THE PELAGIC COPEPODS OF LAMBERT'S BAY:
AN ECOLOGICAL STUDY OF A WEST COAST FISHING GROUND

by

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Data used in this thesis was part of a collection made by the Sea Fisheries Research Institute in Cape Town, South Africa. I began the identification of zooplankton and its subsequent analysis while I was employed there. Recognition of technical assistance in collecting samples at sea, and analysis of related physical and chemical data by other workers, appears in the acknowledgements and in the text where appropriate. None of this material has been submitted by me for any other thesis.

Signed by candidate

Signature removed

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Abstract

Monthly zooplankton samples were collected as part of the Cape Egg and Larva Survey from August 1977 - 1978. A line of stations from the coast to approximately 90 kilometres offshore at Lambert's Bay was selected for intensive study because of its location in the middle of the recruitment area of South African anchovy and pilchard. Examination of physical features showed perennial moderate upwelling, with slight seasonal variation in frequency and intensity. Chlorophyll "a" levels were generally high. Zooplankton standing stock was surprisingly low considering the abundant phytoplankton, and this was attributed to intense predation resulting in high production/biomass ratios. Among the zooplankton, copepods were singled out for special attention because of their importance as food for larval fish. Only six species comprised 83% of the copepod community. These species displayed different spatial and temporal distribution, which appeared to be partly the result of size-determined life histories with indications of time/space niche partitioning. In comparison to the more intense seasonal upwelling area off the Cape Peninsula, there was a trend toward fewer species, larger animals, and more carnivores. This trend was related to changes in the physical and biotic environment.

CHAPTER I

INTRODUCTION

It is well-known that zooplankton, and in particular copepods, compose a large part of the diet of larval, juvenile, and adult pelagic fish (Cushing, 1969; Arthur, 1976; King and McCleod, 1976). Although St. Helena Bay and the immediate area to the north support a productive pelagic fishing industry (approximately 300,000 metric tons annually), little is known of zooplankton dynamics in that region. Whereas euphausiids, chaetognaths, amphipods, salps and doliolids, and fish of the area have been the subject of distribution studies, (Nepgen,1957; Heydorn, 1959; Van Zyl, 1960; Siegfried, 1963), little has been published on copepods of the area. In addition, copepods from other west and south-west coast areas have been analyzed. Hutchings (1979) did a detailed study of the copepod community off the Cape Peninsula and De Decker (1973) described the Agulhas Bank plankton. The Walvis Bay area was studied by Kollmer (1963), Stander and De Decker (1969), and Unteruberbacher (1964). In addition, short reports have been published on St. Helena Bay plankton (De Jager, 1954), and on temperature, currents, salinity and nutrients of the entire west coast region (Clowes, 1954; Buys, 1954). However, to date no detailed study of the copepod distribution in the area north of the bay has been undertaken.

The purpose of this study is to examine the zooplankton population dynamics in the center of the extensive anchovy and pilchard fishing ground off Lambert's Bay, an area some 50 km north of St. Helena Bay. It is in this area that young anchovy (Engraulis capensis), pilchards (Sardinops ocellata), and red-eye (Etrumeus teres) recruit from January through May and during that time must encounter sufficient food in the form of copepods and other zooplankton. The primary emphasis of this paper is on the quantitative and qualitative aspects of copepods species distribution, and on the relationship between copepods and the physical and biotic features of their environment. The spatial and temporal distribution of non-copepod groups is also described and discussed in relation to that of the copepods.

Samples were collected in 1977-78 by the Sea Fisheries Research Institute of South Africa as part of their Cape Egg and Larva Program. Although the sampling was undertaken with the objective of obtaining quantitative fish egg and larval data, valuable new information pertinent to zooplankton distribution was obtained. Spatial and temporal patterns became apparent, which permitted new understanding of the interaction between the plankton and accompanying physical and biological conditions. In general, the topics covered in this study are:

a. a description of the physical environment of Lambert's Bay in which the zooplankton live;

b. a description, both quantitative and qualitative, of the temporal and spatial changes in zooplankton distribution in the area;

c. the relationship between copepod distribution and certain environmental parameters;

d. a description of the non-copepod zooplankton distribution and its relationship to that of the copepods;

e. possible evidence for varying life history strategies in copepod species of different sizes;

f. a comparison between the Lambert's Bay area and other upwelling areas in terms of seasonal variation in zooplankton abundance and production.

Interpretation of the data involves consideration of several relatively distinct problems. In order to facilitate both reading and the evaluation of the different categories of data, discussion of each topic is included in each chapter.

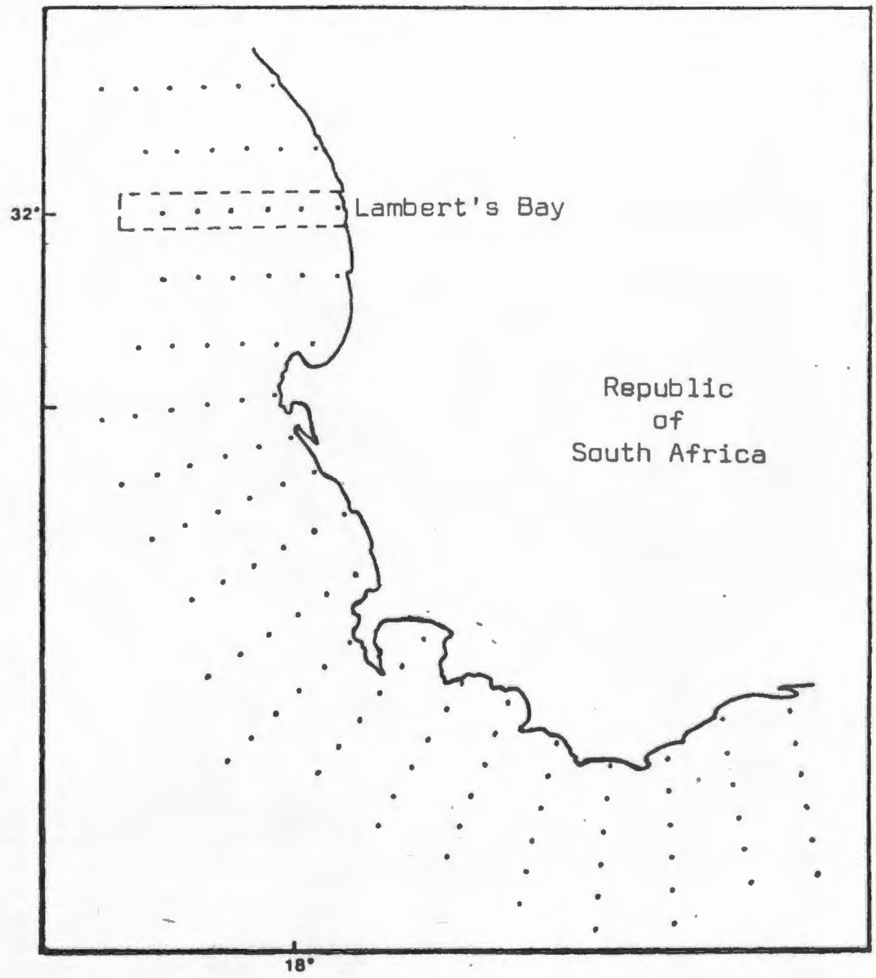

Fig. 2.1. The monthly sampling grid of the Cape Egg and Larvae Program of 1977-78. samples used in the study are from Line 16, shown inside the dotted lines.

CHAPTER II

MATERIALS AND METHODS

Shipboard Sampling

The zooplankton used in this study were part of a collection obtained in 1977-78 for the Cape Egg and Larva Program (CELP) conducted by the Sea Fisheries Research Institute in Cape Town, South Africa. CELP sampling was conducted at approximately one month intervals along lines radiating outward from the south and west coast, six stations to a line, over a period of thirteen months (Fig II.1). In order to gain insight into the zooplankton dynamics of the rich west coast fishing grounds, and to allow a comparison with the previously studied area of intense upwelling farther south (Hutchings, 1980), a single line of stations (Line 16) of the CELP grid was chosen for detailed investigation.[1] This line bisected the area thought to be the primary recruitment site for the west coast anchovy and pilchard populations, and the area most productive in terms of the pelagic fish industry.

The line of sampled stations extends normal to the coast seaward from Lambert's Bay at Latitude 32 5'S.

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1. In the CELP numbering system, the first two digits identify the line of stations. The last two numbers refer to the station on the line, starting inshore with -02 and proceeding in consecutive even numbes in a seaward direction. Hence, 16-02 is the inshore station on Line 16 and 16-12 is the outermost station in the line of six stations.

The first station was two nautical miles (3.2 Km) from the coast, and subsequent stations were at ten-mile intervals. The last station was approximately 52 miles (80 Km) from the coast and just within the 200 m isobath. Bongo nets (Brown and McGowan, 1967) of 57 cm mouth diameter, fitted with 500 and 300 µm nets, were used to collect plankton. Oblique tows, from the surface to bottom or 100 m, averaged 12 minutes at speeds ranging from 0.5 - 2.94 m/sec. Net speed was determined by flow meter. Zooplankton from each haul was washed from the net and preserved in 5% formalin buffered with marble chips.

Because sampling was performed for purposes other than the work done here, certain limitations were inherent in the data. For example, the time of day at which each station was sampled varied each month in an irregular manner, so that the effect of vertical migration may have outweighed the seasonal or geographic variation. Second, the sampling interval ranged from four to six weeks, making it difficult to detect short-term changes due to upwelling and other wind or current variations. Third, plankton was not sampled at discrete depths, so that it was difficult to determine the best way of dealing quantitatively with the numbers of individuals caught in each tow; i.e. if most of the plankton were above the thermocline, then standardization to numbers/1000m^3 of water filtered, as done in this paper, may have distorted rather than simplified data analysis. Standardization in deeper offshore water may indicate a population concentration lower than was actually there. In dealing with this problem in their similar study in Oregon, Peterson and Miller (1977) questioned the significance of all comparative values for inshore and offshore stations that did not differ from each other by more than the factor obtained by dividing the offshore depth by the inshore depth. Fourth, samples were collected for one year only, so that while seasonal variation could be described, there were no comparable data demonstrating that the changes were, in fact, caused by seasonal differences and not other, unknown, factors.

Laboratory Procedures

In the laboratory, the smaller zooplankton (<1.6 mm in diameter) were separated using a 1600 µm sieve. These were weighed after being placed on a mesh and sucked dry for 2 minutes at 10 cm Hg pressure. After resuspension in formalin and settling for 30 minutes, the settled volume was diluted five times. A subsample was then removed with a large-mouth pipette while swirling the diluted sample. Zooplankton were identified under a dissecting microscope until a total of 400 copepods was reached. Repeat counts were made in this way from one sample to determine the reliability of the counting method. Percentage composition of the three dominant species (combined total, 80% of the total sample) was repeatable within a range of 5%.

The subsample of zooplankton greater than 1.6 mm in diameter was subdivided with a 3500 um sieve into medium- and large-sized components. The medium fraction was generally small and all individuals were counted. In the few instances where this was not the case, a settled volume was read as in the small size-fraction, the sample diluted five times, and five 5-ml aliquots were counted. All the zooplankton in the larger size component were counted, with the exception of the largest samples (mostly euphausiids) which were divided with the Folsom splitter to achieve a manageable number for counting. After counting the medium- and large-sized components in the described manner for the purpose of accurate counting, the numbers for each were combined and referred to as the large size-fraction.

Research by Pillar (1982) demonstrated that species smaller than 1.54 mm in length were not caught representatively by the 300 μm Bongo net. As a result, only generalizations can be made about species composition, although fortunately the percentage differences were extremely high and probably represented true qualitative, if not quantitative, population differences. Also, only wet weights and species composition were recorded for the small size-fraction, leaving no way to determine the absolute number of individuals of each species in the sample. Attempts to determine relative weights of each species were not successful, as the amount of fluid retained varied from species to species and distorted the weights, as determined when comparisons were made against samples of known composition. Consequently, relative numbers within each species were estimated using wet weights and percentage composition, assigning equal weights to each species. Although this required the erroneous assumption that all species were of equal average weight, the size range within the small size-fraction was narrow enough to warrant the use of relative numbers in determining the broad trends described below.

Other Methods

Methods used in numerical classification, and other techniques relevant to specific chapters, are described in the appropriate chapters.

CHAPTER III

ENVIRONMENTAL CONDITIONS

Introduction

Several aspects of the physical and biological environment surrounding the study site have an influence upon zooplankton distribution in the area. For example, the contours and composition of the bottom help to determine both current patterns and the type of benthic zooplankton which contribute their larval stages to the zooplankton. Wind patterns, both local and regional, alter the currents and determine the horizontal distribution of phyto- and zooplankton as well as the strength and location of upwelling sites and eddies of varying depth. These last in turn influence zooplankton distribution both through physical dispersal and concentration and by determining the availability of the nutrients necessary for phytoplankton growth. As a final step, phytoplankton availability ultimately provides the potential for zooplankton population growth.

In this chapter, the local characteristics of each of these factors will be described, first individually and then as they relate to each other in determining the characteristics of four water types of specific temperature and salinity ranges to which zooplankton distribution can be related.

Materials and Methods

In addition to plankton samples, wind direction and speed were recorded at each station, and a Bissett-Berman 6600 thermosalinograph was used to record surface temperature and salinity. Temperature sections were compiled from bathythermograph recordings from the surface to the bottom. Chlorophyll "a", as an indicator of phytoplankton abundance, was analyzed by spectrophotometer following the method of UNESCO (1966) from 1-litre samples. Samples were analyzed and plotted by Sybrand Mostert and Gustav Wehmeyer of the Environmental Section of the Sea Fisheries Research Institute. Patterns over the CELP grid each month have since been briefly described by Shannon, et al. (in prep.) Fish eggs and larvae were removed for examination elsewhere.

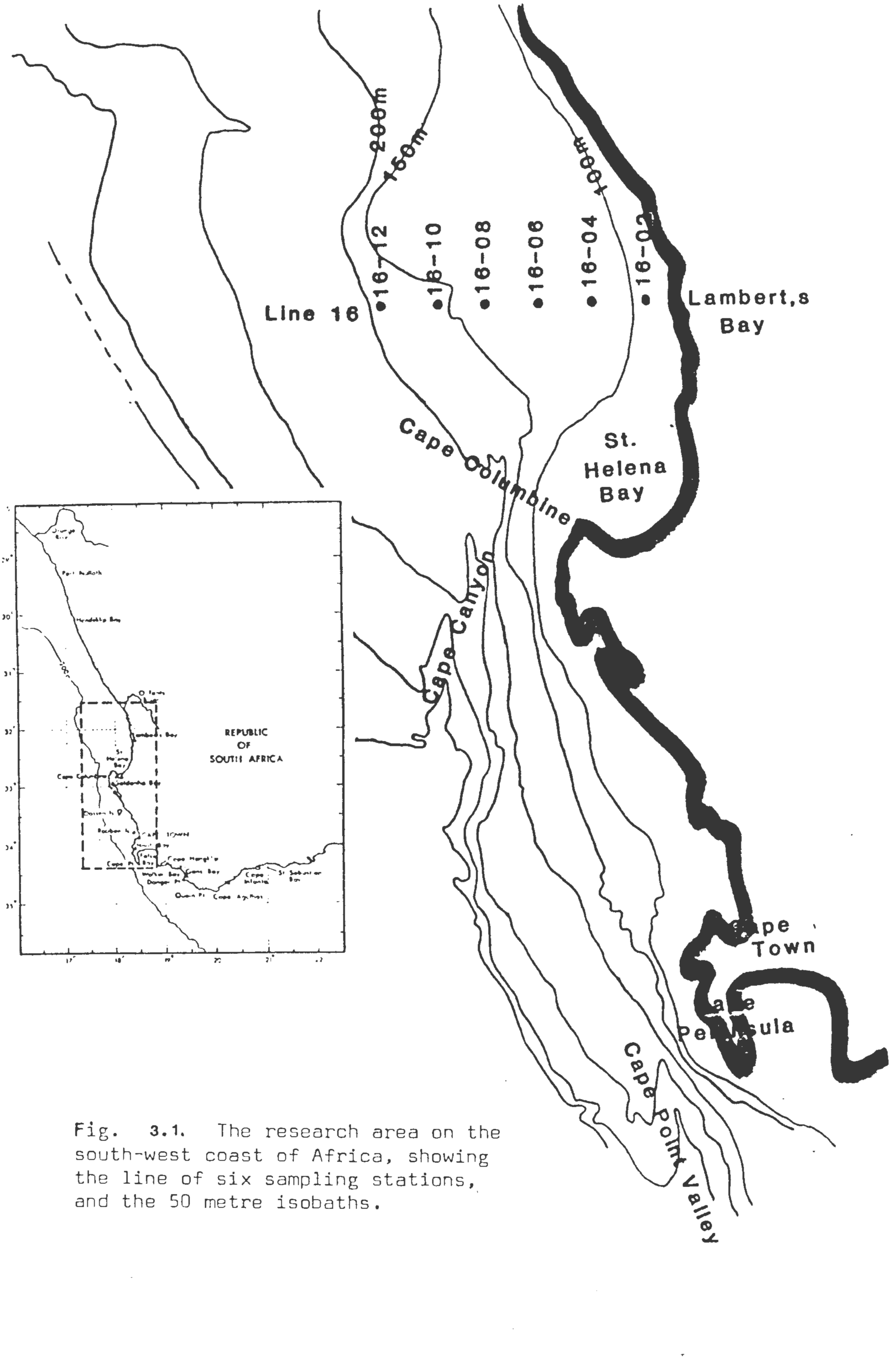


Fig. 3.1. The research area on the south-west coast of Africa, showing the line of six sampling stations, and the 50 metre isobaths.

Results and Discussion

Bottom Topography

The entire area from St. Helena Bay northward through the study line is shallow, with a gently sloping bottom (Fig. 3.1). This topography contrasts sharply with the area immediately to the south, from Cape Point to Cape Columbine, where a marked shelf break and deep canyons occasionally drive the 200 m isobath to within 20 km from the coast. Starting at Cape Columbine, where isobaths are very closely spaced at the head of the Cape Canyon, all isobaths of greater than 200 m depth fan out in a northwest direction. The coast swings eastward into St. Helena Bay, creating a broad continental shelf, which extends north through the research area. Seaward of the 400 m isobath (approximately 140 km from the coast at Line 16), the slope increases considerably, but there is still no marked shelf break. The outermost station studied, Station 16-12, lies just within 200 m depth. This wide, gently-sloping shelf, contrasting so markedly with the area farther south, has a strong influence on the currents of the area (see below).

Along the sampling line, there is a fairly rapid increase in depth to 100 m within the first three miles from shore, followed by a much decreased slope for the remaining distance. The bottom is covered with a green, organically-rich mud at all stations, as evidenced by the debris brought up in the nets when they accidently hit bottom. This was also reported by Buys (1954). The benthos was described by Christie (1976).

Wind

There is a well-documented correlation along the west coast of South Africa between southerly or south-easterly winds and upwelling events (Andrews and Cram, 1969; Andrews, 1975; Andrews and Hutchings, 1980), and several studies have noted the existence of strong and persistent southerly winds in summer from St. Helena Bay northward (Clowes, 1954, from "Weather on the Coasts of Southern Africa," 1943; Hart and Currie, 1960; Shannon, 1966; Visser, 1969). There is a frequent reversal to northerly or north-westerly winds during the late autumn or winter months, which can produce

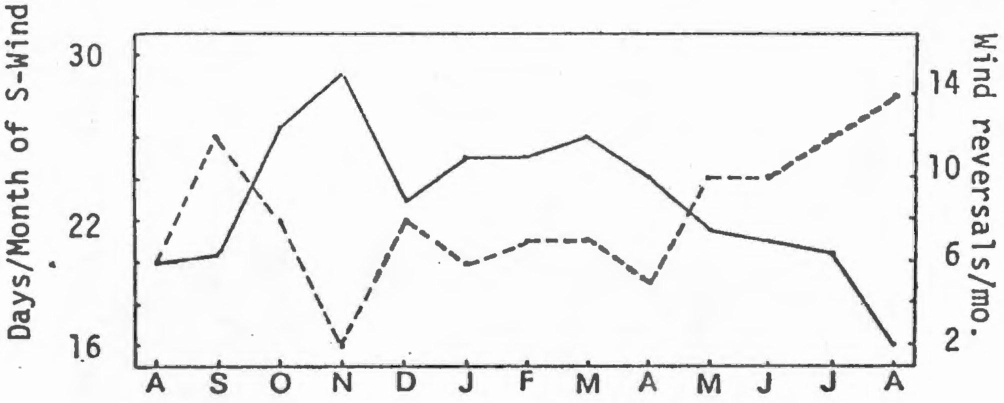


Fig. 3.2. Wind patterns at the Cape Columbine Lighthouse, from August 1977-1978. Solid line represents the number of days/month when the predominant wind was southerly (SE-SW inclusive). Dotted line represents the number of wind reversals/month.

downwelling. The reversal in this area, however, is neither as strong nor as frequent as that farther south off the Cape Peninsula, and important differences exist between the areas. Recent unpublished work by Jury (1979) and by Nelson and Hutchings (in press) all verify and elaborate on the wind patterns described in previous works. The net result is a milder, but more persistent, occurrence of upwelling in the study area throughout the year, as compared to the Cape Peninsula upwelling area.

Wind data directly bearing on this study came from three sources. The first was the Cape Columbine Lighthouse, 70 km to the south of Line 16, which contributed hourly readings of estimated wind speed and direction. Local topography can distort the wind patterns here, causing them to differ from those at sea. Comparison with ship-board readings indicates that the disparity was greater in winter than in summer. Figure 3.2 shows the number of days per month where a southerly (ESE-WSW inclusive), or upwelling, wind predominated at the Cape Columbine Lighthouse. A seasonal difference is apparent, with a southerly wind dominating for 23 or more days each month, from October through April. Southerly winds were least common in August 1978, with only 16 days when the wind was predominantly from the south. The number of wind reversals per month also shifted seasonally, with the fewest between late spring and early autumn and the most between late autumn and early spring.

Secondly, shipboard readings were taken at each station as sampling began. Only one reading per month per station was possible from the ship, and cannot be expected to be representative of average monthly conditions. Even so, a seasonal difference was apparent here also, with 32 southerly reading from October through April, and 16 from May through September, out of the total of 36 for each period.

Thirdly, an automatic weather station established by the Sea Fisheries Research Institute at Nuwedam provided data for progressive vector diagrams for a 10-month period from January to October 1979 (Fig. 3.3). Although these vector diagrams were compiled for the year following sampling, they are valuable for the corroborative data they contain on seasonal trends. In addition to illustrating the dominance of SW winds in late summer and the lessening of the southerly component in late winter and early spring, this figure shows clearly the marked diurnal fluctuation in wind direction. How far

Fig.III.3.a: 19/2/79 through 18/3/79

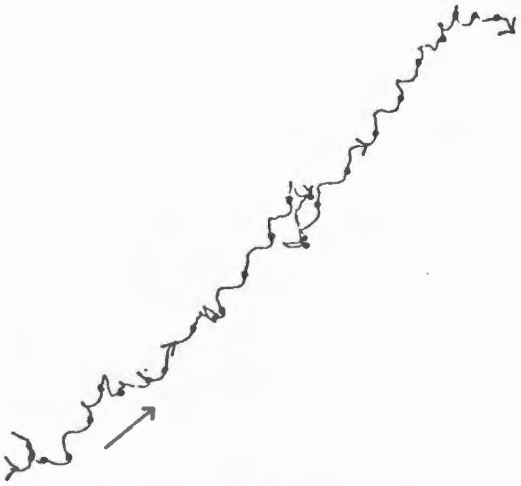


Fig.III.3b: 29/3/79 through 25/5/79.

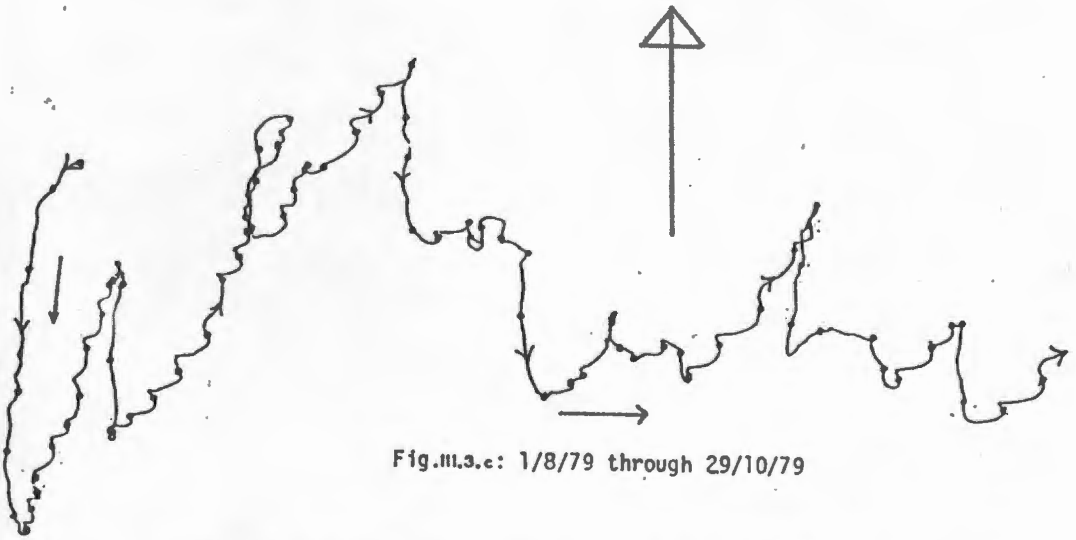


Fig.III.3.c: 1/8/79 through 29/10/79

Fig3.3.a-c. progressive vector diagrams from the Nuwedam weather station, from the direction and average velocities for every hour (unpublished Sea Fisheries Research Institute data). Circles represent daily intervals.

offshore this land-sea breeze effect was felt, is unknown.

Wind data from all locations indicated a slight shift in wind direction from the SE-NW axis predominant off the Cape Peninsula to a more S-N axis north of St. Helena Bay. The coast also swings in that direction and the effects of wind on upwelling are similar in both areas.

Currents and Upwelling

The Benguela Current is the dominant current affecting the study area. It forms the eastern boundary of the permanent anti-clockwise South Atlantic gyre. The current is usually sluggish, but is characterized by its extreme variability (Hart and Currie, 1960). As is typical of an eastern boundary current, density increases in a shoreward direction. The effects of temperature outweigh those of salinity in determining density within the ranges present here. Along Line 16 both values increase in a seaward direction.

Along the Cape Peninsula and again at Cape Columbine, the abrupt continental shelf break, submarine canyons, and strong southerly winds all combine to accelerate the northerly flow into strong jet currents (Nelson and Hutchings, in press). This will be discussed in more detail later in this chapter. Once past Cape Columbine, southerly winds drop in intensity and the bottom contours fan out to the west. Both factors have the effect of reducing the driving force behind the current, allowing eddies, countercurrents, sunwarming, and the sinking of current-transported plankton.

Inshore of the main flow of the Benguela Current are other, more variable currents. Duncan and Nell (1969) described the seasonal variation in the surface currents of the Lambert's Bay area in their drift-card study of 1953-63:

> "North of St. Helena Bay in summer, the drift is mainly northerly with an occasional inshore counter-current. In autumn there is a pronounced southerly current inshore. In winter the dominant drift is southerly, with occasional reversion to the summer pattern. In spring there are often southerly currents close inshore, but the main drift is northerly.
>
> In autumn and winter there is always a southerly inshore current, and the offshore current often flows south" (p. 13).
>
> "The offshore current, however, may flow northwards in autumn and in winter, and this is the summer pattern of flow when upwelling occurs" (p. 14).

Although surface currents have been well documented, the deep-water flows are more difficult to trace. Shannon (1966) states:

> "Results showed that the surface currents were highly dependent on wind speed and direction, while currents below the surface (for example, at 20 metres) often bore no resemblance whatsoever to those at the surface" (p. 17).

Field, *et al.* (1981) report that in shallow, inshore water during the September to May upwelling season off the Cape Peninsula, surface water moved seaward, whereas water below 9 m moved shoreward. Similar occurrences of sub-surface onshore currents during upwelling have been reported off Oregon (Peterson, 1978; Smith, 1981), off Peru (Smith, *et al.*, 1980) and off NW Africa (Smith, 1981; Boucher, 1982). Nelson and Hutchings (in press) report inshore currents to be sluggish in the research area.

De Decker (1970) analyzed hydrographic data collected on the west coast over a ten-year period (1957-67) in a study spurred by the occurrence of several incidents of mass mortality of euphausiids, rock lobsters, and white mussels. He described a subsurface low-oxygen (<2 ml/l) counter-current (i.e., south-flowing), present primarily in late summer to early winter, and often disappearing completely in the spring. (The average oxygen content on the west coast of South Africa is approximately 4 ml/l in the layers from 20 to 100 m.) According to De Decker, the oligoxic water usually, though not always, lay on the bottom. Occasionally, in late summer or early autumn, it rose to a depth of 20 m inshore. It never rose above the 10 m level. The average thickness of the oligoxic current was 20 m (maximum measured thickness, 40 m) and the maximum width 30 miles, narrowing as it moved southward. It never occurred farther offshore than the second station (16-04), although occasionally in winter and autumn it occurred at the second station while skipping the first (16-02). Everywhere it occurred within very narrow temperature and salinity ranges (9-10°C; 34.65-34.75‰).

Bang (1976) confirms the existence of such a counter-current, but believes it to be only occasionally oligoxic. De Decker and Bang also disagree about the origin of the current, but there is little doubt that the inshore south-flowing current does exist, at least in summer and in autumn.

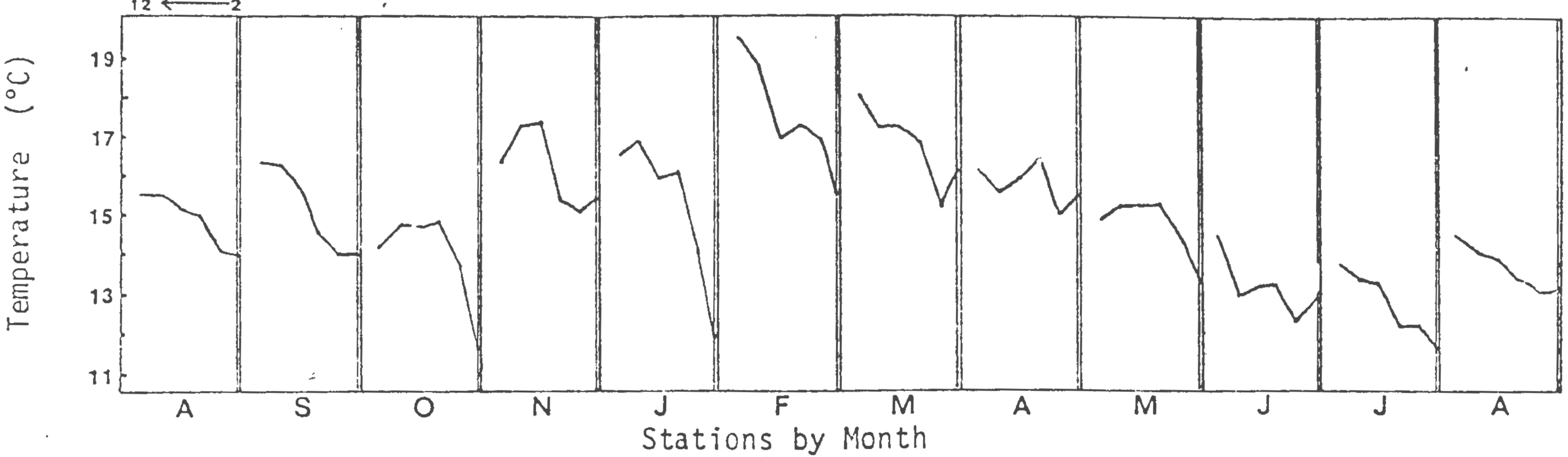
The most significant factor contributing to the productivity of the waters of western South Africa is upwelling. The mechanism of upwelling is described in detail by Clowes (1954) and will not be dealt with here. Multidisciplinary descriptions of upwelling phenomena are described in Boje and Tomczak (1978) and Richards (1981).

The previously mentioned occurrence in the Benguela Current water of light, warm water to seaward and cold, heavy water inshore is augmented by a band of upwelled water of varying width which extends along the west coast of South Africa from Cape Agulhas at 35°S to Cape Frio at 18°S. Off Lambert's Bay, this inshore band of upwelled water is only one of three types of upwelling to affect the area.

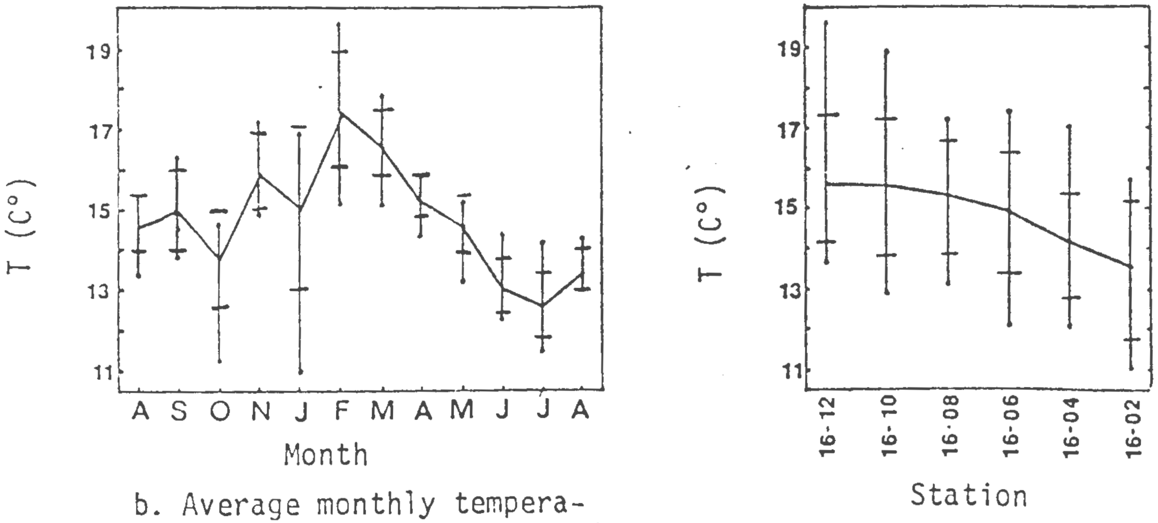
A second source is an upwelling plume caused by the combined effects of the Cape Canyon and southerly winds at Cape Columbine. Off both the Cape Peninsula and Cape Columbine, the narrow shelf and deep underwater canyons provide conditions which enable tremendous rates (20-30 m/day) of upwelling to develop (Bang, 1976). The upwelled water from these two and other lesser upwelling sites feed large amounts of high nutrient, low temperature, and low salinity water into the Benguela Current. The Cape Peninsula plume is probably the southernmost major contributor of upwelled water to the Current (Andrews and Hutchings, 1980). Farther north, given a long period of strong southerly winds, the effects of the Columbine upwelling centre may be felt in an extensive plume of high nutrient water extending to Line 16 and beyond.

The third type of upwelling to influence the Lambert's Bay area is caused by divergence within cyclonic eddies formed by the Cape Columbine Jet during periods of very strong southerly winds farther south. Bang and Andrews (1976) explain the extreme speed of the more southerly Good Hope Jet as the result of excess energy caused by a combination of strong SE winds and the sharp shelf break at the Cape Point Valley, which cannot be completely absorbed by inshore frictional forces. The excess energy is expended in accelerating the Good Hope Jet. It can be assumed, given the similar wind and bottom features, that similar, if not identical, forces are behind the Columbine Jet, which is in turn the cause of large cyclonic and anti-cyclonic eddies north of Cape Columbine. When these eddies are formed, temperature and salinity profiles indicate that they are occasionally of sufficient strength to overwhelm the effects of both the plume and the belt upwelling. Smaller shallow eddies are formed by meanders and dissipation of the jet. Eddies appear in temperature sections as domes or slumps in the isotherms.

Upwelling and current conditions along Line 16 during the time of the study



a. All stations during all months (points go from offshore to onshore in a left-to-right direction within each month.



b. Average monthly temperatures, all stations combined.

c. Average annual station temperatures, all months combined.

Fig. 3.4.a-c. Surface temperature values, taken from the ship just preceding sampling. Vertical lines indicate range; horizontal bars represent standard deviation.

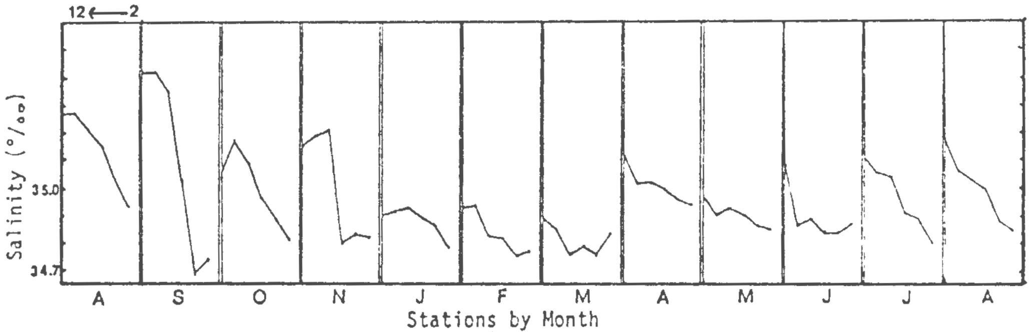
period can be summarized as follows: (1) belt-type inshore upwelling during all but late autumn and winter months, when SE winds dropped inshore, and in November when appropriate winds were present but their effects overridden by a strong cyclonic eddy centred over Station 16-04; (2) occasional less-defined appearances of isolated pockets of colder water at the outer stations which may represent a cross-section of the Cape Columbine plume; (3) strong eddies with accompanying doming or sinking, occurring most markedly in November and January; (4) and an inshore, south-flowing current present to some degree at varying depths during most months. In February and March, upwelling had lessened sufficiently for a sharp thermocline to form over uplifted water. More specific details will be presented in Chapter IV when environmental factors are related to zooplankton abundance.

Temperature and Salinity

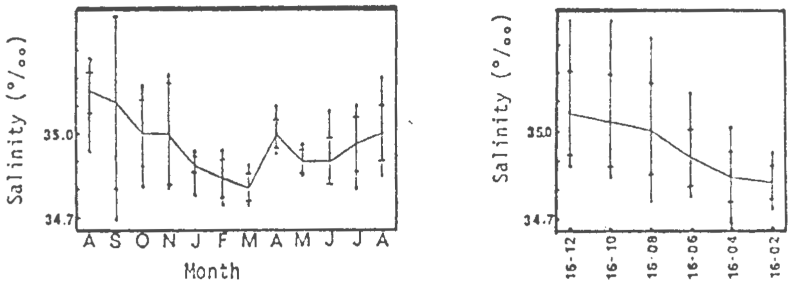
Temperature and salinity data are significant for two reasons. One is that they are useful indicators of the degree of aging in a mass of upwelled water. The values of both increase as upwelled water is affected by sun-warming and evaporation but not necessarily at the same rate, salinity being a more conservative property than temperature. For example, in summer, low temperature and low salinity water indicate upwelling. High temperatures and low salinities can mean sunwarming after relaxed upwelling. In winter, low temperatures and high salinities may indicate the lack of sunwarming on mixed or offshore water. Taken together, temperature and salinity allow a more accurate interpretation of events than does either variable viewed independently.

The second reason for their significance is that both parameters can be effective environmental markers for temperature- or chemo-sensitive zooplankton. Different members of the zooplankton often show a strong preference for water of specific physical properties, using them as niche boundaries (Parsons and Takahashi, 1973). Others are known to use environmental cues to signal the onset of certain types of adaptive behaviour (Levinton, 1982).

Because of the nearly continual upwelling, the entire study area can be characterized as one of low temperatures and low salinities in relation to the main body



a. All stations during all months (points go from offshore to onshore in a left-to-right direction within each month).



b. Average monthly salinities, all stations combined.

c. Average annual station salinities, all months combined.

Figure 3.5. Surface salinity values, taken from the ship just preceding sampling. Vertical lines indicate range; horizontal bars represent standard deviation.

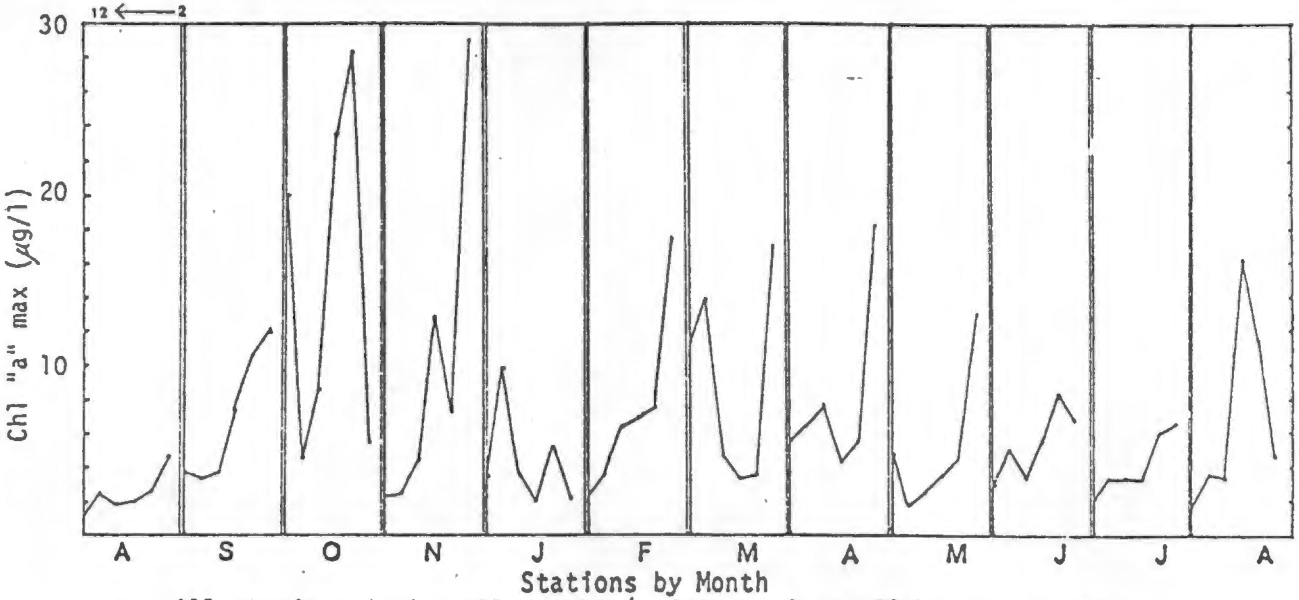
of Benguela Current water farther out to sea. Isohalines and isotherms roughly parallel the coast. South Atlantic Surface Water ranges annually from 16° to 21° C and the main body of the Benguela Current from 14° to 19°C (Shannon, 1966). Figure 3.4.a shows that along the sampling line, surface temperatures (Ts) ranged from 11.0°C in January at Station 16-02 to 19.6°C in February at Station 16-12. Figures 3.4.b-c and show station and monthly averages. Annual average values increased in a regular manner from the coast seaward (13.5°C at 16-02, 15.6°C at 16-12). On average, temperatures were warmer in summer than in winter (16.3°C and 13.5 C°respectively), but when samples were examined individually, that pattern was reversed at the inshore station. At this station, intense summer upwelling overwhelmed the effects of seasonal sunwarming, and explains the existence of both the highest and lowest temperatures occurring within weeks of each other.

Salinity values (Ss) over the entire region (Fig. 3.5. a-c) were low (34.69 - 35.42‰) compared to the oceanic water farther offshore (averaging 35.5‰; Shannon, 1966). Station averages exhibited an increase to seaward and monthly averages increased in winter. Values never rose above 35.00‰ at 16-02 and did so only once at 16-04. When all 72 samples were compared, Ss and Ts values correlated well, but the more conservative nature of salinity as an indicator can be seen by comparing monthly averages for the two parameters (Figs. 3.4,5.b). Salinity sections follow a pattern opposite to that of temperature due to summer conditions of high insolation and the more rapid response of temperature to those conditions.

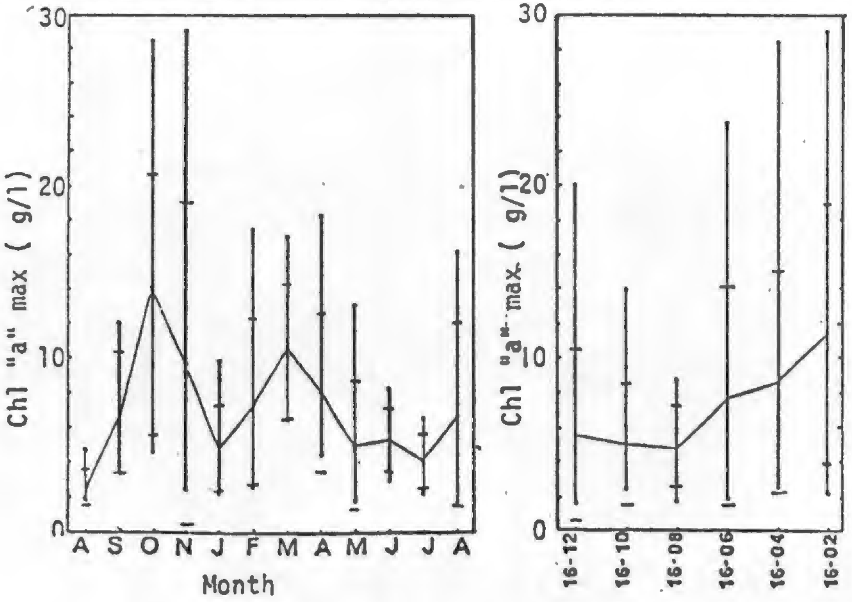
Chlorophyll "a" Maxima

Chlorophyll "a" abundance (in µg/l) is a commonly used measure of phytoplankton abundance. Chlorophyll "a" maxima (chl "a" max), i.e., the maximum single value found in the water column, regardless of depth) correlates well with cell numbers off the Cape Peninsula (Andrews, unpublished data) and in the Walker Bay area (Horstman, 1980). It is assumed that the correlation holds in this study. Although there is disagreement over the exact relationship between pigment content and cell numbers, chl "a" maxima provide a good indication of the amount of food available to zooplankton, most of which are either facultative or obligate herbivores (Lazarus, 1975).

Fig. 3.6. Chlorophyll "a" maxima, readings taken from the ship just preceding sampling. Vertical lines show range; horizontal bars, standard deviation.



a. All stations during all months (points go from offshore to onshore in a left-to-right direction within each month).



b. Average monthly chl "a" max, all stations combined.

c. Average annual chl "a" max values, all months combined.

Little published information exists concerning chlorophyll "a" values in the Lambert's Bay area. Figure 3.6 a-c shows values found along Line 16 during the sampling period. Chl "a" maxima are exceedingly high at all times, falling below 2 µg/l in only four samples. Patchiness is extreme. the lowest value (1.7 µg/l) occurred offshore (Station 16-12) in August, 1977, and the highest (29.0 µg/l) inshore (Station 16-04) in October. Station averages ranged from 11.4 µg/l at Station 16-02 to 4.8 µg/l at Station 16-08. Seaward of Station 16-08 values again climbed, reaching 5.4 µg/l at Station 16-12. Average monthly readings showed phytoplankton to be most plentiful during spring and autumn (October and March respectively) and least abundant during winter, although relative to other south and west coast upwelling areas, high phytoplankton values were present perennially (Hutchings, 1981).

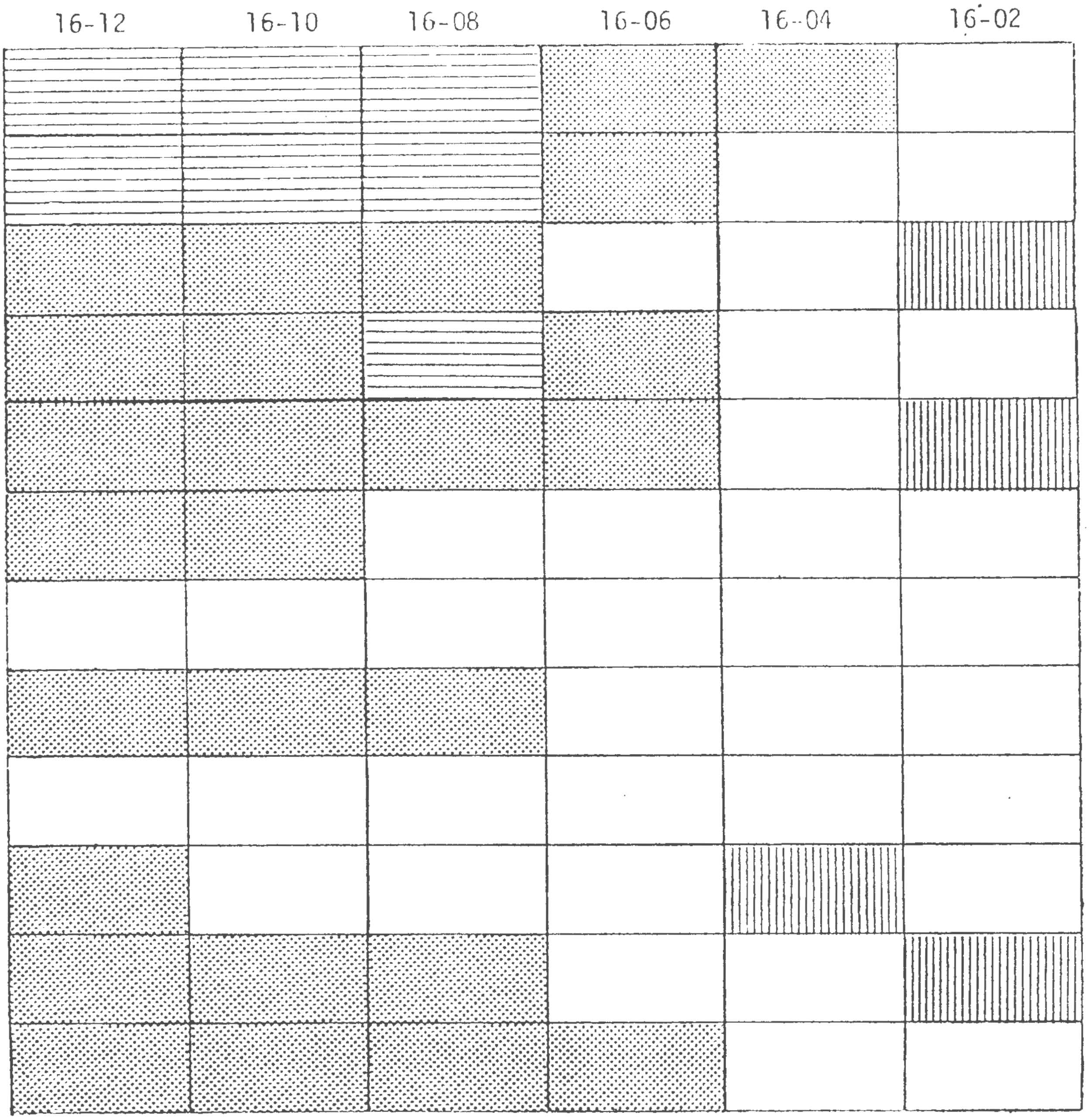
Water Types and Phytoplankton Abundance

The combined effects of bottom topography, wind, and currents are important insofar as they influence dispersal and aggregation. They are even more significant to the productivity of the Lambert's Bay ecosystem as they determine upwelling patterns and the nutrient levels available for phytoplankton growth. Newly upwelled water is nutrient rich, phytoplankton-poor, and characterized by low salinity and temperature. As water ages, temperature and salinity values rise and nutrients become depleted as they are used up by expanding phytoplankton stocks. Due to seasonal fluctuations in sun-warming of the water, wind intensity, and evaporation, and in life cycles and abundance of grazers, linear relationships were neither expected nor found between biotic factors on the one hand, and surface temperature (Ts) and surface salinity (Ss) on the other. However, phyto- and zooplankton maxima showed a distinct relationship to upwelling and the age of water, or water type.

Because Ss and Ts values are functions of water age following upwelling, they may be used to define categories, or water types, while taking into consideration seasonal variation in the relationship between the single variables. The use of water types, rather than any one environmental measure, provides an effective context in which to describe the distributions of both phytoplankton and zooplankton. Longhurst (1967)

Table 3.1. Definition of water types, using Ts, Ss, and temperature profiles.

UW (upwelled water): T < 13.0 C; S < 34.85%
AUW (aged upwelled water): summer; T = 13.0-14.9 C;
      S = 34.85-35.00%
      winter; T = 13.0-13.9 C; S = 34.85-35.00%
MW (mixed water): summer; T = 15.0-16.0 C; S =
35.10-35.20%
      winter; T = 14.0-15.0 C ; S = 35.10-35.20%
WW (warm water): summer; T > 16 C; S > 35.20%
      winter; T > 15.0 C; S > 35.20%



16-12	16-10	16-08	16-06	16-04	16-02	
▤	▤	▤	▒	▒	□	A
▤	▤	▤	▒	□	□	S
▒	▒	▒	□	□	▥	O
▒	▒	▤	▒	□	□	N
▒	▒	▒	▒	□	▥	J
▒	▒	□	□	□	□	F
□	□	□	□	□	□	M
▒	▒	▒	□	□	□	A
□	□	□	□	□	□	M
▒	□	□	□	▥	□	J
▒	▒	▒	□	□	▥	J
▒	▒	▒	▒	□	□	A

Fig. 3.7. The 72 sampling stations, showing water type present at each at the time of sampling. Key: Warm Water (WW)▤, Mixed Water (MW)▒, Aged Upwelled Water □, Upwelled Water (UW)▥.

suggests their applicability for use with zooplankton.

> "Studies such a those of Berner and Reid (1961) have shown that zooplankton species may not be able to follow the rapid movement of the surface isotherm of their limiting temperature during, for instance, the early spring unless a suitable transport mechanism in the form of horizontal advection accompanies the movement of the isotherm. The distribution of a species may thus be linked more closely to the distribution and advection of water types rather than to non-conservative properties such as surface or mixed layer temperatures; this is perhaps more true of the period when movement of the isotherms expands the possible range of a species than during the period of range contraction" (p.396).

Each sampling station was allocated to one of four categories on the basis of Ss and Ts values, T profiles, seasonal ranges of both parameters, and wind regime preceding sampling. The water types were as follows: 1) freshly upwelled water (UW); 2) aged upwelled water (AUW); 3) mixed water (MW); and 4) warm water (WW). Temperature and salinity values for upwelled and warm water were easily determined with the aid of temperature sections and wind records, which clearly identified active upwelling sites and offshore quiescent sites, and the range of values common to those conditions. Criteria for aging upwelled water and for mixed water were determined somewhat more arbitrarily by examining the pattern of increasing values as the water moved offshore, and noting the seasonal differences in the two parameters due to sunwarming, evaporation and wind regime. The distribution of water types among the 72 stations is shown in Figure 3.7. The seasonal Ts and Ss criteria used in categorizing the water types differ somewhat from those used in other upwelling studies (Andrews, 1974; Hutchings, 1979; Barlow, 1980), and are listed in Table 3.1. The same four categories will be used throughout the paper in discussion of distribution patterns.

The temporal progression of upwelled water through the four categories in the Lambert's Bay area follows essentially that described by Hutchings (1979) for the upwelling region off the Cape Peninsula. That region, however, is characterized by extremes of temperature and salinity that are not found in this area of gentler upwelling, more moderate winds, and relatively uniform conditions. A more detailed comparison of the two areas will be presented in Chapter VII.

Because of the position of phytoplankton at the base of the marine food pyramid, it is worthwhile investigating the relationship between phytoplankton abundance and the

Table 3.2. Chl "a" Max against water type.

	Chl "a" max abundance categories (μg/l)			
Water Type	3.0	3.0-6.9	7.0-10.9	11.0
UW (upwelled water)	1	2	1	0
AUW (aged upwelled water)	1	17	7	10
MW (mixed water)	8	11	4	3
WW (warm water)	3	4	0	0
Totals	13	34	12	7

physical conditions present preceding and during sampling. Besides sunlight and nutrients, which limit phytoplankton production in this environment, advection, convection, sinking, and grazing of the phytoplankton species influence distribution. Although average summer values of chl "a" were higher than average winter values, there was much spatial and temporal variation which could not be accounted for solely by the seasonal increase in light. Consequently, it is necessary to look at other factors affecting phytoplankton concentrations.

The chl "a" value for each station was placed into one of four categories, ranging from least to greatest abundance. Table 3.2 illustrates the number of occurrences of each abundance category within each water type. A null hypothesis, i.e., that chlorophyll "a" values were independent of water type, was tested using the RxC Test for Independence with the G test (Sokal and Rohlf, 1969). The details of the test for independence are shown in Appendix A. The null hypothesis was rejected ($p < .01$), and a significant relationship between chl "a" max abundance categories and water types was shown to exist.

As might be predicted from studies in other upwelling areas, recently upwelled water and warm water showed the lowest chl "a" values. In the former, phytoplankton had not yet had time to grow; in the latter, the nutrients were depleted and stocks were no longer able to maintain themselves. Grazing may also be of significance; various studies, however, indicate that grazing probably accounts for from 20 - 70% (Beers, _et al._, 1971) of the phytoplankton stock reduction under upwelling conditions. Hutchings and Olivieri (1983) suggest that grazing takes an average of 46% of phytoplankton biomass off the Cape Peninsula.

The highest phytoplankton concentrations were present in aged upwelled water which had been at the surface long enough for the "seed" plankton to utilize the presence of both increased light levels and high nutrient content. Phytoplankton response has been shown to occur in less than 24 hours off the Cape Peninsula (Andrews and Cram, 1969; Hutchings, 1979; Olivieri, 1981).

Mixed water showed intermediate values. As the name implies, plankton-rich, aged upwelled water, mixed with phytoplankton-poor offshore water and dispersed by wind and current action has resulted in a group of stations whose chl "a" levels fell into a range of intermediate values.

Some difficulties arise in using chl "a" max as an indicator of the amount of phytoplankton present because, although very high levels may have been present, time may have been too short for its concentration into patches. A similar problem exists in turbulent water of any type, due to the breaking up of phytoplankton patches. Homogeneity in phytoplankton distribution will cause underestimation of phytoplankton abundance; however, the effect of very uniform distribution in moderate abundance ranges may be identical to that of food scarcity, if zooplankton require patchiness for energy-efficient grazing (Angel, 1977).

Conclusions

In general, the Lambert's Bay area is characterized by a preponderance of southerly winds, more frequent in spring and summer, that power relatively mild but steady upwelling along the coast. The inshore stations were most affected by this belt-type upwelling, and the lowest temperature and salinity values were found there.

The jets, eddies, and fronts referred to here were all identified through the use of temperature and salinity sections, verified by wind records and sections from the areas to the immediate north and south. The temperature sections are illustrated in Chapter IV, where the distribution of zooplankton can be related to them. Environmental statistics are listed in Appendix B.

Farther offshore, sampling stations came under the influence of the Cape Columbine Jet, which created an area of enriched water north of the Cape and a local front between cold, upwelled water inshore and warmer, older water offshore. When the jet was very intense, as occurred in November and January, eddies (identified by temperature and salinity sections in addition to wind records) were formed on either side of it, causing convergences and divergences depending upon the direction of flow. These eddies were usually centred over Stations 16-04 and 16-08, and often phytoplankton were physically aggregated by them, either toward the centre or toward the eddy edges. Other shallow eddies occurred from time to time at all but the outermost station. These were caused by meanders and dissipation of the Jet.

Upwelling caused by winds and orography at Cape Columbine also created a plume which on occasion extended its influence as far north as Stations 16-04, -06, and -08.

All of these types of upwelling enhanced phytoplankton production, particularly at the inner stations. At no time was phytoplankton very scarce off Lambert's Bay. Chl "a" max values never fell below 1.7 ug/1.

During the winter months, northerly winds were more frequent and remained longer from that direction when they did occur. During these times, warm, low-nutrient water was carried inshore and phytoplankton levels were the lowest of any that occurred (generally < 6.0 ug/l)

In summary, Station 16-02 was subject to mild frequent upwelling, a sub-surface south-flowing counter-current, and periods of wind reversal when upwelling ceased and warm, phytoplankton-poor water was blown in from offshore, e.g. August 1977, July 1978). When upwelling was strongest and when reversals occurred, phytoplankton levels were reduced, but at other times were sufficient to give this station the highest average chl "a" reading of any station.

Station 16-04 was located in a very erratic area, where upwelling sometimes occurred, where it was sometimes the recipient of upwelled water displaced offshore, and where it was sometimes centred in a convergence or a divergence, as shown by a localized uplifting or sinking of isotherms. Consequently conditions were very unstable and unpredictable.

Station 16-06 was the most likely to receive large influxes of phytoplankton-rich water because of its location "downstream" of all three upwelling sources, and at the edge of the local frontal zone. This preferential location was not reflected in exceptionally high phytoplankton levels, but the very high zooplankton densities found at that station (see Chapter IV) suggest that grazing may have been a factor in this case.

Stations 16-08, -10, and -12 show the effects of their increasing distance from upwelling sites, evidenced by increasing temperature and salinity values (see Appendix B) Station 16-08 is, in addition, fairly unstable due to the occasional appearance of eddies generated by the Columbine Jet, but the more offshore stations are generally free from any perturbations of this sort. Station 16-12 was generally the site of mixed or old water but, even at its greater distance from upwelling areas, often had relatively high levels of phytoplankton.

A month-by-month description of environmental conditions vis-a-vis zoooplankton distribution and abundance follows in the next chapter.

CHAPTER IV

SEASONAL CHANGES IN ZOOPLANKTON BIOMASS

Three different aspects of Lambert's Bay zooplankton have been considered in this thesis - total zooplankton biomass, the non-copepod zooplankton, and, finally, the copepod zooplankton. This chapter deals with the first of these. Using biomass as a measure of abundance, all phyla were pooled, divided into large and small size-fractions, and examined in relation to the environmental parameters discussed in the preceding chapter. Because copepods constituted the largest part of the total zooplankton sample, discussion of the relationship between size and water type will be deferred until Chapter VI.

Methods

Biomass has been calculated in grammes wet weight/1000m^3 of water filtered and includes all zooplankton, both copepods and others. Procedures used in weighing and in pumping excess water from the samples, and methods used in dividing the samples into large and small size-fractions, have been described in Chapter II. Weights of each size-fraction and for the total sample from each station are listed in Appendix C. On occasion, results were confounded by large quantities of algae or remains of exploded salps which clogged the nets and the mesh of the laboratory filtering mechanism. This was noted when it occurred.

Results and Discussion

Spatial and Temporal Distribution

Figure 4.1.a-d shows the wet weight of the two size-fractions in terms of: all 72 samples (a), monthly averages (b), smoothing by twos of monthly averages (c), and as station averages (d). Weights for the total sample ranged from a high of 818.8 g/1000m^3 to a low of 55.8 g/1000 m^3. There was a great deal of fluctuation from station to station within each month, and from month to month at each station. In general, biomass was greater inshore, but this trend was easily seen only when station averages were

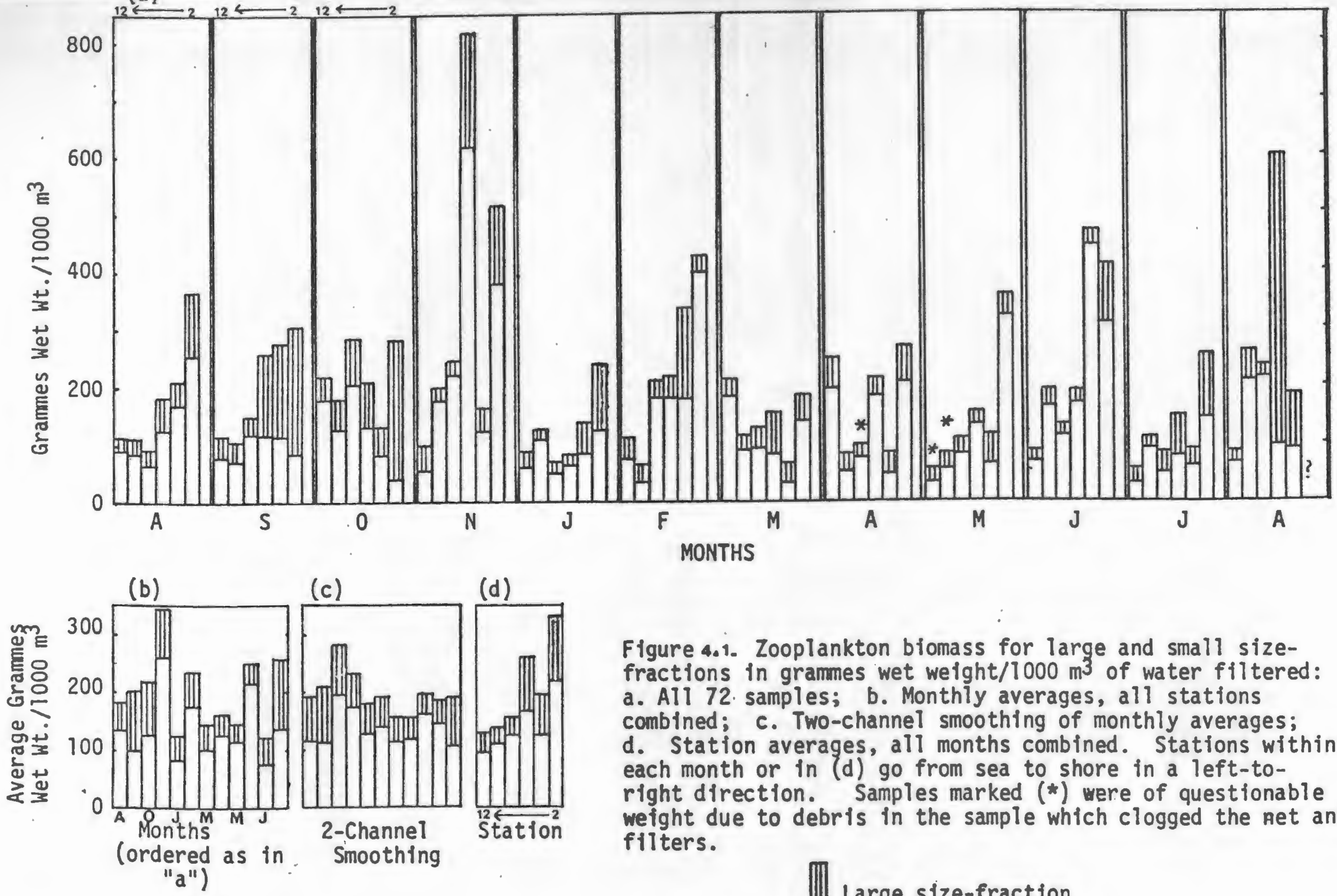


Figure 4.1. Zooplankton biomass for large and small size-fractions in grammes wet weight/1000 m^3 of water filtered: a. All 72 samples; b. Monthly averages, all stations combined; c. Two-channel smoothing of monthly averages; d. Station averages, all months combined. Stations within each month or in (d) go from sea to shore in a left-to-right direction. Samples marked (*) were of questionable weight due to debris in the sample which clogged the net and filters.

Key:
▥ Large size-fraction
□ Small size-fraction

calculated (Fig. 4.1.d). Station 16-02 showed the greatest average monthly biomass (328.6 g/1000m^3), and at Station 16-12 (127.1 g/1000m^3), the lowest. Station 16-04 showed surprisingly low average biomass values in view of its position between two stations of very abundant zooplankton.

Except for generally higher values in spring and summer, the temporal distribution of the total zooplankton population was characterized by great variability from sample to sample. Monthly values, averaged across all stations oscillated from November 1977 through August 1978, the most productive month being November (341.4 g/1000m^3). The month of least biomass was July (123.4 g/1000m^3), but January, March, and May were almost equally low.

In contrast to the fluctuation found in average monthly samples, smoothing by twos demonstrated the remarkable uniformity and lack of seasonal variation in biomass throughout the year. Fig. 4.1.c) suggests a two-phase year, with two periods of increase, one in spring and one in early winter, separated by a winter-early spring plateau, when numbers remained fairly steady. The high levels of phytoplankton available to herbivores in Lambert's Bay during the months of reduced zooplankton abundance suggest that the autumn decrease is in response to predation or to the life cycles of the zooplankton rather than to a seasonal decrease in food which is common in other temperate areas.

The division of station averages into large- and small-sized components provided more insight into the annual zooplankton cycle. The small size-fraction showed the same pattern as the total, i.e., highest values inshore, a sharp drop at Station 16-04, followed by a mid-line bulge at Station 16-06 and a gradual decrease thereafter. Large zooplankton showed the same pattern inshore, but their abundance dropped steeply at midline and stayed low at the three outer stations. They displayed less uniformity in spatial distribution than did the small zooplankton. Patterns for the two size-fractions differed more in quantity than in quality, but the quantitative differences were considerable.

In contrast, monthly averaging of all stations (Fig. 4.1.b) revealed qualitatively different patterns for the two groups. The distribution of the small size-fraction was very similar in pattern to that of the total biomass, showing alternation of increase and decrease from November, 1977 through August, 1978. (Because small zooplankton constituted from 62-80% of the total, the similarity in pattern of increase and decrease between the small size-fraction and the total is not surprising.) The large size-fraction, however, while also displaying alternations of increase and decrease, did so over a time period of several months, rather than one month, from peak to peak. Smoothing by twos (Fig. 4.1.c) indicates more clearly the seasonal difference in peak abundances of the two size-fractions, with large zooplankton most prevalent in the late winter and early spring, and small zooplankton showing general uniformity, within which occurred a multi-peaked cycle with greater average summer abundance.

Correlations With Environmental Parameters

Stavn (1971), in a study of the distribution of the cladoceran, Daphnia, has summarized the major factors responsible for zooplankton distribution. These have been listed in concise form by Parsons and Takahashi (1973) as follows:

> 1) Physical/chemical boundary conditions including light, temperature, and salinity gradients.
>
> 2) Advection effects as in wind or water transport, including small-scale variations due to turbulence.
>
> 3) Reproduction rates within the population.
>
> 4) Social behaviour with populations of the same species.
>
> 5) Coactive factors determined by competition between species" (p.30).

The first two factors are discussed in this chapter in relation to the environmental conditions described in Chapter III. The third and fifth points are considered, along with the additional factor of predation, in Chapters V, VI, and VII.

The attempt to draw correlations between zooplankton distributions and physical or chl "a" parameters has met with only limited success. Fager and McGowan (1963) found only a very loose association between zooplankton numbers in the North Pacific and temperature, salinity, thermocline depth, etc., and concluded that the explanation for distribution patterns was more complex than previously thought. On the other hand, Lance (1962) was able to relate differences in Acartia bifilosa (Copepoda) occurrence to

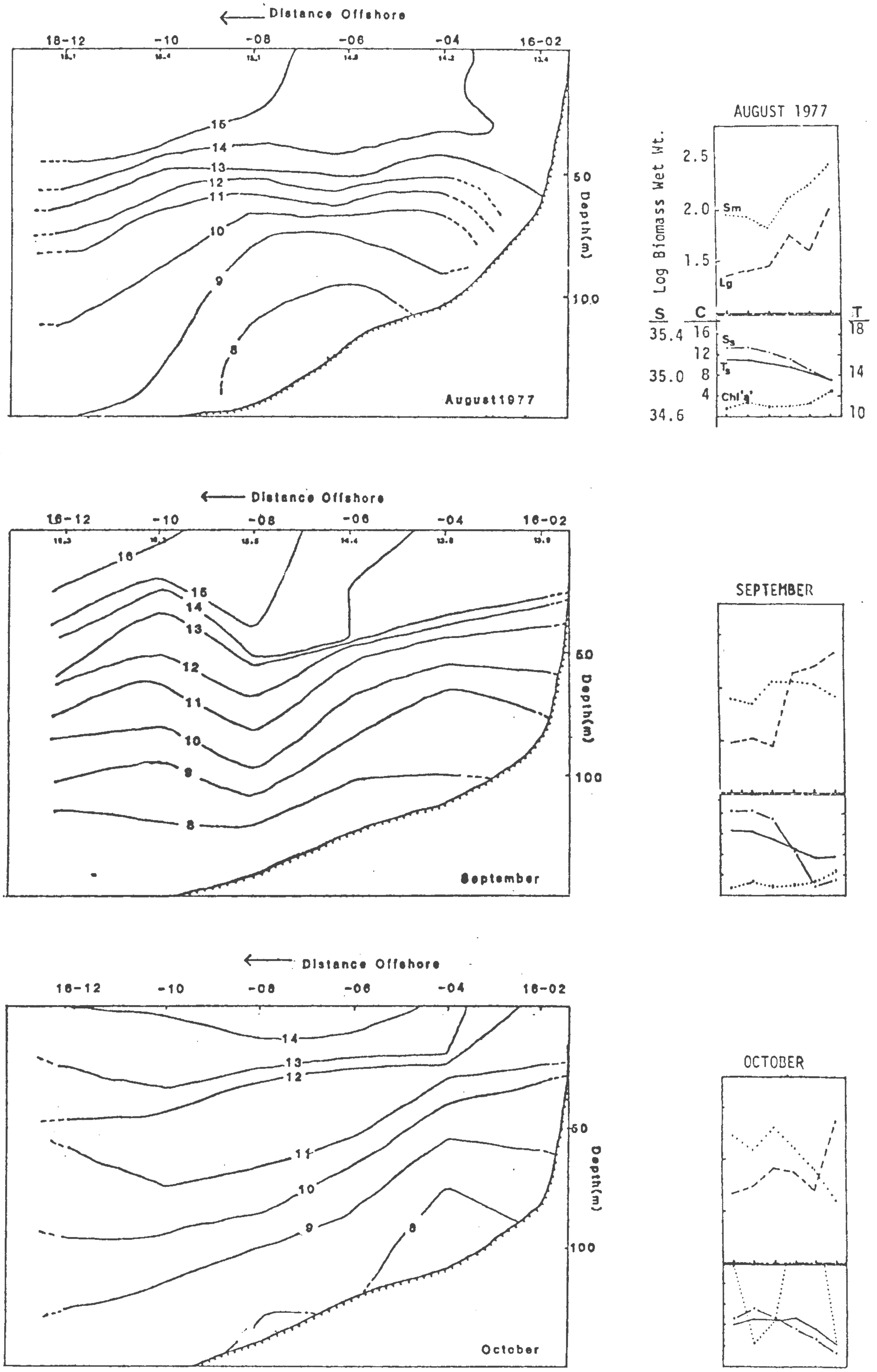


Fig. 4.2.a-1. Temperature sections of Line 16 for each of the twelve months sampled, compared with values for biomass (large and small size-fractions), temperature, salinity, and chl "a" max. Captions for all figures are the same as those for the first month displayed on the page.

salinity changes. These and other studies suggest that success in correlating zooplankton abundances with environmental features is more likely for individual species than for the total zooplankton population. The following month-by-month description presents the zooplankton of Lambert's Bay in their environmental context, and examines the role of size in determining the relationship of zooplankton to environmental features. Individual zooplankton components of the ecosystem will be discussed in later chapters.

Zooplankton in Their Environment:A Month-by-Month Summary

The gross distribution of zooplankton biomass can be examined on a month-by-month basis vis-a-vis upwelling activity, currents, and eddies as interpreted from temperature, salinity, chl "a" and wind data. Figure 4.2.a-1 illustrates the log biomass of each size-fraction in conjunction with accompanying values of Ts, Ss, and chl "a" for each station within each month. Also included is the relevant temperature section.

Two techniques, used in this and in similar studies, must be used with caution: (1) the use of temperature sections for the determination of water flow, and (2) the use of monthly samples in the determination of seasonal cycles. In the former, the upthrusting isotherms generally associated with upwelling, fronts, and eddies may have such interpretations negated by a simultaneous sharp rise in salinity values. The two parameters are inter-related in such a way that the combined effect may preclude the density gradient necessary for such currents to occur (C. Holden, Sea Fisheries Research Institute, pers. comm.). Secondly, surface conditions have recently been found to respond radically within 24 hours to shifts in wind speed and direction (L. Hutchings, C. Holden, Sea Fisheries Research Institute; J. Field, University of Cape Town, pers. comm.). A pattern of isotherms suggestive of long-standing conditions may, in fact, reflect only very short-term events. A knowledge of the wind regime preceding sampling is of great value in interpreting T and S sections and should be examined wherever possible.

In the monthly descriptions which follow, both salinity and temperature sections were used, although only those for temperature are included in the figures; wind records from the shore station were also considered, but the distance from the sampling site to

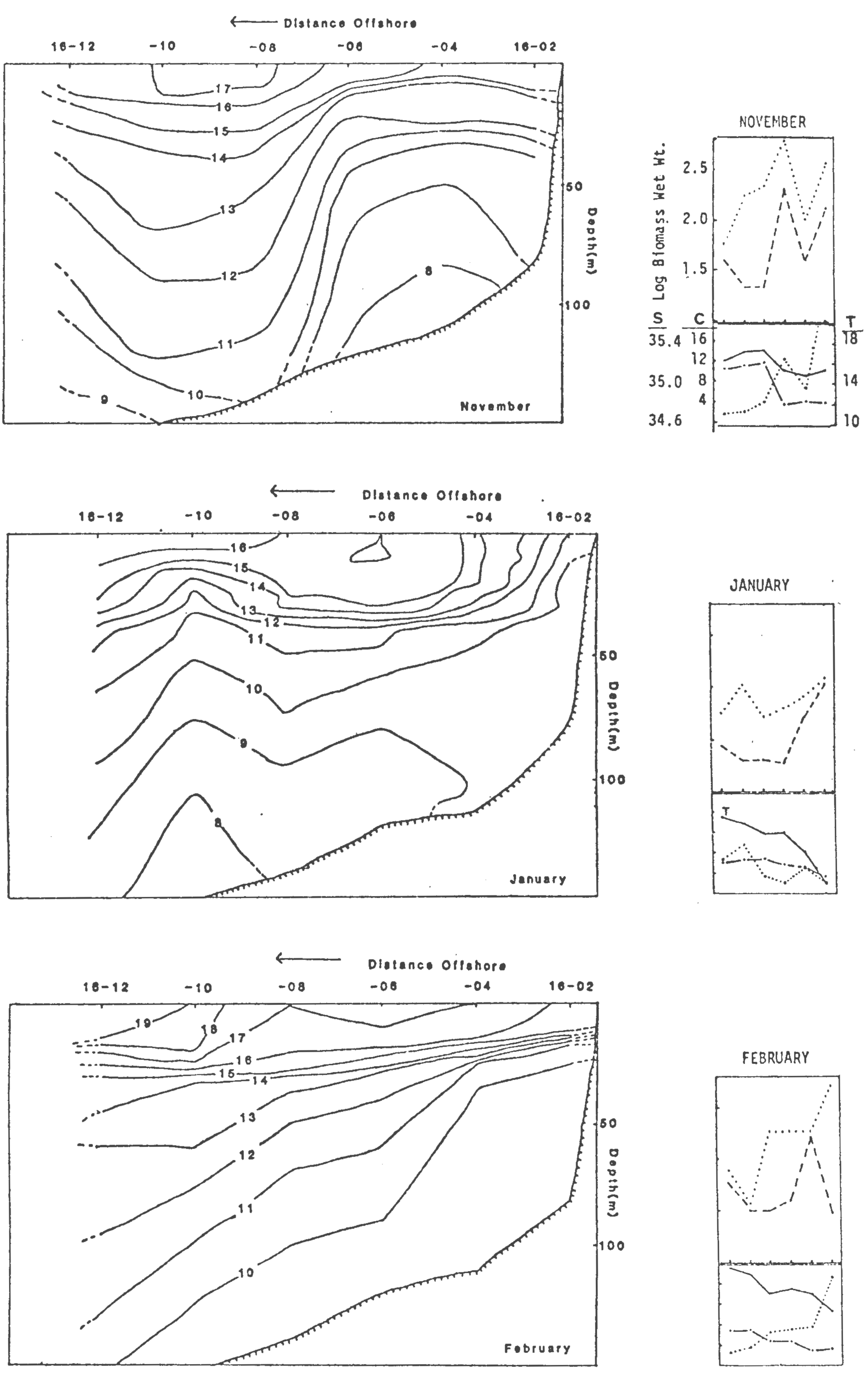


Fig. 4.2. (continued)

the wind station was considerable and may not have been entirely applicable:

August 1977 (Fig. 4.2.a) - This was one of the very few sampling periods when no upwelling was in evidence. Winds had blown steadily from the north-west for a long period preceding sampling, blowing warm, high salinity water toward the inshore stations. Both size-fractions were much more plentiful inshore and probably were physically aggregated there.

September (Fig. 4.2.b) - Upwelling was present at the three inshore stations. Following an increase in southerly winds and the subsequent offshore movement of surface water, phytoplankton was more abundant offshore than it had been in August. The two size-fractions showed differing abundance patterns. Large zooplankton increased considerably inshore over the preceding month, whereas the small size-fraction continued to decline.

October (Fig. 4.2.c) - Station 16-02 exhibited strong upwelling, with very low temperatures. At the middle stations, an isolated pocket of warmer, higher salinity water overlay the upwelled water in the top 20 m. Temperature and salinity sections, as well as the winds preceding sampling, suggest the existence of an eddy over this area. The biomass of large zooplankton again increased in the strongly upwelling water at Station 16-02. The small size-fraction was somewhat more abundant than in September and increased offshore; as with phytoplankton in the previous month, this was probably due to advection. In response to upwelling and increased light levels, chl "a" was markedly higher than in the preceding months.

November (Fig. 4.2.d) - Samples showed a two-fold increase in small zooplankton, whereas the large size-fraction decreased. Chl "a" levels were high. Strong southerly winds for the entire month of October created a jet slightly to seaward of Station 16-06. Wind, and T and S sections all suggest the formation of eddies that extended from the surface to the bottom. The biomass of both size-fractions peaked sharply at the edge of the jet, but showed different distributions in relation to the eddies.

January 1978 (Fig.4.2.e) - Low salinity and temperature values for the entire offshore distance of the study area indicated that weeks of southerly winds without reversals had driven the Columbine Jet seaward of Station 16-12. The two inshore

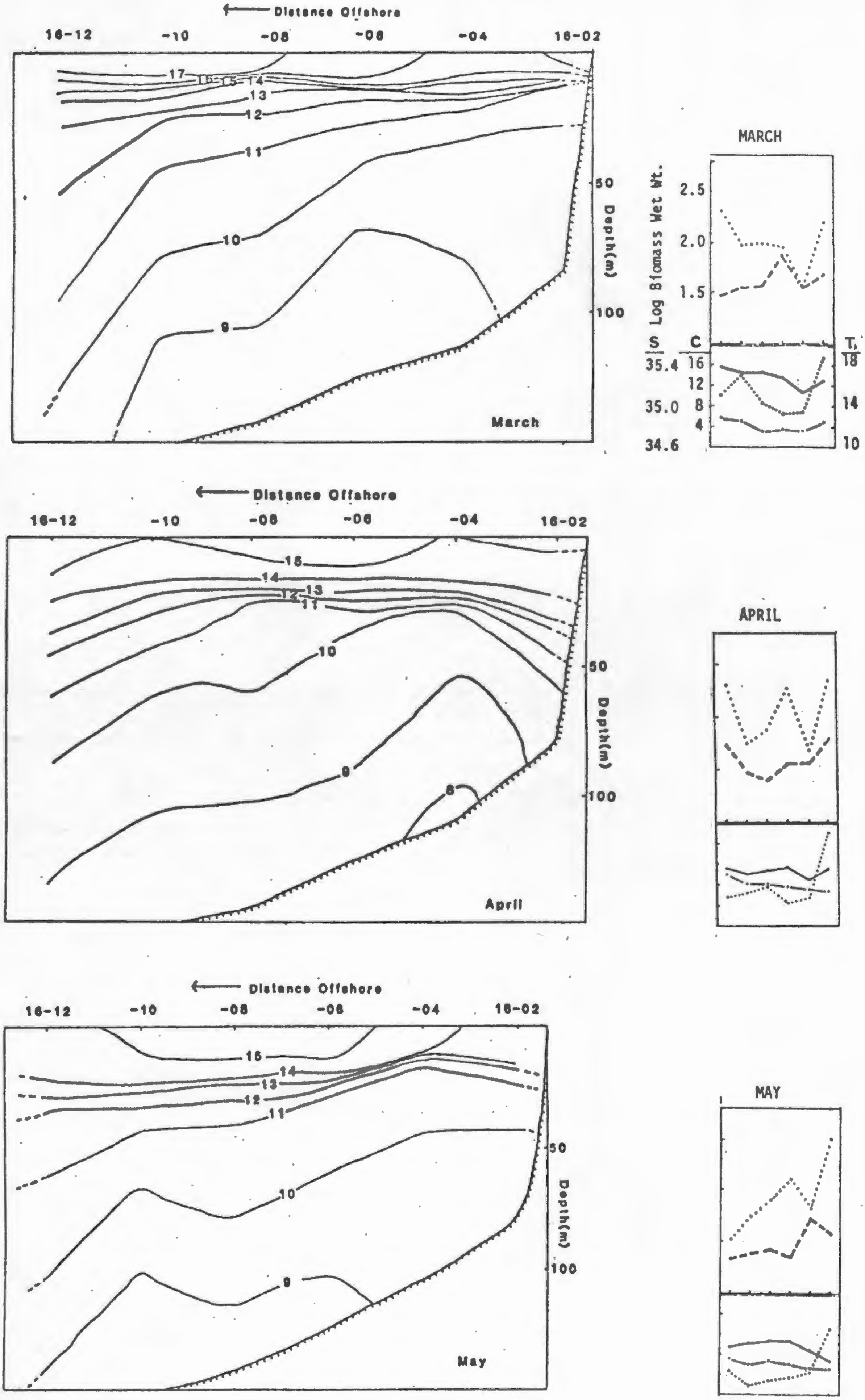


Fig. 4.2. (continued)

stations were located on the edge of an eddy as evidenced by the pattern of isotherms, and biomass values for both size-fractions were highest there. The large size-fraction was much less abundant offshore, whereas the small size-fraction showed a sharp increase again at Station 16-10 in warmer water. There is good reason to suspect that predation acted to reduce zooplankton biomass in the entire area in January (see Chapter VII).

February (Fig. 4.2.f) - Upwelling had relaxed enough to allow the development of a thermocline (particularly sharp at Station 16-02), and chl "a" levels were low relative to the spring months. During this month, and at other times when a sharp thermocline was present, large zooplankton biomass was generally low. At Station 16-04, however, it was much more abundant, coinciding with a rapid rise in the 10 isotherm. Small zooplankton were plentiful inshore and decreased to seaward.

March (Fig. 4.2.g) - Similar conditions were present in March, with a sharp thermocline overlying upwelled water the entire length of the sampling line. Biomass was low except at Stations 16-02 and 16-12, where chl "a" max values and an increase in small zooplankton coincided, and at Station 16-06, where a possible eddy had concentrated large zooplankton near enough to the surface to be caught in the nets.

April (Fig. 4.2.h) - April conditions were very similar to those in March, except that the thermocline was less marked as the result of the seasonal lessening in sunwarming. A south-flowing current, indicated by downward sloping isotherms, was present below 20 m at Station 16-02. A pocket of slightly warmer water lay over the middle stations, with an accompanying large increase in the small size-fraction biomass. The large size-fraction was diminished where the thermocline was most marked.

May (Fig. 4.2.i) - This was the second sampling period to exhibit no upwelling. The slumping of isotherms over the middle stations showed in T sections again in this month and may indicate the existence of a long-term eddy. Variable winds and cooler air temperatures acted to weaken the thermocline somewhat, but it was still strong at the three inshore stations, where the two size-fractions showed opposite patterns of increase and decrease. The increase in non-copepod zooplankton in autumn and winter made the distribution patterns of the two size-fractions less predictable then than in the months when copepods dominated the weight of the sample. However, the large size-fraction still

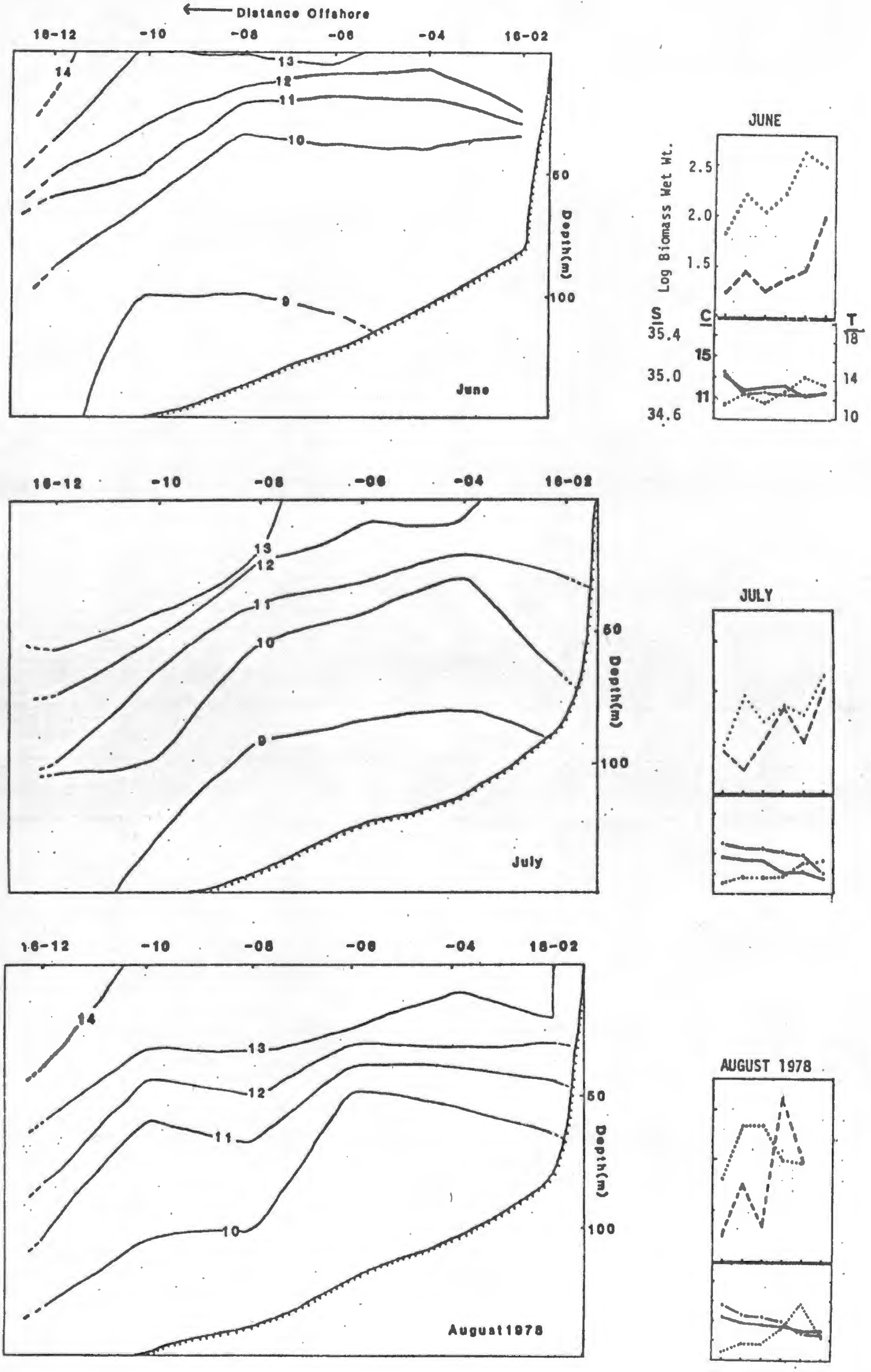


Fig. 4.2. (continued)

increased at the shoreward eddy boundary and the small demonstrated unusually large biomass inshore.

June (Fig. 4.2.j) - Wind reversal near the coast on the day before sampling caused relaxation inshore of Station 16-10 and slight downwelling at Station 16-02. The sharp thermocline, present during the previous three months, was gone. Southerly winds and upwelling were still present offshore. Abundance patterns in the two size-fractions closely paralleled each other.

July (Fig. 4.2.k) - Very cold water was present inshore, the combined effect of upwelling and lack of sunwarming. There was a predictable peak in large zooplankton biomass there, but also an unexpected rise in the small size-fraction biomass which was possibly the result of the great number of bivalve veligers in the sample. This was the only large occurrence of bivalves, and the calcium carbonate in their shells is sufficient to give them weight disproportionate to their numbers (M. LaBarbera, University of Chicago, Pers. comm.). A south-flowing current was present inshore.

August 1978 (Fig. 4.2.l) - Several days of northerly wind before sampling had blown shoreward water 1-2 warmer than that in July in the same area. Large zooplankton peaks occurred at Stations 16-06 and -10 and coincided with marked upsloping of isotherms at all depths. Small zooplankon biomass was most plentiful at Stations 16-08 and -10. Zooplankton data for the inshore station is missing, so cannot be compared.

Standing Stock in Relation to Other Upwelling Areas

Table 4.1 shows the standing stock in gC/m of the Lambert's Bay sampling stations, in relation to other upwelling areas of the world, as compiled by Cushing (1969).

Cushing's values for the Southern Benguela Region are high in relation to those found in this study for Lambert's Bay. Similar nets were used for sampling, and would not have accounted for the difference. However, Cushing (1969, p.12) had little data from the Benguela system on which to draw, and seasonal variation in times of sampling may have been significant. The average monthly values reached in this study showed little seasonal fluctuation, but seasonality is of greater importance in more southern areas. Mean annual values found in this study were, however, consistent with those of

Table 4.1. Standing macrozooplankton biomass, in gC/m2, standardized to 100 metres depth. All figures, except for that of Lambert's Bay, were taken from Cushing (1969).

Upwelling Area		gC/m2
California	Baja California to Point Conception	1.12
	Point Conception to Cape Mendocino	1.68
	Cape Mendocine to Cape Flattery	2.81
Peru	Cape Blanco to 10 S	1.26
	10 S to Africa	1.12
Benguela	Baia dos Tigros to Walvis Bay	4.2
	Walvis Bay to Orange River	2.1
	Orange River to Cape of Good Hope	1.8
	Lambert's Bay	1.05
NW Africa	Freetown to Dakar	2.1
	Dakar to Cap Blanc	2.1

Table 4.2. A comparison of biomass values for the Southern Benguela region by different workers. Data were taken from Hutchings (1979) and converted to gC/m2 (wet weight/ 17.8; Cushing 1969) and standardized to 100 m depth for comparative purposes. References for each value are found in Hutchings (1979).

Worker	gC/m^2	Comments
Andrews & Hutchings	4.45	Highest value, December 1971
	.71	3-year mean
	3.20	Highest value, 1971
De Jager	1.38	Mean summer values
Cushing (1969)	1.8	

recent studies of specific west coast areas, as seen in Table 4.2.

It is somewhat surprising to find that zooplankon biomass values for the Lambert's Bay area were not considerably higher than those found farther south, considering the existence of fairly uniform, perennial upwelling conditions in the area. Because standing stocks of both phytoplankton and fish were high (Crawford, et al., 1980), it follows, unless the fish are planktivorous, that zooplankton would also be abundant. Pilchards and anchovy are known to consume zooplankton until gill rakers are sufficiently developed to allow a change-over to phytoplankton (Crawford, et al., 1980). Consequently, the more likely explanation for the middle range of zooplankton abundance values lies in heavy and consistent fish predation on zooplankton by pelagic fish for several months of the year. Other, invertebrate predators are also abundant year-round in the area (see Chapter V). If this is true, the heavy predation is likely to maintain very high secondary production rates, while keeping a low standing stock (high P/B).

Another factor contributing to the high productivity in Lambert's Bay is the length of the upwelling season. Upwelling was active in nearly all of the twelve months sampled, . Cushing (1971) states that the productivity of upwelling areas lies not so much in the size of their standing stock, but in the length of the upwelling season. If the twelve months sampled in this study were at all representative of conditions in the area, upwelling is a nearly continuous phenomenon. This would provide an extremely long productive season, as well as great environmental predictability. Low standing stock can be explained by predation, and high annual productivity by rapid turnover and the long upwelling season.

Conclusions

The small-fraction, large-fraction, and total biomass values were, in general, high inshore and decreased to seaward, following the same general pattern as that of chl "a". Station 16-06 was an exception to this trend and merits further discussion. The unexpectedly high values at this station exceeded those of even the inshore station several times - twice for total biomass, three times for the small size-fraction, and twice for the large size-fraction. No explanation for this high zooplankton abundance was obvious from the environmental variables. Temperature and salinity values were not unusually low there, nor were chl "a" values especially high. This station was the site of two large population increases, one of small copepods and euphausiids in November, and another of euphausiids in August 1978, but even after those months were excluded from calculation, biomass values remained high. A more likely explanation lies in the fact that this station, more than any other, came under the influence of all of the three types of upwelling described in Chapter III - inshore belt-type upwelling, the plume upwelling associated with Cape Columbine, and upwelling caused by divergences in eddies formed from the Columbine Jet. These three factors did not all operate at any one time, but, depending on the wind regime, each sometimes extended its influence into the area around Station 16-06, decreasing the likelihood of food depletion in mixed, low nutrient, low chl "a" water. In addition, Station 16-06 was often located on the edge of a jet or an eddy, where the additional factor of physical aggregation may have been significant. During the months of strongest upwelling (November and January), Station 16-08 appeared to be similarly affected.

Temporally, total biomass showed several peaks throughout the year, the largest in late spring, and two others in winter. These peaks showed no statistically significant correlation with physical conditions (Appendix D), and no explanation for their temporal distribution was obvious. There were, however, distinct differences in distribution between the two size-fractions, and each pattern, taken individually, was more amenable to interpretation.

As seen in Figure 4.2, only November, April and June showed parallel fluctuations in abundance between the two size-fractions. Large zooplankton showed their greatest increase in September, coinciding with the increase of upwelling. The small zooplankton biomass was still decreasing in September, increased only slightly in October, but more than doubled in November, two months after upwelling was first apparent, and one month after a large phytoplankton increase. Although the abundance of larger animals peaked only twice per year, the smaller animal community oscillated in a bi-monthly cycle in a pattern which was maintained throughout the entire year except for late winter. The large size-fraction showed relatively small biomass fluctuation throughout the year, while the small size-fraction showed a marked fluctuation.

While station biomass averages for both size-fractions generally decreased seaward, the percentage of small zooplankton in the total sample increased in that direction. In addition, the range of the monthly small-to-large ratios at each station was much greater inshore than offshore. This change can be explained by the habitat preferences of the dominant copepods in each size-fraction (see Chapter VI), the large being more abundant in freshly upwelled water and the small showing a preference for warmer, somewhat aged water. For most months, small zooplankton were the more plentiful. However, when very strong upwelling occurred during sampling, they were dispersed offshore and large zooplankton, present in the upwelled water, took their place. When a thermocline developed, the population of large animals declined dramatically and small zooplankton once again dominated the inshore waters. Intermediate conditions produced intermediate ratios.

Different temporal and spatial trends between the size groups can be related to maximizing the efficiency of food utilization in a system which is prone to sporadic and thorough cycling of producers and consumers over short time periods. Both fossil and recent bottom sediments indicate that upwelled areas are inefficient in the sense that food produced is under-utilized to a large degree. Heinrich (1962) states that the efficiency of food utilization between trophic levels depends on coincidence of production peaks with maximum consuming intensity; because both producers and consumers vary seasonally, efficiency is related to the life histories of plankton. He identifies three different strategies for maximizing efficiency: 1) the first spring breeding depends on the spring phytoplankton bloom, and maximum zooplankton biomass follows the maximum phytoplankton biomass; 2) breeding is independent of the spring phytoplankton bloom, often occurring in winter, with the young copepod (copepodid stages IV and V) maximum occurring concurrently with the spring bloom; and 3) reproduction occurs year-round, with brood size dependent upon food availability; in this case, the broods overlap, with several in one year. These strategies are readily applicable to Lambert's Bay zooplankton. Although seasonal variation in primary production is minimal at Lambert's Bay, cycling in upwelling areas has been equated (in terms of response to periods of abundance and scarcity) to a classic temperate cycle (Cushing, 1971; Hutchings, 1979). The pattern of the large zooplankton is very similar to that of Heinrich's second category, while the small zooplankton fit either or both of the first and third categories fairly well.

There are at least five factors which provide evidence that the different species represented in the Lambert's Bay zooplankton differ in a size-related way in their life history strategies:

1) the presence of different cycles of increase and decrease in the two size-fractions, with their spring population peaks occurring at distinctly different times;

2) the presence of large zooplankton inshore in low salinity, low temperature, upwelled water, and on the boundaries of eddies and jets, and the association of small zooplankton with warmer water, with the existence of a sharp thermocline, and with aging but still phytoplankton-rich water;

3) the higher ratios of large to small animals inshore, where physical conditions are more distinct;

4) relatively small fluctuations in the abundance of large zooplankton, and large fluctuations in the small zooplankton population;

5) the presence of visible wax esters in large copepods only. Copepods are known to utilize wax esters during periods of low food availability (Heinle, 1982). The energy storage gained in this way allows survival and egg production during periods of low food availability.

Although size-related variations in abundance may have explanations other than life history (e.g., selective predation, size-dependent sinking rates, etc.) in combination they provide strong supporting evidence for the existence of different life histories. The adaptive value of the different strategies will be discussed when individual copepod species distributions are described.

The ecological significance of these strategies in the specific context of Lambert's Bay is discussed in more detail following the description of copepod species in Chapter VI.

CHAPTER V

NON-COPEPOD ZOOPLANKTON

Introduction

In addition to fluctuations in temperature, salinity, currents, and phytoplankton abundance, copepods must also interact with the other animal groups present in their area as predators, prey, and competitors. In the text that follows, the non-copepod taxa within the macrozooplankton will be discussed in terms of their spatial and temporal abundance and in their roles in relation to copepods. Little attempt has been made to distinguish smaller taxonomic groups within the zooplankton. Fish eggs and larvae were removed from the sample by other workers, and are not included.

Although in the samples studied only euphausiids, cladocerans, doliolids, chaetognaths, and some species of amphipods were holoplanktonic in the true sense, stomatopods and other amphipods were permanent in their relationships to copepods, due to the presence of one or more of their developmental growth stages in the macro-zooplankton at all times. These other groups will be considered permanent in this chapter, and will be described in the first subsection.

The second category to be presented includes those taxa which made only seasonally or spatially isolated appearances, but did so in large numbers. Any group which constituted 10% or more of the entire sample of either size-fraction at least once was included in this category.

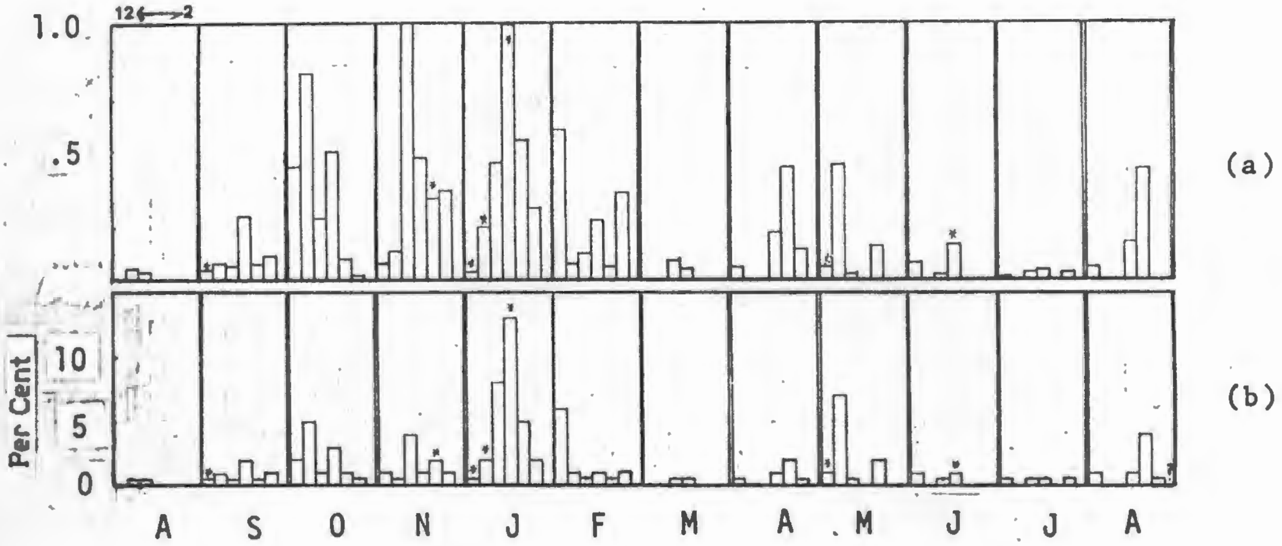
The third group, dealt with very briefly, are those taxa which were present only sporadically or in extremely small numbers, often as only one or a few individuals. The significance of other groups to copepods was not readily apparent, but their indirect effect may have been considerable.

Methods

In the histograms present in this and the next chapter, relative numbers/1000m

AMPHIPODS

Small Size-Fraction



Large Size-Fraction

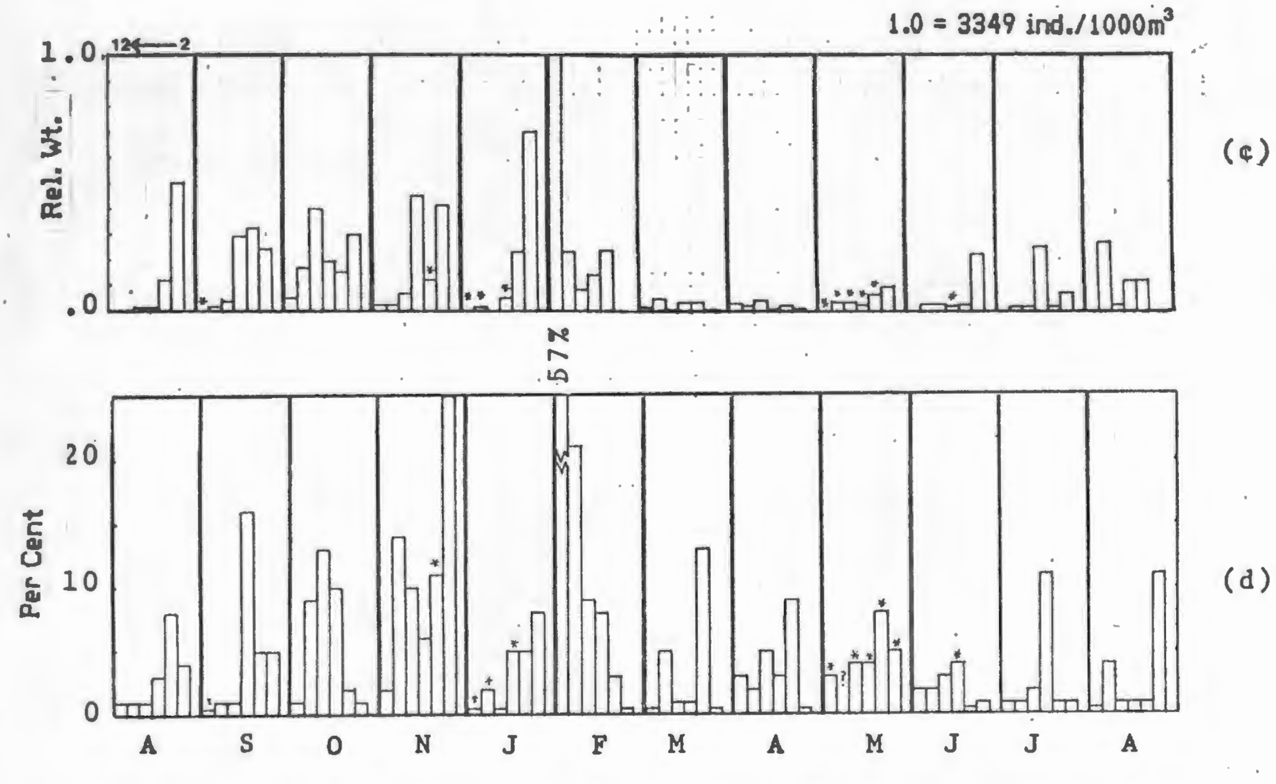


Figure 5.1.- Amphipod Abundance Histograms; a. small size-fraction, <u>relative</u> weights/1000m^3; b. small size-fraction, % of total sample; c. large size-fraction, relative numbers/ 1000m^3; d. large size-fraction, % of total sample. Per cents are shown to the nearest whole number, except that any value less than 0.5% is illustrated as .5% in order to indicate presence. *'s indicate a questionable value due to the condition of the sample. Stations within each month go from offshore to onshore in a left-to-right direction.

within a particular group were obtained by dividing the number or weight of that group for each station by the largest value of the group for all stations. Relative weights for the small size-fraction were calculated similarly. It is important to note that weights and numbers are relative within the group only, and cannot be compared in absolute terms between groups.

Because of the different counting procedures used for the large and small size-fractions, it was difficult to quantify abundance in a taxon that spanned both sizes. Consequently data for the two sizes are often presented separately and the temporal and spatial trends, rather than quantitative descriptions, are summarized.

The Permanent Zooplankton

Amphipods

Amphipods were a very common component of the non-copepod zooplankton sample. They were almost exclusively hyperiid, but there were also very occasional caprellid or gammarid individuals present. These amphipods, in particular Parathemisto gaudichaudi, are known to prey on fish larvae, and are almost certainly predators on copepods. Brownell (1981) writes:

> "Siegfried (1965) had previously found fish larvae among gutcontents of P. gaudichaudi collected in the S.E. Benguela region. Fish larvae were found by Sheader and Evans (1975) to make up 23.4% of this species' diet in their N. Atlantic study area in April-June, which permitted these authors to conclude that P. gaudichaudi is probably 'one of the most important invertebrate predators of fish larvae, as well as being an important competitor with fish larvae for other zooplankton.'" (p. 4).

In the small size-fraction (Fig. 5.1.a,b), amphipods were most abundant in the spring and summer, both in terms of numbers and as a percentage of the total zooplankton sample. From September through February they were present at all stations each month, and comprised anywhere from 1% to more than 13% of the total sample by numbers from each station. These are also the precise months that anchovy and pilchards are spawning, supporting the observation of Sheader and Evans (see above). During the rest of the year they were often absent from one-to-four stations per month, and only twice constituted more than 2% of the total. Numbers increased each month to a peak in November, and reached their maximum in percentage of the total small sample in January. February brought a decline, followed by a more precipitous drop in March. A modest but sustained recovery took place in April and continued for the rest of the year except for a moderate decrease in July. In both absolute numbers and in percentage of sample, amphipods were least abundant at the two inner stations and most abundant at the middle stations.

Amphipods in the large size-fraction (fig. 5.1.c.d) followed a pattern very similar to that of the smaller amphipods, but with peaks appearing from one to two months later, presumably reflecting the progression of the group through growth stages. They comprised a much bigger percentage of the total zooplankton than did the smaller amphipods (up to 57%). Large amphipods were absent from the sample only once, at Station 16-10 in August, 1977. They also were most abundant at the middle stations, except during February, the month of their greatest abundance when the taxon appears to have centred farther offshore.

Progression through growth stages in the amphipod population can be seen by comparing the patterns of abundance peaks throughout the year in the two size-fractions. An overwintering group of late juveniles or adults produced a spring increase in young amphipods which reached its peak in November. The autumn recovery, which does not appear among the larger animals until May, is already apparent in April in the small amphipods, presumably the result of eggs produced in late summer. While the small amphipods are most numerous in November, the large size-fraction is greatest in February. March was the only month when amphipods as a group were not a significant proportion of the total zooplankton biomass somewhere in the study area.

In general, amphipods were characterized by late winter and spring lows and summer and winter highs. The winter high was approximately one-fifth of that in the summer. The evidence shown by the histograms suggests two overlapping generations per year.

Chaetognaths

Chaetognaths are also known predators of copepods (Russell-Hunter, 1979; Levinton, 1982). Due to this fact, and to their extremely large numbers in the inshore area, they must be considered of great importance in any study of the latter. Russell-Hunter (1979) states: "Ecologically, they are predaceous carnivores, feeding on

CHAETOGNATHS

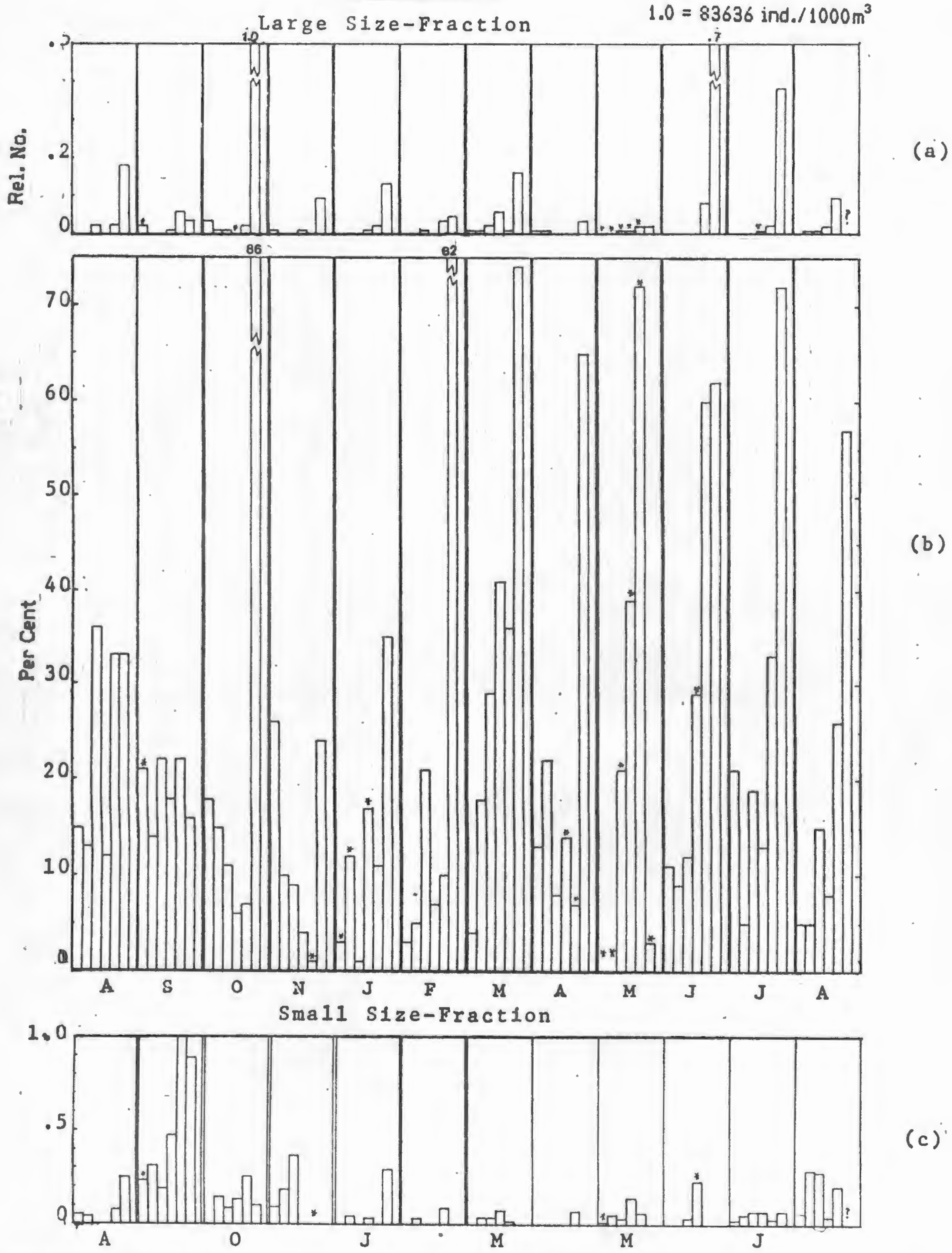


Figure 5.2. - Chaetognath Abundance Histograms: a. large size-fraction, relative numbers/1000m^3; b. large size-fraction, % of total sample; c. small size-fraction, relative weights/1000m^3. No percentage table is shown for small chaetognaths because they never were more than 1% of the total. Per cents are shown to the nearest whole number, except that any value less 0.5% is indicated to show presence. *'s indicate a questionable value. Values for broken lines are displayed above the line. Stations go from offshore to onshore in a left-to-right direction.

forms like Calanus and occasionally destroying whole broods of larval stages, both of invertebrate species and of commercially important fishes" (p. 575). Sagitta has been shown to prefer copepods to fish larvae, when a choice was made available to it (Lasker, 1981).

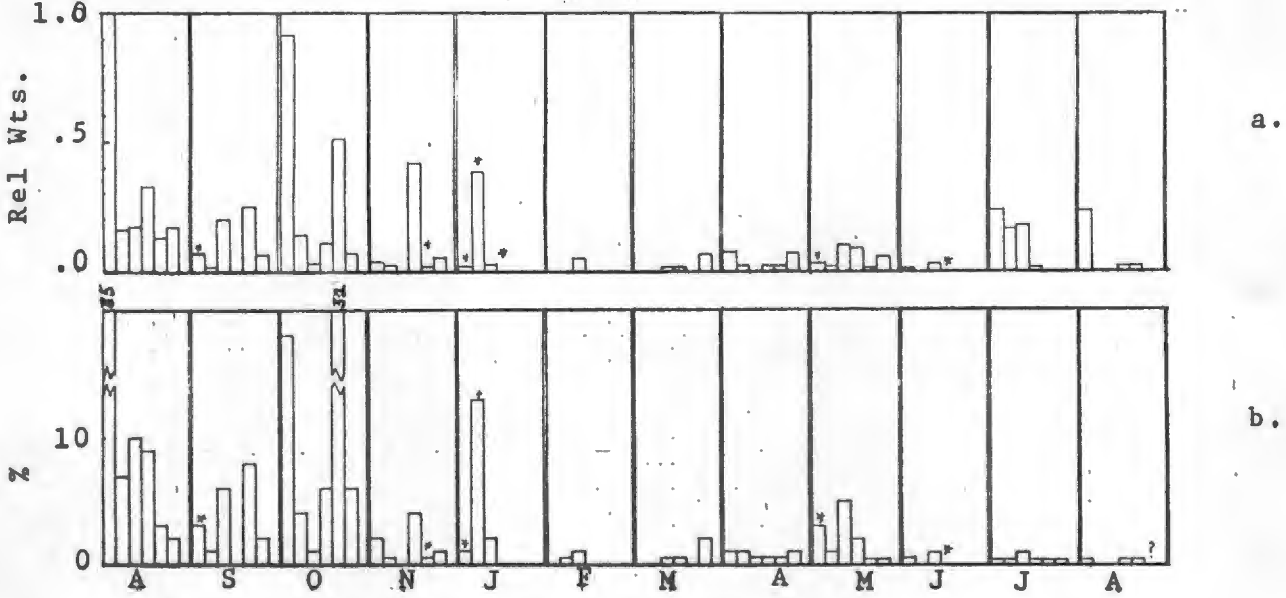
As can be seen in Figure 5.2.a,b the large chaetognaths were predominantly inshore animals, with monthly maxima occurring at Station 16-02 every month but one. There was occasionally a smaller offshore peak somewhere along the line, but it was never more than half the size of the inshore peak. Six different months produced samples containing more than 10,000 individuals/1000m . They were numerically the most abundant of all the non-copepod macrozooplankton at Station 16-02, surpassing even copepods for five months of the year. They made up over 80% of the sample at this station during October and February.

There were fewer chaetognaths in the small size-fraction (Fig. 5.2.c), and they rarely constituted more than 1% of the total sample of small zooplankton. They were, however, present somewhere along the sampling line during all months. Unlike the large chaetognaths, they were primarily offshore animals, found inshore (Station 16-02) only in late winter and early spring, and in January. This group experienced a large inshore expansion in September and was most abundant at all stations during this month. This level was maintained until it began a marked decrease in February. During all other months, numbers were low but constant. Its biggest contribution relative to the other groups present came in September at the two inshore stations, when it constituted 4-5% of the sample.

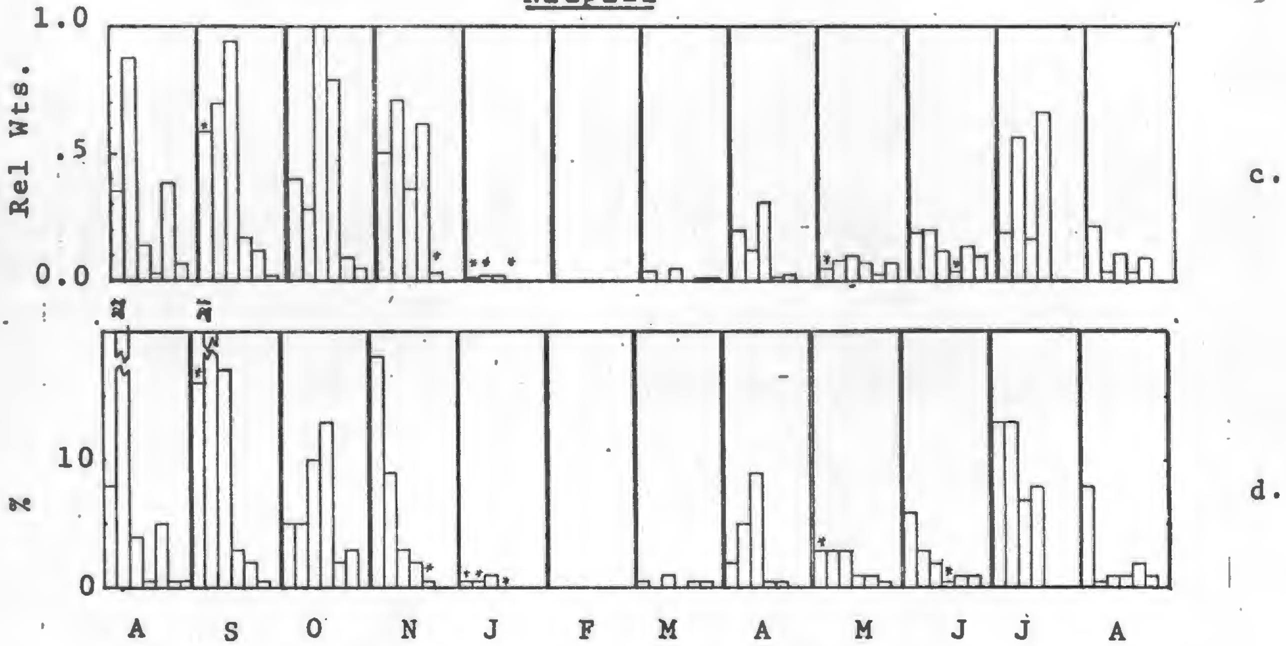
It appears from the histograms that the spring increase among the young chaetognaths is timed to appear simultaneously with the early increase in upwelling and the accompanying increase in small prey in late winter and spring, rather than being a response to these events. The growth of individuals produced a similar expansion in the large chaetognaths two months later. It seems probable that subsequent generations appeared in approximate two-month intervals throughout the summer until late autumn, with generations showing increased overlap as the seasons progressed. The winter drop in numbers, probably the result of a combination of decreased food availability and

EUPHAUSIIDS

Eggs



Nauplii



Calyptopis Stage

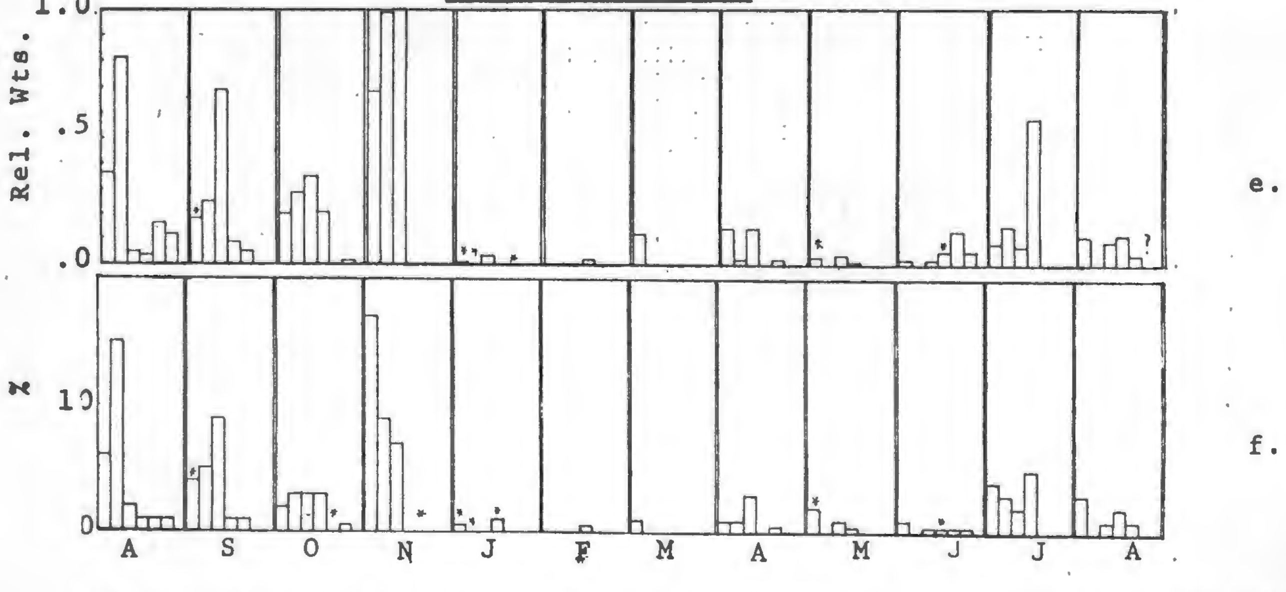
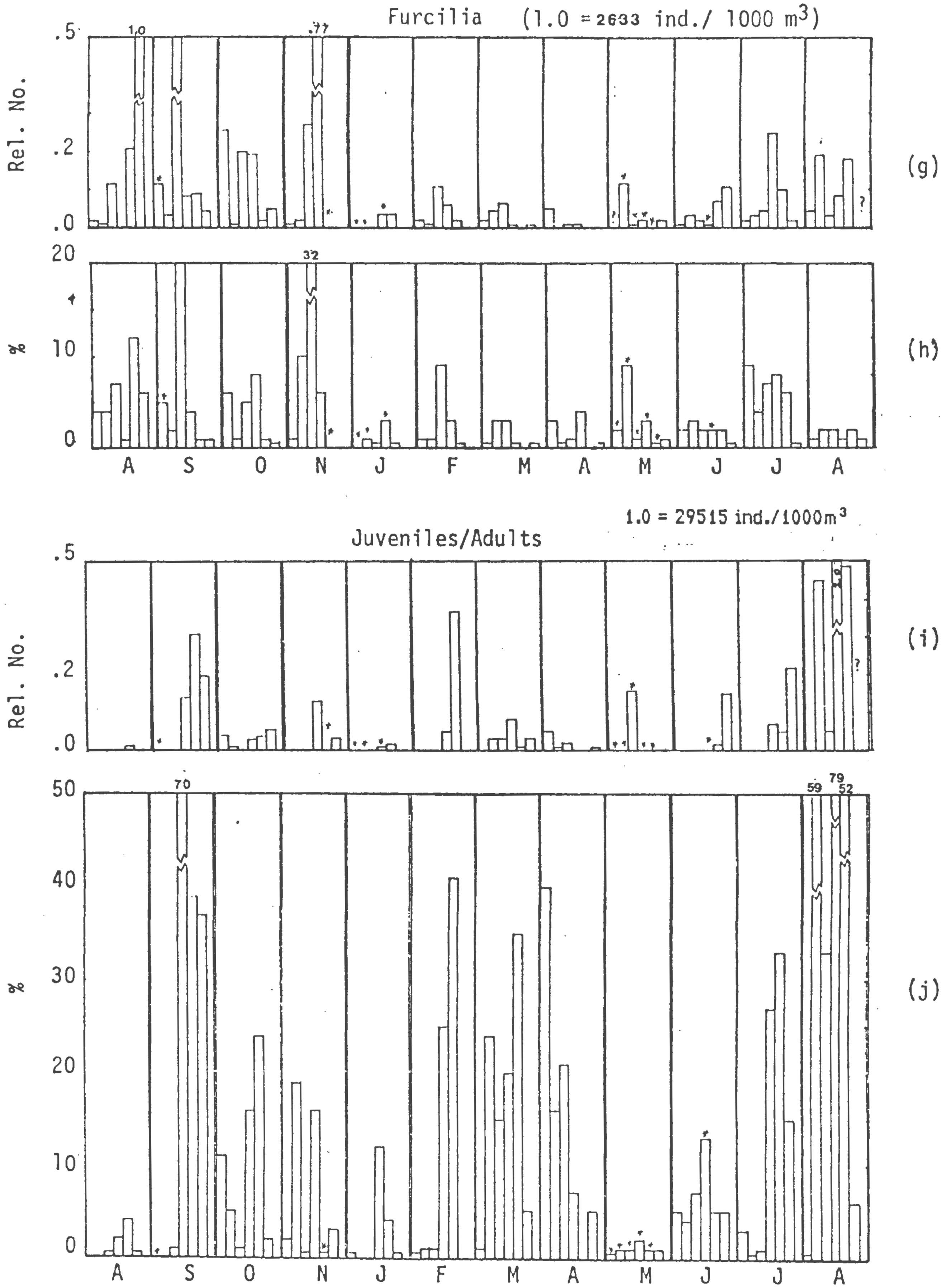


Figure 5.3.- Euphausiid Abundance Histograms (figure text on next pa

EUPHAUSIIDS - continued


Furcilia (1.0 = 2633 ind./ 1000 m^3)

Juveniles/Adults

1.0 = 29515 ind./1000m^3

Figure 5.3. - Euphausiid Abundance Histograms: a. eggs, rel. wt.; b. eggs, %; nauplii, rel. wt.; d. nauplii, %; e. calyptopis stage, rel. wt.; f. calyptopis ge, %; g. furcilia stages, rel. no.; h. furcilia stages, %; i. juv./ad. stages, l. no.; j. juv./ad. stages, %. Per cents are shown to the nearest whole number, cept that any value less than 0.5% is indicated in order to show presence. *'s licate a questionable value. Values for broken lines are shown above the line. tions go from offshore to onshore in a left-to-right direction.

predation by increasing numbers of fish recruits (Shelton and Hutchings, 1979; Crawford, et al., 1980), would bring an end to the repeating cycle until the next spring.

Euphausiids

In terms of biomass, euphausiids were the most abundant of the macro-zooplankton, excluding copepods. They were less numerous than chaetognaths inshore but had a more even distribution, being found along the entire sampling line in substantial numbers. Their abundance and omnipresence make all of their developmental stages - eggs, nauplii, calyptopis and furcilia stages, juveniles, and adults - important to the ecosystem of Lambert's Bay and, in particular, to copepods as prey, competitor, and predator, depending on size. Although once thought to be exclusively herbivorous, coastal and shallow water species in particular are now known to be opportunistic feeders, taking any appropriate food item that presents itself either to a filtering or a raptorial capture system (Theilacker and Lasker, 1974). This ability places them among the potential major predators of both copepods and fish larvae.

The distribution of euphausiid eggs (Fig. 5.3.a,b) showed strong seasonal variation. A late winter and spring group, they were abundant from August, 1977 through January, 1978, and comprised nearly 40% of the zooplankton sample from Station 16-12 in August. After a sharp February drop in number, they remained relatively scarce, but increased fairly steadily through August, and were present at at least two stations per month even during that time. Histograms for relative weights and for percentage of total sample show essentially the same patterns. Euphausiid eggs comprised from 0% to nearly 40% of the entire sample, with wide-ranging fluctuations from month to month and from station to station. While they were found at all stations at some time during the year, they occurred most frequently at the three outer stations, where the warmest water of the area was found.

Nauplii (Fig 5.3.c,d) abundance patterns were very much the same as those for eggs, a finding not unexpected considering that hatching time is short (King, et al; 1978). The autumn increase was more similar in size to that in the spring, perhaps indicating predation pressure in the spring. Also apparent was a more precise relationship with a specific water type.

There were large numbers present when sampling began in August, 1977, and numbers remained high until January. In February, nauplii were absent. Small numbers reappeared in March, and low levels were maintained for the rest of the sampling period except for an isolated two- to three-fold increase in July. Peaks for any given month occurred at Stations 16-08 and 16-10 with only two exceptions. Nauplii were always either non-existent or very rare at Station 16-02, and only slightly more abundant at Station 16-04. The percentage of nauplii in the total sample ranged from 0-22%. The group showed geographical consistency, peaking at the middle stations and diminishing at both ends of the line, and may indicate that even the naupliar stages are not completely passive in their distribution.

As seen in Figure 5.3.e,f, calyptopis stage euphausiids have much the same temporal distribution as eggs and nauplii. However, they continue the trends begun in nauplii of narrowing both the geographical range and the difference in size between the spring and autumn peaks. They ranged from 0-17% of the total sample.

Only the smallest of the furcilia stages were present in the small size-fraction, unlike eggs and naupliar and calyptopis stages which only occur there. There is a slight shoreward movement apparent in the larger individuals. The distribution of those in the large size-fraction is shown in Fig. 5.3.g,h. November showed the greatest absolute number as well as the greatest percentage (14%), but there were additional peaks in September, 1977 and July, 1978. Aside from those peaks, numbers were low and generally constituted less than 5% of the zooplankton total. However, during all months except January were present at three or more stations.

The distribution patterns of number/1000m and percentages of adult and juvenile euphausiids were markedly different from those of the developmental stages which preceded them. Percentages of total sample ranged from 0-70%. Three distinct peaks are apparent in the histograms in Fig. 5.3.i,j - early spring, mid-summer, and winter. The first and last may actually be parts of the same seasonal (winter) increase of different years, shifted somewhat by the annual variation in conditions. Although the maximum abundance for each month still occurred most often at the middle stations, the addition of juveniles and adults to the euphausiid population increased the total number found

STOMATOPODS

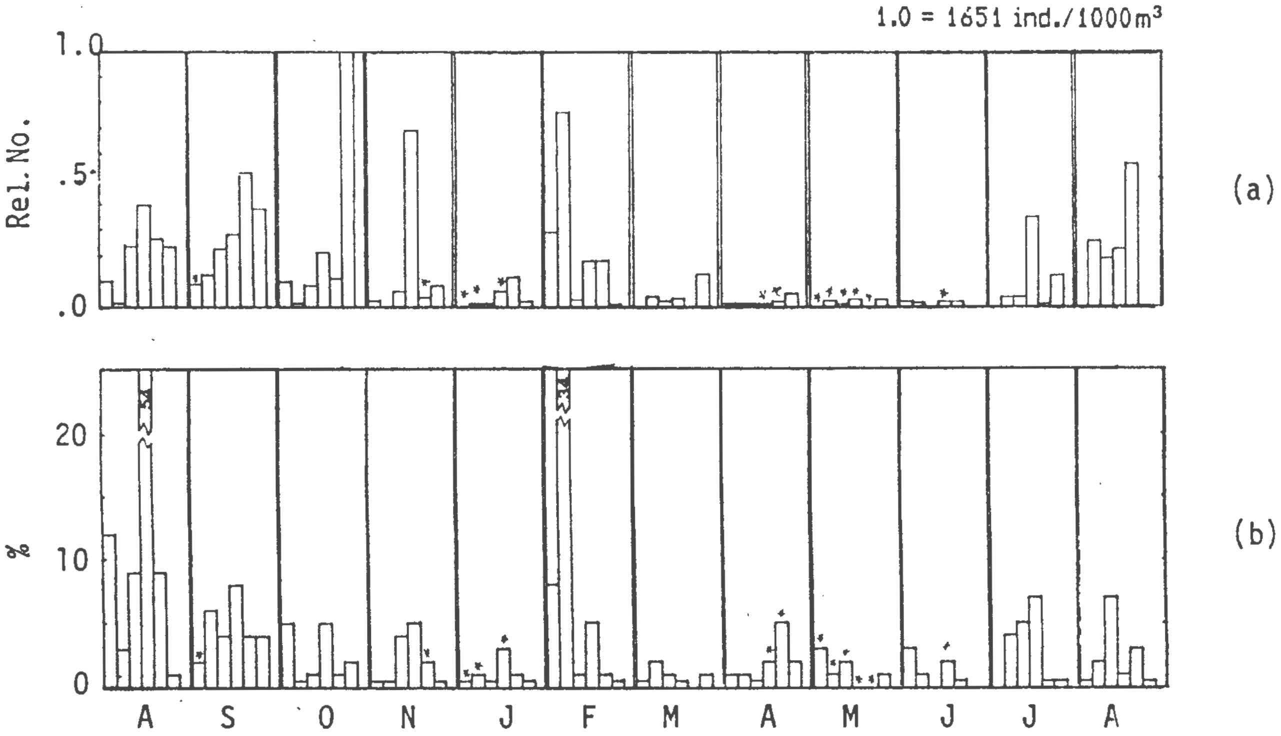


Figure 5.4.- Stomatopod Abundance Histograms: a. rel. no./1000 m^3; b. % Of total sample. Per cents are shown to the nearest whole number, except that any value less than 0.5% is shown as 0.5% in order to indicate presence. *'s indicate a questionable value. Values for broken lines are displayed above the line. Stations go from offshore to to onshore in a left-to-right direction.

inshore in upwelled or aged, upwelled water.

Stomatopod Larvae

With the exception of a few individuals, stomatopod, or mantis-shrimp, larvae were found only in the large size-group. They were surprisingly common in the study area; out of the 72 samples taken, they were absent from only six and constituted up to 34% of the sample at the maximum (Fig. 5.4). For eleven out of the twelve months, stomatopods were most abundant numerically at either Stations 16-02 or 16-04, but outside of these peaks, their numbers were fairly uniform across the study line and often comprised a larger proportion of the zooplankton population offshore. They were abundant in all but the late autumn months, and at a maximum in late winter and early spring. Because they are known to be solitary, bottom-dwelling predators, it was surprising to find so many present in the plankton on a permanent basis. However, Morgan (1980) reports, "The temperate species *Oratosquilla oratoria*, common in Japan, has a 5-month duration in the plankton (Senta, 1967), and *Pterygosquilla armata schizodontia* was discovered to remain in the plankton for up to nine months (Pyne, 1972)." (p. 698.). Morgan goes on to stress their impact on other zooplankton.

> "The abundance and duration of the larvae as part of the plankton may be important factors in the ecology of the Chesapeake Bay, since the larvae not only serve as food for a variety of organisms, including commercially important fishes, but are also rapacious predators themselves, thriving on other members of the planktonic community" (p.693).

The Seasonal Zooplankton

Bivalve Veligers

Bivalve veligers are filter-feeding herbivores (Russell-Hunter, 1979) that occurred only in the small size-fraction. Considering that their shells gave them a weight disproportionate to their numbers (see p. 7) and that numbers were calculated using sample weights, their abundance must be assumed to be very small. Predominantly a winter group, only scattered individuals were found from November through May and moderate numbers appeared in August, 1977 and in June and July, 1978. Twice, however, they constituted a considerable percentage of the total zooplankton sample, 26% in June at Station 16-08 and 15% in July at 16-02. In spite of showing a maximum percentage at

Station 16-08, they were primarily an inshore group, occurring most often at Station 16-02, somewhat less often at Station 16-04, and rarely at the other stations. During three months they occurred only at 16-02. Anchovy are known to feed on them (Hutchings, pers.comm.), and they may compete for food resources with copepod nauplii during times of scarcity. During the year of this study, however, chl "a" max values were within moderate ranges during peaks in bivalve abundance, and competition was unlikely to have been significant.

Cladocerans

Cladocerans, with few exceptions *Evadne*, were almost exclusively an offshore winter group. Although properly a member of the permanent zooplankton, their seasonal appearance in Lambert's Bay makes them more appropriately discussed in this section. Their population showed a slight spring increase, but it was negligible in comparison to the ten-fold increase in winter, when it comprised 16-18% of the total small-sized population at all three of the outer stations in June. No individuals were found from January through March, and very few during any other month. Station 16-12 showed the greatest number of occurrences, and the number dropped steadily in a shoreward direction. As raptorial carnivores (Russell-Hunter, 1979), they must be considered potential predators on copepods.

Decapod Larvae

August through November 1977 were the months of greatest occurrence for decapod larvae, with the maximum occurring in September at Station 16-12. Because their spines prevented them from passing through the finer meshes, all but the very smallest were found in the large size-fraction. No effort was made to identify the several genera represented in the samples. Of interest, however, was the appearance of relatively large numbers (>200/1000m) of a large penaeid (probably *Solenocera*) at the outer three stations, particularly in February, but in lesser numbers from February through April, with occasional appearances at other times. At its peak this decapod composed 7% of the total large zooplankton population. From August until October 1977, decapod larvae were found at all stations along the line. A marked drop occurred in the population in

January when they occurred only at Station 16-02 in small numbers.

It appears that there were two distinct groups of decapod larvae. The first was an inshore, winter-spring group composed of many species and only once totalling more than 5% of the large zooplankton total. The second was an offshore, late summer-autumn group composed of one species which comprised up to 10% of the population. The winter-spring group peaked in September, and the summer-autumn group in February.

Echinoderm Larvae

Echinoderm larvae were present from late autumn to mid-winter, with May the month of greatest abundance. At that time they constituted over 20% of the total zooplankton sample. They were absent during all other months except for a sizeable (6%) but isolated appearance in August, 1977. This may have represented the end of the bloom of the preceding year. The middle stations were populated most heavily. Echinoderm larvae are too small to be serious predators on any but the earliest stages of copepod life. Their significance, if any, to copepods would most likely be as competitors with nauplii for very small food particles, as prey for predacious copepods, or as alternative food source for non-copepod predators.

Tunicates

Tunicates, like cladocerans, are strictly speaking members of the permanent zooplankton. They were nearly all salps and doliolids, and were a winter and spring group, occurring almost exclusively at the three outer stations. The small doliolids were most abundant in July and August (approximately 15%) and the large in August and September, probably reflecting ontogenetic growth within the group. At all other times they ranged from 0-5%, if present at all. Their absolute numbers followed a pattern almost identical to their percentage distribution.

Although only a small part of the total zooplankton community, salps and doliolids are known to be voracious feeders on both small phyto- and zooplankton (Russell-Hunter, 1979) and have been shown to decimate an area when abundance levels are high. However, their filtering mechanisms clog and they have been known to rupture in dense plankton, and so are most efficient in oligotrophic water (Alldredge and Madin, 1982).

The Less Common Groups

Cypris Larvae

Cypris larvae occurred frequently, but were never very abundant, from August through November 1977. During that time they occurred at no more than four stations in any given month. Their population declined in January and only scattered individuals were found for the rest of the sampling period. At no time did they constitute more than 1% of the total sample.

Medusae

Medusae were generally more abundant in winter and inshore, both in terms of numbers and in relation to the total zooplankton population. During June and July they were present at nearly all stations reaching 9% of the total large zooplankton. During the other months of the year they rarely exceeded 1% and were present at scattered locations along the line. They were least common from January through March.

Siphonophores

Siphonophores were never more than 3% of the total sample. They were present in winter and early spring, primarily from July through September for the small members of the group and through November for the large. They were completely absent in May. Siphonophores were most abundant, both in relation to themselves and to the other large zooplankton, at the three offshore stations, particularly Station 16-08. They were never found at Station 16-02. The highest absolute number (497 individuals/1000m) was recorded in September at Station 16-08, and the highest percentage of the sample in August, 1977 (10.2%).

Others

In addition to those phyla whose occurrence in the samples has just been described, there were others which were occasionally present. Their numbers were too small to allow reliable quantitative assertions to be made about their distribution.

They were: cumaceans and mysids, usually found inshore, most often in winter but not exclusively so; gastropod larvae; polychaete worms and ostracods.

Conclusions

On superficial examination, the distribution of zooplankton in Lambert's Bay, with its larger spring and smaller autumn peak, has an apparent two generation annual cycle with population size dependent on the size of the phytoplankton maxima. While this is true in part and is to some degree a matter of scale, a closer look at the fine structure of the Lambert's Bay environment presents a far more complicated picture. The distribution of non-copepod zooplankton described in this chapter hints at some of the intricate interactions between the community members. These will be discussed here in part, and in more detail in the next chapter when the role of copepods will be added to the overall picture.

Firstly, all of the permanent members of the Lambert's Bay community are relatively large, and at least facultative carnivores in their adult form. Chaetognaths and stomatopods are obligate zooplankton predators. All of these permanent groups showed a sizeable spring increase in young stages. By adulthood, this increase was lessened by differential mortality until the adult members showed a fairly even temporal distribution. Stomatopods were an exception to this and showed a more marked autumn decline than the other groups. This may reflect their bottom-dwelling habit, indicating an exodus from surface waters in those months rather than a decrease in numbers. In addition to a smoothing of temporal distribution, there was movement with increasing age toward colder water. (This shoreward movement, in addition to that for copepods, is illustrated in Figs. 6.7,8,9 in the next chapter.) In general, the permanent zooplankton were less specific to either water types or range of phytoplankton abundance. This may have been the result of a number of factors, in particular, size-related increase in tolerance limits for temperature and salinity, decreased dependence on phytoplankton combined with increased effectiveness as carnivores, or increased mobility allowing for foraging over greater ranges.

Secondly, all temporary members of the zooplankton community had population peaks in winter, preceding the large spring influx of permanent predators. In addition, they were usually much farther offshore, outside the range of greatest invertebrate predator abundance. It was impossible to determine from these data whether this pattern was determined by the habitat preference of these species, or whether the abundance peaks occurred where they did because predator populations happened to be sparse there. The species which were represented by a few individuals year-round probably fall into the latter category, whereas those which were never found except at very narrowly defined times and places are more likely to be exhibiting habitat preferences.

In summary, the notable aspects of non-copepod distribution are:

1) the positive association of size, carnivory (obligate or facultative), and freshly-upwelled water between groups;

2) the positive relationship between increased age and freshly-upwelled water within groups; and

3) the small degree of overlap between major groups in space and time in terms of their abundance maxima.

CHAPTER VI

THE COPEPOD COMMUNITY

Introduction

In this chapter, the distribution patterns of copepods as a whole and of individual copepod species will be described in relation to spatial and temporal changes in physical and biological conditions. Questions which will be addressed are:

a. how are copepods distributed in space and time throughout the study area;

b. how is the distribution of dominant species of both size-groups related to water type; and,

c. what is the relationship between copepods and the other zooplankton coexisting in the same area.

Methods

Numerical Classification

In order to process the large amount of data collected on copepods and their environment from the 72 sampling stations, various techniques of numerical classification were employed. These were primarily methods developed originally for use in taxonomic problems and later refined for use in ecological studies (Sneath and Sokal, 1973; Field, et al., 1982). The Bray-Curtis Similarity Measure, utilizing relative weights/1000m , was used for the smaller copepods, and grouped stations according to similarity of species composition using group-average sorting. Data was not transformed. The same method was used with the large size fraction, using standardized numbers rather than weights. An attempt was made to group species and their associated environmental parameters with the McConnaughey Species Analysis, again using group-average sorting with the modifications proposed by Field, et al. (1982). This analysis was based on presence or absence only.

After the station clusters were identified, an R x C Test for Independence (Sokal and Rohlf, 1969; pp. 599-600) was used to quantify the relationship between these clusters and the water types identified in Chapter III. Comparative abundance within the species was shown by using relative weights in the small size-fraction and relative numbers in the large size-fraction.

The Problem of Size Overlap

The majority of the 28 species found in the small size-fraction were exclusive to that size group. However, of the five dominant species of that size-fraction, the second, third, and fourth most abundant species were predominantly juveniles and small adults of species that spanned both size-fractions. This factor complicated both the establishment of absolute numbers of individuals in the intermediate-sized species and the determination of the abundance patterns of the two size groups. Although the other two species comprised more than half the sample most of the time, in interpreting the distribution patterns of the two size groups, the following two factors must be considered.

First, although the presence of young members of the large species may have distorted the small samples, the reverse was not true except where large amounts of gelatinous or phytoplankton debris clogged the nets allowing the retention of smaller animals than usual. In those cases, numbers were clearly questionable for all aspects of the sample and are noted on the histograms. Consequently, the samples from the large size-fraction can be considered as accurate in terms of size-distribution as sampling procedures allow.

Secondly, if large copepods as a group have size-related life histories different from those of small copepods, then their young stages would be expected to smooth out fluctuations in abundance histograms. This was indeed a characteristic of the histograms for copepods in the small size-fraction.

The question of distinguishing whether the relatively uniform average spatial and temporal distribution was either a characteristic of the small species of copepods or was a consequence of the interjection of small growth stages of large species was answered by the close examination of abundance patterns of each of the individual dominant species. Because the dominant species constituted a very large percentage of nearly all samples, this approach made it possible to distinguish the inter-relationship between species life

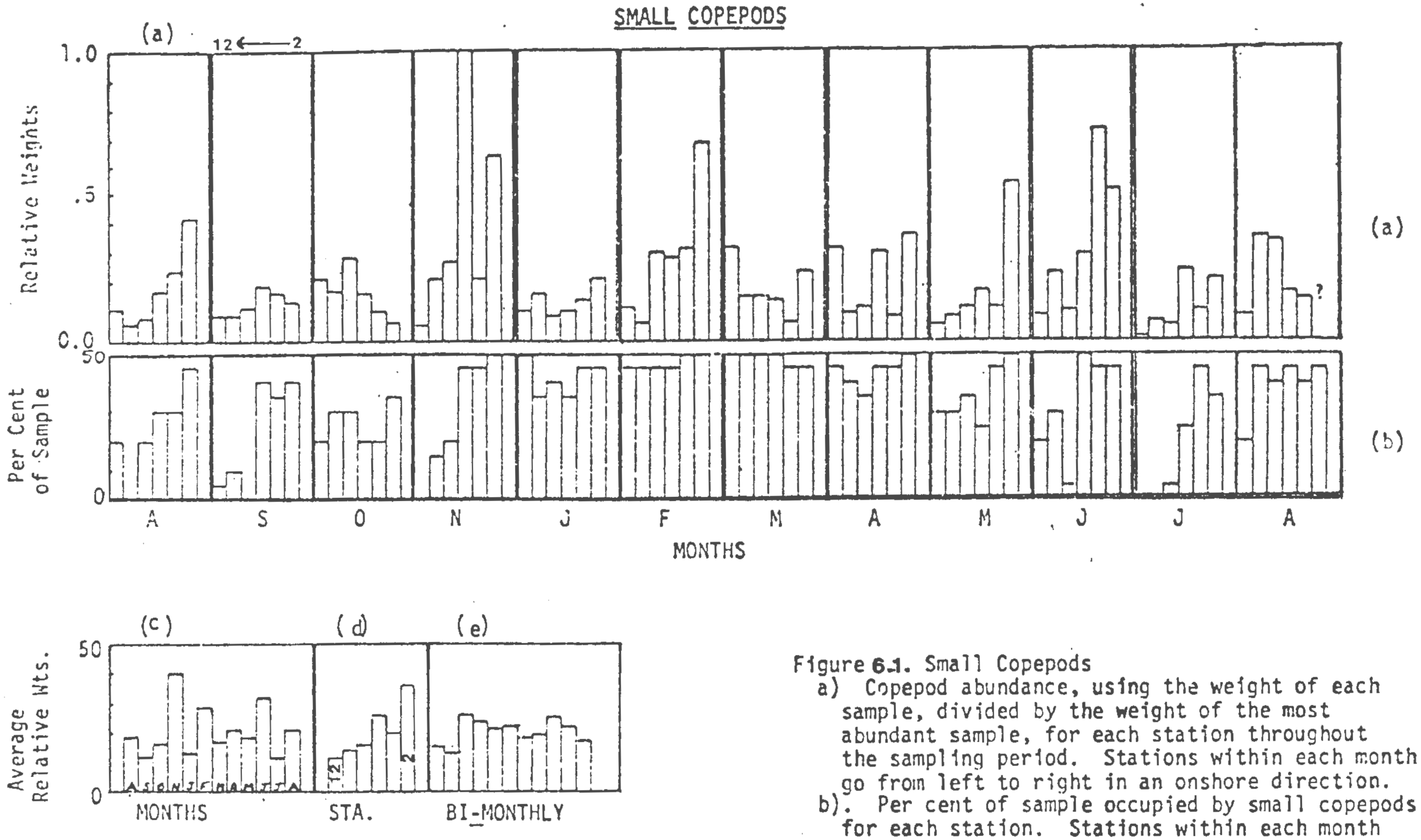


Figure 6.1. Small Copepods
a) Copepod abundance, using the weight of each sample, divided by the weight of the most abundant sample, for each station throughout the sampling period. Stations within each month go from left to right in an onshore direction.
b). Per cent of sample occupied by small copepods for each station. Stations within each month as in (a).
c) Average monthly relative weights, all stations combined.
d) Average station relative weights, all months combined.
e). Average monthly relative weights, after two-channel smoothing.

history patterns and body size.

Results and Discussion

Size-related Distribution

The distribution pattern of each of the two size-groups of copepods was in essential agreement with the size-related distributions within the entire zooplankton sample. In the total sample, the smaller size-group fluctuated a great deal among the 72 stations, and numbers decreased to seaward. In the larger group, there was less short-term fluctuation, a longer time between peaks, and, spatially, a mid-line decrease in abundance.

The similarity in distribution between the small copepods and the entire size-fraction is to be expected because they averaged 83% of the samples. In the large size-fraction, the pattern followed by copepods alone exaggerated the trends of the total sample. Where non-copepod groups formed a larger proportion of the total population, they smoothed out the seasonal and spatial variations which were more clearly visible in the copepods alone.

Thirty species of copepods appeared at least once in the 72 samples collected from the Lambert's Bay transect. In addition, calanid juveniles of undetermined species were pooled to form an additional category of small copepods. These are included as a "species" in the species list and subsequent discussion. Of the 30 species, 28 appeared in the small size-fraction and 15 in the large. Thirteen species occurred in both groups; 15 appeared only in the small size-fraction. Only 2 minor species occurred exclusively in the large group.

The Small Copepods

The small-sized copepods, shown in Fig. 6.1 can be summarized as decreasing in a seaward direction and as maintaining fairly uniform and sizeable numbers year-round. They ranged from 40-99% of the total zooplankton of that size range, and averaged 83%. The biggest proportion of copepods in relation to other groups occurred during the late summer and early autumn. Although absolute weights were highest inshore, small copepods

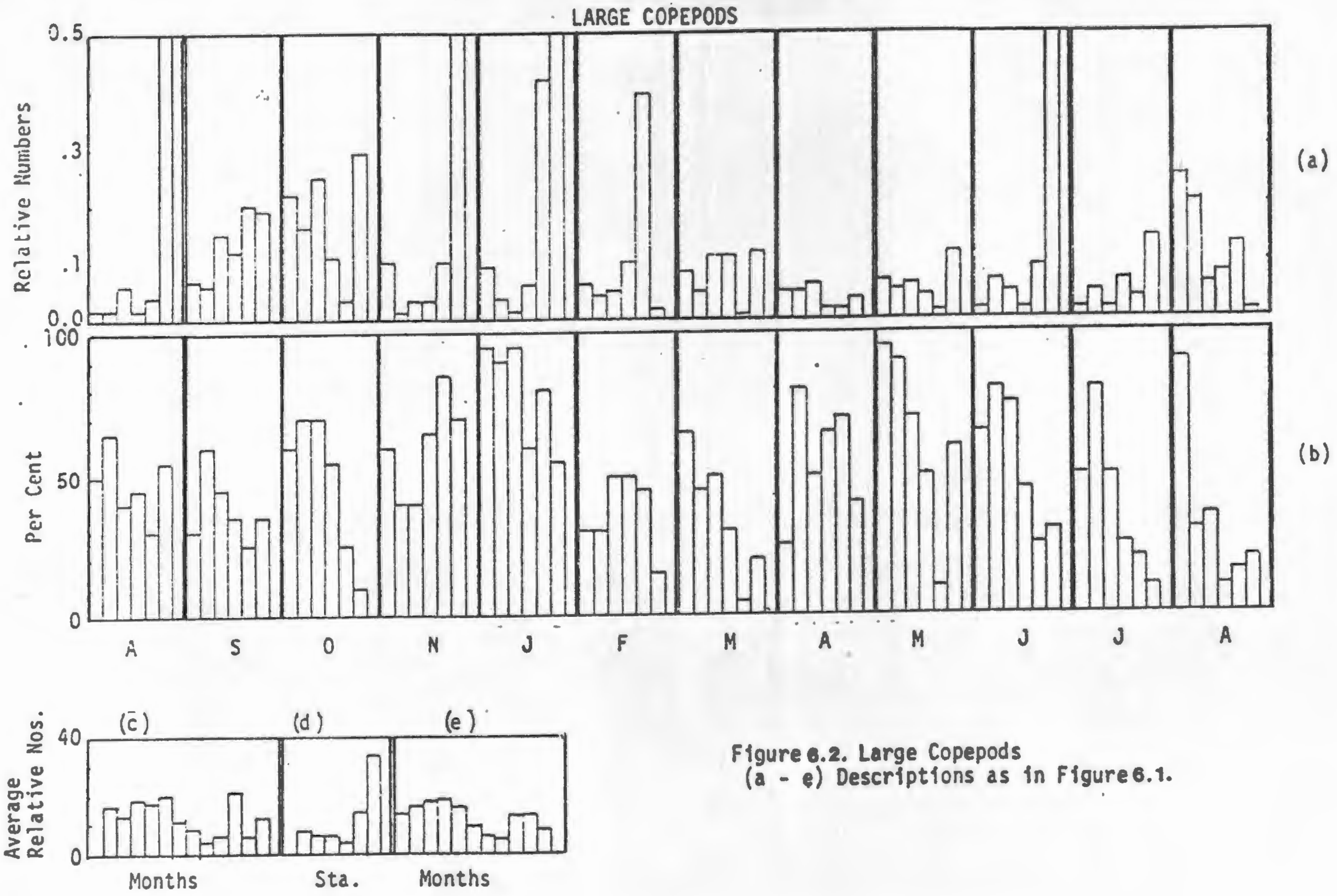


Figure 6.2. Large Copepods
(a - e) Descriptions as in Figure 6.1.

comprised a greater percentage of the total copepod population offshore.

Fig. 6.1.a shows that small copepods were most abundant at Station 16-06 in November and least abundant at Station 16-12 in July. Values for the percentage of copepods in the total size-fraction (Fig. 6.1.b) displayed more uniformity than did the values for relative weights. In general, small copepods made up the greatest fraction of the total in late summer and early autumn, when most other taxa experienced a sharp decline. Numbers also remained fairly high during that time. When averaged over the year (Fig. 6.1.c), relative weights were highest inshore (Station 16-02) and lowest offshore (Station 16-12).

When monthly fluctuations were smoothed by twos (Fig. 6.1.d), the uniform size of the small size-fraction throughout the year became apparent. (However, the large short-term fluctuations were hidden; these fluctuation were not present in all species, and therefore were not considered to be random patchiness.) There were slight spring and autumn increases of similar size, but seasonal variation was surprisingly small. Winter values were somewhat lower than those of the rest of the year.

Figure 6.1.e clearly shows the trend toward decreasing numbers with distance from the coast. As already mentioned in Chapter II, these values must be treated with caution because of the very high probability that most copepods will be found at or above the thermocline. Values at Station 16-04 were lower than the general spatial trend would lead one to expect, while those at Station 16-06 were higher. Both stations frequently came under the influence of powerful eddies and jets, suggesting that values there may be in large part the result of physical dispersal or aggregation (see Chapter IV).

The Large Copepods

Both the spatial and temporal distributions of large copepods were markedly different from those of the small. Figure 6.2.a shows that they were most abundant at Station 16-02 in June, and least abundant at Station 16-04 in March. They constituted from 7-95% of all large zooplankton, with an average of 49% (Fig. 6.2.b). When averaged over the sampling line (Fig. 6.2.c), copepods were most numerous in June, but were almost as plentiful for the entire period from August 1977 through January 1978. April samples contained the fewest. The average inshore (Station 16-02) abundance value was markedly

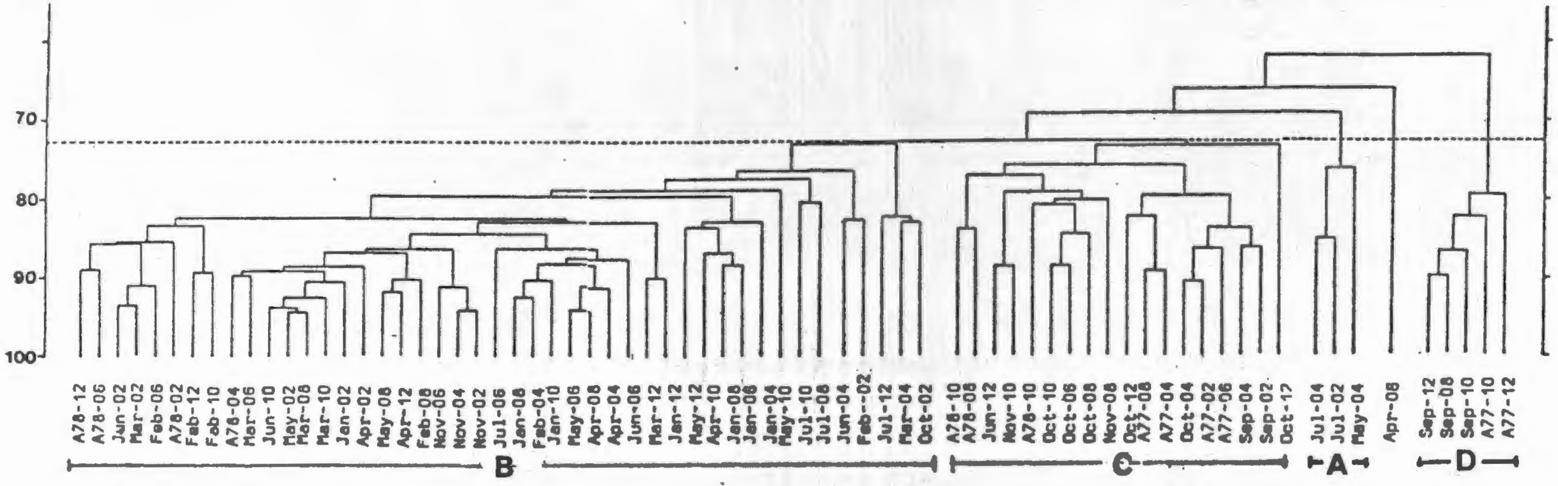
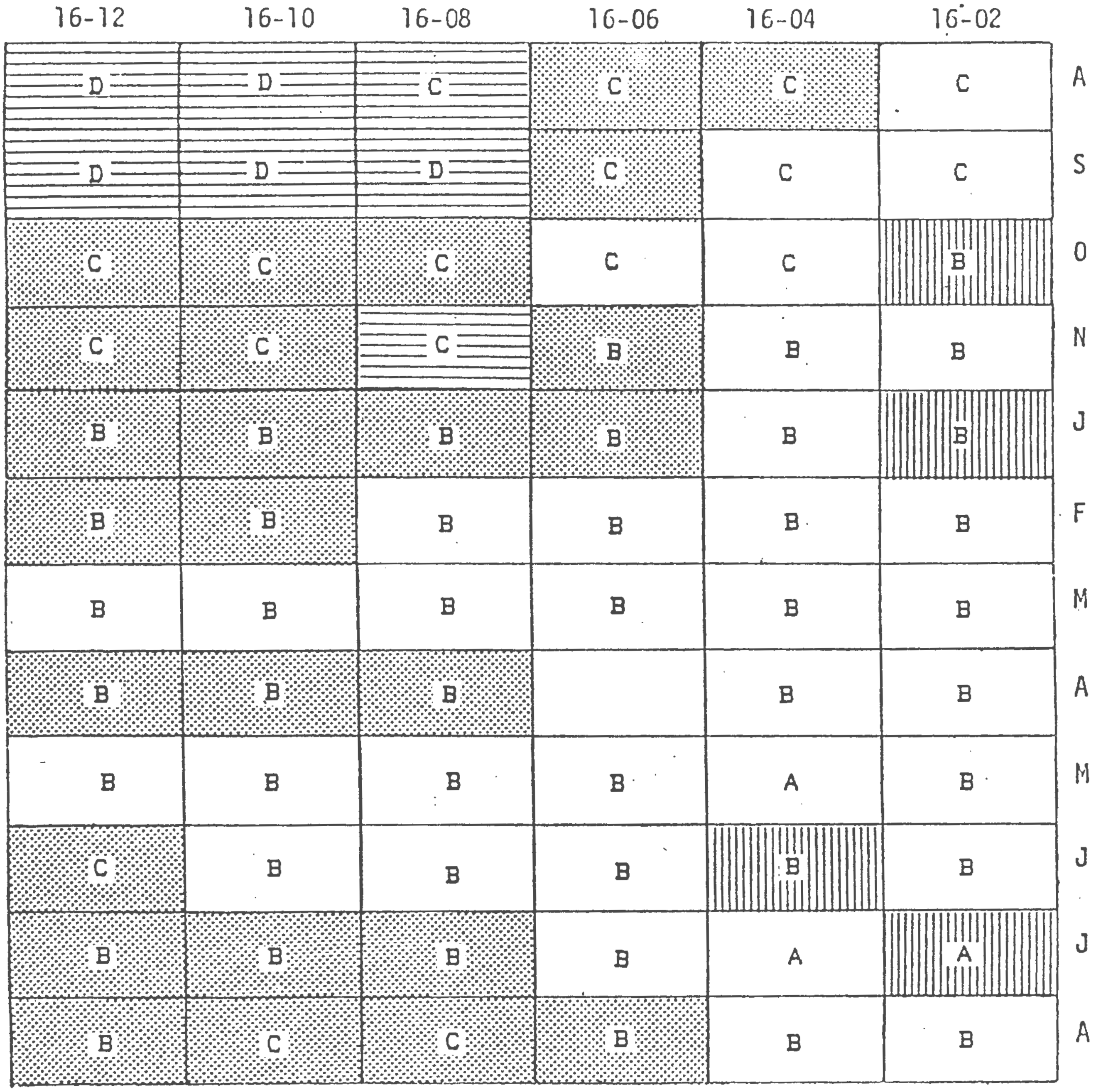


Fig. 6.3. Bray-Curtis Similarity Dendrogram, showing clustering of stations based on species composition of small copepods.



16-12	16-10	16-08	16-06	16-04	16-02	
▤ D	▤ D	▤ C	▒ C	▒ C	C	A
▤ D	▤ D	▤ D	▒ C	C	C	S
▒ C	▒ C	▒ C	C	C	▥ B	O
▒ C	▒ C	▤ C	▒ B	B	B	N
▒ B	▒ B	▒ B	▒ B	B	▥ B	J
▒ B	▒ B	B	B	B	B	F
B	B	B	B	B	B	M
▒ B	▒ B	▒ B		B	B	A
B	B	B	B	A	B	M
▒ C	B	B	B	▥ B	B	J
▒ B	▒ B	▒ B	B	A	▥ A	J
▒ B	▒ C	▒ C	▒ B	B	B	A

Fig. 6.4. Bray-Curtis station groups, based on small copepod species composition, shown against water types.

higher relative to other stations, in contrast to the more even spatial distribution among the small copepods. Station 16-06, where small copepods were plentiful, showed the lowest average value (Fig. 6.2.e). Seaward of Station 16-06, numbers again increased to seaward. Whereas small copepods showed only a two-fold temporal and spatial increase from the least to the most, the large copepods increased approximately four times. Spatially, the average numbers inshore were nearly nine times the offshore low.

Smoothing by twos (Fig. 6.2.d) effectively summarizes the general temporal pattern. Large copepods increased fairly steadily in number from a small winter population, when sampling was initiated, until January when the population began to decline. A sharp February decrease was followed by another smaller increase in the late autumn. In comparison with the smaller ones, the large copepods experienced less short-term fluctuation and more distinct seasonal variation, and were least abundant in the autumn rather than in the winter.

Numerical Classification

The Bray-Curtis similarity measure, applied to the small copepod data, clearly distinguished five different groups of stations at the 73% level of similarity (Fig. 6.3). One group, however, consisted of only one station, and was not considered further. When tested with an R x C Independence Test (SoKal and Rohlf, 1969, pp.599-600), the null hypothesis of independence was rejected ($P < .005$; Appendix D). As shown in Fig. 6.4 and in Table 6.1, Group A was found inshore in the coldest upwelled (UW) or aged upwelled water (AUW). Group B, the largest group, was also found inshore, but extended farther seaward and was associated most strongly with aged upwelled or mixed (MW) water. Group C was never found in newly upwelled water, and was centred still further to seaward in primarily mixed water. Group D was found strictly in warmer, offshore water (WW) in later winter or early spring.

Because the McConnaughey Species Analysis is based on presence-absence, it helped little in identifying species clusters (Fig. 6.5), because differences between species groups in the Lambert's Bay area lie in the relative abundance of species occurrence, rather than in the occurrence or non-occurrence of particular species. All of the major species were included in one group of 93% similarity and associated with cold, low

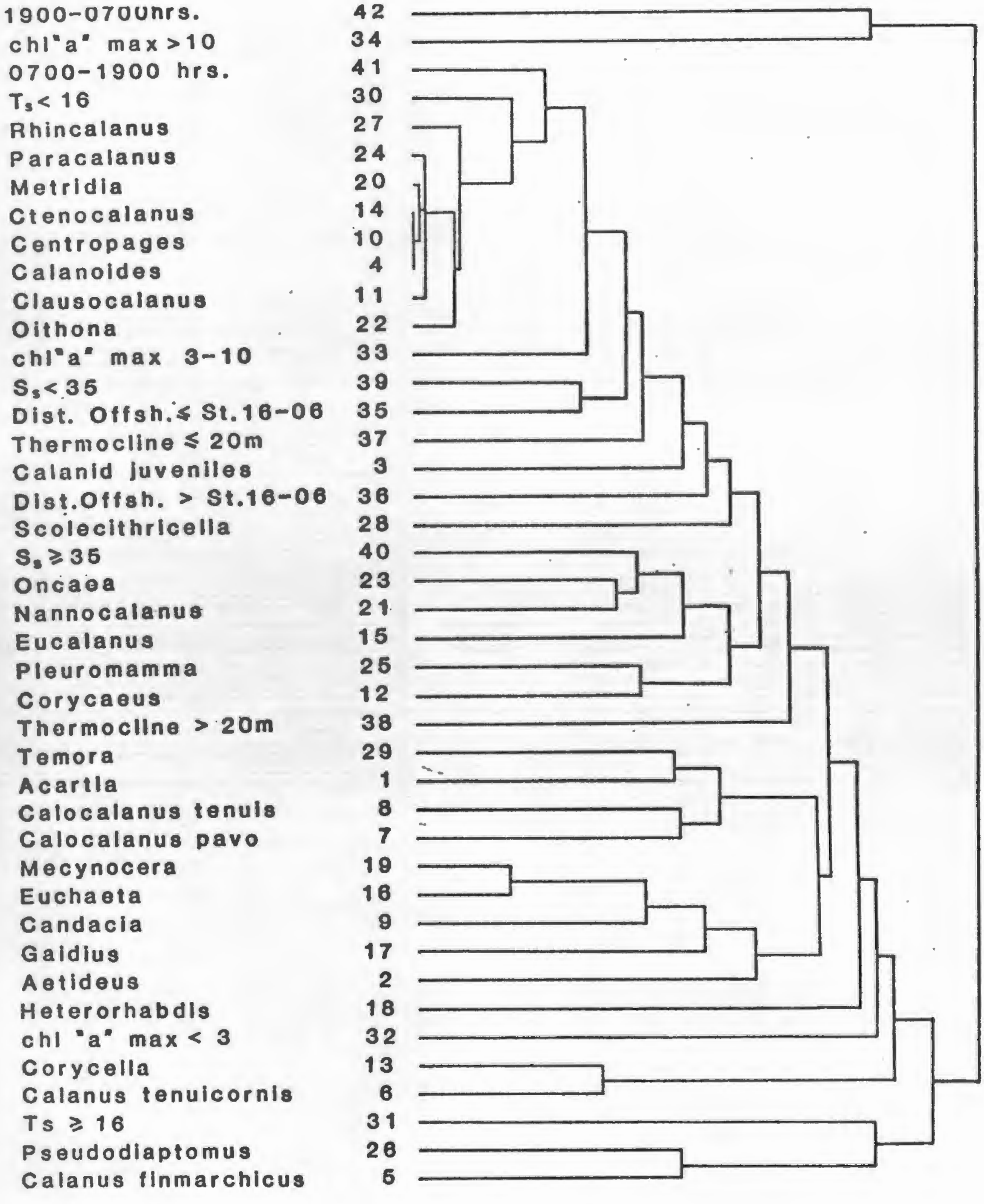


Fig. 6.5. McConnaughey analysis (presence - absence) of small copepod species and environmental features.

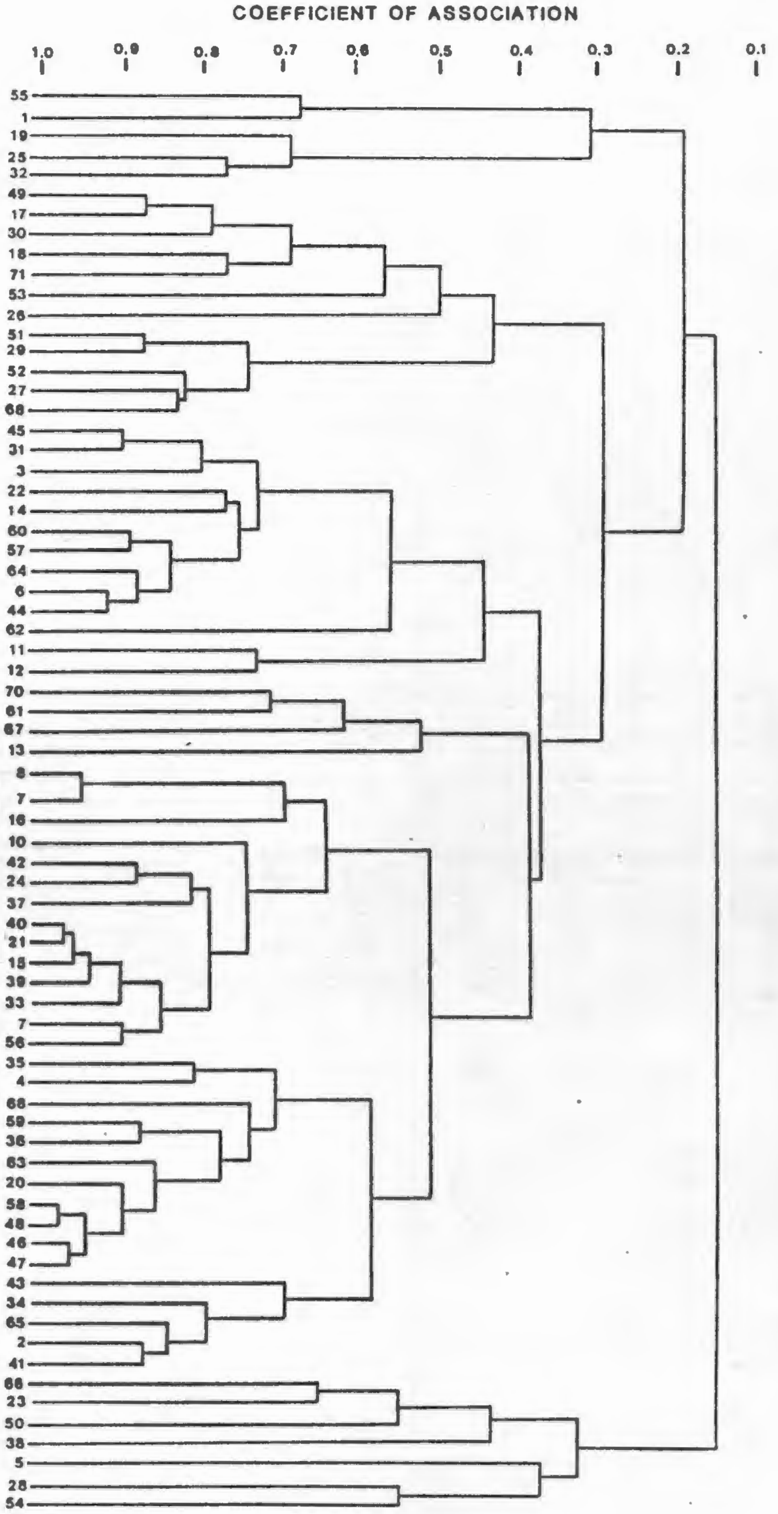
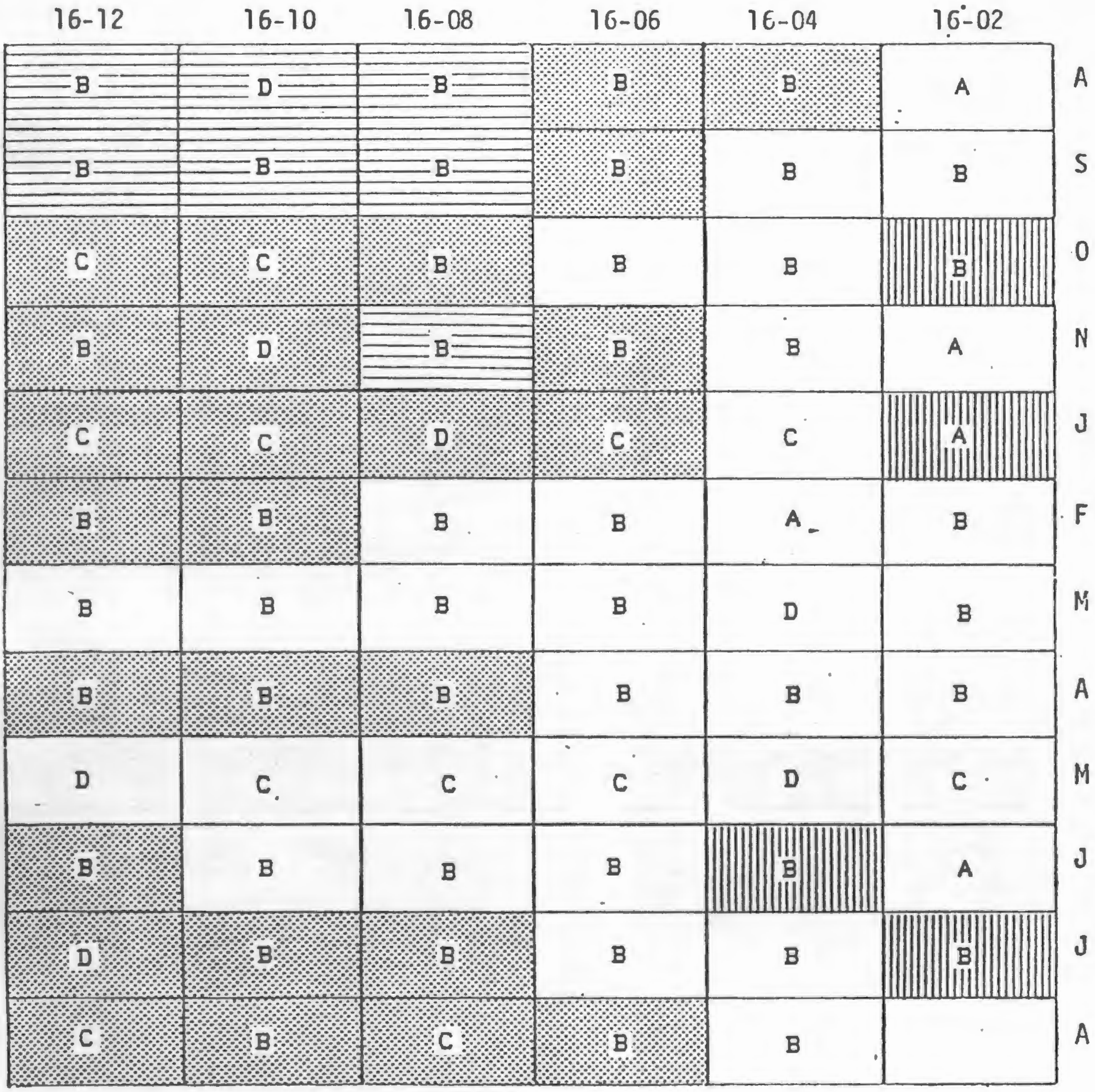


Fig. 6.6. Bray-Curtis dendrogram showing stations grouped on the basis of large copepod composition. Numbering is sequential by month and station; e.g., August, 1977, Stations 2 - 12 are Nos. 1 - 6; September, Stations 2 - 12, Nos. 7 - 12; etc.



16-12	16-10	16-08	16-06	16-04	16-02	
B	D	B	B	B	A	A
B	B	B	B	B	B	S
C	C	B	B	B	B	O
B	D	B	B	B	A	N
C	C	D	C	C	A	J
B	B	B	B	A	B	F
B	B	B	B	D	B	M
B	B	B	B	B	B	A
D	C	C	C	D	C	M
B	B	B	B	B	A	J
D	B	B	B	B	B	J
C	B	C	B	B		A

Fig. 6.7. Bray-Curtis station groups, based on small copepod species composition, shown against water types.

TABLE 6.1

Spatial and temporal abundance distribution of all species, grouped by season and location. Abundance categories - 1 = 1 occurrence; r = rare; c = common; d = dominant. Seasons - winter (Jun-Aug), spring (Sept-Nov), summer (Jan-Feb), and autumn (Mar-May). Locations - inner = Stations 16-02, -04; middle = Stations 16-04, -06; outer = Stations 16-10, -12).

Small Copepods	Wi	Sp	Su	Au	In	Mid	Out	Tot
Acartia spp.	r	r	1	-	1	4	6	11
Aetideus armatus	r	u	r	r	3	6	11	20
calanid juveniles	c	c	r	r	9	14	9	32
Calanoides carinatus	c	c	c	c	24	24	24	72
Calanus finmarchicus	-	r	-	-	-	1	1	2
C. tenuicornis	-	1	-	-	-	1	-	1
Calocalanus pavo	1	1	-	-	-	-	2	2
C. tenuis	r	r	-	-	1	2	4	7
Candacia bipinnata	u	u	-	-	-	2	7	9
Centropages brachiatus	c	c	d	d	24	24	24	72
Clausocalanus spp.	c	c	c	c	24	24	22	70
Corycaeus spp.	r	u	-	r	-	6	6	12
Corycella spp.	-	r	-	-	-	1	1	2
Ctenocalanus vanus	d	d	d	d	24	24	24	72
Eucalanus spp.	r	r	-	-	1	3	5	9
Euchaeta spp.	1	r	-	-	-	-	3	3
Gaidius sp.	1	-	-	-	-	-	1	1
Heterorhabdis spp.	r	r	-	-	1	2	3	6
Mecynocera spp.	r	r	-	-	-	-	4	4
Metridia lucens	d	c	c	d	24	23	24	71
Nannocalanus minor	c	u	r	u	11	11	17	39
Oithona spp.	u	c	u	c	18	23	24	65
Oncaea spp.	u	c	r	r	9	10	14	33
Paracalanus parvus	c	c	c	c	24	24	23	71
Pleuromamma spp.	u	u	r	1	3	8	12	23
Pseudodiaptomus spp.	-	r	-	-	1	3	3	7
Rhincalanus nasutus	u	c	u	c	16	24	24	64
Scolecithricella spp.	r	r	u	u	5	11	12	28
Temora	1	u	-	r	1	3	4	8

Large Copepods	Wi	Sp	Su	Au	In	Mid	Out	Tot
Aetidius armatus	r	u	r	r	2	2	3	7
Calanoides carinatus	d	c	c	c	23	22	22	67
Candacia bipinatta	c	c	r	r	3	12	14	29
Centropages brachiatus	d	d	d	d	22	24	24	70
Corycaeus spp.	u	c	1	-	-	3	4	7
Eucalanus spp.	u	c	r	-	3	8	14	25
Euchaeta spp.	c	c	-	1	1	4	9	13
Heterorhabdis spp.	r	1	1	1	1	2	2	5
Metridia lucens	d	d	u	d	21	16	18	55
Nannocalanus minor	u	r	-	-	2	3	9	14
Oithona spp.	c	c	1	-	-	1	9	10
Pleuromamma spp.	c	u	u	-	2	3	3	8
Rhincalanus nasutus	d	d	d	d	24	24	24	72
Clausocalanus ingens	1	r	-	-	1	1	1	3
Scolecithrix spp.	1	r	-	-	-	1	1	2

salinity water, with other minor species added singly or in small groups in step-ladder fashion. The entire area showed essentially uniform species composition when analyzed in this way. Further information would have been obtainable through Multi-Dimensional Scaling, but because the small number of species made simpler analysis feasible, no further numerical classification methods were used.

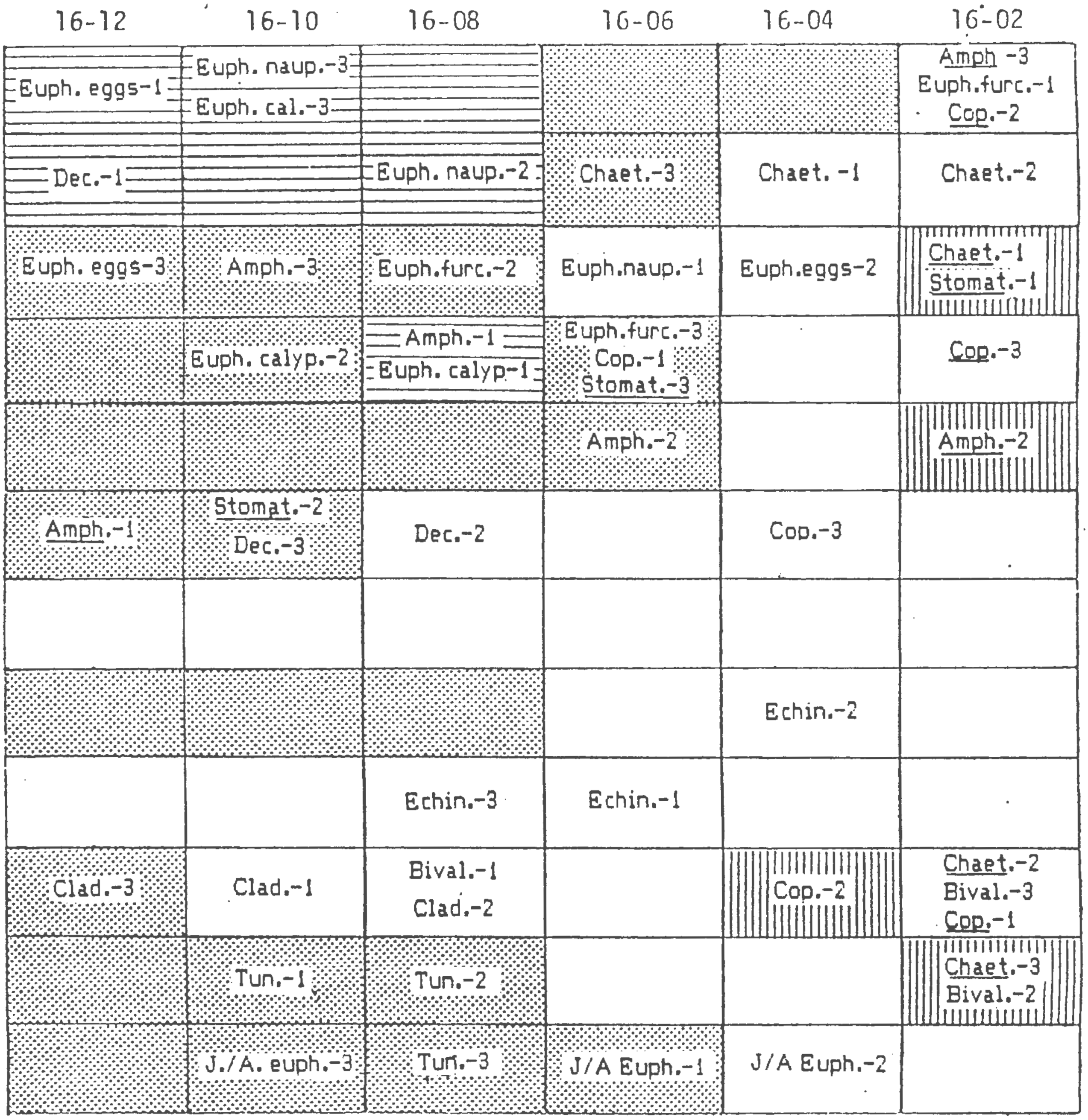
Figure 6.6 shows the Bray-Curtis dendrogram for the large size-fraction. The very high level of similarity between stations found when small copepods were analyzed in this way has decreased, but at the 30% level of association there were again four distinct groups. When displayed against a background of water types (Fig. 6.7; Table 6.2), a more scattered distribution was apparent. The relationship was tested (Appendix E), as was done for the small copepods (p = 0.2) The null hypothesis of independence was not rejected, and no relationship between station clusters, based on species composition, and water types was demonstrated.

Copepods in Relation to Other Taxa

When the three most abundant occurrences of each major zooplankton group were placed on the grid of 72 stations (Fig. 6.8), out of the 39 time-space blocks which were occupied at all, 29 were occupied by only one taxon (or partial taxon, as in the case of euphausiid growth stages). All three of the maxima for large copepods were found at Station 16-02 in aged upwelled water. The three maxima for small copepods, on the other hand, occurred farther offshore at Stations 16-04 and 16-06 in mixed, aged upwelled, and upwelled water, with numbers decreasing in a shoreward direction. They were the least specific to water type of all the taxa, which may have been the result of the larger number of species present in the group, each with its own environmental preferences. Maxima of large copepods appeared singly in one case and coincided with maxima of amphipods and chaetognaths in the others. One of the three small copepod maxima was found in conjunction with stomatopods and furcilia stage euphausiids; the other two occurred alone.

Distribution By Species

Table 6.3 shows the relative seasonal abundance of each genus (based on per cent



16-12	16-10	16-08	16-06	16-04	16-02	
Euph. eggs-1	Euph. naup.-3 Euph. cal.-3				Amph -3 Euph.furc.-1 Cop.-2	A
Dec.-1		Euph. naup.-2	Chaet.-3	Chaet. -1	Chaet.-2	S
Euph. eggs-3	Amph.-3	Euph.furc.-2	Euph.naup.-1	Euph.eggs-2	Chaet.-1 Stomat.-1	O
	Euph. calyp.-2	Amph.-1 Euph. calyp-1	Euph.furc.-3 Cop.-1 Stomat.-3		Cop.-3	N
			Amph.-2		Amph.-2	J
Amph.-1	Stomat.-2 Dec.-3	Dec.-2		Cop.-3		F
						M
				Echin.-2		A
		Echin.-3	Echin.-1			M
Clad.-3	Clad.-1	Bival.-1 Clad.-2		Cop.-2	Chaet.-2 Bival.-3 Cop.-1	J
	Tun.-1	Tun.-2			Chaet.-3 Bival.-2	J
	J./A. euph.-3	Tun.-3	J/A Euph.-1	J/A Euph.-2		A

Fig. 6.3. The three most abundant occurrences of each of the major zooplankton groups, shown against water types: Euphausiid eggs, nauplii, calyptopis stage, furcilia stage, juveniles/adults; amphipods - large and small; chaetognaths - large and small; decapods; stomatopods; cladocerans; tunicates; bivalve veligers; and copepods - large and small.

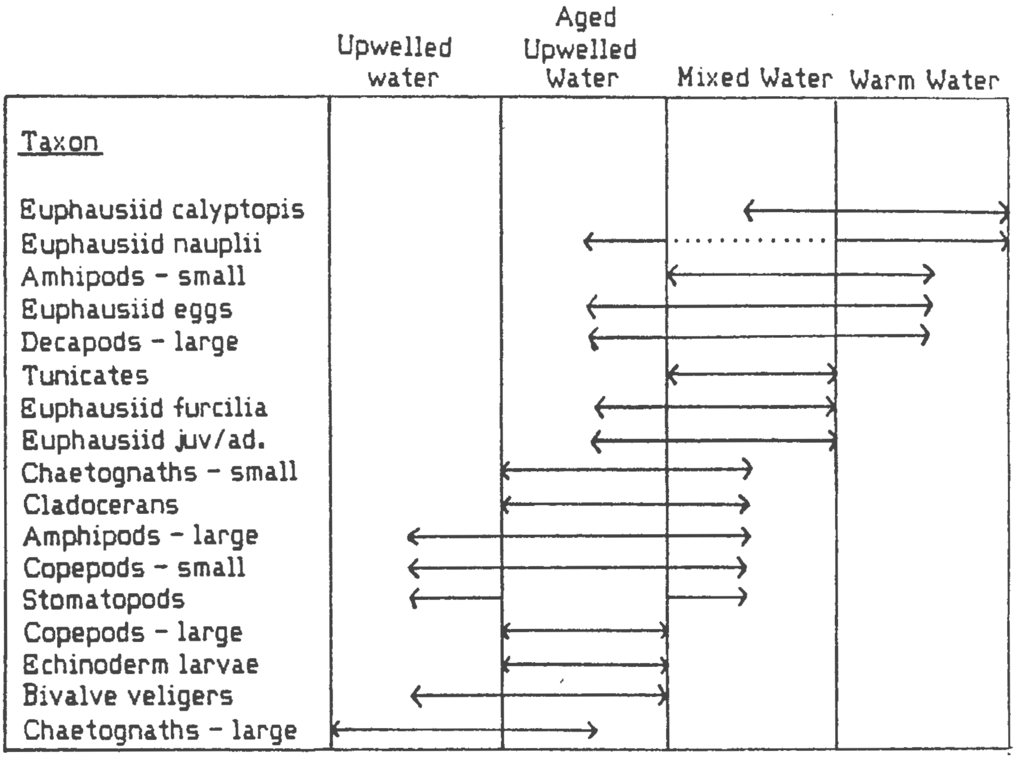


Fig. 6.9. The three most abundant occurrances of each of the major zooplankton groups, shown against water types: Euphausiid eggs, nauplii, calyptopis stage, furcilia stage, juveniles/adults; amphipods - large and small; chaetognaths - large and small; decapods; stomatopods; cladocerans; tunicates; bivalve veligers; and copepods - large and small.

of sample) along the study line. The stations were combined, in groups of two, into inshore (16-02, -04), middle (16-06, -08), and offshore areas (16-10, -12).

Small copepods were dominated, in both absolute numbers and as percentage of total sample, by the following species listed in order of decreasing abundance: Ctenocalanus vanus, Centropages brachiatus, Calanoides carinatus, Metridia lucens, and Paracalanus parvus. Each of these species occurred at a minimum of 71 stations. The dominant species among the large copepods, also in order of decreasing abundance, were: Rhincalanus nasutus, Centropages brachiatus, Calanoides carinatus, and Metridia lucens. Each of these species were found in all 72 samples.

The five major species of the small size-fraction constituted more than 80% of the total zooplankton sample nearly 80% of the time. In the remaining 20% of the samples, the percentage occupied by the five dominants fell gradually to somewhat under 40%. At the other extreme, two species appeared only once, and thirteen species occurred in 10 or fewer samples.

Dominance by a small number of species was even more marked among the large copepods. Out of the 72 samples, the 4 most abundant species comprised 90% of the sample 90% of the time, and at only 3 stations did they fail to reach 50%.

Ctenocalanus vanus and Rhincalanus nasutus were strong dominants in the small and large size-fractions respectively; information on distribution and life history of each was determined only from one size-fraction. Centropages brachiatus, Calanoides carinatus, and Metridia lucens spanned both size groups and consequently absolute numbers of each were difficult to compare with Ctenocalanus vanus and Rhincalanus nasutus. Paracalanus parvus, like Ctenocalanus vanus was found solely among the small copepods, but was not present in the extremely large numbers of the other major species. Each of these six species comprised >10% of 10 or more samples and was present in at least 71 of the 72 samples of one or both size-fractions. They were accordingly given special attention as ecosystem dominants. Each is described separately in the next chapter.

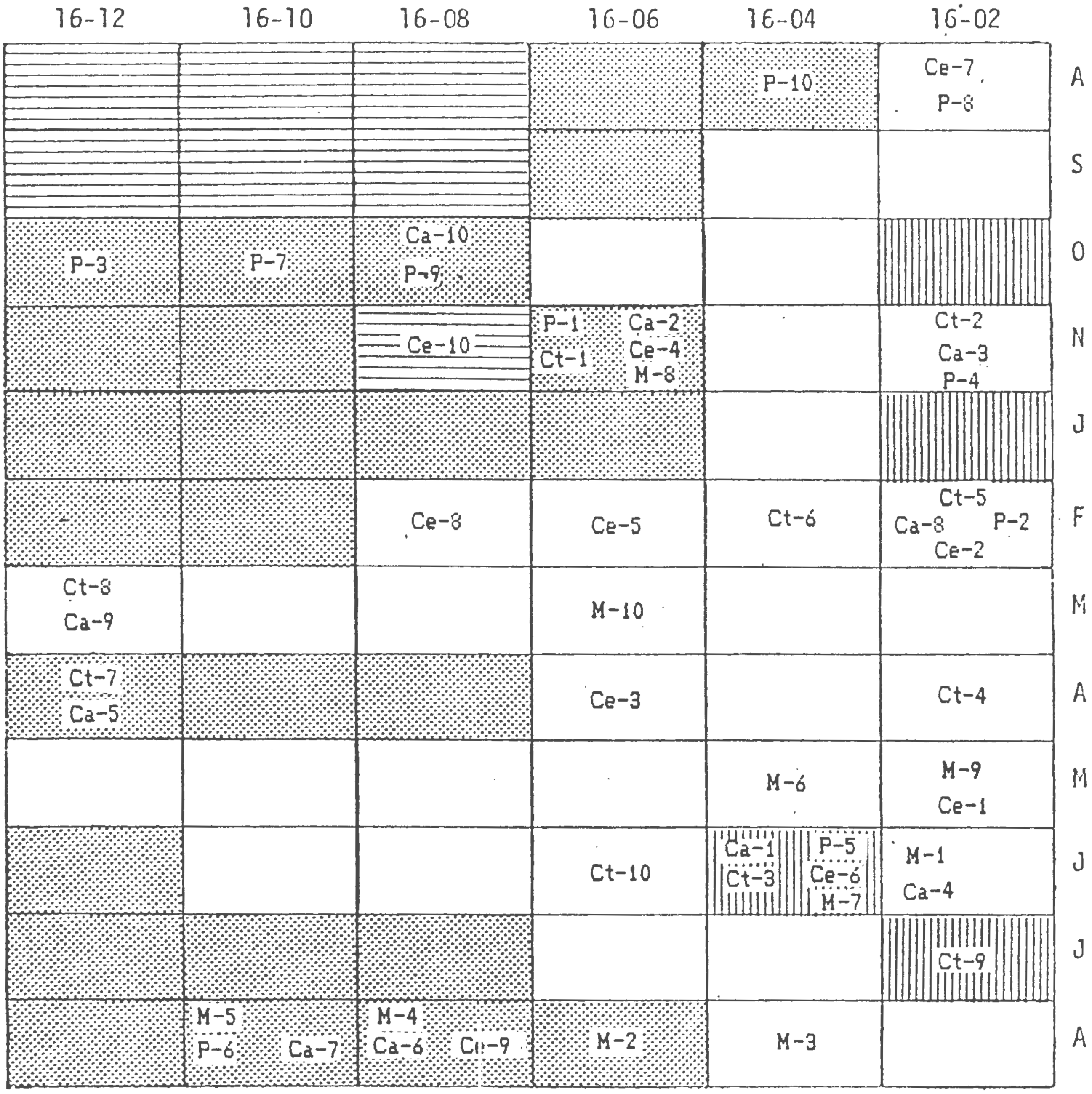
Continuing with the less common genera, those with the narrowest range of occurrence were Calocalanus pavo (2), Euchaeta spp. (3), Gaidius sp. (1),and Mecynocera spp. (4), all of which appeared exclusively at the 2 outer stations. (Here, and in following paragraphs, the number in parentheses denotes the number of samples in which the named genera were found in the small size-fraction, unless the large size-fraction is specifically noted). All of these genera occurred only in the samples of highest salinity and relatively warm water and at the same two stations, during August and September 1977. Their presence can be considered indicative of the presence of warm water.

Expanding their ranges in a shoreward direction, Calanus finmarchicus (2), small Corycaeus spp. (12), Corycella spp. (2), and Scolecithrix spp. (2), the last solely from the large group, were present at both outer and middle stations. Large Corycaeus spp. also occurred at the middle and outer stations in the large size-fraction, but less frequently than did the small members of the genus. Small Candacia bipinnata followed the same distribution pattern, but the large individuals of the species were found in more samples and in much greater abundance inshore than were the small individuals offshore. All of these were winter/spring genera, found rarely, if at all, at any other time of year. They did not occur in recently upwelled water.

Several genera appeared in all three areas, abundance usually increasing with distance from shore. These were: Acartia spp. (11), Aetideus armatus (20 sm. + 7 lg.), Calocalanus tenuis (7), Eucalanus spp. (9 sm. + 25 lg.), Heterorhabdis spp. (6 sm. + 5 lg.), Nannocalanus minor (39 sm. + 14 lg.), Oithona spp. (65 sm. + 10 lg.), Oncaea spp. (33), Pleuromamma spp., (23 sm. + 8 lg.), Pseudodiaptomus spp. (7), Rhincalanus nasutus nauplii and early copepodid stages(64), Scolecithricella spp. (28), and Temora spp. (8). The only genera more common at the middle stations were calanid juveniles too small to be identified to generic level, and Calanus tenuicornis, which appeared only once. Clausocalanus spp. were evenly distributed spatially. All genera in this group may have utilized different water types at specific periods in their life cycles.

Conclusions

Figure 6.9 shows the shift across water types, both within taxa and by different taxa. Any vertical section through the figure provides a grouping of taxa which include both predators and prey. Many taxa fall into both categories, either at different times in their life cycle, or in relation to different groups. Raptorial predators, such as



16-12	16-10	16-08	16-06	16-04	16-02	
▤	▤	▤	▒	▒ P-10	Ce-7 P-8	A
▤	▤	▤	▒			S
▒ P-3	▒ P-7	▒ Ca-10 P-9			▥	O
▒	▒	▤ Ce-10	▒ P-1 Ct-1 Ca-2 Ce-4 M-8		Ct-2 Ca-3 P-4	N
▒	▒	▒	▒		▥	J
▒	▒	Ce-8	Ce-5	Ct-6	Ct-5 Ca-8 P-2 Ce-2	F
Ct-8 Ca-9			M-10			M
▒ Ct-7 Ca-5	▒	▒	Ce-3		Ct-4	A
				M-6	M-9 Ce-1	M
▒			Ct-10	▥ Ca-1 Ct-3 P-5 Ce-6 M-7	M-1 Ca-4	J
▒	▒	▒			▥ Ct-9	J
▒	▒ M-5 P-6 Ca-7	▒ M-4 Ca-6 Ce-9	▒ M-2	M-3		A

Fig. 6.10. The ten most abundant occurrences of each of the five dominant small size-fraction copepod species. Key: Ct = Ctenocalanus vanus, P = Paracalanus parvus, Ce = Centropages brachiatus, Ca = Calanoides carinatus, M = Metridia lucens.

chaetognaths and amphipods, were more common in inshore waters along with large copepods, who themselves qualify as predators on smaller prey. Tunicates were found only offshore in water of lower phytoplankton concentration, where their filtering efficiency is at a maximum (Alldredge and Madin, 1982). Small copepods were unlikely predators on any other taxon included in this study. They would have been detrimental to other taxa only during the very rare instances of scarce phytoplankton, when they would have been possible competitors, both interspecific and to small euphausiids, bivalves, and other filter feeders. They are more likely the most abundant prey item for all of the larger zooplankton, as well as for vertebrate predators. The significance of this likelihood, in terms of life history patterns, will be discussed more fully in the discussion in the next chapter.

Figure 6.10 and 6.11 show the distribution of the samples containing the ten most abundant occurrences for each of the six most common species in the two size-fractions. In general, the large copepod maxima were found in more recently upwelled water than those of the small copepods, and older copepods were found in more recently upwelled water than younger copepods of the same species.

The six dominant species also varied in kind and degree of association with the other copepods. In both size groups, *Centropages brachiatus* and *Metridia lucens* were "loners" whose maxima occurred in conjunction with other species maxima only 40-50% of the time. *Calanoides carinatus* was at the opposite extreme, with all 10 maxima appearing in conjunction with those of other species. Neither size-fraction ever occurred by itself. Small *C. carinatus* were most often found with *Ctenocalanus* and *Paracalanus*, whereas the large were most often associated with *Rhincalanus*. *Rhincalanus nasutus* was often found in abundance with *C. carinatus*, but seldom with *C. brachiatus* or *M. lucens*. *Paracalanus parvus* was associated evenly with the other dominants the other dominants and was found by itself three times.

Taken together, the varying patterns of species association give support to the belief that, within each size group, there is the capability of finding, recognizing, and remaining in a preferred habitat for a period of time, and that the habitat of choice varies from species to species.

In conclusion, the Lambert's Bay copepod community was dominated by very few species, all of which occurred along the entire line during all months. Other species were present in abundance only rarely, in particular when westerly winds had blown warmer, higher salinity water close to the shore. However, in spite of the marked uniformity, the relative abundance of each major species changed from one station to another in ways that do not seem indicative of physical aggregation or random patchiness. More evidence of habitat preference among these species follows in the next chapter.

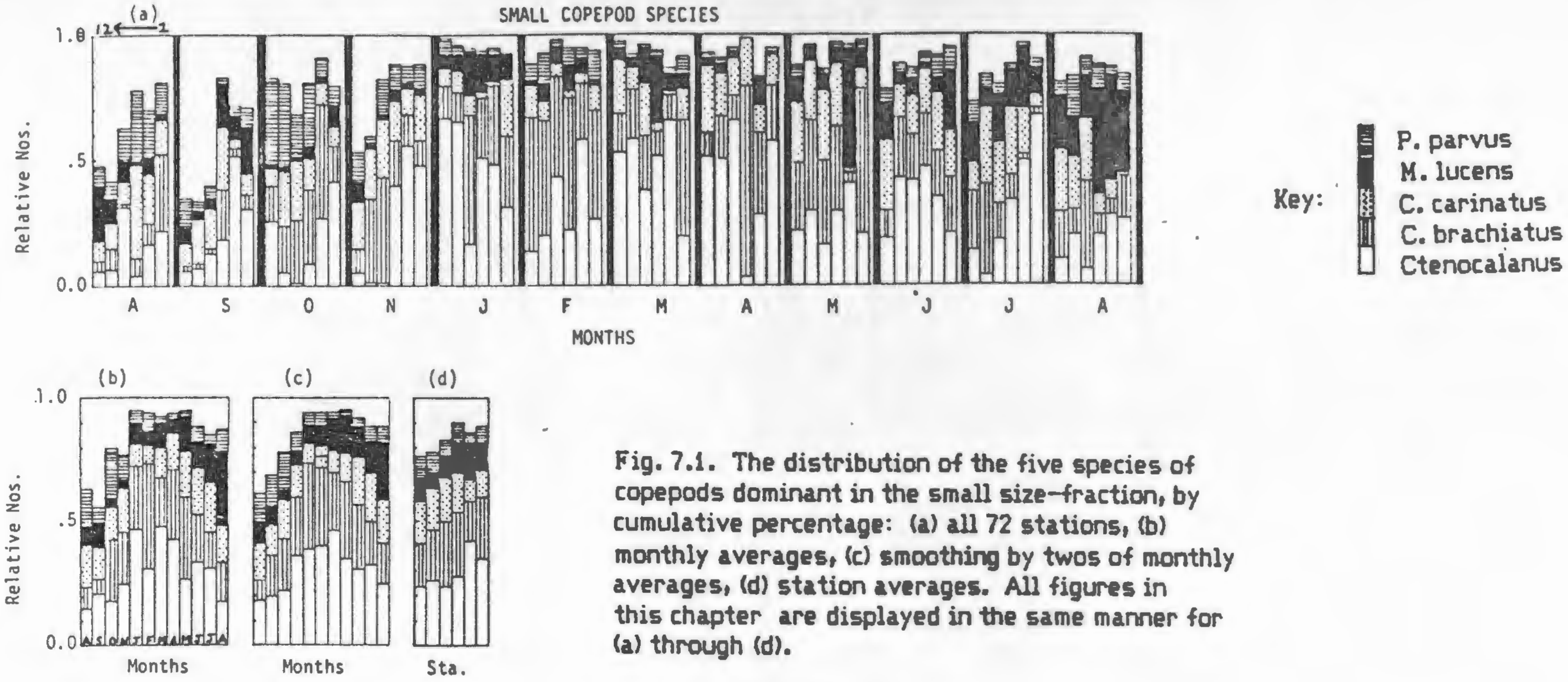


Fig. 7.1. The distribution of the five species of copepods dominant in the small size-fraction, by cumulative percentage: (a) all 72 stations, (b) monthly averages, (c) smoothing by twos of monthly averages, (d) station averages. All figures in this chapter are displayed in the same manner for (a) through (d).

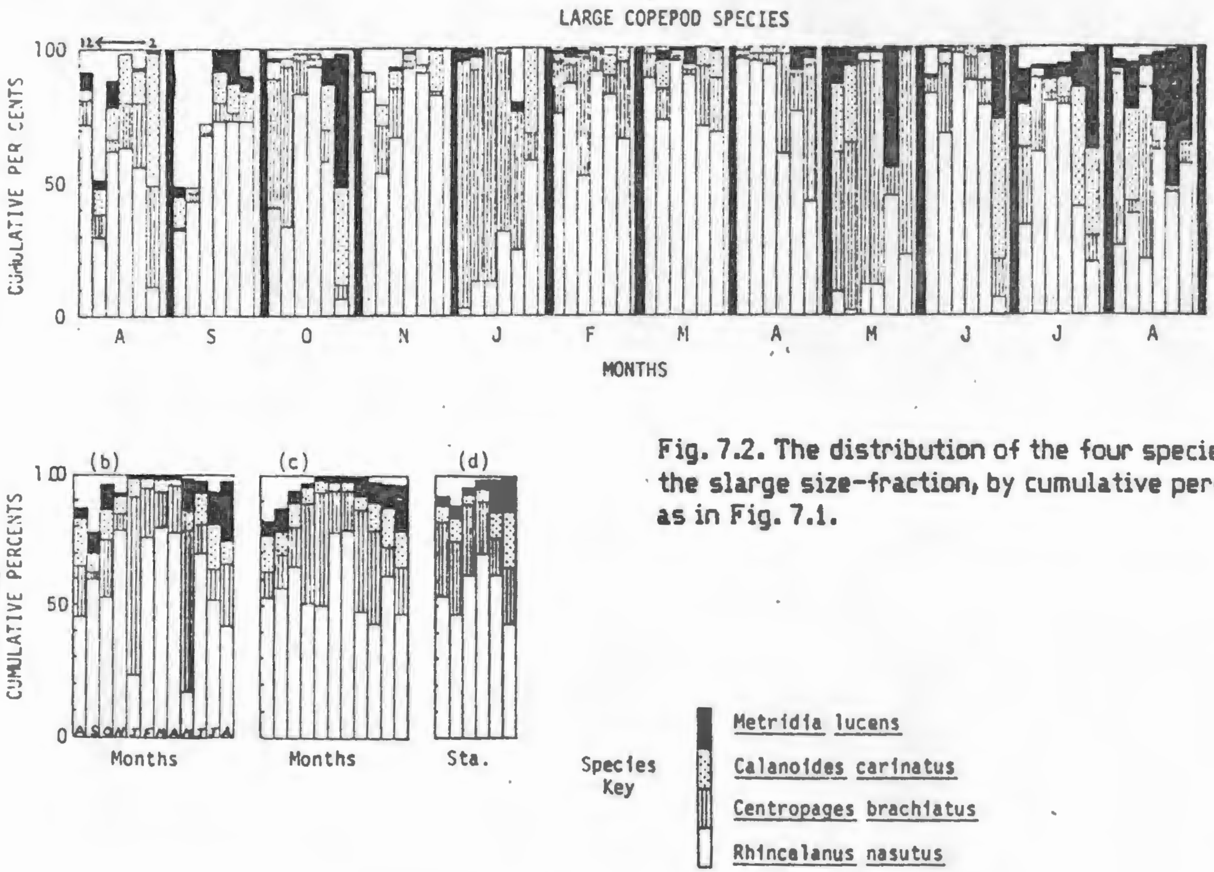


Fig. 7.2. The distribution of the four species of copepods dominant in the slarge size-fraction, by cumulative percentage. Figure explanation as in Fig. 7.1.

CHAPTER VII

NOTES ON THE DOMINANT COPEPOD SPECIES

Introduction

Species diversity was extremely low in the study area, increasing slightly in an offshore direction and in winter. Among the 28 genera represented in the small size-fraction, four to five species comprised an average of 85% (range = 34-99%) of the sample. These were: Ctenocalanus vanus, Paracalanus parvus, Centropages brachiatus, Calanoides carinatus, and Metridia lucens. Of the fifteen genera present in the large size-fraction, the same three species (Rhincalanus nasutus, Centropages brachiatus, and Calanoides carinatus) nearly always dominated the sample year round; a fourth (Metridia lucens) also played a major role in the winter months. Other species occurred either rarely, in very small numbers, or both. Each dominant species was the only representative of its genus.

Figures 7.1 and 7.2 a-d, illustrate the role played by the six dominant species relative to each other and to the rest of the copepod population.

Methods

Methods used in this chapter are the same as those described for Chapter VI.

Results and Discussion

Ctenocalanus vanus

Except for occasional individuals, this species occurred in the small size-fraction only. The exceptions were nearly always males, whose widely-spread antennae made passage through the 1600 m mesh more difficult than for the streamlined females.

Overall, C. vanus was characterized by greatly fluctuating numbers, both spatially and temporally (Fig. 7.3.a-d), and generally greater numbers inshore and in summer. This is in close agreement with the chl "a" distribution pattern, but there was no significant correlation between the two when all 72 samples are compared (r - -.01). Two of the 10 most abundant occurrences were in mixed water, two in upwelled water, and

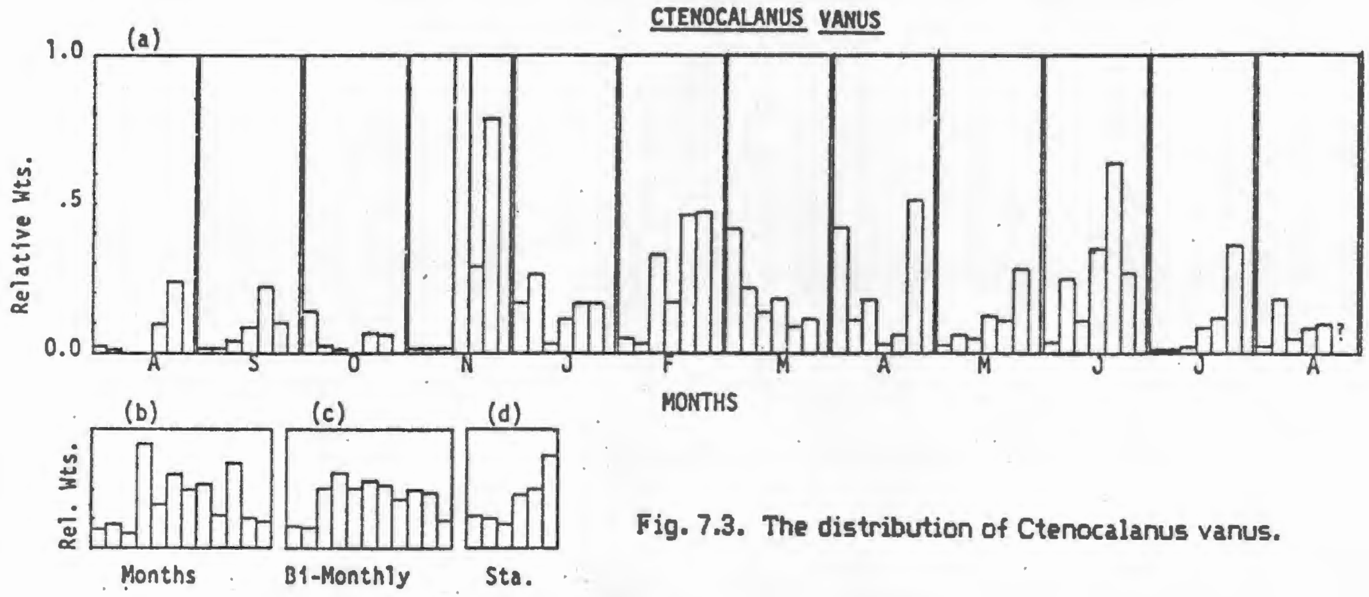


Fig. 7.3. The distribution of Ctenocalanus vanus.

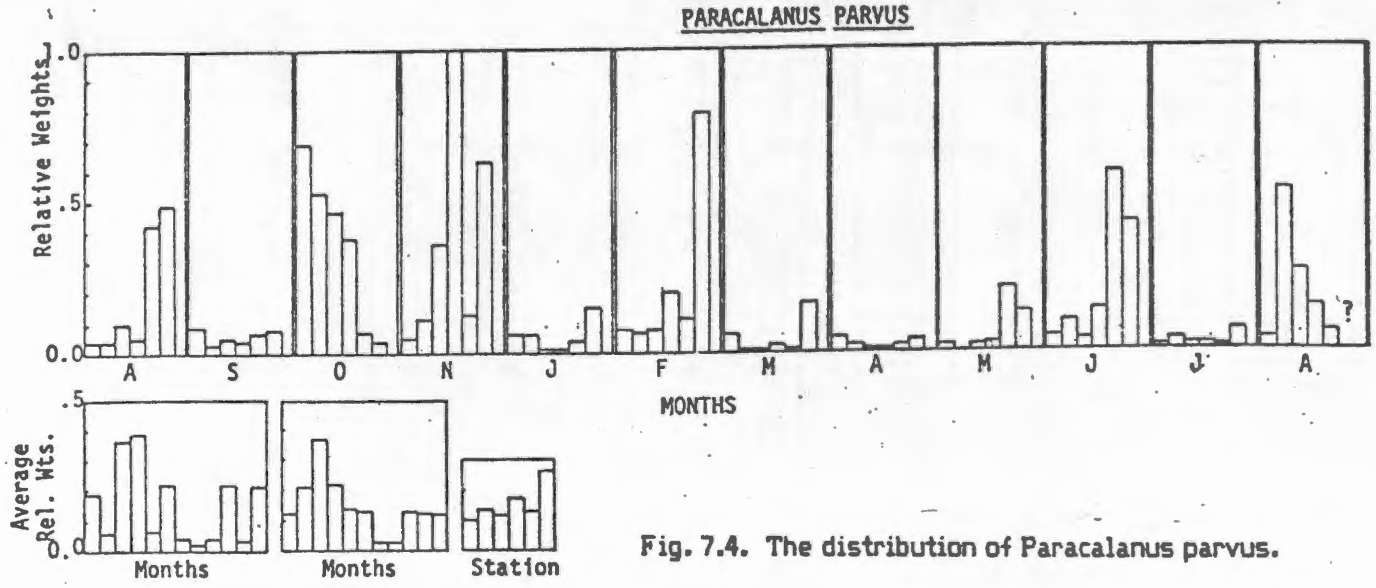


Fig. 7.4. The distribution of Paracalanus parvus.

the remainder in aged upwelled water. Only when samples were pooled and averaged did distinct patterns emerge. This pattern could be attributed both to repeated population increases from new generations and to the effects of wind- and current-induced patchiness. At 26 out of the 72 stations more than a third of the sample was Ctenocalanus, and it comprised up to 66% of the total small zooplankton sample. It was probably the most numerous of all the copepod species in the Lambert's Bay area, although direct numerical comparison with the other most abundant species, Centropages brachiatus and Rhincalanus nasutus, was not possible with this data set. The fact that only adults are caught in the 300um mesh sampling nets suggests that C. vanus are even more important in the area. If anything, these data underestimate the population.

Because of the delay in response to the September phytoplankton increase, it seems most probable that the overwintering population was made up of late juveniles or adults which, with the increase in upwelling intensity, produced the generations that in turn developed into the annual maximum in November. For both C. vanus and P. parvus, described next, a short generation time is probably the most advantageous strategy for reproductive success in an environment characterized by upwelling and patchiness. Neither species showed visible evidence of lipid storage that would permit survival during periods of food scarcity. In species without such mechanisms for energy storage, selection favours generation times shorter than the periods of fluctuation (Hutchinson, 1978).

Paracalanus parvus

This species was the smallest of the dominant copepods, and appeared in the small size-fraction only. P. parvus had a much smaller population size, relative to all of the other species described here, with the exception of the period from August through November (see Fig. 7.1). Fig. 7.4 shows that its spatial distribution to be exceptionally uniform, differing in this regard from C. vanus. It was an early spring species, preceding other small species, in particular Ctenocalanus, with whom it can be assumed to compete for phytoplankton resources. At other times, it maintained a low but steady percentage of the population, with least abundance from March through May. Its maxima occurred more often in mixed water than any other species except small R. nasutus.

The spatial distribution is most easily explained as a susceptibility to physical dispersal. Hutchings (1979) shows P. parvus to be most often found near the surfaces, where it would be most exposed to wind induced water movement in the upper layers. Peaks in the abundance histograms occurred inshore at times of no upwelling and moved offshore in months when southerly winds had blown surface waters offshore, (as determined from temperature profiles). This observation is supported by the findings of Smith et al. (1980), who conclude that "advective effects are extremely important in determining the distribution of Paracalanus parvus" (p. 407). In general, the horizontal distribution of species appears more related to wind and less related to chl "a" distribution and cold, inshore water than was reported for the species by Hutchings (1980) in his description of vertical distribution of this species.

Centropages brachiatus

This species spanned both size-fractions, and in both it was the second most common species. Although this fact made its absolute abundance within the total zooplankton difficult to assess, its appearance in both groups made it easier to observe the passage of age cohorts through time.

As shown in Fig. 7.5 and 7.6, the distribution of Centropages brachiatus was was temporally very similar to that of Ctenocalanus vanus, and also characterized by large temporal and spatial fluctuations in population size. In addition, the two size-fractions showed different distribution patterns. In general, the population of small animals was uniformly high except for midwinter, whereas the large copepods decreased markedly in number during February and March and, to a lesser extent, in July. On average, values were higher in summer than in winter. Two-channel smoothing suggests two major population increases during the year, with the winter/spring peak among the large copepods appearing before that of the small copepods, and the autumn peaks occurring simultaneously. This pattern is explained if the species overwintered as adults, laying eggs when the spring upwelling season began. The large fluctuations may indicate either population bursts in a species with short generation time or physical aggregation and dispersal. Preliminary work by Brownell and Borchers (Sea Fisheries Research Institute, Cape Town) indicates generation times as short as 25-30 days at 12 -

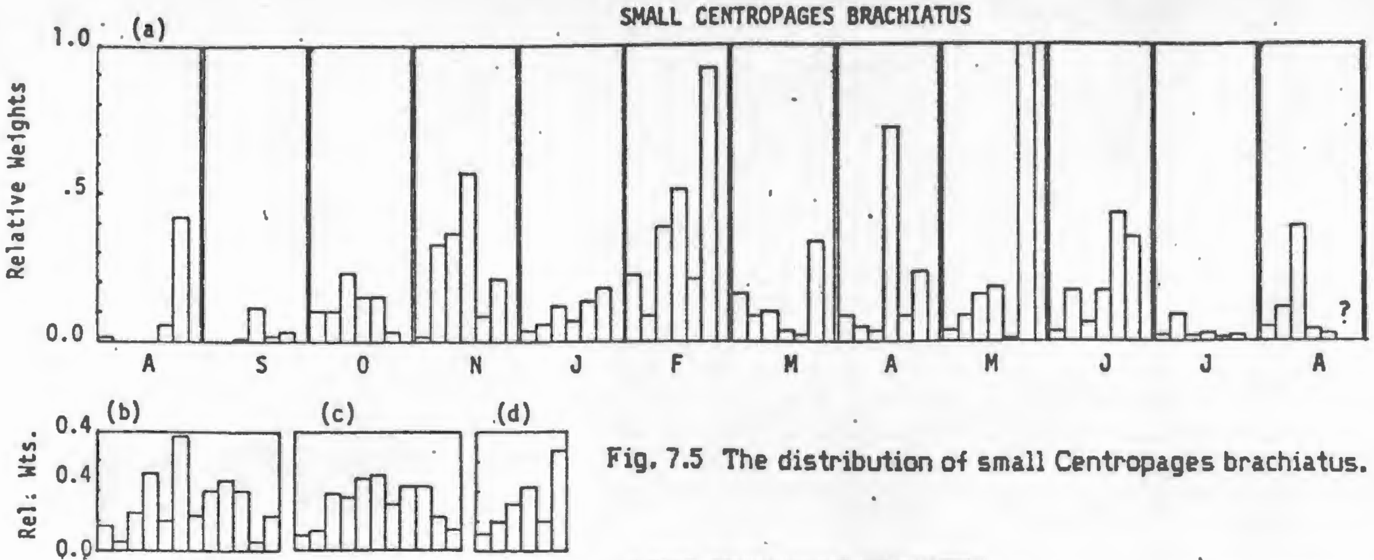


Fig. 7.5 The distribution of small Centropages brachiatus.

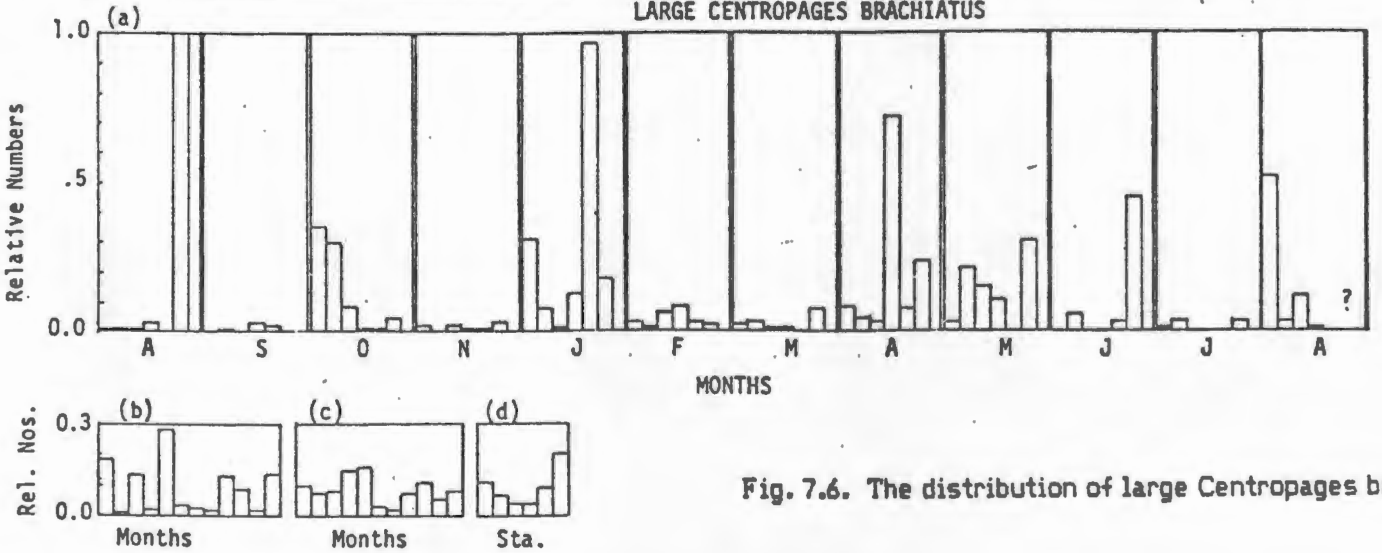


Fig. 7.6. The distribution of large Centropages brachiatus.

Table 7.1. Frequency of occurrence in each water type of the ten most abundant records of the six dominant species. (sm = small. lg. = large).

Species	UW	AUW	MW	WW
C. vanus	2	6	2	0
R. nasutus - small	0	3	6	1
R. nasutus - lg.	1	7	2	0
C. brachiatus - sm.	1	6	2	1
C. brachiatus - lg.	1	5	4	0
C. carinatus - sm.	1	5	4	0
C. carinatus - lg.	3	6	1	0
M. lucens - sm.	1	5	4	0
M. lucens - lg.	1	6	3	0
P. parvus -	1	3	6	0

13° C in laboratory reared animals (Hutchings, pers. comm.), giving some support to the former hypothesis. The bi-annual population increases are more likely to reflect the influence of either food availability or predation pressure, rather than indicating a two-generation per year life cycle. The presence of a spiny carapace in the species suggests the existence of considerable predation pressure.

The small copepods were more common at the middle stations (16-08 and 16-10), although the very high values in February and May at Station 16-02 give that station the biggest average value. Station 16-04 has surprisingly few small Centropages, which may be the result of physical dispersal from the centres of cyclonic gyres. This appears to be the case even in very shallow eddies, and is given support by Hutchings (1979), who reported their greatest abundance in the top 10-20 metres. It appears that this species gains greater ability to control distribution within water types with increased size.

In relation to other small copepods, small C. brachiatus maintained a surprisingly uniform percentage of the sample year round when average values for months and stations are taken (Fig. 7.1,c,d). As a percentage of sample, they are most abundant during autumn and at Stations 16-02, -06, and -08, all stations more prone than others to fronts and density barriers. This is probably due to passive aggregation, but may also be adaptive due to the concomitant concentration of phytoplankton there. Although in biomass they are more abundant in summer than in winter and inshore than offshore, as per cent of sample, they constituted a bigger proportion of small copepods in winter and offshore.

Large individuals of C. brachiatus (Fig. 7.6) showed none of the temporal uniformity of the small individuals, varying in monthly averages from 2.5% to 68%. In January and May they comprised well over half the copepods present. Spatially, however, they were evenly distributed along the study line. They constitute approximately the same proportion of both size-fractions. The two sexes were evenly distributed throughout the large size-fraction.

Both size-fractions showed a strong preference for aged upwelled water, as seen in Table 7.1. It was the only species in which the smaller members of the population were, on average, found in younger water than the adults. No reason is apparent for this

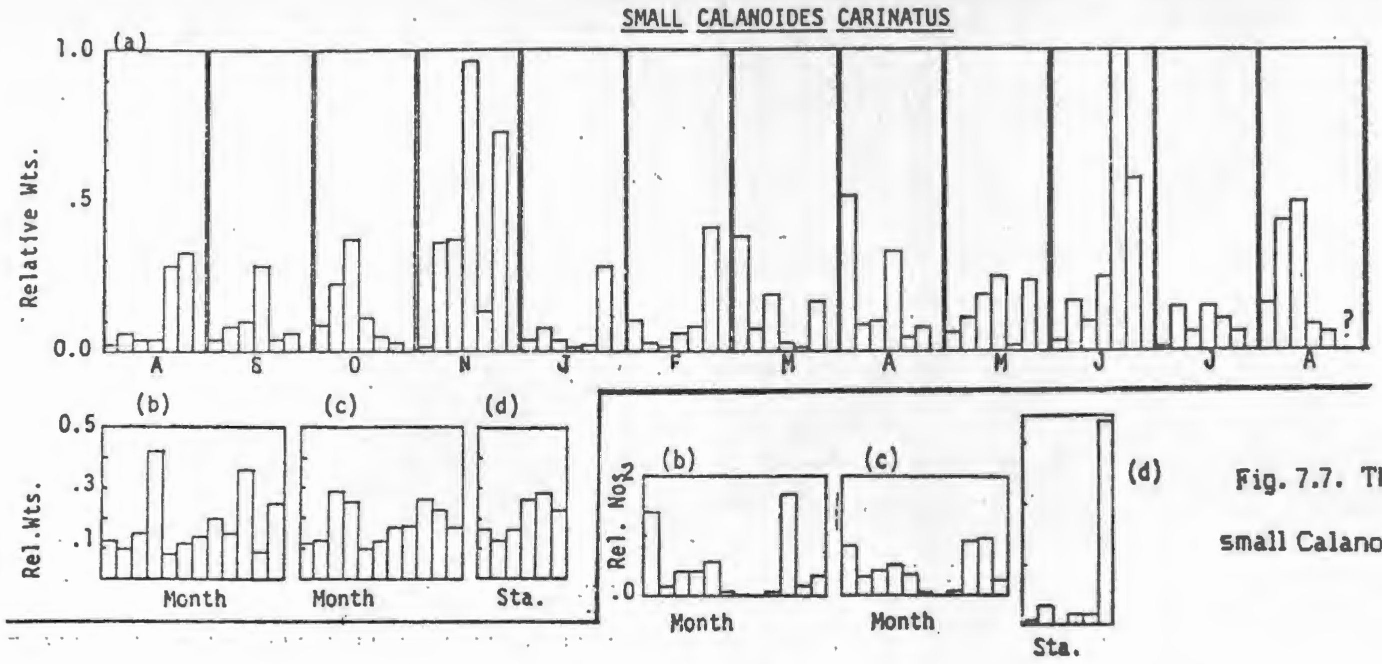


Fig. 7.7. The distribution of small Calanoides carinatus.

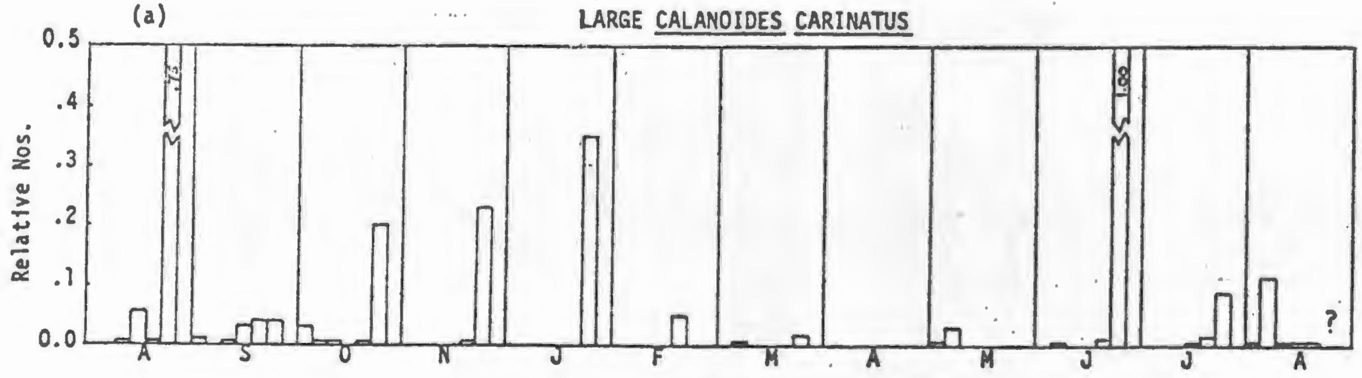


Fig. 7.8. The distribution of large Calanoides carinatus.

reversal.

Calanoides carinatus

As seen in Fig. 7.7, small *C. carinatus* underwent a large November increase following a very uniform, moderate winter population. This short-lived increase preceded a precipitate drop to levels even lower than those of winter, after which came a more gradual, steady increase to a second large peak in June.

Although *C. carinatus* is a large copepod relative to all of the other dominants, with the exception of R. nasutus, its compact shape and positioning of its antennae allow it to pass through the 1600 m mesh smoothly, until its entire body width reaches a specific limiting size. The effect of this morphology was to create a much sharper division of sizes into the two size-fractions. Large *C. carinatus* showed very sharp and distinct peaks of 4- to 5-times the preceding or following month. Their lowest population occurred in autumn, after which there was a steady increase in numbers until an abrupt collapse in January.

The pattern for the two size-fractions, shown in Figures 7.7 and 7.8 suggests a two generation year, although unpublished work by Borchers (Sea Fisheries Research Institute) described generation times of 14-45 days in laboratory reared animals supplied with constant food. Resting stages are almost certainly accomplished by adults or late copepodid stages that lay eggs with the onset of upwelling; the survivors of the generation appear later as a sharp rise in the new adult population in the November increase. The sharp population drop in October may be due to the die-off of adults following the laying of eggs. Smoothing by twos gives an even sharper impression of a two generation year. This would be in keeping with the life cycles described by Marshall and Orr (1972) and others (Heinrich, 1962; Heinle, 1982) for *Calanus finmarchicus* and other closely related species. However, it is contradicted by the laboratory studies of borchers.

Small *C. carinatus* were most abundant at Stations 16-04 and 16-06. Although many species were abundant at the latter, no other species was present in large numbers at the former. Except for this unusual appearance, spatial distribution was fairly uniform across the study line. Large *C. carinatus*, however, contrasted sharply with that pattern

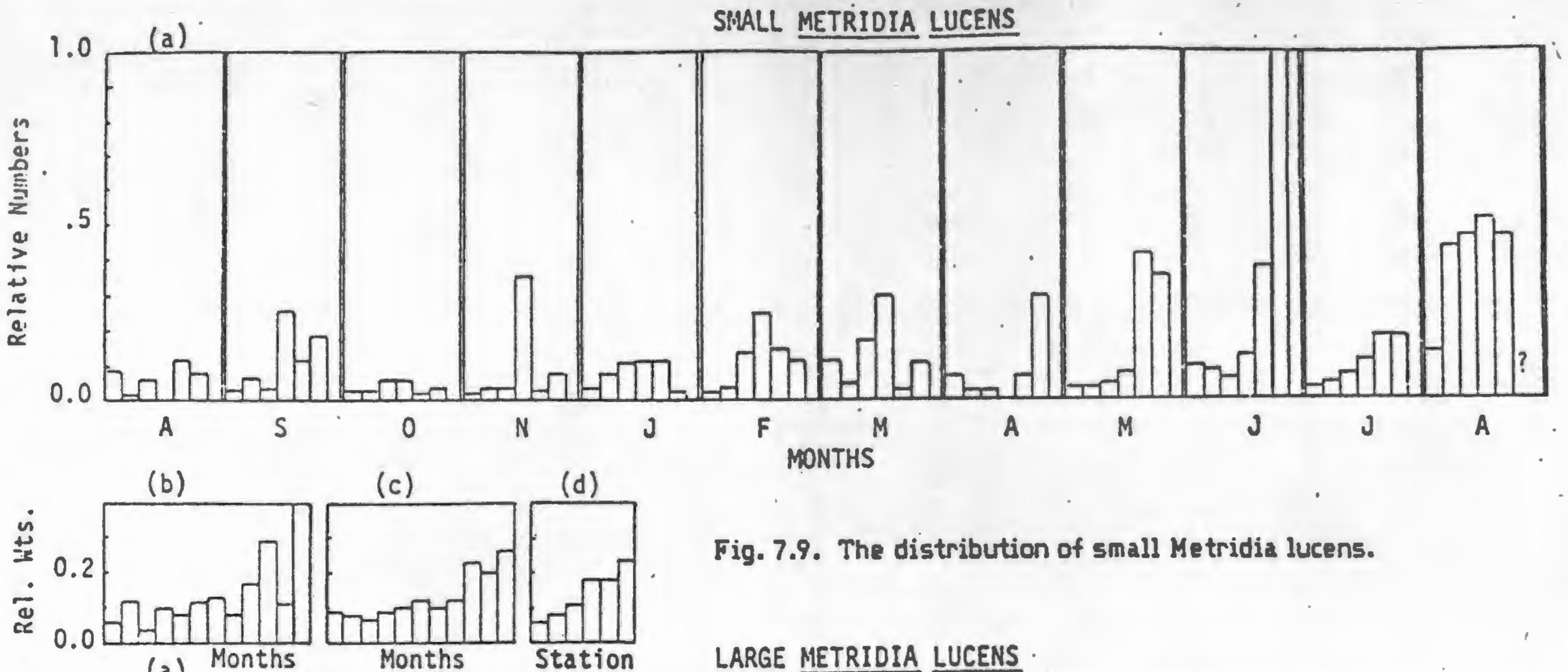


Fig. 7.9. The distribution of small Metridia lucens.

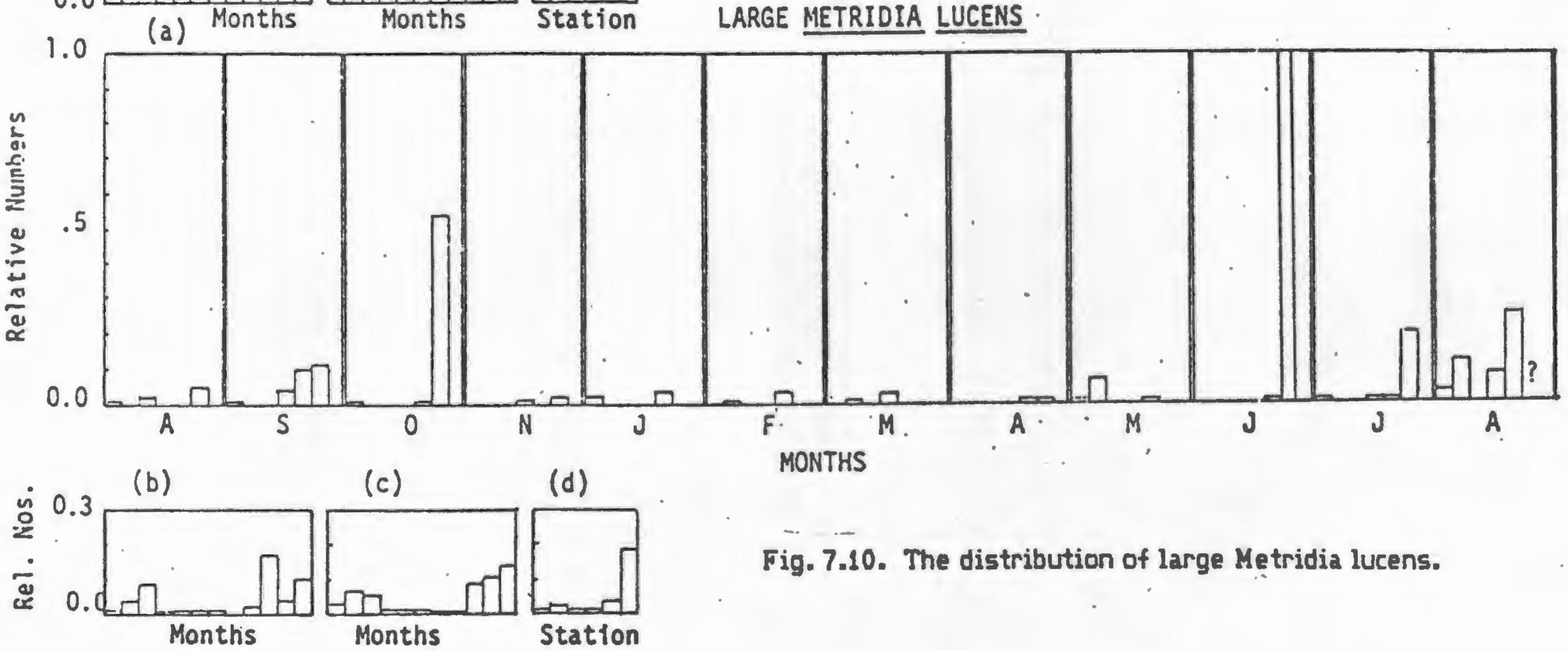


Fig. 7.10. The distribution of large Metridia lucens.

and showed an extremely strong preference for inshore waters, Nearly all monthly maxima for that size-fraction occured there. They were in much smaller numbers at other stations, although those occurrences may have been younger stages that had reached the minimum size necessary for capture. None of the ten maxima for each size-fraction shown in Table 7.1 were strongly associated with cold water and fairly low levels of chlorophyll "a". No maxima are found in WW (warm water); 4 small and 1 large were in MW (mixed water), 5 small and 6 large in AUW (aged, upwelled water), and 1 small and 3 large in UW (upwelled water).

Small C. carinatus were less abundant than either Ctenocalanus or Centropages except during winter and offshore. Large C. carinatus were always much less abundant than Rhincalanus and Centropages except during periods of inshore upwelling when C. carinatus were at their relative peaks. Large members of the species were most abundant relative to other species at the two inshore stations, small members at the 4 offshore stations. There is a movement toward shore with increased size. A facultative carnivory in adults and late copepodids, would allow the maintenance of a population in cold inshore waters, where eggs can be laid simultaneously with upwelling, guaranteeing a ready food supply for young stages as they develop along with phytoplanktion in the moving patch.

Metridia lucens

M. lucens (Figs. 7.9 and 7.10) showed a very different distribution pattern from that of the other dominant species. Both size-fractions were most abundant in winter. Abundance peaks were no associated with vertical migration. An October peak occurred at midday, and other samples of high abundance were scattered throughout the 24-hour day.

In general, the population was relatively uniform, showing few short-term fluctuations. Winter values were approximately double those of summer. Both size-fractions followed essentially the same temporal pattern, allowing for the time delay in peaking attributable to ontogenetic growth. Spatially, the large Metridia, like the large Calanoides, showed a very strong preference for inshore waters and exhibited a five-fold increase at Station 16-02 over the five other stations. Small copepods showed a similar, but more gradual decline to seaward, and had high average numbers at all three

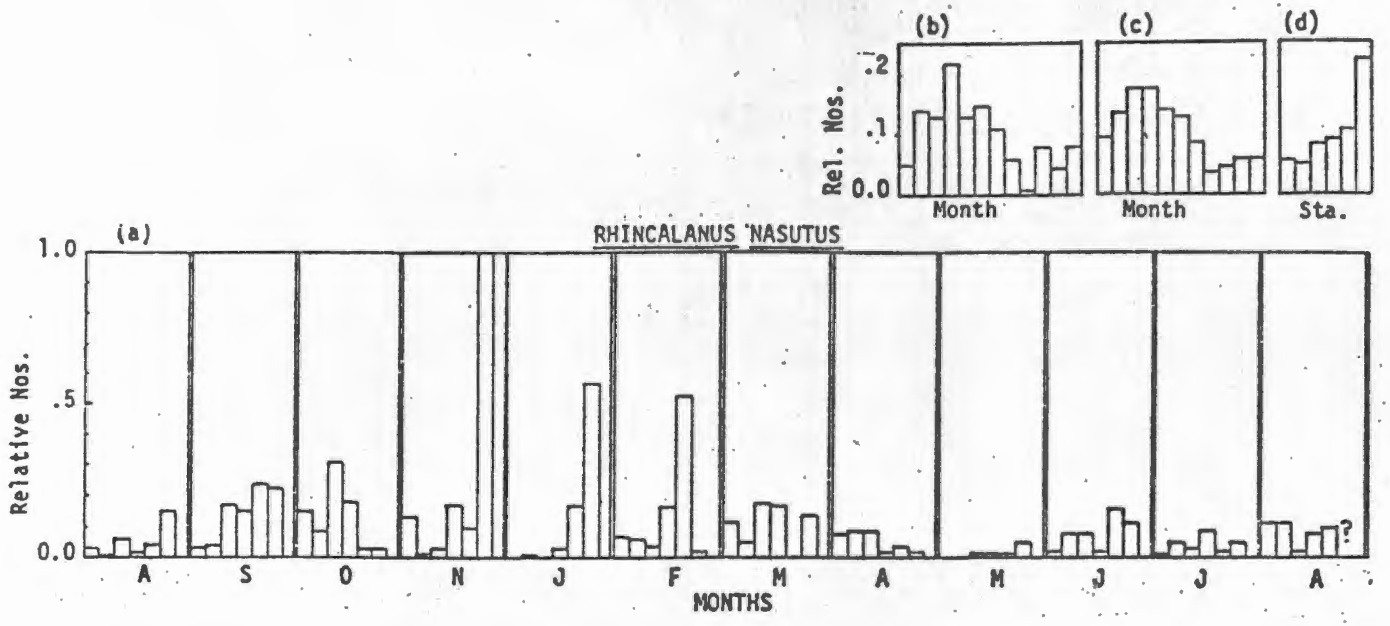


Fig. 7.11. The distribution of Rhincalanus nasutus.

of the inshore stations. Metridia, although present offshore, must be considered primarily an inshore species.

Percentage of sample (see Figs. 7.1 and 7.2) followed the same pattern as for absolute abundance except that the increase in percentage of sample began earlier in the year. Their contribution to the total sample was exceptionally small in the summer months, especially at the inshore stations.

Table 7.1 demonstrates no association between shoreward movement and increased size (age) in Metridia, as occurred in the other species which span both size-fractions. However, the marked sexual dimorphism occurring in this species may explain this absence. Males are much smaller than females, causing a different distribution in the sexes among the two size-fractions, rather than a distribution which is age related. Consequently, it was impossile to determine size-related movement from these samples.

Rhincalanus nasutus

Rhincalanus nasutus was the only species of the genus found in the Lambert's Bay area during the time of this study. R. cornutus was absent, although it was reported as present in the area by De Jager (1954), De Decker (1968), and Unteruberbacher (1964). Hutchings (1979) made no mention of its occurrence in his samples from the area off the Cape Peninsula.

R. nasutus was the strong dominant in the large size-fraction (see Fig. 7.2). It was found in all 72 samples, composing up to more than 60% of all large copepods in over half the samples, reaching a maximum of 98%. There were six occurrences of less than 10% of the sample, but four of these could not be considered reliable indicators, as gelatinous debris clogged the samples making them impossible to count accurately.

Low numbers of R. nasutus appeared in the small size-fraction as nauplii and very early copepodid stages. Only once did it comprise more than 5% of the zooplankton total. All of the 10 most abundant occurrences of R. nasutus occurred in October and November at adjacent stations, strongly suggesting one generation per year, with development beginning inthe spring.

Figure 7.11 a,c shows a clear pattern of seasonal increase and decrease among the large Rhincalanus. A moderate winter population underwent a large spring increase in September, peaked in November, and started to decrease significantly in March. Figure 7.11,d indicates a strong preference for the inshore station, with the population decreasing steadily in an offshore direction. Young individuals, however, were most prevalent farther offshore. Hutchings (1979) reported R. nasutus in cool, deeper water.

Conclusions

In Chapter IV, a list of five factors was presented as evidence for the existence of size-related differences in life-history strategies in Lambert's Bay zooplankton. In summary these were: (1) two different temporal cycles, with the spring increase occurring at different times; (2) preferences for different water types; (3) a wider range of ratios of small-to-large copepods inshore; (4) small fluctuations in large zooplankton abundance, and large fluctuations in small zooplankton abundance; and (5), the existence of wax esters in only the large zooplankton. These characteristics of distribution were then discussed in terms of Heinrich's life history categories (1962) and related to the efficient utilization of food.

In this chapter, the temporal and spatial distribution of copepods and the annual abundance cycles of the dominant species were described. Whereas all of the other aspects listed above continued to suggest the existence of size-related differences, widely varying seasonal cycles were found among copepod species within the same size-group. In addition, the seasonal patterns found among the two size-groups of total zooplankton were not repeated by each of the components of the particular size-group of copepods. All of these factors need further examination..

First, groups of stations identified on the basis of small copepods in Chapter VI (Bray-Curtis) were statistically correlated with water types, whereas those identified on the basis of large copepods were not. At the same time, small copepods ranged more widely over water types than did the large copepods, which showed a very strong preference for inshore stations (Spatial distribution may be, but is not necessarily, closely associated with water types). In all copepod species and in most of the non-copepod groups represented in the samples, there was a movement toward younger and colder water with increased age and size. Although both size-fractions were most abundant at Station 16-02, the small size-fraction diminished in size only gradually in an offshore direction, whereas the large size-fraction dropped abruptly in abundance seaward of Station 16-02. This trend applied both within and between species. Small species were found farther offshore than large species, and the young of small species were found farther offshore than the adults (Centropages brachiatus is a possible exception to this and will be discussed along with comments on predation pressure later in this section).

Considering first the between-species case, small copepod species have three reasons in particular for maintaining at least part of their numbers in offshore waters. First, water is warmer there, allowing faster growth and decreasing time spent in the vulnerable naupliar stages while shortening generation times. Second, the abundance of predators, both copepod and non-copepod, was considerably greater at the inshore stations. Third, the absence of large energy reserves make them vulnerable to periods of intense upwelling when phytoplankton levels fall to very low levels. Large copepod species, however, have fewer invertebrate predators, have longer generation times, and have sizeable energy reserves. The presence of waxy esters in large copepod species reduces their susceptibility to fluctuations in food supply which would be fatal to smaller copepods. Hutchinson (1978) states that in species without mechanisms for energy storage, selection favours generation times shorter than that period of fluctuation. On the other hand, this factor allowed those copepods capable of energy storage greater latitude in generation times, and the increased flexibility in fine-tuning to the environment that is the consequence of a longer life-span. Within species, all of the above factors apply except for the difference in generation times. The desirability of maintaining younger stages in water conducive to rapid growth is probably sufficient reason for the trend seen.

It is easy to see, in this context, the explanation for the changing small-to-large copepod ratios as sampling shifted across water types. Inshore, water types were more sharply defined, with freshly upwelled water strictly the domain of large species, and warmer, stratified water showing almost exclusively small copepod spcies.

In offshore waters conditions were less variable and ratios were more uniform. Consequently, inshore ratios ranged from one extreme to the other, while offshore values stayed close to the middle of the range.

When individual species were examined, short-term fluctuations were found to be characteristic of the three smallest species. This was to be expected in species of probable short generation time and those most susceptible to physical aggregation, by virtue of their small size or preference for surface water (specifically the case in P. parvus, but very likely true in other small copepods as well). The overlapping of generations within species and between species, combined with the intrusion of the young stages of larger species, presented a picture of uniform average distribution over time and large fluctuations within short time periods.

Within the large size-fraction, R. nasutus (with nauplii in evidence only in October and November), and M. lucens (because of its very regular annual abundance cycle), appeared to produce only one generation per year. The distribution of the two size-fractions in C. carinatus , as well as data for sister species, suggests a two generation year. All large species showed a sharp populaton drop in the autumn months, when a sharp thermocline appeared across the sampling line, and generations appeared to become synchronized at that time. The autumn decline was not present in small copepods, suggesting that larger species were subject to some size-related factor not affecting smaller species. This factor was probably predation by recruiting fish, and will be discussed in the concluding chapter.

Although the preceding four characteristics of copepod distribution did not counter the differing size-related life histories suggested by the zooplankton as a whole, the considerable difference between the seasonal cycles of the individual dominant species within each size-group demands closer examination.

Large zooplankton showed the first sizeable increase in September, coinciding with increased upwelling activity. Small zooplankton did not exhibit a similar increase until two months later. The two distinct patterns suggested that individual species would follow the pattern of their size-group when examined individually. This, however, was not the case.

All species, large and small, showed a November increase in the small size-fraction when all stations were averaged. Except for *R. nasutus*, this pattern was not repeated among the large copepods. Consequently, different age categories were involved, e.g., only adults of *C. vanus* and *P. parvus* , late copepodid stages of *C. brachiatus* and *C. carinatus* , and only the youngest copepodids or nauplii in *R. nasutus*. (Sexual dimorphism determines size in *M. lucens*, confusing the age-size relationship; this species showed the smallest November increase.) Because the size range, rather than the growth stage, of each species exhibited the November increase, a more complicated picture emerged than was evident when size alone was examined.

Various interpretations are possible. Strong southerly winds had been blowing for several weeks without a reversal before sampling, causing a very fast-flowing jet to centre over Station 16-06 with accompanying eddies on either side (see Chapter IV). This suggests that the copepods were physically aggregated according to size, an hypothesis supported by the fact that for all species, the peak occurs at Station 16-06. However, in addition to small copepods, a considerable increase in large euphausiids occurred simultaneously, making size-specific aggregation less likely.

Another more likely possibility lies in the predictability of phytoplankton abundance at Station 16-06 at this time of year, as discussed in Chapter III. Because small and young copepods are, in general, more dependent on phytoplankton than larger and older copepods, it is very likely that the dominant species of the area would have evolved life cycles which coordinate the maximum number of the appropriate-sized individuals at the appropriate time. This could apply to euphausiids as easily as to copepods.

Other possible explanations are size-selective predation, which may have allowed the survival of this range of prey, or the chance co-occurence of a number of independent events. However, in combination with other evidence for life histories adapted to upwelling areas, chance seems unlikely as the only explanation. The answer probably lies in a combination of physical aggregation and life history patterns. A significant point, however, is that, although the distribution pattern was size-related and may be the result of life history strategies of the dominant species, it was not a function of the same life cycle being common to all similar-sized copepod species.

In summary, there was sufficient variation in the spatial and temporal distribution of each species to suggest that different species have different life-histories. At the same time, there was also sufficient uniformity in the behaviour of same-sized copepods to indicate that size played an important role in determining the strategies available to a given sized copepod species. Large size allows the enjoyment of certain advantages, e.g. greater energy storage and consequent protection from fluctuations in food availability, longer life spans, a greater choice of possible food items, increased predator protection, and iteroparity with larger eggs. Small size makes possible very short generation times and rapid egg production. Within the limits of their taxon, the copepods of Lambert's Bay appear to exhibit the full range of r- to K-selected life history stategies.

Temporal patterns in small copepods are different from those of large copepods, but it must not be assumed that the same annual cycles apply to each individual component within the size range. Although size-related options dictate the limits of what is possible, there is still a wide range of variation within them. Life history strategies must take into account the desirability of positioning size ranges where they can most effectively utilize the resources of a given time-space niche. The size-related differences in abundance listed in Chapter IV do appear to be indicative of different life history strategies, but at a more complex level than previously indicated. The significance, in an upwelling environment, of the different patterns present among the Lambert's Bay copepods will be discussed in the next chapter.

CHAPTER VIII

CONCLUSIONS

On the basis of the one year of sampling done for this study, and on other wind and current information gathered in subsequent studies (Nelson and Hutchings, in press), upwelling appears to be a nearly constant perennial feature off the coast of Lambert's Bay. The monthly temperature and salinity sections suggest, by the depth to which eddies and fronts extend, less intensity in autumn and winter. This is supported by wind records, which show a marked increase in frequency and strength in southerly winds and a decrease in wind reversals during the spring and summer months. However, it is important to emphasize that this seasonal change is relative and that, even in winter, southerly winds still occurred for half of the month (see Fig III.2). Consequently, in comparison with the major upwelling areas of the California, Oregon, and NW Africa (Cushing, 1969), and with the areas immediately to the south of Lambert's Bay, seasonality is muted and conditions of moderate, nearly constant upwelling are typical of the area. As would be expected under such conditions, phytoplankton levels are also correspondingly high, with chlorophyll "a" maximum (chl "a" max) levels ranging from 1,9 - 29.0 µg/l.

The little variability in zooplankton abundance reflects the perennial nature of upwelling and high phytoplankton abundance with a similar, very uniform, year-round biomass (56.2 - 818.8 g/1000m^3). Total biomass, using average monthly values, showed only a two-fold increase from the least (in January; 113.5 g/1000m^3) to the greatest abundance (in November; 431.3 g/1000m^3). This picture of uniformity was complicated somewhat by the different patterns exhibited by the large and small size-fractions. The small zooplankton followed the same pattern as that described for the total biomass, but the large group showed much more distinct seasonal variation, with winter highs and autumn lows and little of the monthly fluctuation seen in the small size-fraction. This can be explained as a function of the different life histories shown by the major components of each, both copepod and non-copepod.

The major groups of large zooplankton included large copepods, stomatopod larvae, late stages of euphausiids, and large amphipods and chaetognaths. All are at least facultative predators, and all except euphausiids showed a preference for cold inshore water. Small zooplankton (both the adults of small species and the young of larger species), on the other hand, were more often found in phytoplankton-rich, warmer water offshore. This suggests that the breeding members of the large zooplankton are of sufficient size to maintain themselves either entirely through predation, or are able to supplement their diet during times of active upwelling and low phytoplankton abundance through carnivory. Adults can sink to cold water and maintain themselves there until lifted to the surface with upwelled water, where they and their eggs and nauplii are advected offshore along with the surface layers of the water column. Hatching and development of their young occur simultaneously with expansion of phytoplankton stocks in aged, upwelled water (Some species may not eat at all during the adult stage; Marshall and Orr, 1972).

Smaller zooplankton and young members of larger species, more prone to starvation (Dagg, 1977; Borchers, unpublished), were more plentiful in aged upwelled or mixed water where phytoplankton patches are more predictable. The smallest of these groups were more abundant in the surface layers where chl "a" levels were highest (Hutchings, 1980), but also where they and the phytoplankton were subject to the same wind- and current-directed distribution. Although there is evidence that zoo- and phytoplankton are advected at different rates (Andrews and Hutchings, 1980) it can be assumed that there will be some similarity in distribution if both inhabit the same part of the water column. Patchiness, necessary for successful zooplankton feeding (Angel, 1977), is able to develop relatively unhindered in calm, surface waters. Turbulence, and therefore mixing and the break-up of phytoplankton aggregations, are less likely to occur in an area of moderate steady wind, and patches have a longer time in which to develop to a large size. Consequently, gradations occur across the study line in which patches first appear in upwelled water, grow to a large size, and then decline again as water ages. Although phytoplankton levels are always high in this area relative to the California, Oregon, NW Africa, and more southern Benguela regions, herbivorous zooplankton must find and stay with a patch, and be able to survive periods of food shortage between patches. Contact with patches is more probable at the middle stations, where patches have been able to form but are not yet diminished due to grazing and nutrient depletion. It was in these areas that small zooplankton, those most dependent on a constant supply of phytoplankton, were found.

It may be argued that predation, rather than phytoplankton, may be the factor most responsible for the distribution of zooplankton. However, a strong association between increasing size and shoreward movement exists in all groups except one species of copepod (Centropages brachiatus). In addition to the increased probability of finding a phytoplankton patch, another advantage which accrues to young members of large-sized groups in warmer water is the increased rate of growth which occurs there, assuming food is adequate to compensate for increased respiration costs. This minimizes the time spent at sizes more vulnerable to predation and phytoplankton scarcity. Large zooplankton, on the other hand, through their ability to survive longer periods of food scarcity during periods of intense upwelling inshore, are assured of less competition, a readily available food supply for offspring as they develop amidst increasing phytoplankton stocks, and a reduced, energy-saving, metabolic rate in colder water. The benefits from such a distribution suggest that selective pressures are likely to be involved in water preferences.

This does not imply the ability of copepods and other invertebrate groups to swim long distances horizontally. Eddies, counter-currents of varying depths, and the shoreward movement of replacement water during upwelling provide a number of opportunities for animals with an adaptive preference for a particular range of salinity or temperature to find such water through vertical movement. Because of the high reproductive potential (r-max) in copepods and many other small invertebrates, only a small percentage of a population need be successful in locating the right conditions in order for the population to experience its abundance maxima in those places most suited to its development.

In contrast to data compiled by Cushing (1969) and Hutchings (1979), the average standing stock of zooplankton biomass at Lambert's Bay is low compared to other upwelling areas of the world, and within the same ranges as that found by other workers in the Southern Benguela region. However, the season is very long, almost perennial, allowing for greater overall annual production. In addition, large invertebrate predators were always common, and large stocks of pelagic fish under 8-10 cm in length (i.e. those which are dependent upon zooplankton as food; King and McCleod, 1976) are in the area in great numbers from February to June (Crawford, et al., 1980). Pelagic fish stocks are considerably more abundant in the St.Helena Bay-Lambert's Bay area than off the Cape Peninsula, (Centurier-Harris, 1977). Because predatory chaetognaths, amphipods, and stomatopods are common at all other times, standing stocks of zooplankton are kept moderate in spite of the high primary production (see Chapter IV), and turnover times are short. Consequently, it is likely that predation, while keeping biomass down, allows a fast turnover rate (P/B), and hence large secondary production.

Also in comparison with the upwelling area off the Cape Peninsula, the predictability of upwelling has allowed a stable community to develop, if the intricate inter-relationships and niche partitioning found in this study are typical of the usual abundance patterns of its component groups. The occurrence of the abundance maxima of different zooplankton groups and of different species of copepods in distinctly different time-space niches (see Figs. 6.8, 10, 11) could only develop in a predictable and non-catastrophic environment, one regulated by biological as well as physical factors.

It is interesting that all six of the dominant species of Lambert's Bay copepods, and consequently approximately 85% of all copepods in the area through one entire year, fall into only one of the groups recognized by Hutchings (1979) in his 10-day study of Cape Peninsula zooplankton, i.e. that group associated with cold, upwelled water. That fact alone suggests that, in comparison to the area off the Peninsula, Lambert's Bay is extremely uniform. Whereas the more southerly upwelling zone had a total of 65 species of copepods and many groups of non-copepods among the zooplankton of this size-range, Lambert's Bay had only 29, with only 6 present in appreciable numbers for any extended period of time, and very few non-copepod groups other than the chaetognaths, euphausiids, amphipods, and stomatopods mentioned above.

One would expect, in the light of ecological theory relating stability and species diversity (Sanders, 1969; Gould, 1981), that the reverse situation would exist between the two areas. However, in addition to the fact that Hutchings sampled in an area with a narrow shelf and thus his sampling line crossed the oceanic front, the rapid "flushing" of the Cape Peninsula area brings in species from other areas - the Agulhas bank and the oceanic front - which, although they do not occur in large numbers, increase species diversity. This is not the species diversity associated with a static environment, but rather a diversity created by transient habitats. In Lambert's Bay, relative stability has allowed the beginnings of a specialization into different ecological niches even though, considering the entire environmental stability spectrum, the environmental conditions do fluctuate.

Although all species from Lambert's Bay also occurred off the Cape Peninsula, the preponderance of species within various categories changed considerably from south to north - from small species to large species, from herbivorous species to carnivorous species, and from short generations to longer generations. This trend toward the specialized end of the r-K continuum can be explained as a shift in the optimum strategy as environmental conditions become more stable.

The Cape Peninsula is prone to marked seasonality in wind regime and, in consequence, upwelling. Very rapid rates of upwelling (30-40 m/day: Andrews and Hutchings, 1979) have been recorded there. The strong winds and subsurface canyons create a jet which is forced close to the Cape Peninsula coast, cutting off transport to the west during times of strong south-easterly winds, but also carrying species common to the Agulhas Bank into the area. Warm water intrusions during times of northwesterly winds carry with them species from beyond the oceanic front. The extremely strong southerly winds cause turbulence and mixing which commonly break up phytoplankton patches before they are able to be fully exploited, and advect plankton northward. In general, the Cape Peninsula is an unstable, turbulent area compared to the relatively tranquil Lambert's Bay region, with its perennial gentle winds, moderate but steady upwelling, gently sloping bottom, and large eddies (see Chapter

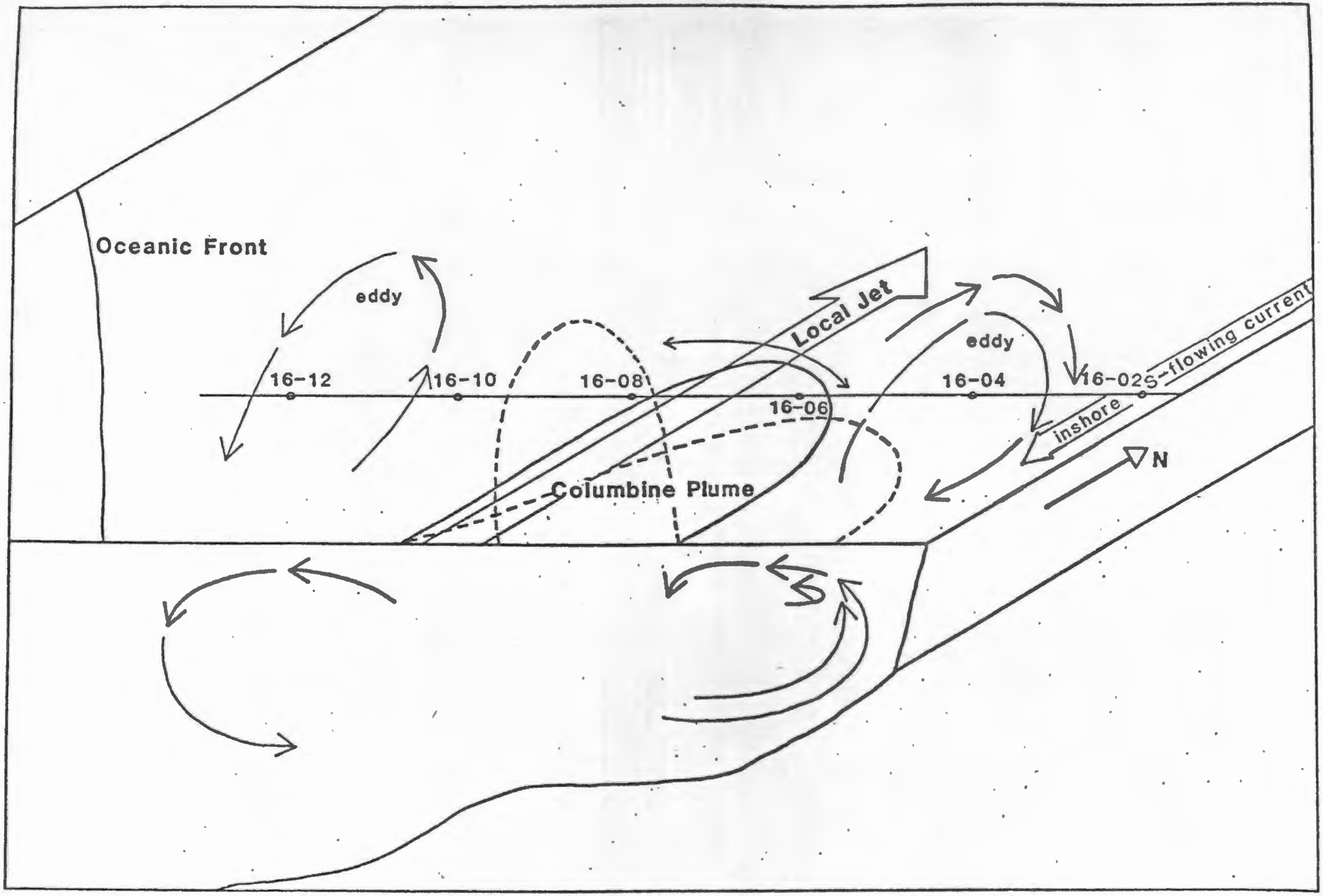


Fig. 8.1. A probable model for circulation within Lambert's Bay.

III) which recirculate much of the plankton within the same area. This is reflected in the patterns of seasonal abundance of zooplankton. Figure VIII.1 shows a stylized circulation map of the area, postulated from the physical and zoological evidence presented in this thesis.

The dominant species from both regions are well adapted to the environment in which they live. Where conditions are favourable only sporadically, as off the Cape Peninsula, it is advantageous to reach reproductive age as quickly as possible. Less energy should be spent in predator avoidance, either spatial, temporal, or morphological, because population control is exerted more strongly from physical conditions than from biological ones. More uniformity in life history would be expected among species in such an area, because harsh conditions allow few variations from extreme r-selection. However, when conditions are predictable, and changes in intensity and frequency of upwelling are not so strong as to be catastrophic, there is more opportunity for selection to operate on populations and for niche partitioning to occur. It is then that species with long generation times, carnivorous habits, means of energy storage, and more possibilities for predator evasion (larger size, stronger vertical migration, and defensive morphological features) become more predominant. Predator-prey interactions become more complicated, and predators become a stronger force in controlling population size.

All of these factors combine to make Lambert's Bay an area of importance, both biologically and economically. Biologically, it offers a set of conditions which allows the observation of the early stages in the transition from an unstable to a more stable environment. Economically, it offers a set of conditions ideal for the nursery ground of pelagic shoaling fish. This study has been aimed at increasing the understanding of both.

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Appendix A

RxC Test for Independence, using G - test (Sokal and Rohlf, 1969; 599-600).

Chl "a" Max vs. Water Type, frequency of occurrence

Water type	Chl "a" max (in $\mu g/l$)				Totals
	< 3.0	3.0 - 6.9	7.0 - 10.9	>11.0	
UW	1	2	1	0	4
AUW	1	17	7	10	35
MW	8	11	4	3	26
WW	3	4	0	0	7
Totals	13	34	12	13	72 = n

G = 2[(Σf ln f for cell frequencies) - (Σf ln f for row and column totals) + n ln n

df = (a - 1)(b - 1) a = rows, b = columns; df = 9

f_i	$f_i \ln f_i$	$f_a \ln f_a$	$f_b \ln f_b$
1	0	5.545	33.344
2	1.386	124.437	119.896
1	0	84.711	29.819
0	0	13.621	33.344
1	0	228.314	216.403
17	48.165		
7	13.621		
10	23.026		
8	16.636		
11	26.377		
4	5.545		
3	3.296		
3	3.296		
4	5.545		
0	0		
0	0		
	= 146.893		

$f_n \ln f_n = 307.920$

$G = 20.192 > \chi^2_{.01\ [9]}$; $P \approx 1.0\%$

APPENDIX B

ENVIRONMENTAL DATA

Mo.	Sta.	W.Type	M3Filt.	Sf.Sal.	Sf.Temp.	Chl"a"
A77	16-02	Auw	79.2	34.92	13.4	4.7
	-04	Mw	165.02	35.03	14.2	2.6
	-06	Mw	92.41	35.15	14.8	2.0
	-08	Ww	228.13	35.22	15.1	1.9
	-10	Ww	223.08	35.27	15.4	2.4
	-12	Ww	265.52	35.27	15.4	1.7
Sept	-02	Auw	184.33	34.74	13.9	12.0
	-04	Auw	213.26	34.69	13.8	10.6
	-06	Mw	194.69	35.03	14.4	7.4
	-08	Ww	217.49	35.35	15.6	3.8
	-10	Ww	181.26	35.42	16.2	3.3
	-12	Ww	213.7	35.42	16.3	3.6
Oct	-02	Uw	155.12	34.81	11.39	5.5
	-04	Auw	183.32	34.88	13.7	28.3
	-06	Auw	174.87	34.97	14.7	23.5
	-08	Mw	230.72	25.09	14.5	8.5
	-10	Mw	213.86	35.17	14.6	4.5
	-12	Mw	240.36	35.07	14.0	20.0
Nov	-02	Auw	171.83	34.82	15.3	29.0
	-04	Auw	253..57	34.83	14.9	7.2
	-06	Mw	288.58	34.80	15.3	12.8
	-08	Ww	269.13	35.21	17.2	4.3
	-10	Mw	240.69	35.19	17.1	2.6
	-12	Mw	193.87	35.15	16.2	2.4
Jan	-02	Uw	237.49	34.78	11.0	2.1
	-04	Auw	307.27	34.87	14.1	5.2
	-06	Mw	279.06	34.89	16.0	2.1
	-08	Mw	292.43	34.93	15.9	3.7
	-10	Mw	301.39	34.92	16.9	9.9
	-12	Mw	199.77	34.90	16.5	6.4
Feb	-02	Auw	252.07	34.77	15.2	17.3
	-04	Auw	254.52	34.75	17.0	7.6
	-06	Auw	216.47	34.82	17.4	7.0
	-08	Auw	210.92	34.83	17.0	6.4
	-10	Mw	248.76	34.94	18.9	3.7
	-12	Mw	273.64	34.93	19.6	2.5
Mar	-02	Auw	198.58	34.83	16.2	17.0
	-04	Auw	178.75	34.75	15.2	6.7
	-06	Auw	267.56	34.78	16.75	6.4
	-08	Auw	252.44	34.76	17.2	8.6
	-10	Auw	178.22	34.85	17.2	13.9
	-12	Auw	185.70	34.89	17.8	10.4

Apr	-02	Auw	113.19	34.93	15.5	18.1
	-04	Auw	227.78	34.96	14.4	5.5
	-06	Auw	251.75	34.99	15.8	4.4
	-08	Mw	293.72	35.01	15.4	7.8
	-10	Mw	257.88	35.01	15.0	6.4
	-12	Mw	179.34	35.1	15.6	5.6
May	-02	Auw	167.98	34.85	13.2	13.0
	-04	Auw	196.78	34.87	14.3	4.4
	-06	Auw	225.59	34.90	15.2	3.4
	-08	Auw	254.19	34.93	15.2	2.6
	-10	Auw	295.72	34.90	15.1	1.9
	-12	Auw	197.24	34.96	14.8	4.8
Jun	-02	Auw	210.11	34.87	12.8	6.8
	-04	Uw	215.42	34.84	12.3	8.2
	-06	Auw	250.46	34.84	13.2	5.4
	-08	Auw	281.74	34.88	13.1	3.3
	-10	Auw	213.27	34.86	12.9	5.0
	-12	Mw	273.66	35.08	14.4	3.0
Jul	-02	Uw	136.28	34.8	11.5	6.6
	-04	Auw	234.23	34.89	12.1	6.0
	-06	Auw	232.17	34.91	12.1	3.5
	-08	Mw	179.5	35.04	13.2	3.3
	-10	Mw	342.5	35.05	13.3	3.3
	-12	Mw	211.59	35.1	13.7	2.1
Aug78	-02	Auw	?	34.85	13.0	4.6
	-04	Auw	284.53	34.88	13.0	11.4
	-06	Mw	234.78	35.0	13.3	16.1
	-08	Mw	344.58	35.03	13.7	3.2
	-10	Mw	368.09	35.06	13.9	3.4
	-12	Mw	319.72	35.16	14.3	1.8

Appendix C

Zooplankton Biomass, Categorized by Size
(in grammes/1000 m water filtered)

Month	Sta.	Small	Large	Total	gC/m^2
Au-77	16-02	262.0	102.8	364.8	2.0
	-04	170.1	39.9	210.0	1.2
	-06	125.6	57.9	183.6	1.0
	-08	65.7	28.1	93.9	0.5
	-10	84.2	25.9	110.1	0.6
	-12	90.3	22.2	112.5	0.6
Sept	16-02	82.8	221.4	304.2	1.7
	-04	113.6	163.6	277.2	1.6
	-06	119.1	139.4	258.5	1.5
	-08	121.8	29.4	151.2	0.8
	-10	73.5	34.1	107.6	0.6
	-12	79.0	37.6	116.6	0.7
Oct	16-02	39.7	242.7	282.4	1.6
	-04	83.3	49.9	133.2	0.7
	-06	131.1	77.3	208.4	1.2
	-08	205.1	82.4	287.5	1.6
	-10	126.3	54.8	181.1	1.0
	-12	176.0	46.9	222.9	1.3
Nov	16-02	377.6	135.9	513.6	2.9
	-04	124.2	40.8	165.0	0.9
	-06	615.7	203.0	818.8	4.6
	-08	224.3	23.8	248.1	1.4
	-10	178.5	22.8	201.3	1.1
	-12	61.2	39.8	101.0	0.6
Jan	16-02	125.2	114.9	240.0	1.3
	-04	85.8	52.7	138.5	0.8
	-06	65.2	19.4	84.5	0.5
	-08	50.9	20.9	71.8	0.4
	-10	107.4	20.4	127.8	0.7
	-12	59.6	28.7	88.4	0.5
Feb	16-02	398.1	30.2	428.4	2.4
	-04	180.7	157.2	337.9	1.9
	-06	182.8	39.4	222.1	1.2
	-08	182.2	31.0	213.2	1.2
	-10	36.1	31.6	67.7	0.4
	-12	76.8	59.0	135.8	0.8
Mar	16-02	139.8	47.1	186.9	1.1
	-04	33.2	35.0	68.2	0.4
	-06	81.5	73.2	154.7	0.9
	-08	89.7	37.4	127.1	0.7
	-10	85.7	34.4	120.1	0.7
	-12	183.0	29.4	212.4	1.2

Month	Sta.	Small	Large	Total	
Apr	16-02	210.1	62.0	272.1	1.5
	-04	48.0	35.0	83.0	0.5
	-06	183.6	33.8	217.4	1.2
	-08	74.9*	24.8*	99.7*	0.6
	-10	53.8	29.5	83.3	0.5
	-12	198.8	51.7	250.5	1.4
May	16-02	321.6	38.6	360.2	2.0
	-04	66.2	53.3	119.5	0.7
	-06	133.4	22.4	155.8	0.9
	-08	80.5	26.7	107.2	0.6
	-10	55.2	24.8*	80.0*	0.5
	-12	34.0	21.6*	55.6*	1.4
Jun	16-02	309.1	99.4	408.6	2.3
	-04	440.6	30.8	471.4	2.6
	-06	171.0	24.9	195.6	1.1
	-08	114.8	19.1	133.9	0.8
	-10	167.8	30.2	198.0	1.1
	-12	68.7	18.5	87.2	0.5
Jul	16-02	145.8	108.1	253.9	1.4
	-04	59.4	31.2	90.6	0.5
	-06	76.7	72.3	149.0	0.8
	-08	50.1	31.9	82.0	0.5
	-10	91.7	16.9	108.6	0.6
	-12	30.8	25.4	56.2	0.3
Au-78	16-02	?	?	?	?
	-04	92.1	92.5	184.5	1.0
	-06	97.3	403.2	500.5	2.8
	-08	213.6	21.7	235.3	1.3
	-10	210.4	57.3	267.7	1.5
	-12	64.2	22.0	86.2	0.5

* indicates that the value is in question, usually because large amounts of algae of fragments of tunicates or cnidarians have clogged the nets and filters.

1. gC/m = wet wt./17.8

Appendix D

R x C Test for Independence, using G - Test (Sokal and Rohlf, 1969; 599 - 600).

Station Groups (based on Bray-Curtis similarity measure) vs. Water Types (defined in Appendix B).

	Station Groups				
Water Type	A	B	C	D	Totals
UW	1	3	0	0	4
AUW	2	27	5	0	34
MW	0	15	11	0	26
OW	0	0	2	5	7
Totals	3	45	18	5	71 = n

$G = 2[(\Sigma f \ln f$ for cell frequencies$) - ($ $f \ln f$ for row and column totals$) + n \ln n]$

df = (a - 1)(b - 1) a = rows, b = column; df = 9

f_i	$f_i \ln f_i$
1	0
3	3.296
0	0
0	0
2	1.386
27	88.988
5	8.047
0	0
0	0
15	40.621
11	26.377
0	0
0	0
0	0
2	1.386
5	8.047
	= 178.348

$f_a \ln f_a$	$f_b \ln f_b$
5.545	3.296
119.896	171.300
84.711	52.027
13.621	8.047
223.773	234.670

$f_n \ln f_n = 302.650$

$G = 45.11 > \chi^2_{.005\,[9]}$; P<0.5%

The null hypothesis, that the species composition of a given station is independent of water type, is rejected.

Appendix E

R x C Test for Independence, using the G - Test (Sokal and Rohlf, 1969; 599 - 600).

Station Groupings based on Species Composition
vs.
Water Types (see Appendix B)

Large Copepods

Water Types	Station Groupings A	B	C	D	Totals
UW	1	3	0	0	4
AUW	4	22	5	3	34
MW	0	16	7	3	26
OW	0	6	0	1	7
Totals	5	47	12	7	71 = n

G = 2[(f ln f for cell frequencies) - f ln f for row and column totals) = n ln n]

f_i	$f_i \ln f_i$	$f_a \ln f_a$	$f_b \ln f_b$
1	0	5.545	8.047
3	3.296	119.896	180.957
0	0	84.711	29.819
0	0	13.621	13.621
4	5.545	223.773	232.444
22	68.003		
5	8.047		
3	3.296		
0	0		
16	44.361		
7	13.621		
3	3.296		
0	0		
6	10.751		
0	0		
1	0		
	160.216		

$f_n \ln f_n = 302.650$

$G = 2(160.216 - 223.773 - 232.444 + 302.650) = 13.30 > \chi^2_{0.1\ [9]}$;

$P \approx 20\%$

The null hypothesis, that the species compositions of stations (large size-fraction) is independent of water type, is not rejected.