the zooplankton, followed by radio-assay of the feeding medium and zooplankton sample to determine a community filtration rate

(Jarvis, 1987). Filtration, or grazing rates, are comparable to the term "clearance rates", but are not equivalent to ingestion rates since particle size retention capabilities and/or discrimination on the basis of the food quality of particles are not accounted for using this technique (Jarvis, 1987).

The method enables measurements of zooplankton community grazing to be made under near-natural conditions and without the normal disturbance, handling, crowding or acclimation stresses associated with most laboratory studies, which have been demonstrated to markedly alter feeding responses (e.g Peters & Downing, 1984). The radio-labelling technique employed allows the food source to be introduced to the grazing compartment in tracer quantities, which avoids substantial alteration of the natural particle food resource of the zooplankton. Generally, an algal monoculture food source is employed which avoids errors in grazing rate measurements arising from the heterogeneity of label uptake by different algal species in natural phytoplankton populations (Jarvis, 1987).

Grazing chamber.

The grazing chamber (Figure 1) was constructed of two perspex cylinders (A and B) which measured 50 cm in length with an internal diameter of 12 cm. The volume of each compartment was 5.6 litres. The compartments were of transparent perspex construction to facilitate natural light conditions *in situ*. Prior to sampling, the lids (a) were fastened into the open position by retaining the wire loops (b) to a trigger pin (c), and a syringe mechanism (d) was inserted into a holder at the top of compartment A (grazing compartment)(Figure 2a). The operation of the chamber by means of a messenger weight, effected the closure of the lids causing a simultaneous introduction of the contents of the syringe into the grazing compartment. Dye tests after Hart & Christmas (1984) demonstrated that complete mixing took place within 30 seconds.

In feeding studies which involve the use of radio-labelled tracers it is essential that the exposure time to the food source is less than the gut passage time, but sufficient to detect appreciable amounts of radio-label consumed by the zooplankton. Published values of gut passage times of numerous species of calanoid copepod are reviewed by Peters (1984). Values range from 25 to 210 minutes and are known to vary in response to body size,

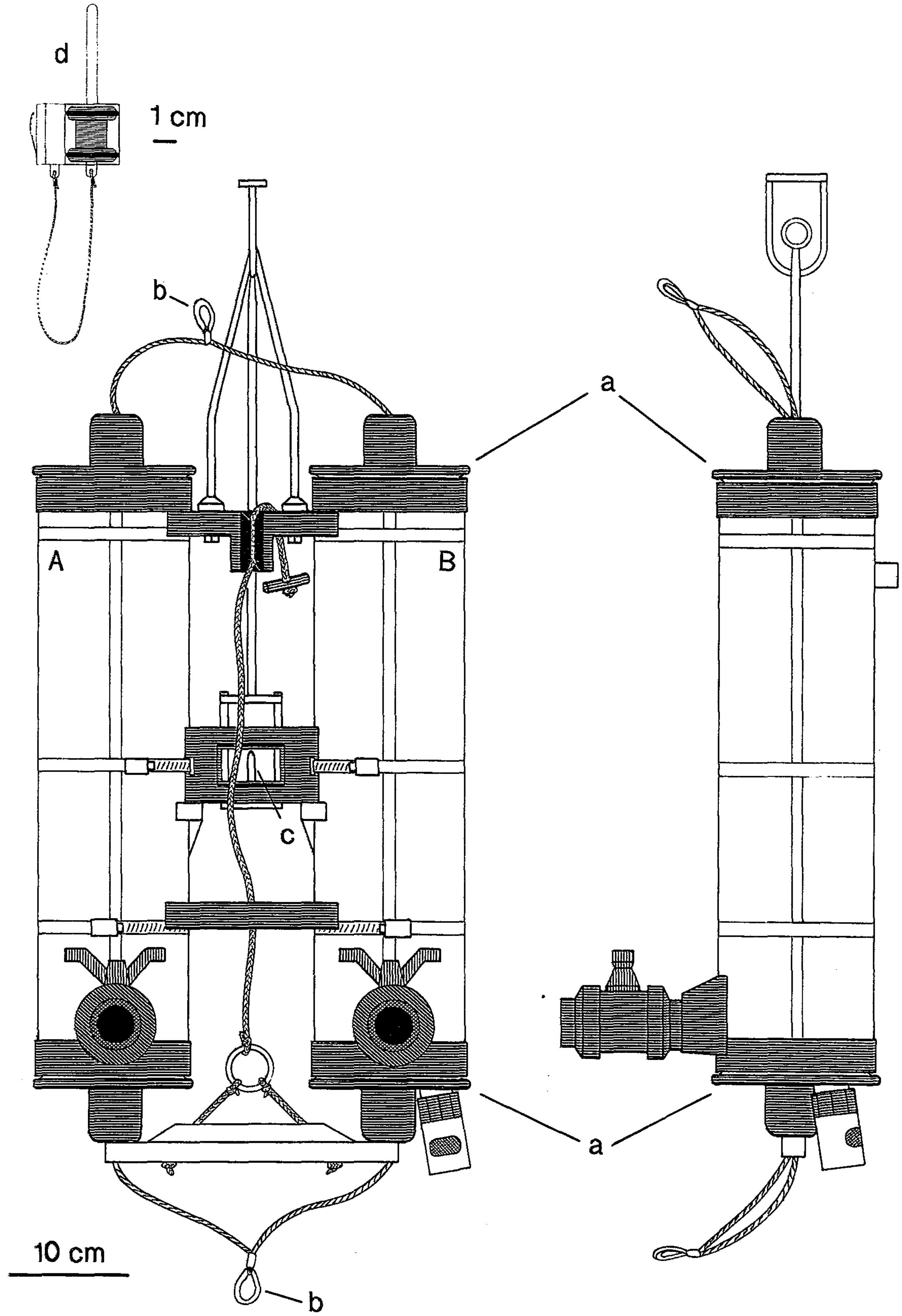


Figure 1. Modified Gliwicz-Haney *in situ* grazing chamber. See Chapter 5, Section 5.1.2 for details.

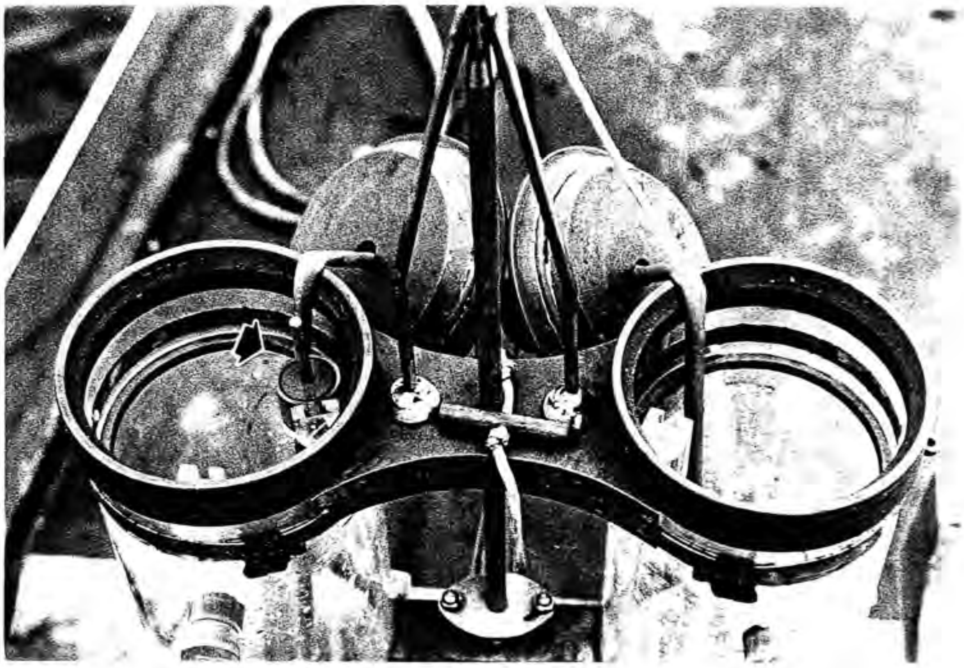


Figure 2a. Photograph of the grazing chamber in the "open" position prior to sampling, showing the syringe mechanism (arrowed) located in the grazing compartment.

Figure 2b. Sampling with the Gliwicz-Haney chamber.

temperature and food concentration (Peters, 1984; and references cited therein). On the basis of the literature values, the duration of feeding experiments in this study was restricted to a period of less than 6½ minutes.

The unicellular green alga *Tetraselmis suecica* (Prasinophyceae) was selected as the food source for the grazing experiments. The cells are ovoid and lack spines, and were readily consumed by zooplankton in laboratory tests. Coulter Counter analyses demonstrated that the modal size class of the algae was similar to those of the particle size distributions measured from natural estuarine samples (Chapter 4, Figure 4b and 6b). In addition, *Tetraselmis* is tolerant of a wide salinity range and was able to tolerate the abrupt decrease in salinity brought about by the release of algae (cultured in seawater medium) into ambient estuarine water, which varied from 0 to 35 ‰, during *in situ* grazing experiments.

Cultures of *Tetraselmis* were maintained at 14 °C under an artificial light source in a seawater-Provasoli culture medium for optimal growth. Cultures in log-growth phase were incubated with radio-isotope at a concentration of 1 μCi ml^{-1} of NaH^{14}CO$_3$ (Amersham) for a period of 16 hours. Thereafter, unincorporated radio-isotope was removed by centrifuging the suspension at low r.p.m., discarding the supernatant, and resuspending the algae in fresh nutrient medium. This process was repeated twice. A 1 ml subsample was removed from the algal "stock" suspension for *in situ* experiments and screened through a 35 μm nytex mesh to remove aggregated algal cells, mixed with 5 ml of estuarine water, and introduced into the syringe mechanism.

The chlorophyll *a* concentration of the radio-labelled food source was restricted to < 10 % of the ambient chlorophyll to avoid unnatural grazing responses due to particle enrichment (e.g. Hart, 1986; Jarvis, 1987). Due to the high natural variability of the seston (particle, and chlorophyll concentrations), no additional standardization of the tracer particles was undertaken.

After approximately 5½ minutes incubation *in situ*, the chamber was retrieved and the duration of each experiment measured from the time the chamber was triggered closed, to the time at which half the chamber volume had been drained (between 6 and 6½ minutes). The contents of both compartments were sieved through 80 μm nytex mesh into buckets. Zooplankton from the non-labelled compartment (B) retained by the mesh were preserved in a 4% formalin solution for subsequent identification, enumeration and conversion to biomass according to the method outlined in Section 5.1.1., with the exception that all individuals were counted and measured.

Zooplankton samples from the grazing compartment were immobilized immediately by immersion in carbonated water to prevent egestion of the gut contents during subsequent treatment. The sample was concentrated onto a 20 mm diameter mesh disc, rinsed thoroughly with filtered estuary water (Whatman GF/F) to remove adhering radio-labelled material and transferred to a scintillation vial containing 0.5 ml of quaternary ammonium hydroxide (Soluene 350 tissue solubilizer, Packard).

The activity of the feeding medium in the grazing compartment was determined from the mean activity (d.p.m.) of two 10 ml aliquots filtered onto 0.45 μm membrane filters, placed in scintillation vials containing 10 ml of Filter Count (Packard) fluor. The remaining radio-labelled feeding medium was stored in a sealed laboratory container.

On return to the laboratory, animal sample scintillation vials were placed in an oven at 55 °C for 12 hours to allow complete solubilization of tissues. Upon cooling to ambient temperature, 10 ml of Insta-Gel (Packard) was added and the sample radio-assayed after the decay of chemoluminescence. Sample activity was measured on a Beckman LS 3801 scintillation counter using the external standards method of quench correction using ^{14}C standards. The instrument was programmed to correct for quench and counting efficiency which permitted sample activity to be expressed as d.p.m.

Community filtration rates (CFR's) were based on the equations of Haney (1973) and calculated according to the formula:

$$\text{Community filtration rate (CFR, ml m}^{-3}\text{ h}^{-1}) = \frac{A_z\,(1 \times 10^6)}{A_m \times V \times t}$$

where, A_z = zooplankton sample activity (d.p.m.)
A_m = mean feeding medium activity (d.p.m. ml^{-1})
V = chamber volume (ml)
t = experimental incubation time (h)

Biomass-specific filtration rates (SFR's, ml mg^{-1} h^{-1})) were calculated by dividing CFR's by the zooplankton biomass determined from the contents of the unlabelled compartment.

During monthly sampling trips, measurements of the seston and environmental variables were made from 80 μm mesh-sieved water, collected concurrently during *in situ* grazing experiments. The procedures and results are reported separately in Chapter 4, and used here to describe the feeding response of the zooplankton to various environmental variables.

5.2 RESULTS

5.2.1 ZOOPLANKTON COMMUNITY COMPOSITION AND BIOMASS.

Temporal, spatial and diel patterns.

Zooplankton standing stocks (mg m^{-3} dry biomass) were calculated from length-biomass relationships of the different species and life-history stages. These relationships are given in Table 1, and the graphs presented in Appendix A.

Table 1. Length-biomass relationships derived for the dominant zooplankton components of the Great Fish and Kariega estuaries.

ZOOPLANKTON	REGRESSION	CORR. COEFF. (R^2)	N	SIGNIF.
Calanoid copepods:				
Acartia spp.				
i) Copepodites/adults:	$Log_{10}Wt(\mu g)=2.754(Log_{10}L(\mu m))-7.283$	0.89	17	$p < 0.0001$
ii) Nauplii:	$Log_{10}Wt(\mu g)=1.210(Log_{10}L(\mu m))-3.417$	0.91	13	$p < 0.0001$
Pseudodiaptomus hessei				
i) Copepodites/adults:	$Log_{10}Wt(\mu g)=2.826(Log_{10}L(\mu m))-7.545$	0.97	18	$p < 0.0001$
ii) Nauplii:	$Log_{10}Wt(\mu g)=1.346(Log_{10}L(\mu m))-3.562$	0.97	13	$p < 0.0001$
Mysids:				
Mesopodopsis slabberi	$Log_{10}Wt(\mu g)=2.819(Log_{10}L(\mu m))-9.489$	0.95	15	$p < 0.0001$

a) Kariega estuary.

The calanoid copepods *Acartia* spp. (*A. longipatella* and *A. natalensis*) and *Pseudodiaptomus hessei* comprised at least 95 % of total grazer biomass in all samples. The mean annual biomass for Stations 1 to 3 (upper, middle, and lower estuary: Chapter 2, Figure 4) are shown in Table 2 and the seasonal fluctuations in community biomass (nighttime data only) are shown in Figure 3. The mean community biomass was highest at Station 2 and lowest at Station 1, attaining 47.3 mg and 30.8 mg m^{-3}, respectively. Total biomass was greatest during the night by a factor of about three as a result of the diel vertical migration movements of some components of the community.

The temporal and spatial patterns of distribution of *Acartia* spp. and *Pseudodiaptomus hessei* during the twelve month period February 1987 to February 1988 are shown in Figures 4 to 7. Clear temporal patterns were observed in all community components. Sampling began during the summer of 1986/87 and a seasonal peak in biomass of *Pseudodiaptomus hessei* copepodites and adults was already in evidence, persisting into May, 1987. An increase in biomass during the following spring occurred in September 1987, but was short-lived and had declined by November. Seasonal biomass peaks were associated with increased temperatures of above ≈ 20 °C.

Connell & Grindley (1974) described only the adult forms of *Acartia natalensis* and *A. longipatella* (specimens collected from estuaries along the east coast of southern Africa). In view of the difficulty in distinguishing these species in the copepodite and naupliar stages, they are grouped together as *Acartia* spp. It is recognized, however, that differences in the spatial and temporal distribution of the two species may occur (e.g. Wooldridge & Melville-Smith, 1979). A seasonal peak of abundance of the copepodite and adult stages of *Acartia* spp. was already well-established when sampling commenced and persisted until sometime during May 1987. During July/August 1987, biomass had once again increased, but this increase became more prominent during September. During this period the peak in biomass was of short duration and was already in decline by November. The seasonal peak in standing stocks took place when temperatures were greater than ≈ 18 °C. The temporal patterns of abundance of the nauplii of both *Acartia* spp. and *Pseudodiaptomus* were similar to those of the copepodite and adult stages.

All species were fairly evenly distributed along the length of the estuary although peak biomass was recorded in the middle reaches of the estuary (Station 2). The copepodites and adults of *Acartia* spp. and *Pseudodiaptomus* demonstrated clear diel patterns of abundance. Copepodites and adults of *Pseudodiaptomus* were normally entirely absent from the watercolumn during daytime. Although some *Acartia* were present during daytime, these individuals represented a small fraction of nighttime densities. By contrast, the nauplii of both genera were present in the watercolumn throughout the diel cycle.

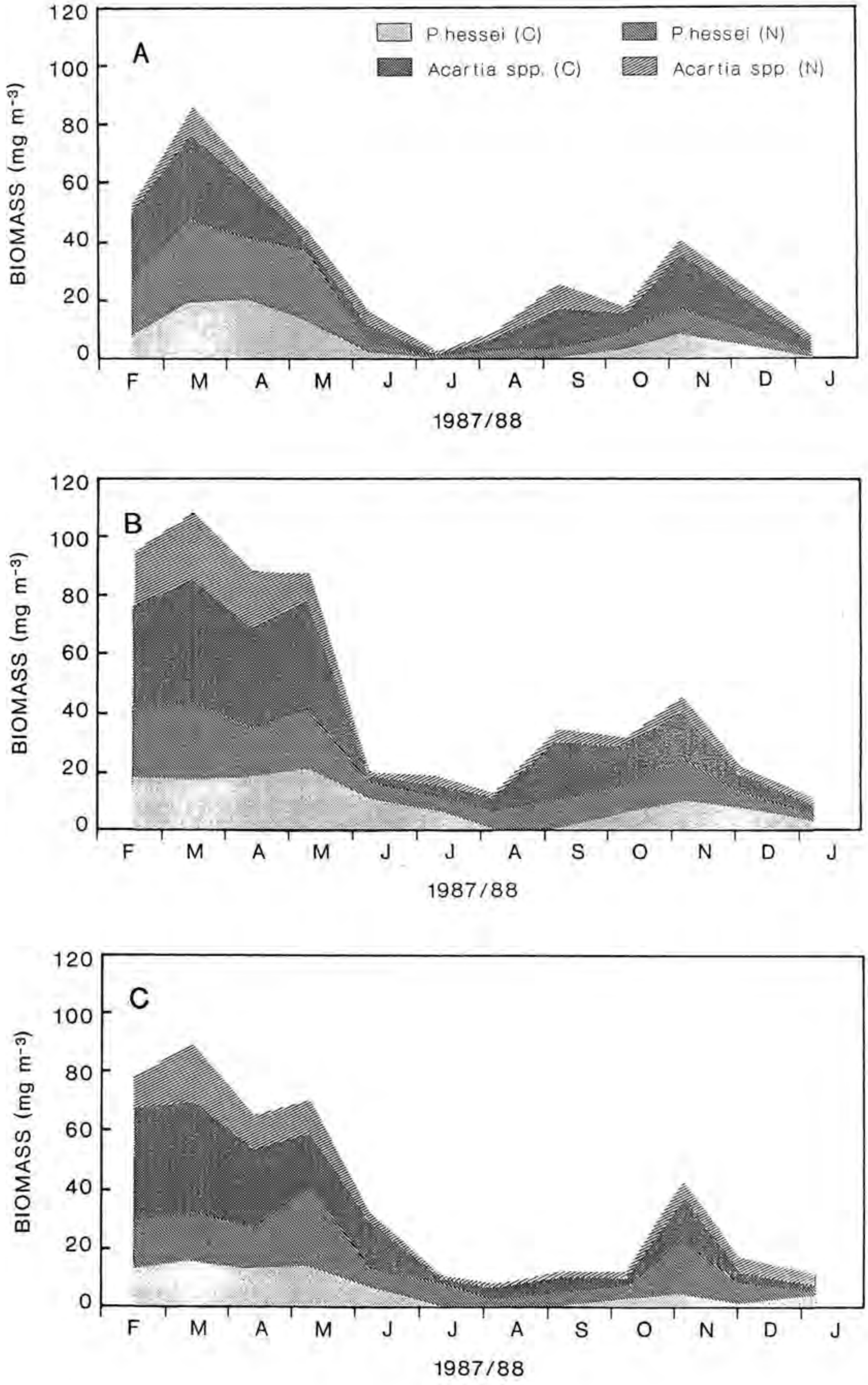


Figure 3. Zooplankton biomass in the upper- (A), middle-(B) and lower (C) reaches of the Kariega estuary, showing the contribution of the dominant species and life-history stages to total biomass. Samples taken monthly from February 1987 to January 1988.

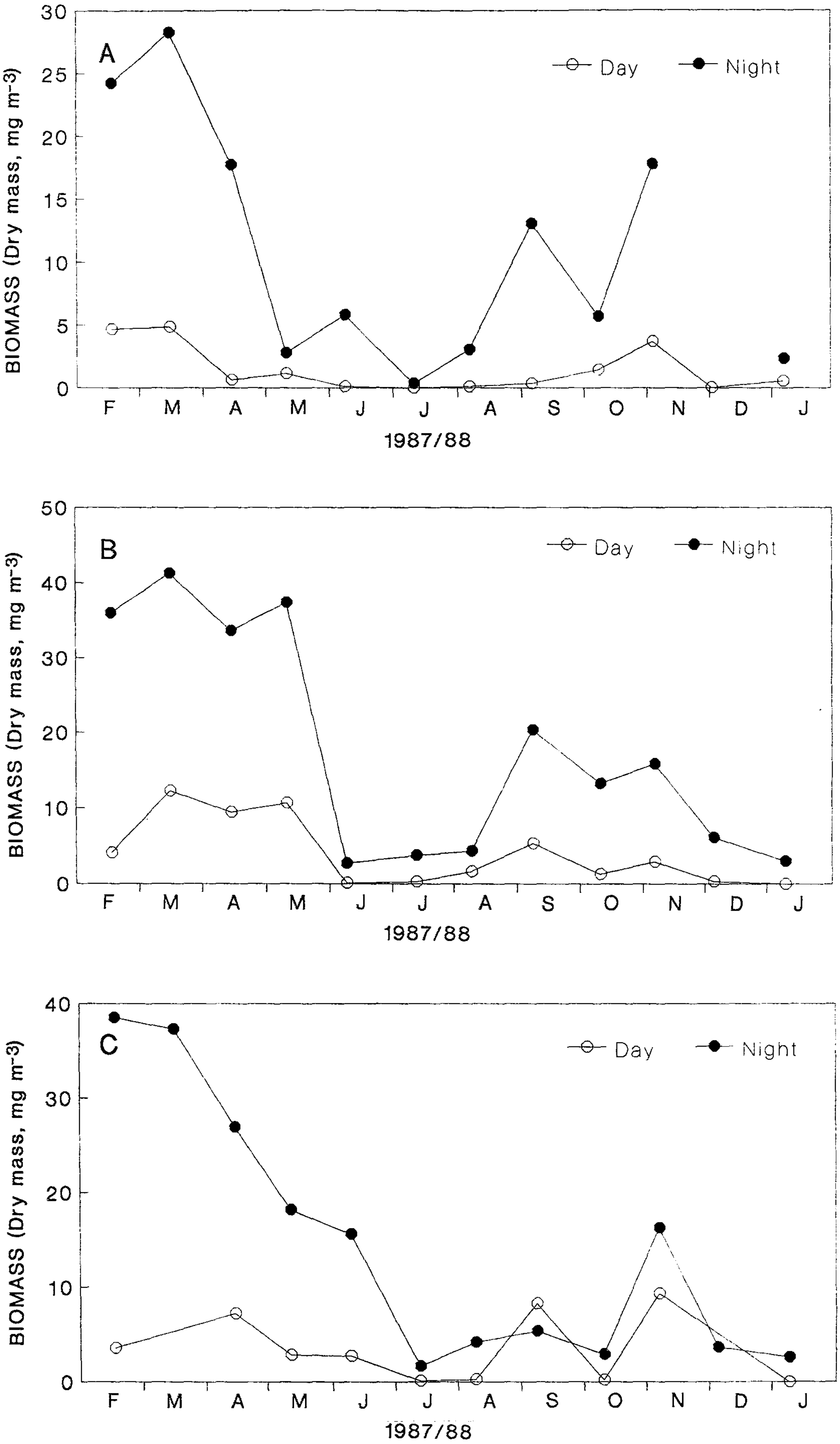


Figure 4. Seasonal biomass distribution of the copepodite and adult stages of *Acartia* spp. in the upper- (A), middle- (B) and lower (C) reaches of the Kariega estuary. Samples taken monthly from February 1987 to January 1988.

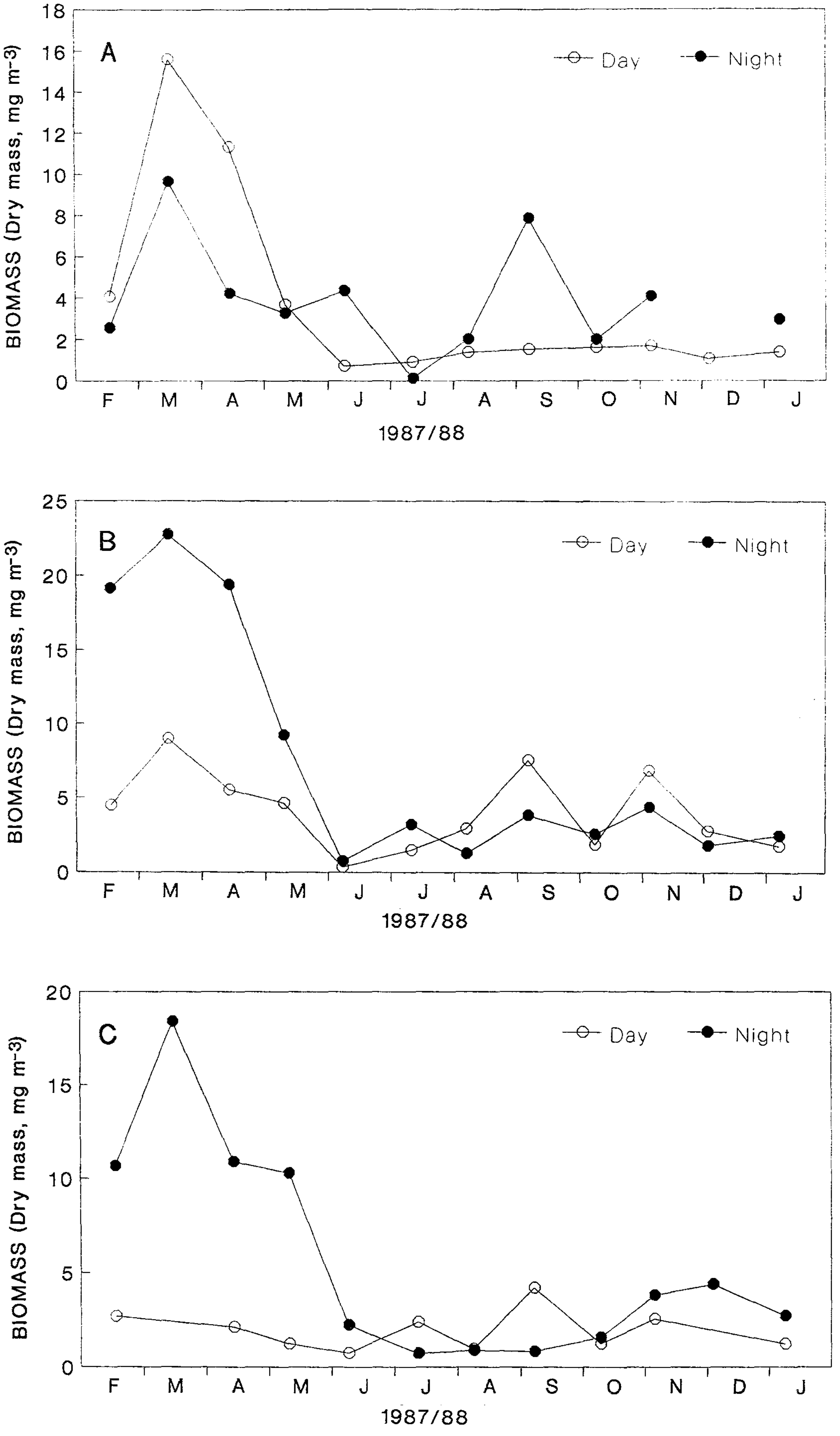


Figure 5. Seasonal biomass distribution of the naupliar stages of *Acartia* spp. in the upper- (A), middle- (B) and lower (C) reaches of the Kariega estuary. Samples taken monthly from 1987 to January 1988.

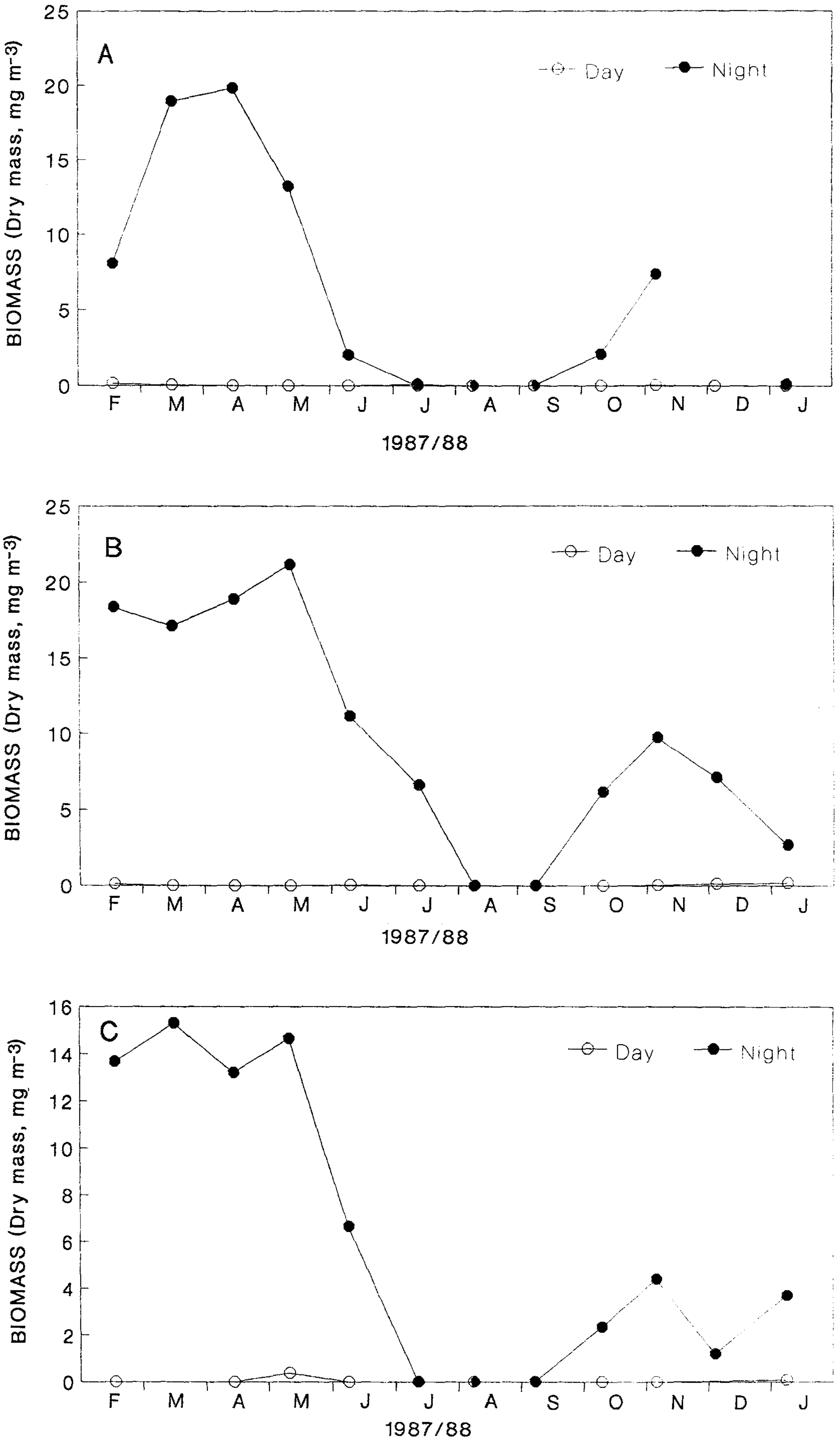


Figure 6. Seasonal biomass distribution of the copepodite and adult stages of *Pseudodiaptomus hessei* in the upper- (A), middle- (B) and lower (C) reaches of the Kariega estuary. Samples taken monthly from February 1987 to January 1988.

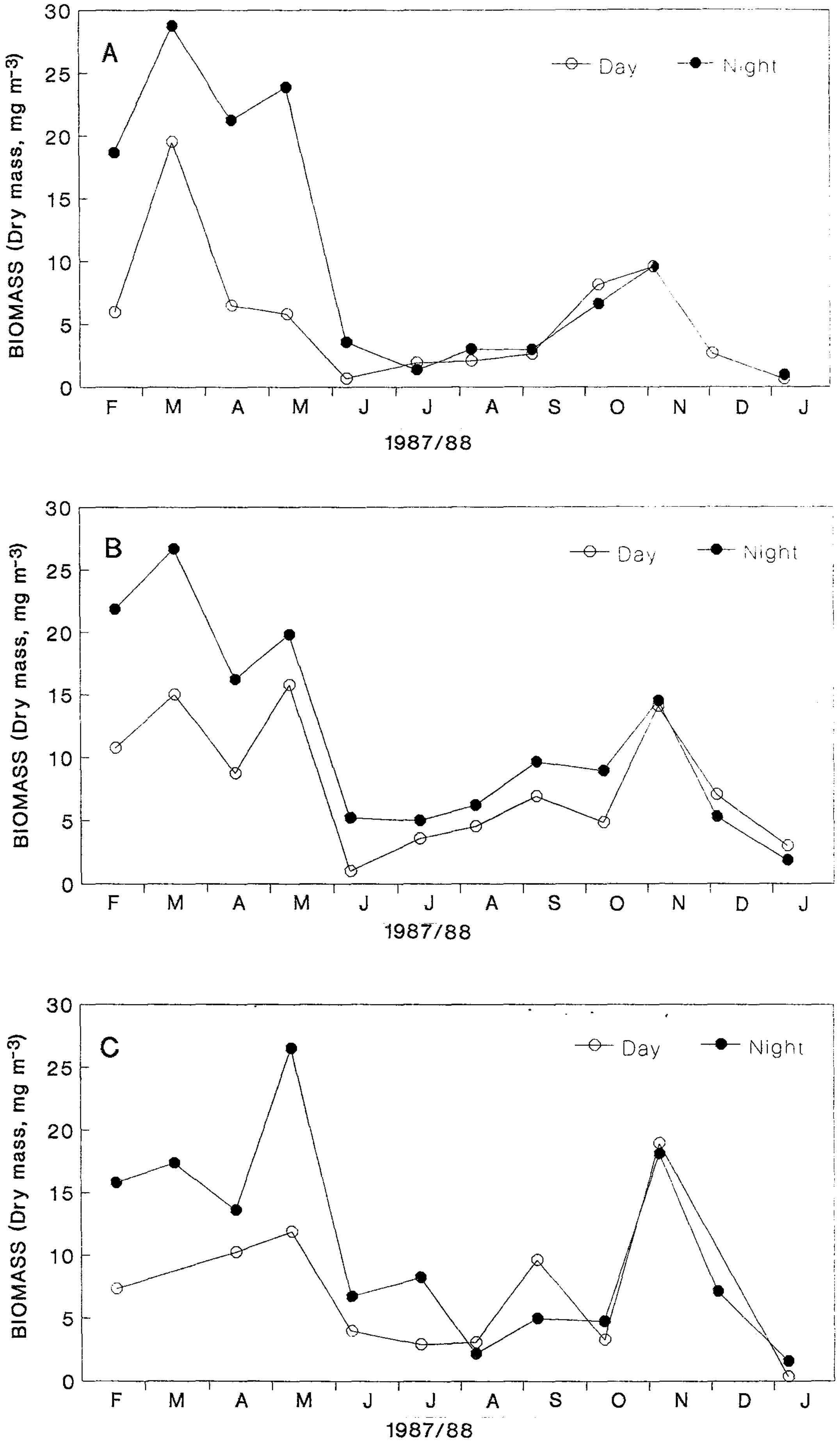


Figure 7. Seasonal biomass distribution of the naupliar stages of *Pseudodiaptomus hessei* in the upper- (A), middle- (B) and lower (C) reaches of the Kariega estuary. Samples taken monthly from February 1987 to January 1988.

Table 2. Zooplankton biomass (Mean ± S.E.) over a twelve month period (Feb. 1987 to Jan. 1988) in the upper, middle and lower reaches of the Kariega estuary.

	STATION		
	1	2	3
Kariega			
a) Daytime:	10.7 ± 1.89	16.0 ± 1.91	12.7 ± 1.82
b) Nighttime:	30.8 ± 4.47	47.3 ± 5.97	36.9 ± 4.99

b) Great Fish estuary.

Two grazer species dominated the zooplankton of the Great Fish estuary. In the upper, freshwater region of the estuary, the zooplankton was comprised exclusively of *P. hessei.* In the middle and lower reaches, where the salinity was greater than ≈ 8 ‰, the mysid *Mesopodopsis slabberi* dominated the community, usually comprising between 90 and 100 % of the biomass, with the remainder composed of *P. hessei.*

Mean annual biomass for Stations 1 to 3 (see Chapter 2, Figure 5) are shown in Table 3 and the seasonal variation (nighttime) in Figure 8. Considerable variation along the length of the estuary was evident and the maximum seasonal mean value of 4253 mg m^{-3} for the estuary was recorded at Station 2 (middle reaches)(Table 3). The lowest value (256 mg m^{-3}) was recorded at Station 1 (upper reaches). Community biomass was higher during the nighttime at Stations 1 and 2, however diel differences at Station 3 were not marked.

The temporal and spatial patterns of distribution of *Pseudodiaptomus hessei* and *Mesopodopsis slabberi* during the twelve month period February 1987 to February 1988 are shown in Figures 9 to 11. Several biomass peaks occurred during this period, during March/April and September/October (1987), and again in December/January (1988). Although maximum biomass was recorded during the warmer months when the temperature was between 19 and 24 °C, biomass peaks were also recorded during the winter months. These coincided with pulses of freshwater inflow into the estuary. A similar pattern of abundance was observed in the nauplii. *Pseudodiaptomus* exhibited a distinct spatial pattern of distribution, and attained highest biomass towards the upper

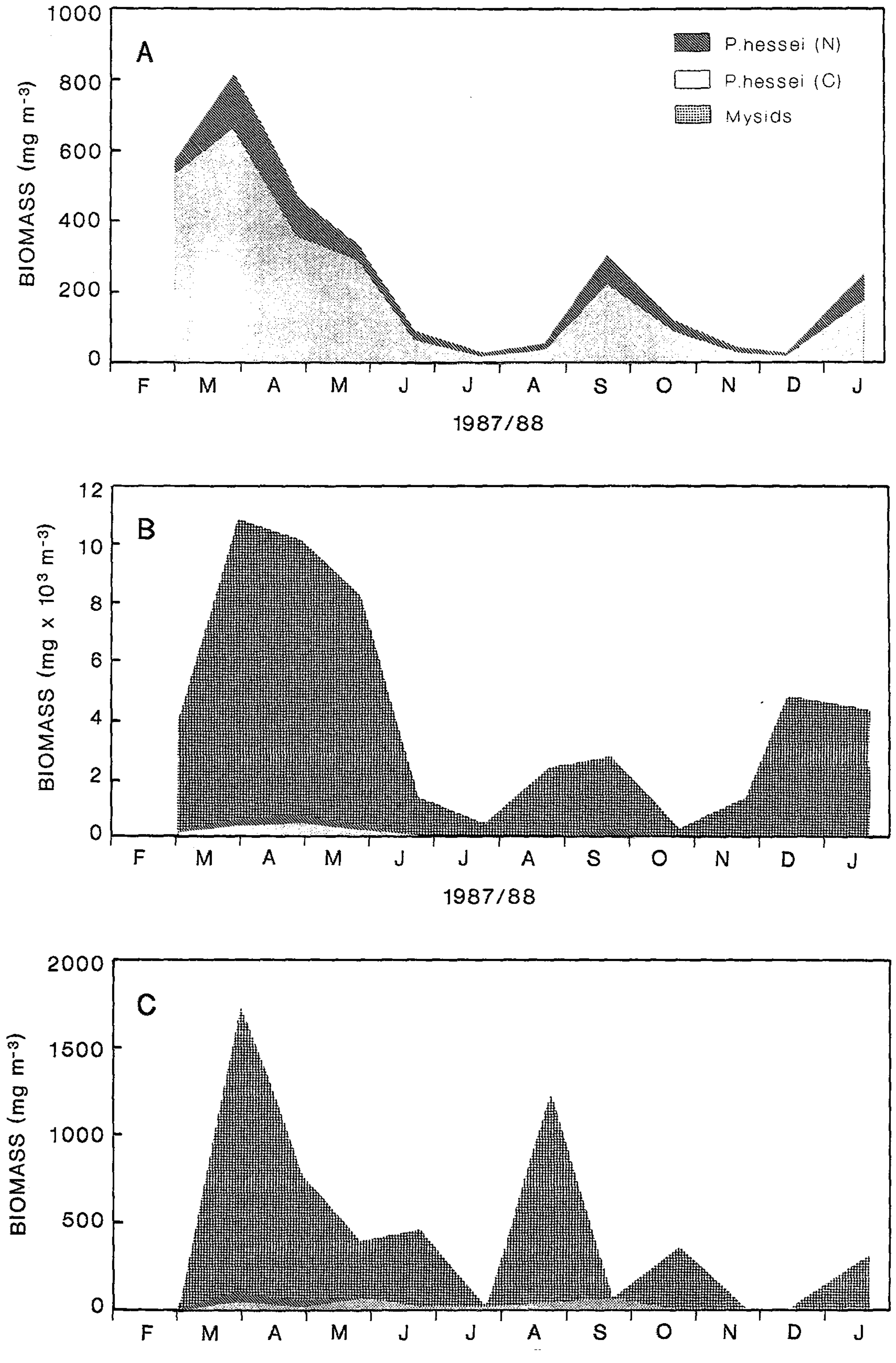


Figure 8. Zooplankton biomass in the upper- (A), middle- (B) and lower (C) reaches of the Great Fish estuary, showing the contribution of the dominant species and life-history stages to total biomass. Samples taken monthly from February 1987 to January 1988. (Note Y-axis scales: A) 0 to 1000, B) 0 to 12 000, C) 0 to 2000).

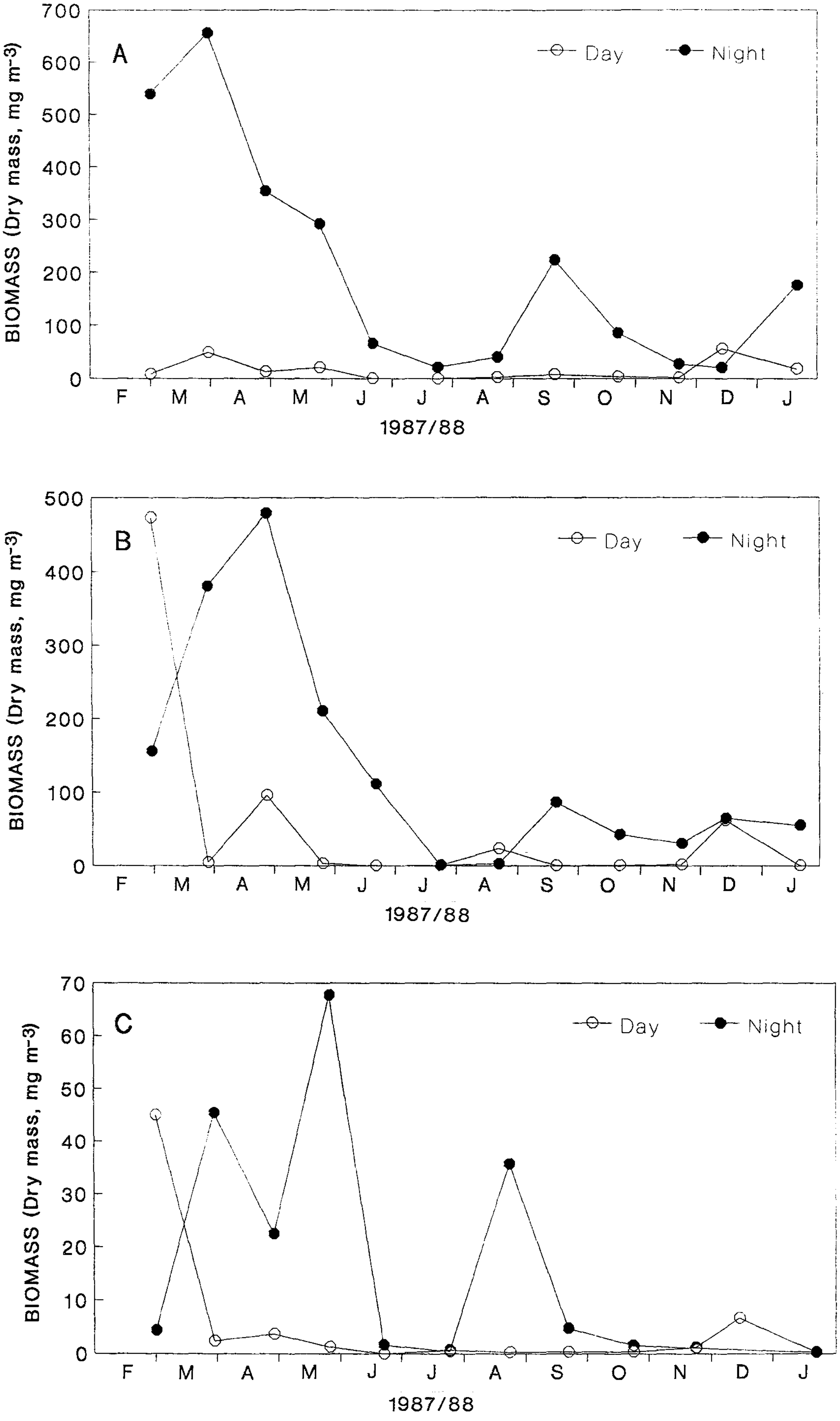


Figure 9. Seasonal biomass distribution of the copepodite and adult stages of *Pseudodiaptomus hessei* in the upper- (A), middle- (B) and lower (C) reaches of the Great Fish estuary. Samples taken monthly from February 1987 to January 1988.

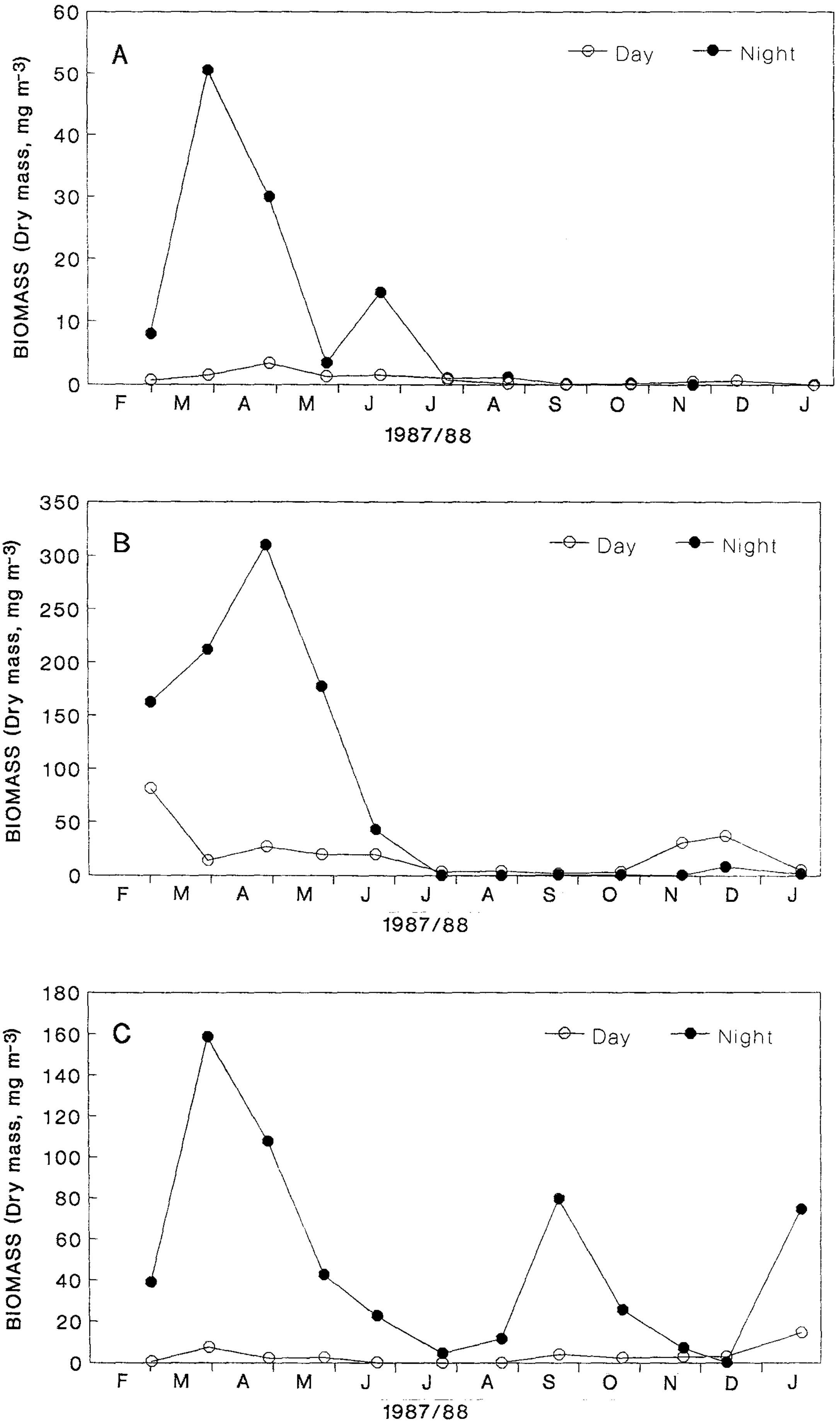


Figure 10. Seasonal biomass distribution of the naupliar stages of *Pseudodiaptomus hessei* in the upper- (A), middle- (B) and lower (C) reaches of the Great Fish estuary. Samples taken monthly from February 1987 to January 1988.

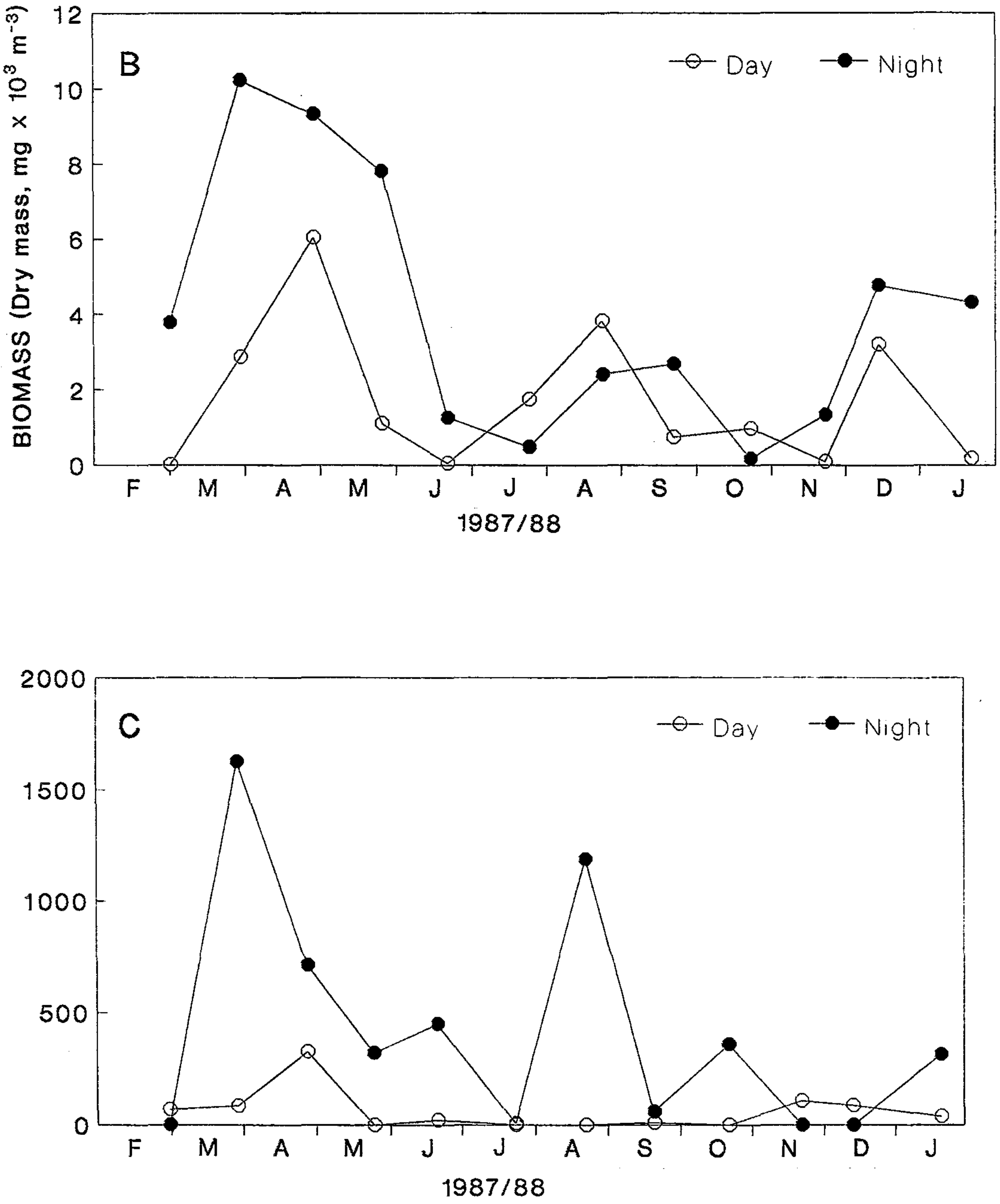


Figure 11. Seasonal biomass distribution of the mysid *Mesopodopsis slabberi* in the middle (B) and lower (C) reaches of the Great Fish estuary. Samples taken monthly from February 1987 to January 1988. (Note Y-axis scales: B) 0 to 12 000, C) 0 to 2000).

reaches. Although the nauplii demonstrated a similar pattern, these stages were on occasions more numerous in the middle reaches. The copepodites and adults demonstrated a clear diel distribution pattern and were generally only present in the watercolumn after dark. Diel differences in the abundance of the naupliar stages were observed although the patterns were not clear.

The mysid *Mesopodopsis slabberi* was only found in the middle and lower reaches of the estuary. Peaks of abundance occurred between March and May, August/September, and again in December/January. Although temporal patterns of abundance appear to be partially in response to seasonal temperature effects, there is a similar influence of freshwater inflow as described for *P. hessei*. Mysid biomass was maximum in the middle reaches of the estuary and somewhat higher at night, although substantial numbers of mysids were also present during the daytime. Diel patterns were not as pronounced in the lower reaches.

Table 3. Zooplankton community biomass (Mean ± S.E.) over a twelve month period (Feb. 1987 to Jan. 1988) in the upper, middle and lower reaches of the Great Fish estuary.

	STATION		
	1	2	3
Great Fish			
a) Daytime:	185 ± 3.4	1765 ± 483.5	667 ± 21.6
b) Nighttime:	256 ± 41.7	4253 ± 605.2	483 ± 122.0

c) Comparisons with other estuaries.

In Table 4., zooplankton community biomass measured during this study is compared with values obtained for other South African estuaries.

Table 4. The standing stock of zooplankton (mg m^{-3} dry biomass) in South African estuaries. *Estimated by Allanson & Read (1987) from authors data. Table after Allanson & Read (1987) with additional data.

ESTUARY	ZOOPLANKTON STANDING STOCK (mg m^{-3}) MEAN	MAXIMUM	REFERENCE
Richards Bay	174	344	Grindley & Wooldridge (1974)
Mboyoti	87	109	Wooldridge (1974)
Msikaba	15	35	Wooldridge (1976)
Mgazana	-	1200	Wooldridge (1977)
Swartkops	17*	95	Grindley (1981)
Sundays	-	8272	Wooldridge & Bailey (1982)
Bot	75	260	Coetzee (1985)
Keiskamma	1627	7497	Allanson & Read (1987)
Kariega	942	4360	Allanson & Read (1987)
Kariega	38	108	This study
Great Fish	9099	19791	Allanson & Read (1987)
Great Fish	1597	11631	This Study

Zooplankton community biomass was considerably higher in the Great Fish estuary compared with the Kariega estuary, and this confirms the findings of Allanson & Read (1987). The actual values obtained in this study were, however, considerably lower. The values obtained for the Great Fish and Kariega estuaries in this study were similar to the upper and lower limits, respectively, of the range recorded in South African estuaries.

5.2.2 ZOOPLANKTON COMMUNITY GRAZING RATES.

a) Temporal, spatial and diel patterns.

i) Kariega estuary.

Spatial, seasonal temporal and diel patterns: Community filtration rates (CFR's, ml m^{-3} h^{-1}) measured in the Kariega estuary during the seven month period July 1987 to January 1988 are shown in Figure 12. During this period, ambient water temperature ranged from 14.5 to 28.5 °C, the seasonal range. A summary of the data, showing differences between sampling Stations and day/night measurements is presented in Table 5.

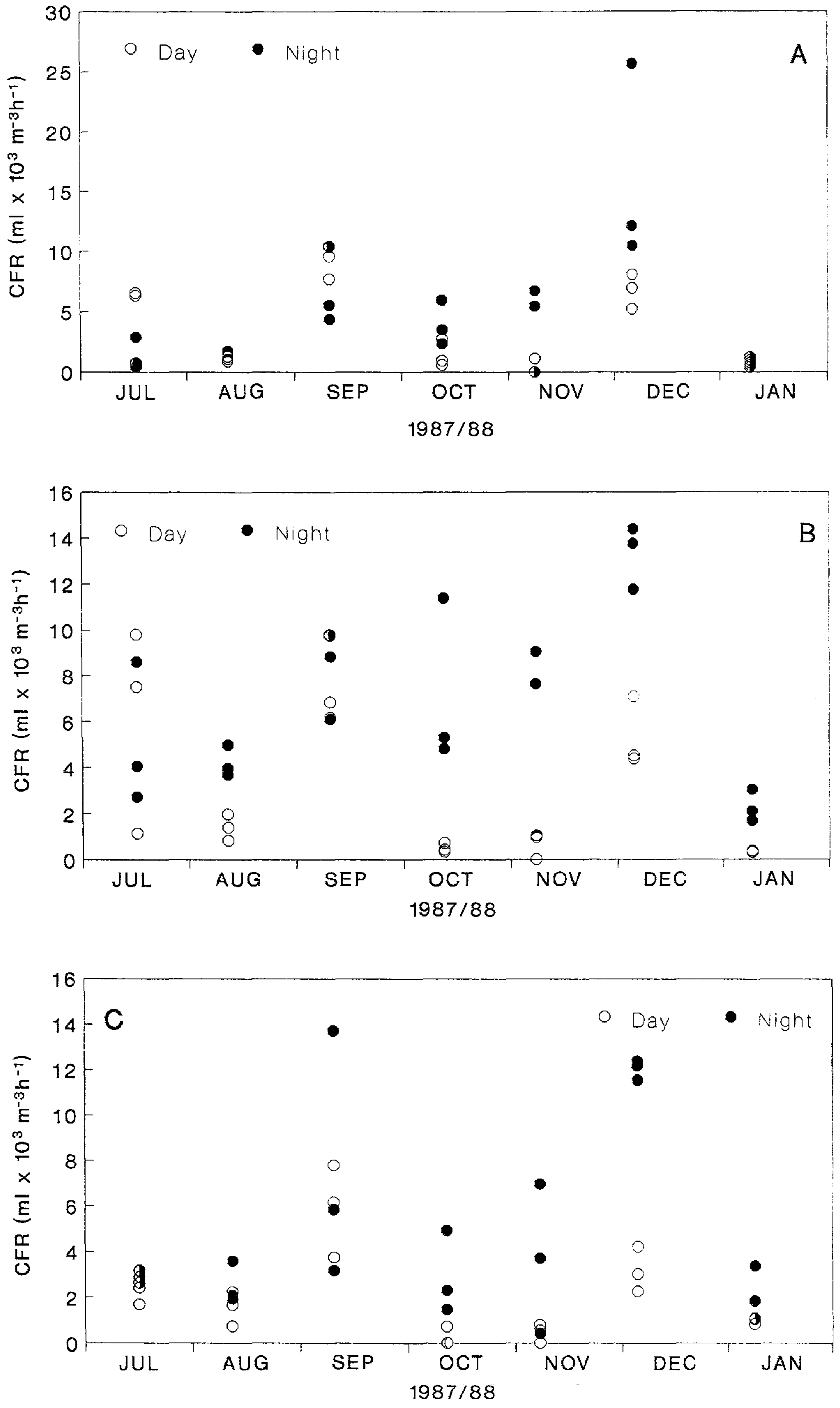


Figure 12. Community filtration rates (CFR's, ml m^{-3} h^{-1}) in the upper- (A), middle- (B) and lower (C) reaches of the Kariega estuary. Samples taken monthly from July 1987 to January 1988. (Note Y-axis scales: A) 0 to 30 000, B) 0 to 16 000, C) 0 to 16 000).

Table 5. Seasonal mean CFR's (ml m^{-3} h^{-1}) at Stations 1 to 3 during day and nighttime in the Kariega estuary.

	COMMUNITY FILTRATION RATES (CFR'S, MEAN ± S.E.)		
	UPPER	MIDDLE	LOWER
i) Daytime:	3461 (n=21) ± 769.2	3081 (n=21) ± 743.1	2094 (n=21) ± 447.5
ii) Nighttime:	3843 (n=20) ± 831.9	6594 (n=21) ± 873.6	4801 (n=21) ± 895.9

The seasonal range of CFR's (ml m^{-3} h^{-1}) varied between 0 and 15 000 and in an exceptional case attained a value of ≈ 25 000. In most cases there was high variability among the three replicate measurements made both at night and during the day on any particular sampling occasion. From July there was a general increase in CFR's which attained a maximum in December, when the temperature was ≈ 25 °C, and declined sharply in January. Temperature increased throughout and attained a maximum in January (≈ 28.5 °C). The mean CFR was higher at Station 2 than at Stations 1 or 3 during both daytime and nighttime, however, analysis of variance indicated that there were no significant differences ($p > 0.05$) in CFR's between Stations (during day or night) (Table 6). Mean nighttime CFR's (Stations 1, 2 and 3) were greater than mean daytime CFR's in all cases. Since no significant differences in the mean CFR between Stations were detected, day/night differences were tested by analysis of variance using data pooled from all three Stations. Day/night differences were found to be significant ($p < 0.01$). It should be noted however, that on several sampling occasions, daytime CFR's exceeded nighttime CFR's. Although no clear seasonal pattern emerges, highest CFR's appeared to occur during December and also, but to a lesser extent, during September. This observation was made at all three sampling Stations.

Table 6. Analysis of variance to test the effect of sampling Station on mean CFR in the Kariega estuary. n.s. = not significant, ($p > 0.05$).

DATA SET	SOURCE	DF	SS	MS	F
a) Kariega (day):	Station	2	20.9078	10.4539	1.111 n.s.
b) Kariega (night):	Station	2	43.0982	21.5491	0.942 n.s.

Grazing pressure: A community grazing rate (CGR, % d^{-1}), the amount of watercolumn "cleared" by the zooplankton community over a 24 hour period, was calculated for each sampling occasion at all three Stations. CGR's were measured as the sum of daytime and nighttime filtration rates, by extrapolation of each to a 12 hour period. This required the assumption that CFR's were maintained constant for the duration. The minimum and maximum watercolumn "cleared" by the zooplankton community was calculated by deriving CGR's (% d^{-1}) from the lowest and the highest of three replicate CFR measurements made during the day and at nighttime. The results are presented in Table 7.

Table 7. Maximum and minimum CGR's (% d^{-1}) estimated for Stations 1 to 3 in the Kariega estuary during the seven month period Jul. 1987 to Jan. 1988.

	COMMUNITY GRAZING RATE (CGR, % d^{-1})					
	UPPER		MIDDLE		LOWER	
DATE	MIN.	MAX.	MIN.	MAX.	MIN.	MAX.
15/7/87	1.35	11.30	4.60	22.05	4.90	7.55
11/8/87	2.09	3.54	5.38	8.30	3.19	6.96
10/9/87	14.50	24.95	14.70	23.24	8.30	25.80
13/10/87	3.50	10.40	6.15	14.50	1.75	6.75
9/11/87	0	9.35	1.25	12.00	0.50	9.30
8/12/87	18.80	40.45	7.25	25.75	16.55	19.90
12/1/88	1.10	2.60	3.25	4.10	2.25	5.35

The results of Table 7 demonstrate that at certain times of the year, the zooplankton community in the Kariega estuary exerted considerable grazing pressure and "cleared" up to 40 % of the watercolumn over a 24 hour period, with values in the region of 25 % not uncommon. Considerable differences between maximum and minimum values were obtained, however.

Specific Filtration Rates: The seasonal patterns of biomass-specific filtration rate (SFR, ml mg^{-1} h^{-1}) for each Station are shown in Figure 13, and the seasonal means in Table 8. Although no obvious seasonal trend in SFR was apparent, highest SFR's were recorded at all Stations during December 1987 when the temperature was comparatively high. Higher SFR's were recorded in the upper reaches, particularly during the daytime when the community was dominated by calanoid nauplii (Table 8). Mean day, and nighttime SFR's at other Stations were reasonably similar.

Table 8. Seasonal mean SFR (ml mg^{-1} h^{-1}) during daytime and nighttime for Stations 1 to 3 in the Kariega estuary.

	SPECIFIC FILTRATION RATES (SFR'S, MEAN ± S.E.)		
	UPPER	MIDDLE	LOWER
i) Daytime:	918 (n=21) ± 227.0	293 (n=21) ± 79.5	274 (n=20) ± 44.6
ii) Nighttime:	416 (n=19) ± 145.3	301 (n=21) ± 51.5	341 (n=21) ± 49.2

ii) Great Fish estuary.

Spatial, seasonal temporal and diel patterns: Community filtration rates (CFR's, ml m^{-3} h^{-1}) measured in the Great Fish estuary during the seven month period July 1987 to January 1988 are shown in Figure 14. During this period, ambient water temperature ranged from 13 to 24.5 °C, the seasonal range. A summary of the data, showing differences between sampling Stations and day/night measurements is presented in Table 9.

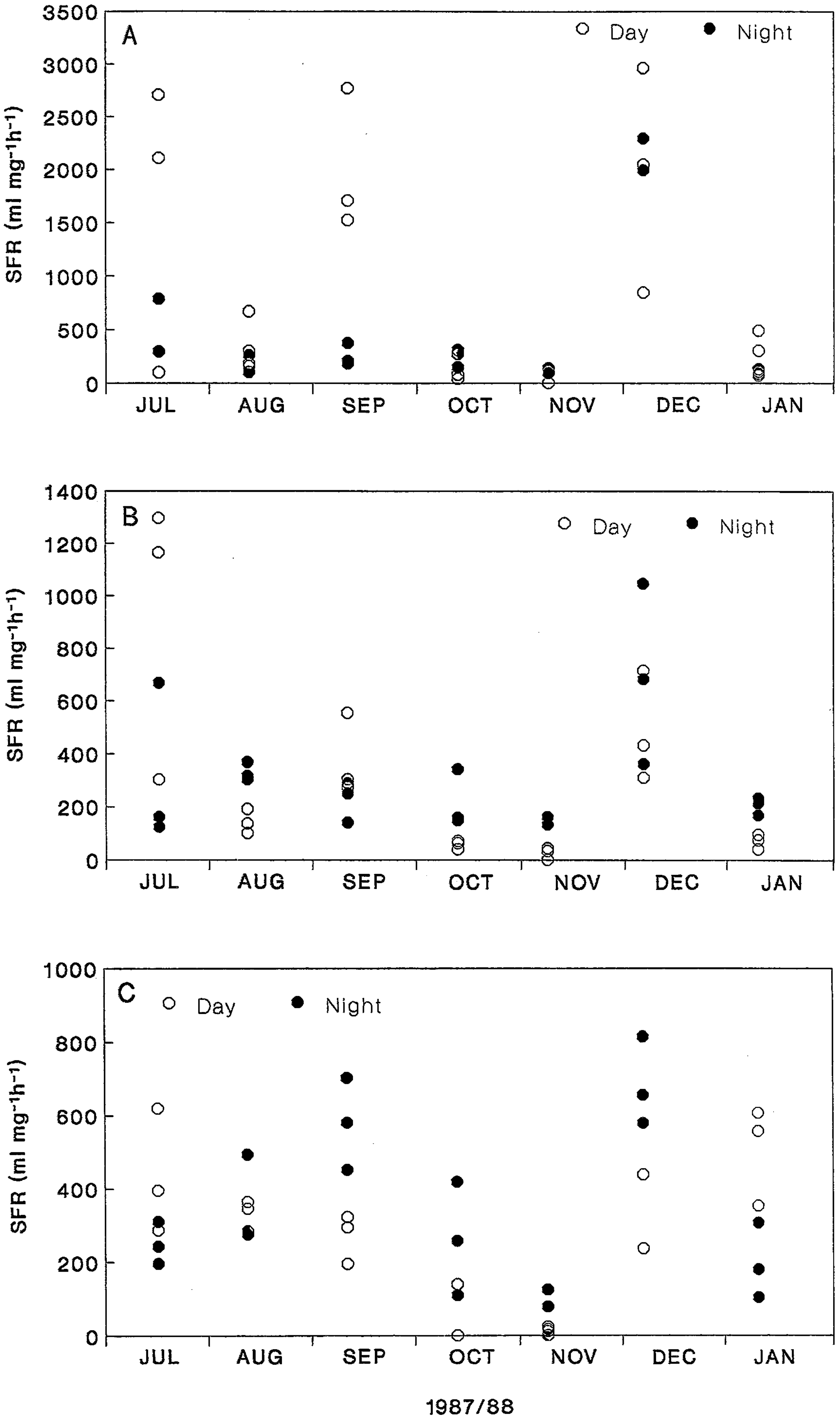


Figure 13. Specific filtration rates (SFR's, ml mg^{-1} h^{-1}) in the upper- (A), middle- (B) and lower (C) reaches of the Kariega estuary. Samples taken monthly from July 1987 to January 1988.

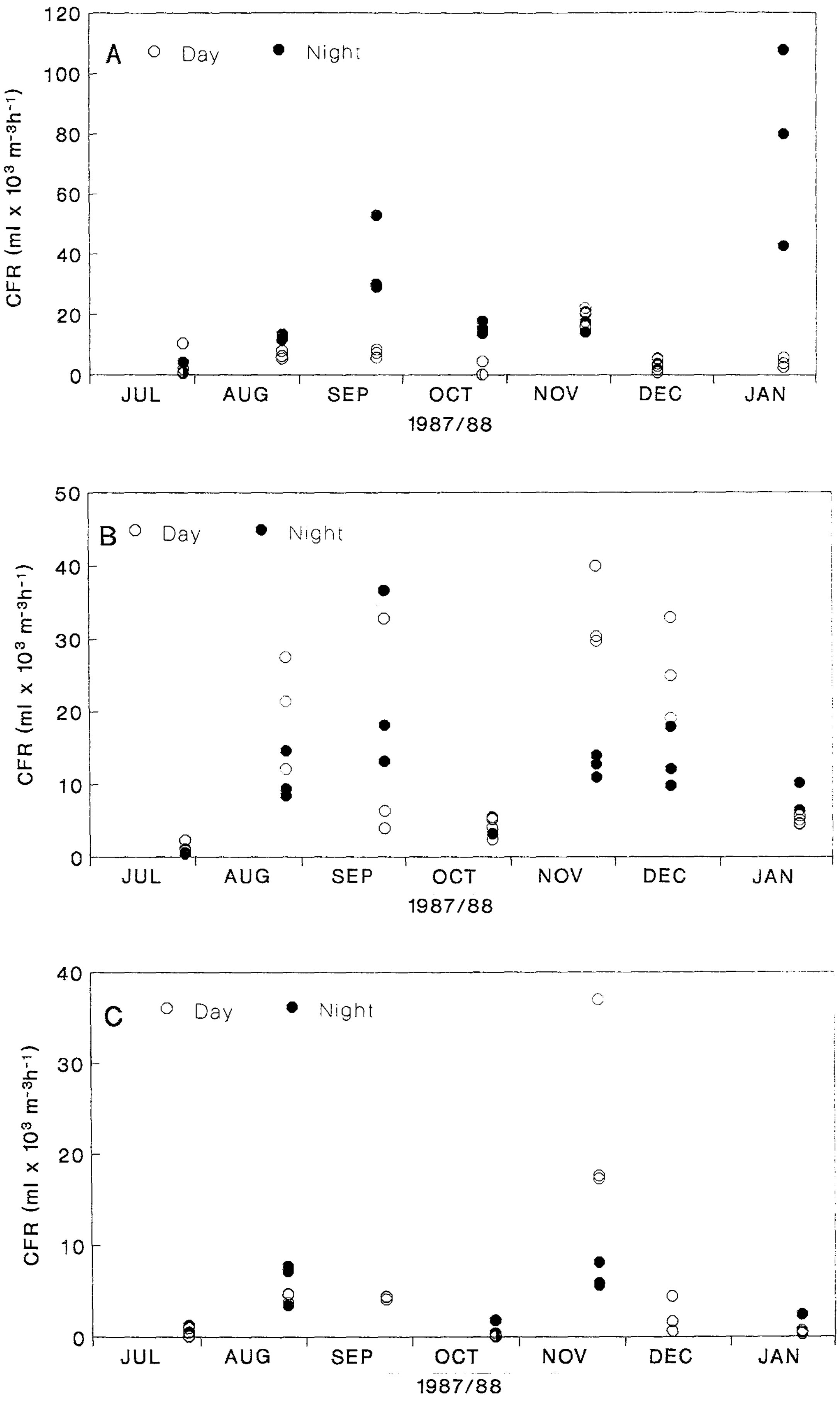


Figure 14. Community filtration rates (CFR's, ml m^{-3} h^{-1}) in the upper- (A), middle- (B) and lower (C) reaches of the Great Fish estuary. Samples taken at monthly intervals from July 1987 to January 1988. (Note Y-axis scales: A) 0 to 120 000, B) 0 to 50 000, C) 0 to 40 000).

Table 9. Seasonal mean CFR's (ml m^{-3} h^{-1}) at Stations 1 to 3 during daytime and nighttime in the Great Fish estuary.

	COMMUNITY FILTRATION RATES (CFR'S, MEAN ± S.E.)		
	UPPER	MIDDLE	LOWER
i) Daytime:	6673 (n=21) ± 1331	14762 (n=21) ± 2887	5138 (n=21) ± 1926
ii) Nighttime:	23344 (n=21) ± 5971	10260 (n=21) ± 1748	2963 (n=15) ± 789

Seasonal, diel, and Station-specific variation in CFR's followed a somewhat different pattern in the Great Fish estuary. No obvious seasonal pattern was observed. The highest seasonal mean CFR was obtained at Station 2 during the daytime, and at Station 1 during nighttime (Table 9).

Analysis of variance indicated that CFR's between Stations were significantly different, both during daytime and nighttime ($p < 0.01$) (Table 10). Consequently, further analysis of variance to examine differences between day/night CFR's was conducted for each Station separately.

Table 10. Analysis of variance to test the effect of sampling Station on mean CFR in the Great Fish estuary. * = significant ($p < 0.01$), i) 6 missing values in (b).

DATA SET	SOURCE	DF	SS	MS	F
a) Great Fish (day):	Station	2	1122.714	561.357	5.804 *
b) Great Fish (night):	Station	2	3913.922	1956.96	6.449 * (i)

At Station 1, the mean nighttime CFR was considerably higher than the mean daytime value and analysis of variance indicated that this difference was significant ($p < 0.01$) (Table 11). Although the mean CFR was slightly higher during the daytime at both Stations 2 and 3 (middle and lower reaches), analysis of variance indicated that these differences were not significant.

Table 11. Analysis of variance to test the influence of day, and nighttime measurements on mean CFR in the Great Fish estuary. * = significant ($p < 0.01$). n.s. = not significant, ($p > 0.05$).

DATA SET	SOURCE	DF	SS	MS	F
a) Station 1:	day/night	1	2917.85	2917.85	7.426 *
b) Station 2:	day/night	1	212.75	212.75	1.779 n.s.
c) Station 3:	day/night	1	41.38	41.38	0.833 n.s.

Grazing pressure: The fraction of the watercolumn "cleared" by the zooplankton community was calculated according to the method described previously for the Kariega estuary, and the results are given in Table 12.

Table 12. Maximum and minimum CGR's (% d^{-1}) estimated for Stations 1 to 3 in the Great Fish estuary during the seven month period Jul. 1987 to Jan. 1988.

	COMMUNITY GRAZING RATE (CGR, % d^{-1})					
	UPPER		MIDDLE		LOWER	
DATE	MIN.	MAX.	MIN.	MAX.	MIN.	MAX.
27/7/87	1.30	17.35	1.15	4.00	0.54	2.55
26/8/87	20.34	25.45	24.55	50.44	8.50	14.80
24/9/87	41.54	73.45	20.45	83.29	data missing	
26/10/87	16.30	26.35	6.65	12.80	0.50	2.35
26/11/87	35.74	50.44	48.79	64.79	27.40	54.09
18/12/87	4.45	12.70	34.59	60.94	data missing	
25/1/88	54.29	135.93	11.95	18.15	0.80	3.60

The zooplankton community exerted considerable grazing pressure at certain times of the year (e.g. Station 1, Jan 1988) and values were generally considerably higher than in the Kariega estuary. Results indicate that at certain times, the zooplankton community "cleared" the entire watercolumn during a 24 hour period. CFR's of between 50 and 80 % d^{-1} were common.

Specific filtration rates: The seasonal patterns of biomass-specific filtration rates (SFR, ml mg^{-1} h^{-1}) for each Station are shown in Figure 15, and the seasonal means in Table 13. No clear seasonal trends in SFR were apparent (Figure 15). In Table 13, the mean daytime SFR in the upper reaches was considerably higher than the nighttime mean, which suggests that the nauplii exhibit higher SFR's than the copepodite and adult forms. The considerable difference between mean SFR in the middle and lower reaches suggests the influence of some environmental factor on mysid feeding activity.

Table 13. Seasonal mean SFR (ml mg^{-1} h^{-1}) during daytime and nighttime for Stations 1 to 3 in the Great Fish estuary.

	SPECIFIC FILTRATION RATES (SFR'S, MEAN ± S.E.)		
	UPPER	MIDDLE	LOWER
i) Daytime:	2680 (n=19) ± 1080.3	104 (n=21) ± 53.8	2667 (n=21) ± 1101.1
ii) Nighttime:	205 (n=21) ± 33.0	138 (n=21) ± 103.6	1141 (n=16) ± 649.8

b) Factors influencing CFR's.

In general, much of the variation between either daytime or nighttime replicate CFR measurements made on the same sampling date was attributable to sampling patchily distributed zooplankton due to the comparatively small sampling size of the grazing chamber, since SFR's were generally more comparable.

Diel variation: In the Kariega estuary, the generally higher nighttime CFR's were as a result of elevated biomass resulting from diel vertical migration of zooplankton into the watercolumn after dark. Daytime CFR's were attributed to the non-migratory component of the community, specifically the naupliar forms of both *Pseudodiaptomus* and *Acartia*, although copepodites of *Acartia* were occasionally present in low numbers (see Section 5.2.1, a) Kariega estuary).

In the Great Fish estuary, diel differences in CFR were noticeably pronounced at Station 1 (upper reaches) only. The zooplankton community in this region of the estuary was

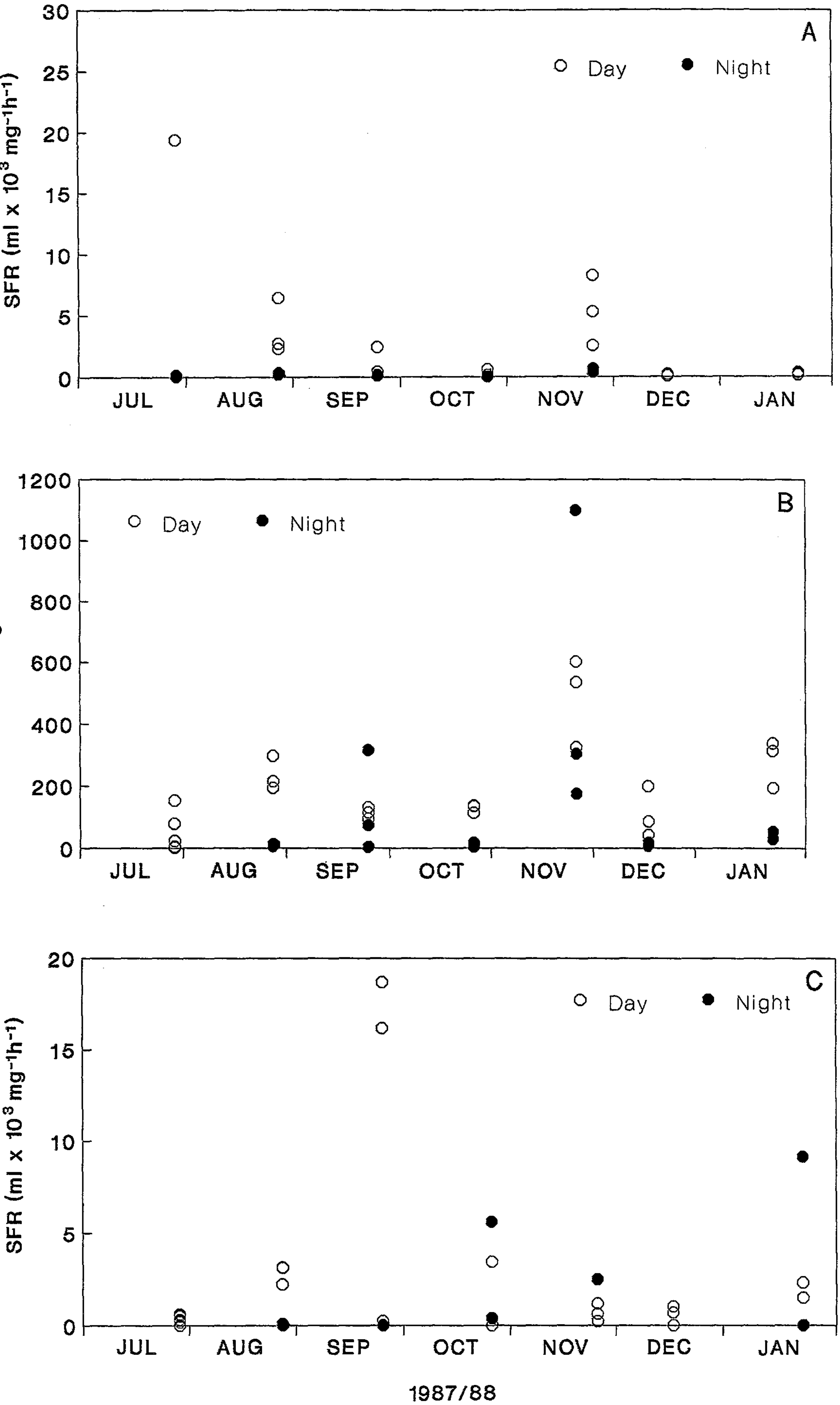


Figure 15. Specific filtration rates (SFR's, ml mg^{-1} h^{-1}) in the upper- (A), middle- (B) and lower (C) reaches of the Great Fish estuary. Samples taken at monthly intervals from July 1987 to January 1988. (Note Y-axis scales: A) 0 to 30 000, B) 0 to 1 200, C) 0 to 20 000).

comprised solely of *Pseudodiaptomus hessei*. Thus, diel differences in CFR's in the upper reaches occurred in response to vertical migration movements as described for the Kariega estuary. In the middle reaches of the estuary, differences between daytime and nighttime feeding were not significant despite the fact that community biomass (dominated by the mysid *Mesopodopsis*) was approximately a factor of 2.5 greater at night. This suggests that feeding activity was generally lower during the nighttime. Similar observations were made at Station 3.

Community biomass and environmental factors: In several studies of zooplankton community feeding, multiple regression has been employed to determine the main factors contributing to variability in feeding rates (e.g. Hart, 1984; 1986; Jarvis, 1987; Kleppel, 1992). A similar analysis of the data was attempted in this study. A preliminary examination of the variation in CFR's in response to changes in i) community biomass, ii) temperature, iii) chlorophyll *a* and iv) seston concentration was conducted by means of simple linear regression (Jarvis, 1987). Only zooplankton community biomass (Kariega), and temperature and seston (Great Fish) were significantly correlated with CFR's, however, correlation coefficients for all variables were low. In general, linear relationships were inadequate to describe the response of CFR to the variables tested. Despite the low correlations, stepwise multiple regression was performed to test the applicability of the analysis to the data sets. Predictably, results were inconclusive and consequently are not included. Scatterplots are shown in Figures 16 and 17.

Several problems associated with the use of multiple regression were identified. The possible influences of species-specific filtration rates (SFR's) in a mixed community assemblage are described above under that heading. In order for multiple regression to explain variation in CFR's successfully, the relationship between CFR's and environmental variables must be linear, however, there is evidence to suggest that this is not always the case. For example, the relationship between CFR and temperature appeared to be biphasic with maximum CFR's occurring at between 23 and 26 °C. It was not possible to establish this with any certainty, however, since wide scatter of the data points was evident. Further problems arise in determining the true source of variation in CFR's if two or more of the independent variables co-vary. Linear regression analyses were performed to test

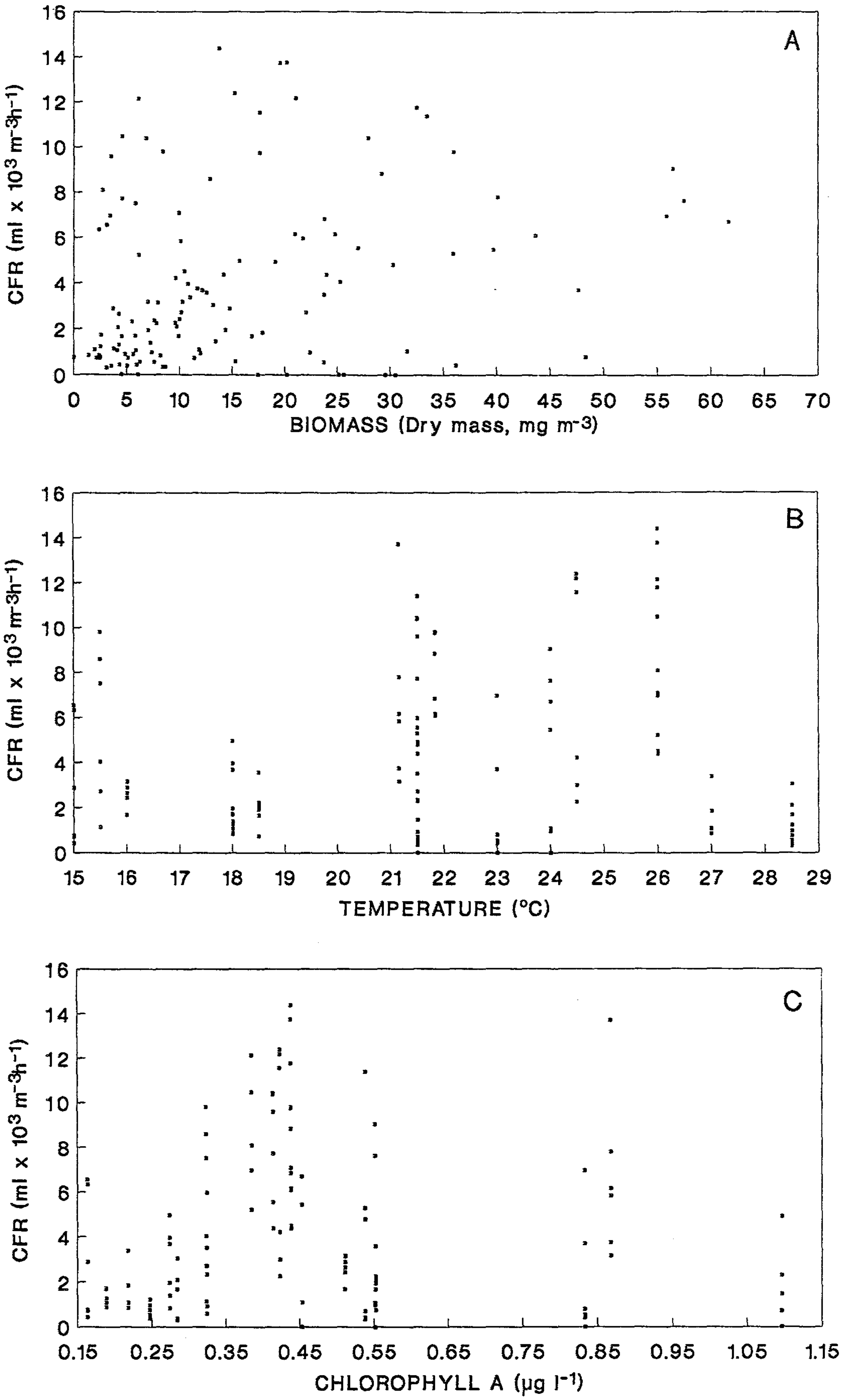


Figure 16. Scatterplots of CFR (ml m^{-3} h^{-1}) as a function of Zooplankton biomass (mg m^{-3}) (A), Temperature (°C) (B), Chlorophyll *a* (µg l^{-1}) (C) and Seston (TPM, mg l^{-1}) (D) in the Kariega estuary. (Note Y-axis scales: A) to D) 0 to 16 000).

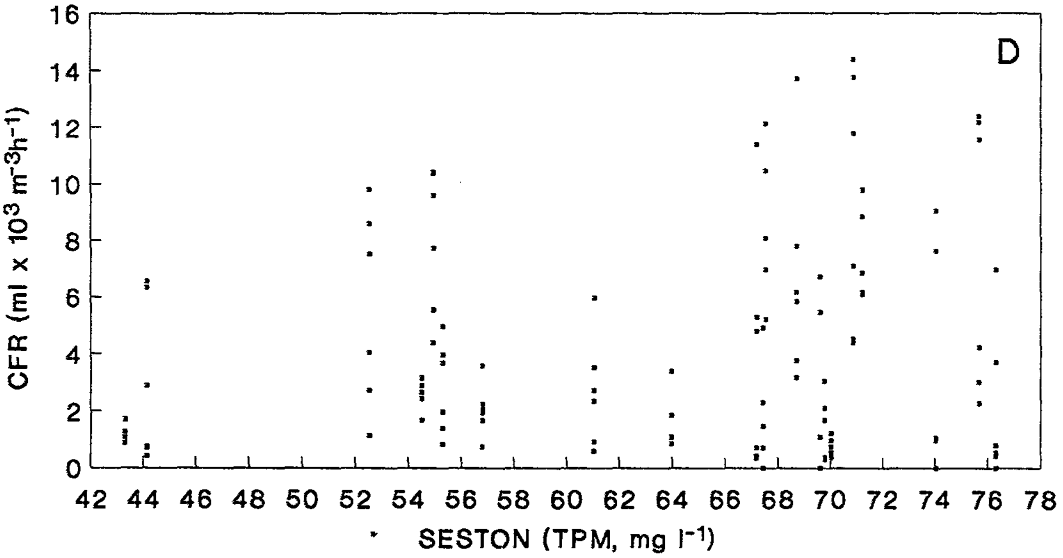


Figure 16 (continued).

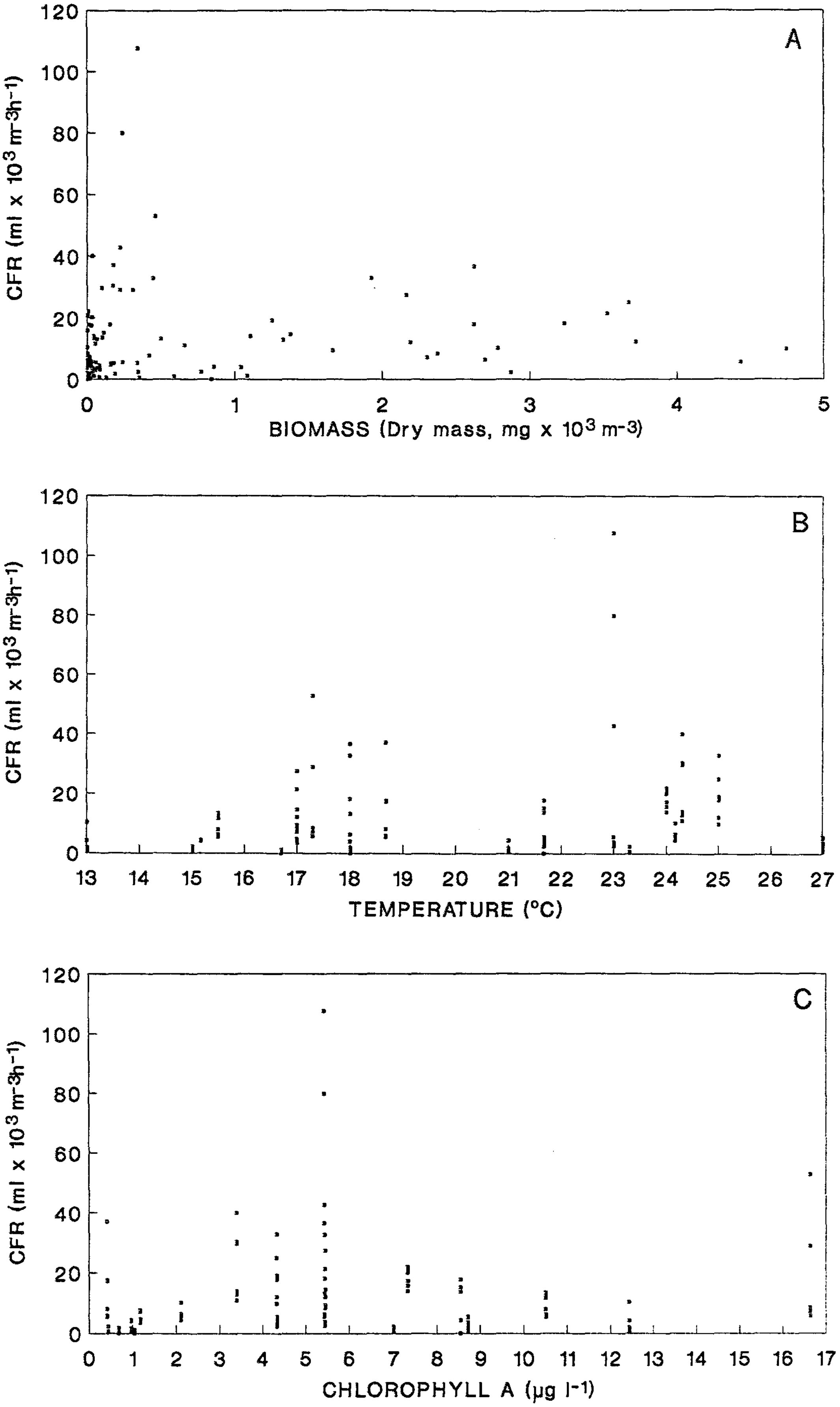


Figure 17. Scatterplots of CFR (ml m^{-3} h^{-1}) as a function of Zooplankton Biomass (mg m^{-3}) (A), Temperature (°C) (B), Chlorophyll *a* (μg l^{-1}) (C) and Seston (TPM, mg l^{-1}) (D) in the Great Fish estuary. (Note Y-axis scales: A) to D) 0 to 120 000).

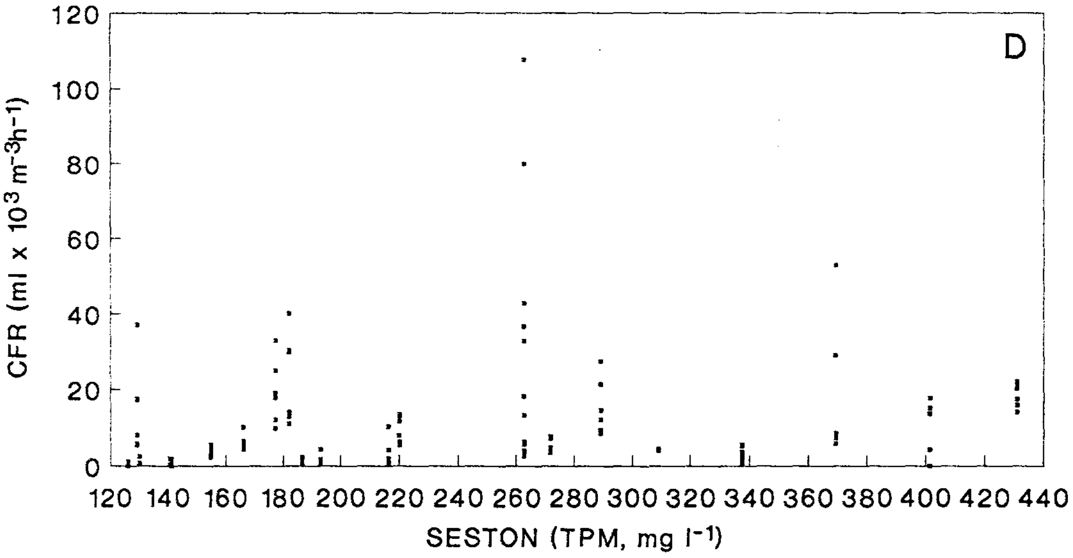


Figure 17 (continued).

for co-variance. In the Kariega data, temperature and seston, and seston and chlorophyll *a* co-varied ($r^2=0.56$, $n=124$, $p < 0.01$; $r^2=0.21$, $n=124$, $p < 0.01$, respectively). In the Great Fish data, seston and chlorophyll *a* co-varied ($r^2=0.32$, $n=124$, $p < 0.01$). Consequently, it is not possible to determine which independent variables were responsible for the majority of observed variability in CFR's.

In summary, multiple regression analysis was concluded to be inappropriate to this study for the following reasons:

a) In some circumstances, CFR's were poorly correlated with biomass because changes in species composition occurred in which the biomass-specific filtration rates (SFR's) of the community components were observed to be different. b) The response of the dependent variable (CFR) to certain environmental parameters was not linear. c) Co-variance of two or more independent variables was found to occur. d) Interactions between the above.

5.3 DISCUSSION

Several studies have recognized the importance of temperature and freshwater inflow in determining zooplankton distribution and abundance in estuaries of the eastern Cape (e.g. Wooldridge & Melville-Smith, 1979; Wooldridge & Bailey, 1982; Allanson & Read, 1987). Although temperature fluctuations are subject to a predictable seasonal cycle, the extent and timing of freshwater inflow is, by comparison, extremely variable. Due to the nature of the climate, and differences in catchment size and regulation, estuaries in the eastern Cape range from marine-dominated systems in which the upper reaches may temporarily become hypersaline, to freshwater-dominated systems, in which a well-developed salinity gradient is evident (Chapter 2).

Elevated freshwater inflow has several important consequences for zooplankton. These include osmotic stress in response to fluctuating salinity (Grindley, 1981) as well as problems in maintaining position in the estuary as a result of a higher flushing rate (Grindley, 1972; Wooldridge & Erasmus, 1980; Castel & Veiga, 1990). The trophic status, however, is generally higher due to the input of nutrients and detritus associated with freshwater inflow (Allanson & Read, 1987).

Although zooplankton communities of the Kariega and Great Fish estuaries contrasted markedly, they were comparable with other marine-, and freshwater-dominated estuaries of the eastern Cape, respectively. The transition from a community dominated by calanoid copepods of the genera *Acartia* and *Pseudodiaptomus* in marine-dominated systems, to a community comprising *Pseudodiaptomus* and mysid shrimps in estuaries subject to elevated freshwater inflow appears to be a common feature of eastern Cape estuaries and has been described in several studies (Wooldridge & Melville-Smith, 1979; Wooldridge & Bailey, 1982; Allanson & Read, 1987). Diel variation in abundance resulting from diel vertical migration of the zooplankton community confirmed the findings of Grindley (1972) and is discussed in more detail in Chapter 6.

Differences in species-specific tolerance to reduced salinity have been demonstrated to be a major factor influencing the distribution and composition of eastern Cape zooplankton communities (Wooldridge & Melville-Smith, 1979). Although *Acartia* spp. are a major component of marine-dominated estuaries, they fail to become established in estuaries such as the Sundays (Wooldridge & Melville-Smith, 1979) and are completely absent in the Great Fish estuary. Both of these estuaries are subject to high freshwater inflows and the absence of this genera in substantial numbers probably reflects the low tolerance of reduced salinity described by Connell & Grindley (1974). *Acartia natalensis* is, however, slightly more tolerant of reduced salinity than *A. longipatella* and this has been demonstrated to influence spatial patterns of distribution due to the competitive advantage of *A. natalensis* towards the upper reaches of an estuary, depending upon the extent of freshwater inflow (Wooldridge & Melville-Smith, 1979). By contrast, *Pseudodiaptomus hessei* is a ubiquitous species and has been recorded in substantial numbers in estuaries ranging from freshwater-dominated systems to those which periodically become hypersaline (Wooldridge & Melville-Smith, 1979; Wooldridge & Bailey, 1982; Allanson & Read, 1987), reflecting the ability of this species to withstand a wide salinity range (Grindley, 1972). Although mysids were extremely abundant in estuaries subject to high freshwater inflow, their notable absence in the upper reaches where salinities of below 8 to 10 ‰ were recorded suggests that their distribution may be limited by osmotic problems experienced in low salinity water.

The positive influence of temperature on zooplankton production is widely recognized (Jerling & Wooldridge, 1991; and references cited therein) and in this study highest zooplankton standing stocks were observed during the warmer months. Although the zooplankton community demonstrated peak biomass when temperatures were maximal, Wooldridge & Melville-Smith (1979) have described a temporal pattern of succession between *Acartia natalensis* and *A. longipatella*. The former was more abundant during summer and as the temperature dropped to below 20 °C, was succeeded by its congeneric. Although a similar pattern of succession is likely to have occurred in the Kariega estuary, this was not demonstrated in this study since *Acartia* spp. were not distinguished.

According to Wooldridge & Melville-Smith (1979), the response of zooplankton to temperature and salinity cannot alone account for observed patterns of zooplankton distribution and abundance.. In addition to the differences in community composition, several studies have noted that zooplankton community biomass is considerably higher in estuaries subject to elevated freshwater inflow. Allanson & Read (1987) have suggested that this observation may be linked to the higher trophic status of freshwater-dominated estuaries. The positive influence of freshwater inflow in determining food resources for zooplankton communities is discussed in Chapter 4.

Several observations demonstrated the importance of food resources in determining zooplankton standing stocks. In the Kariega estuary, considerable differences were observed between the magnitude and duration of the seasonal zooplankton biomass peaks which occurred during the summers of 1986/87 and 1987/88, respectively. During the former, zooplankton standing stocks were higher and were sustained throughout the summer period. During the following summer, the spring increase in zooplankton biomass was short-lived and despite the continued increase in temperature, was already in decline by November. These patterns appear to be in response to food availability. Sustained phytoplankton growth during the summer of 1986/87 was attributed to a pulse of freshwater inflow which occurred during the spring. No further inflow occurred prior to the following summer and it was assumed that the low phytoplankton levels recorded were as a result of severe nutrient limitation (Chapter 4). Prolonged periods of low freshwater inflow are characteristic of the Kariega estuary (Chapter 2) and consequently zooplankton biomass peaks of short duration and minor extent are likely to be common.

As a result of the reduction in freshwater inflow, only minor spatial variability in food resources occurred along the Kariega estuary. A slight peak in the seston was observed in the middle reaches and Allanson & Read (1987) have attributed this to the effects of tidal shear and wind-induced turbulence. Lowest food resource concentrations were recorded in the upper reaches and were attributed to the reduced tidal currents which would be expected in this region. Although spatial differences were minor, mean annual zooplankton standing stocks reflect this trend precisely and this suggests that tidal re-suspension may have an additional role to play in determining zooplankton standing stocks, particularly in estuaries where freshwater inflow is reduced.

Although highest zooplankton biomass in the Great Fish estuary was recorded during the warmer months, numerous biomass peaks occurred throughout the year and coincided with fluctuations in food resources arising from pulses of freshwater inflow. Wooldridge & Melville-Smith (1979) have described the rapid proliferation of *Pseudodiaptomus* in the "new waters" following flood events and current evidence suggests that this is partially due to the associated increase in food resources. Considerable spatial variation in food resources was evident in the Great Fish estuary and was due to the point source influence of freshwater inflow and to physical processes such as hydrodynamic trapping (Chapter 4). Although food resources were highest in the upper reaches, maximum biomass was recorded in the middle reaches. Mysids usually comprised more than 70 % of zooplankton community biomass and their absence from water less than 8 to 10 ‰ suggests that the observed distribution is in response to both salinity tolerance and food resources. The euryhaline *Pseudodiaptomus hessei* by comparison, was always most abundant in the upper reaches.

In situ zooplankton community filtration rates provide a useful index for estimating the grazing pressure of zooplankton on natural particulate assemblages (Conover & Huntley, 1980), and the considerably higher values obtained in the Great Fish estuary reflect the potential for higher rates of trophic transfer and zooplankton secondary production compared with the Kariega estuary. The extent of grazing pressure exerted in the Great Fish estuary was associated with the higher herbivore standing stocks supported in this system due to the elevated trophic status as a result of freshwater inflow (Chapter 4). Although it is useful to compare results from the Kariega and Great Fish estuaries with other studies of *in situ* grazing by estuarine zooplankton communities, at the present time, these are restricted to several studies of the Newport river estuary in North Carolina, U.S.A. (Williams *et al.*, 1968; Fulton, 1984; Stearns *et al.*, 1987). Since these studies employed the gut fluorescence technique (Mackas & Bohrer, 1976) to provide an estimate of the fraction of primary production "removed" by the zooplankton communities, the results of this study are not strictly comparable.

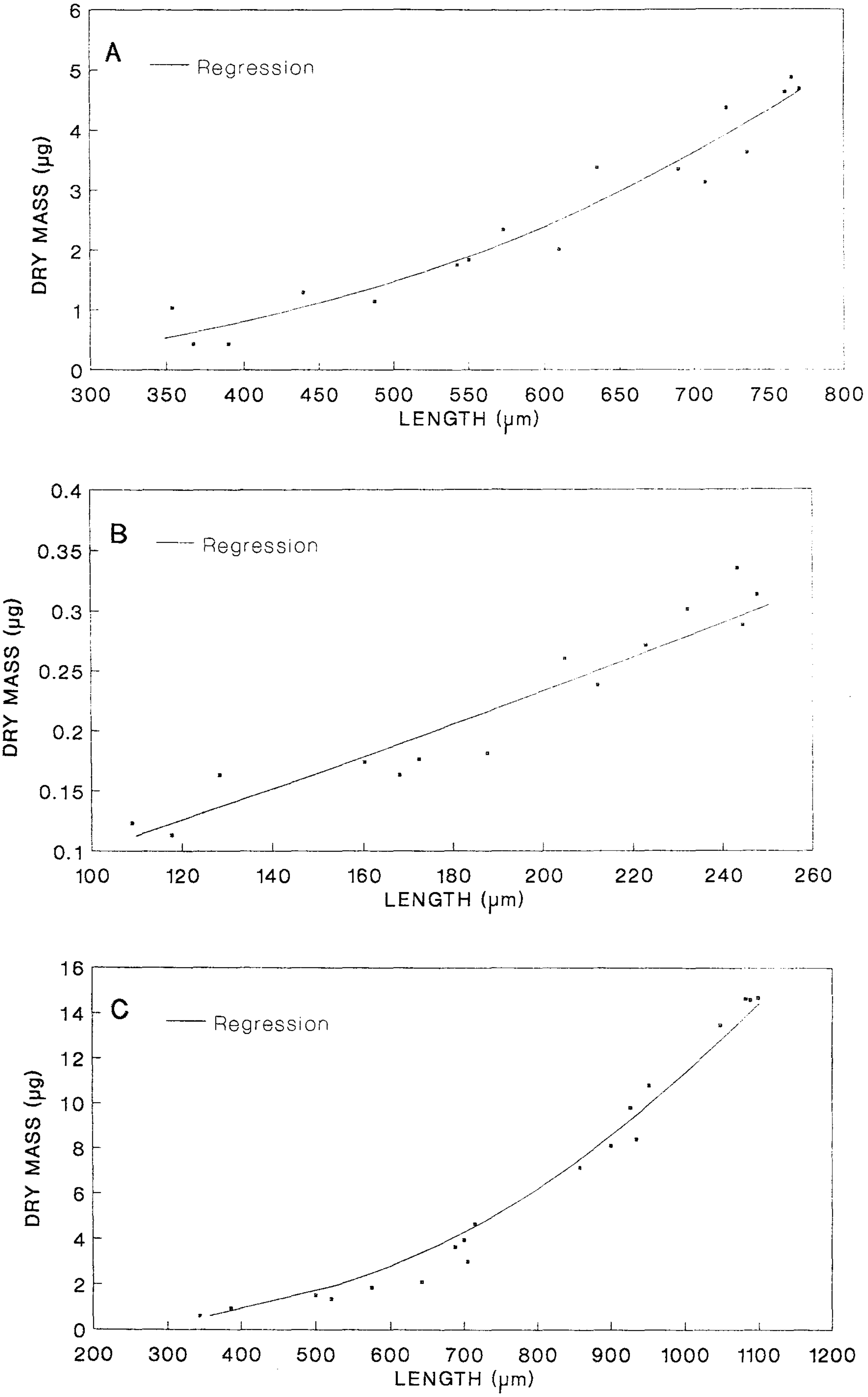
Grazing pressure varied considerably over a diel cycle in the Kariega estuary and in the upper reaches of the Great Fish, and was associated with the vertical migration movements of part of the zooplankton community. Diel grazing pressure was estimated on the assumption that measured daytime and nighttime community filtration rates (CFR's) were maintained relatively constant. The validity of this assumption requires testing, consequently, the relationship between diel vertical migration and feeding activity is investigated further in Chapter 6.

Although there was a positive relationship between zooplankton community biomass and CFR's, the correlation was low for both the Kariega and Great Fish estuary data, suggesting that other factors are important in influencing zooplankton feeding. Although variability in SFR's may be ascribed in part to changes in community composition, it is not possible to differentiate between this, and the influence of other environmental factors. Filtration rates have been demonstrated to vary in response to environmental factors, particularly temperature (Deason, 1980). In the Great Fish estuary, maximum CFR's were recorded at about 20 °C, which suggested that CFR's demonstrated a biphasic response to temperature over the seasonal range (e.g. Deason, 1980; Gulati *et al.*, 1982; Jarvis, 1987). In view of the wide scatter of the data points, further work is required to establish this beyond doubt. Although the influence of temperature on CFR's in the

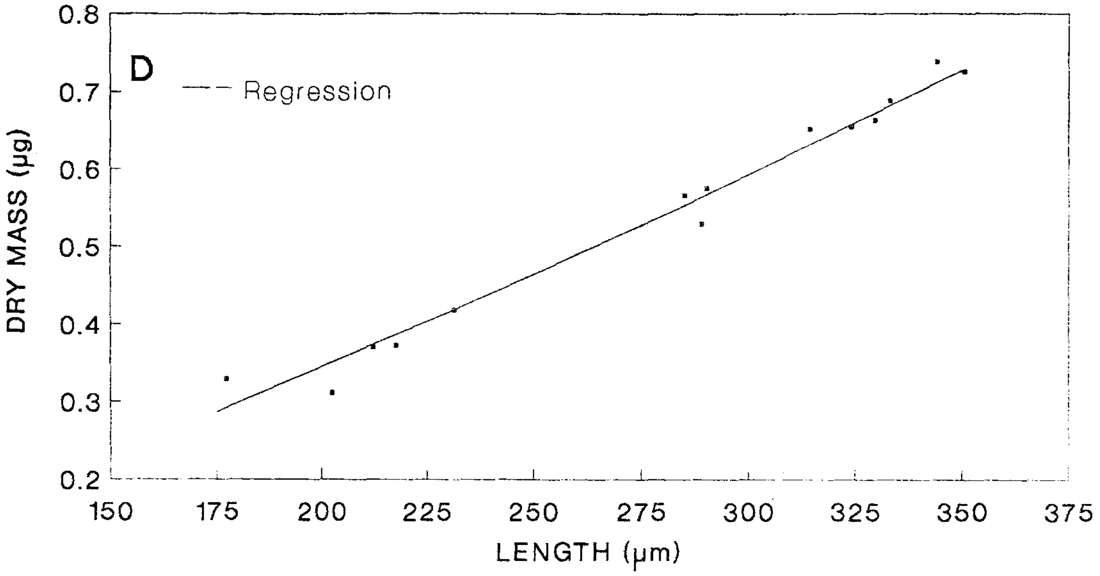
Kariega estuary appeared to be similar, it cannot be demonstrated with certainty due to the confounding influence of seston concentration. Despite the seasonal temperature regime, a lack of seasonality in CFR's was observed in either the Kariega or the Great Fish estuaries. This was probably due to changes in community biomass which were not correlated with seasonal temperature changes. In the Kariega this was in part due to food resource limitation, and in the Great Fish estuary due to fluctuating food resources resulting from sporadic freshwater inflow.

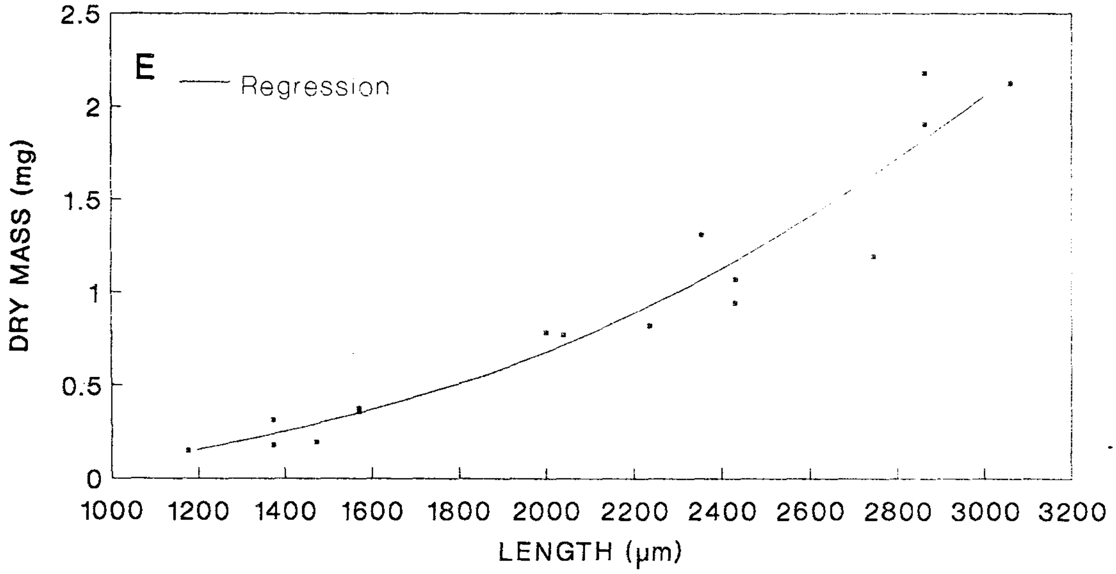
Attempts to ascribe variability in CFR's to changes in food quality and quantity were largely unsuccessful partly due to the co-variance of seston and chlorophyll in both the Great Fish and the Kariega estuaries, and the co-variance of seston with temperature in the latter. Consequently, it was difficult to determine the individual influences of these factors. Size, quality and quantity of food resources as well as feeding pre-history are considered to be of major importance in determining feeding rates in many zooplankton (see Introduction). Since the quality and quantity of food resources was demonstrated to be extremely variable, both seasonally and in the short term, resulting from the influence of freshwater inflow and tidal re-suspension (Chapter 4), the influence of these factors warrants further attention, aspects of which are investigated in Chapter 7.

CFR's and SFR's measured in this study represent the combined filtration rates of various species and life-history stages which potentially responded differently to the various parameters (e.g. food, temperature) measured. Interpretations of results were therefore difficult and I conclude that in future work, it will be necessary to determine the contribution of individual species, and life-history stage filtration rates in order to resolve the factors responsible for the variability in SFR's and CFR's observed.



Appendix A. Length-biomass relationships for *Acartia* spp. copepodites and adults (A), *Acartia* spp. nauplii (B), *Pseudodiaptomus hessei* copepodites and adults (C), *P. hessei* nauplii (D) and the mysid *Mesopdopsis slabberi* (E). Regressions given in the text.


D
Regression
DRY MASS (µg)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
150
175
200
225
250
275
300
325
350
375
LENGTH (µm)


E
Regression
DRY MASS (mg)
2.5
2
1.5
1
0.5
0
1000
1200
1400
1600
1800
2000
2200
2400
2600
2800
3000
3200
LENGTH (µm)

CHAPTER SIX

DIEL GRAZING PATTERNS AND THE INFLUENCE OF FEEDING ACTIVITY RHYTHMS, VERTICAL MIGRATION AND COMMUNITY COMPOSITION

6.0 INTRODUCTION

In recent years, the development of techniques for *in situ* feeding rate determination have enabled the grazing impact of zooplankton communities to be studied under near-natural conditions (e.g. Haney, 1973; Duval & Geen, 1976; Mackas & Bohrer, 1976; Roman & Rublee, 1981; Simard *et al.*, 1985; Stearns, 1986; Dagg *et al.*, 1989; Ishii, 1990). Generally, these experiments have been of short duration (usually < 1 h), and the results extrapolated to provide an estimate of grazing impact over a diel cycle (Duval & Geen, 1976). This assumes that a constant filtration rate is maintained (Hart, 1986).

Several studies have demonstrated short term variation in the feeding behaviour of zooplankton. This commonly involves an elevation of feeding rates at night (e.g. Hayward, 1980; Head *et al.*, 1984; Kleppel *et al.*, 1985; Christoffersen & Jespersen, 1986; Stearns, 1986; Bautista *et al.*, 1988; Tiselius, 1988; Dagg *et al.*, 1989; Durbin *et al.*, 1990), although more complicated bimodal activity patterns have been observed in which intensive feeding activity coincides with dusk and dawn (Haney & Hall, 1975; Duval & Geen, 1976; Mackas & Bohrer, 1976; Dagg & Grill, 1980; Simard *et al.*, 1985; Ishii, 1990). In order to make accurate predictions of diel grazing pressure, it is necessary to take into account short term variations of the feeding behaviour (Mourelatos *et al.*, 1989).

Increased feeding pressure is associated with the vertical migration of actively feeding zooplankton into the surface waters (e.g. Gauld, 1953; Haney, 1973; Boyd *et al.*, 1980; Dagg & Wyman, 1983; Baars & Oosterhuis, 1984; Head *et al.*, 1984; Mayzaud *et al.*, 1984a; Huntley *et al.*, 1987). This behaviour may be interactive or mutually exclusive (Roman *et al.*, 1988), since there is evidence of, for example, nocturnal feeding in non-migratory copepods (e.g. Mackas & Bohrer, 1976; Boyd *et al.*, 1980; Nicolajsen *et al.*, 1983; Ishii, 1990). In addition, there are instances of feeding rhythms associated with reverse migratory patterns (Ohman *et al.*, 1983), daytime feeding maxima (Starkweather, 1978) and an absence of diel feeding rhythmicity (Richman & Rogers, 1969; Haney, 1973; Mourelatos *et al.*, 1989).

The mechanism controlling vertical migration and feeding activity is important since it is ultimately responsible for the duration and extent of the grazing pressure. Enright and Hamner (1967) demonstrated that vertical migration may be triggered by changes in the light regime and a similar inference has been made for feeding periodicity, based upon the many observations of higher grazing rates after dark (Ishii, 1990). While light cues may control the timing of this behaviour, there is evidence to suggest that these activities may be under endogenous control (Stearns, 1986). Although physical factors appear to be implicated in the control of feeding and vertical migration, there may be considerable flexibility. Huntley & Brooks (1982), for example, have shown that vertical migration may cease during periods of low food availability.

Diel vertical distribution of the zooplankton communities in eastern Cape estuaries, as well as in South African estuaries in general, have been studied in some detail (Grindley, 1964; 1972; 1977). The existence of diel feeding rhythms in estuarine zooplankton species is limited to Hart's (1977) study of a non-estuarine population of *Pseudodiaptomus hessei*.

The majority of the dominant species migrate into the watercolumn after dark and descend before dawn (Grindley, 1981). There is evidence of endogenous control in at least one species (*Pseudodiaptomus hessei*) (Grindley, 1972; Hart & Allanson, 1976). The pattern of vertical migration differs between species and in some cases vertical migration is more pronounced in older life-history stages (Grindley, 1977). Changes in species and life-history stage composition are likely to accompany patterns of zooplankton abundance resulting from vertical migration. Consequently, grazing periodicity in which higher feeding rates occur after dark would be expected, and determined by the interaction between species/stage-specific feeding rates, feeding activity rhythms and vertical migration patterns.

By virtue of their estuarine existence, and partly due to special circumstances encountered in eastern Cape estuaries, zooplankton communities are subject to a number of unique biological and physical factors which may influence temporal feeding and vertical migration patterns. Vertical migration is restricted to movements of only a few metres due to the present shallow nature of most eastern Cape estuaries (Grindley, 1972). Tidal-current induced turbulence may prevent zooplankton from maintaining a preferred depth and obscure fine-scale patterns of vertical distribution (Huntley & Brooks, 1982; Fancett & Kimmerer, 1985). Turbulent mixing also ensures that food availability is relatively homogeneous throughout the watercolumn (Fancett & Kimmerer, 1985).

Grindley (1964) has shown that vertical migration may be restricted in the presence of low-salinity surface water. This behaviour is thought to enable zooplankton to maintain position in the estuary by avoiding outward flowing currents of freshwater. High turbidity associated with freshwater inflow results in altered light regimes, however the effect on zooplankton, which may rely on light cues in the timing of vertical migration, is not known.

In this study, I describe zooplankton community grazing patterns over several diel cycles in the Kariega and Great Fish estuaries and the role of feeding activity rhythms, community structure and vertical distribution of the zooplankton. Community filtration rates were measured *in situ* using the modified Gliwicz-Haney grazing chamber described in Chapter 5, and in addition, a modification of the method was employed to measure species-, and stage-specific filtration rates.

6.1 METHODS

6.1.1 SAMPLING.

Studies of diel vertical migration and feeding activity rhythms of the zooplankton communities were carried out on three occasions, on the 24/25 March and the 9/10 May 1988 in the Kariega estuary (K1 and K2), and on the 16/17 March 1989 in the Great Fish estuary (F1). Sampling was carried out from a boat in midstream at Station P in the Kariega and Station H in the Great Fish estuary (see Chapter 2). Samples were collected over a period of 18 hours, at approximately hourly intervals, incorporating the dark phase of the diel cycle and some of the light cycle. Measurements of water temperature, salinity, light penetration of the watercolumn and concentration of suspended particulate matter were also made.

Environmental variables.

i) Seston: Total particulate material (TPM, mg l^{-1}) was obtained from water pre-filtered through an 80 μm nytex mesh. Seston TPM was measured by the mass difference after filtering known volumes of water through pre-weighed Whatman GF/F glass-fibre filters, which were subsequently dried at 55 °C for 24 hours and re-weighed.

ii) Chlorophyll: Determinations were made on water samples pre-screened through a 35 μm nytex mesh and filtered onto Whatman GF/F filters. These were then wrapped in aluminium foil to exclude light and stored on ice until return to the laboratory. Subsequent extraction of pigments and spectrophotometric analysis followed the method outlined in Chapter 4, Section 4.1.2.

iii) Light profiles: Light profiles were made using a Li-Cor Model 185 photometer fitted with a submersible probe.

iv) Temperature/salinity: Temperature was recorded to the nearest half degree Celsius (°C) using a standard mercury-in-glass thermometer. Salinity (‰) was measured to the nearest part-per-thousand with an Atago S-10 refractometer.

Vertical distribution of zooplankton.

Analysis of vertical migration patterns was made from plankton samples collected at two depths using a 0.25 kW submersible centrifugal pump operated for a period of 5 minutes. The surface sample was collected at 0.5 metres depth and the near-bottom sample from 0.5 metres above the bottom sediments. Mid-channel depth was generally 2 to 2.5 metres. The mean volume output of the pump was measured at 114.1 ℓ min^{-1} for the upper strata and 113.9 ℓ min^{-1} for the lower strata. These values were used to convert sample counts to natural population densities.

Water from the pump samples was sieved through an 80 μm nytex mesh plankton net suspended at the water surface. The net contents were concentrated into the cod-end, transferred to formalin bottles and preserved in a final concentration of ≈ 4 % seawater-formalin solution. In the laboratory, identification, enumeration and measurements for length-biomass regression were made from subsamples taken using a modification of the method of Allanson & Kerrich (1961). Counting was restricted to dominant zooplankton types, which in any case account for > 95 % of the total community biomass.

6.1.2 DETERMINATION OF ZOOPLANKTON GRAZING RATES.

Community filtration rates.

Community filtration rates (CFR's) were obtained using the method outlined in Chapter 5, Section 5.1.2.

Specific filtration rates.

Species-specific filtration rates were derived by a modification of the procedure used to determine CFR's. Community filtration rates were obtained from compartment A of the grazing chamber in the normal way and, in addition, radio-labelled algal tracer cells were simultaneously injected into compartment B using the same syringe arrangement employed in compartment A (Figure 1). For these experiments, the plankton bucket attached to the bottom lid of compartment B was replaced by a screw-cap. At the end of the incubation, the usual procedure and processing of samples were applied to the contents of compartment A (Chapter 5, Section 5.1.2.). The contents of compartment B were drained

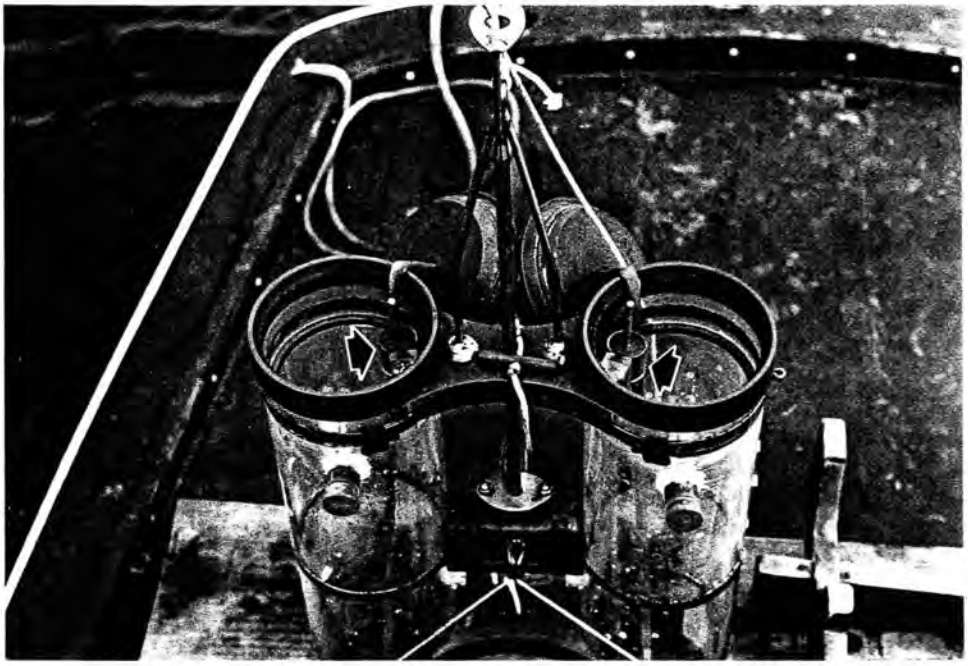


Figure 1. The *in situ* grazing chamber in the "open" position illustrating the twin syringe arrangement (arrowed) used for sampling, where specific filtration rates (SFR's), in addition to community filtration rates (CFR's), are determined by simultaneous labelling of compartments A and B.

through an 80 μm nytex mesh-bottomed tube and the zooplankton retained anaesthetized in carbonated water before being killed and preserved in a 4 % formalin-seawater solution.

In the laboratory, labelled zooplankton from compartment B were sorted at the earliest opportunity, in an attempt to avoid loss of label from preserved samples (e.g. Holtby & Knoechel, 1981). In practice, samples were processed between 16 to 30 hours after collection. Length-frequency distribution analysis was made from a subsample and the entire sample sorted by placing the contents in a petri dish and separating the dominant components under a binocular microscope. Each subcomponent was concentrated onto a 20 mm diameter 80 μm nytex mesh disc and placed in a scintillation vial containing 0.3 ml of quaternary ammonium hydroxide (Soluene 350 tissue solubilizer, Packard). The remaining procedure for scintillation counting was by the method outlined in Chapter 5, Section 5.1.2.

i) Species/stage-specific filtration rates (fractions of CFR) were calculated using the following formula:

Specific filtration rate (SFR, ml m^{-3} h^{-1}) =

$$\frac{A_{zj}}{\sum_{j} A_{zj}} \times F_a \qquad \text{.............} (1)$$

where, A_{zj} = activity (d.p.m.) of zooplankton community species/stage component *j* (*j*= 1,2,.....,n)
$\sum_{j} A_{zj}$ = summation of activity (d.p.m.) over all *j* (*j*=1,2,.....,n) species/stage components.
F_a = community filtration rate (ml m^{-3} h^{-1}) measured concurrently in compartment A.

ii) Biomass-specific filtration rates of the community components were then calculated by the following formula:

Specific filtration rate (SFR, ml h^{-1} μg dry $mass^{-1}$) =

$$\frac{V}{b_j} \text{ x } (1)$$

where, b_j = biomass (μg dry mass) of the species/stage sample j (j=1,2,.....,n)
V = compartment volume (m^3).

6.2 RESULTS

Environmental variables.

Ambient water temperature recorded during K1, K2 and F1 was 24.5, 20.5 and 22.5 °C respectively. There was no temperature stratification with depth and values remained constant for the duration of each survey. In the Kariega estuary, salinity was uniform at 35 ‰, however in the Great Fish estuary, values ranged from 6 to 32 ‰ as a result of the tidal movement of partially-stratified water. Seston concentrations (measured as total particulate material, TPM, mg l^{-1}) varied considerably, presumably as a result of tidal re-suspension, and in the Great Fish estuary, additionally due to tidal movement of a more pronounced upstream/downstream seston concentration gradient. Diel patterns of variability are shown in Figure 2. Diel light cycles (day/night) and predicted tides are superimposed on diel vertical distribution graphs (see below). Cloud cover in each study was minimal, and played no part in determining watercolumn light profiles. The moon was in the first quarter during K1 and F1 and in the last quarter during K2.

6.2.1 DIEL VERTICAL DISTRIBUTION PATTERNS.

Interpretation of vertical migration movements from trends in zooplankton distribution were difficult, principally due to the effect of alternate upstream/downstream displacement of the zooplankton community caused by tidal currents, combined with the limited extent of vertical migration imposed by the shallow nature of these estuaries. Consequently, data sets were smoothed using a 3-point moving average. Community, species-, and stage-specific diel vertical migration patterns are described as follows:

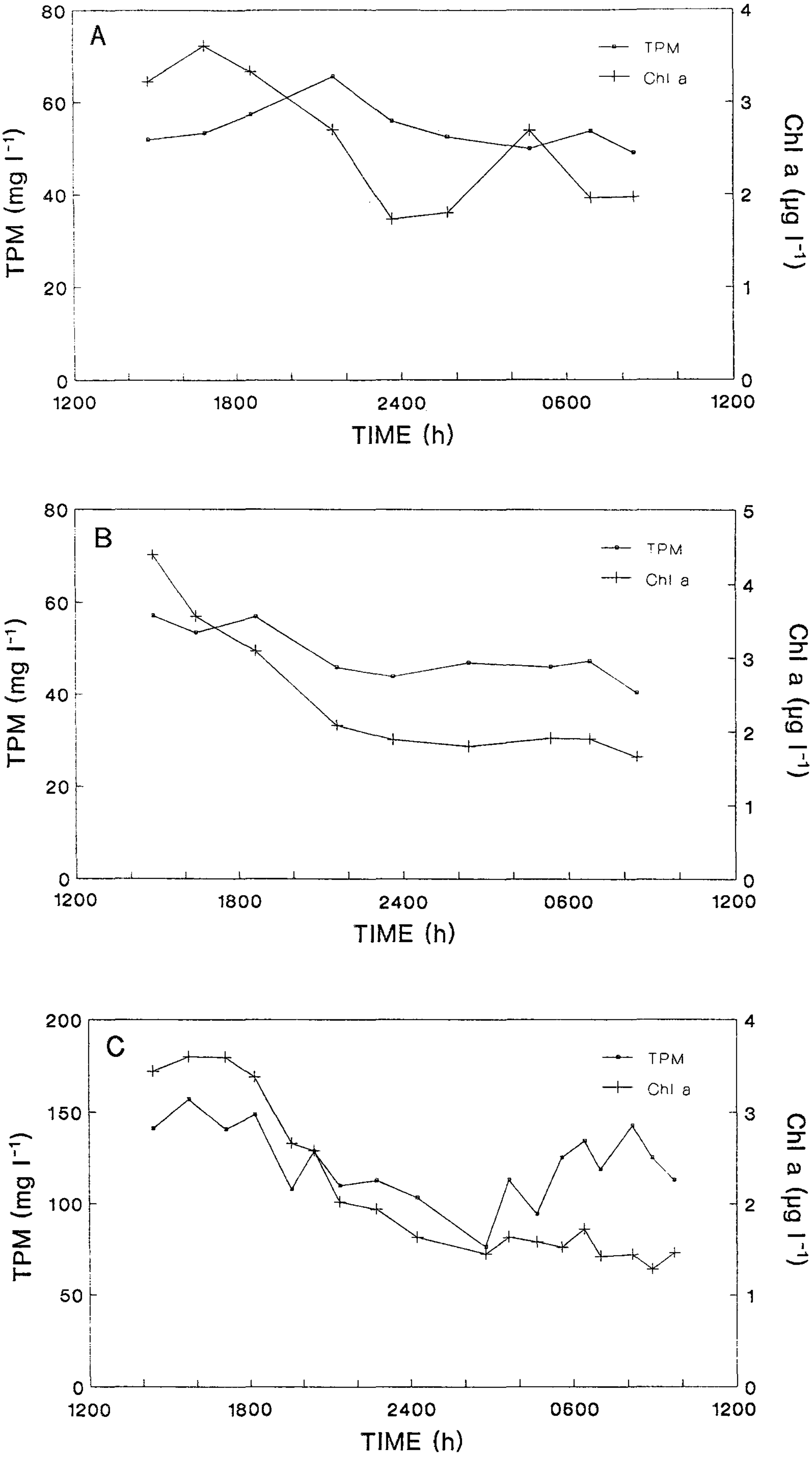


Figure 2. Diel variation in Seston (TPM, mg l^{-1}) and Chlorophyll *a* (µg l^{-1}) during diel cycles K1 (A), K2 (B) and F1 (C).

a) Total biomass.

In each of the three diel surveys, community biomass was elevated at night as a result of the vertical migration activity of the zooplankton (Figure 3). Concurrent increases in biomass in near-bottom samples indicate that the zooplankton migrated from a position below 0.5 metres above the sediment surface. During K2 and F1, the increase in community biomass was characterized by a single peak occurring during the middle of the night, however, the pattern in K1 was more complex with additional peaks of abundance at dusk and dawn. A combination of differences in community composition and species-, and stage-specific vertical migration activity patterns provide the most probable explanation for the precise diel vertical distribution patterns observed in each survey. These are described below:

b) Copepodites and adults.

i) *Pseudodiaptomus hessei* (Figure 4): This species contributed substantially to zooplankton community biomass in both the Great Fish and the Kariega estuaries. The diel pattern of distribution was unimodal and similar in each of the surveys undertaken. The onset of migration was timed around dusk and the majority of copepods had returned to the sediments before dawn. A single peak of abundance occurred at the surface at approximately midnight during K1 and K2 but somewhat earlier (± 2200 h) during F1. Although this difference may be real, it is thought likely that the decrease in abundance at the surface after 2200 h is more likely a result of decreased biomass associated with higher salinity water on the incoming tide. The reduced biomass observed in the near-bottom samples in the middle of the night during K1 and F1 was probably associated with the migration of the majority of the population into the upper strata. The nocturnal distribution pattern suggests that light levels are implicated in the control of vertical migration.

Hart & Allanson (1976) presented evidence of endogenous control in a study conducted on a population of *Pseudodiaptomus hessei* from a deep freshwater lake. According to Grindley (1972), this mechanism of control accounts for the observation that *P. hessei* only begins to migrate **after** dusk and returns to the sediments **before** dawn. Although the abundance of *P.hessei* was substantially higher after dark, from the data it is not

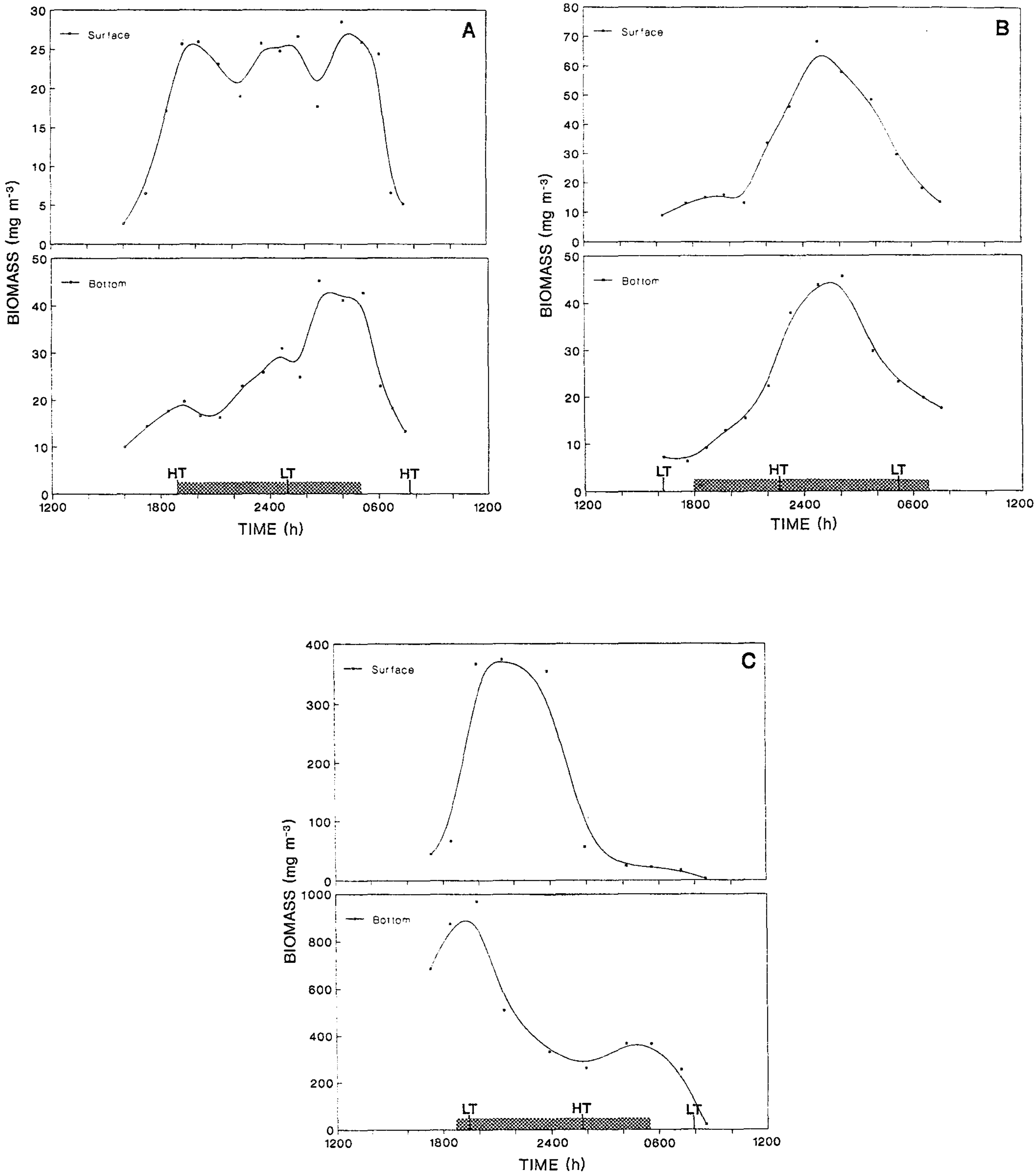


Figure 3. Fluctuations in zooplankton community biomass over three diel cycles, K1 (A), K2 (B) and F1 (C). Diel vertical migration patterns were determined after smoothing the data using a three-point moving average. Changes at the near-surface (upper panel) and near-bottom (lower panel) of the watercolumn are shown. The day/night cycle and predicted tides are shown along the X-axes.

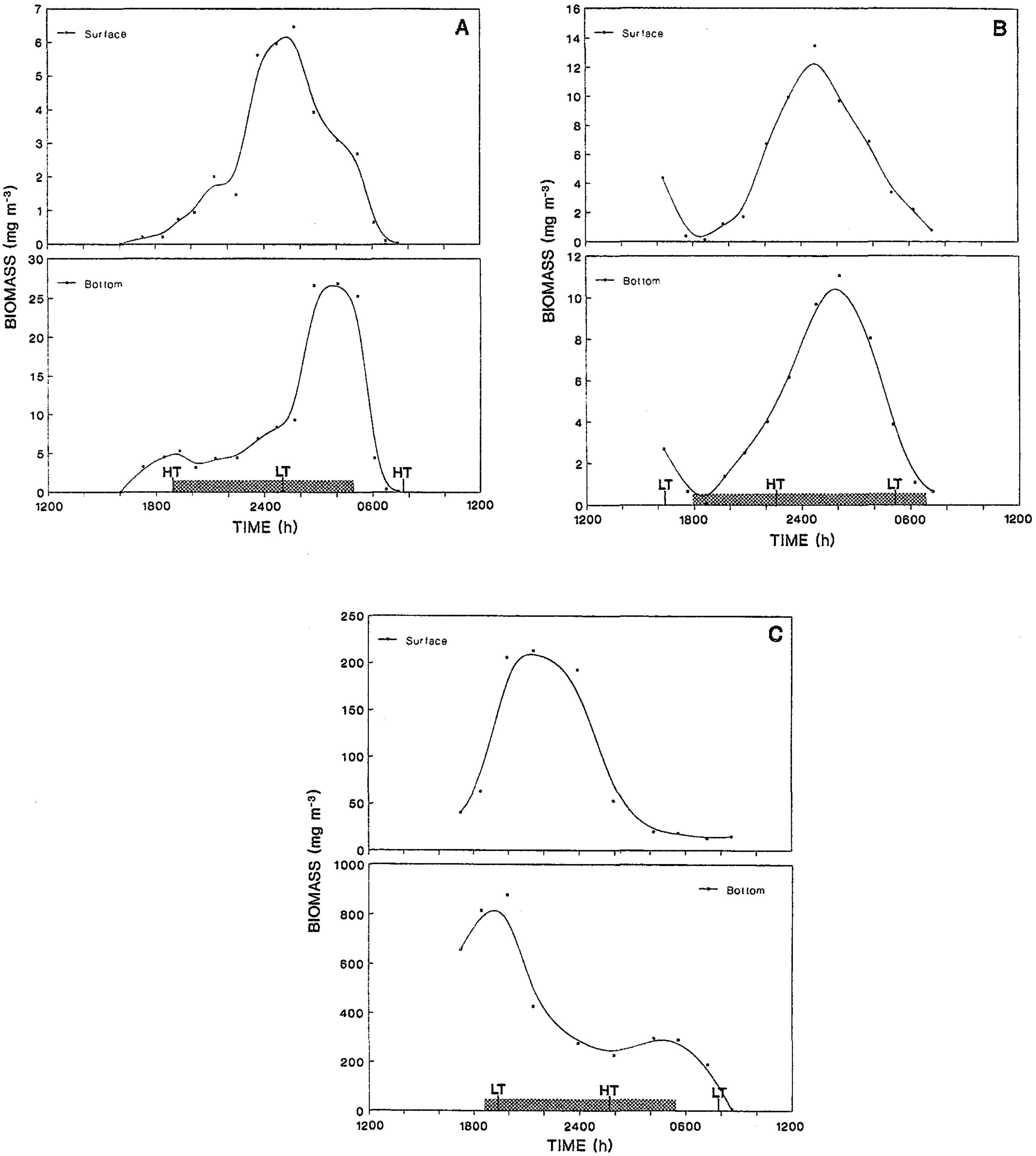


Figure 4. Fluctuation of zooplankton biomass comprising copepodites and adults of *Pseudodiaptomus hessei* over three diel cycles, K1 (A), K2 (B) and F1 (C). Changes at the near-surface (upper panel) and near-bottom (lower panel) of the watercolumn are shown. The day/night cycle and tide state are shown on the X-axes.

possible to confirm the exact timing of the onset of migration although in this case there did appear to be some activity before dark.

The absence of individuals captured in pump samples from the lower strata (≈ 0.5 metres above the sediments) during the day suggests that this species is resident below this depth during daytime. According to Fancett & Kimmerer (1985), members of the family Pseudodiaptomidae are demersal, and live in association with the sediments during the daytime. There is evidence that *P. hessei* not only attaches to the sediments but actually burrows beneath the surface (Grindley, 1972; Hart & Allanson, 1976).

ii) *Acartia* spp. (Figure 5): Copepodites and adults showed a distinct elevation in biomass at night as a result of nocturnal vertical migration activity. *Acartia* is not thought to be benthically associated during the day, however the low numbers sampled in the near-bottom depth samples during daylight indicate that they are resident below this depth during daytime. Although *Acartia* spp. are generally abundant nocturnally, Grindley (1977) has reported occasional surface elevations in biomass during daylight.

A comparison of vertical migration during K1 and K2 revealed that although the migratory activity was nocturnal in both cases, the patterns of diel distribution were dissimilar. A subsequent inspection revealed that on the second occasion (K2), adult *Acartia* spp. were comprised almost entirely of *A. longipatella*, whereas during the previous survey (K1), numbers were more evenly divided between both *A. longipatella* and *A. natalensis*. It is likely that the differences in diel distribution reflect different vertical migration behaviours. Assuming that this interpretation is correct, the diel distribution pattern of *A. longipatella* is unimodal, with peak surface biomass occurring at about midnight. By contrast, the diel distribution of *A. natalensis* exhibited a characteristic bimodal pattern with surface biomass peaks at dusk and dawn and a "midnight sink" to greater depth. The three peaks of abundance that occurred in the first survey therefore represent the overlap of a unimodal, and a bimodal vertical migration pattern. *A. natalensis* and *A. longipatella* show seasonal succession (Wooldridge & Melville-Smith, 1979) with the former more abundant in summer, and replaced by the latter in winter. Therefore, the two surveys, K1 and K2 are representative of a transitional autumn, and a winter state, respectively.

Further work is required to determine conclusively whether different vertical migration behaviours are employed, or whether these differences simply represent the variable nature of vertical migration in South African estuarine zooplankton (Grindley, 1977).

c) Naupliar larvae.

The biomass of *Pseudodiaptomus* and *Acartia* naupliar larvae showed periodic elevations which were apparently synchronous, but not linked to the day/night cycle (Figure 6). According to Grindley (1972), the nauplii of *P. hessei* and *Paracartia* (*Acartia*) *longipatella* do not undergo diel vertical migration. In other studies (e.g. Huntley & Brooks, 1982), it has been shown that the onset of migration begins in the nauplius stage III larvae. In this study, the density/biomass ratio (not shown) for both *P. hessei* and *Acartia* spp. nauplii was lower at night, indicating a higher proportion of late-stage nauplii during this time. The fluctuations in biomass exhibited periodic peaks during daytime as well as nighttime which suggests that the majority of nauplii did not migrate in response to light. The possibility remains that the fluctuations observed were tidally-mediated, either patterns of distribution due to turbulence, or the movement of patchiness into and out of the sampling station. There is no consistent evidence to suggest that migration occurred in response to tidal state.

d) Mysids.

Mysids (Figure 7) were represented by one species, *Mesopodopsis slabberi*, a common component of estuarine zooplankton which is also found in the open ocean (Wooldridge & Erasmus, 1980). Although this species is known to undergo diel vertical migration (Grindley, 1972), the distribution of biomass recorded in the Great Fish estuary during F1 appeared to be tidally-mediated rather than as a result of vertical migration movements. Although vertical migration patterns may contribute to the observed pattern of distribution, it is thought that tidal effects are considerably more important since *Mesopodopsis* was nearly always found in highest numbers associated with the region of mixing, or "saltwedge".

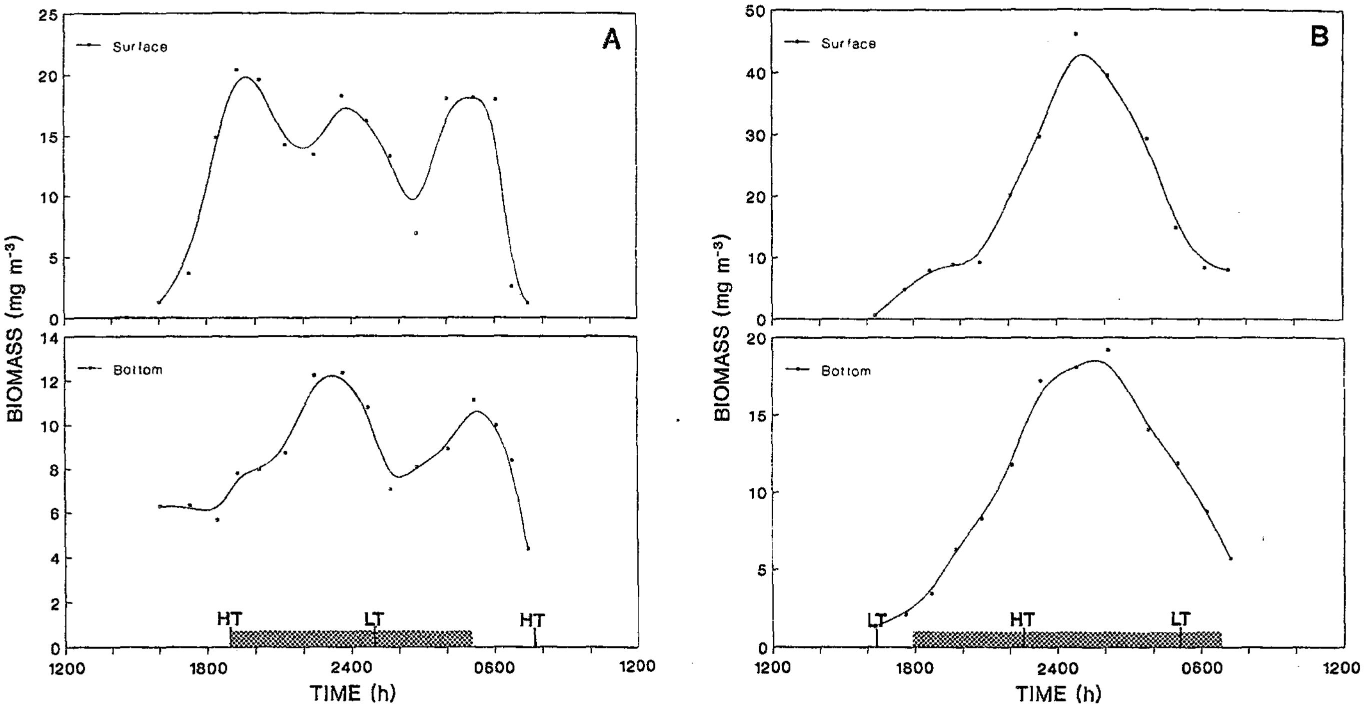


Figure 5. Fluctuation of zooplankton biomass comprising copepodites and adults of *Acartia* spp. (*A. natalensis* and *A. longipatella*) over two diel cycles, K1 (A) and K2 (B). Changes at the near-surface (upper panel) and near-bottom (lower panel) of the watercolumn are shown. The day/night cycle and tide state are shown on the X-axes.

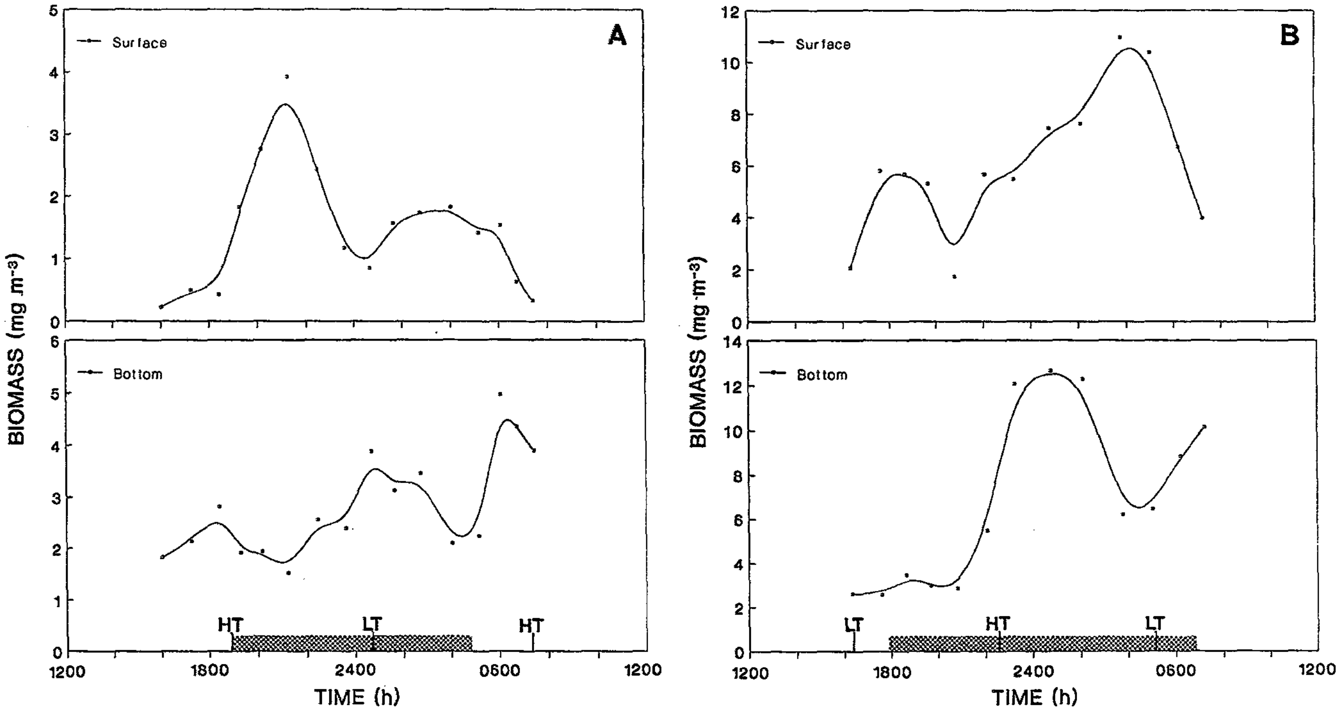


Figure 6. Diel fluctuation of zooplankton biomass comprising calanoid naupliar stages. (A), (B) and (C) show the changes in biomass of *P. hessei* nauplii during diel cycles K1, K2 and F1, respectively. (D) and (E) show the changes in *Acartia* spp. nauplii during diel cycles K1 and K2, respectively. (upper panel = near-surface, and lower panel = near-bottom of the watercolumn). The day/night cycles and tide state are shown on the X-axes.

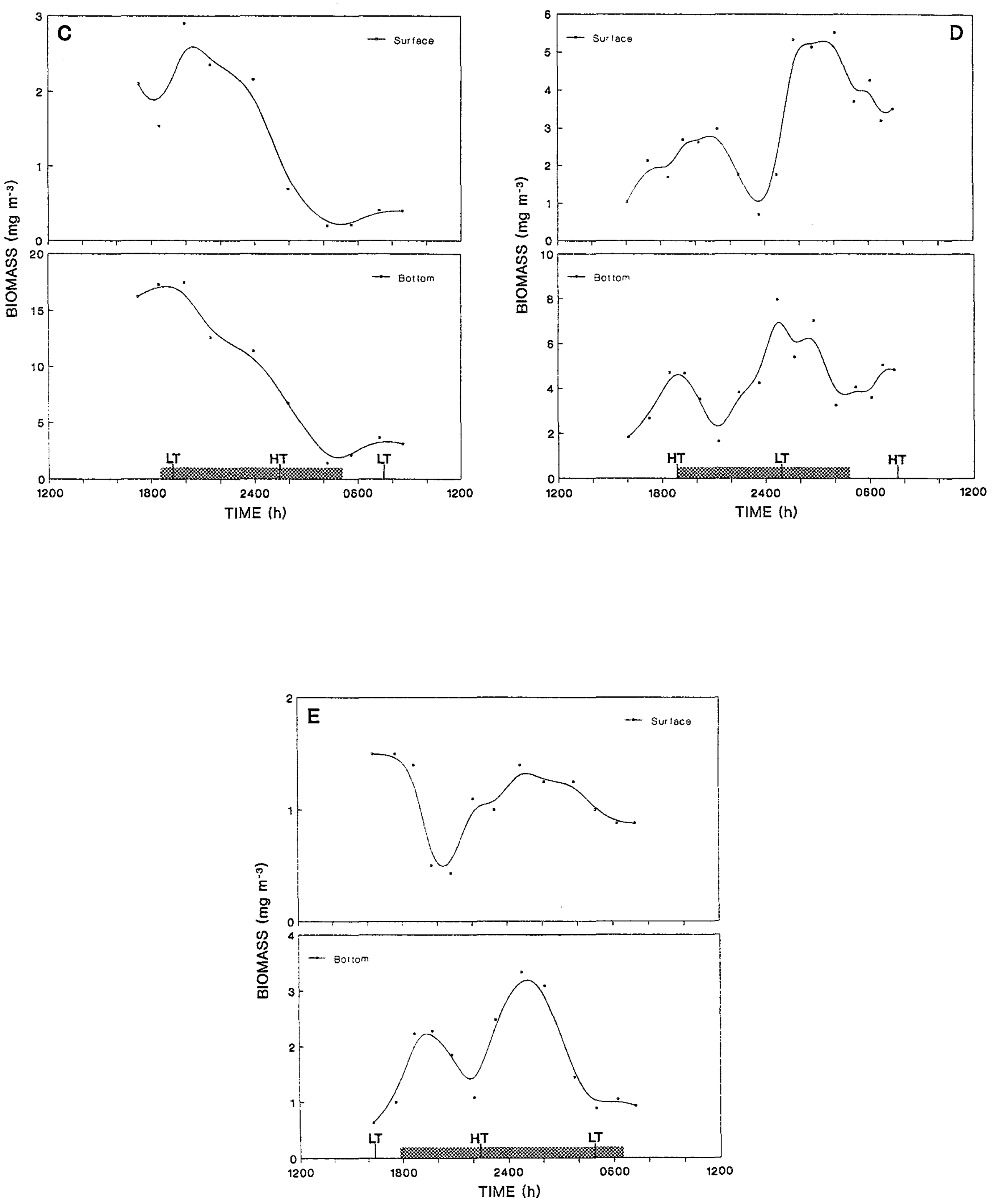


Figure 6 (continued).

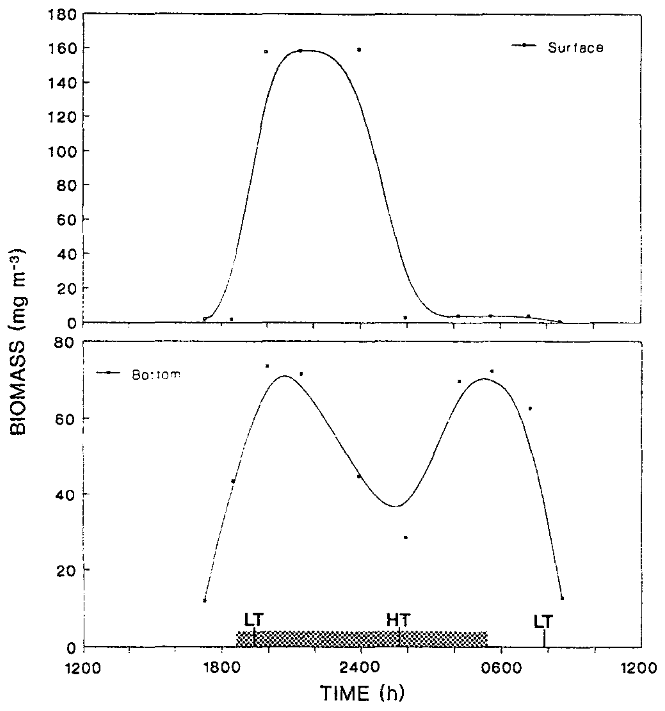


Figure 7. Fluctuation of zooplankton biomass comprising the mysid *Mesopodopsis slabberi* during diel cycle F1. Changes at the near-surface (upper panel) and near-bottom (lower panel) of the watercolumn are shown. The day/night cycle and tide state are shown on the X-axes.

6.2.2 DIEL COMMUNITY FEEDING.

Diel community filtration patterns.

Diel community filtration rates measured during this study were generally higher during the night and these observations were consistent with elevated community biomass due to nocturnal vertical migration. The diel feeding pattern varied between the three diel surveys. The pattern was bimodal during K1, approximately unimodal during K2 and variable during F1 (Figure 8). During K1 and K2, the pattern of community filtration was associated with the diel distribution of biomass, although on both occasions, peaks in biomass around midnight did not coincide with elevations in filtration rate. The bimodal pattern observed in K1 was probably indirectly as a result of the abundance and diel vertical migration pattern of *Acartia natalensis* which exhibited dusk and dawn surface peaks. The low community filtration rate/biomass ratio around midnight (Figures 8a and b) infers that biomass-specific filtration rates around midnight were generally low, or that there was a shift in community composition to a species with a lower specific filtration rate. The less definable pattern of community filtration activity in the Great Fish estuary is attributed to the less uniform nature of the environment in which patterns of zooplankton abundance were more variable. Diel community grazing pressures were estimated by integrating the area under the curve, formed by linking adjacent data points, although this necessitated the extrapolation of daytime values to a full diel cycle (Figure 8, Table 1).

Although the majority of diel grazing pressure occurred nocturnally, daytime values accounted for a significant fraction (Table 1). Daytime filtration rates were largely determined by the non-migratory zooplankton, particularly the naupliar stages, and to an extent by migratory zooplankton at dusk and dawn.

Table 1. Zooplankton community grazing pressure (% d^{-1}) over a complete diel cycle for K1, K2 and F1. Grazing pressure obtained by integrating the area under the curve formed by linking the adjacent community filtration rate data points (Figure 8a, b and c, upper panels) and extrapolating to a full 24 hour period. The contributions of nighttime and daytime grazing to diel total, are also shown.

DIEL SURVEY	DIEL GRAZING PRESSURE (% d^{-1})	NIGHTTIME GRAZING PRESSURE (% d^{-1})	DAYTIME GRAZING PRESSURE (% d^{-1})
Kariega (K1)	7.0	63.6	36.4
Kariega (K2)	13.0	86.4	13.6
Great Fish (F1)	49.2	75.8	24.2

Influence of community composition and biomass.

The community biomass values obtained from the *in situ* grazing chamber were generally higher than values obtained from pump samples used to determine diel vertical migration patterns. Consequently, no attempt was made to compare data collected by different sampling methods.

Species composition may be important in determining biomass-specific filtration rates (Tiselius, 1988). Species composition in eastern Cape estuaries depends partly on patterns of seasonal abundance and succession, but also on the characteristic hydrography of the system. The highest community filtration rates were measured in the Great Fish estuary where the recorded biomass commonly reached upwards of 1000 mg m^{-3} and on one occasion over 6000 mg m^{-3} (Figure 8c). Although the community filtration rates measured in the Great Fish estuary are associated with highest recorded biomass, the results of the two diel surveys undertaken in the Kariega estuary suggest that zooplankton community filtration rates are not directly correlated with community biomass. Diel grazing pressure during the second survey conducted in the Kariega estuary was approximately double the value obtained during the previous survey despite the fact that community biomass was substantially less.

Although there is considerable variation in diel biomass-specific filtration rates (SFR's) (Figure 9), between-survey comparisons show that SFR's are lowest in K1, intermediate

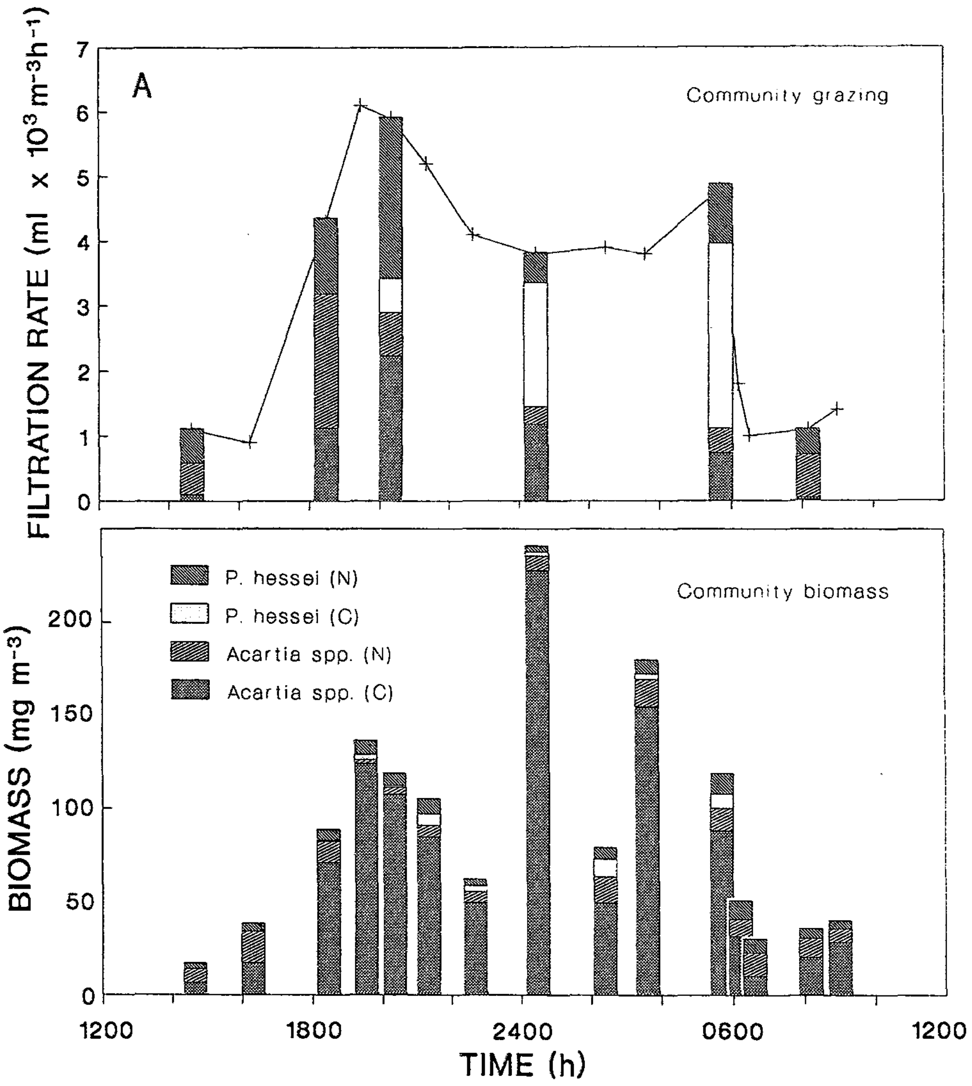


Figure 8. Fluctuations in community filtration rates (CFR's) (upper panel) and corresponding community biomass (lower panel) measured over three diel cycles, K1 (A), K2 (B) and F1 (C), using the Gliwicz-Haney chamber. Species-, and life-history stage contribution to total biomass is shown for all samples in the lower panel. In the top panel, species-, and life-history stage contribution to grazing pressure is shown for the samples in which specific filtration rates (SFR's) were obtained.

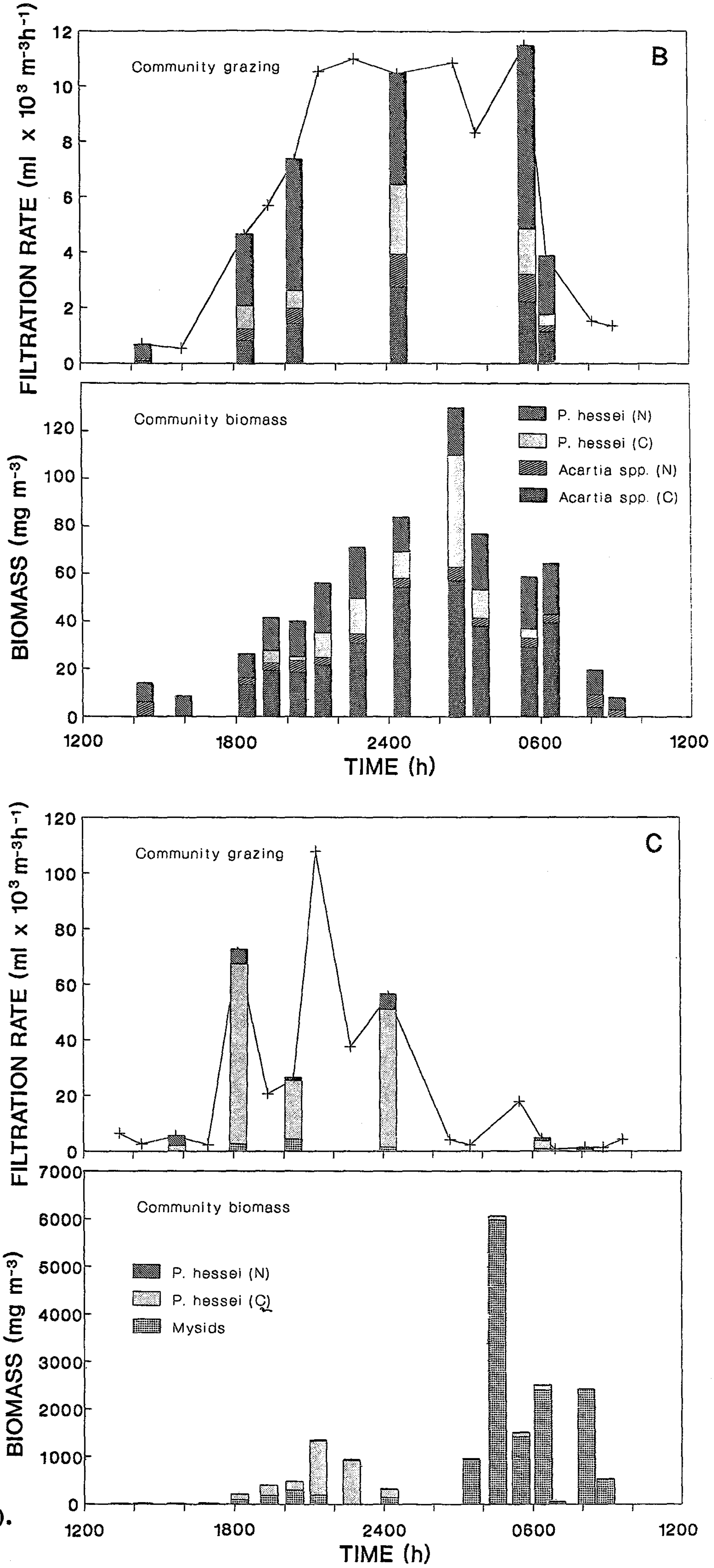


Figure 8 (continued).

in K2, and highest in F1 with the exception of the last six data points, in which mysids contributed most of the community biomass. The change in community composition provides an explanation for these observations. During K1, *Acartia* spp. nauplii and copepodites contributed up to 94 % of community biomass (Figure 8a), but considerably less during K2 (up to 69 %) and were absent in F1. Low SFR's in the Great Fish occurred in the presence of high mysid biomass. Filtration rates generally showed a positive correlation with community biomass, however, this relationship is modified by community composition. Thus, in situations where *P. hessei* dominated the biomass, SFR's were higher than in situations where either mysids (in the Great Fish estuary), or *Acartia* spp. (in the Kariega estuary), were abundant.

Species/life-history stage diel filtration rates.

Species-, and life-history stage-specific filtration rates obtained for the dominant zooplankton over the three diel surveys are shown in Figure 10, and the ranges are summarized in Table 2. Despite the considerable variability, results confirm that diel mass-specific filtration rates of *Pseudodiaptomus hessei* were generally higher, up to an order of magnitude greater than those obtained for either *Acartia* spp. or the mysid *Mesopodopsis slabberi*. With the exception of the results from the Great Fish estuary survey, specific filtration rates of *P. hessei* copepodites and adults, were higher than those of the nauplii. The converse was true for *Acartia* spp., in which naupliar specific filtration rates were higher.

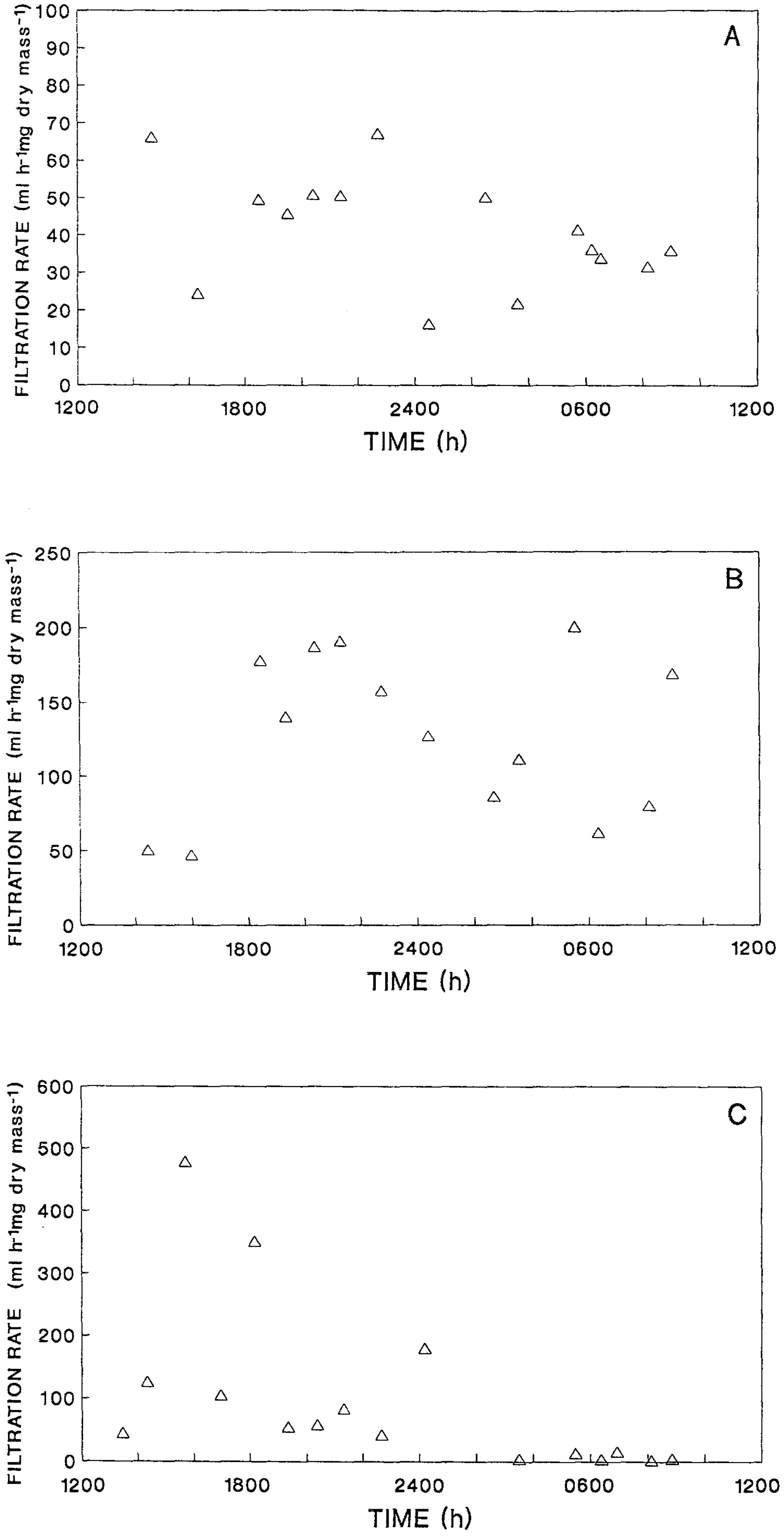


Figure 9. Fluctuations in zooplankton community biomass-specific filtration rates (SFR's) measured over three diel cycles, K1 (A), K2 (B) and F1 (C).

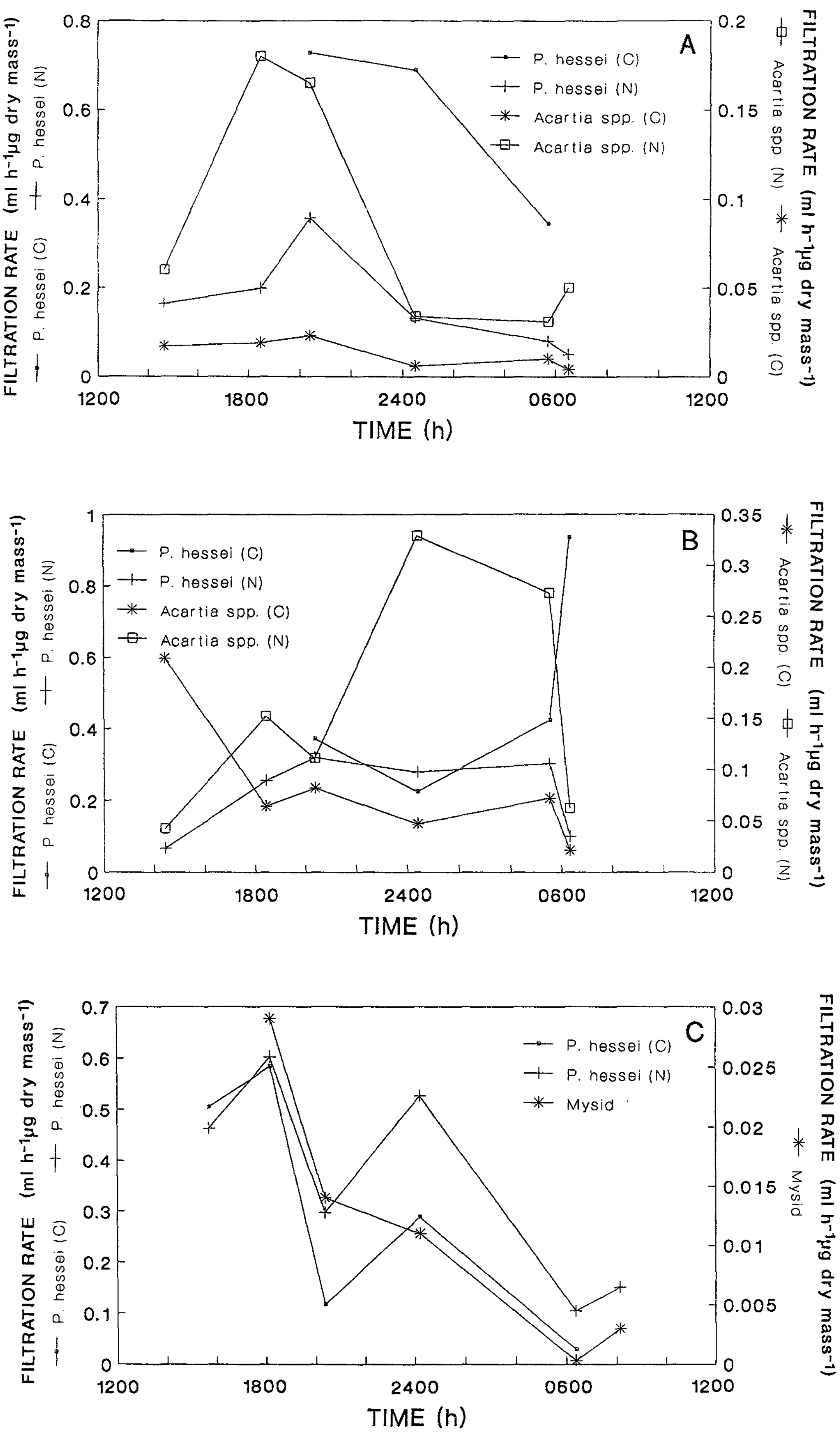


Figure 10. Fluctuations in species-, and stage-specific filtration rates (SFR's) measured over three diel cycles, K1 (A), K2 (B) and F1 (C).

Table 2. Ranges in specific filtration rates (ml h^{-1} μg dry mass^{-1}) determined for each species and/or life-history stage over the course of three diel cycles (K1, K2 and F1).

	FILTRATION RATE (ml h^{-1} μg dry mass^{-1})		
SPECIES/STAGE	KARIEGA (K1)	KARIEGA (K2)	GREAT FISH (F1)
P. hessei			
a) copepodites:	0.344 -0.728 (n=3)*	0.224 -0.935 (n=4)*	0.029 -0.584 (n=5)*
b) Nauplii:	0.050 -0.357	0.066 -0.319	0.105 -0.602
Acartia spp.			
a) copepodites:	0.004 -0.023	0.021 -0.209	none
b) nauplii:	0.031 -0.180	0.042 -0.329	none
Mespodopsis slabberi	none	none	0.003 - 0.009

*Range taken from six samples unless otherwise indicated.

The variation in diel filtration rates provides inconclusive evidence of diel feeding activity rhythms since no consistent patterns were evident in any of the feeding groups. Filtration rates, however, were only determined for animals present in the watercolumn, and could not be obtained for animals inhabiting near-bottom water or the sediment surface during the daytime.

6.3 DISCUSSION

6.3.1 VERTICAL MIGRATION.

The patterns of diel vertical migration observed in this study were generally in agreement with the results of Grindley (1972) based on observations of other South African estuaries and lagoons. Migration patterns were characterized by the "normal" pattern of nocturnal diel vertical migration described by Hutchinson (1967). Migratory behaviour was characterized by a dusk ascent from the bottom, and a dawn return to the sediments, although there is circumstantial evidence that *Acartia natalensis* exhibits the more complex "twilight" migration pattern which involves a "midnight sink". It is assumed that light provides the stimulus for zooplankton undertaking diel migration movements (e.g. Duval & Geen, 1976; Simard *et al.*, 1985; Stearns, 1986), although in at least one of the species (*Pseudodiaptomus hessei*), there is evidence from other studies that these movements are under endogenous control, with light serving only to synchronize the circadian rhythm (Hart & Allanson, 1976; Grindley, 1977). There was no evidence of; i) migration in response to tidal flow as described by Wooldridge & Erasmus (1980), or ii) inhibition of vertical migration by salinity stratification (Grindley, 1964).

Zooplankton may either migrate in synchrony, with the result that depth distributions are obvious as distinct bands, or they may migrate from a common depth and become evenly distributed throughout the watercolumn (Lampert, 1989). The latter situation applies in this study since, at the onset of dusk, numbers of zooplankton increased at the surface and near bottom simultaneously and further changes in distribution were generally reflected at both depths. Since the change in distribution with time may only represent the net effect of migratory movements, the dispersion of animals throughout the watercolumn may indicate considerable individual variation in the timing and direction of these movements (Lampert, 1989). Alternatively, turbulence generated by the relatively strong tidal currents, coupled with the shallow depth of the estuaries, may prevent the zooplankton from maintaining a preferred depth (Huntley & Brooks, 1982; Fancett & Kimmerer, 1985).

Ontogenetic change in diel vertical migration behaviour, which was observed in both *Acartia* spp. and *P. hessei*, is not unusual in copepods, having been described in a number of studies (Grindley, 1972; Hart & Allanson, 1976; Pearre, 1979; and references cited therein; Huntley & Brooks, 1982). The onset of vertical migration is believed to occur in the copepodite IV of *Calanus pacificus* (Frost, 1988), although Huntley & Brooks (1982) have provided evidence of limited migratory movements in as early as the stage III nauplius. Although Grindley (1972) found no evidence of vertical migration in either *Pseudodiaptomus* or *Acartia* spp. nauplii, results of this study indicated that late stage nauplii do undertake some migratory movement. The adaptive significance is discussed further in Section 6.3.3.

6.3.2 DIEL FEEDING PATTERNS.

Feeding periodicity.

Zooplankton community grazing pressure is often elevated at night and associated with nocturnal diel vertical migration patterns (e.g. Dagg & Wyman, 1983; Baars & Oosterhuis, 1984; Head *et al.*, 1984). Similar patterns of grazing pressure were observed in this study. The majority of the zooplankton community migrated into the watercolumn at night and there was an associated increase in community grazing pressure. Although feeding activity was elevated at night, daytime grazing accounted for up to 36 % of the diel total. This was due to non-migrating naupliar larvae which, depending on their presence and abundance, may be important in determining the extent of daytime grazing as well as the overall pattern of diel grazing pressure.

Unlike their many deep-lake, or oceanic counterparts, which may migrate to deeper water during daytime, estuarine zooplankton migrate to the bottom where they remain on or near the sediments (Grindley, 1972; Stearns, 1986). Most of the migratory component of the community was therefore not sampled throughout the day, and evidence of cessation of feeding during this time is largely circumstantial. Hart (1977) questioned the ability of *P. hessei* to feed effectively while living infaunally during the daytime. The majority of individuals sampled from the lower strata by the plankton pump shortly after the onset of migration were found to be devoid of gut contents, suggesting that they had not been feeding. Daytime cessation of feeding in nocturnally migrating copepods has not been conclusively shown, however, and consequently this point warrants further investigation.

Filtration rates.

a) Specific filtration rates.

There were marked differences in biomass-specific filtration rates despite the large variation measured. Specific filtration rates can vary in response to life-history stage composition since the feeding rate, proportional to body size, may not be the same for small copepods relative to larger ones (Dagg & Grill, 1980). In addition, the onset of feeding only occurs in the stage III nauplius onwards in some species (Huntley & Brooks, 1982), consequently a change in community composition in which greater numbers of non-feeding stages contribute to naupliar biomass, would therefore yield an apparently lower specific filtration rate.

Some species have higher energy requirements related to the periodicity in feeding associated with vertical migration. Fancett & Kimmerer (1985) have shown that *Pseudodiaptomus* is able to store lipids, which enhances starvation resistance. They suggested that feeding rates are elevated during periods of active feeding so that sufficient energy is ingested to convert to reserves.

Community structure therefore plays an important role in determining biomass-specific community filtration rates. Community structure may change temporally due to seasonal succession as well as over diel cycles due to differences in species-, or life-history stage vertical migration patterns. Therefore, some knowledge of community structure is required to make accurate predictions of community filtration rates based on community biomass.

b) Feeding activity rhythms.

A number of studies have demonstrated the presence of feeding activity rhythms which are independent of food availability and may serve to modify day/night feeding periodicity (Dagg & Grill, 1980; Nicolajsen *et al.*, 1983; Welschmeyer *et al.*, 1984; Stearns *et al.*, 1987; Bautista *et al.*, 1988). Although the occurrence of these feeding rhythms is common, they are by no means universal (Haney, 1973; Haney & Hall, 1975; Mourelatos *et al.*, 1989).

The variations in filtration rates observed in this study showed no particular pattern, and were not consistent between cycles. It seems unlikely, therefore, that feeding rhythms were primarily responsible for the variations observed. Other studies have shown 3 to 4.5-fold increases in filtration rate as a result of feeding activity rhythms (Stearns, 1986; Stearns *et al.*, 1987; Kleppel *et al.*, 1988). These were considerably less than the amplitude in the filtration rates measured in this study. Inaccuracies in the method employed to determine specific filtration rates cannot be discounted, however, it is significant that the between-survey range of values recorded for each species-, and life-history stage were in all cases comparable (see Table 2).

Although the existence of a feeding rhythm cannot be discounted, I conclude that the response of the zooplankton to other factors are responsible for the variability observed which obscure any feeding rhythm evident. The filtration rate of zooplankton is known to vary in response to several factors which include the size of food particles, their concentration and quality, as well as environmental factors, notably temperature (Chapter 5, Introduction). The concentration of the food resource was the only variable to change significantly over the course of a diel cycle. This was mostly due to patterns of tidal re-suspension, and also in the Great Fish estuary as a result of the tidal movement of an upstream/downstream seston gradient. The precise form of the functional response curve and the concentration at which maximal feeding rates are attained (the "incipient limiting level"), may vary between species as a result of differences in feeding behaviour (Mullin *et al.*, 1975). Without some prior knowledge of the functional response of the dominant zooplankton, it is not possible to determine the precise influence of diel changes in seston concentration on the filtration rates of the zooplankton, or whether these obscured feeding activity rhythms.

6.3.3 ADAPTIVE SIGNIFICANCE OF DIEL FEEDING AND VERTICAL MIGRATION.

The widespread occurrence of diel vertical migration suggests that the behaviour has some adaptive value for zooplankton (Lampert, 1989), and numerous hypotheses to account for its significance have been proposed. These include metabolic models (e.g. McLaren, 1963), resource-related models (e.g. Enright, 1977), predator avoidance mechanisms (e.g. Hutchinson, 1967; Zaret & Suffern, 1976) and avoidance of light damage (e.g. Hairston, 1980). Metabolic, and resource related hypotheses can be discounted for shallow estuarine environments since vertical stratification of either temperature or food resources, which is intrinsic to these models, is not a feature of these habitats (Fancett & Kimmerer, 1985; Frost, 1988).

Avoidance of light damage provides a logical explanation for diel vertical migration in zooplankton, particularly in clear, shallow systems (Haney, 1988), however, observations in South African estuaries are not consistent with this theory. Grindley (1977), for example, has described how *Acartia*, which lacks protective pigmentation, is often present in surface waters during the daytime. In addition, pronounced vertical migration of *P. hessei*, a species which is heavily pigmented, was observed. Also, there were no obvious differences in the diel vertical migration pattern of *P. hessei* between the Kariega and Great Fish estuaries despite the low penetration of light in the latter as a consequence of high turbidity.

Lampert (1989) stated that "the concept of predator evasion is the most straightforward of the various hypotheses". It is not possible to demonstrate that vertical migration behaviour in this case is in response to predators, however, there is circumstantial evidence to support the idea that predator avoidance is important in these zooplankton communities. South African estuaries support large numbers of post-larval marine fish (Whitfield, 1983) as well as small estuarine-dependent fish which inhabit estuaries for the entire duration of their life-cycle (Wallace *et al.*, 1984; Talbot & Baird, 1985). The importance of zooplankton in the diet of these fish has been demonstrated in a number of studies (Coetzee, 1981; Whitfield, 1985; Talbot & Baird, 1985; Blaber, 1987).

Talbot & Baird (1985) demonstrated that the round herring *Gilchristella aestuaria*, a common endemic estuarine species, was primarily a visual feeder rather than a non-selective filter-feeder. The diel feeding pattern was characterized by two periods of activity of approximately 6 hours duration with peaks at 1600 h and 0800 h during summer when food was abundant. *Gilchristella* was found to be capable of feeding even in very dim light, equivalent to bright moonlight. Since there is some dependence on light for visual feeding in at least some of the planktivorous fish, a considerable advantage is conferred on zooplankton that migrate into the watercolumn after dark, and descend to the sediments before dawn.

The work of Fancett & Kimmerer (1985) on a shallow estuary in Australia supporting a zooplankton community dominated by co-existing *Pseudodiaptomus* and *Acartia* (of different species to this study), has shown that planktivorous fish select the former species more readily. This is attributed to greater conspicuousness in the larger, pigmented *Pseudodiaptomus*. Therefore, the ability to remain on, or in the sediments during the daytime is probably of greater significance in *Pseudodiaptomus*. They were able to show that *Pseudodiaptomus* was better able to withstand periods of non-feeding than *Acartia* since it stored energy in the form of lipids. The presence of clearly visible lipid globules observed in *P. hessei* at certain times suggests that they have a similar capacity for storing reserves, and may account for the relatively higher feeding rates measured for this species. Since calanoid naupliar larvae are commonly found in the gut contents of fish predators (Coetzee, 1981), the question of why the nauplii do not undertake vertical migration remains. This may be explained by the fact that juvenile stages generally have smaller energy reserves and higher specific metabolic rates, and may be unable to tolerate a cessation of feeding during daylight (Pearre, 1979; and references cited therein).

It is reasonable to assume that the periodicity in feeding invoked by vertical migration behaviour is a compromise between maximum energy gain and avoidance of predators (Lampert, 1989). The numerous observations that show a cessation of vertical migration activity during conditions of low food availability (e.g. Boyd *et al.*, 1980; Huntley & Brooks, 1982), suggest that it is a flexible behaviour that may be modified by prevailing food conditions. Trade-off theory predicts that where zooplankton are subject to predation pressure, food availability should determine the pattern of vertical migration (Lampert, 1989). This may account for the daytime surface occurrence of *Acartia* observed by Grindley (1977), since members of this genus are considered to be less able to withstand intermittent periods without food than *Pseudodiaptomus* (Fancett & Kimmerer, 1985).

CHAPTER SEVEN

THE INFLUENCE OF PARTICLE SIZE AND CONCENTRATION ON THE FEEDING RESPONSES OF PSEUDODIAPTOMUS HESSEI AND ACARTIA SPP. IN NATURAL SESTON ASSEMBLAGES

7.0 INTRODUCTION

In eastern Cape estuaries, the transition in hydrodynamic conditions from marine-dominated, to freshwater-dominated systems, due to variation in river discharge, results in a marked change in zooplankton community composition (e.g. Wooldridge & Melville-Smith, 1979; Allanson & Read, 1987; Chapter 5, this study). In estuaries such as the Kariega, which are subject to low freshwater inflow, particulate suspended food resources are often limiting and the zooplankton community is dominated by calanoid copepods of the genera *Pseudodiaptomus* and *Acartia*. In estuaries such as the Great Fish, which receive sustained freshwater inflow, *Acartia* are either present in low numbers, or excluded, and zooplankton biomass is usually dominated by mysid shrimps (particularly *Mesopodopsis* and *Gastrosaccus*), although *Pseudodiaptomus* are generally present in high densities.

It is generally accepted that herbivorous zooplankton communities are structured by the effects of resource limitation and predation (Rothhaupt, 1990; and references cited therein), although in estuaries, the influence of salinity is also important (Grindley, 1981). The distributions of *Acartia* and *Pseudodiaptomus* indicated that there are differences in respect of the influence of one or more of these factors.

Salinity has been demonstrated to influence the distribution of *Acartia* since this genera, in contrast to *Pseudodiaptomus*, is not able to withstand the low salinities encountered in the upper reaches of estuaries subject to high freshwater inflow (Wooldridge & Melville-

Smith, 1979; Grindley, 1981). Their absence from the middle and lower reaches of these estuaries could not be explained in these terms, consequently, Wooldridge & Melville-Smith (1979) concluded that other factors were probably responsible. The exclusion of *Acartia* from freshwater-dominated systems is unlikely to be as a result of predation since in mixed zooplankton assemblages comprising *Pseudodiaptomus* and *Acartia*, the former is more susceptible to predation (Fancett & Kimmerer, 1985). In addition, the risk of predation in freshwater-dominated estuaries is reduced as a result of increased turbidity as a result of inorganic seston (e.g. Hart, 1986). At the present time, there are no studies on the potential role of food resources in determining community structure in eastern Cape estuaries.

The quality and quantity of particulate suspended food resources is significantly influenced by the amount of freshwater inflow (Allanson & Read, 1987; Chapter 4, this study). Under conditions of high freshwater inflow, the quantity of food resources was considerably higher compared with marine-dominated systems, however, the overall quality was lower due to the "masking" effect of inorganic seston. In addition, marked variability in food resource concentration was evident as a result of the influence of tidal re-suspension and sporadic pulses of freshwater inflow. The size distribution of seston in eastern Cape estuaries is characterized by a predominance of nanoplanktonic size fractions (Chapter 4).

The co-existence of several copepod species suggests that they potentially compete for the same food resources, however, there are several ways in which competition can be avoided. These include temporal or spatial separation (Greenwood, 1981; Alcaraz, 1983; Hessen, 1990), however, this was not observed between *Pseudodiaptomus* and *Acartia*. Although periodic increases in food abundance may provide a temporary release from competition (Greenwood, 1981), this is unlikely in marine-dominated estuaries such as the Kariega where food resources were generally limiting throughout the year (Chapter 4). Co-existence of copepods with different competitive abilities with regard to food quantity is possible in non-steady state conditions such as significant variability or oscillations in food resources (Hessen, 1990; Rothhaupt, 1990). Alternatively, copepods may avoid competition if there are differences in respect of their resource utilization (Rothhaupt, 1990; and references cited therein). Although food resources are probably not limiting in freshwater-dominated estuaries, decreased seston quality, resulting from high suspended inorganic loads may adversely influence copepod filter-feeding (Arruda *et al.*, 1983), which, depending on the functional feeding characteristics, may result in the exclusion of certain species from these environments.

In this study, interspecific differences in functional feeding are identified as possible factors influencing co-existence, competition and resource utilization. A comparison of i) the feeding response to seston concentration, ii) particle size retention capabilities, and iii) feeding appendage morphology of *Pseudodiaptomus* and *Acartia* was made in order to answer the following questions:

1) Do co-existing species overlap in their feeding requirements, and thereby compete for shared resources ?

2) Can the distributions of copepods in estuaries of varying hydrodynamic conditions be explained in terms of interspecific differences in the response to the range of food resource concentration and, if so, what are the implications of different functional responses for community filtration rates ?

3) Can morphological studies of copepod mouthparts be used to predict particle size retention efficiency, or provide supportive evidence of feeding mode ?

7.1 METHODS

7.1.1 SESTON CONCENTRATION AND FILTRATION RATES.

A series of experiments was designed in which artificial seston gradients were used to test the feeding responses of *Pseudodiaptomus hessei* and *Acartia* spp. over the natural range of seston concentration occurring in eastern Cape estuaries (Chapter 4). These comprised a total of ten experiments; six corresponding to the range of seston concentration measured in the Great Fish estuary, and four corresponding to the range measured in the Kariega estuary.

Collection of zooplankton.

Natural zooplankton assemblages, consisting mainly of *P. hessei* and *Acartia* spp. were collected from the middle reaches of the Kariega estuary after dusk. Sampling was carried out at mid-water depth using a Clarke-Bumpus plankton sampler fitted with an 80 μm nytex mesh net and cod-end. Net tows were restricted to about thirty seconds to avoid damaging the zooplankton. The sample was screened through a coarse mesh filter to remove the larger calanoid copepods (e.g. *Tortanus* sp.) and mysids. No further attempt was made to sort the sample at this stage and a suitable sample density was obtained by a visual inspection. This sample was divided into 16 subsamples using a plankton splitter, two of which were preserved in a 4 % seawater-formalin solution for subsequent enumeration. The remaining zooplankton subsamples were transferred to 2 litre experimental feeding bottles by sieving the sample through an 80 μm nytex mesh, and washing the zooplankton retained on the mesh into the feeding bottle using pre-prepared feeding medium. Subsample densities never exceeded maximum population values recorded during this study (Chapter 5). In the laboratory, feeding bottles were maintained at ± 2 °C ambient water temperature, which, during these experiments ranged between 24 and 26 °C.

Preparation of concentration gradients.

Feeding media were derived from a "stock" suspension of particulate material obtained by resuspending surface sediments from the littoral margins of the Kariega estuary. In the laboratory, the "stock" suspension was first screened through 80 μm nytex mesh to remove coarse particulate material and the total particulate material determined by filtering a subsample onto pre-weighed Whatman GF/F filters and re-weighing after drying the filter at 60 °C for 3 hours. In each experiment, the "stock" suspension was diluted with Whatman GF/F filtered seawater to create a series of feeding suspensions (1 to 7), each with two replicates, over a pre-determined range (either the natural seasonal range of the Kariega estuary, or the Great Fish estuary). Total seston volume (mm^3 l^{-1}) in the particle size range 1.4 to 28 μm (equivalent spherical diameter, ESD) was determined for each suspension (1 to 7) using a Model Z_B Coulter Counter fitted with a 70 μm aperture. Particle volume distributions obtained were similar to those of natural seston (see Figure 1, example).

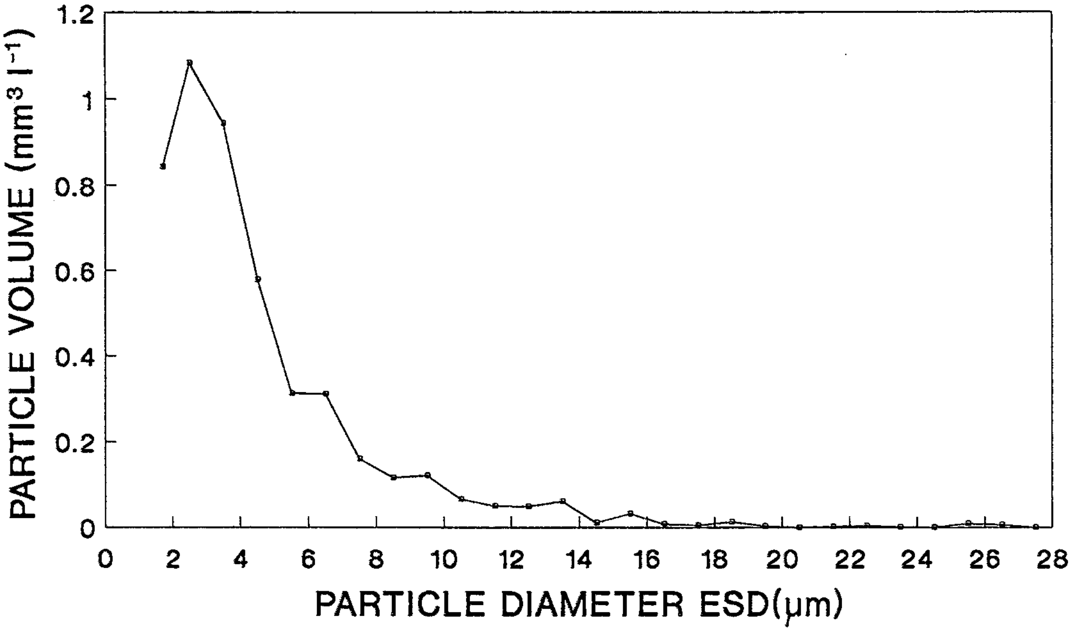


Figure 1. Characteristic particle size distribution of estuarine water samples. Measured using a Model Z_B Coulter Counter fitted with a 70 μm aperture.

Feeding experiments.

Since the dominant zooplankton exhibited diel vertical migration with highest densities occurring at nighttime (Chapter 6), field collection of zooplankton and laboratory feeding experiments took place on the same night. Experiments were carried out between 0100 and 0300 h, the time at which the zooplankton are actively feeding (Chapter 6). Consequently, the period of acclimation to the experimental feeding medium was restricted to between 7 and 10 hours.

Filtration rates were determined indirectly from the ingestion rate of radio-labelled algal cells (Peters, 1984). Preparation of radio-labelled *Tetraselmis* algae was carried out according to the procedure given in Chapter 5, Section 5.1.2. At the start of the feeding experiment, 1 ml of *Tetraselmis* suspension was added to the contents of the experimental bottle and mixed thoroughly by gently inverting the bottle several times to ensure an even distribution of labelled algal cells. Zooplankton were exposed to the labelled feeding medium for 6 minutes, which was adequate time to detect the presence of ingested radio-label, but insufficient to cause the loss of radio-label by egestion. The experiment was terminated by pouring the feeding medium through an 80 μm nytex mesh. The zooplankton retained by the mesh were immobilized in carbonated water, rinsed thoroughly with filtered seawater and concentrated onto a small 80 μm nytex mesh disc. Heat-killed copepods, exposed to the same experimental procedure, were used as controls to correct for the absorption of radio-label by processes other than feeding. Subsequent preparation of copepod samples for enumeration and radio-assay followed the method of Berberovic & Pinto-Coehlo (1989). The labelled samples (mesh + disc) were placed in plastic vials and frozen in liquid air immediately, and subsequently freeze-dried. This method avoids the loss of label associated with more traditional preservation methods (Holtby & Knoechel, 1981; Berberovic & Pinto-Coehlo, 1989).

Thirty late stage (stage V and VI) copepodites of *P. hessei* and *Acartia* spp. were sorted from each freeze-dried sample and prepared for separate radio-assay. These were placed into scintillation vials containing 0.2 ml quartenary ammonium hydroxide (Soluene 350 tissue solubilizer, Packard). Vials were placed in an oven at 60 °C for 24 hours. After solubilization, 10 ml of Insta-Gel (Packard) was added and the sample activity (d.p.m.)

measured on a Beckman LS 3801 scintillation counter after the dissipation of chemoluminescence (Chapter 5, Section 5.1.2). The activity of the feeding medium was determined from the mean activity (d.p.m.) of two 10 ml aliquots filtered onto 0.45 μm membrane filters, placed in scintillation vials containing 10 ml of Filter Count (Packard) fluor.

Calculation of filtration rates.

Absorption controls were subtracted from experimental values and the filtration rates calculated by the following formula:

$$G = \frac{(A_a)60}{A_s nt}$$

where,

G = filtration rate (ml individual^{-1} h^{-1})
A_a = activity of animal sample (d.p.m.)
A_s = feeding suspension activity (d.p.m. ml^{-1})
n = number of animals in sample
t = duration of experiment (minutes) (Peters, 1984)

7.1.2 PARTICLE SIZE-SELECTION.

a) Particle size-retention efficiency.

Two basic methods are used in experimental studies of zooplankton feeding that employ particle counters. These are, i) end-point determinations (e.g. Gauld, 1951; Frost, 1972; Richman *et al.*, 1977; Vanderploeg, 1981) and ii) time series measurement (e.g. McClatchie & Lewis, 1986). The end-point method of Richman *et al.* (1977), modified by Vanderploeg (1981) was used in this study. Various criticisms have been levelled at both the use of particle counters in zooplankton feeding studies, and end-point determination of filtration rate. Two major disadvantages are associated with electronic particle counting compared with direct observations such as microscopy (e.g. the Utermöhl counting chamber technique). Firstly, particle size is measured as equivalent spherical diameter (ESD) which may bias size distributions unless all the particles in the sample are spherical, which is unlikely in natural seston suspensions. Secondly, particle counters offer no information on the nature of the particles counted. The main advantage of electronic counting techniques is the rapid analytical speed, which allows a greater number of experiments to be performed (Peters, 1984).

End-point experiments rely on the measurable depletion of particles in the experimental bottle through the feeding activity of the zooplankton. If the particle concentration is above the incipient limiting level (ILL) (see Review, Chapter 3) at the outset, and the copepods detect a decrease below it during the course of the experiment, the behavioural adjustment will bias the average filtration rate (Williams, 1982). To avoid this, McClatchie & Lewis (1986) recommended that the initial particle concentration be kept low.

Another problem that arises is, if certain size classes are retained with greater efficiency than others, the particle size spectra available to the zooplankton at any given time becomes progressively altered by the relative increase of the less efficiently retained particles. This is partially avoided by reducing the number of particles grazed to the minimum detectable by the particle counting method employed. Marin *et al.* (1986) achieved this by manipulating the density of grazers in the experimental bottle and the duration of the experiment, using *a priori* knowledge of gross filtration rate of the grazer species. They found that a drop of approximately 14 % with respect to the initial concentration was necessary for counting purposes. Average filtration rates of *Acartia* spp. and *P. hessei* taken from *in situ* measurement of diel feeding activity were used in this study (see Chapter 6). Using the equations of Marin *et al.* (1986) as guidelines to set the experimental variables, experiments with *P. hessei* were run for 18 hours with 15 individuals (10 ml per individual) and with *Acartia* spp. for 24 hours with 30 individuals (5 ml per individual).

Collection of zooplankton.

Zooplankton were collected using the same method outlined in Section 7.1.1. Zooplankton samples were brought to the laboratory approximately three hours after collection and were kept overnight in 5 litre containers in a constant environment room in darkness at ± 2 °C ambient water temperature which, in this series of experiments, ranged from 19 to 22 °C. Stage VI *P. hessei* and *Acartia* spp. adults were sorted using a wide-mouth pipette and transferred to separate petri dishes containing 80 μm nytex mesh-screened estuary water.

Size-selection experiments.

Particle size-selection by the dominant zooplankton (*P. hessei* and *Acartia* spp.), feeding in natural particle assemblages, was measured. In each experiment, six replicate experimental bottles and two control bottles (150 ml) were used for each feeding group (ie., *Pseudodiaptomus* and *Acartia* spp.). Water samples from the Kariega estuary were used since particle concentrations were generally low and the seston size distributions are characteristic of estuaries in the region. Estuary water was collected on the same day experiments were performed in order to minimize particle modification from containment effects. Prior to the experiment, water was poured through an 80 μm mesh screen to remove coarse particles which might interfere with the counting procedure.

The zooplankton samples in the petri dishes were checked just before the experiment to ensure that all individuals were healthy and active and any necessary adjustments were made. All experiments commenced at 1800 h, which coincided with the onset of feeding under natural conditions as zooplankton migrate into the watercolumn (Chapter 6). At the start of the experiment, the contents of the petri dishes were sieved through an 80 μm mesh to retain the zooplankton and rinsed from the mesh into an experimental bottle using 150 ml of feeding medium. The same procedure, but without zooplankton was used for the controls. A sub-sample of the feeding suspension was retained at the start of each experiment for Coulter Counter analysis. The experimental and control bottles were attached to a plankton wheel which was rotated at 1 revolution per minute (rpm) and maintained in the dark at ambient water temperature ± 2 °C.

After the pre-determined time, the experiments were terminated by sieving the contents of the bottles through an 80 μm nytex mesh screen. The zooplankton retained by the mesh were transferred back into petri dishes, examined, and mortality among samples noted. The feeding media, minus zooplankton, were retained in clean 150 ml bottles for Coulter Counter analysis. The same procedure was adopted for control bottles.

Coulter Counting.

Particle size distributions were determined with a Model Z_B Coulter Counter according to the method of Sheldon & Parsons (1967). The characteristic size distribution of the estuarine seston, in which particles < 20 μm ESD comprised ≈ 95 % of particulate volume (Chapter 4), allowed the full size spectrum to be counted using a 70 μm aperture. Four replicate counts were made of each of the 13 size "windows" covering the entire spectrum. Experimental and control particle concentrations were converted to particle volumes and plotted against particle size (ESD). In no instances were particle counts in excess of the coincidence limit for the aperture, consequently, dilution prior to counting was not necessary. Since the salinity in the middle reaches of the estuary was constant at 35 ‰, the natural conductivity of the medium was within the optimum operating limits of the instrument (Kersting, 1985).

Calculations.

Filtration rate (F) was calculated for each size class using the Richman *et al.* (1977) modification of Gauld's (1951) equation:

$$F = \frac{\ln C_i - \ln E_i}{t} v$$

where, F = filtration rate (ml cleared h^{-1} copepod^{-1}).
C_i = concentration of particles of size i in control.
E_i = concentration of particles of size i in experimental bottle.
t = experimental duration (hours).
v = number of ml animal^{-1} in the experimental bottle.

Where control concentrations were higher than experimental bottle values the filtration rate was assigned zero since negative filtration rates are not possible (Vanderploeg, 1981).

Lechowicz (1982) in his review of various selectivity indices found the index of Vanderploeg & Scavia (1979) to be the most useful measure of feeding preference and amenable to statistical analyses. The selectivity coefficient (W'), which is mathematically equivalent to retention efficiency (Vanderploeg, 1981), was calculated by dividing the filtration rate (F) of a particular size class *i* by the maximum filtration rate (F_{max}) observed across all size classes (Vanderploeg & Scavia, 1979).

b) Feeding appendage morphology.

Second maxillae (M2) were dissected from formalin-preserved stage VI *Pseudodiaptomus* and *Acartia* spp. and pre-treated for scanning electron microscopy (SEM) examination according to the method of Paerl & Shimp (1973). Samples were prepared by gradual ethanol replacement followed by transfer into amylacetate as a transitional fluid and then critical-point dried with CO_2. M2 were mounted on glue-coated brass stubs, sputter-coated with gold, and examined on a JEOL-JSM 840 SEM. In addition, whole mounts of copepods were prepared and the region of the second maxillae, photographed under SEM.

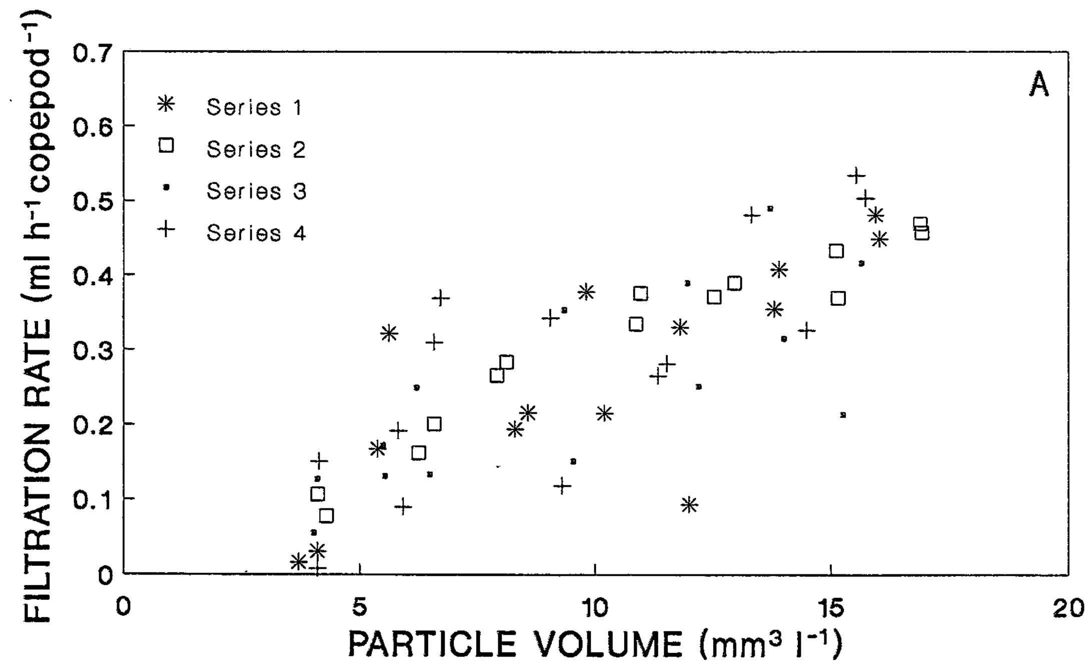
Observations of maxillary structure were made on six individuals of each species. Photographs of M2 were used to measure the intersetule distances which were calculated by subtracting the setule diameter from the distance between the midpoints of the setules on either side of the space. The filtering area of the second maxillae was determined using the method of Nival & Nival (1976).

7.2 RESULTS

7.2.1 SESTON CONCENTRATION AND FILTRATION RATES.

The filtration rates of *Pseudodiaptomus* and *Acartia* spp., measured over the range in seston concentration (as total particle volume, $mm^3\ l^{-1}$) occurring naturally in the Kariega estuary, are shown in Figures 2a and b, respectively. Similarly, the filtration rates over the natural seston range recorded in the Great Fish estuary are shown in Figures 2c and d.

It was useful to convert seston concentration expressed as total particle volume, into units of total particulate material (TPM, $mg\ l^{-1}$) since the latter is more commonly encountered in the literature. The relationship between total particulate matter (TPM, $mg\ l^{-1}$) and total particle volume (TPV, $mm^3\ l^{-1}$) is shown in Figure 3. Although the linear regression provides a convenient conversion, the relationship is likely to vary somewhat in response to changes in the nature of the particulate material.



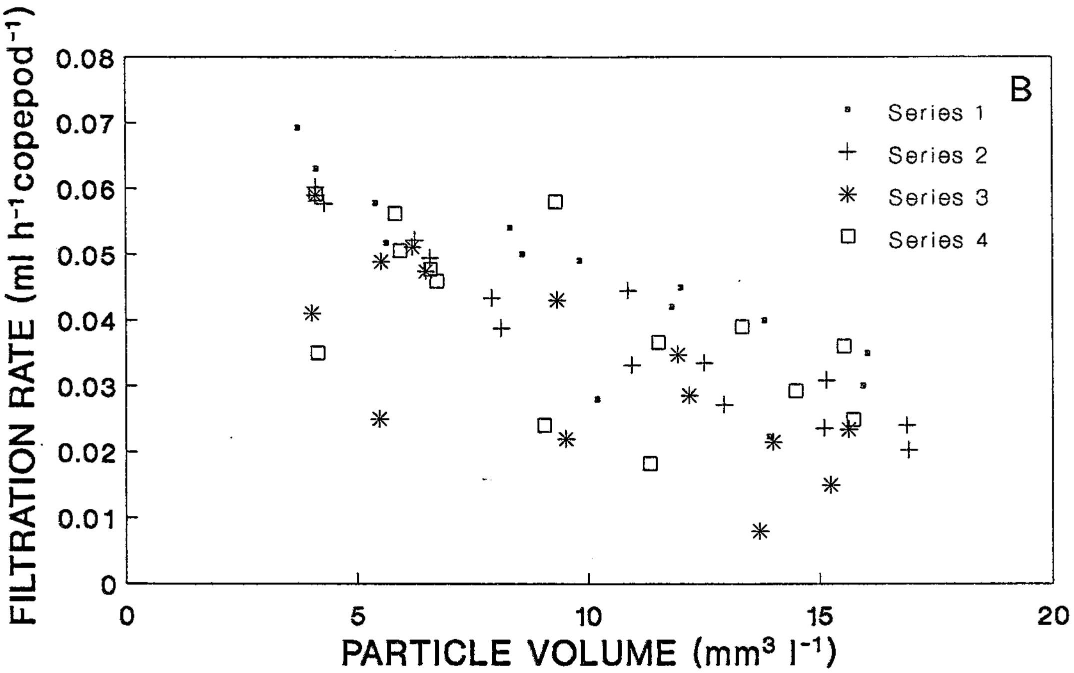


Figure 2. Filtration rates (ml h^{-1} $copepod^{-1}$) of *Pseudodiaptomus hessei* (A) and *Acartia* spp. (B) over the natural range in seston concentration (expressed as total particle volume per litre of water) occurring in the Kariega estuary.

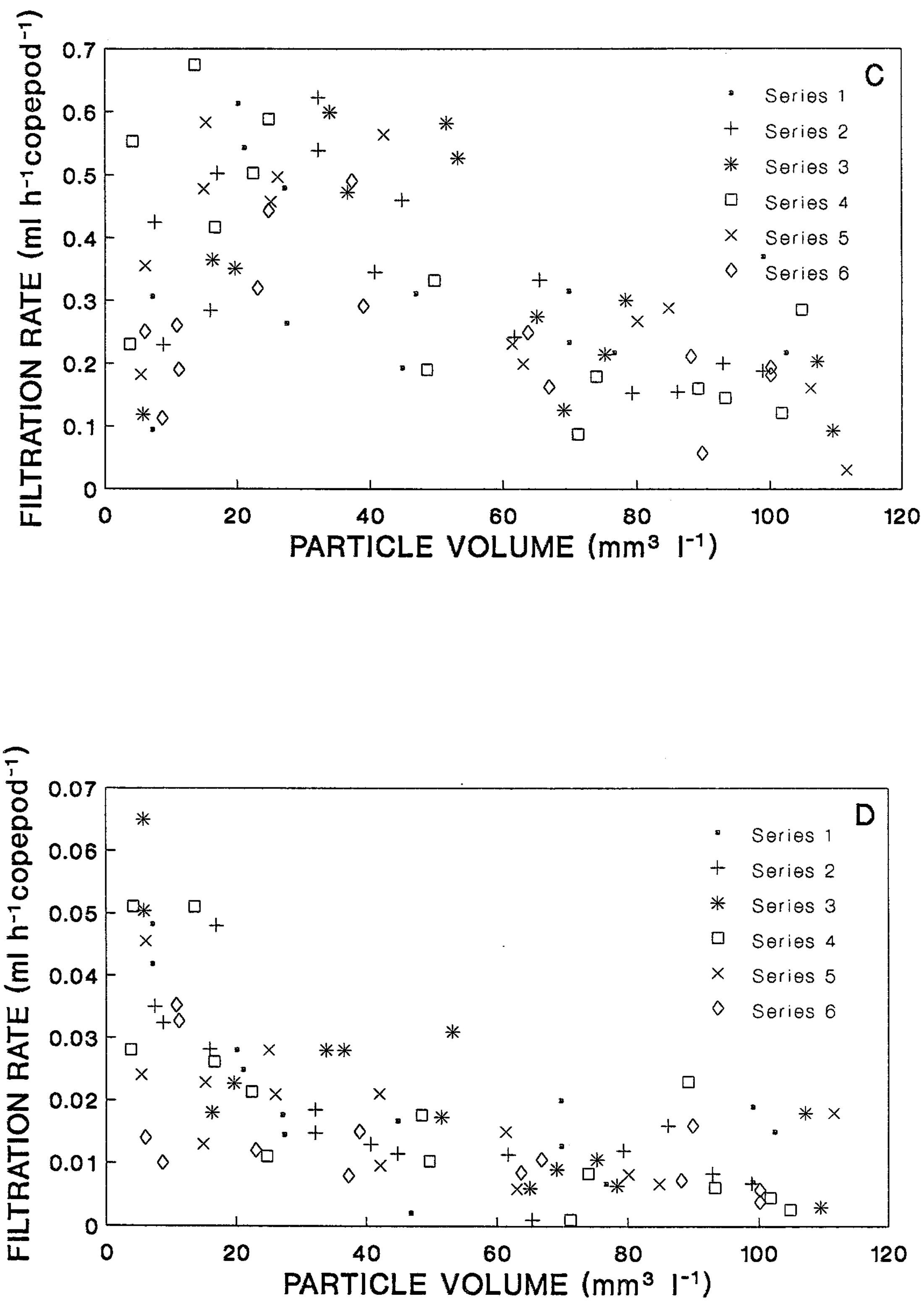


Figure 2 (continued). Filtration rates (ml h^{-1} copepod^{-1}) of *P. hessei* (C) and *Acartia* spp. (D) over the natural range in seston concentration in the Great Fish estuary.

Filtration rates of *P. hessei* showed a positive linear response to seston concentration across the normal seston range of the Kariega estuary (Figure 2a). In Figure 2c, filtration rates of *P. hessei* showed that an incipient limiting level (ILL) (see Review, Chapter 3) was attained at approximately 30 $mm^3\ l^{-1}$, which is within the natural seston range of the Great Fish estuary. Filtration rates of *Acartia* spp. showed a negative response to seston concentration across the seston range of the Kariega estuary (Figure 2b), and were noticeably reduced at much higher seston concentrations (Figure 2d). An ILL for *Acartia* spp. was not evident across the range in seston concentration used in these experiments.

The average dry mass of individuals used in these experiments was 6.19 μg for *P. hessei* and 2.28 μg for *Acartia* spp. Thus, maximum mass-specific filtration rates derived from the response curves are 0.087 ml $\mu g\ h^{-1}$ for *P. hessei* and 0.030 ml $\mu g\ h^{-1}$ for *Acartia* spp., although this may represent an underestimation in *Acartia* since the maximal filtration rate at ILL was not determined. Models of the response curves of *Pseudodiaptomus* and *Acartia* over the entire seston concentration range, based on the data shown in Figures 2a to d, are shown in Figure 4.

7.2.2 PARTICLE SIZE-SELECTION.

a) Particle size-retention efficiency.

The results of five particle size-selectivity experiments are shown in chronological order in Figures 5a to e. In each case, the particle size distributions on which the zooplankton were feeding were consistent with natural seston. In each experiment, particle volume distributions of the control and experimental bottle (replicate$_1$) at the end of the experiment are given in the upper (*P. hessei*) and middle (*Acartia* spp.) panels. The remaining five replicates in each case (*P. hessei* and *Acartia* spp.) were omitted for clarity but showed essentially the same trend. The full data set is given in Appendix A. The particle size-selectivity coefficients (W') of *P. hessei* and *Acartia* spp., shown as means (of six replicates) with 95 % confidence limits about the mean, are given in the lower panel. The date and ambient water temperature are given in the upper panel.

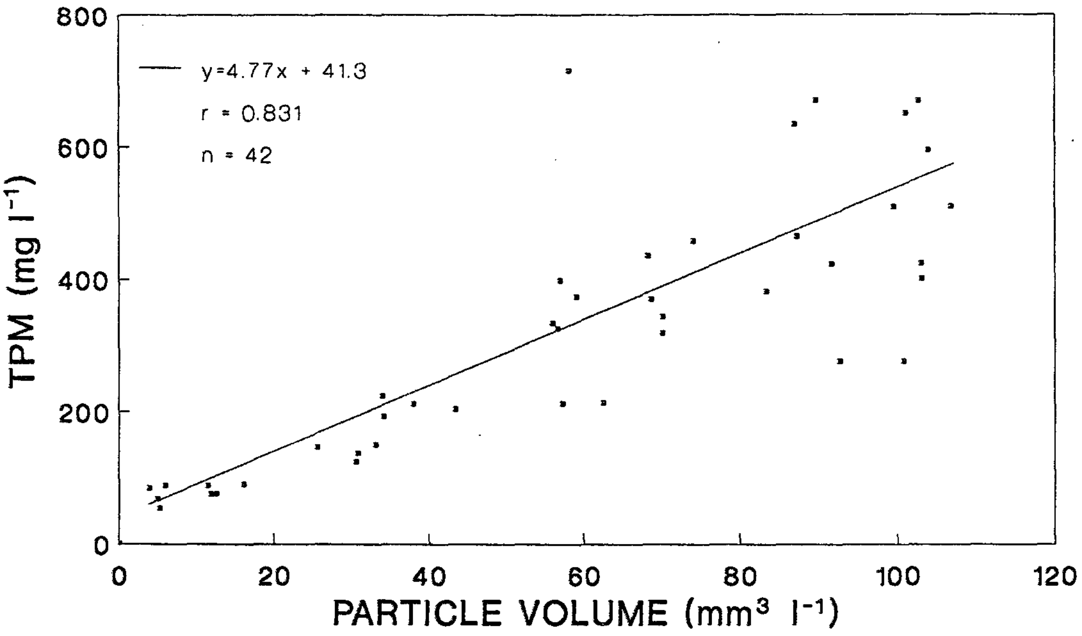


Figure 3. The linear relationship (shown by regression) between total seston volume (TPV, mm^3 l^{-1}) measured using a Coulter Counter, and total particulate matter (TPM, mg l^{-1}) obtained by filtering known volumes onto Whatman GF/F filters.

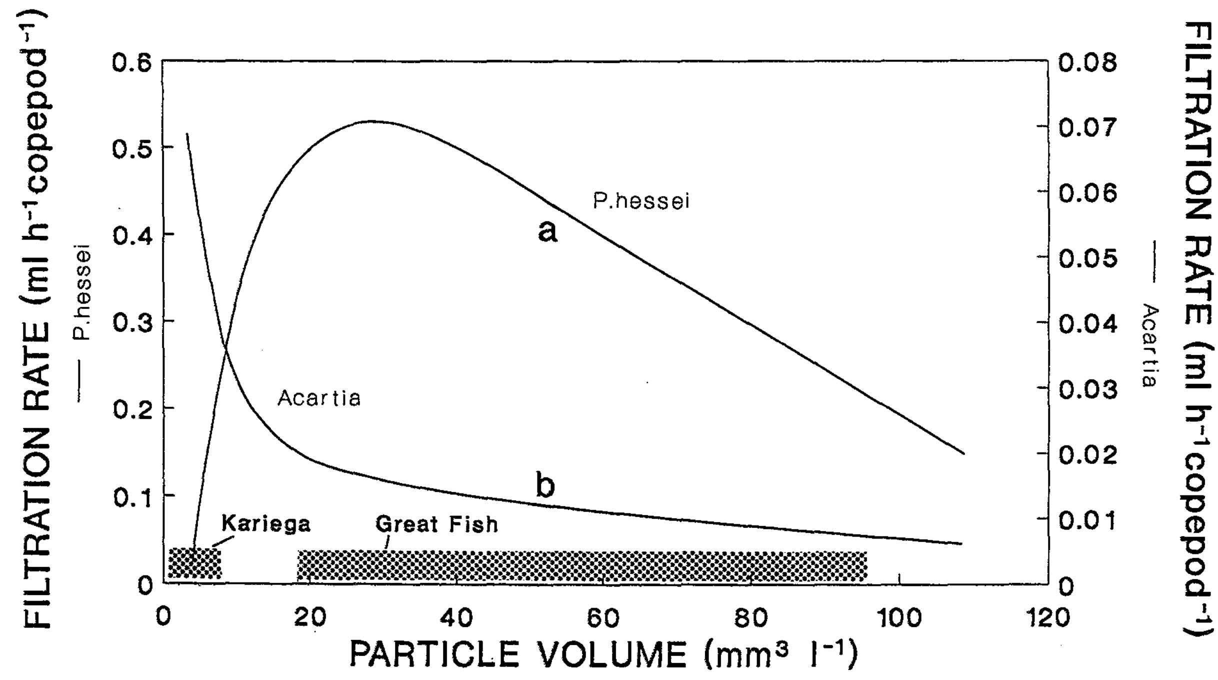
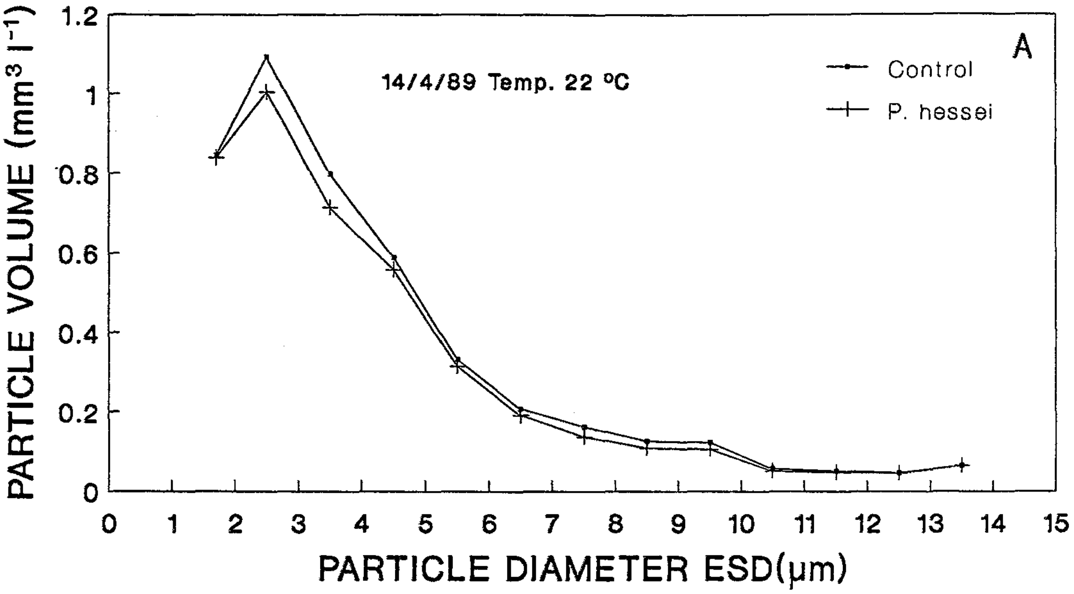
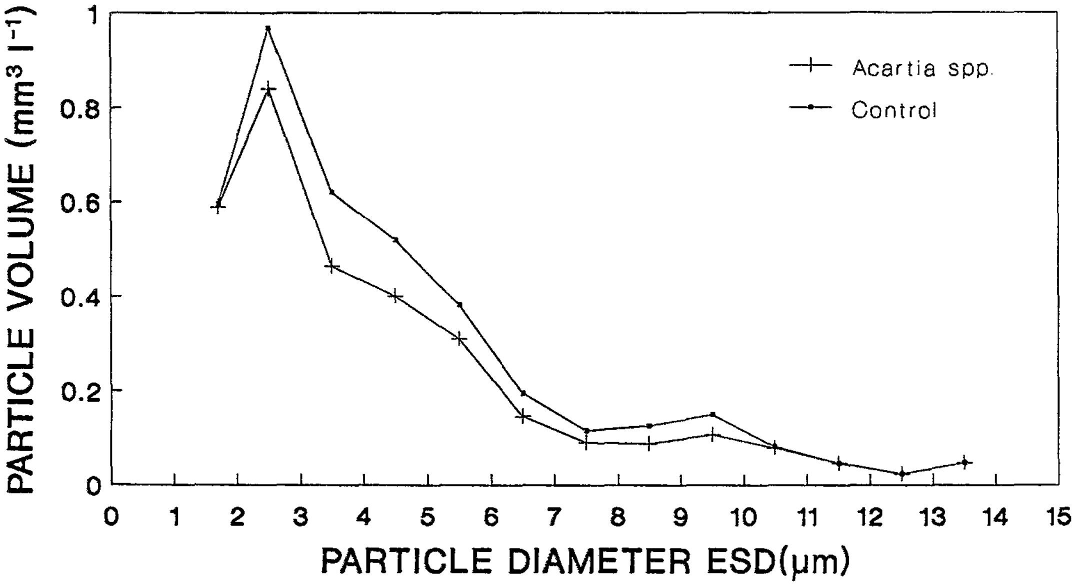
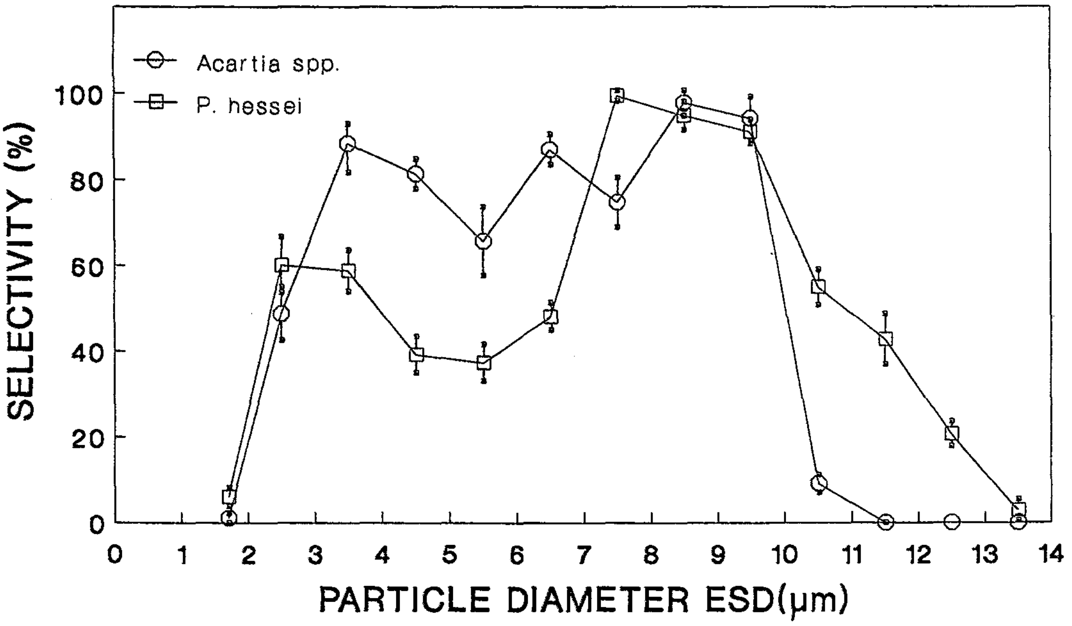


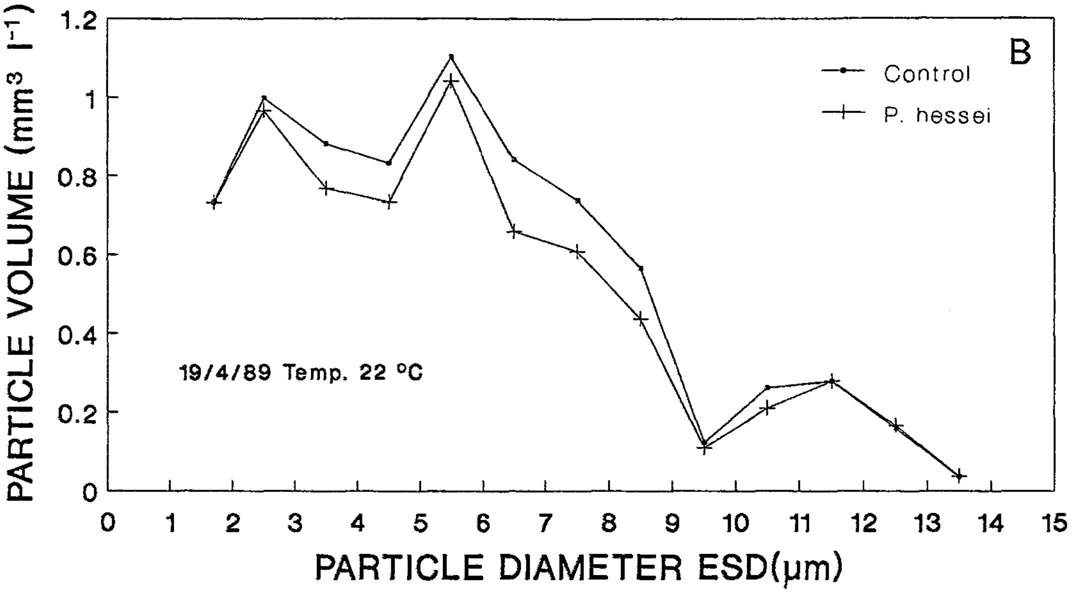
Figure 4. Model of the functional feeding of *Pseudodiaptomus hessei* (a) and *Acartia* spp. (b) constructed from data presented in Figure 2. The ranges in seston concentration in the Kariega, and Great Fish estuaries are shown along the X-axis.

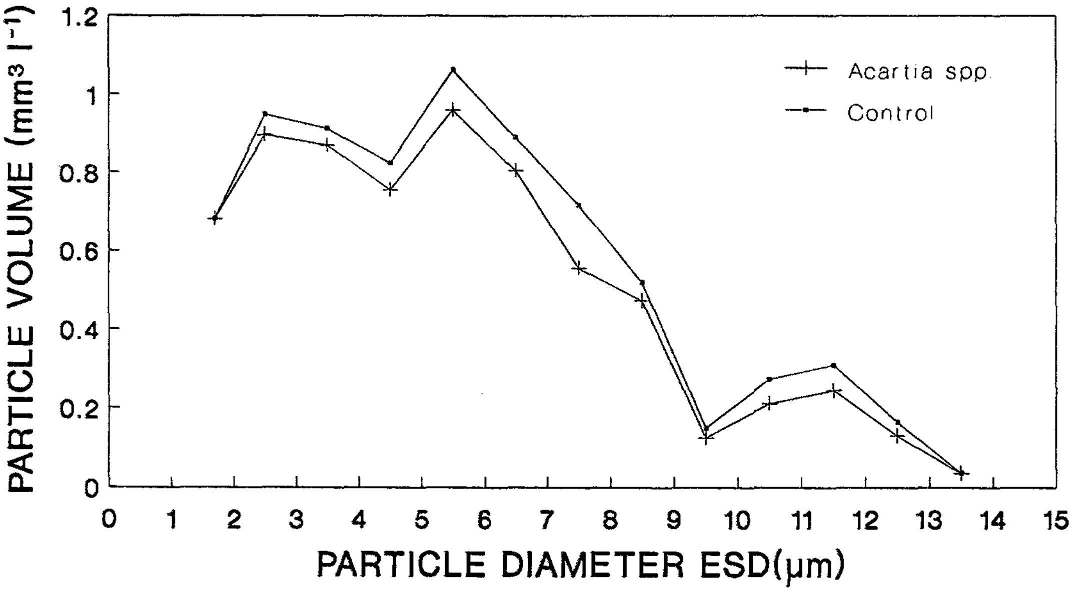
Figure 5. Results of five (a to e) size-selection feeding experiments with *P. hessei* and *Acartia* spp. In each experiment, the top panel illustrates particle-size distribution (TPV) at experiment end in the i) the control bottle, and ii) replicate$_1$ bottle (of six) for *P. hessei*. The middle panel illustrates particle size distribution (TPV) at experiment end in i) the control bottle, and ii) replicate$_1$ bottle (of six) for *Acartia* spp. Ambient water temperature and the date of the experiment are shown. The mean selectivity coefficients of (W') of six replicates with 95 % confidence limits for both *P. hessei* and *Acartia* spp. are shown in the bottom panel.

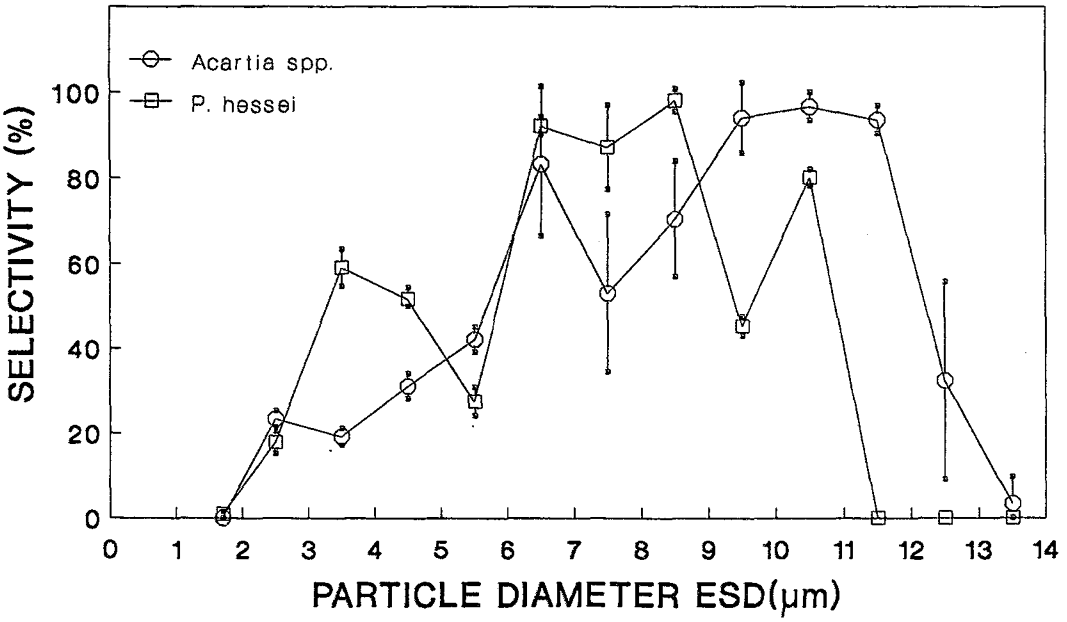

A
14/4/89 Temp. 22 °C
Control
P. hessei
PARTICLE VOLUME (mm³ l⁻¹)
0
0.2
0.4
0.6
0.8
1
1.2
PARTICLE DIAMETER ESD(μm)
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15

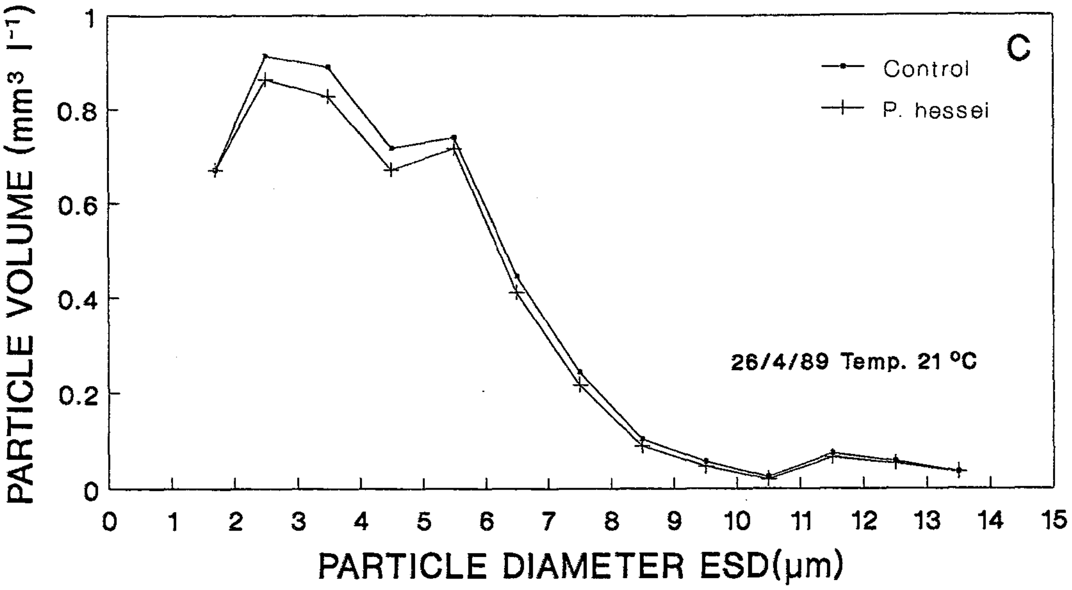

Acartia spp.
Control
PARTICLE VOLUME (mm³ l⁻¹)
0
0.2
0.4
0.6
0.8
1
PARTICLE DIAMETER ESD(μm)
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15

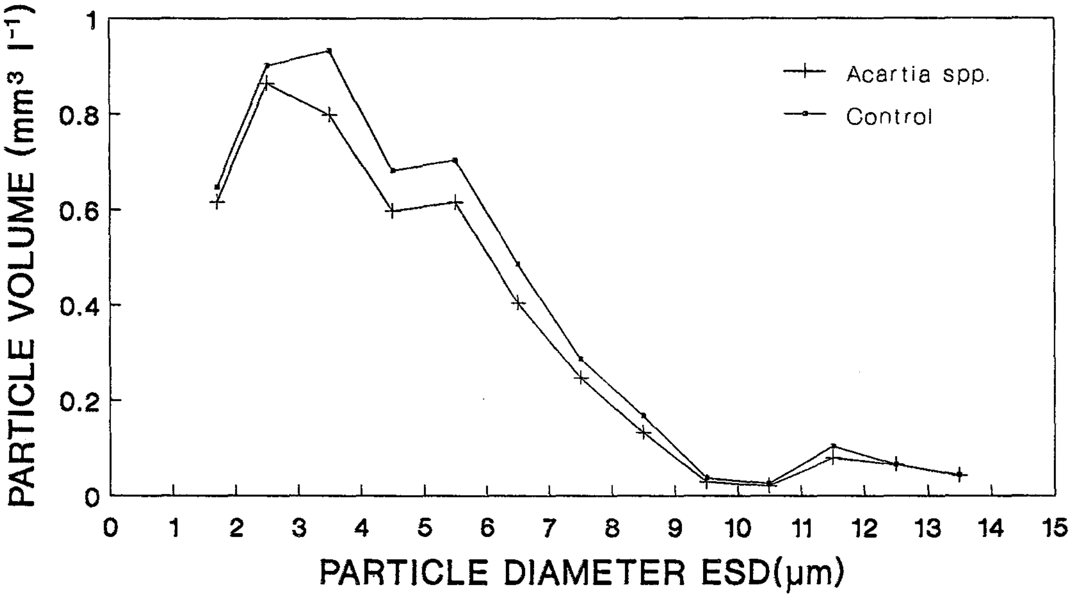

Acartia spp.
P. hessei
SELECTIVITY (%)
0
20
40
60
80
100
PARTICLE DIAMETER ESD(μm)
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14

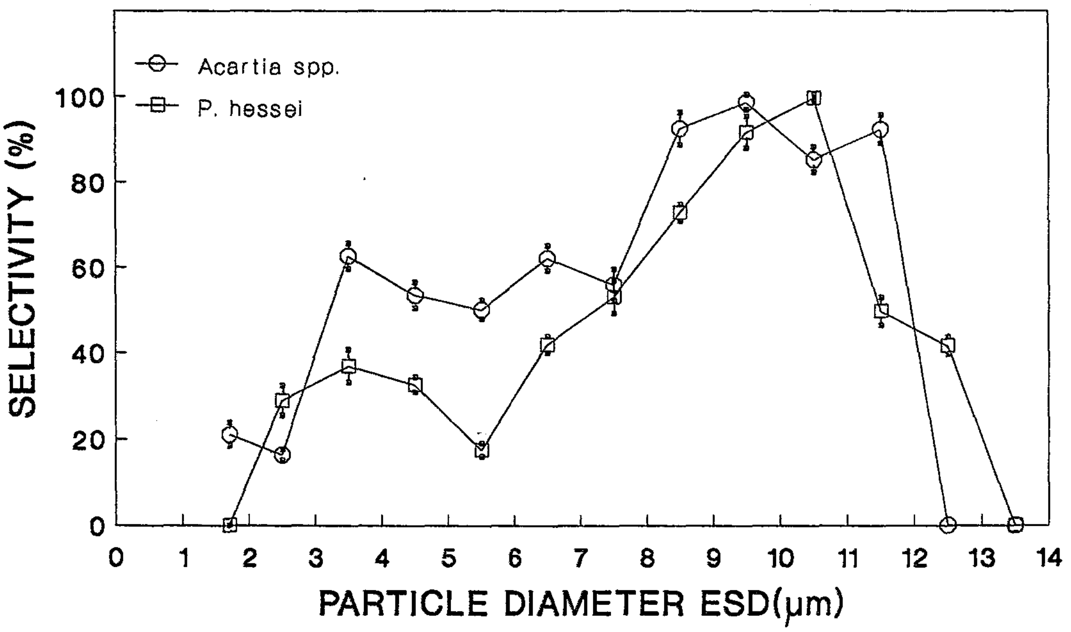

B
Control
P. hessei
19/4/89 Temp. 22 °C
PARTICLE VOLUME (mm³ l⁻¹)
PARTICLE DIAMETER ESD(µm)
0
0.2
0.4
0.6
0.8
1
1.2
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15

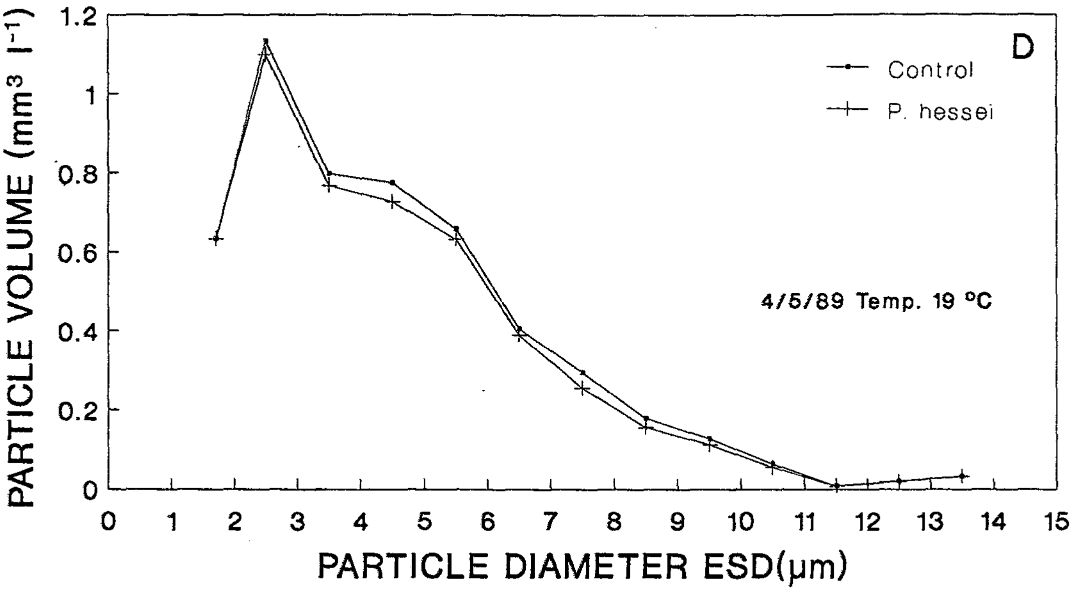

Acartia spp.
Control
PARTICLE VOLUME (mm³ l⁻¹)
PARTICLE DIAMETER ESD(µm)
0
0.2
0.4
0.6
0.8
1
1.2
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15

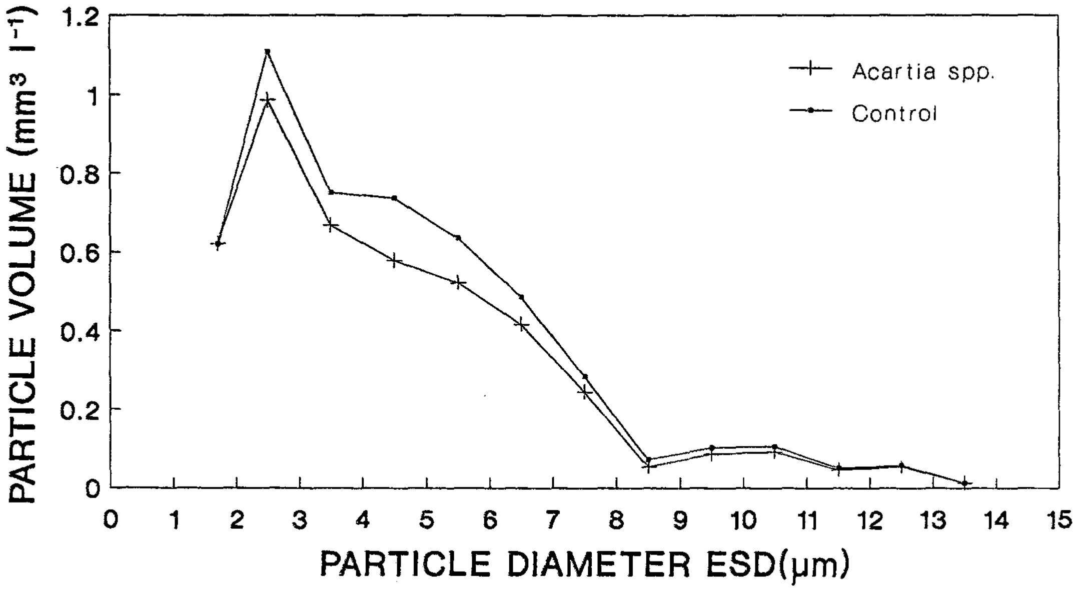

Acartia spp.
P. hessei
SELECTIVITY (%)
PARTICLE DIAMETER ESD(µm)
0
20
40
60
80
100
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14

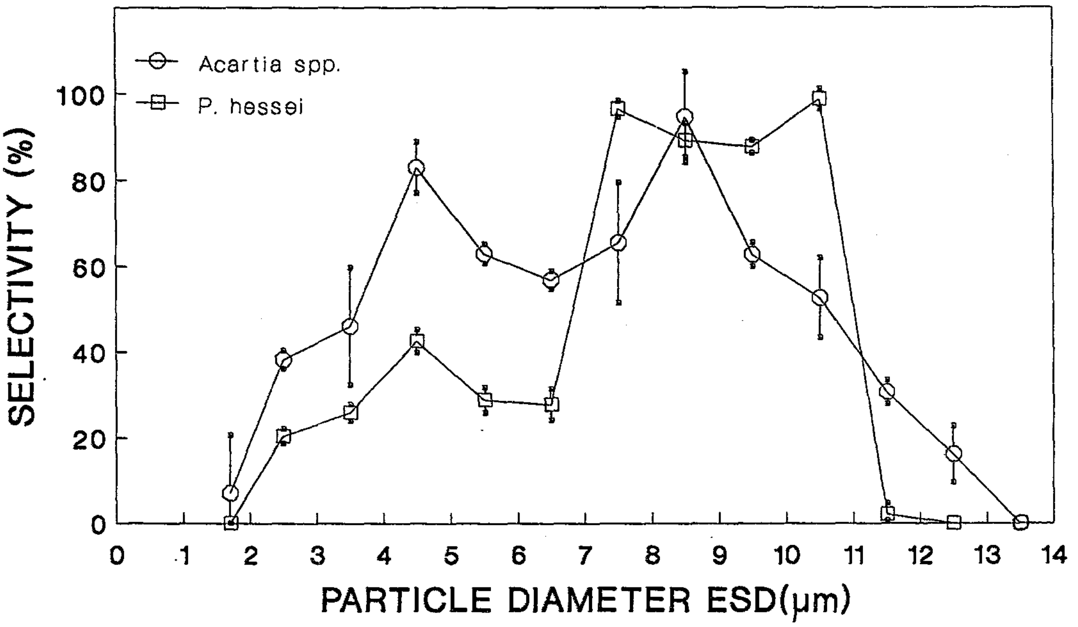

C
Control
P. hessei
26/4/89 Temp. 21 °C
PARTICLE VOLUME (mm^3 l^{-1})
0
0.2
0.4
0.6
0.8
1
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
PARTICLE DIAMETER ESD(μm)

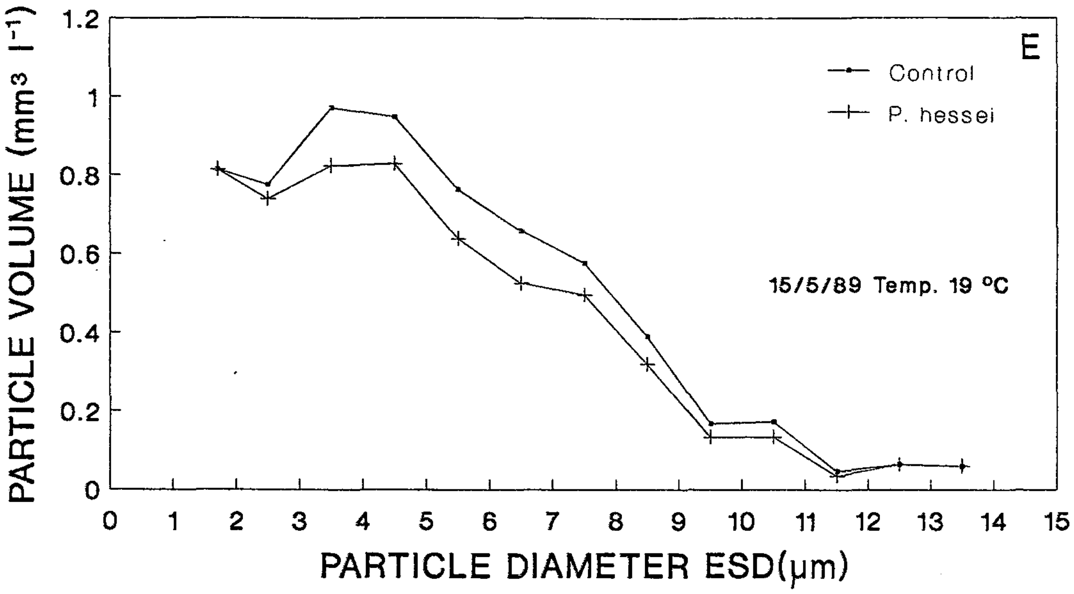

Acartia spp.
Control
PARTICLE VOLUME (mm^3 l^{-1})
0
0.2
0.4
0.6
0.8
1
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
PARTICLE DIAMETER ESD(μm)

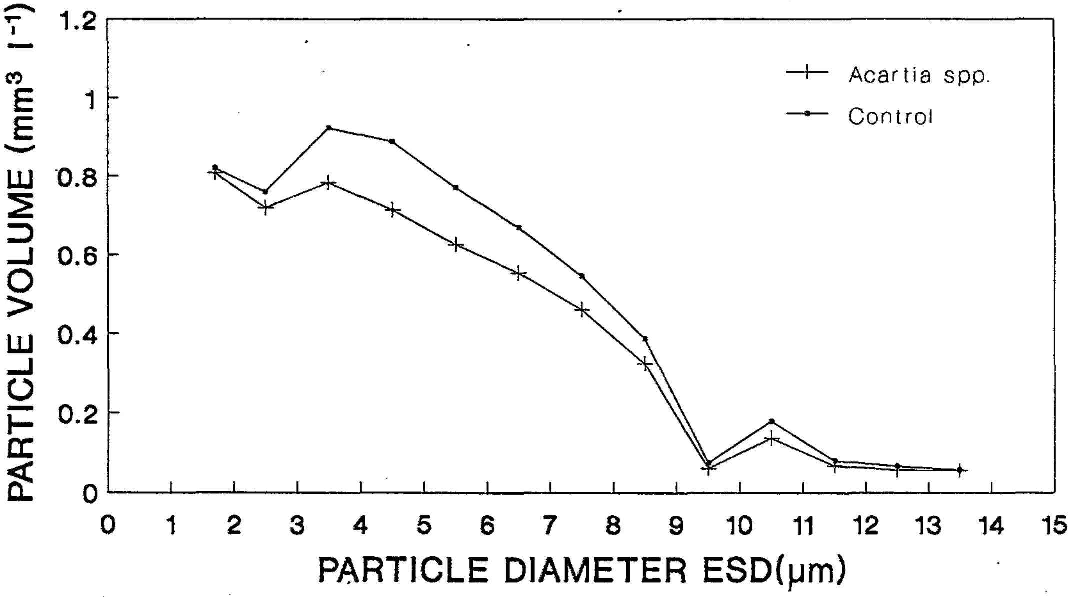

Acartia spp.
P. hessei
SELECTIVITY (%)
0
20
40
60
80
100
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14
PARTICLE DIAMETER ESD(μm)

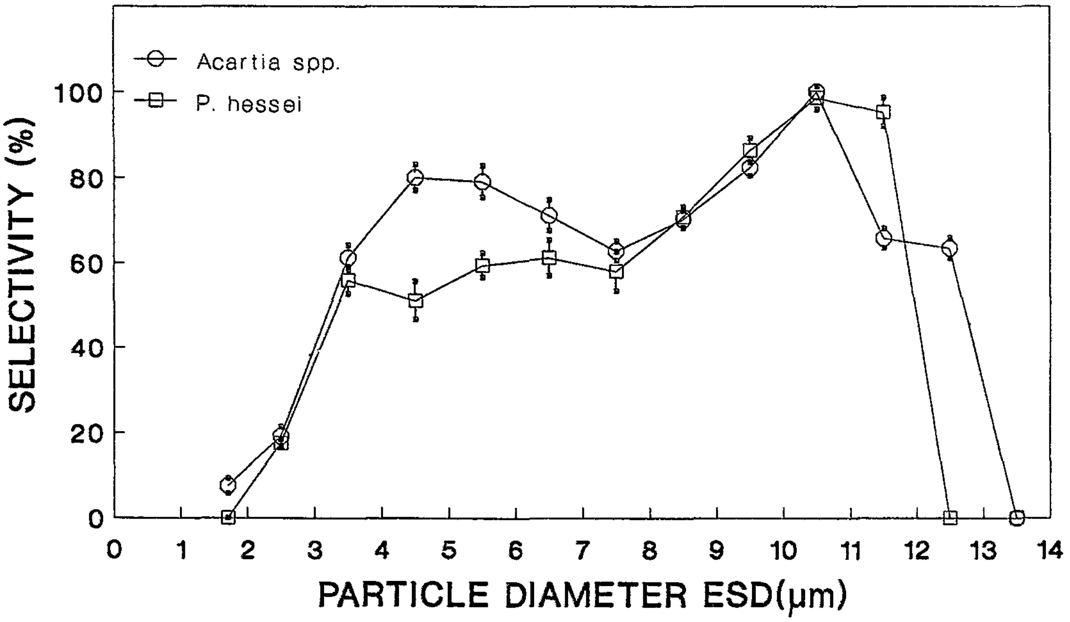

D
Control
P. hessei
4/5/89 Temp. 19 °C
PARTICLE VOLUME (mm³ l⁻¹)
1.2
1
0.8
0.6
0.4
0.2
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
PARTICLE DIAMETER ESD(μm)


Acartia spp.
Control
PARTICLE VOLUME (mm³ l⁻¹)
1.2
1
0.8
0.6
0.4
0.2
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
PARTICLE DIAMETER ESD(μm)


Acartia spp.
P. hessei
SELECTIVITY (%)
100
80
60
40
20
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14
PARTICLE DIAMETER ESD(μm)


E
Control
P. hessei
15/5/89 Temp. 19 °C
PARTICLE VOLUME (mm³ l⁻¹)
1.2
1
0.8
0.6
0.4
0.2
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
PARTICLE DIAMETER ESD(μm)


Acartia spp.
Control
PARTICLE VOLUME (mm³ l⁻¹)
1.2
1
0.8
0.6
0.4
0.2
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
PARTICLE DIAMETER ESD(μm)


Acartia spp.
P. hessei
SELECTIVITY (%)
100
80
60
40
20
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14
PARTICLE DIAMETER ESD(μm)

In each experiment (a to e), mean selectivity coefficients of *P. hessei* and *Acartia* spp. in each size class were compared statistically using a two-tailed t-test. Significance was tested at the 5 % level ($p < 0.025$) (see Table 1). Several points emerge from a comparison of the W' plots. There are no examples in which the patterns of selectivity are similar to the particle size distribution. Thus, particles are filtered at rates which are not in proportion to their abundance in the feeding medium. For both *P. hessei* and *Acartia* spp., the maximum filtration rate (F_{max}) generally occurred in the larger size classes (between 7 and 13 μm ESD), although it is not possible to distinguish a particular size class of F_{max} for either. In both *P. hessei* and *Acartia* feeding experiments, selectivity for particles above 13 μm ESD decreased substantially and is attributed to the relatively low concentration of particles above this size class.

The statistical analysis in Table 1 shows that in four out of five experiments (a, c, d and e), *Acartia* spp. demonstrated a statistically higher selection for particles less than ≈ 7 μm ESD compared with *P. hessei*. Thus, *Acartia* spp., feeding on natural seston, generally utilized the smaller particle size fractions to a greater extent than *P. hessei*.

A comparison of the controls at the start and end of the experiments revealed that in the smallest size classes (1.4 to 3 μm ESD), an increase in particle concentration occurred which may result in unrealistically low filtration rates, although major error is unlikely. In addition, since different experimental feeding times were used for *P. hessei* and *Acartia* spp., the effects of particle modification processes on particle size-selection may be different. A more comprehensive review of particle modification effects in Coulter Counter feeding experiments is given in Vanderploeg (1981).

Table 1. Comparison of the mean selectivity coefficients (W') of *P. hessei* (PH) and *Acartia* spp. (AC). For each experiment (a to e), the larger W' in each size class is indicated by (x). Significance at the 5 % level (two-tailed t-test, $p < 0.025$) is indicated by (*), non significant differences by (n.s.), and where one W' value in a pair was zero, (-) indicates that no test was performed.

PARTICLE	EXPT. A			EXPT. B			EXPT. C			EXPT. D			EXPT. E		
SIZE CLASS	MEAN W'		SIGNIF.	MEAN W'		SIGNIF.	MEAN W'		SIGNIF.	MEAN W'		SIGNIF.	MEAN W'		SIGNIF.
(μm)	PH	AC	p<0.025	PH	AC	p<0.025	PH	AC	p<0.025	PH	AC	p<0.025	PH	AC	p<0.025
1.4 - 2.0	x		-	x		-		x	-		x	-		x	-
2.0 - 3.0	x		*		x	*	x		*		x	*		x	n.s.
3.0 - 4.0		x	*	x		*		x	*		x	*		x	*
4.0 - 5.0		x	*	x		*		x	*		x	*		x	*
5.0 - 6.0		x	*		x	*		x	*		x	*		x	*
6.0 - 7.0		x	*	x		n.s.		x	*		x	*		x	*
7.0 - 8.0	x		*	x		*		x	n.s.	x		*		x	*
8.0 - 9.0		x	n.s.	x		*		x	*		x	n.s.		x	n.s.
9.0 - 10.0		x	n.s.		x	*		x	*	x		*	x		*
10.0 - 11.0	x		*		x	*	x		*	x		*	x		-
11.0 - 12.0	x		-		x	-		x	*		x	*		x	*
12.0 - 13.0	x		-		x	-	x		-		x	-	x		-
13.0 - 14.0	x		-		x	-			-		-	-		x	

b) Mouthpart morphology.

Structure of the main filtering appendages, the second maxillae (M2), are shown in Figures 6a to f. Gross morphology of the M2 are shown in Figure 6a (*P. hessei*) and d (*Acartia* spp.). Despite the fact that adult *Acartia* spp. are considerably smaller than *P. hessei* adults, the overall dimensions of the M2 were considerably larger. Maxillary setae are generally longer in *Acartia* spp., but are fewer in number than the maxillae of *P. hessei*. For comparative purposes, Figure 6b (*P. hessei*) and e (*Acartia* spp.) provide an indication of M2 gross morphology in relation to metasome size. The fine structure of the M2 is shown in Figure 6c (*P. hessei*) and 6f (*Acartia* spp.). Intersetule distances were measured from a series of photomicrographs of six adults of each species. An examination of the entire maxillary area revealed no evidence of regional differences in intersetular spacing. Maxilla area was calculated according to the method of Nival &

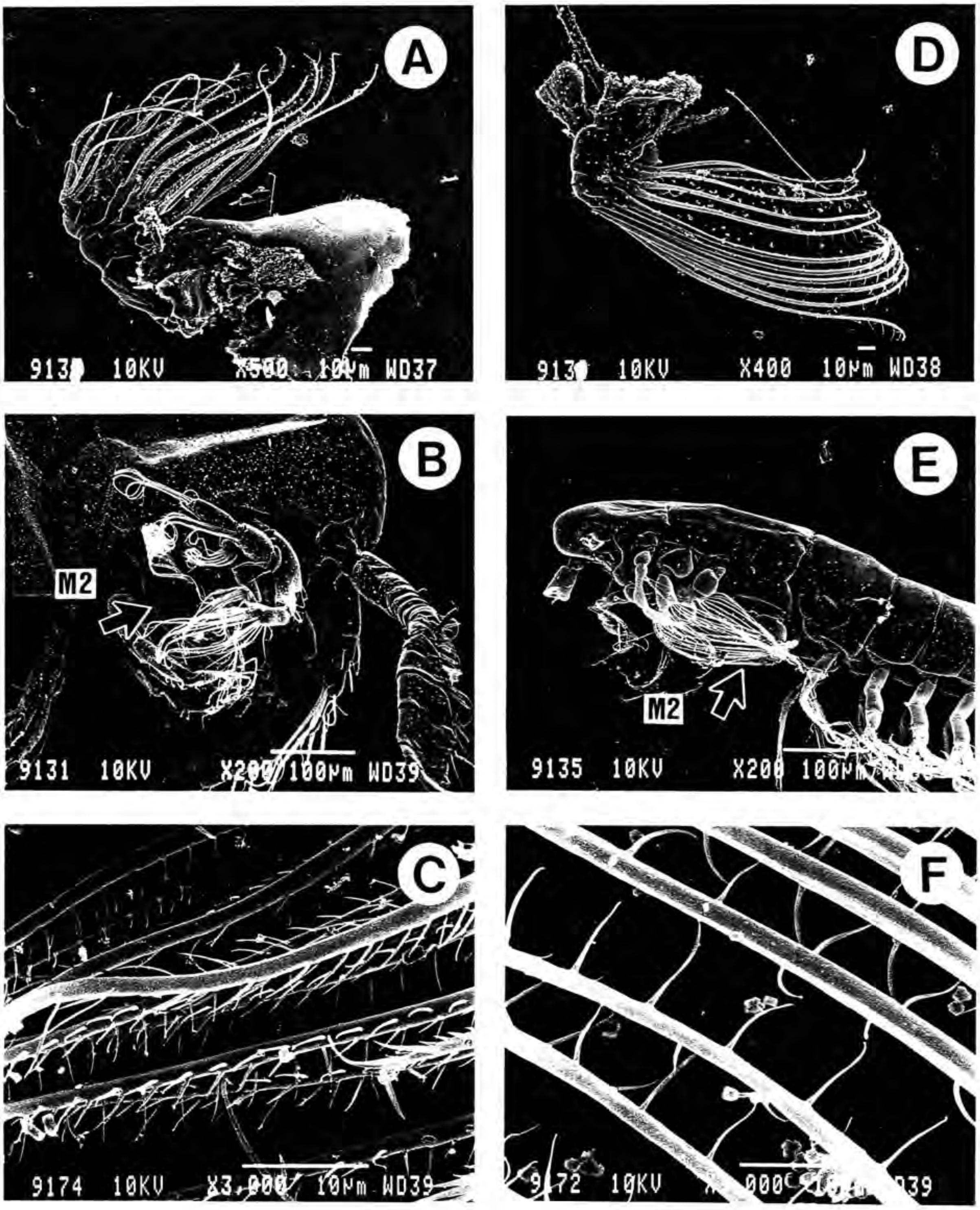


Figure 6. Scanning electron micrographs of the filtering appendages (second maxillae) of *P. hessei* and *Acartia* spp. Maxillae of *P. hessei* are shown in A to C, and maxillae of *Acartia* spp. are shown in D to F.

Nival (1976). The values obtained, and intersetule distances, are given in Table 2, compared with other studies.

Table 2. Filter area and intersetule distances of the second maxillae of *P. hessei* and *Acartia* spp. (this study), compared with other related copepods.

COPEPOD SPECIES	MAXILLAE FILTER AREA (μm^2)	MEAN INTERSETULE SPACING (μm)	SOURCE
Pseudodiaptomus hessei	3 850	2.8	this study
Pseudodiaptomus hessei	-	2 - 4	Hart, 1973
Acartia spp.	7 670	≈ 3 - 4	this study
Diaptomus sicilis	15 500	7.3	Vanderploeg & Ondricek-Fallscheer (1982)
Acartia clausi	≈ 14 000	≈ 10	Nival & Nival (1976)
Acartia tonsa	-	≈ 6 - 7	Bartram (1981)

7.3 DISCUSSION

7.3.1 FUNCTIONAL RESPONSE.

The dominant calanoid copepods of eastern Cape estuaries, *P. hessei* and *Acartia* spp., demonstrated a marked contrast in functional feeding response. The seston concentration at which the filtration rate of *P. hessei* was maximal, known as the incipient limiting level (ILL), was comparatively high (≈ 30 $mm^3\ l^{-1}$, or by conversion ≈ 185 $mg\ l^{-1}$) and occurred within the range of seston concentrations characteristic of estuaries subject to high freshwater inflow (e.g. Great Fish estuary). The decrease in the filtration rate, or feeding effort, below the ILL is thought to be a strategy to conserve energy during drops in the food level (Lam & Frost, 1976; Lehman, 1976; Frost, 1980; Paffenhöfer & Stearns, 1988). The ILL of *P. hessei* indicated that filtration rates are reduced in marine-dominated estuaries such as the Kariega, where the feeding environment is relatively "dilute" (Chapter 4). Despite this observation, *Pseudodiaptomus* is nonetheless a dominant component of the zooplankton community of the Kariega estuary throughout the year and this is possibly explained by the potentially higher energetic benefit derived from feeding on higher quality seston (Figure 7).

The ILL of *Acartia* spp. could not be determined in this study, however, the form of the functional response curve suggested that an ILL, if present, would occur below the minimum seston concentration used in this series of experiments, indicating an ILL of between 0 and 3.7 $mm^3 l^{-1}$ (or between 0 and 59 mg l^{-1} TPM, by conversion). Experiments suggested that maximal filtration rates of *Acartia* spp. would occur at seston concentrations below the natural range of even marine-dominated estuaries such as the Kariega, which are relatively "dilute" feeding environments, which suggests that satiated feeding conditions predominate in the natural environment.

A number of studies have demonstrated that the functional response varies in response to several factors including particle size and the quality of the food resource (Lam & Frost, 1976; Lehman, 1976; Roman, 1984; Houde & Roman, 1987; Kiφrboe, 1989; Stφttrup & Jensen, 1990). Although the size structure of natural seston is relatively consistent in eastern Cape estuaries, seston quality is variable (see Figure 7). In this study, the functional feeding of *Pseudodiaptomus* and *Acartia* spp. was determined under conditions of constant food quality, thus attempts to extrapolate results to field conditions are somewhat limited since the quality of natural seston generally showed an inverse relationship with seston concentration.

Threshold response (e.g. Frost, 1975; Lampert & Schober, 1980; Muck & Lampert, 1980), in which feeding activity ceases below a certain threshold feeding concentration (see Review, Chapter 3) could not be demonstrated in this study, however, is probably relatively unimportant in estuaries of the eastern Cape, since the seston rarely, if ever, approaches concentrations low enough to elicit this response.

7.3.2 PARTICLE SIZE-SELECTION.

The observation that *P. hessei* and *Acartia* spp. ingested large particles disproportionately to the frequency of these particles in the feeding medium is consistent with the results of a number of other studies (e.g. Mullin, 1963; Richman & Rogers, 1969; Frost, 1972;

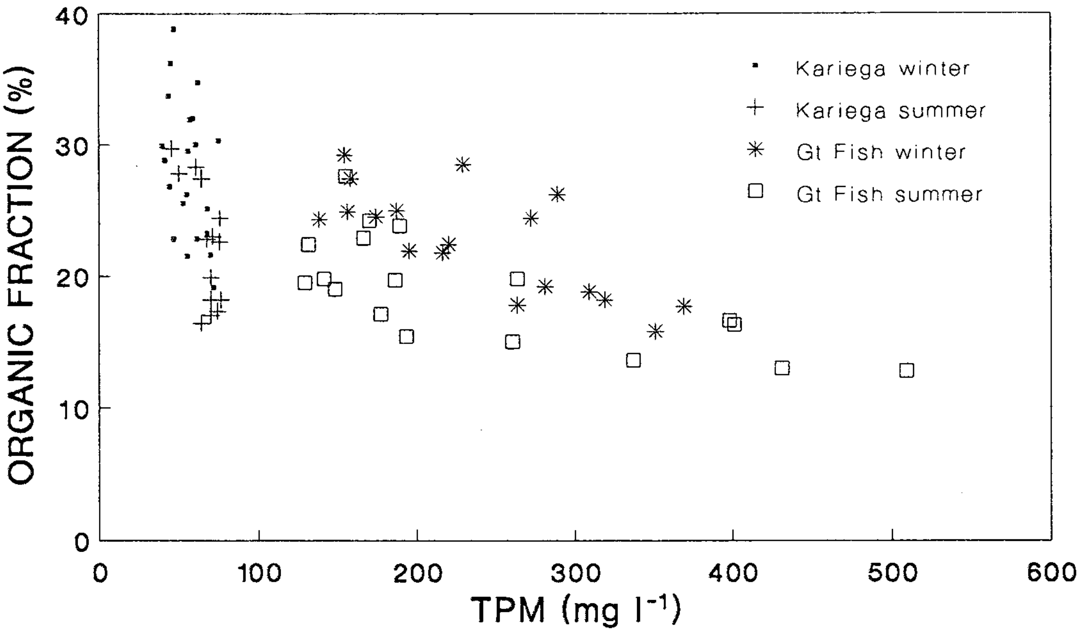


Figure 7. Seasonal variation in seston quality (as determined by organic content) in relation to seston concentration. Data recorded from the marine-dominated Kariega estuary and the freshwater-dominated Great Fish estuary during 1987/88.

Paffenhöfer & Knowles, 1978). This suggests that copepods either retained larger particles with greater efficiency, or actively selected particles in these size classes. Despite variations in the retention curves of the five experiments (Figures 5a to e), results suggest that selectivity increases significantly for particles greater than ≈ 6 to 8 μm ESD, although this was more readily apparent in experiments with *P. hessei* than *Acartia* spp.

Direct observations of the feeding behaviour of copepods have only been made in a few studies (e.g. Koehl & Strickler, 1981; Price & Paffenhöfer, 1986a; 1986b) and there are none involving South African zooplankton species. Despite this, it is useful if the results of this study can be discussed in terms of feeding behaviour by reference to related feeding groups (e.g. Bartram, 1981). For the purposes of this discussion, *Pseudodiaptomus* is grouped with the diaptomid copepods, since there is evidence that the i) feeding mode (Alcaraz *et al.*, 1980; Vanderploeg & Paffenhöfer, 1985), ii) maxillary filter structure (Vanderploeg & Ondricek-Fallscheer, 1982) and iii) turbidity tolerance (Vanderploeg, 1981; Allanson & Read, 1987) show close similarities. Feeding behaviour in the Acartiidae has been described by Rosenberg (1980).

Vanderploeg (1981) categorized feeding behaviour in copepods and grouped a number of genera into what he termed the "*Calanus*-like" copepods, which included the diaptomid copepods but not the Acartiidae. A general account of mouthpart movement during feeding in this group is given by Price *et al.* (1983) (see Review, Chapter 3). The higher filtration rates on larger particles demonstrated by "*Calanus*-like" copepods can be explained by cinematographical studies that show two modes of feeding. "Large" particles are individually detected and elicit an **active** capture response and "small" particles are accumulated by **passive** filtration and handled in groups (Price *et al.*, 1983; Vanderploeg & Paffenhöfer, 1985; Price & Paffenhöfer, 1986a; 1986b). This behaviour greatly enhances the capture probability of large particles since a large volume of water is scanned, and the perception of a particle in the feeding current is required to elicit a capture response. Also, one might expect that the small filter area of the M2 of *P. hessei* would reduce the area for passive accumulation during the capture of an individually perceived particle.

The size threshold for individual detection and capture, rather than passive accumulation, may explain the apparent increase in selectivity above ≈ 4 to 6 μm ESD for *P. hessei*, however, this is unlikely to account for the similar observation in *Acartia* spp. since the feeding mode is dissimilar. The Acartiidae show a reduced chemosensory ability (Barrientos-Chacon, 1980) and the comparatively large M2 are used in a "scoop-net" feeding action (Gauld, 1964; Rosenberg, 1980). Consequently, *Acartia* do not respond to particles in the near vicinity or alter the flow field (Paffenhöfer & Stearns, 1988), therefore patterns of particle-size retention efficiency are more likely to reflect the combined influences of M2 filter characteristics and post-capture selection processes.

The utilization of seston particles in size classes approaching the lower threshold for particle retention is likely to have important consequences for zooplankton in eastern Cape estuaries, since the majority of natural seston occurred in the < 5 μm ESD size fraction (Chapter 4). The lower size threshold of both *P. hessei* and *Acartia* was between 2 and 3 μm ESD, which was comparable to values described for *Diaptomus* (Vanderploeg, 1981) and for *Acartia* (Nival & Nival, 1976; Berggreen *et al.*, 1988). These results indicated that there was no significant difference in interspecific utilization of seston at the lower threshold based on particle size. The structure of the feeding appendages did not provide a good indication of lower size threshold, since marked differences in intersetular spacing on the M2 (Table 2) between *P. hessei* and *Acartia* spp. were not reflected in the particle retention capabilities (cf. Bartram, 1981).

The principles of fluid dynamics, in which copepod feeding appendages operate at low Reynolds numbers characterized by viscous forces, provide a likely explanation for this observation (Alcaraz *et al.*, 1980; Koehl & Strickler, 1981; Jørgensen, 1983). In several studies, estimates of the boundary layer surrounding the setules of the M2 were greater than half the intersetular distance suggesting that these appendages act as paddles rather than sieves (Vanderploeg & Paffenhöfer, 1985). A more comprehensive discussion of these principles is presented in the Review (Chapter 3).

The considerable overlap in particle size retention by *Acartia* spp. and *P. hessei* suggested that differences in seston utilization were not significant. The use of electronic particle counters in particle size selection experiments is, however, limited by the fact that the technique is unable to discriminate between particles of a different nature and therefore provides no information about behavioural selection processes. This capability is thought to be an important adaptation to living in the estuarine environment where low quality food particles predominate (Paffenhöfer & Van Sant, 1985). Although selective feeding capabilities have been demonstrated in both diaptomid-type copepods (Richman *et al.*, 1980), and *Acartia* (Donaghay & Small, 1979; Donaghay, 1980), such copepods also ingest large amounts of low quality particles in the presence of phytoplankton. *Acartia* is known to ingest large quantities of detritus (Roman, 1984), and several studies have demonstrated the presence of fine inorganic particles in the faecal pellets of *Diaptomus* (Vanderploeg, 1981), *P. hessei* (pers. obs.) and *Acartia* (Turner, 1984). This is often interpreted as evidence for non-discriminate feeding (e.g. Turner & Tester, 1989), however, several authors have proposed that organic material adsorbed onto mineral particles may act as a energy subsidy where food quality is low (Arruda *et al.*, 1983; Hart, 1987).

7.3.3 ECOLOGICAL IMPLICATIONS.

Competition between co-existing species of copepods is difficult to demonstrate in the natural environment (e.g. Hessen *et al.*, 1986; Hessen, 1990), however, limiting food resources (Chapter 4), coupled with the considerable dietary overlap (Section 7.3.2), indicated that competition between *P. hessei* and *Acartia* spp. is likely to occur in the Kariega estuary. Despite the predictions of ecological theory, competition between different species of copepod rarely seems to result in competitive exclusion (Alcaraz, 1983). There are several explanations for the co-existence of competing species (Hessen, 1990), the most common of which explains co-existence in terms of oscillating food abundance (Hessen, 1990; Rothhaupt, 1990). This provides a possible explanation for co-existence in this case, since cyclical tidal influences and pulses of freshwater inflow resulted in considerable short-term variability in the food resources (Chapter 4). The functional feeding responses of *P. hessei* and *Acartia* spp. implied differences in competitive ability with regard to food quantity, consequently, conditions in the Kariega estuary should confer a competitive advantage on both as food resources alternate between high and low abundance.

In other studies which attempt to explain the variance in feeding rates using multiple regression (Hart, 1984; 1986; Jarvis, 1987), zooplankton community biomass was generally a good indicator of zooplankton feeding, usually accounting for a significant proportion of the variance in CFR's. This was not apparent in this study, however (Chapter 5), and the results of this Chapter indicate that this may be explained at least in part by a combination of zooplankton communities comprising species with different functional responses, and the extreme variation in food resource abundance.

High food resource abundance alone does not account for the absence of *Acartia* spp. in freshwater-dominated systems such as the Great Fish estuary. Although food resources may not be limiting at all times, the characteristic size distribution of the seston in eastern Cape estuaries (Chapter 4) may pose special problems for suspension-feeders. The major fraction of the seston falls into the nanoplanktonic size category in which particles are unlikely to be perceived individually, therefore limiting the capacity for selective feeding on high quality particles (Price *et al.*, 1983; Review, Chapter 3). This may present a problem, particularly in freshwater-dominated systems where, despite high food resource concentrations, the quality is greatly reduced by the presence of suspended silt particles. This may explain the absence of *Acartia* spp. in the Great Fish estuary, although, the influence of salinity or selective predation, for example, cannot be ruled out.

Particle Size Class (um)	EXPERIMENT A													
	P. hessei							Acartia spp.						
	C	R 1	R 2	R 3	R 4	R 5	R 6	C	R 1	R 2	R 3	R 4	R 5	R 6
1.4 - 2.0	0.844	0.838	0.836	0.835	0.829	0.840	0.836	0.595	0.589	0.593	0.595	0.595	0.595	0.590
2.0 - 3.0	1.092	1.005	0.991	0.978	0.992	0.969	0.998	0.968	0.839	0.821	0.785	0.768	0.805	0.809
3.0 - 4.0	0.798	0.714	0.729	0.726	0.733	0.729	0.711	0.621	0.464	0.450	0.427	0.448	0.441	0.440
4.0 - 5.0	0.589	0.558	0.554	0.546	0.551	0.552	0.549	0.520	0.401	0.393	0.377	0.371	0.377	0.370
5.0 - 6.0	0.332	0.314	0.311	0.308	0.312	0.311	0.315	0.381	0.311	0.321	0.287	0.284	0.292	0.286
6.0 - 7.0	0.208	0.191	0.193	0.194	0.193	0.190	0.191	0.195	0.146	0.143	0.136	0.143	0.138	0.135
7.0 - 8.0	0.162	0.137	0.138	0.137	0.138	0.137	0.136	0.116	0.091	0.088	0.086	0.090	0.085	0.081
8.0 - 9.0	0.126	0.109	0.108	0.107	0.107	0.107	0.108	0.126	0.088	0.090	0.088	0.086	0.085	0.084
9.0 - 10.0	0.123	0.106	0.105	0.106	0.107	0.105	0.105	0.150	0.107	0.110	0.101	0.110	0.103	0.099
10.0 - 11.0	0.055	0.051	0.051	0.050	0.050	0.051	0.051	0.081	0.079	0.078	0.077	0.079	0.078	0.078
11.0 - 12.0	0.051	0.048	0.047	0.048	0.047	0.047	0.047	0.046	0.046	0.046	0.046	0.046	0.046	0.046
12.0 - 13.0	0.046	0.045	0.045	0.045	0.045	0.044	0.045	0.023	0.023	0.023	0.023	0.023	0.023	0.023
13.0 - 14.0	0.064	0.063	0.063	0.064	0.064	0.063	0.063	0.047	0.047	0.047	0.047	0.047	0.047	0.047

Particle Size Class (um)	EXPERIMENT B													
	P. hessei							Acartia spp.						
	C	R 1	R 2	R 3	R 4	R 5	R 6	C	R 1	R 2	R 3	R 4	R 5	R 6
1.4 - 2.0	0.734	0.732	0.733	0.731	0.734	0.731	0.734	0.682	0.682	0.682	0.682	0.682	0.682	0.682
2.0 - 3.0	0.999	0.965	0.950	0.959	0.952	0.955	0.940	0.948	0.897	0.887	0.894	0.897	0.896	0.902
3.0 - 4.0	0.883	0.769	0.767	0.739	0.761	0.746	0.758	0.913	0.871	0.875	0.873	0.864	0.869	0.878
4.0 - 5.0	0.834	0.734	0.716	0.735	0.734	0.727	0.725	0.824	0.756	0.772	0.755	0.765	0.763	0.771
5.0 - 6.0	1.101	1.041	1.020	1.035	1.028	1.015	1.011	1.061	0.959	0.960	0.951	0.950	0.954	0.969
6.0 - 7.0	0.842	0.658	0.662	0.668	0.669	0.655	0.659	0.890	0.805	0.710	0.713	0.721	0.699	0.710
7.0 - 8.0	0.739	0.608	0.577	0.567	0.601	0.566	0.612	0.717	0.556	0.642	0.642	0.654	0.644	0.643
8.0 - 9.0	0.567	0.437	0.434	0.440	0.441	0.443	0.436	0.520	0.473	0.429	0.430	0.429	0.429	0.440
9.0 - 10.0	0.123	0.110	0.110	0.109	0.110	0.109	0.108	0.150	0.125	0.118	0.120	0.119	0.117	0.118
10.0 - 11.0	0.261	0.210	0.212	0.212	0.214	0.210	0.213	0.272	0.211	0.218	0.214	0.217	0.215	0.213
11.0 - 12.0	0.279	0.279	0.279	0.279	0.279	0.279	0.279	0.309	0.245	0.246	0.250	0.246	0.243	0.243
12.0 - 13.0	0.167	0.167	0.167	0.167	0.167	0.167	0.167	0.165	0.131	0.158	0.158	0.157	0.157	0.156
13.0 - 14.0	0.038	0.038	0.038	0.038	0.038	0.038	0.038	0.037	0.035	0.037	0.037	0.037	0.037	0.037

Appendix A. Total particle volumes (mm^3 l^{-1}, per size class) of the control and replicates 1 to 6 at experiment end, for each experimental series (a to e). results for *P. hessei* shown in the left hand panel, and results for *Acartia* spp. shown in the right hand panel.

Particle Size Class (um)	EXPERIMENT C													
	P. hessei							Acartia spp.						
	C	R 1	R 2	R 3	R 4	R 5	R 6	C	R 1	R 2	R 3	R 4	R 5	R 6
1.4 - 2.0	0.671	0.671	0.671	0.671	0.671	0.671	0.671	0.647	0.616	0.608	0.601	0.614	0.609	0.608
2.0 - 3.0	0.913	0.863	0.871	0.848	0.851	0.861	0.863	0.900	0.863	0.864	0.859	0.860	0.858	0.849
3.0 - 4.0	0.890	0.827	0.811	0.820	0.835	0.820	0.828	0.932	0.798	0.777	0.784	0.758	0.781	0.768
4.0 - 5.0	0.717	0.670	0.668	0.672	0.663	0.669	0.674	0.682	0.597	0.595	0.579	0.577	0.584	0.575
5.0 - 6.0	0.740	0.716	0.715	0.713	0.709	0.711	0.714	0.703	0.615	0.603	0.612	0.608	0.606	0.606
6.0 - 7.0	0.445	0.410	0.404	0.405	0.407	0.409	0.409	0.486	0.405	0.413	0.412	0.405	0.404	0.397
7.0 - 8.0	0.243	0.216	0.213	0.217	0.219	0.220	0.218	0.287	0.247	0.251	0.244	0.239	0.243	0.239
8.0 - 9.0	0.103	0.089	0.089	0.088	0.087	0.088	0.089	0.168	0.132	0.130	0.131	0.124	0.127	0.125
9.0 - 10.0	0.056	0.046	0.045	0.047	0.046	0.047	0.047	0.037	0.028	0.028	0.028	0.028	0.027	0.027
10.0 - 11.0	0.024	0.020	0.020	0.020	0.020	0.020	0.020	0.025	0.021	0.020	0.020	0.020	0.020	0.019
11.0 - 12.0	0.073	0.065	0.065	0.066	0.066	0.066	0.066	0.103	0.079	0.080	0.080	0.078	0.078	0.078
12.0 - 13.0	0.057	0.052	0.052	0.052	0.051	0.052	0.052	0.065	0.065	0.065	0.065	0.065	0.065	0.065
13.0 - 14.0	0.035	0.035	0.035	0.035	0.035	0.035	0.035	0.043	0.043	0.043	0.043	0.043	0.043	0.043

Particle Size Class (um)	EXPERIMENT D													
	P. hessei								Acartia spp.					
	C	R 1	R 2	R 3	R 4	R 5	R 6	C	R 1	R 2	R 3	R 4	R 5	R 6
1.4 - 2.0	0.634	0.634	0.634	0.634	0.634	0.634	0.634	0.622	0.622	0.622	0.622	0.622	0.557	0.622
2.0 - 3.0	1.133	1.099	1.101	1.096	1.094	1.099	1.105	1.108	0.987	0.994	1.007	0.990	1.008	0.988
3.0 - 4.0	0.798	0.767	0.767	0.771	0.762	0.767	0.769	0.751	0.668	0.669	0.680	0.682	0.607	0.664
4.0 - 5.0	0.775	0.728	0.732	0.721	0.722	0.724	0.731	0.737	0.579	0.571	0.587	0.589	0.615	0.568
5.0 - 6.0	0.659	0.632	0.634	0.628	0.636	0.627	0.628	0.636	0.522	0.536	0.536	0.543	0.540	0.522
6.0 - 7.0	0.405	0.389	0.390	0.384	0.385	0.390	0.390	0.485	0.416	0.409	0.415	0.420	0.419	0.407
7.0 - 8.0	0.294	0.255	0.256	0.255	0.252	0.250	0.255	0.284	0.245	0.237	0.243	0.243	0.218	0.237
8.0 - 9.0	0.178	0.156	0.158	0.155	0.154	0.153	0.157	0.073	0.054	0.055	0.056	0.056	0.061	0.054
9.0 - 10.0	0.127	0.112	0.112	0.111	0.112	0.110	0.112	0.103	0.086	0.085	0.087	0.088	0.087	0.084
10.0 - 11.0	0.064	0.055	0.055	0.055	0.055	0.054	0.055	0.106	0.092	0.090	0.091	0.090	0.098	0.090
11.0 - 12.0	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.051	0.047	0.047	0.047	0.046	0.048	0.046
12.0 - 13.0	0.020	0.020	0.020	0.020	0.020	0.020	0.020	0.057	0.054	0.054	0.054	0.053	0.057	0.053
13.0 - 14.0	0.032	0.032	0.032	0.032	0.032	0.032	0.032	0.013	0.013	0.013	0.013	0.013	0.013	0.013

Particle Size Class (um)	EXPERIMENT E													
	P. hessei							Acartia spp.						
	C	R 1	R 2	R 3	R 4	R 5	R 6	C	R 1	R 2	R 3	R 4	R 5	R 6
1.4 - 2.0	0.815	0.815	0.815	0.815	0.815	0.815	0.815	0.820	0.808	0.800	0.799	0.795	0.809	0.805
2.0 - 3.0	0.775	0.739	0.732	0.737	0.738	0.742	0.739	0.760	0.719	0.723	0.710	0.713	0.720	0.726
3.0 - 4.0	0.971	0.823	0.838	0.835	0.837	0.818	0.838	0.924	0.784	0.775	0.779	0.768	0.742	0.784
4.0 - 5.0	0.948	0.828	0.815	0.814	0.806	0.843	0.826	0.889	0.714	0.707	0.694	0.702	0.682	0.716
5.0 - 6.0	0.763	0.638	0.633	0.654	0.654	0.649	0.652	0.772	0.627	0.616	0.627	0.594	0.590	0.615
6.0 - 7.0	0.659	0.545	0.563	0.555	0.565	0.549	0.559	0.671	0.555	0.547	0.540	0.529	0.541	0.558
7.0 - 8.0	0.576	0.495	0.482	0.491	0.478	0.500	0.494	0.546	0.461	0.455	0.453	0.451	0.451	0.451
8.0 - 9.0	0.390	0.319	0.322	0.321	0.317	0.318	0.322	0.388	0.324	0.318	0.316	0.309	0.311	0.318
9.0 - 10.0	0.168	0.133	0.129	0.133	0.131	0.133	0.133	0.075	0.061	0.060	0.060	0.058	0.058	0.059
10.0 - 11.0	0.173	0.133	0.130	0.132	0.131	0.132	0.132	0.180	0.137	0.136	0.135	0.132	0.130	0.136
11.0 - 12.0	0.046	0.035	0.036	0.035	0.036	0.036	0.036	0.080	0.067	0.066	0.065	0.065	0.064	0.066
12.0 - 13.0	0.064	0.064	0.064	0.064	0.064	0.064	0.064	0.066	0.056	0.055	0.055	0.055	0.053	0.055
13.0 - 14.0	0.060	0.060	0.060	0.060	0.060	0.060	0.060	0.057	0.057	0.057	0.057	0.057	0.057	0.057

CHAPTER EIGHT

GENERAL DISCUSSION

8.0 INTRODUCTION.

Reduced catchment run-off, a result of increased impoundment, and accentuated by recent drought conditions, has stimulated research towards predicting the influences of reduced freshwater inflow on estuaries in the eastern Cape region of South Africa (e.g. Reddering, 1988a; 1988b; Whitfield & Bruton, 1989; Reddering & Rust, 1990). At present, only a few studies have dealt specifically with the role of freshwater inflow on the biological functioning of eastern Cape estuaries (e.g. Allanson & Read, 1987; Whitfield & Bruton, 1989).

In this study, the influence of freshwater inflow in regulating estuarine zooplankton community structure and standing stocks was investigated. A comparison was made of the potential food resources and feeding rates of zooplankton communities in two estuaries subject to marked differences in freshwater inflow. In general, increased freshwater inflow resulted in elevated suspended particulate food resources, higher zooplankton community standing stocks and altered community structure. Estimates of daily grazing rates demonstrated that the zooplankton communities were capable of "clearing" substantial proportions of the watercolumn at certain times, indicating the potential for depletion of food resources and high rates of trophic transfer. The majority of the zooplankton community underwent diel vertical migration, and elevated nighttime feeding rates were associated with these movements. Although zooplankton community grazing rates were positively correlated with zooplankton biomass, considerable variability was evident. Multiple regression analysis failed to discriminate the major factors influencing feeding rates, although evidence has been provided which suggests that interspecific differences in response to fluctuations in the quality and quantity of particulate food resources may have been implicated.

8.1 THE INFLUENCE OF HYDRODYNAMIC CONDITIONS ON THE TROPHIC STATUS OF EASTERN CAPE ESTUARIES.

The estuaries in this study (the Kariega and Great Fish) represent extremes of a continuum of hydrodynamic conditions characteristic of eastern Cape systems (Chapter 2), and were selected in order to identify the effects of reduced freshwater inflow. Although freshwater run-off into estuaries in the region is generally low, marked differences between systems are evident, and largely due to catchment size and regulation (e.g. Allanson & Read, 1987; Reddering & Rust, 1990). The Kariega estuary is a clearwater, homogeneously marine system along its entire length, a result of minimal freshwater inflow (Allanson & Read, 1987). By contrast, the Great Fish estuary is turbid, exhibits a well-developed salinity gradient and is partially-stratified (Lucas, 1986; Allanson & Read, 1987). Despite differences in freshwater inflow, both estuaries share a number of general features common to eastern Cape estuaries. Several of these characteristics were of importance in this study: Estuaries in the eastern Cape region are shallow (< 5 m depth), channel-like systems with small tidal prisms ($< 10^6$ m^3)(Reddering, 1988a; 1988b; Reddering & Rust, 1990). With a maximum tidal range of about 1.61 metres, the estuaries are microtidal (MacKay & Schumann, 1990). Changes in water level occur in response to the semi-diurnal and spring-neap tidal cycles, and most estuaries exhibit flood tide domination as a result of constricted mouth regions (MacKay & Schumann, 1990).

Generally, estuaries are allochthonous-dominated systems (Whitfield & Bruton, 1989), and it was clear that the input of organic material and nutrients via freshwater inflow was the major factor determining food resources for planktonic suspension-feeders (Chapter 4). In addition, alternate re-suspension and settling of particulate food resources in response to tidal currents had an important modifying influence on the availability of food resources. A reduction in freshwater inflow has several important effects: There is a decreased input of nutrients and organic matter into the system (Allanson & Read, 1987), although the lower flushing rate reduces losses to the coastal shelf. Despite the higher flushing rates of freshwater-dominated systems, a "turbidity maximum" zone in the middle reaches (Lucas, 1986; Allanson & Read, 1987) is evidence of the retention and re-circulation of seston by hydrodynamic trapping. Distinct turbidity maxima only occur at moderate river discharge since particles escape from the estuary during floods (e.g. Festa & Hansen, 1978; Cloern *et al.*, 1983). This suggests that there is an optimal freshwater flow for maximum retention of material by hydrodynamic trapping. At present, there are no published data on the biological implications of this process in South African estuaries. In view of the small tidal prism volumes of eastern Cape estuaries (Reddering, 1988a; 1988b; Reddering & Rust, 1990), a small change in river discharge will effect comparatively large hydrodynamic changes. Consequently, the rate of freshwater inflow at which seston retention by hydrodynamic trapping is optimal, is likely to be comparatively low compared with northern Hemisphere estuaries. This has important implications for the regulation and management of catchments and warrants further investigation.

Correlation analyses between seston components (see Chapter 4) indicated that a long term reduction in freshwater inflow results in a marked alteration in the composition of the seston. Detritus comprised a greater proportion of the organic fraction of the seston in marine-dominated systems whereas the phytoplankton contribution was more important in freshwater systems (see also Allanson & Read, 1987). This implies that food resources for suspension-feeders in freshwater-dominated systems were of higher quality since detritus is generally considered to be of inferior nutritional value (Roman, 1984). Riverine inflow, however, results in high suspended silt loads (Lucas, 1986; Hart, 1986; Allanson & Read, 1987), consequently, the masking effect of inorganic particles is much greater where freshwater inflow is high. In addition, hydrodynamic trapping results in more efficient retention of denser inorganic particles (Festa & Hansen, 1978; Cloern *et al.*, 1983). Differences in the nature of the seston were, indirectly, a result of the reduced nutrient status and higher salinities in marine-dominated estuaries, which resulted in decreased phytoplankton standing stocks, and an increased emphasis on primary production by fringing macrophytes (Allanson & Read, 1987; de Villiers, 1989; Hilmer & Bate, 1990). Since only a small fraction of macrophyte production is utilized directly (Rublee & Roman, 1982), the majority enters the detrital "pool". It has been estimated that even in the Kariega estuary, which receives minimal freshwater inflow, phytoplankton production accounts for about 75 % of the total primary production (Allanson & Read, 1987). Although the predominance of suspended detrital material seems contradictory to this, de Villiers (1989) has suggested that marine-dominated estuaries, such as the Kariega, act as "detrital traps".

The naturally dynamic state of estuaries (Knox, 1986) has important implications for the temporal availability of food resources for suspension-feeders. Conditions in eastern Cape estuaries depend largely on the interaction of numerous cyclic and sporadic events occurring on different time scales (Lucas, 1986). Food resources varied markedly in response to the semi-diurnal tidal cycle and the seasonal temperature cycle (Chapter 4). The spring-neap tidal cycle is also likely to be important, however this was not demonstrated. The occurrence of sporadic events, notably floods, disrupt predictable cyclical patterns and result in the establishment of a new equilibrium (Whitfield & Bruton, 1989). Consequently, although estuaries may be predominantly marine-, or freshwater-dominated, classification is difficult since conditions change constantly in response to fluctuations in the environment. In general, estuaries subject to reduced freshwater inflow are likely to be more stable systems due to the greater predominance of cyclical, rather than sporadic, influences. These attributes are summarized in Table 1.

Table 1. Summary of hydrodynamic conditions and seston characteristics of eastern Cape estuaries subject to high, and low freshwater inflow.

	FRESHWATER INFLOW	
	HIGH (E.G. GREAT FISH)	LOW (E.G. KARIEGA)
1) Physical factors.		
Flushing rate:	High	Low
Allochthonous input:	High	Low
Tidal influence:	Semi-diurnal/spring-neap	Semi-diurnal/spring-neap
Turbidity:	High	Low
Salinity gradient:	Present	Generally absent
Depth stratification (salinity/temp.):	Sometimes	Weak
Stability:	Low	Moderate
2) Food factors.		
Food abundance:	High	Low
Food quality:	High	Low/Moderate
Inorganic load:	High	Moderate/Low
Predictability:	Poor	Moderate
Particle spectra:	Nanoplanktonic dominance	Nanoplanktonic dominance

8.2 ZOOPLANKTON COMMUNITY COMPOSITION AND BIOMASS.

A comparison of the zooplankton communities in the Great Fish and Kariega estuaries demonstrated that the change in the trophic status and salinity regime resulting from a large reduction in freshwater inflow had a marked influence on the distribution, abundance and composition of zooplankton standing stocks (Chapter 5). The holoplankton of estuaries is normally characterized by low specific diversity comprising mainly calanoid copepods (Alcaraz, 1983). In eastern Cape estuaries, zooplankton communities were comprised mainly of calanoid copepods of the genera *Pseudodiaptomus* and *Acartia* under conditions of marine-domination. However, a transition to a mixed calanoid/mysid shrimp-dominated community, comprised mainly of the genera *Pseudodiaptomus*

(Copepoda), *Mesopodopsis* and *Rhopalophthalmus* (Mysidaceae) occurred under conditions of high, sustained freshwater inflow (Wooldridge & Melville-Smith, 1979; Wooldridge & Erasmus, 1980; Wooldridge & Bailey, 1982; Wooldridge, 1986; Allanson & Read, 1987; Chapter 5, this study). Although the relationship between the phytoplankton and zooplankton standing stocks are unlikely to be clear where detrital and/or inorganic material dominate the seston, a comparison of the two estuaries shows that zooplankton biomass generally reflected the trophic status of the estuary (Figures 1 and 2). Zooplankton standing stocks in the region of an order of magnitude higher in the Great Fish estuary, compared with the Kariega estuary, were evidence of this.

Marked spatial variation in zooplankton biomass occurred under conditions of sustained freshwater inflow but was virtually absent where freshwater inflow was minimal. Spatial patterns were determined largely by a combination of the variation in food resources and the salinity regime. Where freshwater inflow was sustained (Great Fish estuary), food resources were higher towards the upper reaches whereas the salinity increased in the opposite direction. Zooplankton demonstrated an increase in biomass towards the upper reaches corresponding to the increase in food resources (Figure 2b and c), but declined above the region where the salinity was less than about 8 ‰ (Figure 2a). This was due to the distribution of the mysid *Mesopodopsis slabberi*, since this species comprised the majority of zooplankton community biomass. By contrast, in the Kariega estuary, there was virtually no spatial variability in the food resources and salinity, and this is reflected in the uniform distribution of zooplankton biomass (Figure 1).

The extent of freshwater inflow had important implications for the temporal distribution of zooplankton. In the Great Fish estuary, zooplankton community biomass increased rapidly in response to high food resource availability resulting from elevated river discharge (Chapter 5). Consequently, peaks in zooplankton community biomass occurred throughout the year in response to sporadic pulses of freshwater inflow, most noticeably in the upper reaches (Figure 2a). Although floods may also result in zooplankton being swept out of an estuary, it is clear that the pulses of freshwater which occurred during the study period (up to 20×10^6 m^3 $month^{-1}$)(see Chapter 4) were not of sufficient magnitude for this to occur, since zooplankton standing stocks were maintained. By comparison, the

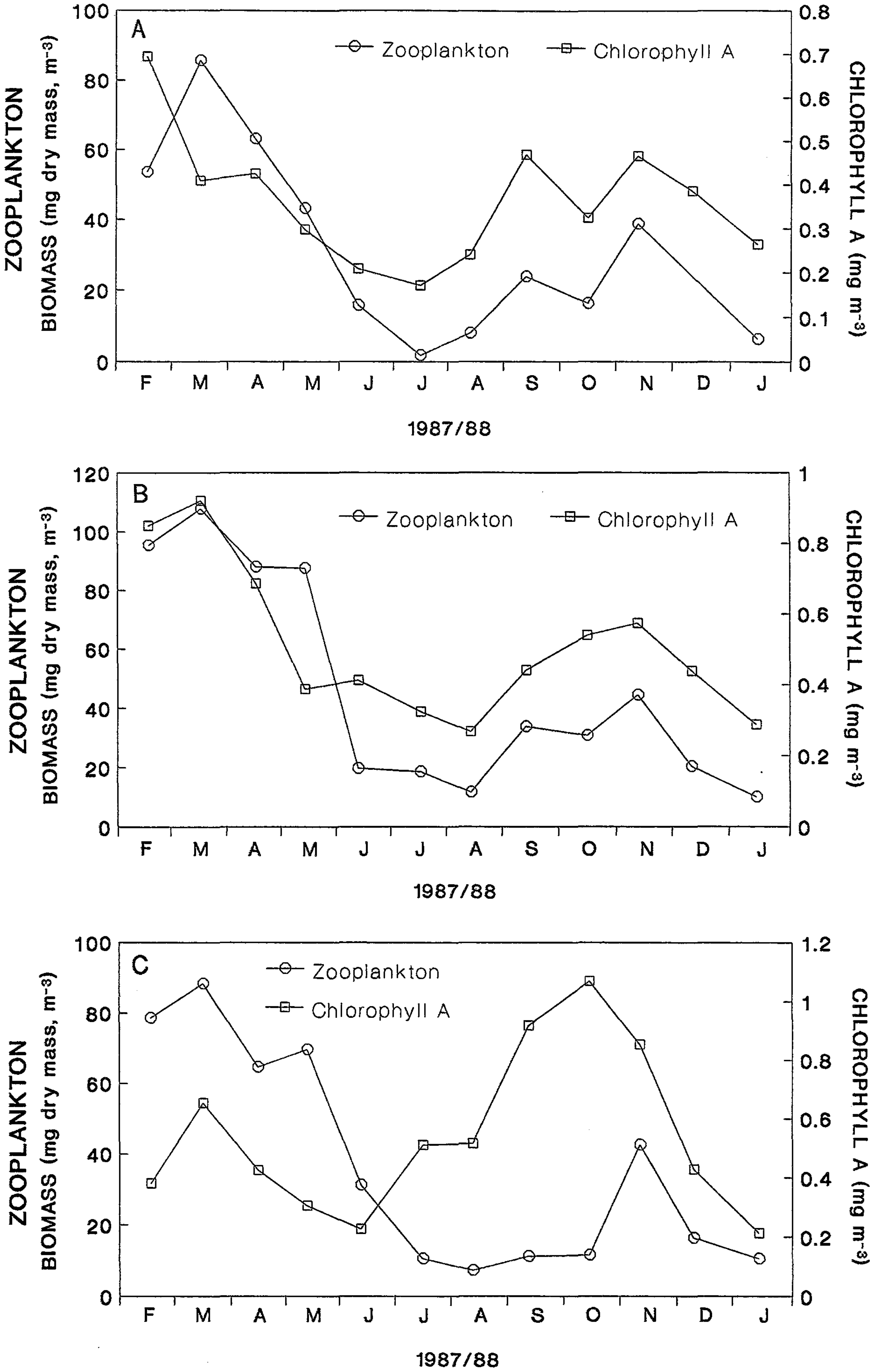


Figure 1. The relationship between Chlorophyll *a* and Zooplankton biomass in the upper- (A), middle- (B) and lower (C) reaches of the Kariega estuary during 1987/88.

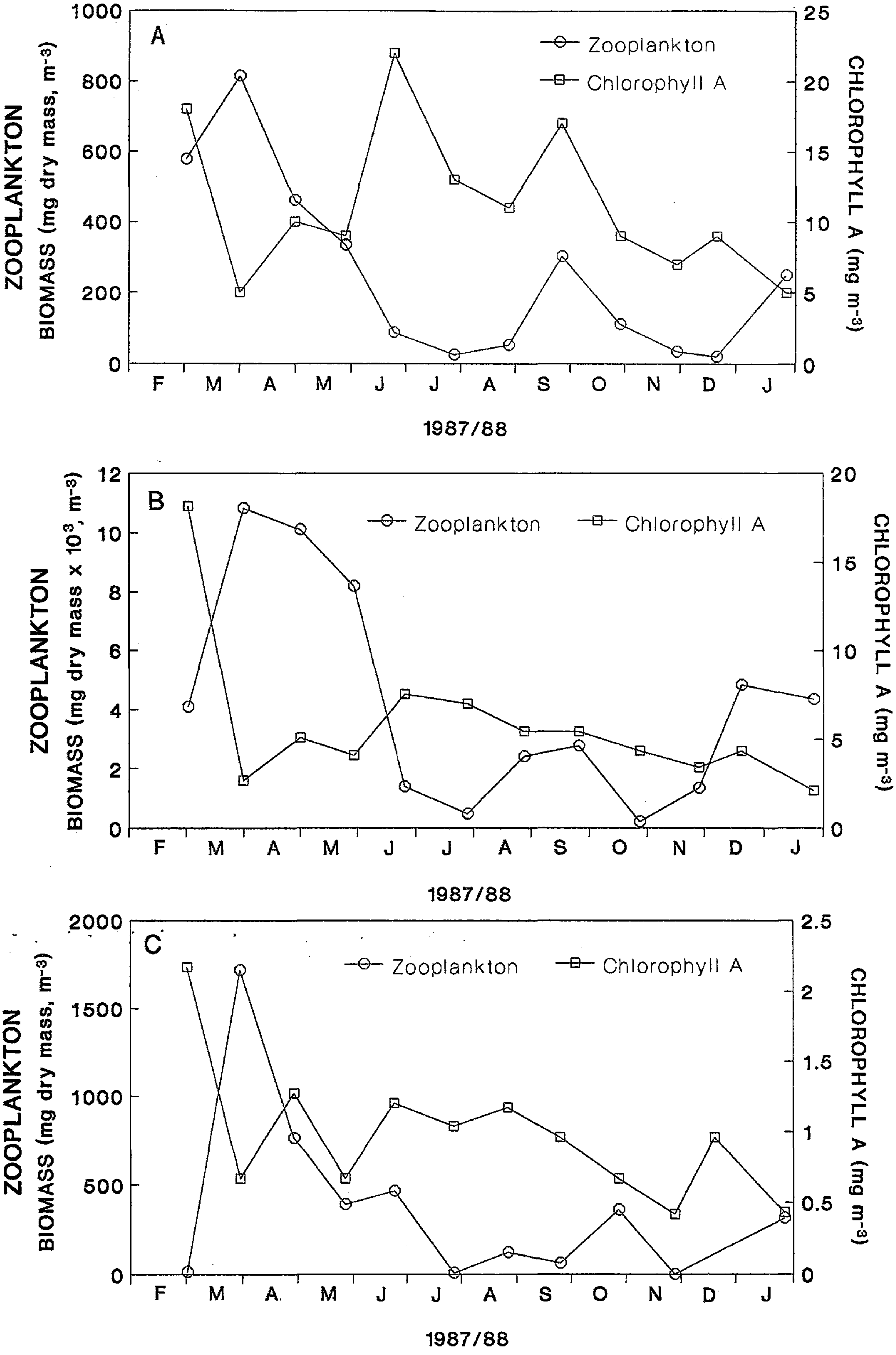


Figure 2. The relationship between Chlorophyll *a* and Zooplankton biomass in the upper- (A), middle- (B) and lower (C) reaches of the Great Fish estuary during 1987/88.

absence of freshwater inflow in the Kariega estuary resulted in a strong seasonal component in the temporal distribution of the zooplankton. A slight elevation in community biomass occurred during the early summer in response to the phytoplankton bloom which was of short duration and low magnitude (Figure 1). Extremely low biomass throughout the remainder of the year suggested that the zooplankton were frequently limited by food resources.

8.3 ZOOPLANKTON COMMUNITY GRAZING PRESSURE.

Feeding rates described in this study (Chapter 5) represent the first attempts to evaluate the grazing impact of zooplankton communities in South African estuaries. The choice of an *in situ* approach employing the Gliwicz-Haney method (Haney, 1971; 1973) enabled grazing rates of natural populations to be determined under as near-natural conditions as possible. Limitations of the method are discussed in Chapter 5. The zooplankton communities were capable of "clearing" substantial proportions of the watercolumn at certain times, and it is concluded that they are capable of substantial grazing impact on phytoplankton standing stocks. Highest community filtration rates (CFR's) were recorded in the Great Fish estuary and were frequently in the order of 50 to 80 % d^{-1} although values up to 135 % d^{-1} were measured. In the Kariega estuary, maximum grazing pressures were commonly in the region of 25 % d^{-1} although the highest value obtained was 40 % d^{-1}. The temporal and spatial variability in grazing pressure generally reflected the distribution and abundance of zooplankton standing stocks previously described in Section 8.2.

This study demonstrated the importance of diel vertical migration behaviour of the zooplankton community in influencing short term grazing patterns (see also Stearns *et al.*, 1987; Mourelatos *et al.*, 1989). Consequently, extrapolation of short time interval grazing experiments to daily rates must take account of diel variability. Fluctuations in grazing rates were generally associated with the diel distribution of biomass, determined by the vertical migration behaviour of the species, and life history stages which comprised the zooplankton community (see also Gauld, 1953; Haney, 1973; Boyd *et al.*, 1980; Dagg & Wyman, 1983; Baars & Oosterhuis, 1984; Head *et al.*, 1984; Mayzaud *et al.*, 1984b; Huntley *et al.*, 1987). Calanoid copepods of eastern Cape estuaries are characterized by ontogenetic differences in vertical migration behaviour (Grindley, 1972; 1981). The copepodite and adult stages demonstrated the "normal" pattern of nocturnal diel vertical migration (Hutchinson, 1967), however, the naupliar stages demonstrated little if any response. Vertical migration in the mysid *Mesopodopsis* was not clear and substantial numbers were present during both the day and night. Consequently, although zooplankton grazing pressure was commonly highest at night, daytime grazing by naupliar stages or mysids often comprised a substantial fraction of the diel grazing pressure. The importance of grazing pressure by sub-adult stages has previously been recognized (Stearns *et al.*, 1987; Berggreen *et al.*, 1988). After the onset of vertical migration, zooplankton were relatively evenly distributed in the watercolumn, and marked differences in depth-specific grazing pressure are unlikely. It was not possible to determine whether uniform vertical distribution was as a result of non-synchronous vertical migration (Lampert, 1989), or due to turbulence associated with tidal currents combined with the shallow nature of the estuaries, which may prevent zooplankton from maintaining a preferred depth (Huntley & Brooks, 1982; Fancett & Kimmerer, 1985).

8.4 FACTORS AFFECTING FILTRATION RATES.

Although considerable information is available on the functional feeding of zooplankton (see Review, Chapter 3), most studies have been laboratory based and problems associated with extrapolating the results to field conditions are recognized (e.g. Boyd *et al.*, 1980; Dagg & Grill, 1980; Frost, 1980; Kiφrboe *et al.*, 1982; Dagg & Wyman, 1983). Laboratory studies may suffer from a high degree of artificiality due to containment effects and do not take into account the variability of the natural environment. Consequently the need for greater emphasis on *in situ* techniques was recognized (e.g. Wang & Conover, 1986). However, due to the simultaneous influence of a variety of factors, results are often difficult to interpret. Multiple regression has been employed successfully in a few studies to investigate the main factors giving rise to the variability in zooplankton filtration rates measured *in situ* (e.g. Hart, 1984; 1986; Jarvis, 1987). In this study, attempts to explain the variability in filtration rates using the same technique were inconclusive. The use of this technique is not necessarily precluded, but several factors will need to be considered in future studies:

As several of the independent variables were found to co-vary, the true source of variability in CFR's was obscured. This problem may be resolved by a larger data set in which wider ranging conditions are encountered. Multiple regression analyses also depend upon a linear relationship between the dependent variable (CFR) and the independent variables (environmental factors). There is evidence to suggest that this is not always the case, e.g., some studies have demonstrated a biphasic response to temperature (Deason, 1980; Gulati *et al.*, 1982; Jarvis, 1987), thus precluding adequate modelling by multiple regression.

A more serious limitation of this study was the inability to determine individual filtration rates of the various life-history stages which comprised the zooplankton community (Chapter 5). This presented a problem in explaining the variability in filtration rates by multiple regression analysis since different species may filter at different mass-specific rates (Paffenhöfer, 1988). In addition, there is evidence to suggest that there is no simple relationship between developmental stage and filtration rate (Allan *et al.*, 1977; Stearns *et al.*, 1987; and references cited therein), and there may be differences in functional response between species. Difficulties encountered in interpreting the variation in filtration rates were attributed to the mixed species assemblage of the community, coupled with the high natural variability of the seston. In view of the variable nature of the seston, the functional response of the zooplankton is likely to be an important factor influencing filtration rates, and was investigated further:

Theory suggests that co-existence of species with pronounced niche overlap should result in competitive exclusion, but this is rarely demonstrated. Generally, this is either due to the effects of selective predation on competitively superior species, or differences in some aspects of the utilization of food resources (Hessen, 1990). The distribution of *Pseudodiaptomus* and *Acartia* (Section 8.2.) indicated interspecific differences in response to environmental factors. In an analysis of previous studies which considered competition between cladoceran species, or between herbivorous cladocerans and calanoid copepods, Hessen (1990) found that the most common explanation of co-existence was the combination of differences in functional feeding and oscillating food abundance. This provides a possible explanation for co-existence as well as unexplained variability in community filtration rates observed in this study.

The question arises whether there is niche overlap with respect to the utilization of food resources. This was difficult to determine conclusively, although particle size selection experiments (Chapter 7) indicated that there was considerable overlap regarding the size spectrum of the particles ingested. However, it was not possible to determine whether selection based on food quality occurred. Possible differences in feeding strategy and selective ability, based on the structure of the feeding appendages and comparisons with observations of similar species are discussed in Chapter 7. Despite arguments for different selective capabilities, it is important to note that the majority of seston (usually > 85 % by mass) occurred in the < 5 μm size fraction, and there is considerable doubt concerning the ability of copepods to distinguish the quality of particles smaller than 6 to 12 μm diameter (Price *et al.*, 1983; Vanderploeg & Paffenhöfer, 1985; Price & Paffenhöfer, 1986b).

Experiments carried out under controlled laboratory conditions to determine the influence of particle concentration on filtration rates demonstrated that filtration rates of *Pseudodiaptomus* attained an incipient limiting level at a seston concentration considerably higher than that of *Acartia* (Chapter 7). This indicated that *Pseudodiaptomus* feeds optimally at relatively high seston concentrations. The filtration rates of *Acartia* were depressed at high seston concentrations which suggested that either ingestion was saturated, or possibly that clogging of the feeding apparatus had occurred. Estuarine food quality was normally reduced under conditions of high seston concentration due to the influence of silt associated with freshwater inflow. Under these conditions, a combination of low filtration rates and poor food quality may prevent copepods of the genera *Acartia* attaining their nutritional requirements, and contribute to their exclusion from freshwater-dominated systems.

8.5 FUTURE RESEARCH.

This study has contributed to an understanding of the role of freshwater inflow in the biological functioning of eastern Cape estuaries. Zooplankton are the vital link between the detrital and phytoplankton energy base, and secondary production. Freshwater availability indirectly influences zooplankton production through their feeding by determining food resources, and is therefore one of the driving abiotic variables which affects estuarine production. In view of the importance of maintaining estuaries as productive habitats, and the decline in freshwater inflow into eastern Cape estuaries, this study emphasizes the urgent need for an estuarine management policy to be included in the management of freshwater resources. Future research directions, which have been indicated in the text, could include:

1) The relationship between freshwater inflow, hydrodynamic trapping and the quality and quantity of food resources available for suspension-feeders.

2) Measurement of species-, and life-history stage filtration rates *in situ* over the semi-diurnal and spring-neap tidal cycles in order to examine the influence of short-term, cyclical changes in food resources*.

3) Determination of; a) selective feeding capabilities by the dominant zooplankton in natural particle assemblages and elucidation of the role of inorganic particles and detritus in feeding behaviour, and b) the natural diet of the dominant zooplankton.

*There are several possible modifications to the Gliwicz-Haney method which, if incorporated in future studies, would enable individual species, and life history stage filtration rates to be measured in *in situ* experiments. The method suggested by Gulati (1985) and described in detail by Berberovic & Pinto-Coehlo (1989) would appear to offer the best option. Their method involves freeze drying the radio-labelled zooplankton assemblage which enables the subsequent enumeration and separate radioassay of community components without the loss of label reported for other methods of preservation (e.g. Holtby & Knoechel, 1981).

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