DISTRIBUTION AND POPULATION DYNAMICS OF <u>EUPHAUSIA LUCENS</u> (EUPHAUSIACEA) IN THE SOUTHERN BENGUELA CURRENT

BY

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DECLARATION

All counts and identification of preserved material were carried out by myself including the laboratory experiments on live specimens which formed the basis of the growth and development study in Chapter 3. Dr V Stuart was largely responsible for the laboratory experiments on live specimens which are presented in Chapter 6 of this thesis. The zooplankton review (Chapter 2) is a section of a paper by Dr V Shannon and myself entitled, "The Benguela Ecosystem. 3. Plankton", published in 'Oceanography and Marine Biology. An Annual Review. Vol.23'. I was entirely responsible for the section presented in this thesis. Chapters 3 and 4 are published papers written by myself, and Chapter 5 and 6 are collaborative works by Dr V Stuart and myself, and have been submitted for publication. For presentation purposes the references of both published and unpublished material are listed together. In all other respects I lay claim to concepts, hypotheses and conclusions contained in this thesis.

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ABSTRACT

The thesis first reviews the research on zooplankton ecology in the Benguela system and then evaluates the contribution of euphausiids to the zooplankton biomass of the southern Benguela region. The study further investigates the population dynamics and maintenance of the dominant euphausiid, Euphausia lucens, principally in the St Helena Bay region because of its importance as a recruitment area for the pelagic fishery.

On the basis of night-time Bongo net collections taken monthly between August 1977 and August 1978 off the west and south-west coasts of South Africa, the temporal and spatial patterns of euphausiid and copepod biomass (mg dry wt.m^{-2}) were examined. Biomasses of both euphausiids and copepods were higher on the west coast than on the Agulhas Bank and monthly variations within each group differed between these two areas. Euphausiid biomass did not show seasonal changes characteristic of the west coast upwelling areas; however, copepod biomass showed an apparent seasonal pattern in the Cape Peninsula area with maximum abundances in late spring and summer (November to March) which is the major upwelling season. During this period there is evidence of offshore displacement of copepods in the St Helena Bay/Cape Columbine area as a consequence of upwelling events.

From laboratory experiments, a mixed algal (Tetraselmis) and animal (Artemia nauplii) diet produced slightly faster growth in E.lucens larvae than did a pure algal or animal diet. The intermoult period was 3-4 days, being independent of the age of the larvae. The ontogeny of E.lucens followed two main pathways of development being independent of feeding conditions.

Data drawn from two lines of stations from the coast to approximately 90km offshore of St Helena Bay showed that gravid females (stage IV) and young larvae of E.lucens were present throughout the year, thereby suggesting continuous breeding. Spawning was most intense from August to October (late winter to early spring) just prior to the onset of upwelling and the associated increase in phytoplankton. Recruitment was high through to early summer and decreased to a low level throughout autumn and early winter (February to June). The proportion of gravid females increased with distance despite relatively low chlorophyll a concentrations offshore. It is inferred from the high frequency of gravid females in the population that multiple spawning occurs and is in the order of approximately one batch of eggs.$female^{-1}$.$month^{-1}$.

The growth rate of larvae and juveniles of E.lucens from laboratory studies ranged from 0.131 to 0.047 mm.d^{-1} and from monthly size-frequency distribution the growth rate for adults was estimated to be 0.026 mm.d^{-1}. The mean annual biomass in the St Helena Bay region ranged from 9.75-47.29 mg.dry wt.m^{-3}, with highest biomass inshore. Production due to growth was estimated to be 92.71-185.60 mg dry wt.m^{-3}.$year^{-1}$, while moult production varied between 60.01 and 281.38 mg dry wt.m^{-3}.$year^{-1}$. Production of eggs ranged from 5.07-12.39 mg dry wt.m^{-3}.$year^{-1}$, the lowest value being obtained in the inshore region. Moult production was six times the mean biomass while the P/B ratio for flesh production varied from 3.92-8.91, the highest ratio being obtained in the offshore region. Total P/B ratios ranged from 10.14 to 16.01.

The ontogenetic migration of E.lucens, whereby eggs and nauplii remain in the near-surface layer, is different from the developmental ascent which is characteristic of oceanic species. The exploitation of differential current regimes between shallow and deep water by different developmental stages may be important mechanisms whereby E.lucens populations can be maintained within the southern Benguela system.

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CHAPTER 1

GENERAL INTRODUCTION

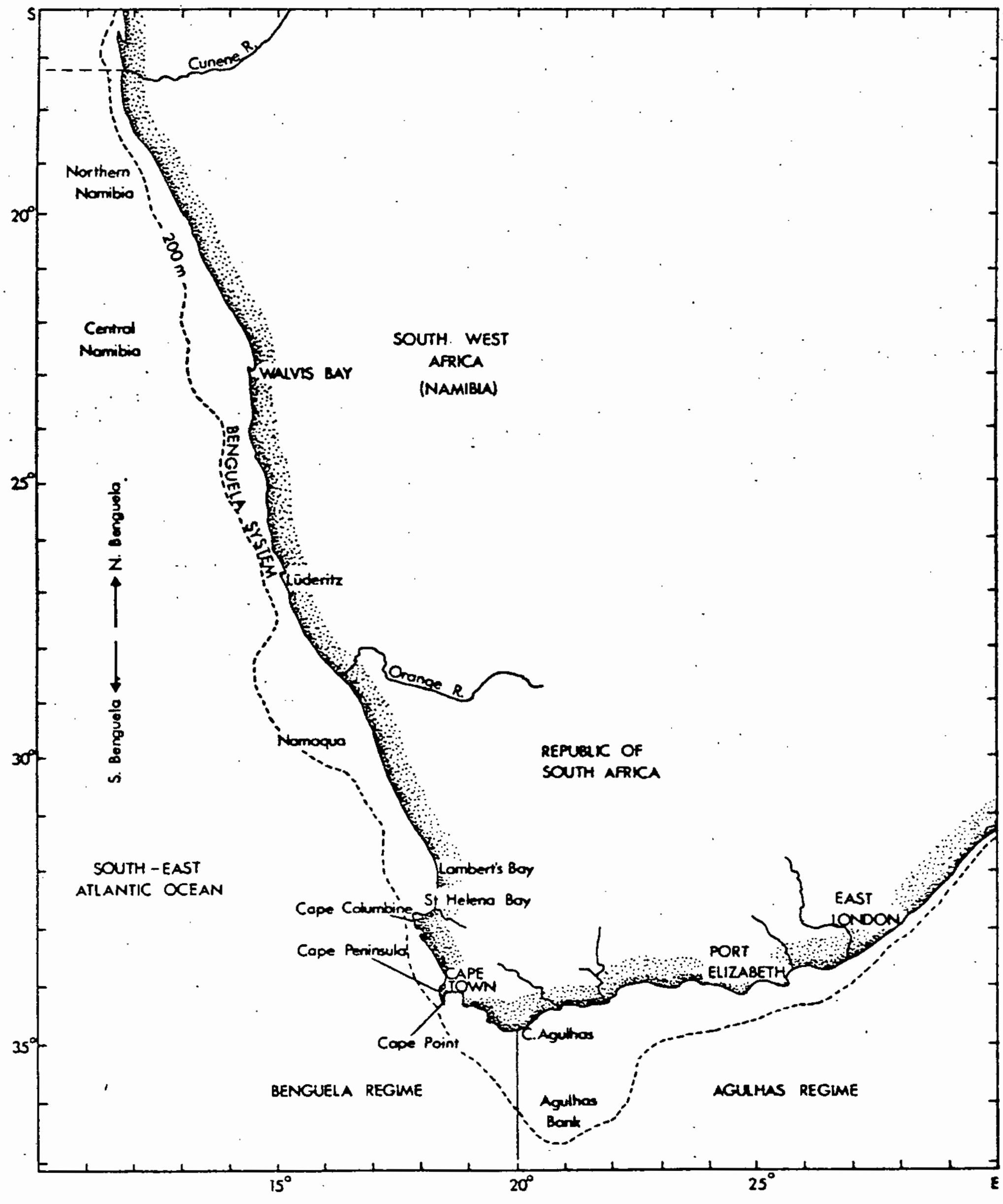

Figure 1.1 The south and west coasts of southern Africa showing the main oceanographic regions which are referred to in the text

With the development of the pelagic fisheries in the St Helena Bay area during the early 1950's, regular zooplankton collections from this area and later from more extensive surveys off South West Africa (Namibia) and around the south western Cape (Figure 1.1), formed the basis of a number of systematic and distributional studies of the local zooplankton fauna. Chapter 2 of this thesis serves as a review of this research and its contribution towards our understanding of zooplankton ecology of the Benguela system. In recent years the direction of research has changed and more emphasis has been placed on understanding the functional aspects of zooplankton populations of single dominant species to which the concepts of population dynamics may best be applied. This thesis describes the population dynamics of the dominant euphausiid, Euphausia lucens, of the southern Benguela region.

Euphausiids have a fundamental position in the food chain, being intermediate between the small mesoplankton and the large pelagic carnivores. In the southern Benguela region they are important prey items for a large variety of commercially important fish such as anchovy Engraulis capensis, pilchard Sardinops ocellatus (King and Macleod, 1976; James, 1987), hake Merluccius spp. (Botha, 1980; Payne et al., 1987) and snoek Thyrsites atum (Nepgen, 1979). Yet little is known about the temporal and spatial distribution or general ecology of local euphausiid species.

Euphausia lucens is the dominant euphausiid species in the southern Benguela region. Its range extends northwards from the cooler coastal waters of the western Agulhas Bank (Talbot, 1974) to the southern

Namibian waters (Boden, 1955). Swarms of E.lucens have been reported off the western and south-western coasts (De Decker, 1973) and the occurrence of daytime surface swarms have been recorded by Nicol et.al. (1987). Laboratory studies by Stuart (1986) has shown E.lucens to be omnivorous and having the potential to exert a considerable predatory impact on newly hatched anchovy larvae. Pillar (1984a) has shown that E.lucens undertakes diel vertical migration and therefore has the ability to exploit a variety of food types. It is plausible that the general enrichment of upwelled areas in the southern Benguela induces the abundance of E.lucens and consequently makes them an important link in the transfer of energy to the higher trophic levels. The main objective of this thesis is to define the trophic status of E.lucens in the southern Benguela, particularly in the St Helena Bay area. This area was chosen because of its importance as a recruitment area for commercially exploited pelagic fish (Crawford et.al., 1980; Shelton et.al., 1985). Also, environmental parameters such as wind and current patterns have been well documented (see review by Shannon, 1985, and more recently by Holden (1987) and Nelson and Polito, (1987)), hence some understanding of the physical environment is available to study the dynamics of E.lucens in this region.

Chapter 3 is aimed at evaluating the contribution of euphausiids to the zooplankton biomass of the southern Benguela region and to ascertain their centres of abundance in relation to the principle upwelling areas of the west coast. Questions as to whether euphausiid biomass respond to seasonal changes characteristic of these areas, such as increased abundance in association with elevated phytoplankton concentrations, offshore displacement during upwelling conditions, are addressed and compared to the seasonal changes in the smaller mesoplankton, principally copepods.

Because of the inconsistencies in the larval description of E.lucens (Boden, 1955; Bary, 1956; Talbot, 1974) and the necessity of identifying variant forms in preserved materials, larvae of E.lucens were reared in the laboratory. Chapter 4 describes the role of diet in determining larval growth rates, development times and developmental pathways.

Chapter 5 provides a description of the population dynamics of E.lucens in the St Helena Bay region. Features such as abundance, size distribution, age structure and reproductive cycles are described in relation to the seasonal, physical and biotic characteristics of the area. Since eggs have been recorded throughout the year in the St Helena Bay area (De Jager, 1954; Nepgen, 1957), it may be proposed that E.lucens has a protracted spawning season and multiple spawning may exist in the population. To test this hypothesis, brood characteristics were examined to determine the timing and duration of the spawning frequency in the female population.

Chapter 6 considers the growth and production of E.lucens in the St Helena Bay region. If E.lucens exhibits continuous breeding a high production:biomass ratio (P/B) would be expected. Also, since euphausiids moult regularly throughout their lifespan, this contribution of organic matter to detrital food webs would be significant. The relative contributions of flesh, moults and eggs to the total annual production are estimated and P/B ratios presented for three different areas (inshore, intermediate and offshore) in the St Helena Bay region.

Chapter 7 addresses the significance of vertical migration in the life history strategy of E.lucens. By migrating between layers of water moving in different directions and at different velocities, a vertically migrating population is offered a suite of opportunities for maintaining or expanding their species range. Diel vertical migration in E.lucens has been described by Pillar (1984a). However, because the entire water column was not sampled, the extent of migration was not known. More quantitative data are drawn from collections using an RMT 1x6 multiple net system which sampled different depth strata throughout virtually the whole water column. From recent knowledge of the current regime of St Helena Bay (Holden, 1987) and of the west coast (Nelson and Hutchings, 1987; Nelson and Polito, 1987), mechanisms are proposed whereby populations of E.lucens may be maintained within the southern Benguela region.

The significance of this work is that it is the first attempt at describing the life history and ecology of a dominant zooplankton species of the southern Benguela region. Hutchings (1979) and Hopson (1983) studied population dynamics of local zooplankton over a wide range of species from knowledge of their vertical and horizontal distributions, however, details of their life histories remain unknown. A knowledge of the population dynamics and life history of *E.lucens* in the southern Benguela region should contribute to our understanding of the energy flow and production of the higher trophic levels of this ecosystem.

CHAPTER 2

REVIEW OF ZOOPLANKTON STUDIES IN THE BENGUELA CURRENT

2.1 INTRODUCTION

The most important contributions to the systematics of South African zooplankton are those by Cleve (1905) and Stebbing (1910). Their general catalogues of the zooplankton fauna were later supplemented by studies on individual taxa such as Wolfenden (1911) on copepods, Tattersall (1925) and Illig (1930) on euphausiids and Barnard (1932, 1940) on amphipods. The two surveys of the Benguela Current by the R.S.S. WILLIAM SCORESBY between 20°S and 35°S during 1950 (Hart and Currie, 1960) provided the first detailed studies of individual zooplankton taxa from the Benguela system. Some of the findings stemming from these surveys were reported by Iles (1953) on ostracods, Boden (1954, 1955) on euphausiids, Tatersall (1955) on mysids, and Jones (1955) on cumaceans. With the development of the Cape and Namibian pelagic fisheries during the early 1950s regular zooplankton sampling began, first in the St Helena Bay area where fishing activities were more concentrated. The first account of the local zooplankton groups from this region was provided by De Jager (1954) from monthly sampling of an area bounded by Saldanha Bay (33°S) in the south and Lambert's Bay (32°S) in the north. This was later extended southwards to Table Bay and is referred to in the text as the 'Cape routine area' (Figure 2.1a). Regular collections from this area formed the basis of several distributional studies which include Nepgen (1957) on euphausiids, Van Zyl (1960) on tunicates, Heydorn (1959) on chaetognaths, and Siegfried (1963) on hyperiid amphipods.

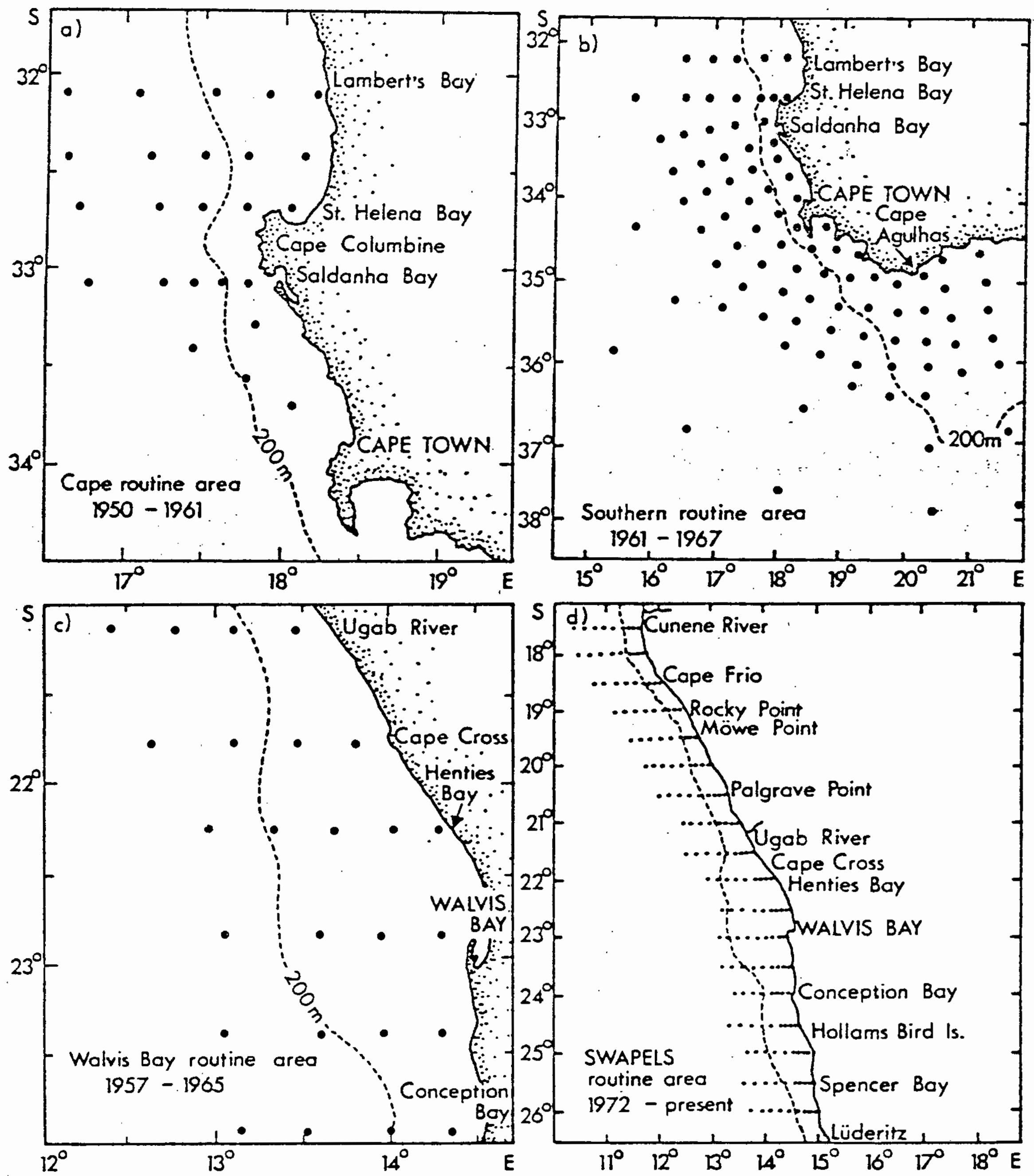

Figure 2.1 Zooplankton routine and research areas in the Benguela region between 1950 and 1977

During the early 1960s the southern limit of the 'Cape routine area' was extended southwards to encompass the Agulhas Bank regions (38°S). The eastern limit of this area, referred to as the 'Southern routine area' (Figure 2.1b) was at San Sebastian Bay (21°E). Between 1963 and 1967, this area was sampled monthly and later on a quarterly basis which yielded further contributions to our knowledge of the major zooplankton groups. De Decker (1973) summarised most of the research effort in his account of the Agulhas Bank plankton. Other works include Lazarus (1967) and Lazarus and Dowler (1980) on the distribution of phyllosoma larvae and pelagic tunicates, respectively.

In the Namibian region of the northern Benguela system, material collected from an area stretching from Conception Bay in the south (24°S) to the Ugab River in the north (21°S), referred to as the 'Walvis Bay routine area' (Figure 2.1c), provided the first account of the centres of abundance of the major zooplankton groups (Kollmer, 1963). Later studies in this area by Unterüberbacher (1964) and Venter (1969) provided accounts of the copepod and chaetognath fauna. During the early 1970s, this area was extended northwards to the Kunene River (18°S) and southward to just north of Luderitz (26°S), by the initiation of the South West African Pelagic Egg and Larval Survey (SWAPELS). Regular ongoing sampling of the 'SWAPELS routine area' (Figure 2.1d) has yielded vast amounts of zooplankton material. No attempt has yet been made, however, to analyse individual zooplankton groups. Zooplankton biomass has been monitored regularly, but few published data are available (Kruger, 1983; Kruger and Boyd, 1984).

During the late 1960s, zooplankton sampling in the southern Benguela changed from monthly routine surveys over large areas to more intensive and discrete studies in time and space. These changes were initiated to provided better insight into the changes in zooplankton communities during local upwelling events. During December 1969 samples were collected over a 13-day period at discrete depth intervals using a centrifugal pump (Hutchings et.al., 1970) and WP-2 nets (Currie and Foxton, 1957) equipped with flowmeters. This net was considered more quantitative than the 'Discovery'-type gear which had been used previously on routine surveys. From 1971-1973 a transect of stations running northwest of the Cape Peninsula was monitored monthly to observe seasonal changes in zooplankton standing stock. In 1974, this line of stations was extended northwards by three lines to Cape Columbine which were monitored quarterly over a one-year period. The results of these surveys were reported by Hutchings (1979, 1981) and Andrews and Hutchings (1980). Between 1977 and 1978 monthly surveys, principally aimed at mapping the distribution of pelagic fish eggs and larvae around the South African western and southern coasts (Cape Egg and Larval Programme: CELP), provided material for further studies on local zooplankton communities. Collections from along one transect off Lambert's Bay, formed the basis of a study on the inshore-offshore and temporal distribution of the copepod community of this area, with notes on other major taxonomic groups (Hopson, 1983).

During nine deep-sea and two inshore cruises by the R.S. AFRICANA II, between 1961-1968, a pump situated at keel depth of about 3m, was used to collect zooplankton while steaming between hydrological stations. The cruises encompassed an area between the Indian Ocean (26°S), the South

Atlantic Convergence (47°S) and the southeastern Atlantic Ocean bordering the western coast mainland to as far north as Walvis Bay (23°S). Data collected from these cruises were recently presented by De Decker (1984) in his comprehensive account of the copepod distribution in the southern African seaboard.

The following paragraphs are not intended as an account of the progress in zooplankton faunistic studies of the Benguela system. They should serve as a summary of pertinent work on taxonomic and distributional studies, rather than an attempt to address zooplankton on a functional basis. The account should be viewed as a reference text to augment our understanding of the distribution of local zooplankton taxa. In recent years the direction of research has changed and more emphasis has been placed on the investigation of functional aspects of zooplankton ecology, rather than descriptive distributional studies. An outline of ongoing and future studies is included in the text to elaborate on this change in approach.

2.2 DISTRIBUTION OF BIOMASS AND SEASONAL CHANGES

2.2.1 Northern Benguela

Earlier studies by Kollmer (1963) and Unterüberbacher (1964) provided some insight into the distribution and seasonal changes in zooplankton abundance in the northern Benguela. From data collected in the 'Walvis Bay routine area' between 1958 and 1962, they noted consistently high biomasses of zooplankton in an area west and northwest of Walvis Bay along the inferred upwelling plume which was characterised by low temperatures and salinities. Unterüberbacher (1964) observed two annual zooplankton peaks, one during the late spring and early summer (November-December) and the other mainly during the autumn (March-May). These findings agreed with the peaks of phytoplankton abundances recorded by Kollmer (1963). Later studies by Visser et.al., (1973) and Wessels et.al., (1974) showed that zooplankton and phytoplankton maxima occurred in belts parallel with the coastline. The phytoplankton maxima occurred inshore in cool upwelled water while the zooplankton peaked further offshore. Data shown from the South West African Pelagic Egg and Larval Surveys (SWAPELS) has provided some information on the distribution of zooplankton in the northern Benguela. Kruger (1983) has shown the inshore-offshore distribution of zooplankton in relation to phytoplankton abundance during the period from September to March 1980-1981 and 1981-1982. The pattern of high inshore phytoplankton concentrations and offshore peaks of zooplankton biomass estimates from the SWAPELS material, however, are of a semi-quantitative nature due to the imprecise method of measuring plankton volume, i.e. relative zooplankton/phytoplankton ratios, rather than direct measurement. Furthermore, the type of gear used, i.e. 80 μm mesh 'Discovery'-type N50 net, is inefficient as regards the capture of the larger zooplankton and the small mesh would be susceptible to clogging which would confound biomass estimates. Consequently, limited conclusions on biomass distribution and seasonal changes can be drawn from these data. Recent analysis of zooplankton from Bongo net collections taken during the SWAPELS surveys is providing more quantitative data on zooplankton biomass.

2.2.2 Southern Benguela

The first study of seasonal changes of zooplankton in the southern Benguela was by De Jager (1954) from his collections from the 'Cape routine area' between 1950 and 1951. He observed that biomass was lowest during winter when upwelling was minimal and highest during spring and summer when upwelling sustained high phytoplankton concentrations in his study area. He noted a three to four-fold decrease in zooplankton settled volume from inshore to offshore. De Decker (1973) showed higher zooplankton concentrations over the Agulhas Bank than off the western coast from data collected between 1961 and 1967 in the 'Southern routine area'. This observation he noted as paradoxical considering the comparatively lower phytoplankton production over the Agulhas Bank. The author explained this observation as a bias in the settled volume estimates caused by large numbers of pelagic tunicates from the Bank collections which far exceeded those collected off the western coast.

Settled volume biomass estimates from the above studies were based on collections using the 'Discovery'-type N70 net which was limited quantitatively due to the absence of flow monitoring or depth recording instrumentation and no cognizance of vertical migration. Consequently, the data indicated little more than seasonal trends in zooplankton biomass. Data collected from October 1970 to March 1973 off the Cape Peninsula, using the more quantitative WP-2 net, enabled Hutchings (1979, 1981) and Andrews and Hutchings (1980) to define more clearly local seasonal cycles of zooplankton biomass. A transect of seven to ten stations running northwest from the Cape Peninsula, referred to as the 'Upwelling monitoring line', was sampled monthly to observe the physical and biotic changes along

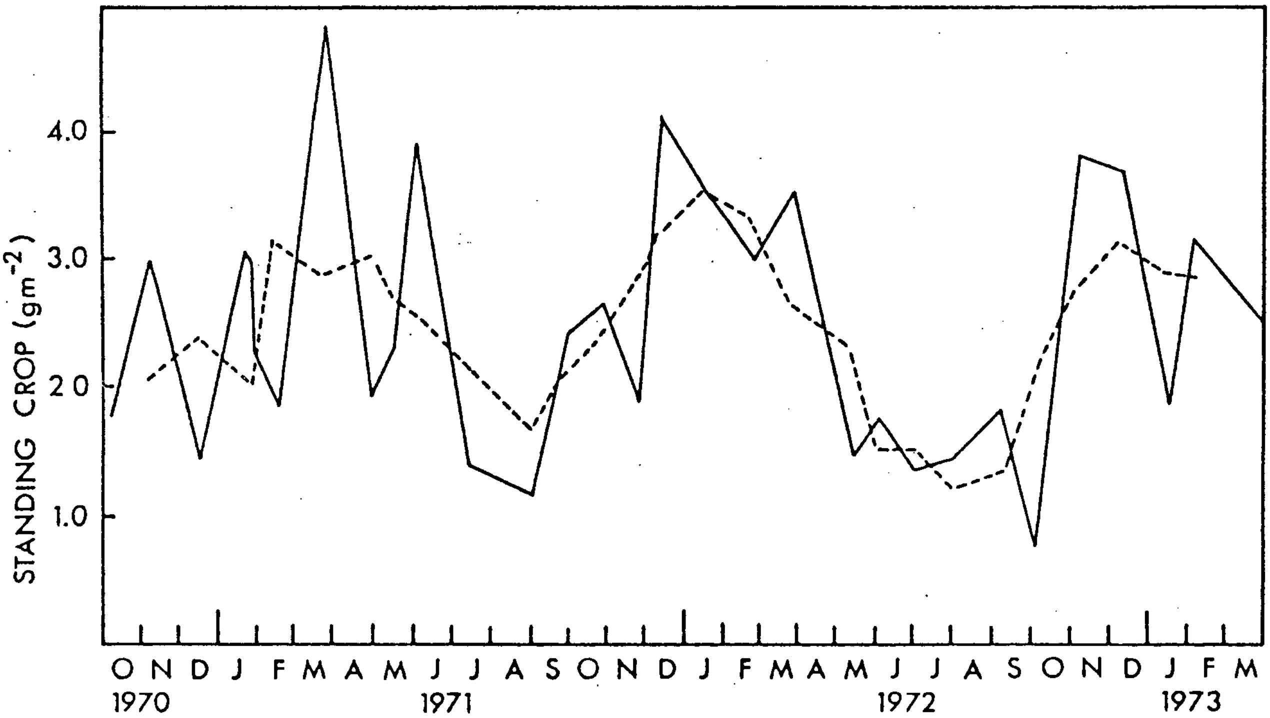

Figure 2.2 Seasonal variations of the mean zooplankton standing stock (g dry wt.m^{-2}) along the Upwelling Monitoring Line running north-west off the Cape Peninsula between 1970 and 1973 (from Andrews and Hutchings, 1980)

the axis of the inferred upwelling plume. The authors used dry weight per unit area (g $DW.m^{-2}$) which they considered to be a more suitable measure of zooplankton standing stock than the previously used settled volume biomass estimates ($ml.1000m^{-3}$).

The monthly changes in standing stock along the 'Upwelling monitoring line', as illustrated by Andrews and Hutchings (1980), are shown in Figure 2.2. Considerable variability between successive months is evident but when a three-month running mean is applied to the data, distinct seasonal patterns are apparent. High values were recorded in the upwelling season between December to February and lowest values in the non-upwelling season between June to August. A two- to three-fold difference in standing stock was noted between these periods with an overall mean of 2.3g $DW.m^{-2}$. At a nearshore site in a kelp bed zone off the Cape Peninsula, Carter (1983) observed similar seasonal fluctuations in zooplankton biomass. Highest biomasses were noted in summer with reduced levels in autumn and lowest in winter with an overall mean biomass of 2.14g $DW.m^{-2}$. By comparison, St Helena Bay, some 150km to the north was characterised by higher and more consistent standing stock than off the Cape Peninsula (Hutchings, 1981). The author relates his findings to the comparative homogeneity of the St Helena Bay region. Based on long term wind data, he found that upwelling-favourable winds were more common in St Helena Bay (45%) than off the Cape Peninsula (33%). Also the cyclonic water circulation within the St Helena Bay area favoured water retention with mild but prolonged upwelling events, thus contributing further to the stability of this area relative to the more variable seasonal upwelling fluctuations associated with the Cape Peninsula. Hopson (1983) noted that

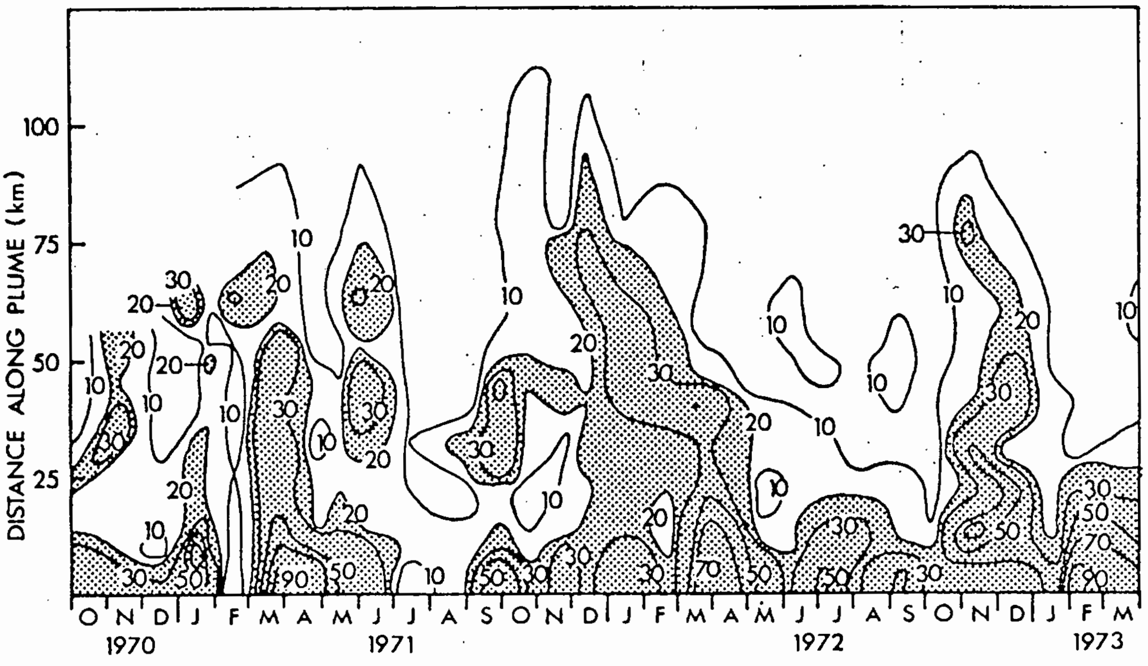

Figure 2.3 Seasonal and spatial changes of zooplankton standing stock (mg dry wt.m^{-3}) along the Upwelling Monitoring Line between 1970 and 1973 (from Andrews and Hutchings, 1980)

upwelling was active during most of her monthly zooplankton collections in an area just north of St Helena Bay (Lambert's Bay) (32°S) between August 1977 and August 1978. Supporting the finding by Hutchings (1981) she noted uniformity and a lack of seasonal variation in biomass throughout the year.

The seasonal inshore-offshore fluctuations of zooplankton biomass along the Cape Peninsula upwelling plume, as illustrated by Andrews and Hutchings (1980) are shown in Figure 2.3. During the spring and summer multiple peaks of zooplankton occurred offshore as a result of offshore displacement during active upwelling. In winter when upwelling was minimal zooplankton peaks were smaller and closer inshore. The zones of high concentrations corresponded to temperatures between 10° and 16°C. Intrusions of warmer water towards the coast, especially during winter months limited zooplankton to the inshore regions. The authors pointed out that the transect was occupied only once amonth and between each collection four to five wind reversals could occur with subsequent marked changes in the relative distribution of the zooplankton. From data collected during December 1969 off the Cape Peninsula, Hutchings (1981) was able to describe the short-term changes in zooplankton standing stock during a brief wind reversal. As the wind blew from the west after a period of upwelling, the inshore surface water warmed rapidly and the zooplankton was more concentrated near the coast during this period of downwelling. As the wind backed to the southeast and increased in speed, upwelling resumed, and cold water reappeared which rapidly spread offshore displacing the zooplankton in a northwesterly direction. The author concludes that the duration of the southeasterly winds would influence the displacement of zooplankton. Typically, these winds seldom persist for more than four to six days, consequently it is estimated that patches of zooplankton could be displaced some 40-90km during this period.

Andrews and Hutchings (1980) attempted to relate zooplankton biomass to phytoplankton on a seasonal basis. By expressing the biomasses in terms of carbon, they found that zooplankton biomass formed 4-25% of the phytoplankton biomass with maximum values occurring during the summer and lowest during the winter. These correspond to periods with highest zooplankton biomass and phytoplankton biomass, respectively. Carter (1983) also noted similar seasonal cycles in zooplankton/phytoplankton ratios which form a 5% minimum during winter to a 64% maximum during summer. Using the mean zooplankton/phytoplankton biomass ratio (12%) from the data of Andrews and Hutchings (1980) and a higher ratio of 20% estimated from data compiled by Olivieri and Hutchings (1983), Shannon and Field (1985) estimated the lower and upper limits of the annual zooplankton production of the active upwelling area of the southern Benguela (40 000km^2), to be 2.0-6.7 x 10^6 tonnes carbon, respectively. The estimated mean annual zooplankton production of 3.6 x 10^6 tonnes carbon was equivalent to 9% of the phytoplankton production. Andrews and Hutchings (1980) reported spatial and temporal mismatch along the upwelling plume between zooplankton and phytoplankton, yet found a correlation ($0.01 < P < 0.05$) between zooplankton standing stock and gross phytoplankton production. No seasonal pattern was evident. Carter (1983) found no relationship between either zooplankton and phytoplankton biomass or gross phytoplankton production. The author, however, pointed out that his findings were not conclusive owing to the spatial and temporal limitations of his data. Hutchings (1981) noted that because of the more rapid response of phytoplankton than

TABLE 2.1: Zooplankton standing stock estimates from the Southern and Northern Benguela: the estimates denoted by an asterisk were taken from the original source, and others were taken from Hutchings (1979); all data were converted to $gC.m^{-2}$ using a conversion factor of 6.5% of wet weight (Cushing, 1971); dry weight is considered 10% of wet weight (Hutchings, 1979)

Area		Source	Mean depth sampled (m)	Gear	Mesh width (μm)	Standing stock ($gC.m^{-2}$)	Comments
Southern Benguela	1.	De Jager, 1954	100	N70V	200-460	1.59	Summer samples only 1950/51; 'Cape routine area'
	2.	De Decker, 1973	100	N70V	200-460	1.02	Annual mean 1961/67; 'Southern routine area'
	3.	Andrews and Hutchings, 1980	180	WP-2	200	1.49	Annual mean 1970/73; Cape Peninsula upwelling plume
	4.	Hopson, 1983	100	Bongo	300	1.29*	Annual mean 1977/78; Lambert's Bay area
	5.	Carter, 1983 Carter, 1983	20 20	Pump Pump	44 149	1.39* 1.11*	January, May, August and October/November 1979 (mean); kelp bed zone off the Cape Peninsula
Northern Benguela	1.	Kollmer, 1963	100	N70V	200-460	2.04	Annual mean 1958/59; 'Walvis Bay routine area'
	2.	Unterüberbacher, 1964	100	N70V	200-460	1.34	Annual mean 1959/62; 'Walvis Bay routine area'
	3.	Visser et.al., 1974	116	WP-2	200	0.96*	May-November 1971, April-October 1972 (mean) 19-23°S
	4.	Wessels et.al., 1975	116	WP-2	200	0.63*	June and July (mean) 19-23°S

zooplankton to upwelling and downwelling events, it is expected that there would be inconsistent patterns of zooplankton and phytoplankton distribution of the Cape Peninsula.

Hutchings (1979) and Hopson (1983) compared their zooplankton standing stock estimates with those of previous records from the Benguela system as well as those from other upwelling areas, e.g. California, Peru, Northwest Africa. Carter (1983) confined his comparisons to those of Andrews and Hutchings (1980). These authors, however, have stressed that the data must be viewed with several restrictions placed on the validity of the comparisons. The effect of spatial, seasonal and diel variations are important sources of bias. Also those associated with sampling gear such as mesh size and avoidance of the sampler, particularly by the larger zooplankton, can confound valid comparisons when different samplers are used. Pillar (1984b) has shown that towing bridles similar to those in front of the 'Discovery'-type N70 nets and the WP-2 nets, increased the avoidance response of the larger zooplankton, such as euphausiids, to the net. This resulted in lower biomass estimates using these nets than when using Bongo nets which were free from bridle obstructions. The author showed that mesh size was of critical importance in biomass of local copepod fauna as a mesh of 200μm retained two to three times the biomass of a 300μm meshed net.

Considering the aforementioned, the standing stock values listed in Table 2.1 should be considered reliable for regional comparative purposes only when similar sampling gear is used. Meaningful regional comparisons are therefore premature until data on the temporal variability of the zooplankton are available from collections covering the whole depth range of the fauna. Despite these restrictions, the data presented should provide a useful reference as an overview of the zooplankton standing stock of the Benguela system.

2.3 Copepoda

Copepods are numerically the most abundant and diverse group of zooplankton in South African waters. De Decker (1964) gave a systematic review of earlier contributions to copepod faunal studies of South Africa, citing Cleve (1905), Stebbing (1910), Wolfenden (1911), and Tanaka (1960) as the major works. He identified 92 copepod species of which 28 were first records for South African waters (Table 2.2). He lists three species which he regarded as typical members of the Agulhas Current, i.e. Clausocalanus furcatus, Corycella concinna, and Temora discaudata and five species, Calanus finmarchicus, Euterpina acutifrons, Temora turbinata, Pseudodiaptomus nudus, and Calocalanus tenuis as being specific to the Agulhas Bank fauna, while eight species were regarded as typical members of the cold water community of the Benguela Current, i.e. Centropages brachiatus, Calanoides carinatus, Metridia lucens, Nannocalanus minor, Clausocalanus arcuicornis, Paracalanus parvus, Paracalanus crassirostris and Ctenocalanus vanus. Subsequent studies by De Decker (1973) have confirmed the dominance of these species in the Benguela system. The more recent and comprehensive account by this author (De Decker, 1984) on the copepod fauna of southern African waters is based on widespread collections in the area between the Indian Ocean (26°S) and the southeastern Atlantic

TABLE 2.2: Copepod species recorded from South African waters (from De Decker, 1964)

Acartia amboinesis	Eucalanus attentuatus
danae	elongatus
negligens	monachus
Acrocalanus gracilis	mucronatus
monachus	pileatus
Calanoides carinatus	subcrassus
Calanopia minor	Euchaeta wolfendeni
Calanus finmarchicus	Euterpina acutifrons
tenuicornis	Labidocera acutum
Calocalanus contractus	minutum
pavo	Macrosetella gracilis
plumulosus	Mecynocera clausi
satyliremis	Metridia lucens
tenuis	Microsetella norvegica
Candacia armata	rosea
bipinnata	Nannocalanus minor
catula	Oithona fallax
curta	nana
truncata	plumifera
Canthocalanus pauper	rigida
Centropages brachiatus	tenuis
calaninus	Oncaea clevei
elongatus	media
furcatus	mediterranea
gracilis	subtilis
pacificus	venusta
Clausocalanus arcuicornis	Pachos tuberosum
furcatus	Paracalanus aculeatus
paululus	crassirostris
Clytemnestra rostrata	denudatus
scutellata	parvus
Copilia mediterranea	Pleuromamma abdominalis
mirabilis	gracilis
Corycaeus africanus	robusta
agilis	Pontellina plumata
asiaticus	Pseudodiaptomus nudus
crassiusculus	Rhincalanus cornutus
dubius	nasutus
latus	Sapphirina gastrica
longistylis	nigromaculata
pacificus	ovatolanceolata-gemma
speciosus	Scolecithrix danae
subtilis	Temora discaudata
Corycella concinna	turbinata
curta	Undinula darwinii
gibbula	vulgaris
Ctenocalanus vanus	

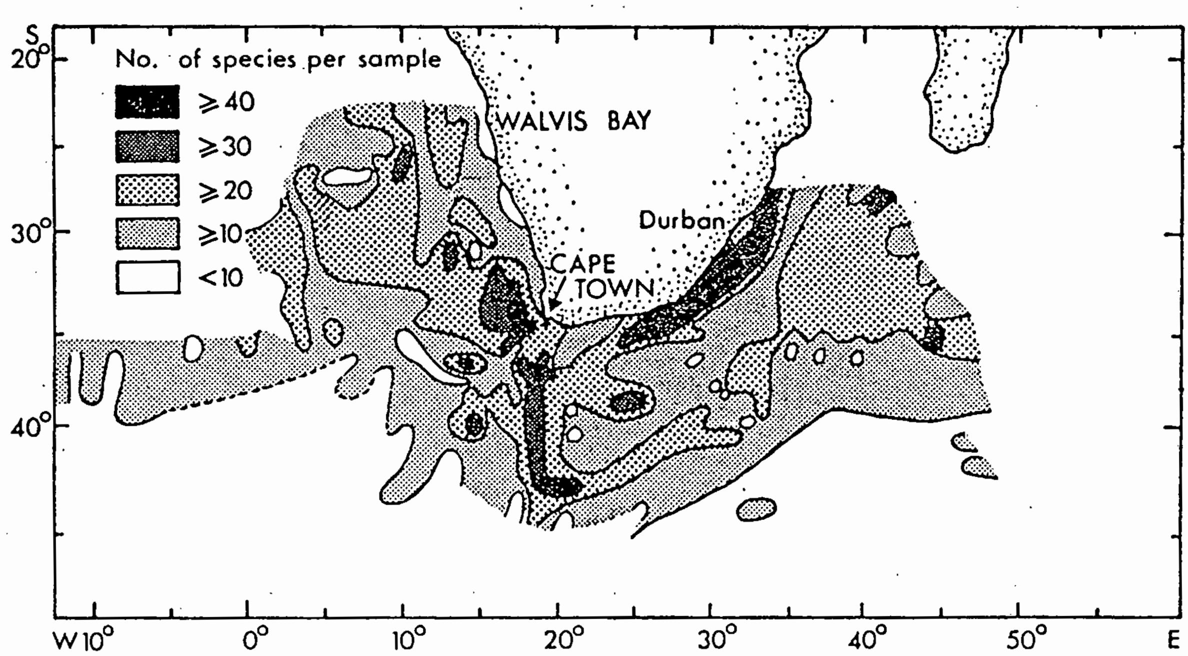

Figure 2.4 Diversity distribution of copepods collected off southern Africa from cumulative data drawn from eleven cruises between 1961 and 1968 (from De Decker, 1984)

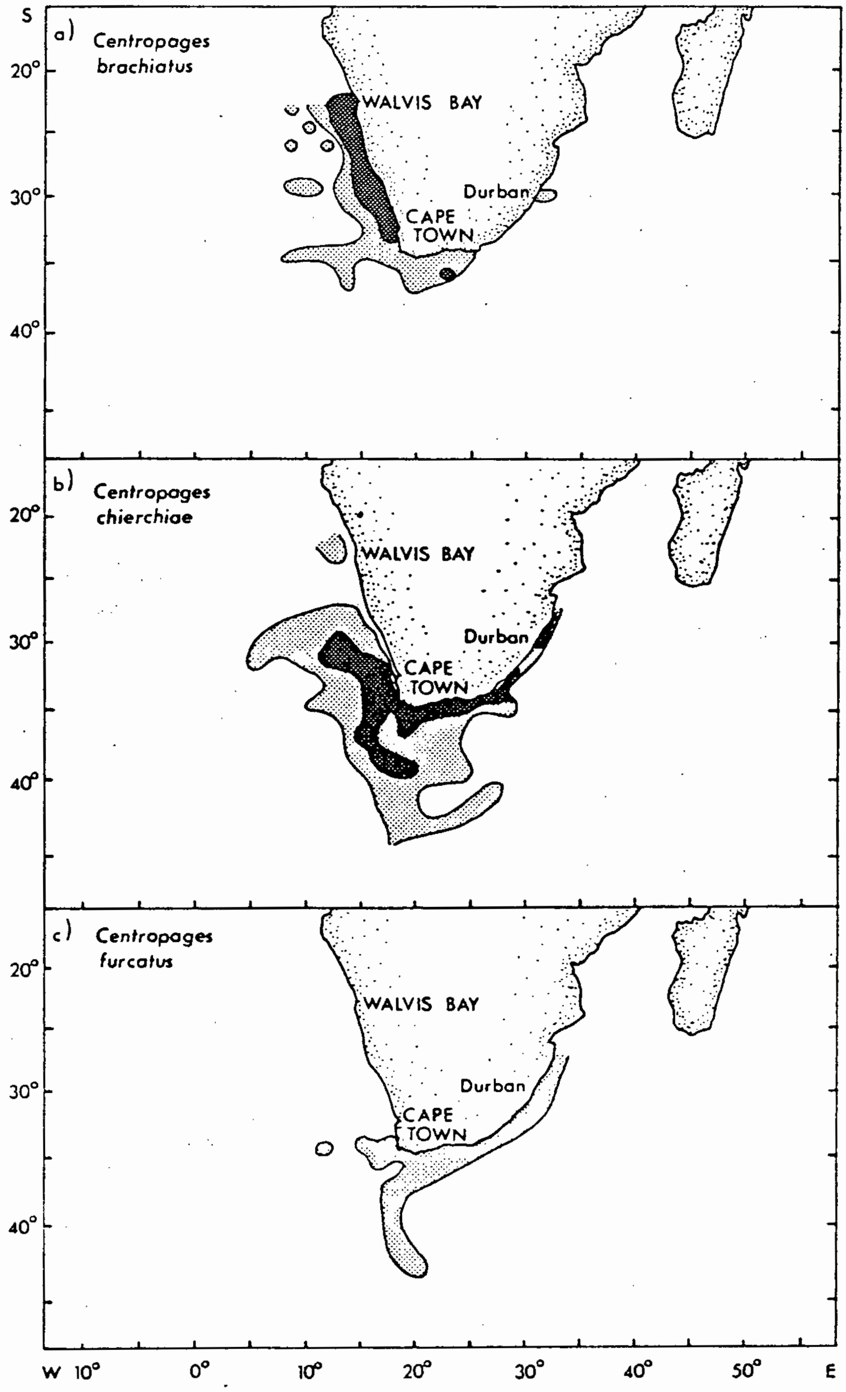

Figure 2.5 Distribution of (a) Centropages brachiatus, (b) Centropages chierchiae, and (c) Centropages furcatus: shaded areas suggest distribution patterns; darker shading indicates areas of higher abundance (from De Decker, 1984)

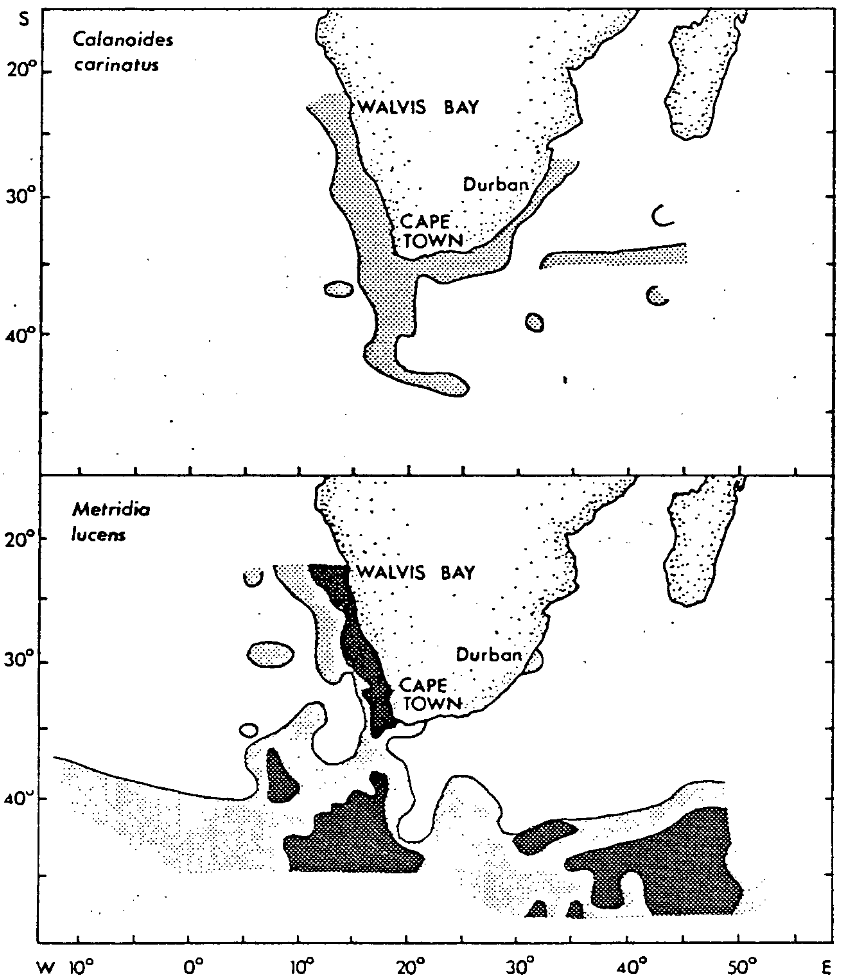

Figure 2.6 Distribution of (a) Calanoides carinatus and (b) Metridia lucens; shading as for Figure 5 (from De Decker, 1984)

Ocean (23-47°S). The author provided distributional maps of 80 species which he considered occurred in sufficient numbers to warrant description. His cumulative data illustrate the low species diversity in the Benguela Current system compared with the Agulhas Current and Agulhas Bank regions (Figure 2.4). The decrease in diversity from the Bank northwards along the west coast supports the findings that the cool Benguela inshore waters limit the dispersal of a number of warm-water species of Agulhas origin, while supporting a larger but less diverse population of cool-water species. This is adequately reflected in the distribution maps of three species of the genus Centropages (Figure 2.5). C.furcatus, an Indo-Pacific species, is shown to be indicative of the Agulhas Current with little penetration into the Benguela system. C.chierchiae, a member of the Agulhas Bank community, has a wider distribution which reflects the advection of Agulhas Bank water into the Benguela system. Contrary to C.chierchiae, C.brachiatus thrives in the inshore waters in the Cape and the Namibian regions of the Benguela. C.brachiatus is shown to be less able to withstand advection than C.chierchiae. The southward penetration shown by C.chierchiae is only faintly displayed by C.brachiatus. To the north C.brachiatus is considered not to extend further than Namibia while C.chierchiae has been recorded along the African Atlantic coast (Thiriot, 1978).

De Decker (1984) also discussed the distribution of Metridia lucens and Calanoides carinatus, in relation to that of Centropages brachiatus (Figure 2.6). Although they proliferate and co-occur in the Benguela, their distributions differ in the eastern Atlantic. Metridia lucens extends northwards from the Subantarctic to northern Namibia and it has been recorded further north until approximately 15°N which is regarded as the southern limit of its northern population (Thiriot, 1978). De Decker (1984) noted that Calanoides carinatus was more eurythermic than Centropages brachiatus which explains its more extensive southward and northeasterly distribution in his study area. Thiriot (1978) has recorded Calanoides carinatus as being a dominant copepod species on the eastern Atlantic seaboard.

Working in the 'Walvis Bay routine area', Kollmer (1963) noted the importance of the genus Paracartia as a nearshore copepod and Centropages brachiatus, Calanoides carinatus, and Metridia lucens as being numerically dominant over the continental shelf, while the boundary area was typified by the presence of Rhincalanus nasutus. Unterüberbacher (1964) provided a more comprehensive account of the copepod fauna of this area. He found Paracalanus crassirostris and Paracartia africana to be a strictly neritic species while the cool-water community was represented mainly by Centropages brachiatus, Calanoides carinatus and Metridia lucens which together with Paracalanus parvus and Oithona similis comprise about 80% of the copepods in the area studied. The author listed a number of copepod species which he considered to be members of the offshore warm-water community, with Nannocalanus minor being numerically the most important.

The data of Unterüberbacher (1964) provided a base line for studying the effect on the biotic fauna during the Benguela 'El Nino' in 1963 when water with anomalously high temperature and salinity and unusual dissolved oxygen concentrations moved southwards into the northern Benguela from the tropical Atlantic (Stander and De Decker, 1969). The notable increase in numbers of Nannocalanus minor and the marked decline of some cool-water copepods, principally Paracalanus parvus, was suggested by the authors as a consequence of the warm-water intrusion. Furthermore, the occurrence of several species of copepods in the area, which were only known to occur further north, contributed towards their conclusion that the observed anomaly was not a result of local conditions, but due to a southward advance of warm surface water from Angola. The use of copepods as an indicator of water masses was also demonstrated by De Decker and Coetzee (1979) in their studies of the oil yield fluctuations from pelagic fish in the Namibian fishing grounds. They showed an inverse correlation between oil yield with the southward extension of a warm saline water mass of Angolan Current origin into the Namibian shelf region. This influx of water was marked by the presence of the neritic copepods Temora turbinata and Euterpina acutifrons which were regarded by the authors as of practical value in the interpretation and the identification of different water masses in the northern Benguela regions.

Coetzee (1974) discussed the vertical distribution of Calanoides carinatus, Centropages brachiatus and Metridia lucens in the upper 50m of the waters in the vicinity of Walvis Bay during April and August 1972. Despite gross environmental changes as observed from the stable highly stratified conditions during April to strong coastal upwelling with minimal stratification later in the year, there were no apparent changes in the vertical distribution of Calanoides carinatus or Centropages brachiatus. A strong diurnal vertical migration was displayed by Metridia lucens during both months with maximum numbers encountered in the surface layers during the night.

Lazarus (1975) provided a systematic account of the zooplankton communities from four sheltered bays in the southern Benguela system between the Cape Peninsula and St Helena Bay. Typical members of the cool nearshore copepod community were Calanoides carinatus, Centropages brachiatus, Paracalanus crassirostris and Oithona similis which dominated the zooplankton throughout three years of observations (1964-1966). Other dominant Benguela species, such as Nannocalanus minor and Metridia lucens were relatively scarce in his collections, indicating their affinity for warmer offshore waters.

From an ecological rather than a systematic viewpoint, Hutchings (1979) produced a comprehensive study of the vertical and horizontal distribution of zooplankton in the southern Benguela upwelling region. Using more quantitative sampling methods than used on previous studies, his work was the first detailed investigation of the coupling between the biological and physical processes which act to control local zooplankton communities. Copepods collected at 36 hour intervals, over a ten-day period from oceanic, newly upwelled and mature upwelled water, showed that temperature and chlorophyll abundance had an effect on the vertical structure of different species. Species were separated into three groups using association indices and typical members of each group were described in relation to hydrological conditions. The largest group of copepods were typical of the cool upwelled water consisting mainly of those species described by earlier workers (e.g. De Decker, 1964, 1973) as preferring this habitat. With the exception of M.lucens there was very little indication of any extensive vertical migration in this group with the majority remaining in the mixed upper layer where chlorophyll concentrations were highest. A second group typified the frontal zone which borders the cool upwelled water and were represented by Paracalanus crassirostris and Calocalanus tenius. Strong vertical temperature gradients exerted a considerable influence on these species, as evidenced by their close association with the thermocline. Those species inhabiting the warm waters beyond the front formed the third group, which the author considered to be species characteristic of the Agulhas Bank, such as Calanus finmarchicus.

From the above data and from those drawn from additional material, Hutchings (1979) was able to postulate several possible mechanisms whereby the zooplankton community was maintained in the southern Benguela system. He suggested that sinking at the oceanic front, combined with the periodic shoreward movement when upwelling relaxed and downwelling at the coast prevailed, could be sufficient to allow the zooplankton to return to the inshore regions. The southward surface currents and low oxygen undercurrents such as those described by Duncan and Nell (1969) and De Decker (1970) were also suggested by the author as a system of currents which could be responsible for replenishing the local zooplankton population.

In her studies on the temporal and inshore-offshore variations of zooplankton in the pelagic fish nursery and recruitment grounds in the Lambert's Bay area, Hopson (1983) singled out the copepod community for special attention because of their importance as potential food items of young fish. Only six species comprised 86% of the copepod community and there were sufficient variations in their distribution to suggest that different species had different life histories. Attention was drawn by the author to the fact that young and mature members of larger species such as Calanoides carinatus were found closer inshore than the smaller species Paracalanus parvus and Ctenoclanus vanus, the young of which were found further offshore than the adults. This size-determined life history was discussed by the author in relation to changes in the physical and biotic environment.

The zooplankton community of a nearshore southern Benguela kelp bed was found by Carter (1983) to be dominated by copepods typical of the cool-water groups of the Benguela system. Their vertical distributions were consistent with the community structure of those defined by Hutchings (1979), supporting the conclusions by Field et.al. (1980) that little captive water is maintained in the west coast kelp beds. Respiration rates were determined by the author for Centropages brachiatus at three different temperatures (8°, 9.5° and 13.5°C). Rates ranged from 3.41-5.11 $\mu l O_2 . mg\ DW^{-1} . h^{-1}$ and the low Q_{10} values found for this species showed that it was well equipped to withstand frequent large temperature variations which characterised its normal habitat. In laboratory studies Borchers and Hutchings (1986) found the copepod Calanoides carinatus was highly adapted to the patchy food regime typical of the southern Benguela region. This tolerance of starvation was ascribed to an exceptionally large lipid reserve. Newly hatched and young copepodite stages were most vulnerable to starvation, depending on the temperature.

Lazarus (1975) found that certain of the smaller copepod species such as Oithona similis, Paracalanus parvus and Paracalanus crassirostris were entirely herbivorous while several of the larger species such as Calinoides carinatus, Centropages brachiatus and Metridia lucens had remains of both phytoplankton and zooplankton, principally copepods, in their guts.

2.4 Euphausiacea

The study of Boden (1954) provides the most comprehensive account of the euphausiids of southern African waters. He described and illustrated 42 species and constructed keys to the euphausiids from both the eastern and western seaboards of South Africa. He subsequently reported on 14 species drawn from material collected off Namibia by the R.S.S. WILLIAM SCORESBY (Boden, 1955). Nepgen (1957) reported on 18 species of euphausiids from collections in the 'Cape routine area' (Table 2.3) of which Euphausia lucens and Nyctiphanes capensis were numerically the dominant species, constituting 76% and 23% respectively, of his total collections from two years of monthly sampling (1954-1956). Boden (1955) first described the larval developmental stages of both these species, but later Bary (1956) and Talbot (1974) concluded that Boden's description of E.lucens was incorrect. Rearing studies by Pillar (1984c, 1985) confirmed both Bary's and Talbot's descriptions of E.lucens as being correct, while supporting Boden's original description of N.capensis larvae.

TABLE 2.3: Euphausiid species recorded off the west coast of South Africa (from Nepgen, 1957)

Euphausia lucens	Nematoscelis megalops
Euphausia recurva	Nematoscelis microps
Euphausia similis var. armata	Stylocheiron carinatum
Euphausia similis	Stylocheiron longicorne
Euphausia hanseni	Stylocheiron elongatum
Euphausia mutica	Stylocheiron abbreviatum
Nyctiphanes capensis	Stylocheiron affine
Thysanoëssa gregaria	Stylocheiron maximum
Thysanoëssa parva	Nematobrachion flexipes

The distribution of euphausiid eggs was first documented by De Jager (1954) in the 'Cape routine area', where he found maximum concentrations during winter and spring and a decline during summer and autumn. He showed maximum occurrence of eggs in waters approximately 37km from the coast where the temperature was generally higher than 14°C. Nepgen (1957) working in a similar area recorded maximum egg production during spring and summer at a similar distance offshore in waters with temperatures ranging from 11°-14°C (integrated over 0-50m depth). More recent work by Hopson (1983) in Lambert's Bay showed a later winter to spring peak in egg production, again offshore in the relatively warmer water. As N.capensis do not release their eggs directly into the water it appears that the above authors were reporting on the distribution of the eggs of E.lucens. Although peaks were recorded by these authors, egg production was noted throughout the year as were the occurrence of euphausiid larvae. Larval peaks were in accordance with the seasons of maximum egg production.

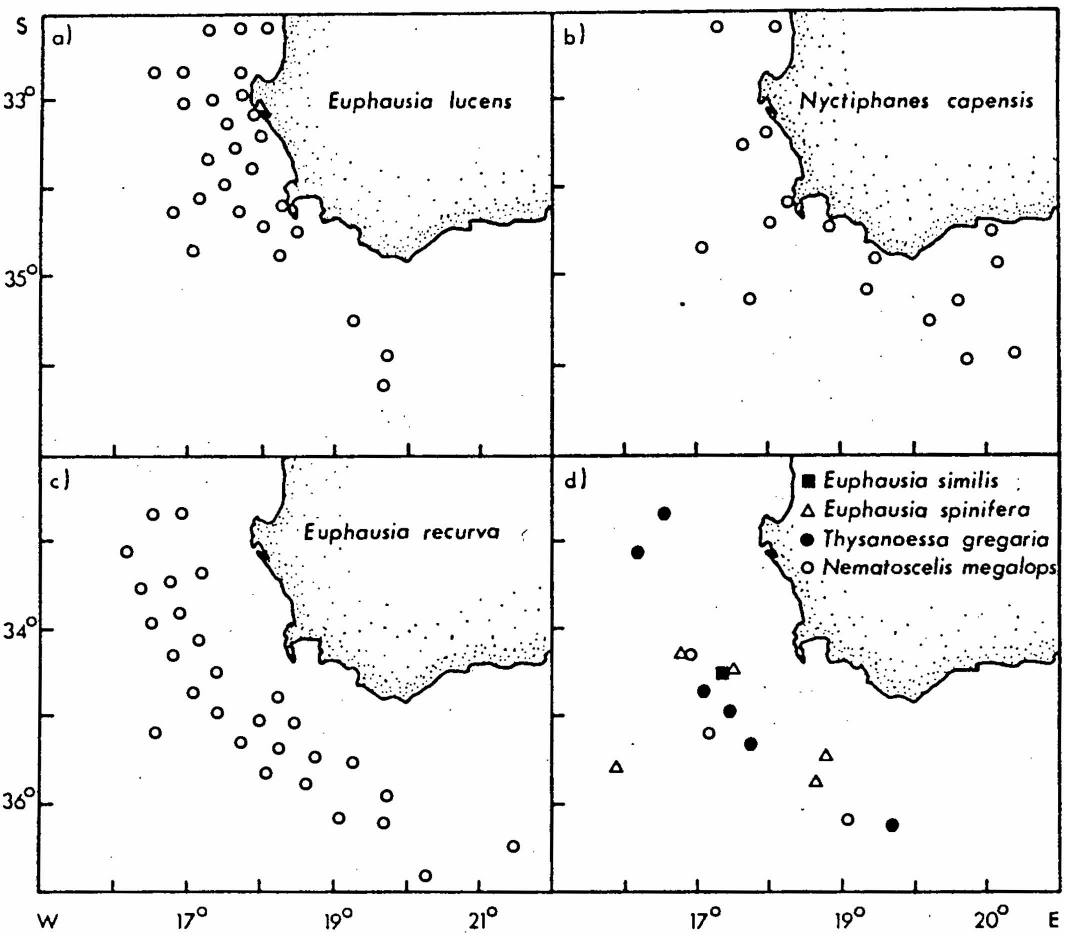

Figure 2.7 The occurrence of euphausiid swarms off the western and south western coast of South Africa from cumulative data from 1964-1966 (from De Decker, 1973)

In the southern Benguela, Nepgen (1957) and Gow (unpubl.data) cited by De Decker (1973), found that swarms of E.lucens and N.capensis occurred closer inshore than those of E.recurva. Less abundant species such as E.similis, E.spinifera, Thysanoëssa gregaria and Nematoscelis megalops occurred further offshore in warm oceanic waters (Figure 2.7). E.lucens was dominant in Gow's material and were caught in the Lambert's Bay area in the winter, while summer swarms were located further south as far as 75km west of Cape Point. Winter and spring concentrations of N.capensis extended from Lambert's Bay southwards as far as 160km south of Cape Agulhas, while very few swarms were recorded during the summer months. Hopson (1983) also found winter and spring euphausiid maxima in the Lambert's Bay area. Further south, Talbot (1974) found that E.lucens and N.capensis were only found in the cooler coastal waters of the western Agulhas Bank during the winter when temperatures were lowest and the influence of the Agulhas Current was weakest. She concluded that during the summer E.lucens was shifted westward into the Benguela system due to the influx of warm tropical waters from the east coast. Talbot (1974) concluded that both N.capensis and E.lucens were resident species of the Benguela system and not indicative of the Agulhas Current zooplankton community.

Hutchings (1979) discussed the vertical distribution of the larval stages of E.lucens during a period of active upwelling off the Cape Peninsula. He found that the early stage larvae (calyptopis) were concentrated higher in the water column than the older furcilia larvae. Pillar (1984a) examined the vertical distribution and diel movement of E.lucens from material collected in an area 65km west of St Helena Bay (33°S) during a comparative

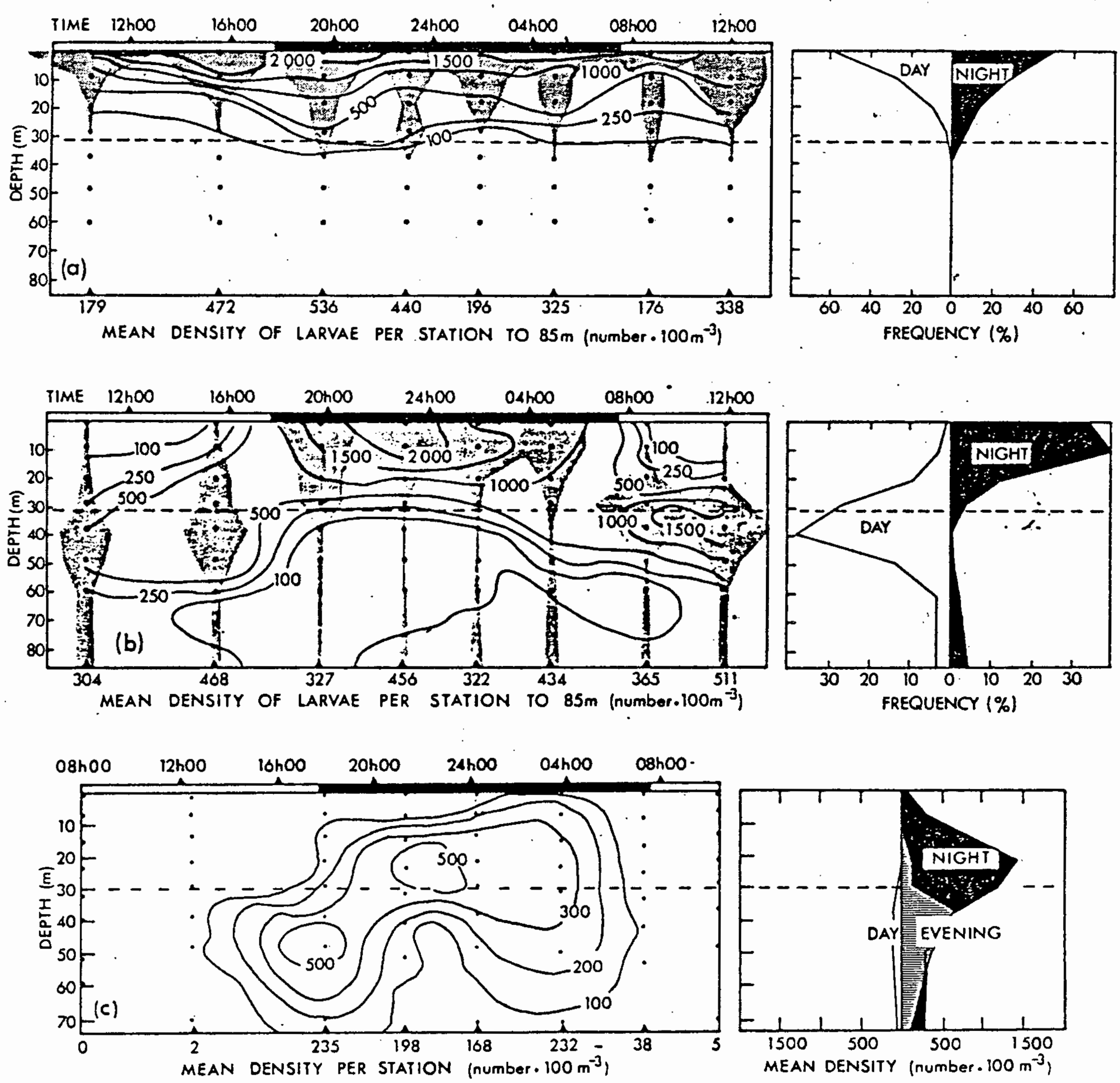

Figure 2.8 Vertical distribution of (a) calyptopis larvae and (b) furcilia larvae of Euphausia lucens based on pump collections and (c) juvenile and adults based on Miller net collections: the thermocline is denoted by a broken line, the sampling depths as dots and the proportion of animals at each depth by a shaded area (from Pillar, 1984a)

study of the sampling performance of zooplankton nets (Pillar, 1984b). He showed evidence of ontogenetic layering in the vertical range of this species. While the calyptopis larvae remained near the surface and did not migrate, the older stages did, with the juveniles and adults moving through a greater depth range than the younger furcilia larvae (Figure 2.8).

The euphausiids of the northern Benguela current have received less attention than those further south in the Cape waters. Boden (1955) recorded N.capensis as the dominant species in inshore Namibian waters. He concluded that E.lucens, which was scarce in his collections, had approached the northern limits of its range in the Benguela system. While N.capensis has been recorded further north, as far as 23°N, E.lucens has not been recorded north of Namibia (17°S) (Thiriot, 1978). Unterüberbacher (1964) reported euphausiid larvae to be abundant beyond the shelf off Walvis Bay, and D'Arcangues (1977) described the vertical distribution of larvae which she observed during February and May 1974 and February 1975. She showed that two distinct layers exist in the water column, one concentrated in the upper layers in temperatures ranging from 14°-18°C and the other deeper in 12°-13°C. She also found the larvae to be tolerant of a wide range of dissolved oxygen levels ($1.2-7.3 m\ell.\ell^{-1}$). During November in inshore waters off Walvis Bay, Thomas (1980) observed extensive day-time surface swarms of early larval stages of N.capensis. Night-time surface swarms of adults were observed by Cram and Schülein (1974) during an unusual occurrence of surface-shoaling Cape hake (Merluccius capensis). N.capensis have been encountered in sound-scattering layers off Namibia by D'Arcangues (1977).

The feeding habits of the local euphausiid fauna was first reported by Nepgen (1957) who found them to be omnivorous. Observations on N.capensis by Lazarus (1975) showed that the larval stages contained only diatoms whereas the juvenile and adults contained, in addition to diatoms, copepod and amphipod remains. Larval stages of euphausiids in the gut indicated them to be cannibalistic. Pillar (1984c, 1985) carried out selective feeding experiments with larval stages of E.lucens and N.capensis using mixtures of Artemia nauplii, copepod nauplii and phytoplankton as food. He showed that a mixed or pure diet of phytoplankton (Tetraselmis chuii) and Artemia nauplii, but not a diet of copepod nauplii, was sufficient for proper larval development. He pointed out, however, that Artemia nauplii is a poor indicator of carnivorous feeding behaviour since it is captured as a passive particle, whereas the larvae would have more difficulty in capturing the more active copepod nauplii. Nevertheless, he provided evidence that they can capture and utilise copepod nauplii at later stages of their larval development.

Field observations by Pillar (1983) have shown the co-occurrence both horizontally and vertically of E.lucens and anchovy larvae in the southern Benguela system. Laboratory studies indicate that juvenile and adult stages of this euphausiid are capable of capturing and ingesting 1 to 2-day-old anchovy larvae, which increased significantly with increasing age of predator.

2.5 Chaetognatha

Heydorn (1959), in a survey of works by Ritter-Zahony (1909, 1911), Gray (1923), Fraser (1937) and Thomson (1947), recorded 19 species of chaetognaths in South African waters, 12 species of which were present in his own material collected in the 'Cape routine area'. The chaetognath community of the Agulhas Current has been investigated by Stone (1969) who recorded 18 species, the majority being cosmopolitan warm-water forms of Indo-Pacific origin. From material collected in the 'Southern routine area', Masson (1973) recorded 24 species of chaetognaths (Table 2.4) which included all those reported by both Heydorn (1959) and Stone (1969). Venter (1969) reported on the occurrence of 10 species from collections in the 'Walvis Bay routine area', which were also included in Masson's material. As evidenced in the data obtained by the above authors, there is a close relationship of different chaetognath species with specific water masses in the Benguela system. Sagitta friderici, which is the most commonly occurring chaetognath, is indicative of cold neritic water, while S.minima, the second most common species, prefers the warmer offshore waters of mixed origin. Heydorn (1959) describes S.enflata and S.regularis as useful indicators of the penetration of water of Agulhas Current origin into the Benguela system. Other less common species are also considered to be useful in labelling water masses and determining their origin, even after there has been substantial mixing. S.serratodentata and S.tasmanica are indicative of the influx of South Atlantic subtropical surface water in the region. The occurrence of bathypelagic species such as Eukrohnia hamata and S.decipiens in coastal regions and the offshore displacement of S.friderici is considered as evidence of recent upwelling (Masson, 1973; Thiriot, 1978).

TABLE 2.4: Chaetognath species recorded off the west and southwest coast of South Africa (from Masson, 1973)

Sagitta friderici	Sagitta enflata
Sagitta lyra	Sagitta tasmanica
Sagitta robusta	Sagitta regularis
Sagitta decipiens	Sagitta serratodentata
Sagitta macrocephala	Sagitta neglecta
Sagitta pacifica	Sagitta bipunctata
Sagitta hexaptera	Eukrohnia bathypelagica
Sagitta pulchra	Eukrohnia fowleri
Sagitta bedoti	Eukrohnia hamata
Sagitta minima	Krohnitta pacifica
Sagitta ferox	Krohnitta subtilis
Sagitta planctonis	Pterosagitta draco

The degree of penetration of chaetognaths into the Benguela system either from Agulhas Current water or from South Atlantic subtropical surface water is dependent on the amount of upwelling that has recently occurred. The cold upwelled waters of the western coast act as a barrier to the northern extension of some species of chaetognaths. When this barrier is relaxed, many chaetognath species are transported northwards by the Benguela Current. The scarcity, however, of some typically Indo-Pacific species such as S.robusta and S.neglecta indicates the restricted movement of these forms into the Benguela system. Venter (1969) recorded no Indo-Pacific species in his material collected in the northern Benguela region which seems to suggest that the Lüderitz upwelling zone is an effective environmental barrier to certain species in the Benguela.

Masson (1973) found that both S.friderici and S.minima spawned continuously throughout the year. There were, however, notable peaks in spawning in winter and spring in accordance with the maximum occurrence of the adult population. He postulated that there were at least five generations of S.friderici per year in the southern regions and noted a tendency for spawning to occur inshore in the winter and offshore during the summer. For certain species, such as S.lyra and Eukrohnia hamata, immature stages were found to inhabit shallower water than the adults. This pattern has been documented for other species in other areas (Alvarino, 1965), hence any surface current will have a pronounced effect on the juveniles and less effect on the adult distribution. The fact that the juveniles are more widely distributed than the adults of a particular species can be explained by their susceptibility to surface water movement. Masson (1974) also attributes this observation to the possibility that the juveniles have a greater tolerance to changing conditions when transported out of their preferred habitat.

Venter (1969) noted the neritic preference of S.friderici in Namibian waters. It constituted numerically 90% of all the species recorded in coastal waters there while forming only 24% of the chaetognath population in the offshore regions. Although it was described as being associated with cold water it was noted that its maximum occurrence was not coincidental with periods of upwelling. Its seasonal occurrence in this region is similar to that found in the southern Benguela, being maximum during the winter and spring. In the northern Benguela Current S.tasmanica occupies the place held by S.minima in the warm offshore waters of the southern Benguela regions. The former species represented 70% of the chaetognath population in the offshore waters while the latter species only constituted 3% of the whole chaetognath community (Venter, 1969). Although both S.friderici and S.tasmanica are reported by Thiriot (1978) as being particularly dominant in upwelled areas along the African Atlantic coast, S.friderici is often located far beyond the centre of upwelling along the west African seaboard.

The carnivorous feeding behaviour of chaetognaths was supported by Lazarus (1975) who identified 19 types of prey in the gut of S.friderici. Only one species of phytoplankton was recorded, and occurred only in 1% of the specimens. Copepods, cirripede nauplii, decapod larvae, and hyperiid amphipods all formed important parts of their diet, also the cannibalistic nature of this species was noted by the author. No fish larvae remains were noted in the gut contents. Consumption of fish larvae by chaetognaths has, however, been frequently inferred elsewhere from both examination of field specimens and from laboratory experiments (Hunter, 1984), but is role as a predator in the Benguela system is not well documented.

2.6 Amphipoda, Hyperiidae

Using material drawn mainly from the reports of Barnard (1932, 1940), Siegfried (1963) compiled a list of 77 hyperiid species found off the western coasts of South Africa and Namibia (Table 2.5). From material collected from an area between the Agulhas Bank on the southern coast (38°S) to the northern border of Namibia (17°S), he found most species occurred north of the Cape of Good Hope with 27 occurring off the southern coast. Dick (1970) examined material covering the southwestern and eastern coasts of South Africa and recorded 105 species, of which 20 were additional to the western coast fauna. The numerical importance of Themisto gaudichaudi (recorded as Parathemisto gaudichaudi by Siegfried, 1963) in the amphipod fauna of the Benguela system is confirmed by the above authors and by Siegfried (1965), who reported it as being one of the most characteristic and abundant members of the neritic plankton off the western coast of South Africa.

TABLE 2.5: Hyperiid amphipod species recorded off the western coast of South African and Namibia (from Siegfried, 1963)

Lanceolidae

Lanceola serrata
Lanceola pacifica
Scypholanceola vanhoeffeni

Scinidae

Scina crassicornis
S. curvidactyla
S. incerta
S. langhansi
S. borealis
S. uncipes f. affinis
S. oedicarpus
S. woltereckí
S. rattrayi
S. tullbergi
S. nana
S. exisa
S. stenopus

Vibilidae

Vibilia viatrix
V. propinqua
V. antarctica
V. armata
V. cultripes
V. chuni
Cyllopus magellanicus

Paraphronimidae

Paraphronima gracilis
P. crassipes

Cystisomatidae

Cystisoma coalitum

Phrosinidae

Phrosina semilunata
Primno macropa
Anchylomera blossevillei

Lycaeopsidae

Lycaeopsis themistoides

Pronoidae

Eupronoe minuta
E. maculata
E. armata
Parapronoe crustulum
P. campbelli
Sympronoe parva

Lycaeidae

Tryphana malmi
Lycaea nasuta

Brachyscelidae

Brachyscelus crusculum
B. rapax
Thamneus platyrhynchus

Oxycephalidae

Simorhynchotus antennarius
Oxycephalus clausi
O. latirostris
Streetsia pronoides
S. porcella
S. steenstrupi
Cranocephalus scleroticus
Leptocotis tenuirostris
Rhabdosoma whitei

TABLE 2.5: continued

Hyperiidae	Parascelidae
Hyperia galba	Parascelus edwardsi
H. promontorii	Schizocelus ornatus
Hyperioides longipes	Thyropus sphaeroma
Hyperoche medusarum	
Parathemisto (Euthemisto) gaudichaudi*	**Platyscelidae**
Phronimopsis spinifera	
	Platyscelus ovoides
Dairellidae	P. armatus
	P. serratulus
Dairella latissima	Hemityphis rapax
	Amphithyrus bispinosus
Phronimidae	A. sculpturatus
	Paratyphis maculatus
Phronima sedentaria	Tetrathyrus forcipatus
P. atlantica	
P. atlantica var. solitaria	
P. pacifica	
P. colletti	
P. stebbingi	
Phronimella elongata	

* Themisto gaudichaudi

Siegfried (1963) found ovigerous females of T.gaudichaudi throughout the year. Further observations by Siegfried (1965) from the 'Cape routine area', showed an increase in their abundance during the spring and a low occurrence during the winter. The maximum reproductive activity displayed during the spring was reflected in his data by an increase in the abundance of mature individuals during the summer and autumn. This early attainment of maturity allowed for the production of a number of successive

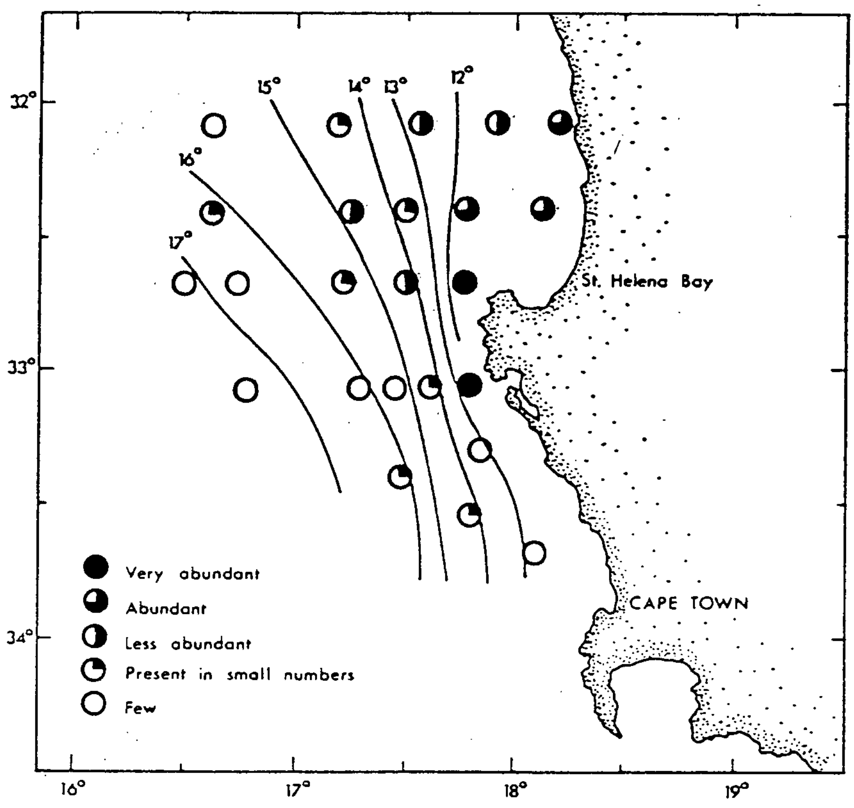

Figure 2.9 Density distribution of Themisto gaudichaudi and average of 0-50m integral temperatures from April 1954- March 1955 (after Siegfried, 1965)

generations each spring and summer, which he suggested maintained an abundant population in the southern Benguela region. Hopson (1983) found a progression of growth stages of T.gaudichaudi in her collections off the Lambert's Bay area. In agreement with Siegfried (1965), her data suggested continuous reproduction throughout the year with an overwintering group of adults which produced a spring spawning, which in turn produced another generation in late summer.

The cool neritic preference of T.gaudichaudi (Figure 2.9) was shown by Siegfried (1963, 1965), and Hutchings (1979) and Hopson (1983) also found it more abundant in cool inshore waters off the western coast during periods of active upwelling. It has also been reported in appreciable numbers over the Agulhas Bank where small populations were found centred over an area of upwelling (De Decker, 1973).

Siegfried (1965) found T.gaudichaudi to be a voracious feeder on plankton and to be unselective in their feeding habits. In most cases he found the frequency of occurrence of prey in their guts reflected the frequency with which the prey occurred in the water. Zooplankton items ranged from small copepodite stages to juvenile euphausiids, decapod larvae and fish larvae. He identified five genera of phytoplankton which were consumed to a greater degree by the juveniles than by the adults. Lazarus (1975) found 61 different kinds of food in the guts of this species of which 12% consisted of zooplankton remains. Field evidence indicates this species to be strongly predatory on fish larvae (Hunter, 1984).

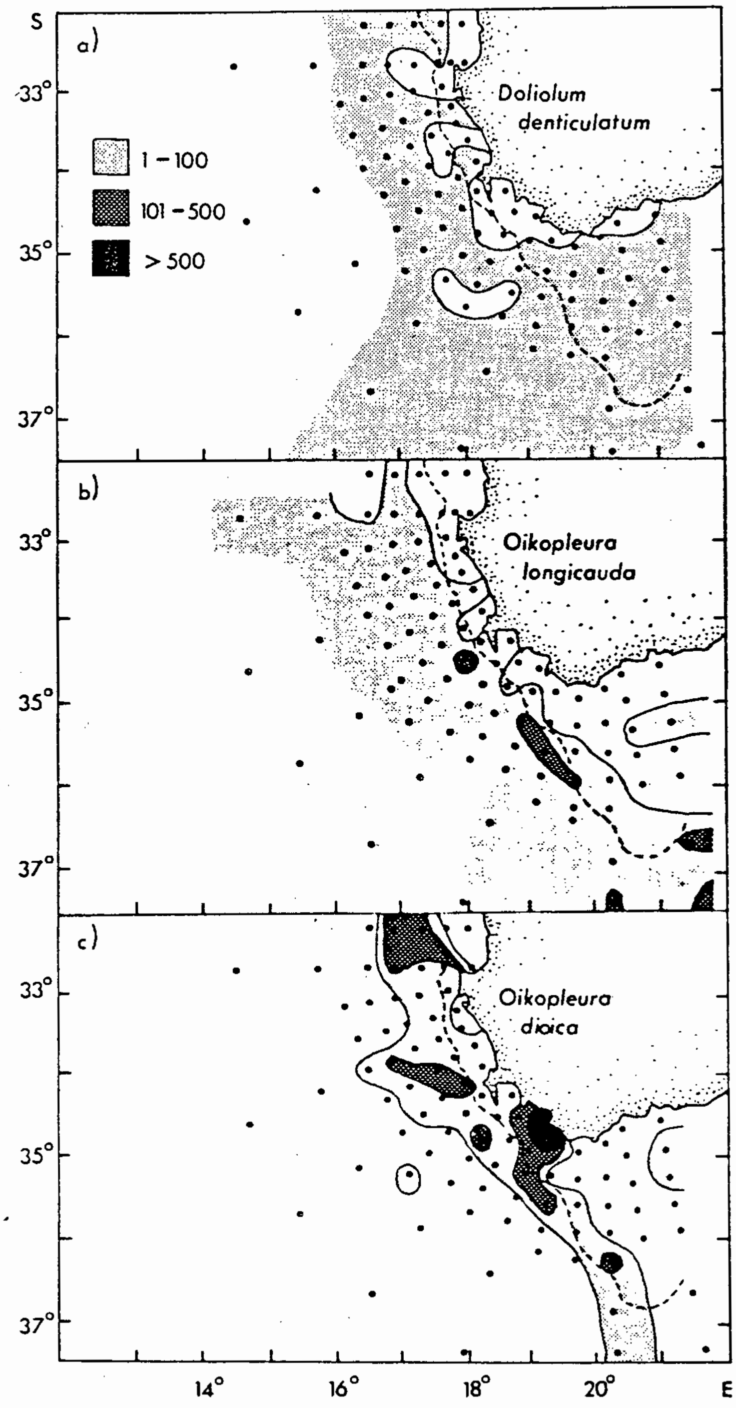

Figure 2.10 Distribution of (a) Doliolum denticulatum, (b) Oikopleura longicauda and (c) Oikopleura dioica during the summer and winter period of 1964 (after Lazarus and Dowler, 1980)

2.7 Tunicata

Van Zyl (1960) investigated the distribution of doliolids and salps in the 'Cape routine area' and listed 11 species of thaliaceans. A follow-up of this work by Lazarus and Dowler (1980) reported on 23 species of thaliaceans and 26 species of appendicularians from material collected monthly over a two-year period (1964-1965), from the 'Southern routine area' (Table 2.6). A brief summary of unpublished data by Dowler was incorporated into an earlier report by De Decker (1973) in his account of the Agulhas Bank plankton. The seven most commonly occurring western coast tunicates recorded by Lazarus and Dowler (1980) were three thaliaceans, *Thalia democratica*, *Salpa fusiformis* and *Doliolum denticulatum*, and four appendicularians, *Oikopleura longicauda*, *O.dioica*, *Fritillaria formica* and *F.pellucida*. The use of several of these species as indicators of different water masses was demonstrated by De Decker (1973) and Lazarus and Dowler (1980).

Of the thaliaceans, *T.democratica* and *D.denticulatum* are indicative of warm water and good indicators of water of Agulhas origin. In the typical forms of *D.denticulatum*, there is a strong tendency for the oozoids (nurse stages), the phorozoids (solitary stages) and the gonozoids (aggregate stages) to avoid the cool inshore waters. The restriction placed by temperature on the distribution of *D.denticulatum* in the southern Benguela region was illustrated by Lazarus and Dowler (1980) during their October 1965 collections when areas of cool water in the Walker Bay, Cape Peninsula and St Helena Bay regions excluded this species (Figure 2.10a). They noted

TABLE 2.6: Thaliacea and Appendicularia species recorded off the western and southwestern coasts of South Africa (from Lazarus and Dowler, 1980)

Oikopleura intermedia	Fritillaria sp.
Oikopleura fusiformis	Folia sp.
Oikopleura longicauda	Oikopleura sp.
Oikopleura cophocerca	Kowalevskaia oceanica
Oikopleura rufescens	Thalia democratica
Oikopleura dioica	Thalia longicauda
Oikopleura parva	Salpa fusiformis
Oikopleura cornutogastra	Salpa maxima
Oikopleura albicans	Salpa cylindrica
Megalocercus huxleyi	Ihlea magalhanica
Stegosoma magnum	Iasis zonaria
Althoffia tumida	Traustedtia multitentaculata
Tectillaria fertilis	Pegea confoederata
Fritillaria formica	Cylcosalpa pinnata
Fritillaria borealis	Doliolum denticulatum
Fritillaria pellucida	Doliolum nationalis
Fritillaria megachile	Doliolum denticulatum var. ehrenbergii
Fritillaria haplostoma	Doliolum mirabilis
Fritillaria fraudax	Doliolетta gegenbauri
Fritillaria bicornis	Doliolетta tritonis
Fritillaria taeniogona	Pyrosoma sp.

that this species was abundant in the warmer well-mixed waters further off the western coast and over the Agulhas Bank. Only when the warmer waters ($>14°C$) penetrated inshore on the western coast did the authors observe D.denticulatum near the coast. This distributional pattern was also observed in T.democratica and to a lesser extent in S.fusiformis. They were not found in areas associated with cool water and were only observed offshore in mixed warm water.

Among the less abundant species of thaliaceans reported by De Decker (1973), only Doliolum nationalis showed a preference for areas of cool water. On the rare occasions when it was observed it occurred inshore in upwelling areas off the western coast. The affinity of this species for low temperatures was also noted by Van Zyl (1960). D.nationalis is exceptional among local thaliacean species in having its maximum occurrence during winter when the other species show a decline during this period. The peak abundances of the other species were reported by the above authors as occurring during the spring and summer.

Of the common appendicularian species reported by Lazarus and Dowler (1980), Oikopleura dioica and Fritillaria formica showed a preference for cool water, whereas Oikopleura longicaudata and Fritillaria pellucida showed a preference for warmer waters. This pattern was clearly indicated in their July 1964 distribution maps showing the two species of the genera Oikopleura (Figures 10b and 10c). During this period, inshore upwelling was noted east of the Cape Peninsula. There was very little penetration into this area of O.longicauda; further offshore in warmer waters the species was, however, well represented. Contrary to this, O.dioica occurred in abundance close inshore in the cooler waters while progressively decreasing in numbers offshore. The former species is shown to be indicative of the warm waters of Agulhas origin, while the latter proved to be indicative of cooler upwelled water. A comparison of the abundance of these two species by the above authors showed that over the entire area studied O.dioica was the less abundant species. It, however, was predominant in the appendicularian community of the western coast. Similar findings were also noted by Lazarus (1975) from inshore collections taken between Table Bay and St Helena Bay.

Analysis of gut contents by Van Zyl (1960) showed that thaliaceans fed mainly on phytoplankton in inshore areas and zooplankton in offshore areas. Zooplankton remains consisted mainly of young stages of copepods, amphipods and euphausiids. Large salps such as Salpa maxima had traces of fish eggs together with phytoplankton remains in their stomachs. Lazarus (1975) found inshore specimens of appendicularians to be entirely herbivorous.

2.8 Decapod larvae

Decapod larval studies in the Benguela system have been principally concerned with the development and distribution of the phyllosoma stages of the commercially important rock lobster, Jasus lalandii. Lazarus (1967) examined phyllosoma larvae from material collected over a three-year period (1961-1964) in the 'Southern routine area' and identified 13 larval stages. He estimated that these larvae spent between 9-11 months in the plankton after hatching from eggs in September to November each year. The early stage larvae were found in large numbers in nearshore waters during the summer but thereafter middle and late stage larvae were rarely encountered in his inshore collections. Late stage larvae were only found well offshore as far as 300km west during the winter. Later studies by Pollock and Goosen (1983) in the southeastern Atlantic confirmed the offshore distribution of the late stage phyllosoma larvae, although relatively few individuals were caught. They found their distribution extended westward over the shelf break to as far as 13°30'E. The contention of both Lazarus (1967) and Pollock and Goosen (1983), that some of the larvae encountered further west are those of *Jasus tristani* of Tristan da Cunha origin, is still inconclusive owing to the taxonomic difficulties in distinguishing between these two species at the phyllosoma stage.

Since phyllosoma larvae are unable to swim against currents of any appreciable magnitude, return transport mechanisms are thought to play an important role in preventing all the larvae from being advected out of the Benguela system. The role of vertical migratory behaviour coupled with underlying inshore countercurrents and eddies have been proposed by Lazarus (1967), Duncan and Nell (1969) and Pollock and Goosen (1983) as being possible return mechanisms. Pollock and Goosen (1983) also reported late larval stages occurring in the top 11m at night and deeper than 200m during the day. No significant data on the distribution of the older puerulus stages could be gleaned from their collections due to their ability to avoid the sampling gear. They speculated that once metamorphosis from phyllosoma into puerulus occurs offshore, their progressively stronger swimming capabilities enables them to return to the shallow coastal waters.

Lazarus (1975) found only early phyllosoma larvae and the occasional puerulus stage of *J.lalandii* in his nearshore collections. Gut contents of the former yielded only phytoplankton remains, whereas the latter were principally carnivorous, feeding mainly on crustaceans and larval bivalves.

2.9 Other species

Table 2.7 lists six other zooplankton taxa that have been studies to a lesser degree than those discussed earlier. The major contributions to the study of these groups was by Lazarus (1975) from inshore collections between the Cape Peninsula and St Helena Bay.

TABLE 2.7: Synopsis of work on six other taxa

Taxa	Details of findings	References
Cladocera	Dominant species in the southern Benguela are Evadne spinifera and Podon sp. They prefer thermoclines or warm surface water. Minimum during winter in nearshore water. Penilia avirostris is found off the western coast but is considered a typical member of the Agulhas Bank community.	De Decker, 1973; Hutchings, 1979; Carter, 1983
	Dominant species in the northern Benguela are Podon polyphemoides and Evadne nordmanni. Both species are abundant throughout the year. The former found inshore of the shelf while the latter species extends beyond the shelf.	Unterüberbacher, 1964
Mysidacea	The dominant species is Mysidopsis major with Mysidopsis similis, Mysidopsis schultzei, Anchialina truncata and Gastrosaccus psammodytes being present in appreciable numbers. Breeding is continuous throughout the year with a spring maxima and a winter low.	Lazarus, 1975
	The mean biomass of Mysidopsis major in a southern Benguela kelp bed was estimated to be 116mg dry wt.m^{-2} being an order of magnitude less than the smaller zooplankton biomass (principally copepods). Their mean daily ration requirements represented only 0.08% of the total primary production. Production of this species in the study area was estimated as 246mgC.m^{-2}.yr^{-1} with an annual P/B estimate of 5.7.	Carter, 1983

TABLE 2.7: continued

Ctenophora	Two species, Pleurobrachia pileus and Beroe forskali recorded in nearshore Cape waters. Maximum occurrence of the former species during winter and the latter during summer and autumn. Noted as being carnivorous and a potential predator of fish larvae.	Lazarus, 1975
Cnidaria	Eleven genera recorded in nearshore Cape waters. Sizes and seasonality of different genera discussed. Zooplankton remains were observed in the stomachs of a number of species.	Lazarus, 1975
	Stranding of Physalia on the beaches in the South Western Cape during January 1983 is considered to be a consequence of the anomalous meteorological oceanographical conditions during the 1982-1983 summer period.	Shannon and Chapman, 1983
Cirripedia	Abundance and distribution of cypris nauplii and larval stages of the western coast are described for Balanus algicola (the most dominant species) and for Balanus amphitrite var. denticulata, Tetraclita serrata and Octomeris angulosa. Their abundance declined during the winter months.	Lazarus, 1975
	Cypris nauplii and larvae recorded as preferring warm water.	Hutchings, 1979; Carter, 1983
Isopoda	Seven species are recorded of which Eurydice longicornis and Paridotea ungulata comprised numerically 87 and 9%, respectively, of the population. Peaks of abundance and maximum breeding occurs during the spring months.	Lazarus, 1975

2.10 PRESENT AND FUTURE ZOOLPLANKTON RESEARCH IN THE BENGUELA

The main direction of zooplankton research in recent years has been towards a better understanding of the functional aspects of zooplankton populations, not as a single entity, but on dominant species to which the concept of population dynamics may best be applied. Research in this direction has lagged behind that of the physical, chemical and phytoplankton work, largely because of the lack of intensive short-term surveys such as those first reported by Hutchings (1979) in the Cape Peninsula. With the exception of the work by Carter (1983) on the energetics of zooplankton in the kelp-bed zone, when time scales in the order of hours to days were used, the only attempts at elucidating the dynamics of local zooplankton are from surveys of at least one month apart. Under such sampling programmes documentation is limited to large scale phenomena, such as faunal changes associated with seasonal hydrographic changes and faunal differences between nearshore and offshore regions. Nevertheless, surveys such as The Cape Egg and Larval Programme (CELP) have provided material which has added considerably to our knowledge of the spatial and temporal distribution of local zooplankton communities, e.g. Hopson (1983). These collections, using Bongo nets, are considerably more quantitative than earlier investigations. In addition, the superior catching ability of these nets has facilitated more reliable mapping of the distribution and abundance of larger zooplankton such as euphausiids. The mesh size of these nets (300μm) has allowed for a quantitative evaluation of all developing stages of the local, dominant euphausiid species, Euphausia lucens. These data are at present being documented in relation to concomitant physical-chemical data as a basis towards a better understanding of the life history adaptations of this species in the southern Benguela system.

Recent developments in the techniques for sampling zooplankton have resulted in the construction of a small meshed (200μm) large-mouth multiple net system (RMT 1x6), which can sample up to six different depths in one operation using electronically operated opening and closing devices. This net has allowed for the examination of the vertical distribution of a wide size range of zooplankton organisms. In addition, it allows sampling of the entire water column so that organisms may not migrate beyond the tracking range of the net. On-going hydroacoustic surveys for mapping pelagic fish stocks off the South African seaboard have incorporated the RMT 1+6 in their sampling programme in order to address questions regarding the importance of zooplankton in the feeding ecology of economically important fish species. These collections have provided useful material for examining the depth distribution of key zooplankton species in relation to environmental factors such that their transport and maintenance mechanisms can now be quantitatively evaluated.

In considering future research, short-term studies will be conducted primarily in the Cape Columbine and St Helena Bay area. In this important fishery recruitment area environmental conditions, such as wind and current patterns, have been closely monitored over a number of years, hence some physical understanding of the processes is available and could be used in the study of the dynamics of zooplankton in this region. A major emphasis will be placed on the formation of patches of suitable zooplankton food organisms and the rates of consumption of young and adult fish in these patches. Given that reasonable estimates of zooplankton production can be derived from biomass estimates in the field and laboratory and field-derived estimates of grazing, growth and generation times from ongoing research, the relative rates of growth versus feeding and dispersion need to be examined in order to derive better estimates of the carrying capacity in terms of zooplankton in important recruitment and spawning areas of the Benguela system. Central to this approach would be the deployment of a continuous depth profiling sampler such as the Batfish (Herman and Denman, 1977) which may soon be operational. The high vertical and horizontal resolution capabilities of this instrument offer tremendous scope for refining our present broad-scale studies so that critical relationship concepts between zooplankton and environmental variables can be formulated and tested more efficiently. This instrument will form the basis of a monitoring programme which will be initially deployed between Lambert's Bay and the Cape Peninsula to include the important St Helena Bay nursery area and will later be extended to include the Agulhas Bank spawning area.

The interest in quantitative analysis of zooplankton dynamics has resulted in the development of culturing and rearing facilities which was initiated in the early 1980s. Two main categories of study are at present being investigated. First, continuous cultures have been used as an aid in taxonomic work. The young stages of many of the commoner species in the Southern Hemisphere are poorly described and this information is vital to any work using a population dynamics approach. In rearing the euphausiids _Euphausia lucens_ and _Nyctiphanes capensis_, Pillar (1984c, 1985) studied their larval development under different trophic conditions. He showed that morphological characters were influenced by feeding condition, with similar morphological variations existing in wild populations. Culturing of dominant local copepod species such as Centropages brachiatus and Calanoides carinatus has contributed significantly to an improved understanding of their successive larval stages. To date nearly 60 species of planktonic marine and estuarine organisms, mainly fish larvae and copepods, have been successfully reared or cultured in the laboratory.

From a consideration of standing stock and laboratory determined respiration, feeding and excretion rates, Carter (1983) estimated the production and daily ration requirements of the zooplankton community of a kelp-bed zone off the Cape Peninsula. This approach is at present being extended towards the construction of energy and nitrogen budgets of the dominant euphausiid, Euphausia lucens. Factors influencing the physiological processes such as temperature, swimming speeds, feeding behaviour, food type and feeding rates are being investigated in this study. As techniques are improved, further studies on other major zooplankton groups are envisaged.

To investigate the idea that invertebrate predation on the commercially important anchovy larvae is of significance, extensive observations are being made on the food preferences and the effectiveness of various zooplankton groups as predators on these larvae. Having anchovy larvae of various sizes as well as juveniles and adults in captivity, has also permitted studies on cannibalistic behaviour in the laboratory.

The emphasis for future culture work lies in estimating quantitative values for the tropho-population dynamics of selected zooplankton groups. Olivieri (1985) and Carter (1983) have estimated that local zooplankton populations exert little impact on the phytoplankton community. It is suggested that the important factor limiting local zooplankton populations may be the transient nature of food availability and their inability to return to sites of high primary production. Laboratory studies by Borchers and Hutchings (1986) have shown that the adults of the common west coast copepod <u>Calanoides carinatus</u> are resistant to periods of starvation (8-12 days) but the juvenile stages are less so. There is clearly room for more laboratory studies on the feeding, growth, starvation tolerance and survival of zooplankton, such processes which cannot be successfully monitored in the ocean. These studies should be combined with field work for studying patchiness and its general significance to the trophodynamics of the zooplankton community. Knowledge of their general vertical and horizontal distributions and the system of currents and counter-currents needs to be drawn together to provide a picture of the life history adaptations of representative species.

CHAPTER 3

TEMPORAL AND SPATIAL VARIATIONS IN COPEPOD AND EUPHAUSIID BIOMASS OFF THE SOUTHERN AND SOUTH-WESTERN COASTS OF SOUTH AFRICA IN 1977/78

3.1 INTRODUCTION

Although a number of authors have discussed the distribution of major zooplankton groups of the South-Western Cape (see review by Shannon and Pillar, 1986), relatively little quantitative information has been published on the seasonal variation and inshore-offshore distribution of zooplankton on a scale covering the whole of this region. Estimates of settled-volume biomass by De Jager (1954) and De Decker (1973) provided little more than evidence of seasonal trends in zooplankton biomass in local waters. More quantitative data by Hutchings (1979, 1981) and Andrews and Hutchings (1980) provided a good understanding of the temporal and spatial distribution of mesozooplankton biomass in response to upwelling events off the Cape Peninsula. However, the type of sampling gear used for their studies (WP-2 net) did not representatively capture the larger, more motile macroplankton such as euphausiids (Pillar, 1984b). Hopson (1983) described the seasonal and inshore-offshore fluctuations of zooplankton biomass off Lambert's Bay (32°S) in relation to changes in the physical and the biotic environment. However, her conclusions did not take cognizance of the significance of diurnal vertical migration of the zooplankton, principally euphausiids.

Between August 1977 and August 1978 a monthly survey with Bongo nets was undertaken around the South-Western Cape by the Sea Fisheries Research Institute as part of the Cape Egg and Larval Programme (CELP). Of a total of 1 380 collections, 540 were made during the night. These extensive surveys provided material for a quantitative study of the mesoscale distribution of zooplankton biomass, especially of euphausiids, which are effectively captured by the Bongo net (Pillar, 1984b). The present study considers CELP data with the aim of contributing to the knowledge of the seasonal and inshore-offshore variations of zooplankton biomass with special reference to copepods and euphausiids. The information is discussed mainly in relation to existing knowledge of the physical and biotic characteristics of the southern Benguela region reviewed recently by Shannon (1985) and Shannon and Pillar (1986). These works complement earlier important studies by Andrews and Hutchings (1980), Nelson and Hutchings (1983) and Parrish et al. (1983).

3.2 MATERIALS AND METHODS

Samples were collected by double oblique hauls from the surface to either 100m or to 10m from the bottom in shallower water with a paired Bongo net (McGowan and Brown, 1966) of 0.57-m mouth diameter and fitted with 300 and 500 μm meshed nets. The volume of water filtered was computed from a calibrated digital flowmeter mounted centrally in the mouth of each net. Ship's speed, while towing, was regulated at approximately $1m.s^{-1}$ (2 knots) in order to maintain a wire angle as near as possible to 45°. The depth attained by the net was recorded by a bathythermograph. The collections were preserved in 5-per-cent buffered formalin.

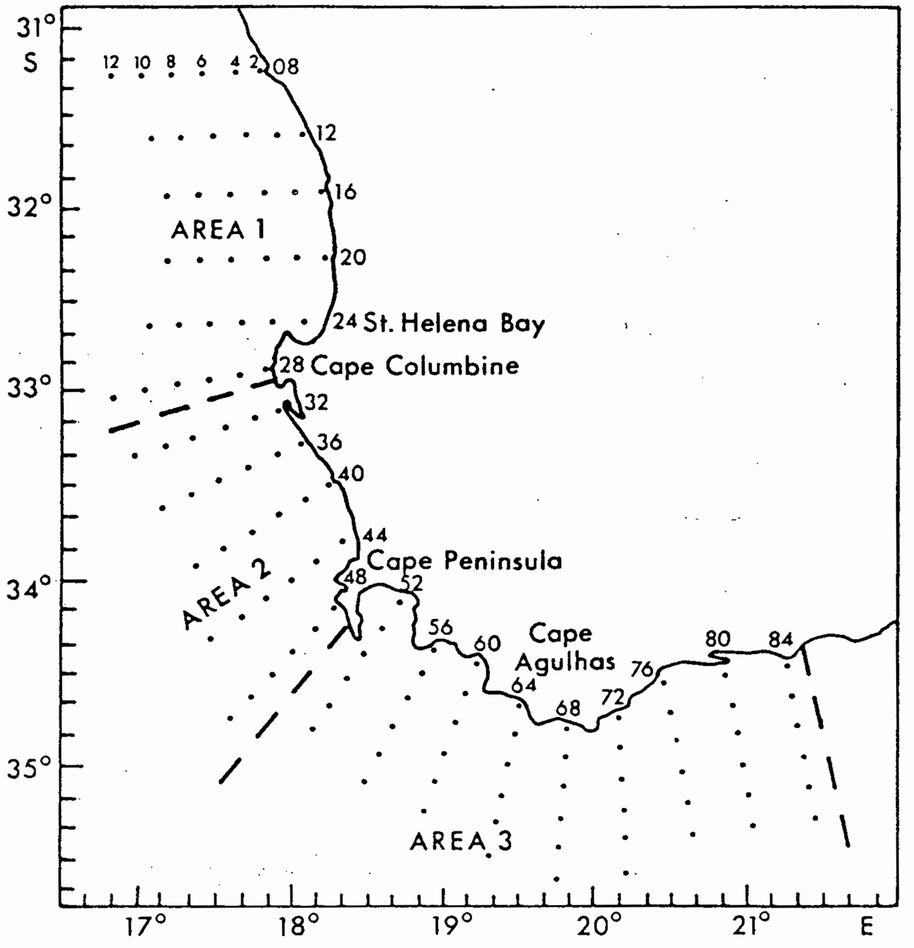

Figure 3.1 Station grid of the Cape Egg and Larval Programme (CELP) sampled monthly between August 1977 and August 1978 and Areas 1 (St Helena Bay/Cape Columbine, 2 (Cape Peninsula) and 3 (Agulhas Bank)

The CELP study area consisted of 120 stations around the south-western seaboard of South Africa, covering an area of approximately 78 000km^2. The stations were arranged in a grid pattern consisting of 20 lines, each 20 nautical miles (37km) apart with six stations to a line (Figure 3.1). The first station on each line was 2 miles (3.7km) from the coast and the remaining five were at 10-mile (18.5km) intervals offshore. Only night-time samples were used because juvenile and adult euphausiids would not be sampled representatively during the daylight hauls owing to their vertical migratory behaviour (Pillar, 1984a). Those samples considered to be non-quantitative because of either gear malfunction or suspected clogging of the net by phytoplankton were excluded. Night was taken to be the period from one hour after sunset to one hour before sunrise. From a total of 540 night-time collections, 519 were selected for analysis.

The collections with the 300 μm mesh net were selected for biomass studies. The samples were halved in a Folsom splitter and, after removing gelatinous organisms (mainly tunicates), one half was passed through a 1 600 μm mesh to sieve out the larger organisms. The other half was not used in the present analysis. The larger fraction contained all late larvae and adults of euphausiids, which formed the dominant taxon in this fraction. When other taxa (principally amphipods and chaetognaths) were present they were removed and analysed separately as 'other zooplankton'. The smaller fraction contained mostly copepods. Early larval stages of larger organisms were observed, but their contribution to the biomass of this 'copepod' fraction was considered to be small for the purposes of the present study. Dry weights of each category (i.e. copepods, euphausiids and 'others') were measured after draining the sample on a metal filter of

180 μm mesh for two minutes at 66mb vacuum and drying at 60°C for twenty-four hours (Lovegrove, 1966). The biomass estimates were standardised to milligrams under $1m^2$ of surface from a knowledge of the volume of water filtered and the depth range sampled by the net.

Within selected taxonomic groups, i.e. euphausiids and copepods, analysis of variance (ANOVA) procedures were used to detect areal (A) and monthly (M) differences, the effect of distance offshore (D) and interaction effects (if appropriate). Three areas contrasting in physical and biotic conditions were selected for the analysis and are illustrated in Figure 11. Area 1, the St Helena Bay/Cape Columbine area (Lines 08-28), is typified by a more stable environment than Area 2, the Cape Peninsula area (Lines 32-48), which is characterised by frequent pulses of upwelling resulting in a highly variable and unstable environment. Area 3, the Agulhas Bank area (Lines 52-84), is influenced by the warm water of the Agulhas Current, especially during the summer months when a strong thermocline is established (Brown, 1981; Shannon et.al., 1984; Shannon, 1985).

Preliminary inspection of the data revealed that variances were positively correlated with means, and therefore a $\log_{10}(x + 1)$ transformation was used to equalize variances and to normalise the data. The ANOVA used for the analysis was a fixed-effects model with unequal sizes and was computed with SAS, a Statistical Analysis System (SAS Institute Inc., 1982). A posteriori comparisons of the ANOVA results were made by means of the Scheffé test (Zar, 1974). This test indicated how the variations were apportioned between the subclasses. Additional non-parametric methods employed are described in Zar (1974).

TABLE 3.1: Mean biomass (mg dry wt/m^{-2}) and percentage composition of each zooplankton category for the areas illustrated in Figure 11

Parameter	Euphausiids	Copepods	Others	Total
Area 1 - St Helena Bay/Cape Columbine				
Mean biomass	1 164	1 167	124	2 455
Percentage of total biomass	47.4	47.5	5.1	
Number of samples				157
Area 2 - Cape Peninsula				
Mean biomass	464	873	148	1 485
Percentage of total biomass	31.3	58.8	9.9	
Number of samples				135
Area 3 - Agulhas Bank				
Mean biomass	270	610	11	891
Percentage of total biomass	30.3	68.5	1.2	
Number of samples				227

3.3 RESULTS

Table 3.1 gives the mean and the percentage of the total biomass of each zooplankton category for the three areas illustrated in Figure 3.1. The highest biomass was in Area 1, where similar proportions of euphausiids and

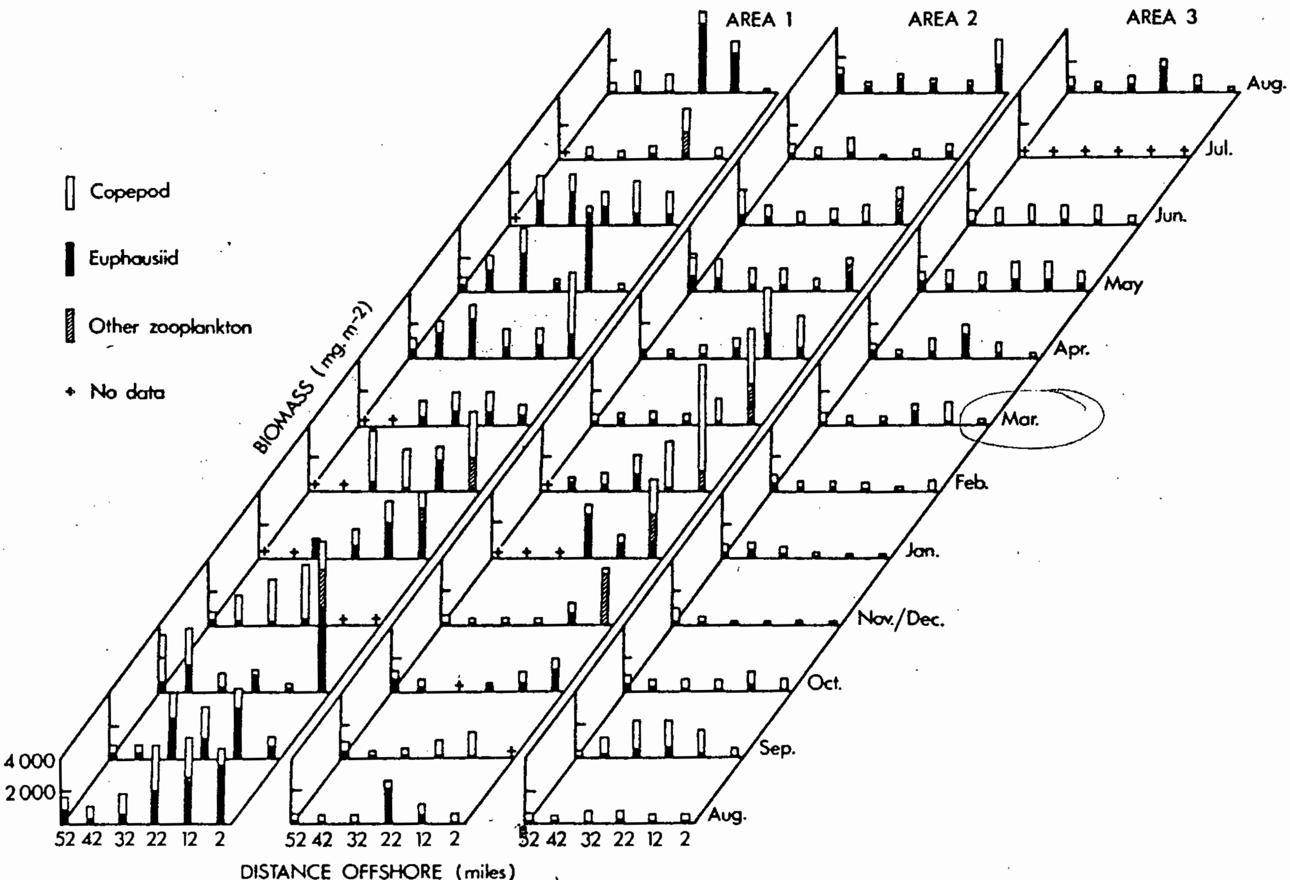

Figure 3.2 Three-dimensional display of spatial and temporal distribution of euphausiid, copepod and 'other zooplankton' biomass (mg dry wt.m^{-2}) for Areas 1, 2 and 3. Biomasses 50mg-m^{-2} are not shown

copepods made up 95 per cent of the total biomass. In Area 2, euphausiids and copepods constituted 90 per cent of the total biomass with larger proportions of copepods than euphausiids. In Area 3, copepods made up 68 per cent of the total biomass with euphausiids constituting most of the remainder.

Figure 3.2 illustrates the mean biomasses of euphausiids, copepods and 'other zooplankton' for each of the three areas with respect to distance offshore and month of sampling. Several patterns are apparent from this Figure. Both the euphausiid and copepod biomasses were consistently higher in Area I than in Area 2, where again they were generally higher than in Area 3. Biomasses of the three groups were highest inshore to within 22 miles of the coast and decreased with distance seaward. This trend differed in varying degrees depending on the area and the time of year. It is noteworthy that the relatively high biomasses of the 'other zooplankton' at the innermost stations in Areas 1 and 2 were due to abundant concentrations of gammarid amphipods at only two stations during the study period, i.e. the innermost stations on Lines 20 and 40 (Figure 3.1). Although amphipods were present at other stations, their abundance was relatively low and, together with chaetognaths and miscellaneous taxa, the contribution of 'other zooplankton' biomass to the total zooplankton, with the exception of the above-mentioned stations, is considered to be insignificant in the present analysis. Consequently only the features of spatial and temporal distribution of euphausiids and copepods were tested by means of ANOVA, as described earlier. A summary of the results is given in Table 3.2.

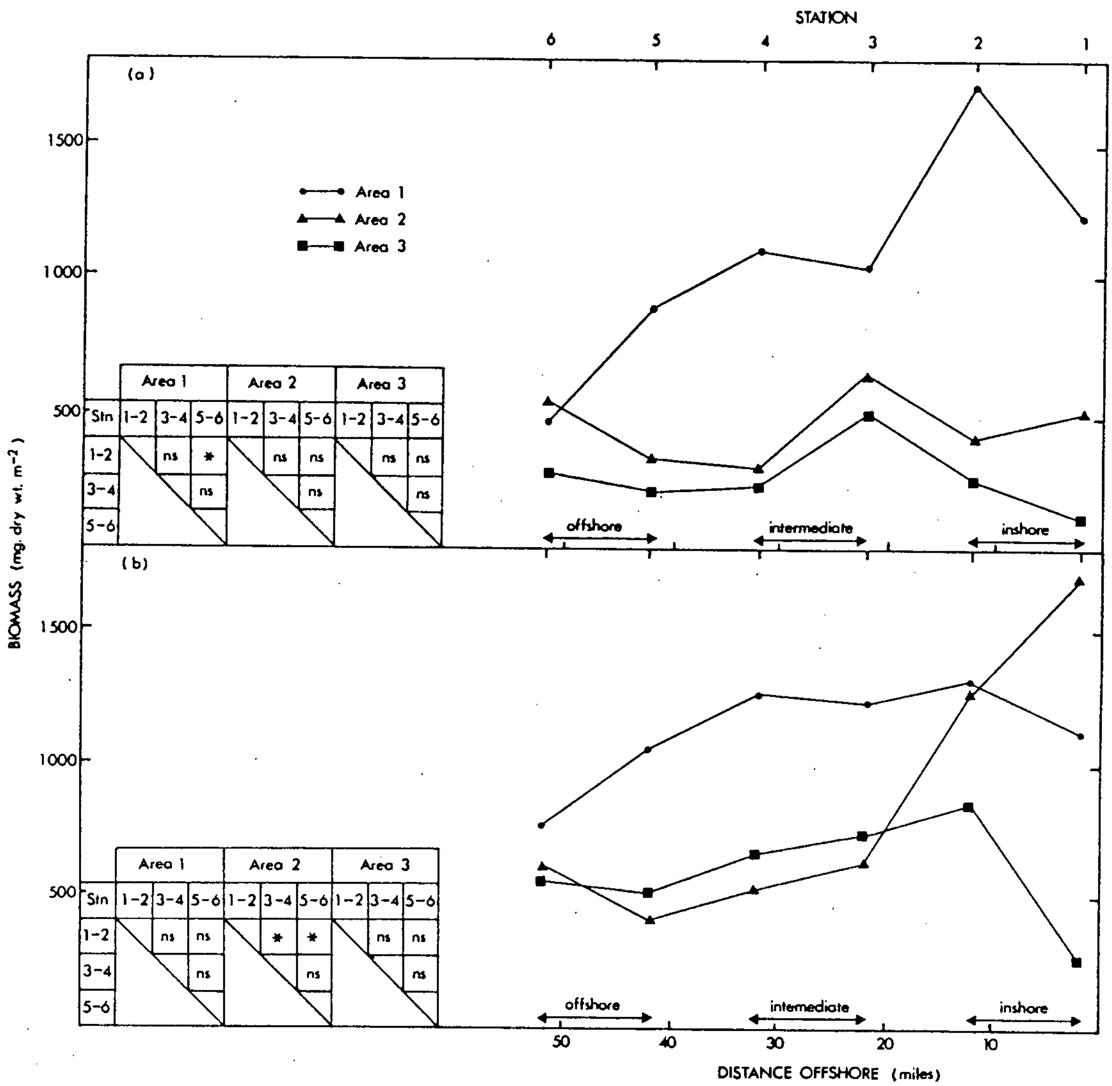

Figure 3.3 Areal and inshore-offshore variations in the biomass (mg dry wt.m^{-2}) of (a) euphausiids and (b) copepods. The results of the Scheffé test are given where * denotes $p < 0.05$ (significant) and ns denotes $p > 0.05$ (not significant). 1-2, 3-4, 5-6 denote inshore, intermediate and offshore respectively

3.3.1 Areal and inshore–offshore variations

Euphausiids – The A x D interaction was not significant, but the main effects A and D were significant (Table 3.2). Inspection of the subclass means shown in Table 3.1 reveals the areal differences. When examined further using the Scheffé test (Zar, 1974), significantly higher biomass was found in Area 1 than in Area 2, while the latter area had significantly higher biomass than Area 3.

TABLE 3.2: Analysis of variance of the euphausiid and copepod biomass categories (mg/m^{-2} log-transformed) showing the components of variance for each category

Source of variation	Euphausiids			Copepods		
	df	Mean square	Variance ratio F	df	Mean square	Variance ratio F
Area (A)	2	20.31	37.18*	2	2.67	22.70*
Distance offshore (D)	5	4.48	8.20*	5	0.29	2.50*
Month (M)	11	2.63	4.82*	11	0.40	3.40*
A x D	10	0.40	0.74	10	0.41	3.49*
A x M	22	0.97	1.86*	22	0.47	4.24*
D x M	55	0.71	1.29	55	0.11	0.97

* $p < 0.05$

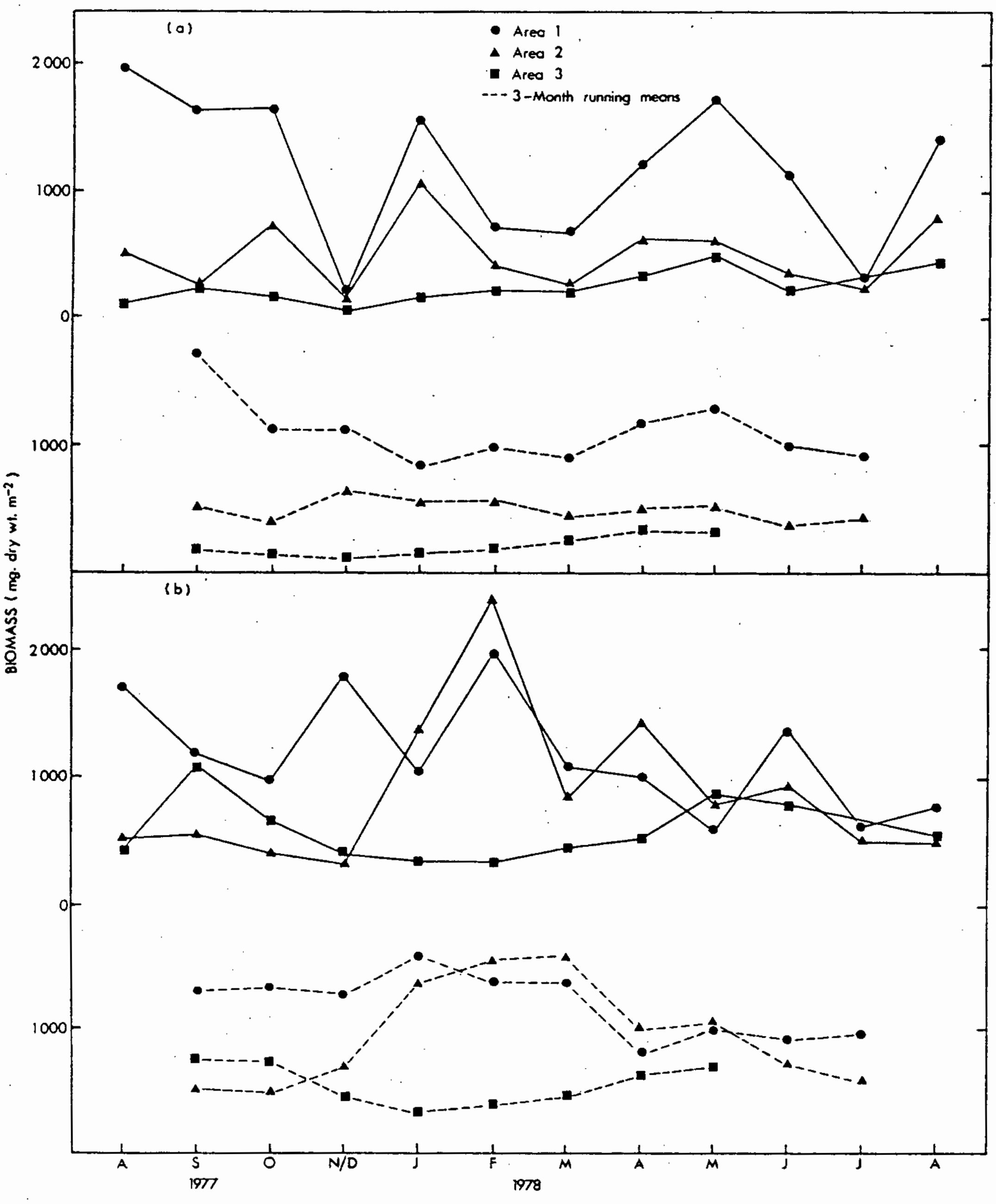

Figure 3.4 Areal and monthly variations in the biomass (mg dry wt.m^{-2}) of (a) euphausiids and (b) copepods

The subclass means of the main effect D were examined for each area, as shown in Figure 3.3a. The distance offshore was subdivided into inshore (2-12 miles), intermediate (22-32 miles) and offshore (42-52 miles), the corresponding means of each sub-division being pooled and examined statistically by means of the Scheffé test (Figure 3.3a). The results revealed that only Area 1 had significant inshore-offshore differences with higher biomass inshore than offshore. No significant difference in biomass existed between the intermediate stations and those further inshore or offshore in any of the three areas.

Copepods - The A x D interaction was significant, as were the main effects A and D (Table 3.2). From the Scheffé test, significantly higher biomass was recorded in Area 1 than in Area 2, but no sigificant difference existed between Areas 2 and 3. As regards inshore/offshore differences, only in Area 2 was there significantly higher biomass inshore (Figure 3.3b).

3.3.2 Monthly variability

Highly significant monthly differences in biomass were observed for both the euphausiid and copepod groups (Table 3.2). Subclass means based on pooled monthly biomasses for the different areas are shown in Figure 3.4. Monthly variations in biomass within each group and possible relationships between the groups were examined with Friedman's concordance test (Zar, 1974). Both the euphausiid and copepod biomasses displayed significant temporal concordance between Areas 1 and 2 ($p < 0,05$), but no significant similarity existed between these two areas and Area 3. No similarity in monthly variations between the different groups was displayed for any of the three areas, suggesting that euphausiids and copepods generally responded differently to monthly changes in the environment.

No marked fluctuations are apparent in any area for either group when the data are smoothed by 3-month running means, though the copepod group seemed to display a summer maximum and a winter minimum in Area 2 (Figure 3.4b). Seasonal variations are discussed in more detail in the next section.

3.3.3 Seasonal variability

Temporal variations were further investigated to determine any seasonal effect on the inshore/offshore distribution of the two zooplankton groups. Seasonal variations of each group for the three areas are illustrated in Figure 15 for two general seasons: September-March, representing summer and approximating the upwelling season when strong inshore/offshore gradients in physical properties occur, and April-August, representing winter when upwelling is minimal and inshore/offshore gradients are weakest within the study areas (Andrews and Hutchings, 1980). Seasonal differences in the inshore/offshore biomass were examined by the Scheffê test.

Euphausiids - Differences within this group in Area 1 were only significant 32 nautical miles offshore, where higher biomass was found during winter

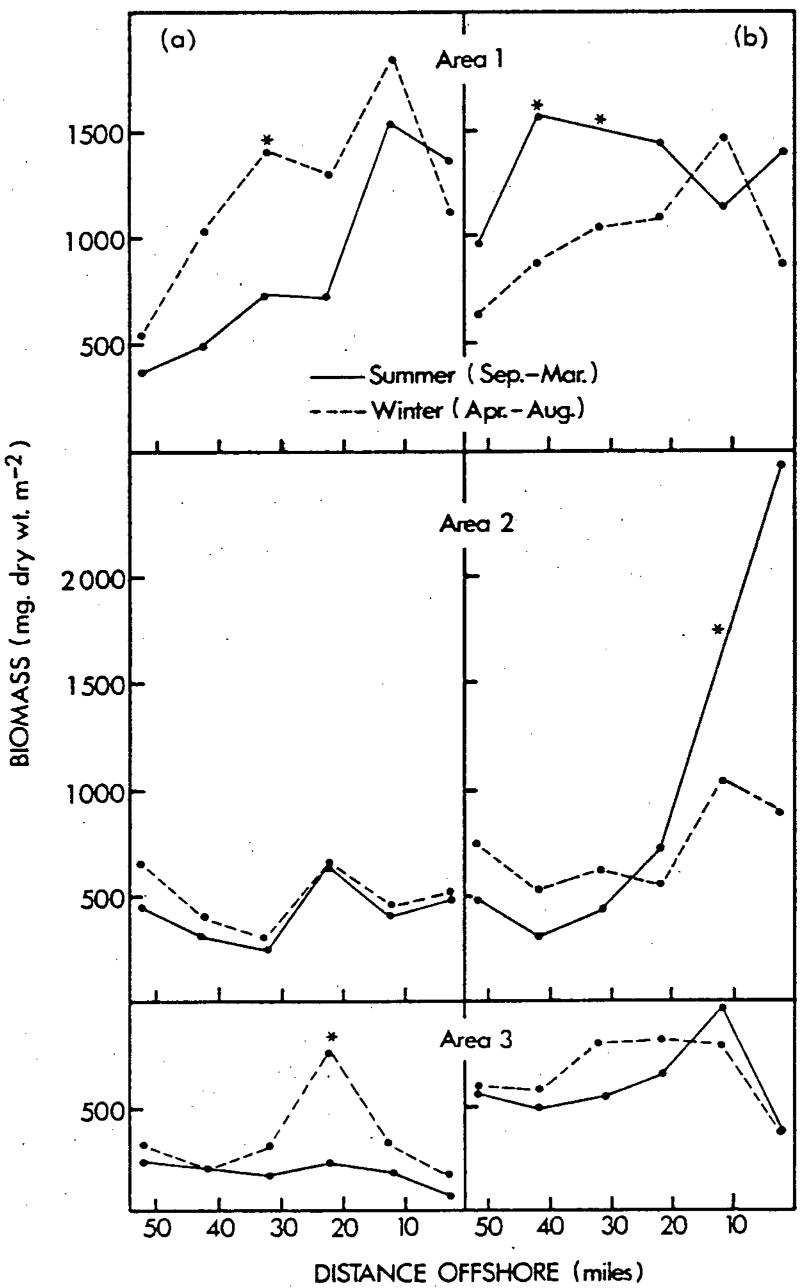

Figure 3.5 Areal and inshore-offshore variations in the biomass (mg dry wt.m^{-2}) during summer (September-March) and winter (April-August) of (a) euphausiids and (b) copepods. The results of the Scheffé test are given where * denotes $p < 0.05$ (significant)

(Figure 3.5a). In contrast to the situation pertaining to Area 1, the biomasses in Area 2 showed a marked lack of seasonal variation at all stations. The only significant seasonal difference in Area 3 occurred 22 miles offshore, where the biomass in winter was some three times greater than in summer.

Copepods - Few seasonal differences existed within this group (Figure 3.5b). The only apparent differences were 32 and 42 miles offshore in Area 1, where the biomass in summer was approximately double that in winter, and 12 miles offshore in Area 2, where the biomass was higher in summer. There was a three-fold increase during summer at the inshore station (2 miles from the coast) in Area 1. However, this difference was not statistically significant. This finding can be attributed to the large variability in copepod biomass there resulting from one collection which yielded a biomass some 13 times the summer mean.

Both taxa - In general there was close similarity between biomasses in the two seasons for both groups. Those apparent seasonal variations that were not statistically different may be explained by large variability that makes seasonal differences difficult to detect. Figure 3.6 shows the variability of both the euphausiid and copepod biomasses for each area and station over the sampling period. A marked decrease in the variability of both groups is shown from inshore to offshore in all three areas. Euphausiid biomass was generally more variable than copepod biomass regardless of the area.

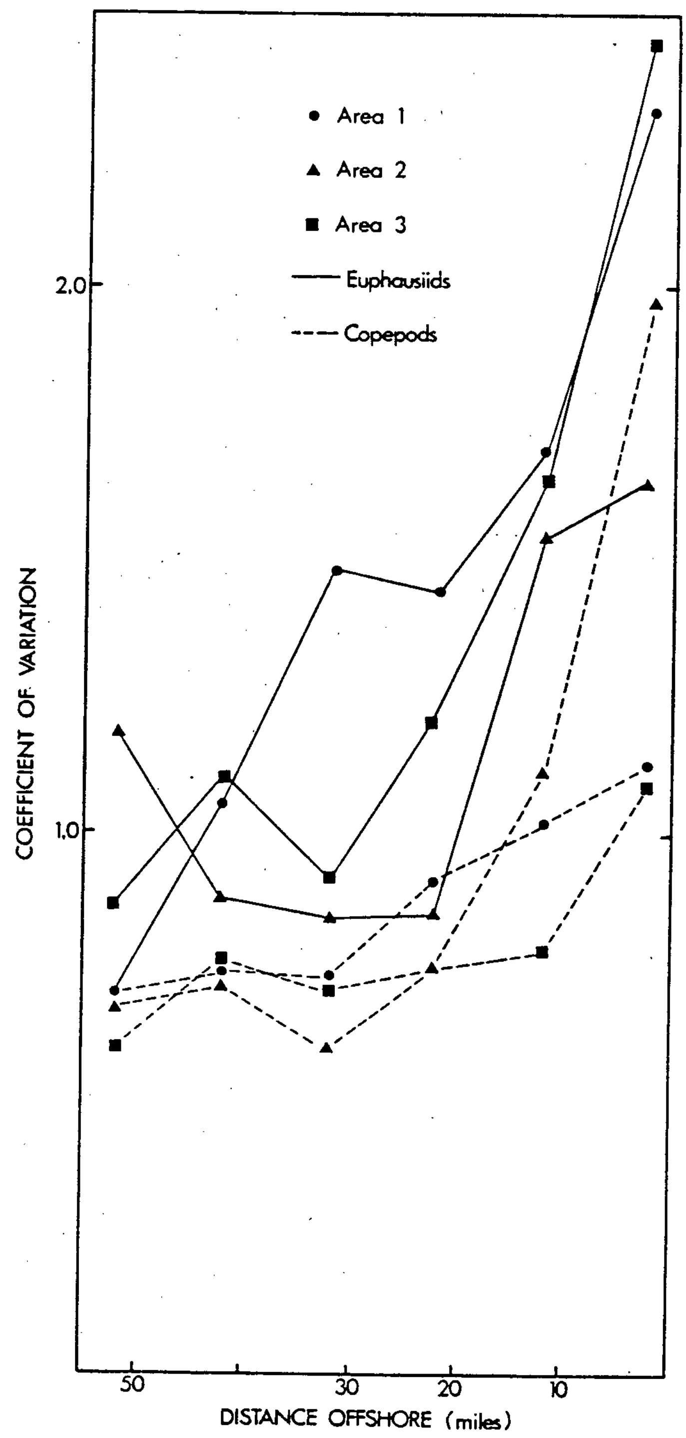

Figure 3.6 Inshore–offshore variability of the biomass of euphausiids and copepods with respect to area. Variability is expressed as coefficients of variation based on mg dry wt.m^{-2}

TABLE 3.3: Regional comparison of euphausiid and copepod biomass (mg dry wt.m^{-2}) from this study with those of Verheye and Hutchings (in press). The adjusted copepod biomasses are shown in parenthesis.

Area	Euphausiids			Copepods			Information source and sampling gear
	May	November	Annual mean	May	November	Annual mean	
Oliphants River - Cape Town	1 220	484	843	692 (1 280)	1 032 (1 909)	1 030 (1 906)	This study: Bongo 300 μm Pillar (1984b)
Western sector	2 102	444		1 080	1 609		Verheye and Hutchings (in press): RMT 1x6 200 μm
Cape Point - Cape Infanta	550	60	270	872 (1 613)	366 (677)	610 (1 129)	This study: Bongo 300 μm Pillar (1984b)
Southern sector		167		2 080	940		Verheye and Hutchings (in press): RMT 1x6 200 μm

3.4 DISCUSSION

3.4.1 Regional comparisons of zooplankton biomass

The higher biomass of copepods and euphausiids observed off the West Coast, relative to that in the Agulhas Bank area, is in accord with the results of Verheye and Hutchings, (in press) for the months of May and November (Table 3.3). This table shows that the copepod biomasses of this study are similar to those of Verheye and Hutchings (in press) after the present data have been adjusted to compensate for the differences in mesh size of the nets (Pillar, 1984b). De Decker (1973) found larger settled volumes of zooplankton over the Agulhas Bank than off the West Coast after a seven-year study of the southern Benguela region. He found this observation paradoxical, considering the three-fold greater phytoplankton biomass off the West Coast. De Decker further explained this observation as a bias in the settled volume estimates caused by the perennial presence of large numbers of pelagic tunicates in the Bank collections, which far exceeded those collected from the West Coast.

Andrews and Hutchings (1980) found a positive correlation between zooplankton and phytoplankton biomass and Hutchings (1981) used this feature to explain his observation of higher zooplankton biomass in St Helena Bay relative to that off the Cape Peninsula. Several authors have shown a progressive decrease in chlorophyll a concentrations from St Helena Bay to the Agulhas Bank (e.g. Hutchings et.al., 1983). This trend may account for the areal differences in zooplankton biomass evident from the present study.

copepod biomass in the Agulhas Bank area is not consistent with the marked seasonal changes in zooplankton biomass (principally copepods) observed by Hutchings and Nelson (1985) on the western edge of the Bank. These authors noted a positive relationship with the summer maxima of phytoplankton biomass during upwelling-favourable south-easterly winds.

The uniformity of euphausiid biomass recorded in this study is in contrast to the observations of Gow (unpublished data, cited by De Decker, 1973), who noted a winter maximum off the South-West Coast and over the Agulhas Bank. Conversely, Nepgen (1957) found a marked summer maximum during his two-year study of the St Helena Bay/Cape Columbine area. Hopson (1983) found both a winter and a summer peak in euphausiid concentration from a one-year study just north of St Helena Bay. However, it should be emphasised that none of these previous studies has taken cognizance of the effects of diel migration and the significance of this bias in estimating euphausiid abundance from pooled day-and-night data. Neither were these earlier findings substantiated statistically.

Seasonal inshore/offshore fluctuations of zooplankton biomass off the Cape Peninsula were observed by Andrews and Hutchings (1980). During spring and summer, multiple peaks of zooplankton occurred offshore as a result of displacement during active upwelling. Hutchings (1981) described the movement of zooplankton patches during a complete wind cycle off the Cape Peninsula. He concluded that zooplankton could be displaced some 40-90km offshore during an active upwelling event. Evidence for this mechanism is suggested in the St Helena/Cape Columbine area, where significant increases in copepod biomass are displayed at the stations 32 and 42 miles offshore

CHAPTER 4

LABORATORY STUDIES ON THE LARVAL GROWTH AND DEVELOPMENT OF *EUPHAUSIA LUCENS* (EUPHAUSIACEA)

4.1 INTRODUCTION

Boden (1955) first described what he believed to be the early stages of Euphausia lucens from a small collection from the Benguela Current. He was unable to describe the later larval stages in detail because his specimens were accidently destroyed. With material collected from New Zealand waters, Bary (1956) described different morphological characters for the larval stages of E.lucens, claiming that his series rather than Boden's belonged to this species. He presented a complete series of the larval stages from the first calyptopis through to the last furcilia stage. Talbot (1974) found larval forms conforming to Boden's description in the warm Agulhas Current and larval forms conforming to Bary's description in the cooler waters over the Agulhas Bank. Because E.lucens had not been previously recorded from the Agulhas Current, Talbot concluded that Bary's description of E.lucens larval stages was correct. Among the larvae described by Talbot as being E.lucens, some early furcilia did not conform to Bary's description. This she assumed represented an alternative pathway of development in the species.

E.lucens has a circumpolar distribution and is mainly restricted to a narrow zone just north of the Antarctic Convergence between 30° and 45°S. It is one of the two dominant euphausiid species (the other is Nyctiphanes capensis) off the west coast of South Africa (Nepgen, 1957; De Decker, 1973), and therefore it constitutes one of the key elements of the macroplankton of the Benguela ecosystem. Because of the inconsistencies in the larval description, laboratory studies were carried out to study in more detail its early developmental stages. In studying live animals, it was also possible to determine the duration of each stage, the number of moults and the growth between each stage of development. Similar studies on N.capensis (Pillar, 1985) has allowed larval stages of both species to be distinguished in field samples.

4.2 MATERIALS AND METHODS

Larvae of E.lucens were captured in a 1-m diameter surface-towed plankton net during November at a position approximately 16km south-west of the Cape Peninsula (34°10'S, 18°15'E). In the laboratory, calptopis II stages were isolated and kept individually in 80-ml crystallizing dishes, each containing 50ml of seawater filtered through 10 μm mesh and held in the dark at a temperature of 13°C.

The animals were fed daily according to one of three regimes (Table 4.1). The algal culture was grown in Walnes medium at approximately 20°C and cooled to 13°C before use. Only newly hatched Artemia nauplii were used for each feeding.

The larvae were examined daily. When moulting had occurred, the moult was removed and the larvae were measured and examined for pleopod development and reduction in number of telson spines. Body length was measured by ocular micrometer from the anterior end of the rostrum to the tip of the telson.

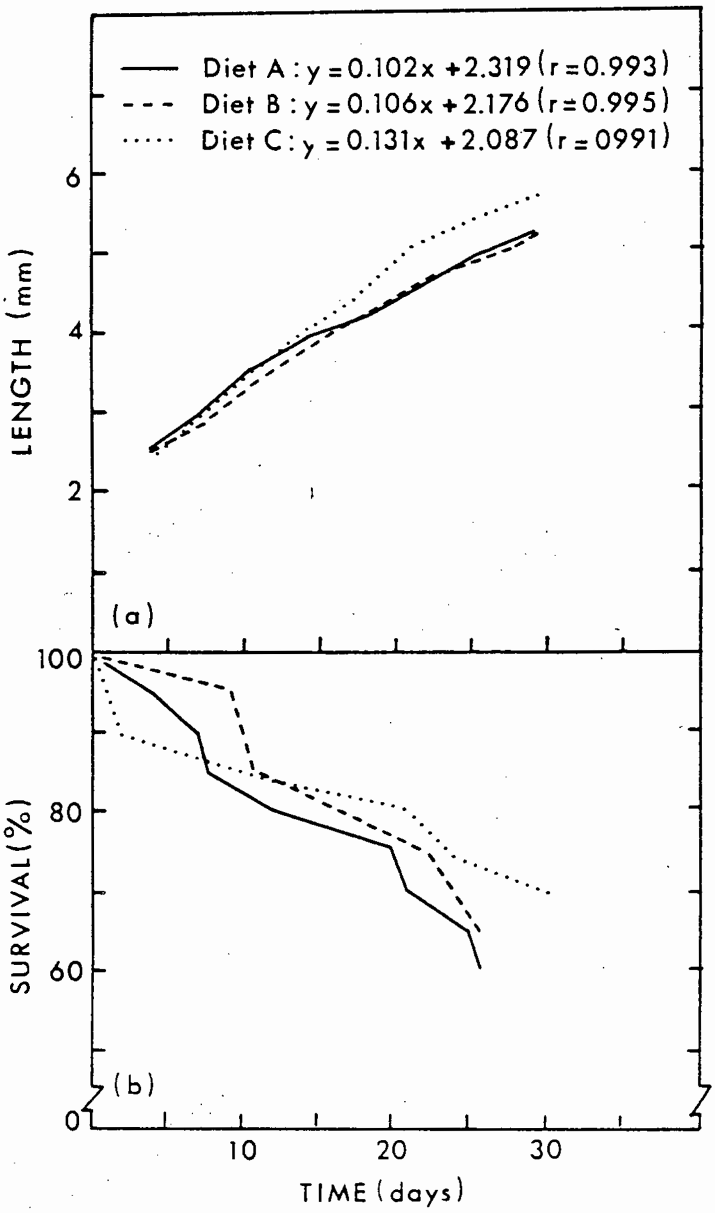

Figure 4.1 Effect of different diets on (a) growth and (b) survival of larval E.lucens

TABLE 4.1: The type of food and concentrations fed to larvae

Diet	Food type	Daily ration	Initial number of larvae
A	Tetraselmis chuii	2ml	20
B	Artemia nauplii	20 individuals	20
C	Mixture of A and B	2ml of algae and 20 individual nauplii	20

4.3 RESULTS

The growth and the survival rates of larvae fed on different diets are shown in Figure 4.1. The larvae raised on a mixed diet of Artemia nauplii and Tetraselmis achieved the highest growth rate (0.131 mm/day^{-1}). The different diets did not strongly influence the survival of the larvae in attaining the first juvenile stage. Survival ranged from 60 per cent with the pure algal diet to 70 per cent for the mixed algal and animal diet.

A second approach to analysing growth rates was made by expressing the increment at each moult as a percentage of the pre-moult body length. Mauchline (1977a) termed this growth increment a growth factor and demonstrated, for several species of decapods, that the log transformation of this growth factor was linearly related and decreased when regressed against the body length of the animal. Table 4.2 shows that the growth factor decreased throughout successive furcilia stages of E.lucens and is log-linearly related to body length of the larvae.

TABLE 4.2: Regression analyses of the log of the growth factor (y) on body length in mm (x)

Diet	Regression constants log y = bx + a		Correlation co-efficient (r)
	a	b	
A	5.336	-0.110	-0.802
B	5.778	-0.148	-0.922
C	6.663	-0.179	-0.924

The duration of intermoult periods and their range for the three diets are shown in Table 4.3. The number of days ranges from 2 to 7 with mean values between 3.0 and 4.2. The most frequent intermoult period regardless of type of diet or stage of larvae is 3 days. It was noticed that the intermoult period increased prior to death of the larvae.

Table 4.4 shows the existence of eight different pathways of pleopod development of the furcilia stages. The frequency distribution indicates the existence of two main pathways of development between the third calyptopis stage (CIII) and the final stage of pleopod development, i.e. 5 setose pleopods. The pathway F4 → F4'1 → F5' is dominant over the pathway F3 → F3'2 → F5'. In both cases, two furcilia moults are required to reach the final sequence of pleopod development i.e. the third furcilia stage. In all cases a setose pleopod appeared where a non-setose pleopod existed before.

TABLE 4.3: Mean and range of the intermoult period of each larval stage of E.lucens fed on the different diets

Developmental stage	Diet A (days)		Diet B (days)		Diet C (days)	
	Mean	Range	Mean	Range	Mean	Range
CIII	3.5	3-4	4.2	3-7	3.4	3-4
FI	3.4	3-4	3.5	3-4	3.0	2-4
FII	3.7	3-5	4.0	2-7	3.4	3-5
FIII	3.3	2-4	3.2	2-4	3.2	3-4
FIV	3.1	3-4	3.1	3-4	3.0	2-4
FV	4.1	2-7	4.0	3-6	3.9	3-7
FVI	3.2	3-4	3.1	2-4	3.0	2-4

TABLE 4.4: Pathways of pleopod development of E.lucens and the number of moults needed to attain 5 setose pleopods

Furcilia moults					Number of individuals partaking of each diet			
1	2	3	4	5	A	B	C	A + B + C
F1→	F1'2→	F3'2→	F4'1→	F5'	1		1	2
F1→	F1'3→	F4'1→	F5'		1	1		2
F2→	F2'1→	F3'1→	F4'1→	F5'	1		1	2
F2→	F2'2→	F4'1→	F5'			1	1	2
F2→	F2'3→	F4'1→	F5'		2	1	2	5
F2→	F2'3→	F5'				1		1
F3→	F3'2→	F5'			3	3	4	10
F4→	F4'1→	F5'			8	10	8	26
TOTAL					16	17	17	50

N.B. CIII: 3rd calyptopis
F: furcilia
('): setose pleopods, e.g. F4'1 denotes a furcilia larvae with 4 setose and 1 non-setose pleopods

TABLE 4.5: Pathway of telson spine reduction of the furcilia stages of E.lucens

Furcilia stages							Number of individuals partaking of each diet			
FII		FIII	FIV	FV		FVI	A	B	C	A + B + C
7		6	3	2		2		2		2
7		6	5	2		1	1		1	2
7		6	5	3		1		1	1	2
7		5	5	3		1	7	6	10	23
7		5	4	3		1	3	1		4
7	7	5	3	3		1		1	1	2
7		5	5	4	3	1	1	1		2
7		5	5	5	3	1	1	1	1	3
TOTAL							13	13	14	40

The number of terminal spines of the telson reduces from 7 to 1 only after the second furcilia stage. The combination 7-5-5-3-1 is the most frequent pattern regardless of food type, and in most cases one moult occurred between each successive stage (Table 4.4).

4.4 DISCUSSION

A mixed diet of Tetraselmis and Artemia nauplii produced slightly better growth in the larvae of E.lucens than did either of the components taken separately. This agrees with the observations of Le Roux (1973) and Pillar (1985) in laboratory experiments on larvae of Nyctiphanes couchi and N.capensis respectively. Both these workers showed that underfed individuals and those fed exclusively on an algal culture grew more slowly than did those offered a diet of mixed Artemia nauplii and algae. They concluded that the larvae were capable of omnivorous feeding from as early as the third calyptopis stage. In the present study, Artemia nauplii were ingested from at least the final calyptopis stage.

The mean daily growth rates (0.102 to 0.132 $mm.day^{-1}$) compare favourably with the range quoted for several other laboratory-reared euphausiid larvae. A growth rate of 0.10 - 0.12 $mm.day^{-1}$ was found by Gopalakrishnan (1973) for Nematoscelis difficilis, and Le Roux (1973) and Pillar (1985) observed growth rates of 0.13 and 0.092 $mm.day^{-1}$ in Nyctiphanes couchi and N.capensis respectively. Lasker (1966) determined a much lower rate of 0.048 $mm.day^{-1}$ for juvenile Euphausia pacifica. Higher rates than those observed in the laboratory by Lasker (op.cit.) have been estimated from natural populations of E.pacifica off Oregon (Smiles and Pearcy, 1971) and off Southern California (Brinton, 1976). Off Oregon the mean growth rate of E.pacifica was 0.065$mm.day^{-1}$ with a maximum of 0.095$mm.day^{-1}$, whereas off California growth was estimated to be about 0.1$mm.day^{-1}$. The life expectancy was estimated to be one year in these regions. Smiles and Pearcy (1971) compared the growth rates of E.pacifica in different regions of the Pacific and noted that growth was about twice as fast inshore than further offshore, where the life span was estimated as two years (Nemoto, 1957). This shortening of the life cycle was related to high primary production during the summer caused by coastal upwelling and the lack of large seasonal temperature fluctuations in nearshore waters. Both the growth rates and habitat of E.lucens are sufficiently similar to those of E.pacifica to suggest that E.lucens also has a life expectancy of one year in South African waters.

The present study yielded no evidence to show that the intermoult period was dependent on the diets tested. The fastest growing larvae became juveniles at approximately the same time, but at a larger size than the slower larvae. Both fast and slow-growing larvae followed a similar developmental sequence. Le Roux (1973, 1974) and Pillar (1985) found that, when food was nutritionally discontinuous or low, the growth rate of euphausiid larvae was slower and the intermoult period was longer and more variable than in the more healthy individuals. This finding implies that food type may affect growth rates of individuals, but under favourable dietary conditions (as may be assumed for the present study) the developmental sequence and time are not appreciably affected.

The work reported here demonstrated no dependence of moult frequency on age. This contradicts the statement by Mauchline (1977b) that the intermoult period of euphausiids increases at successive moults. Mauchline's observations were based on experimental data on three species (*Nyctiphanes couchi*, *Nematoscelis difficilis* and *Meganyctiphanes norvegica*, though little or no degree of correlation was found in some of the regressions. Results for other euphausiid larvae of Le Roux (1974), Antezana-Jerêz (1978), Ross (1981) and Pillar (1985) displayed no age dependence of intermoult periods. Studies on adult euphausiids by Fowler *et.al*. (1971) suggest that intermoult period increases as a function of body weight. On the other hand, Jerde and Lasker (1966) and Mackintosh (1967) found no weight or size dependence of moulting frequency.

The 3-4 days intermoult period for E.lucens larvae agrees with the moulting frequency of larval, juvenile and adult E.pacifica (Lasker, 1966), but it is slightly shorter than estimates of moulting frequencies for other euphausiids. Antezana-Jerêz (1978) and Mauchline (1980) summarised the moulting frequencies from numerous studies on larval, juvenile and adult euphausiids and, with the exception of the larger species, e.g. Meganyctiphanes norvegica and E.superba, the frequency ranged from 4 to 6 days. Similar intermoult durations were found for the larval development of Nyctiphanes capensis by Pillar (1985).

The ontogeny of E.lucens followed two main pathways of development which were independent of the diets offered in this study. These dominant pathways were shorter and more direct than the other variants observed, where sometimes more than one moult was needed to achieve a succeeding stage. Variations in the pleopod pathway and number of moults in the larval development of euphausiids have been found to be strongly associated with trophic conditions in the laboratory. Le Roux (1973) and Pillar (1985) have shown that unfavourable diet and deprivation of food will produce additional moults and variant forms in the larval development of Nyctiphanes couchi and N.capensis. Other authors have assumed environmental factors such as temperature and salinity to be responsible for variability in larval forms (Sheard, 1953; Makarov, 1974). The flexibility of the developmental pathway of the larvae has been shown to be associated with their locality and habitat. Most oceanic species have relatively non-variable pleopod development whereas coastal populations have many variants and ill-defined forms (Einarsson, 1945; Sheard, 1953; Bøden, 1955; Le Roux, 1973, 1974; Knight, 1975, 1976). The existence of

TABLE 4.6: Summary of the larval characteristics of <u>E.lucens</u> from Boden (1955), Bary (1956) and the present study

Stage	Character	Boden	Bary	This study
Calyptopis III	Pleopods	none	none	none
	Telson spines	7	7	7
	Length (mm)	2.2	2.3	2.5
Furcilia I	Pleopods	1 non-setose	4 non-setose	4 non-setose
	Telson spines	7	7	7
	Length (mm)	3.0	3.0	3.0
Furcilia II	Pleopods	1 setose 4 non-setose	4 setose 1 non-setose	4 setose 1 non-setose
	Telson spines	7	7	7
	Length (mm)	3.5	3.8	3.5
Furcilia III	Pleopods	5 setose	5 setose	5 setose
	Telson spines	7	5	5
	Length (mm)	-	4.7	4.0
Furcilia IV	Pleopods	5 setose	5 setose	5 setose
	Telson spines	5	5	5
	Length (mm)	-	5.2	4.4
Furcilia V	Pleopods	5 setose	5 setose	5 setose
	Telson spines	3	3	3
	Length (mm)	-	5.4	5.0
Furcilia VI	Pleopods	5 setose	5 setose	5 setose
	Telson spines	1	1	1
	Length (mm)	-	5.6	5.4

several major pathways and variant forms places E.lucens into the latter category, i.e. coastal.

Information summarised in Table 4.6 permits comparison of the developmental sequence of E.lucens from this study with that described by Boden (1955) and Bary (1956). As the early furcilia stages described by Talbot (1974) were considered by her to be supplementary to Bary's description, they were excluded from the Table.

Although the lengths of the larvae in Bary's (1956) material are greater than those of specimens raised in the laboratory, there is little doubt that they are from the same species and that Bary's description of E.lucens is correct. It is questionable, however, that the sequence of pleopod development described by Bary is as rigidly fixed as is assumed by the exclusion of variant forms from his descriptions. This interpretation is based on the present results and those of Talbot (1974), and it should be noted that variants do exist in natural populations of E.lucens.

In summary, the results indicate that the ontogeny of E.lucens follows a sequence of development which is not lost under laboratory conditions. Moulting and growth are independent of each other, the moulting frequency being characterised by a continuous process of short intermoult periods (3-4 days) independent of rate of development or age of the larvae. The growth rate decreases with successive moults.

Further laboratory studies on older animals will be necessary to determine if these features continue for juvenile and adult stages of development. Concomitant field work is underway, after which it is hoped to present a definitive life history of E.lucens and a treatment of the environmental parameters influencing its distribution in South African coastal waters.

CHAPTER 5

POPULATION STRUCTURE, REPRODUCTIVE BIOLOGY AND MAINTENANCE OF *EUPHAUSIA LUCENS* IN THE SOUTHERN BENGUELA CURRENT

5.1 INTRODUCTION

Euphausia lucens is the dominant euphausiid species in the southern Benguela system (Nepgen, 1957) and is a major consumer of phytoplankton and zooplankton (Stuart, 1986), as well as prey for a large variety of fish (Davies, 1957; King and Macleod, 1976; Nepgen, 1979; Botha, 1980; James, 1987). Studies to date have examined various aspects of the general biology of E.lucens such as larval development, feeding and metabolism, biomass and distribution (Pillar, 1984c; Stuart, 1986; Pillar, 1986), however, little is known about the species population structure and reproductive behaviour. To understand energy flow from the zooplankton community to the higher trophic levels, it is necessary to examine all factors contributing to critical trophic links in the food chain.

The reproductive output of an individual euphausiid may be considerable (Mauchline, 1980), and hence the eggs and larvae may represent an important food source for other organisms. Brood size (the number of eggs produced by a female in a single spawning event) has been calculated for E.lucens using preserved material (Stuart and Nicol, 1986), but the number of broods produced per year remains unknown.

Since all attempts to induce ripe females to lay eggs in the laboratory have been unsuccessful, a one year series of preserved material have been used to determine the timing and duration of the spawning season, and to make some estimates of the fecundity of E.lucens. Data analysed were selected from collections taken between August 1977 and August 1978 from

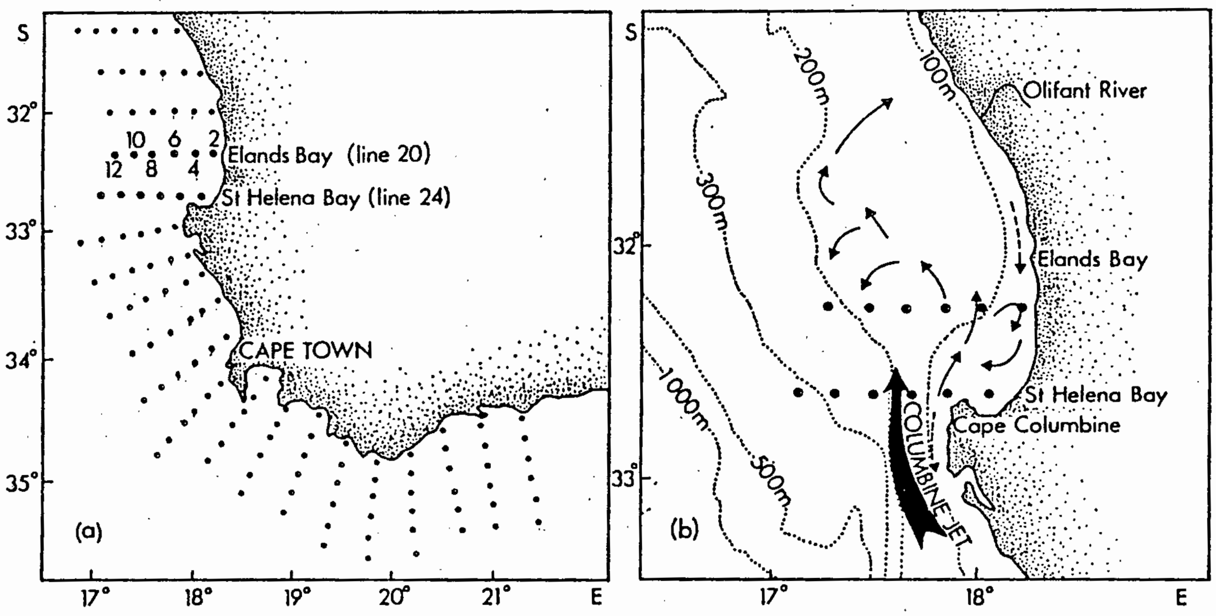

Figure 5.1 (a) The Cape Egg and Larval Programme (CELP) station grid with larger dots denoting the stations used in this study, (b) The bathymetry and schematic presentation of currents in the vicinity of the study area (from Shannon, 1985)

the southern and western coasts of South Africa by the Sea Fisheries Research Institute as part of the Cape Egg and Larva Programme (CELP) (Figure 18a). Collections from the St Helena Bay area have indicated that it is an area of enhanced primary and secondary productivity (Shannon *et.al*., 1984; Pillar, 1986), and an important recruitment area for the pelagic fishery (Crawford, 1980). The present study attempts to establish the predominant spawning locations and maintenance strategies of *E.lucens* in this area, and to investigate the population structure relative to seasonal and inshore-offshore variations in physical and biotic characteristics. It should be noted that the outermost stations of the CELP grid off St Helena Bay do not extend across the shelf break and associated front between the cool inshore water and oceanic water (Shannon, 1985). The study forms part of a broader investigation aimed at defining the trophic status of *E.lucens* in the southern Benguela current.

5.2 MATERIALS AND METHODS

The CELP grid (Figure 5.1a) comprised 120 stations consisting of 20 lines, each 20 nautical miles (37km) apart, with six stations to a line. The first station was 2 nautical miles (3.7km) from the coast (station 2) and the remainder at 10 nautical miles (18.5km) intervals offshore (stations 4, 6, 8, 10, 12). Zooplankton samples were collected using a Bongo net (300 m mesh, 57cm diameter) towed obliquely to a depth of either 100m or to 10m from the bottom in shallower water. The collections were preserved in 5% formalin. The volume of water filtered was measured using a calibrated digital flow meter mounted centrally in the mouth of each net. At each station, the surface water temperature was measured and recorded at depth using a bathythermograph. Discrete water samples were collected at 10m depth intervals up to 70m for analysis of salinity and chlorophyll a (Shannon et.al., 1984). A continuous record of wind data was obtained from Cape Columbine, which is situated approximately 50km from the study site.

Collections from two lines (lines 20 and 24) were used from the CELP samples (Figure 5.1a). Only night-time collections (one hour after sunset to one hour before sunrise) were used to estimate abundance of juveniles and adults due to the vertical migratory behaviour of this species (Pillar, 1984a). The stations were subdivided into three regions: inshore (station 4), intermediate (stations 6 and 8) and offshore (stations 10 and 12). Material from station 2 was not considered in the analysis due to the perennial abundance of gammarid amphipods and very low concentrations of euphausiids. This observation is not characteristic of the surrounding inshore stations (Pillar, 1986) and the inclusion of this data would underestimate the abundance of euphausiids in the inshore region.

Counts were made of all developmental stages of E.lucens i.e. egg, nauplii, calyptopis, furcilia, juvenile and adult, and expressed as numbers per m^3. A comparative net study showed that the eggs and all larval stages, with the exception of the first naupliar stage, were representatively retained by the 300 μm mesh net. Subsamples were taken using a Folsom splitter, and the total length of specimens was measured (tip of rostrum to distal end of telson). Generally the entire sample was examined for this analysis, large samples were split until at least 200 specimens were available. Ovaries were dissected out of adult females and the eggs teased onto a microscope slide for examination. Four ovarian stages were assigned according to the scheme proposed by Mauchline (1968): Stage I eggs are small and immature, they grow through Stages II and III, and they reach maturity at the end of Stage IV when the eggs become large and opaque and are filled with globules of yolk. Females were examined for presence/absence of a spermatophore in the thelycum and the condition of the spermatophores in the males was noted.

5.3 RESULTS

5.3.1 Wind, temperature and salinity regimes

Annual upwelling cycles can be inferred from the monthly wind indices based on the integrated northward component. The mean monthly northward displacement from August 1977 to August 1978 and those averaged over 9 years between 1978 to 1986 were extracted from the SFRI wind analysis system and presented in Figure 5.2a. The data show a consistent northward component indicating perennial occurrence of upwelling inducing winds. The mean cumulative northward displacement for the five days prior to sampling, the typical periodicity of south-easterly winds (Hutchings, 1981), is consistent with the monthly averages and shows maximum upwelling intensity from late spring to early autumn (October to March). Variations in mean

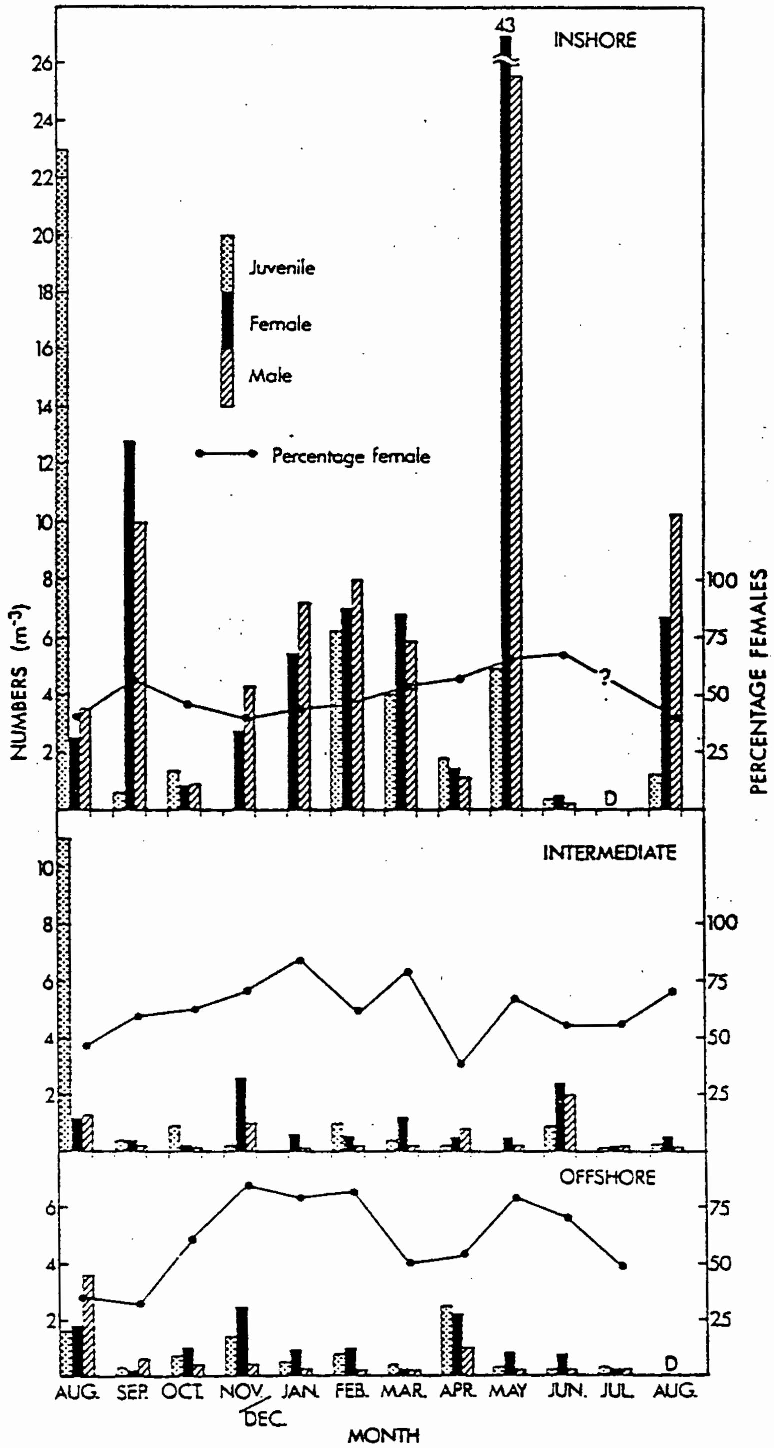

Figure 5.3 Monthly changes in the inshore-offshore abundances of juveniles, females and stages of E.lucens. The closed circles denote the sex ratio expressed as the percentage of females in relation to total adults. 'D' denotes daytime sampling

monthly surface temperature and salinity (Figures 5.2 a and b) can also be used as possible indicators of upwelling. At the inshore station, minimum salinities ($< 34.8^{0}/_{00}$) occurred between October and March, indicating the presence of upwelled water. Although temperature during this period increased (presumably as a result of sun-warming during the summer months), it was nevertheless lower than the offshore region. Temperature and salinity both increased significantly with distance offshore ($p<0.05$, t-test). All three regions showed similar seasonal temperature patterns, but only the intermediate and offshore regions exhibited similar monthly variations in salinity ($p<0.05$, Friedman's concordance test [Zar, 1974]). This finding suggests that salinity is a more conservative property in revealing upwelling in the inshore region. Waldron (1985) emphasised the value of salinity as a means of identifying upwelled water.

5.3.2 Species composition and abundance

Euphausia lucens constituted approximately 99% of the euphausiids in the collections. Larvae, juvenile and adult Nyctiphanes capensis occurred infrequently, mostly during summer and autumn (January to May), however, their numbers never exceeded 5% of the counts in any one monthly collection. This scarcity is noteworthy, since Nepgen (1957) found that N.capensis accounted for 23% and E.lucens 76% of the euphausiids collected from monthly sampling during 1954 to 1956 in the St Helena Bay/Lambert's Bay area.

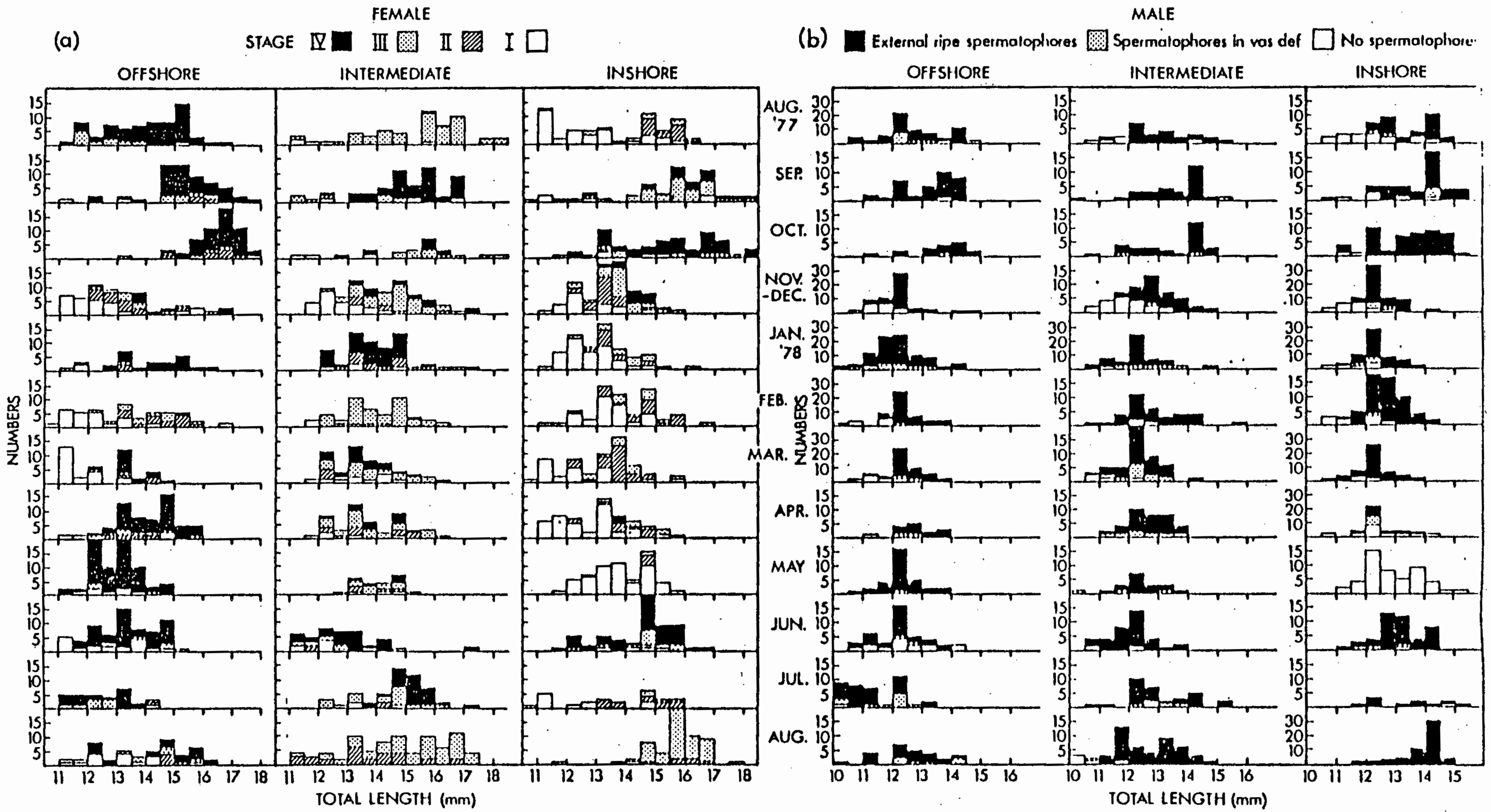

Figure 5.4 Monthly changes in the inshore-offshore size distribution and stages of sexual maturity of (a) females, classified into stages I-IV of ovarian development (after Mauchline, 1968) and (b) males, classified into condition of reproductive organs

The monthly variations in the abundance of juvenile and adults of E.lucens for the three regions are shown in Figure 5.3. Densities are markedly higher in the inshore region and undergo considerable variation throughout the year. There are no apparent seasonal trends in the adult population, however, the juveniles show late summer to autumn (February to March) and late winter (August) peaks. The female population appears to outnumber the males for most months of the year especially in the offshore region. This feature has also been noted for other euphausiid species (Brinton, 1976; Hosie and Ritz, 1983).

5.3.3 Size and sexual maturity

Figures 5.4 a and b show the size distributions and maturity stages for adult female and male E.lucens from the inshore, intermediate and offshore areas, for each month between August 1977 and August 1978. The stage of development of the ovaries ranging from Stage I (immature) to Stage IV (ready to spawn), as well as the condition of the male reproductive organs are indicated.

Females matured at a mean length of 11mm and attained a greater size than males. Males matured around 10mm total length and reached a maximum length of ~15mm. The largest sexually mature females were found in early spring (September/October), with a maximum total length of 18.4mm being recorded, whereas during the autumn and winter months (March to July) the maximum size of females was only ~15.5mm. Mature males followed a similar pattern

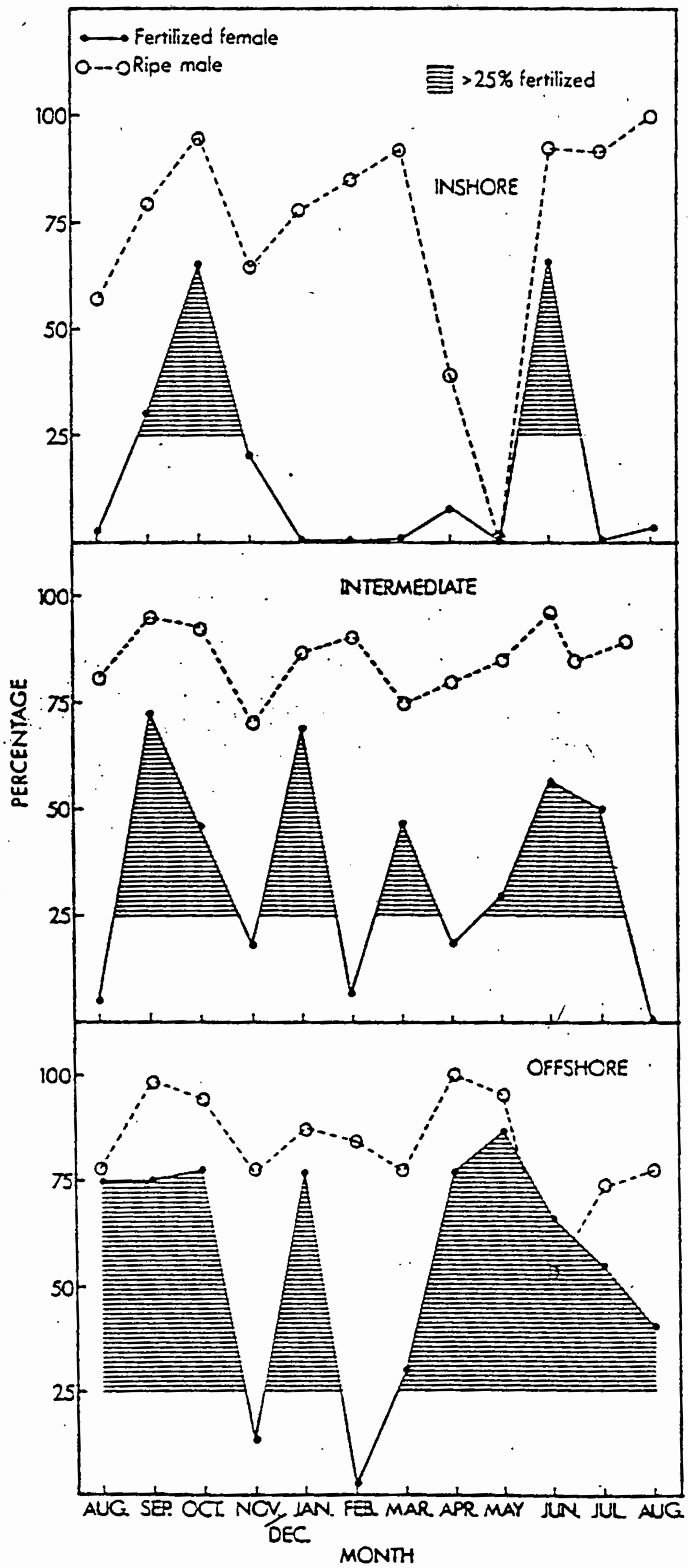

Figure 5.5 Monthly changes in the percentage of fertilised females and ripe males of <u>E.lucens</u> in the inshore, intermediate and offshore regions. The periods when fertilised females comprised > 25% of the female population are denoted by horizontal bars (see text)

with the largest specimens occurring in spring and the smallest in autumn and winter. A conspicuous feature of the male size distribution was the predominance of a 12-12.5mm modal size class for most months of the year (see Figure 5.4b). The cause of this feature is unknown, but may indicate retardment in growth due to energy being utilised for the production of spermatophores. Brinton (1976) found a similar 'piling up' at the 11-12mm increment for Euphausia pacifica, which he attributed to growth being faster into the new adult phase than out of it, due to energy being diverted to gonad development.

Nearshore, female E.lucens had immature eggs (Stage I and II) in their ovaries for most of the year, whereas further offshore Stage III and IV eggs were common (Figure 5.4a). This can be related to the percentage of fertilised females throughout the year (Figure 5.5), since it was found that the majority of fertilised females (94.8% ± 7.8) also had ripe Stage IV eggs in their ovaries. The presence of a spermatophore in the thelycum of a female thus serves as a useful indicator of the number of females which are about to spawn. Using this criterion, there appear to be two to three periods of intensive spawning throughout the year (Figure 5.5). Inshore, this was mainly confined to the spring months (September/October), although a large proportion of ripe females occurred in June. Further offshore, breeding was almost continuous throughout the year, increasing in intensity seawards. The longest period of breeding occurred at the outermost stations where at least 25% of the adult females were fertilised and ready to spawn for 10 months of the year. More intensive breeding (>50% of fertilised females) occurred during the spring, late autumn and winter months. The majority of males also had ripe, fully developed

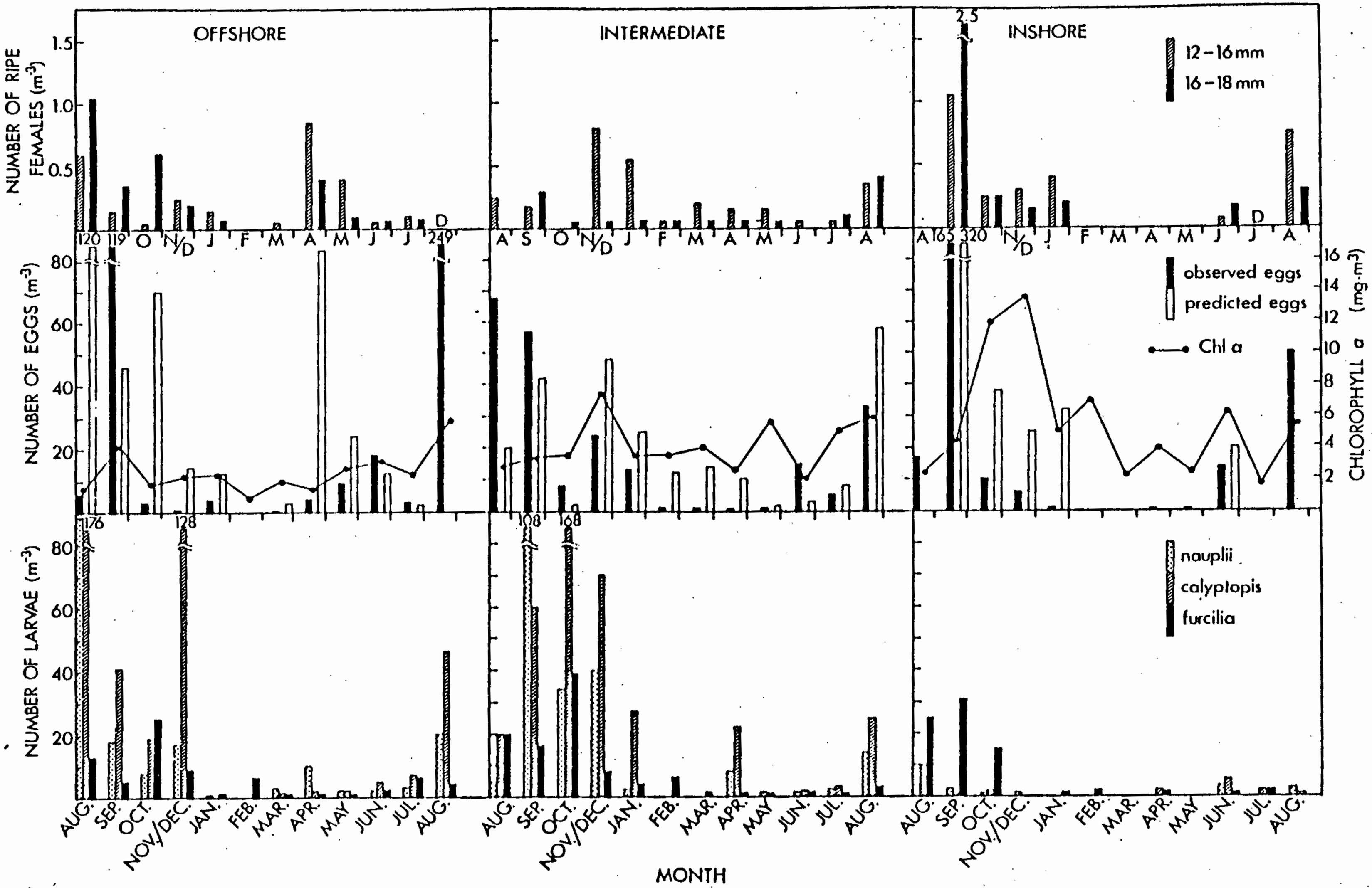

Figure 5.6 Monthly changes in the inshore-offshore population structure of E.lucens with respect to (a) the size structure of the spawning stock, (b) the observed and predicted egg production in relation to chlorophyll a concentration (integrated over the upper 20m of the water column) and (c) the different stages of larvae. 'D' denotes daytime sampling

spermatophores all year round, (apart from the months of April and May in the inshore area), which would ensure fertilisation of females whenever they ripen.

It is notable from Figure 5.4a that the majority of ovaries examined contained a large range of eggs of different stages, suggesting continuous maturation of the ovary and the production of multiple broods. Very few undeveloped or spent ovaries were found, indicating that the ovaries do not regress to a resting stage.

5.3.4 Spawning and recruitment

The size structure of the spawning stock and the monthly production of eggs and larvae in relation to phytoplankton concentration for the inshore, intermediate and offshore regions are shown in Figure 5.6. Substantial egg production occurred in early spring (August/September) and was accomplished mostly by large females (16-18mm). Spawning in mid-summer (November - January) and winter (May - July) by smaller euphausiids led to reduced egg numbers. Fertilised females in March, April and May did not produce many viable eggs, except in the offshore region. The spawning potential of females at each station was estimated from the number of fertilised females in each size class, multiplied by the mean number of ripe Stage IV eggs in the ovary, derived from the relationship established by Stuart and Nicol (1986). These estimates of predicted egg production were significantly correlated with the observed egg production ($p < 0.05$, Spearman rank correlation [Zar, 1974]), suggesting that direct egg counts provided a reliable indication of the duration of spawning.

No relationship existed between either the observed or predicted egg production and phytoplankton concentration ($p > 0.05$, Spearman rank correlation [Zar, 1974]). From Figure 5.6b it can be seen that in the inshore region the major peak of eggs occurred just before the onset of upwelling and associated spring bloom (12-14mg chlorophyll a m^{-3}). Conversely, egg production fell to near zero when phytoplankton concentration dropped below 4mg chlorophyll a.m^{-3} (March, April, May, July). This was not the case further offshore, where chlorophyll a concentrations were lower (2-4mg m^{-3}) and more consistent all year round, although the two major peaks in egg production do appear to coincide with marginally higher chlorophyll levels.

The spring spawning peaks were accompanied by substantial recruitment of early larvae (nauplii and calyptopis), and were followed by peaks of late larvae (furcilia) generally one month later (Figure 5.6c). Most of this recruitment took place in the intermediate and offshore areas despite the high chlorophyll levels close inshore. It should also be noted that the number of larvae in the intermediate and offshore areas were occasionally higher than egg counts. This observation may be a consequence of the longer residence time in the plankton of larvae, due to their longer development period (~1 month), compared to 1-2 days for egg development.

5.4 DISCUSSION

The Euphausia lucens population off the St Helena Bay area includes Stage IV females and newly hatched larvae all year round, suggesting continuous breeding. Recruitment was highest from August to October, with two periods of intense breeding in the inshore region and at least three periods of breeding further offshore (see Figure 5.4). The egg production maxima for E.lucens (August-October) was similar to previous observations of euphausiid egg production off the west coast of South Africa (De Jager, 1954; Hopson, 1983). Although Nepgen (1957) showed a later peak from October to March during 1954-1955, he showed an earlier peak (August-November) the following year, indicating the breeding patterns may vary in successive years.

Assuming that spawning takes place between moults (to avoid loss of the spermatophore), each fertilised female would be expected to spawn within one week, since the intermoult period of adult E.lucens is 4-5 days (Stuart, 1986). This assumption can be further verified by the work of Anderson et.al. (1984), who showed that late Stage IV eggs (described by these authors as oocytes with prominent cortical specialisations) of the prawn Sicyonia ingentis were frequently spawned within a week. It can then be predicted that for every month in which at least 25% of the adult female population was fertilised, each individual would spawn at least once a month. If the proportion is greater than 25%, then X/25 broods will be laid each month, where X is the percentage of fertilised females. By applying a growth rate of $0.026mm.day^{-1}$ for adults (see Chapter 6), a female could be reproductively active for a maximum of 9 months (11-18mm total length), and using the above criteria, could release between 3 (inshore region) and 10 (offshore region) broods per lifetime). These results are similar to those of Hosie and Ritz (1983), who estimated that Nyctiphanes australis produced approximately one brood per month over 8 months, while Brinton (1976) estimated that Euphausia pacifica spawned about three times a year. In contrast to this, Ross et.al. (1982) estimated that small female E.pacifica released a maximum of 11-12 broods over a one month period, and large females released a maximum of 25-30 broods over a two month period. In the light of the findings by Clarke (1980), who measured a loss of 54% of total lipid for female Euphausia superba after spawning, it is unlikely that E.lucens could sustain such a high rate of egg production over an extremely long breeding period (9 months of the year in the offshore area). Since the spawning potential of fertilised females was generally of the same order of magnitude as eggs collected in the plankton (Figure 5.6), it is likely that egg production is of the order of approximately 1 to 3 batches of eggs per female per month (i.e. 3-16 broods per year, depending on location). The discrepancy between the different areas suggests that the E.lucens population is not uniform, and that the length and timing of the spawning season can vary even within a general geographical area (Hulsizer, 1979, quoted by Ross et.al., 1982).

The major peak in spawning occurs just prior to the onset of upwelling and the associated increase in phytoplankton (Figure 5.6). Several authors have reported a close association between the increase in chlorophyll a concentrations and maximum spawning of euphausiids. Smiles and Pearcy

(1971) and Brinton (1976) found that spawning of E.pacifica off the Oregon and southern Californian coasts was more intense during the periods of upwelling and associated phytoplankton blooms. In the northern Puget Sound Ross et.al. (1982) noted that spawning of E.pacifica was earlier in 1975 and 1978 than in other years, corresponding to early peaks in chlorophyll a concentrations. In other upwelling areas such as the Chile-Peru current, the heaviest spawning of Euphausia mucronata was noted as a result of increased phytoplankton concentrations stimulated by upwelling (Antezana-, Jerez, 1978).

The present results were thus unexpected, since they indicate a marked increase in the proportion of females carrying ripe eggs with distance offshore, despite the relatively low chlorophyll a concentrations in the offshore regions. The potential food environment of the spawning stock may, however, not be adequately described by chlorophyll a concentrations alone, since the size of the phytoplankton cells and abundance of zooplankton may also be important factors. Peterson (1985) has shown that egg production rates of the copepod Temora longicornis were only related to chlorophyll levels when cells $>10\mu m$ were considered, implying that they could not efficiently ingest smaller cells. The effect of phytoplankton size on the egg production of other copepods was implicated by Checkley (1980). It has also been demonstrated that euphausiids feed more efficiently on larger particles such as diatoms, than smaller flagellates (Parsons et.al., 1967; Holm-Hansen and Huntley, 1984; Quetin and Ross, 1985). Secondly, it should be noted that E.lucens is omnivorous (Nepgen, 1957) and that this feeding behaviour could provide greater energy returns than herbivory for both the adults and the larval stages (Pillar, 1984; Stuart, 1986).

In local waters Hutchings et.al. (1986) and Armstrong et.al. (1987) have found peaks of micro- and mesoplankton at the vicinity of the front. Pillar (1986) observed significantly higher copepod biomass offshore in the St Helena Bay area during the upwelling season (September-March) when the front is more pronounced (Shannon, 1985). It has been established elsewhere that frontal zones are also sites of enhanced secondary production (Mooers et.al., 1978; Scrope-Howe and Jones, 1985; Smith et.al., 1986). Associated with the Cape Columbine upwelling front are strong northward flowing jet currents (Bang and Andrews, 1974; Nelson, 1985), which would facilitate the transport of biological material into the offshore regions of St Helena Bay.

Temperature and salinity do not appear to be important factors in controlling spawning, as ripe females occurred over a wide temperature (12-20°C) and salinity (34.75-35.35$^{0}/_{00}$) range. Large tolerances to these variables were noted by Nepgen (1957) in St Helena Bay, although Talbot (1974) found that the warm Agulhas current (>20°C) restricted E.lucens to the cooler west and south western coasts of South Africa. However, the transport of eggs into warmer offshore water during periods of upwelling may facilitate faster egg development, resulting in increased early larval survival. Food such as microzooplankton which may be swept offshore in the surface waters may be significant to the feeding and survival of larvae.

Although spawning and recruitment reached a maximum during spring, mainly as a result of spawning by larger females, lower numbers of newly hatched larvae were present throughout the rest of the year (Figure 5.6).

Similarly, Hopson (1983) noted a summer reduction in recruitment, which can perhaps be explained by the preponderance of smaller females in the spawning stock. This is compatible with other studies which show that the size composition of ripe females determines recruitment strength (Mauchline, 1980).

Several mechanisms may underlie the observation that recruitment of younger larvae (nauplii and calyptopis) occurred offshore, while older larvae (furcilia) were present both inshore and offshore, a finding also noted by Hopson (1983). Since furcilia exhibit a strong vertical migration pattern, their net dispersal would be less than that of non-migratory, near-surface-dwelling, younger larvae. Continuous advection of young larvae offshore would therefore be facilitated by the more consistent belt-type upwelling regime which extends along the coastline northwards from St Helena Bay, as opposed to the episodic plume-type upwelling exhibited further south (Jury, 1980; Taunton-Clarke, 1985). A further mechanism for the increased abundance of young larvae offshore would be entrainment in the northward flowing jet currents associated with the Cape Columbine and Cape Peninsula upwelling fronts (Bang and Andrews, 1974), which have also been implicated in the transport of anchovy eggs and larvae up the west coast (Shelton and Hutchings, 1982; Shelton et.al., 1985). This current is strongest in the upper layers (Nelson, 1985), and since most early E.lucens larvae are found in the surface layers (Pillar, 1984b; Hutchings, 1985), this would favour the transport of euphausiid larvae from breeding grounds further south.

There was no evidence to suggest significant offshore transport of the juvenile and adult stages of E.lucens even during the period of strongest upwelling (October-March). It is assumed that a large proportion of these individuals in the intermediate and offshore regions are not of local origin but originate upstream of the study site. The high inshore concentration of juveniles and adults may, in part, be a result of the accumulation of animals being carried northwards and entrained into the inshore zone by cyclonic eddies associated with the front. These eddies have been proposed as mechanisms to facilitate the transport of anchovy larvae from the west coast jet current offshore into the nursery grounds in the St Helena Bay area (Shannon et.al., 1984; Shelton et.al., 1985). The inshore euphausiid population may also be supplemented by material being transported from further north by the inshore southward flowing undercurrent (De Decker, 1970; Holden, 1985; Nelson, 1985). Holden (1987) has demonstrated this countercurrent to be a perennial feature and has speculated it to be of mesoscale dimensions alongshore, extending southwards from Namibian waters along the entire west coast of South Africa. This subsurface countercurrent in association with shoreward surface movement of material further north generated by the influence of northerly winds (Shannon, 1985; Holden, 1987) all appear as likely mechanisms for maintaining E.lucens populations within the southern Benguela current.

The ability of older stages of E.lucens to migrate vertically would allow them to maintain or expand their distributional range within an upwelling region. The coastal currents in the vicinity of the study site are generally sluggish (Clowes, 1954; Holden, 1985) and the cyclonic gyre and associated eddies of varying depths within St Helena Bay would provide a number of opportunities for individuals to maintain themselves within the coastal zone. Equally they could remove themselves from the zone in a similar manner to the young larvae by migrating into the upper layers which would carry them offshore during the dominant southerly winds. The residence time of water in St Helena Bay is substantial, in the order of 25 days (Waldron, 1985), which contributes further to the concentration of older animals within the coastal zone relative to the offshore regions.

The reproductive strategy of E.lucens in the southern Benguela may be adapted to late winter and spring conditions when standing stocks of phytoplankton and zooplankton are more uniform and widespread (Shannon et.al., 1984; Shelton et.al., 1985) and offshore transport is at a minimum especially during the onset of spawning (August-September). The combined effect of a protracted spawning season, particularly in the offshore regions, accompanied by multiple spawning would enable E.lucens populations to withstand unfavourable short-term variability in the environment. Given the general northward and offshore flow of the upper layers, by Ekman transport combined with the shoreward movement of water during downwelling and a net southerly and inshore component at depth (Holden, 1987), a vertically migrating population is offered a suite of opportunities for maintenance within the southern Benguela system.

CHAPTER 6

GROWTH AND PRODUCTION OF *EUPHAUSIA LUCENS* IN THE SOUTHERN BENGUELA CURRENT

6.1 INTRODUCTION

In a previous study on variations in the biomass of euphausiids and copepods around the southern and south western coasts of South Africa, it was noted that the area around St Helena Bay (32°30'S, 18°E) had an abundance of euphausiids all year round. This area is one of the principal upwelling regions on the west coast, and is commonly associated with large phytoplankton concentrations (Shannon et.al., 1984). It is also one of the major recruitment areas for the anchovy (Engraulis capensis) fishery (Crawford, 1980).

Since many species of fish, including the commercially important anchovy, frequently consume large numbers of euphausiids (Botha, 1980; James, 1987; Payne et.al., 1987)), variations in euphausiid abundance may have far-reaching effects on the fish stock dynamics. For this reason, a study was undertaken on the reproductive biology and population dynamics of the dominant euphausiid, Euphausia lucens, as related to the seasonal, physical and biotic characteristics of the area (see Chapter 5). Another step in this study was to estimate the production rate of E.lucens, as well as to obtain estimates of the contribution of eggs and moults to total production.

Lasker (1964) has suggested that euphausiid moults make a substantial contribution to the detritus of the ocean, although only a few estimates of moult production are available to date (Jerde and Lasker, 1966; Sameoto, 1976; Ikeda and Dixon, 1982; Hosie and Ritz, 1983).

In this paper estimates are presented for somatic flesh production by E.lucens from three different areas (inshore, intermediate and offshore) in the St Helena Bay region, as well as estimates for additional production (moults and eggs), based on some of the results from previous work (see Chapter 5).

6.3 MATERIALS AND METHODS

Euphausiids were collected at monthly intervals between August 1977 and August 1978 by the Sea Fisheries Research Institute, as part of the Cape Egg and Larval Programme (CELP). Samples were ananlysed from two lines of stations running seaward from St Helena Bay (see Chapter 5 for details of location and methods). These stations were divided into three regions, based on the distance from the shore: inshore (~20km), intermediate (~60km) and offshore (~90km from the coast). Data for each region comprised the mean of four sampling stations except for the inshore region, which consisted of only two stations due to the perennial abundance of amphipods in the most proximal station to the coast.

Only samples which were collected during the night were used in the analysis of juvenile and adult Euphausia lucens, because the species is known to migrate to deeper waters during the day (Pillar, 1984a) resulting in daylight net samples being under-representative. Sub-samples were taken from each haul using a Folsom splitter, and the number and total length (tip of rostrum to distal end of telson) of all development stages of E.lucens (from calyptopis I larval stage to adults) were measured. The total number of eggs in each sample was also counted, but comparative net studies has shown that nauplii were not quantitatively retained by the nets (see Chapter 5), so these were omitted from the analysis. Adult males and females were categorised according to the state of sexual maturity. Criteria used were the presence or absence of spermatophores in the males, and the extent of ovarian development and presence of a spermatophore in the thelycum of the females (indicating fertilisation). The dry mass of individual eggs and different larval stages was determined by placing a known number of each stage onto pre-weighed GF/C filters and drying at 60°C for 24h.

Estimates for the intermoult period of different sized E.lucens were obtained by maintaining specimens ranging in size from 2,5 to 15mm total length, in the laboratory at 13°C for up to two months. Euphausiids were kept individually in 80-1000ml containers (depending on specimen size) in the dark and fed on a mixture of diatoms (Thalassiosira weissflogii) and newly hatched Artemia nauplii. The water was changed twice a week and the containers were examined daily for the presence of moults. On each occasion the moult was retrieved, the uropods were measured under a dissecting microscope and the moult briefly rinsed in distilled water, dried in an oven at 60°C and weighed. The increase in length of the uropods provided a measure of growth, since uropod length is directly proportional to total body length (Stuart, 1986). After two months, the laboratory animals were sacrificed and weighed after drying at 60°C for 48h. The final moult dry weights were expressed as a percentage of total body dry weight.

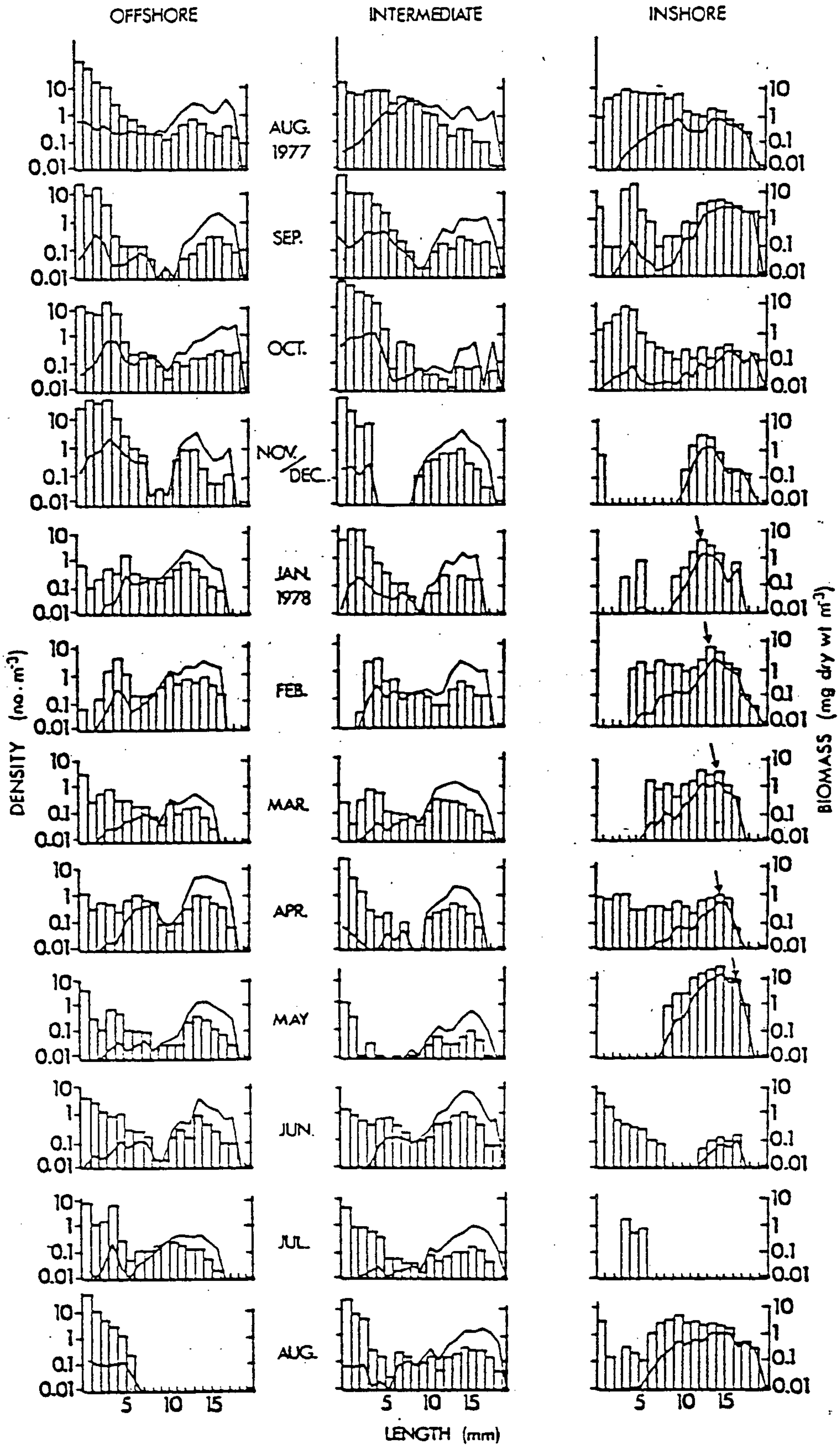

Figure 6.1 Monthly size-frequency distribution (bar graphs) and biomass (line-graphs) of E.lucens from August 1977 to August 1978 for the inshore, intermediate and offshore areas. The arrows refer to the size-class of adults used for estimating growth rates

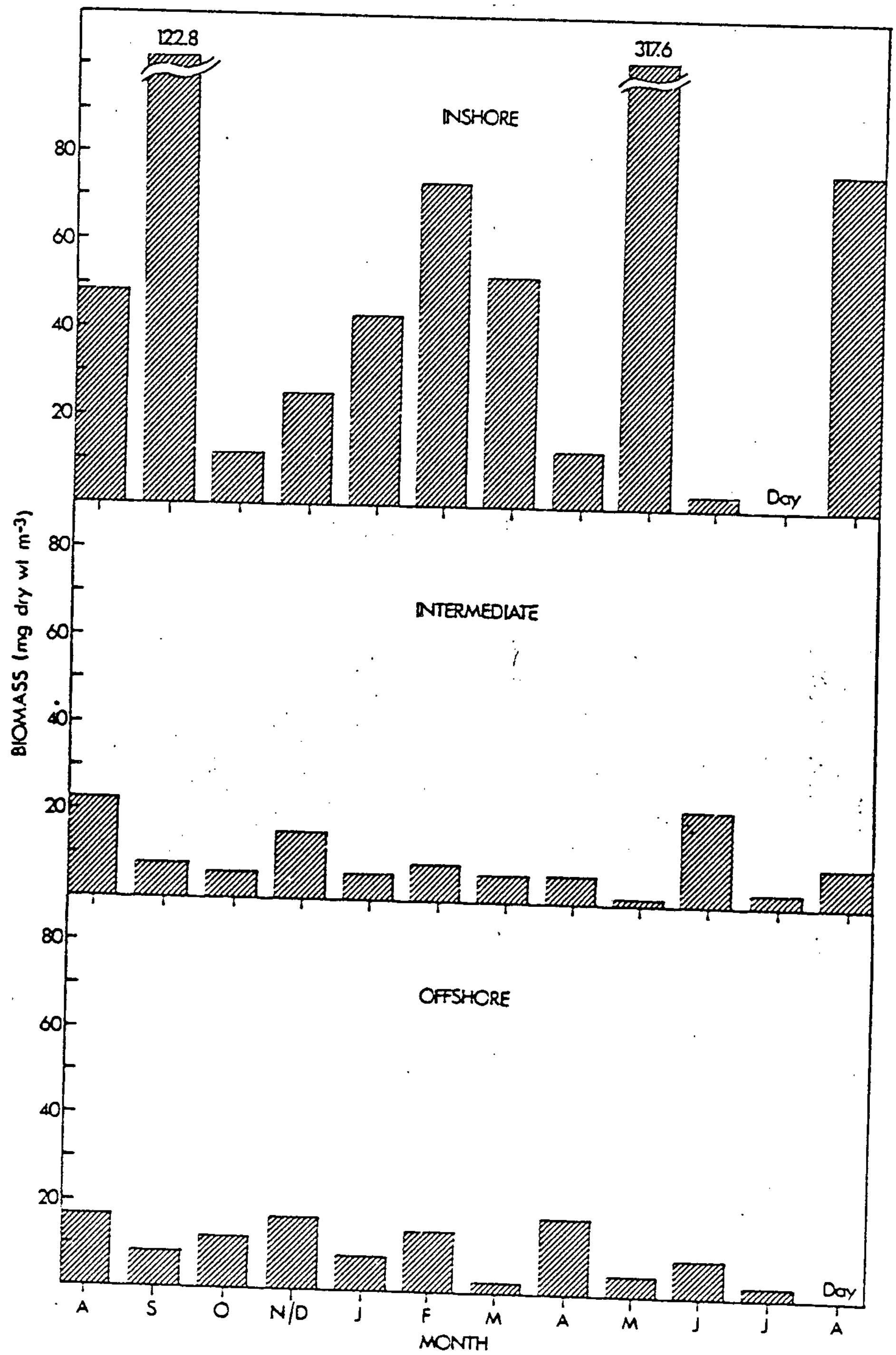

Figure 6.2 Total monthly biomass (mg dry wt.m^{-3}) of E.lucens (calyptopis larvae to adults) for the inshore, intermediate and offshore regions

Daily production due to growth (Pg) and exuvial production (Pe) was calculated for 1mm size-classes of E.lucens (1-1.99mm to 18-18.99mm) from the inshore, intermediate and offshore areas. A spreadsheet (Lotus Development Corp. (c) 1985) was used to manipulate the data. For these calculations it had to be assumed that the same data was sampled in each area, or at least that the sampled populations had similar age structures and growth rates. Reproductive production (Pr) was estimated for adult females larger that 11mm total length by calculating the number of eggs produced per month. These estimates were then converted to daily or annual production rates.

6.3 RESULTS

6.3.1 Population size distribution and density

Figure 6.1 shows the monthly population size distribution of E.lucens from the calyptopis I stage (~1mm) to 18mm adults, for the inshore, intermediate and offshore areas. The biomass of each size-class was estimated from the length/dry weight relationship of Stuart (1986) where $DW = 0.0012\ L^{3.16}$. The data have been plotted on a $\log_{10}$ scale to emphasise the proportionally smaller contribution of older stages to density and larval stages to biomass. Distributions show that in the inshore region, density and biomass underwent considerable variations throughout the year, with monthly biomass estimates ranging from 3.4 to 317.6mg. m^{-3} (Figure 6.2). Extensive

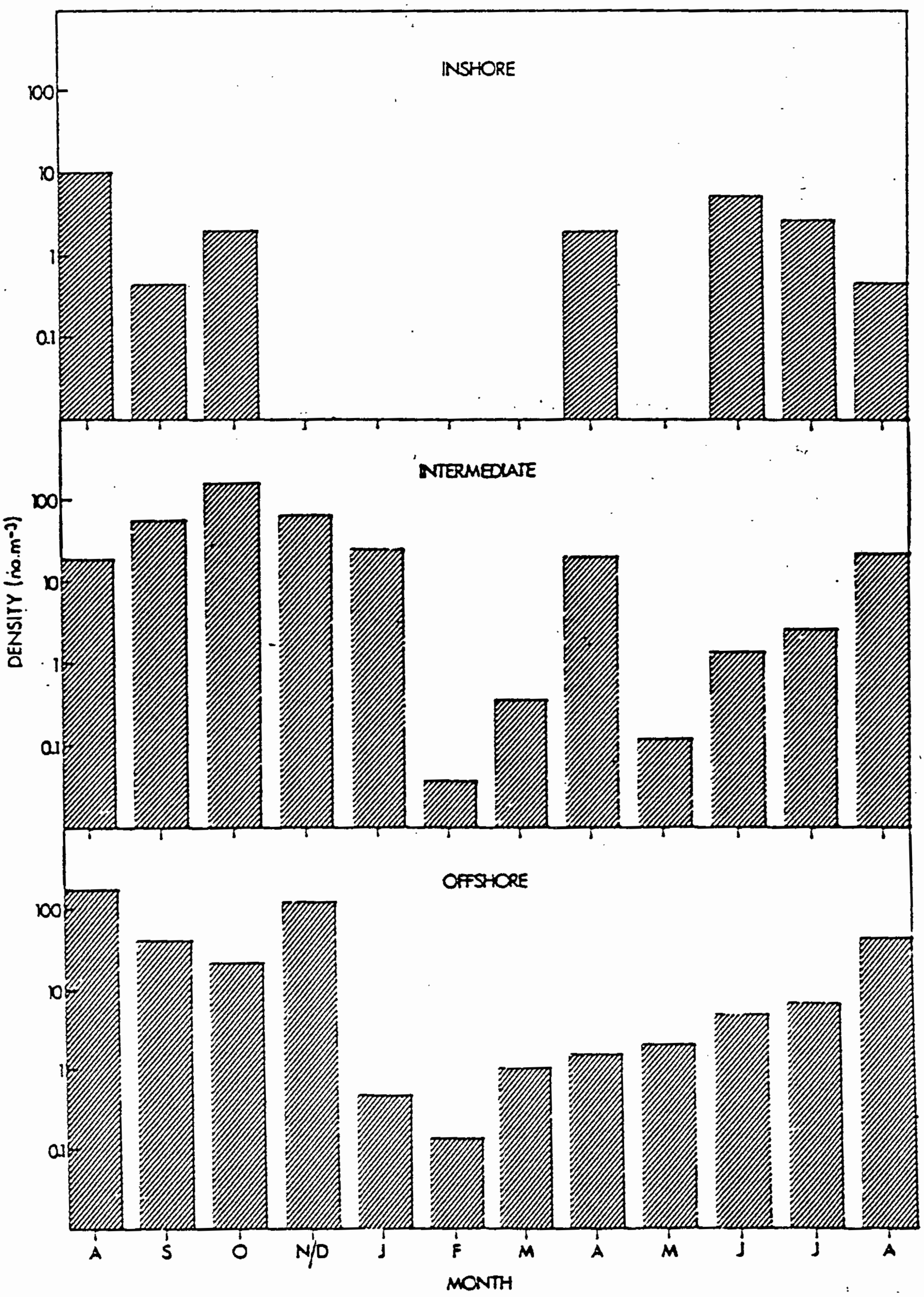

Figure 6.3 Density (no.m^{-3}) of calyptopis larvae (CI, CII and CIII) throughout the year, from the inshore, intermediate and offshore regions

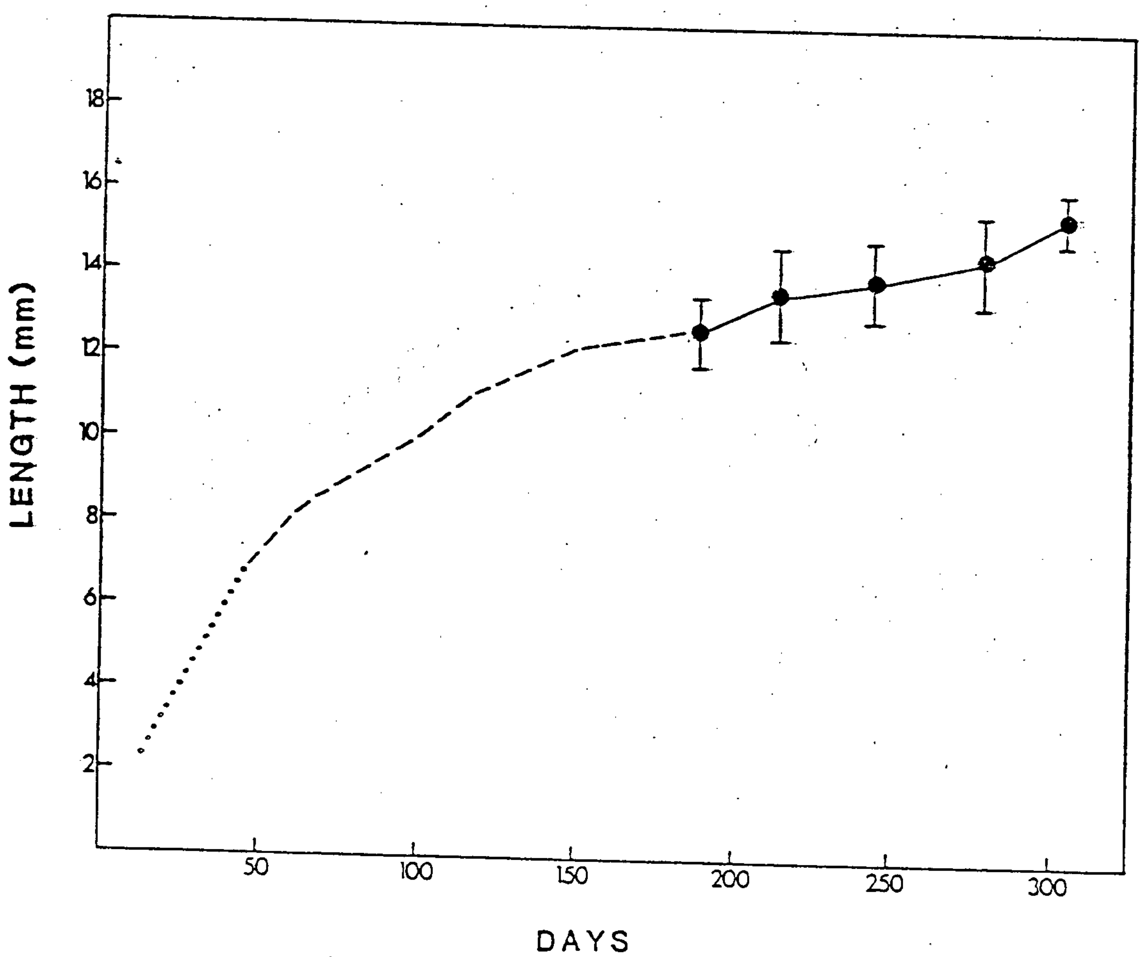

Figure 6.4 Growth curve for E.lucens. Larval growth rates (......) were taken from the laboratory study of Pillar (1984c), juvenile growth rates are from the present laboratory study (–·–·–·–·–·–) and the growth rate of the adults (•) was estimated from the population size-frequency distributions for the inshore region from January to May. The bar refers to one standard deviation

swarming inshore (De Decker, 1973; Nicol et.al., 1987) may be the cause of the exceptionally large numbers recorded in May. The intermediate and offshore areas exhibited a less abundant but more stable population throughout the year and the biomass in these regions was approximately 5 times lower than that of the inshore area.

Recruitment is more or less continuous throughout the year (Figure 6.1), with larval stages (1-6mm total length) being present for most months of the year. Despite the greater biomass in the inshore area, recruitment appears to be poor in this region considering the low density of calyptopis larvae (Figure 6.3). Calyptopis larvae (CI, CII and CIII) are abundant all year round, except in the inshore area during the summer months.

6.3 2 Growth rates

Results indicate that E.lucens spawns over a prolonged breeding season (Figure 6.3), which is reflected in a complex size-frequency distribution and considerable overlap of size ranges. Discrete cohorts are thus difficult to follow for more than a few months at a time. For this reason the growth rates of individuals from 2.5mm to 12mm total length were estimated from laboratory studies and using the data of Pillar (1984b) for the larvae. Adult growth rates were estimated from the population size-frequency distributions from January to May in the inshore region (Figure 6.1). A probability plot (Harding, 1949) was used to separate overlapping populations. The resultant growth curve is presented in Figure 6.4. It is evident that the growth rate declines with age, ranging

TABLE 6.1: Total daily flesh (Pg), moult (Pe) and egg (Pr) production (mg dry wt. $m^{-3}.d^{-1}$) for all size classes of E.lucens in the inshore, intermediate and offshore regions.

Month	Inshore			Intermediate			Offshore		
	Pg	Pe	Pr	Pg	Pe	Pr	Pg	Pe	Pr
August	1.0573	0.8894	0.0000	0.6532	0.4398	0.0078	0.4759	0.2741	0.0953
September	1.1980	1.9776	0.2099	0.2918	0.1422	0.0253	0.1813	0.1299	0.0275
October	0.2726	0.1957	0.0242	0.6076	0.1427	0.0000	0.3466	0.2036	0.0449
November/December	0.1895	0.4103	0.0181	0.2326	0.2512	0.0285	1.0118	0.3525	0.0259
January	0.3426	0.7002	0.0203	0.1271	0.0990	0.0161	0.1161	0.1415	0.0078
February	0.6252	1.1687	0.0000	0.1475	0.1416	0.0067	0.1969	0.2399	0.0000
March	0.4547	0.8461	0.0000	0.0681	0.1036	0.0065	0.0505	0.0473	0.0022
April	0.1353	0.2119	0.0034	0.0736	0.1030	0.0062	0.1785	0.2813	0.0516
May	2.2194*	4.9154*	0.0000*	0.0126	0.0256	0.0000	0.5014	0.0790	0.0155
June	0.0458	0.0541	0.0123	0.1839	0.3367	0.0005	0.0989	0.1412	0.0068
July		DAY		0.0370	0.0500	0.0056	0.0859	0.0514	0.0027
August	0.7636	1.2555	0.0514	0.1034	0.1378	0.0358		DAY	
Mean	0.5085	0.7709	0.0340	0.2115	0.1644	0.0116	0.2540	0.1764	0.0255
SD	0.6074	0.5926	0.0638	0.2025	0.1153	0.0121	0.2697	0.0966	0.0290

* Swarm, therefore not included in the calculation of mean daily production.

TABLE 6.2: Mean annual production (mg dry wt. $m^{-3}.year^{-1} \pm$ SD) of flesh (Pg), moults (Pe) and eggs (Pr) for the inshore, intermediate and offshore regions, and the percentage of the total production for each category. Biomass (mg dry wt. $m^{-3} \pm$ SD) and P/B ratios for all three regions are also given.

	Production (mg dry wt. $m^{-3}.year^{-1}$)	% of P (total)	P/B ratios	Biomass (mg dry wt $.m^{-3}$)
INSHORE:				
Pg	185.60 ± 136.40	38.72	3.92	47.29 ± 34.93
Pe	281.38 ± 205.20	58.70	5.95	
Pr	12.39 ± 21.79	2.58	0.26	
P (total)	479.39	100.00	10.14	
INTERMEDIATE				
Pg	77.20 ± 74.91	54.26	7.92	9.75 ± 6.53
Pe	60.01 ± 42.08	42.18	6.15	
Pr	5.07 ± 4.07	3.56	0.52	
P (total)	142.28	100.00	14.59	
OFFSHORE				
Pg	92.71 ± 98.44	55.73	8.91	10.40 ± 5.42
Pe	64.39 ± 35.26	38.69	6.19	
Pr	9.31 ± 9.96	5.59	0.89	
P (total)	166.41	100.00	16.01	

from 0.132mm.d^{-1} for the larvae (Pillar, 1984b), 0.047mm.d^{-1} for the juveniles (7-11mm total length) and approximately 0.026mm.d^{-1} for the adults.

6.3.3 Flesh production

The production due to growth (Pg) of E.lucens was estimated using the equation developed by Petrovich et.al. (1964), as modified by Ritz and Hosie (1982) and which is suited to animals exhibiting continuous recruitment. In this equation, production is estimated by summing the growth increments of each size-class multiplied by the density of each size-class as follows:

$$Pg = \sum_{1+1}^{s} (\frac{W_{1+1} - W_1}{D_1}) \times N_1) \quad \ldots\ldots\ldots \quad 1$$

where Pg is the daily flesh production (mg dry wt. $m^{-3}.d^{-1}$), W_1 is the weight at the beginning of the size interval, W_{1+1} is the weight at the end of the interval (i.e. the initial weight of the next size-class), D_1 is the developmental time in days for each size-class (calculated from Figure 6.4), N_1 is the monthly density (no. m^{-3}) of each size-class and s is the total number of size-classes (i.e. 18, ranging from 1-1.99 to 18-18.99). The weight increments for each size-class were calculated from the length/weight regression derived by Stuart (1986).

Daily flesh production (Pg) was calculated for each month for all three

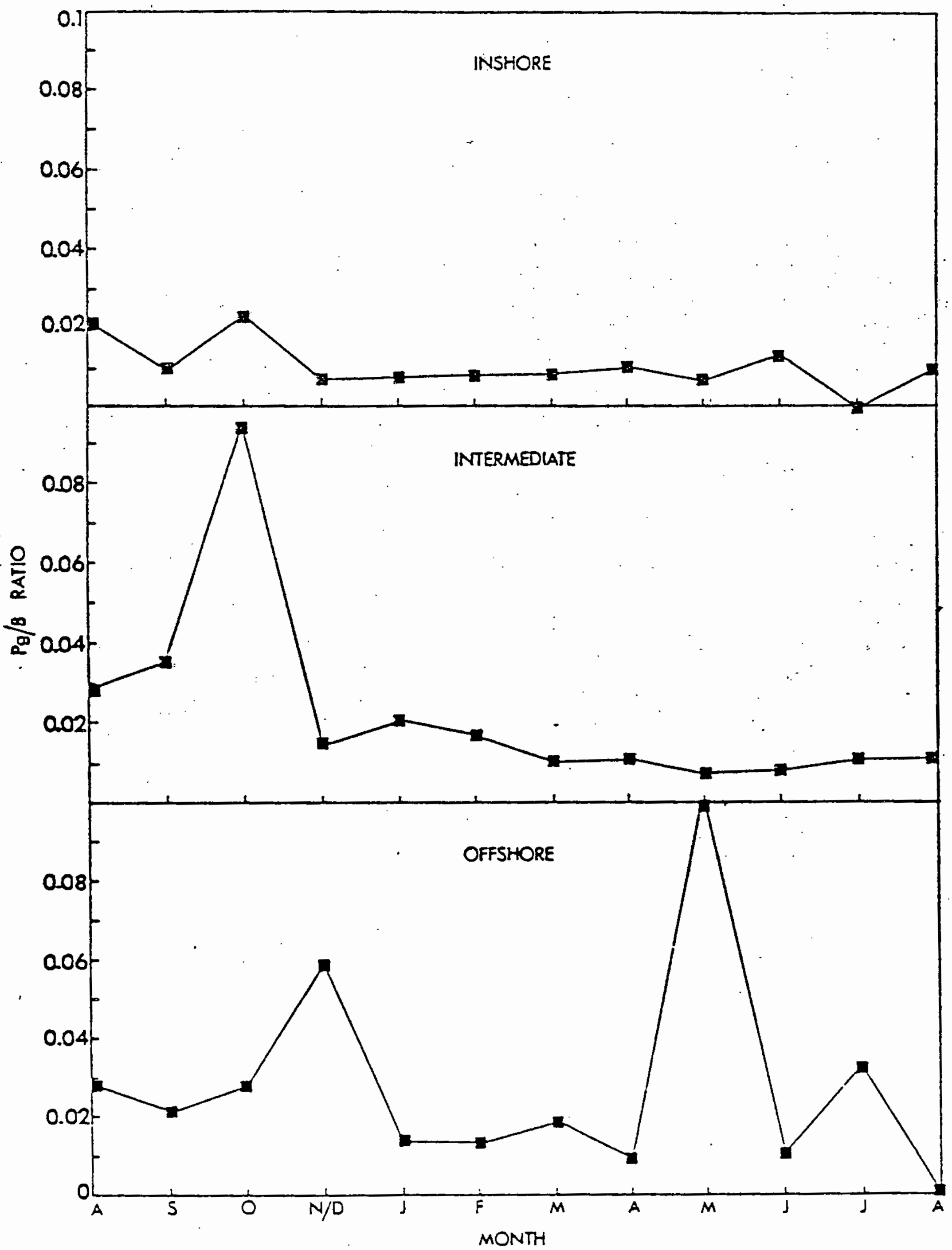

Figure 6.5 Daily P/B ratios for flesh production of E.lucens for the inshore, intermediate and offshore regions

regions and is presented in Table 6.1, while the mean annual Pg estimates are shown in Table 6.2 Mean daily flesh production ranged from 0.2115mg. $m^{-3}.d^{-1}$ (intermediate region) to 0.5085mg. $m^{-3}.d^{-1}$ (inshore region), which represents 77.2 to 185.6mg dry wt. $m^{-3}.year^{-1}$. Production was highest in the inshore regions due to the greater density of animals in this area. Daily P/B ratios for flesh production for each month are illustrated in Figure 6.5. A peak in the P/B ratios corresponded with periods of maximum recruitment of larvae, which occurred in October in the intermediate area and November/December in the offshore area (Figure 6.3). The ratios are also inversely related to biomass, resulting in a low P/B ratio for months having a very high biomass (September and May in the inshore region), and vice versa. The annual P/B ratio for flesh production ranged from 3.92 in the inshore region to 8.91 in the offshore region, indicating higher production offshore. This is substantiated by the fact that the recruitment of calyptopic larvae was also highest in the outermost areas (see Figure 6.3).

6.3 4 Moult production

The intermoult period (IMP) for animals ranging in size from ~1mm (CI larvae) to 15mm was estimated using individuals maintained in the laboratory at 13°C for up to 2 months. The IMP increased with body size, ranging from 3-4 days for the larvae to 4-6 days for the older stages and can be expressed by the following equation:

$$\ln IMP = 1.0224 + 0.0410\ TL \quad (r^2 = 0.79;\ p < 0.001) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ 2$$

The mean moult dry weight was 6.75% (± 0.47) of the body dry weight and production of moults was calculated for each size-class using the formula devised by Sameoto (1976):

$$Pe = \sum_{1=1}^{s} \left(\frac{W_1 \times N_1 \times 0.0675}{D_1}\right) \quad \ldots\ldots 3$$

where Pe is the production of exuvia in mg. $m^{-3}.d^{-1}$, W_1 is the mean weight of each size-class, N_1 is the monthly density of each size-class, 0.0675 is the dry weight of the moults as a percentage of body dry weight and D_1 is the IMP in days calculated from equation 2.

Using equation 3, moult production was calculated for each size-class over the entire year. Total daily moult production for each month is shown in Table 6.1, while the mean annual moult production is presented in Table 6.2 The production of moults is directly influenced by the size distribution of the population. A population with a large proportion of adults (e.g. March, inshore region) has a higher Pe than Pg, due to slower growth of the larger individuals which still continue to moult regularly. In contrast, a population with a large number of larvae (e.g. August 1977, offshore region) has a much higher Pg than Pe, due to the higher growth rates of the larvae. Total daily moult production for all size-classes ranged from 0.1764 to 0.7709mg dry wt. m^{-3} (Table 6.1). Annual production due to moulting represents approximately 6 times the mean annual biomass.

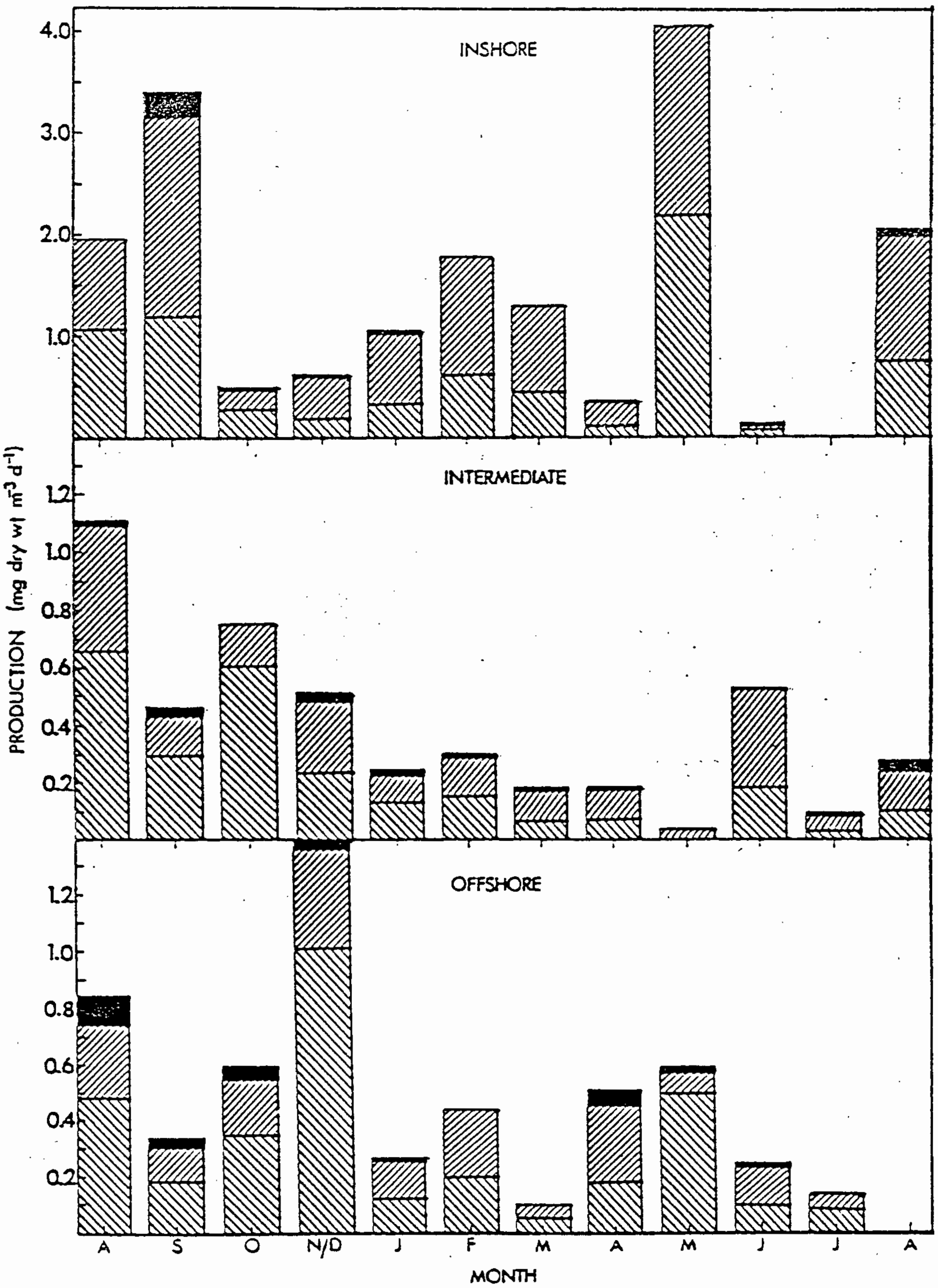

Figure 6.6 Production (mg dry wt.m^{-3}.d^{-1}) of flesh ▧, moults ▨, and eggs ■ by E.lucens from the inshore, intermediate and offshore areas

6.3.5 Egg production

Monthly production due to reproductive efforts (Pr) was estimated for females from 11-18mm total length using equation 4, which is based on the assumption that all fertilised females lay their eggs within a week (see Chapter 5). Thus for any population in which 25% of the females are fertilised, each female will lay one batch of eggs per month. Where this proportion is greater than 25%, more than one batch of eggs will be laid each month. The number of eggs laid by each size-class of females was calculated from the equation established by Stuart and Nicol (1986) relating brood size of E.lucens to total body length. The mean dry mass of a newly-laid egg was found to be 4.3 μg ($\pm$ 0.03). Secondary production in the form of eggs was thus calculated as follows:

$$Pr = \sum_{l=1}^{s} \left(\frac{S_l}{25} \times N_l \times F_l \times 0.0043\right) \qquad \ldots\ldots 4$$

where Pr is the production due to reproductive efforts (eggs) in mg. m^{-3}. $month^{-1}$, S_l is the proportion of adult females which are fertilised (spermatophore attached), N_l is the number of adult females in each size-class, F_l is the number of eggs per female, and 0.0043 is the dry weight of an egg in mg. The monthly Pr thus obtained was divided by 30 and expressed in mg dry wt. $m^{-3}.d^{-1}$ (Table 6.1). Annual production of eggs is shown in Table 6.2 and amounts to some 2.58-5.59% of the total annual production (Pg + Pe + Pr). The contribution of growth, moults and eggs to the total daily production for each month is illustrated in Figure 6.6.

6.4 DISCUSSION

In the inshore region, biomass estimates for Euphausia lucens varied considerably from month to month (3.37-317.63mg dry wt. m^{-3}), indicating a patchy distribution. These estimates were often higher than is commonly found for most other euphausiid species, which are reported to range from 1-15mg dry wt. m^{-3} (Mauchline, 1980). Simard et.al. (1986) also noted a patchy distribution of euphausiids in the St Lawrence estuary, with a mean biomass of 60mg dry wt. m^{-3} being recorded. Biomass estimates in the intermediate and offshore regions fall within the range reported by Brinton (1976) for Euphausia pacifica. The average biomass in the inshore region was about 5 times higher than further offshore (see Table 6.2). Similarly, Smiles and Pearcy (1971) also recorded a higher population density of E.pacifica closer to the coast than in the offshore oceanic waters. This aggregation of euphausiids may be explained by the accumulation of animals retained by the action of surrounding ocean currents (see Chapter 5), or by the interaction between upwelling and residual circulation with the negative phototactive behaviour of euphausiids (Simard et.al., 1986).

Growth rates of juveniles (0.047mm. d^{-1}) and adults (0.026mm. d^{-1}) are comparable to those of Nyctiphanes australis, a euphausiid of similar size to E.lucens (Ritz and Hosie, 1982). In studies of E.pacifica, however, population growth rates were twice as fast (Smiles and Pearcy, 1971; Brinton, 1976; Ross, 1979), although it should be noted that E.pacifica is a larger species. Growth slows down with increasing age and females attain a larger body size than males (see Chapter 5) probably through increased growth rates and increased longevity (Mauchline, 1980).

Production due to growth (Pg) was relatively high as a result of the high biomass and ranged from 77-186mg dry wt. $m^{-3}.year^{-1}$. This is comparable with the mean annual production for Nyctiphanes australis of 78.29mg. $m^{-3}.year^{-1}$ (Ritz and Hosie, 1982), although considerably higher than values obtained by Lindley (1978, 1980, 1982a and b) for several other species in the North Atlantic Ocean and by Berkes (1977) for Thysanoëssa raschii in the Gulf of St Lawrence. Lindley (1978, 1980, 1982a and b) only sampled the top 10m both by day and night which may have led to underestimation of euphausiid biomass and production due to the vertical migratory behaviour of most euphausiid species.

E.lucens was found to exhibit continuous breeding throughout most of the year (see Figure 26) which has only been observed in relatively few other euphausiid species confined most to the equatorial regions and mid latitudes. Gros and Cochard (1978) found continuous breeding in a population of Nyctiphanes couchii and Jillet (1971) and Ritz and Hosie (1982) observed multiple generations in populations of N.australis in New Zealand. In addition, Smiles and Pearcy (1971) and Brinton (1976) found that E.pacifica off Oregon and southern California had breeding females at all times of the year with furcilia larvae being perenially abundant.

Associated with a prolonged breeding season are high P/B ratios. This is particularly evident in the offshore area where high densities of calyptopis larvae were found throughout the year and an annual Pg/B ratio of 8.91 was computed. In contrast to this, the inshore area had lower densities of calyptopis larvae, indicative of less breeding, with a Pg/B ratio of only 3.92 (Table 6.2). Lindley (1978) also observed contrasting P/B ratios for the euphausiid Thysanoëssa longicaudata in different geographical areas, with a ratio of up to 11.6 in areas where two generations were produced annually and only 2 in areas where a single generation was produced. The higher P/B ratios were attributed to warmer waters, resulting in faster metabolism and increased turnover of materials. This may also be the reason for the higher P/B ratio in the offshore region in the present study, since temperatures in this region were on average 2-3°C higher than in the inshore region (see Chapter 5). However, it should be borne in mind that since E.lucens undergoes strong vertical migrations (Pillar, 1984a) both populations would be subjected to a wide range of temperatures during the course of the day. Populations of euphausiids in higher latitudes with large seasonal temperature fluctuations and severe winters have much lower P/B ratios, as is found in Thysanoëssa inermis and Thysanoëssa raschii where P/B ratios of 1.3-4.2 were recorded (Lindley, 1980) and in Euphausia superba which has P/B ratios ranging from 1.19-2.8 (Allen, 1971; Miller et.al., 1985). In contrast, species from warmer areas, which lack large seasonal temperature changes, such as N.australis of South East Tasmania and E.pacifica off Oregon, exhibit fast turnovers, with P/B ratios of 14.5 and 8.7 respectively (Ritz and Hosie, 1982; Smiles and Pearcy, 1971).

The duration of the intermoult period (IMP) for E.lucens at 13°C was found to increase logarithmically with body size (see Equation 2), as has been found in many other euphausiid species (Fowler et.al., 1971; Murano et.al., 1979; Mauchline, 1980). Production due to moulting (Pe) has only been estimated for relatively few other species. Hosie and Ritz (1983) estimated the production of moults for N.australis to be 42.01mg. m^{-3}.$year^{-1}$, which is comparable to the present production estimates of 60-281mg. m^{-3}.$year^{-1}$, or 6 times the mean euphausiid biomass. Assuming an average depth of 100m for the present study, moult production can also be expressed in terms of g.m^{-2}, resulting in estimates of 6-28g dry wt. m^{-2}.$year^{-1}$. This is comparable to the moult production estimates of 4.6g dry wt. m^{-2}.$year^{-1}$ for the total population of euphausiids in the Gulf of St Lawrence (Sameoto, 1976) and to E.pacifica which has an estimated moult production of 1.5g dry wt. m^{-2}.$year^{-1}$ or 7 times the mean euphausiid biomass (Lasker, 1966). E.superba, which lives in much colder waters and has an intermoult period of approximately 27 days, has a somewhat lower moult production of 0.45g dry wt. m^{-2}.$year^{-1}$ (Ikeda and Dixon, 1982). These moults are rapidly colonised by numerous bacteria and ciliates (Stuart, 1986) and may thus either represent a substantial food source for other organisms in the form of detritus or they may be rapidly decomposed and thereby play an important role in nutrient regeneration. In the present study, dry weight production due to growth (Pg) was of the same order of magnitude as production due to moulting (Pe) (see Table 6.2) indicating the great extent of moult production by euphausiids.

Production due to reproductive output (Pr) has also been largely ignored in previous studies. For E.lucens this amounts to 5-12mg dry wt. m^{-3}.$year^{-1}$

Total annual production (Pg + Pe + Pr) for E.lucens off St Helena Bay is thus remarkably high (142-479mg dry wt. m^{-3}.$year^{-1}$) and the resulting annual P/B ratios of 10-16 (Table 6.2) indicate this to be an area of high secondary production. Borchers and Hutchings (1986) tentatively estimated total zooplankton production (excluding microplankton) to be 50gC.m^{-2}.$year^{-1}$, a value derived from the mean zooplankton standing stock in the southern Benguela region and assuming a mean generation time of 1 month. The total production of E.lucens expressed in terms of carbon is 5-15gC.m^{-2}.$year^{-1}$ which is equivalent to 10-30% of the annual zooplankton production. However, since the St Helena Bay region only represents a portion of the range of E.lucens and given the paucity of data on the production of other local zooplankton, this calculation should be viewed as a preliminary estimate of the importance of E.lucens as a secondary producer in the southern Benguela region.

The abundant food supply, set up by the interplay between coastal upwelling, strong offshore fronts and advective processes, the prolonged breeding season, lack of a severe winter and relatively warm water all year round are all contributing factors to the high production of E.lucens in the St Helena Bay region. Several species of commercially important fish, including anchovy (Engraulis capensis), display their strongest recruitment in the this region (Crawford et.al., 1980). This reflects the benefits of the large zooplankton production of which E.lucens comprises a substantial proportion.

CHAPTER 7

THE ROLE OF DIEL VERTICAL MIGRATION IN THE LIFE HISTORY STRATEGY OF *EUPHAUSIA LUCENS* IN THE SOUTHERN BENGUELA CURRENT

7.1 INTRODUCTION

Several hypotheses regarding the role of diel vertical migration in zooplankton have been reviewed by such workers as Longhurst (1976) and Pearre (1979), and more recently by Angel (1985) and Kerfoot (1985). Advantages of residing at depth during the day were suggested as being the decreased risk of predation (Pearre, 1973; Zaret and Suffern, 1976; Stich and Lampert, 1981) and conservation of energy in cooler waters (McLaren, 1963; Enright, 1977). The nocturnal ascent has generally been attributed to nutritional advantage of being in warmer, more productive, surface water (e.g. Enright and Honegger, 1977). Transport by differential current systems has also been advanced as a possible advantage of diel migration (Isaacs et.al., 1974). These hypotheses are, however, still in dispute and the conclusion is that no single benefit hypothesis can explain diel migration in zooplankton and that to some degree all of the above-mentioned hypotheses may be applicable.

Diel migration is common in most euphausiid species as well as ontogenetic migration, whereby progressively deeper levels are occupied by older stages during the day, while during the night most of the population congregate in the upper layers of the water column (Brinton, 1979; Mauchline, 1980; Roe et.al., 1984). A characteristic of most oceanic species is the developmental ascent, whereby the eggs sink and hatch into nauplii at depth, and ascend to the upper layers as first-feeding calyptopis larvae when ontogenetic migration begins (Marr, 1962; Hempel et.al., 1979; Williams and Lindley, 1982). By contrast, in neritic and shelf-dwelling species the eggs and nauplii have been shown to be restricted to the upper layers, while the larvae and older stages migrate through different depth ranges throughout the water column (Hirota et.al., 1984; Williams and Fragopoulu, 1985). The coastal environment is characterised by stronger horizontal and vertical circulation systems and more complex advective processes than the oceanic environment. Neritic species would therefore have to interact with markedly different current regimes in order to maintain themselves within the coastal environment. Because of the ontogenetic shift in the pattern of migration, the currents acting on early reproductive stages may be different from those acting on older larvae and adult stages.

Ontongenetic layering has been reported for Euphausia lucens in the Southern Benguela region from preliminary studies by Pillar (1984a), but information was not provided on the vertical distribution of the eggs and nauplii or on the daytime distribution of the juveniles and adults, since they migrated below the tracking range of the net. It is therefore not known if E.lucens possesses the characteristics typical of neritic species. The intentions of this study are to gain more insight into the vertical and ontogenetic distribution patterns of E.lucens and to consider what physical processes interact with these patterns to maintain the population within the Southern Benguela system.

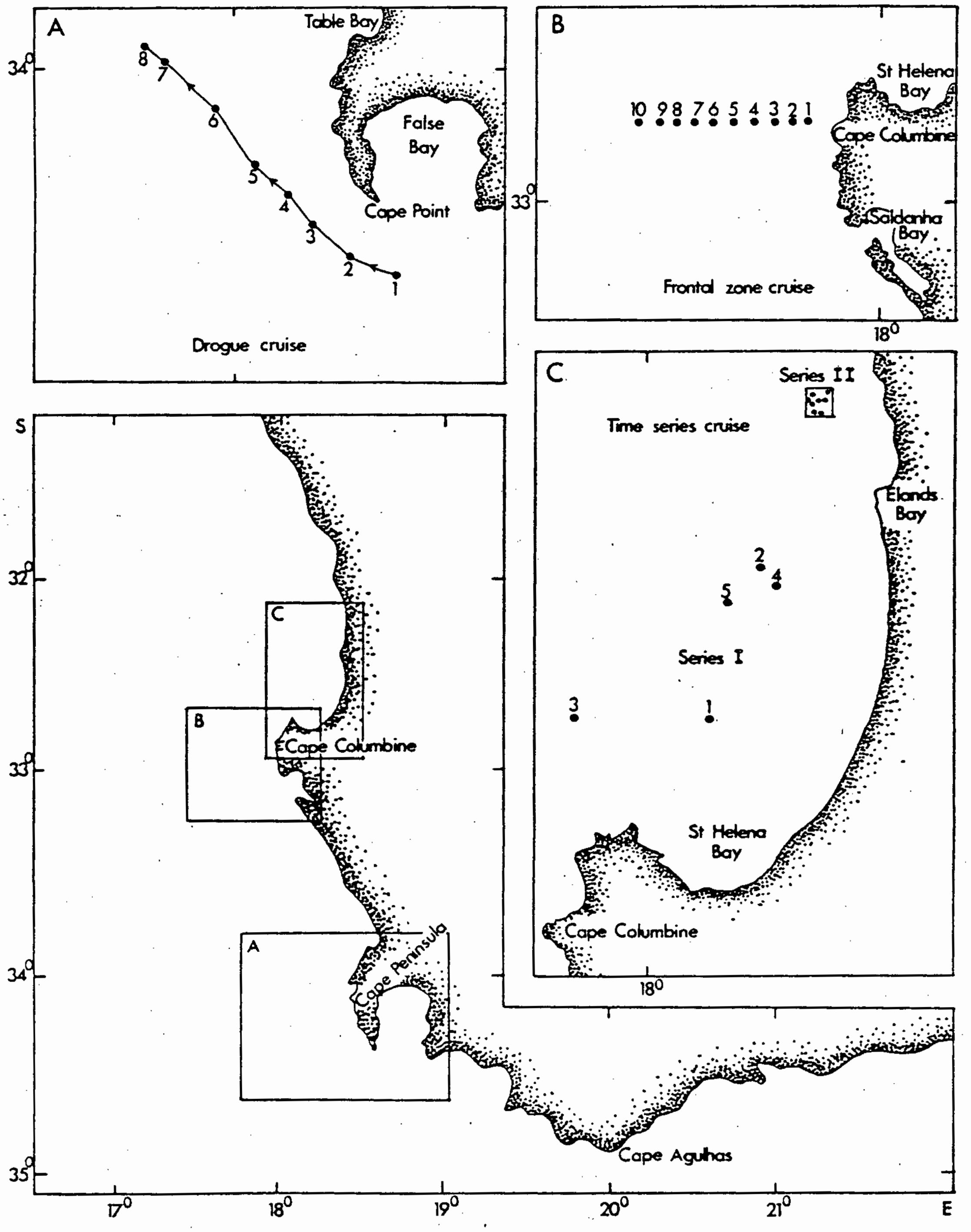

Figure 7.1 Study areas showing stations occupied during (a) the Drogue cruise, (b) the Frontal zone cruise and (c) the Time series cruise

7.2 MATERIALS AND METHODS

Data were obtained from zooplankton collections from three cruises. The first was during October 1976 in the vicinity of Cape Point, when a parachute drogue set at 10m was followed for a period of 68 hours in a north-westerly direction for 136kms (Figure 7.1a). Zooplankton collections were taken at approximately 8-hourly intervals using a flight of 'Miller nets' (Miller, 1961). Each net consisted of an 80cm long PVC tube with an internal diameter of 14.5cm, and an attached 125cm long cylindro-conical 300 μm meshed net. The nets were distributed between the surface and 75 metres, and were towed at 3 knots for 60 minutes. The depth of the water column ranged from 165-265 metres during the study period. Full details of biological and physical data collections made are presented in Shelton and Hutchings (1982) and it is referred to in the text as the 'drogue cruise'.

The second cruise from which data are drawn consisted of two series of six-hourly RMT 1x6 collections in the St Helena Bay region during May 1984, and is referred to as the 'time series cruise' (Figure 7.1c). The first series (series I) consisted of a random sampling grid which was designed to cover a large area of St Helena Bay, and the second series (series II) represented a more intensive grid covering an area of approximately one square nautical mile (3.2km^2). At each station, zooplankton samples were collected with a 1m^2 multiple opening and closing Rectangular Midwater Trawl fitted with six 200 μm meshed nets (RMT 1x6). The net was towed at two knots and fished in five depth strata during the ascent from close to the bottom to the surface.

The third cruise, referred to as the 'frontal zone cruise', was designed to study the front associated with the Cape Columbine upwelling centre, which also provided information on the inshore-offshore differences in the vertical structure of the euphausiid community. During 11-13 December 1984, a transect of 10 stations, each 3 nautical miles (5.5km) apart, were sampled shoreward to within 10km of the coast (Figure 7.1b). Zooplankton was collected from close to the bottom to the surface, using the same method as described earlier for the RMT 1x6 net. Subsequent analysis of the collections showed possible malfunctioning of the trigger mechanism of the RMT1x6, such that it necessitated pooling the data from the upper two and middle two depth strata. Since these depths were selected on the basis of thermocline depth, the three strata sampled could be considered to represent the layers above, within and below the thermocline. Details of the physical, chemical and biological sampling are described by Armstrong et.al. (1987).

In the laboratory, counts were made of all developmental stages of Euphausia lucens, i.e. egg, nauplii, calyptopis, juveniles (post-larvae and immatures) and adults. Females were examined for presence/absence of a spermatophore in the thelycum, and the condition of the spermatophores in the males was noted. Counts of large samples were obtained from sub-samples using a Folsom splitter. All counts were standardised to numbers per m^3 from a knowledge of the volume of water filtered by the nets.

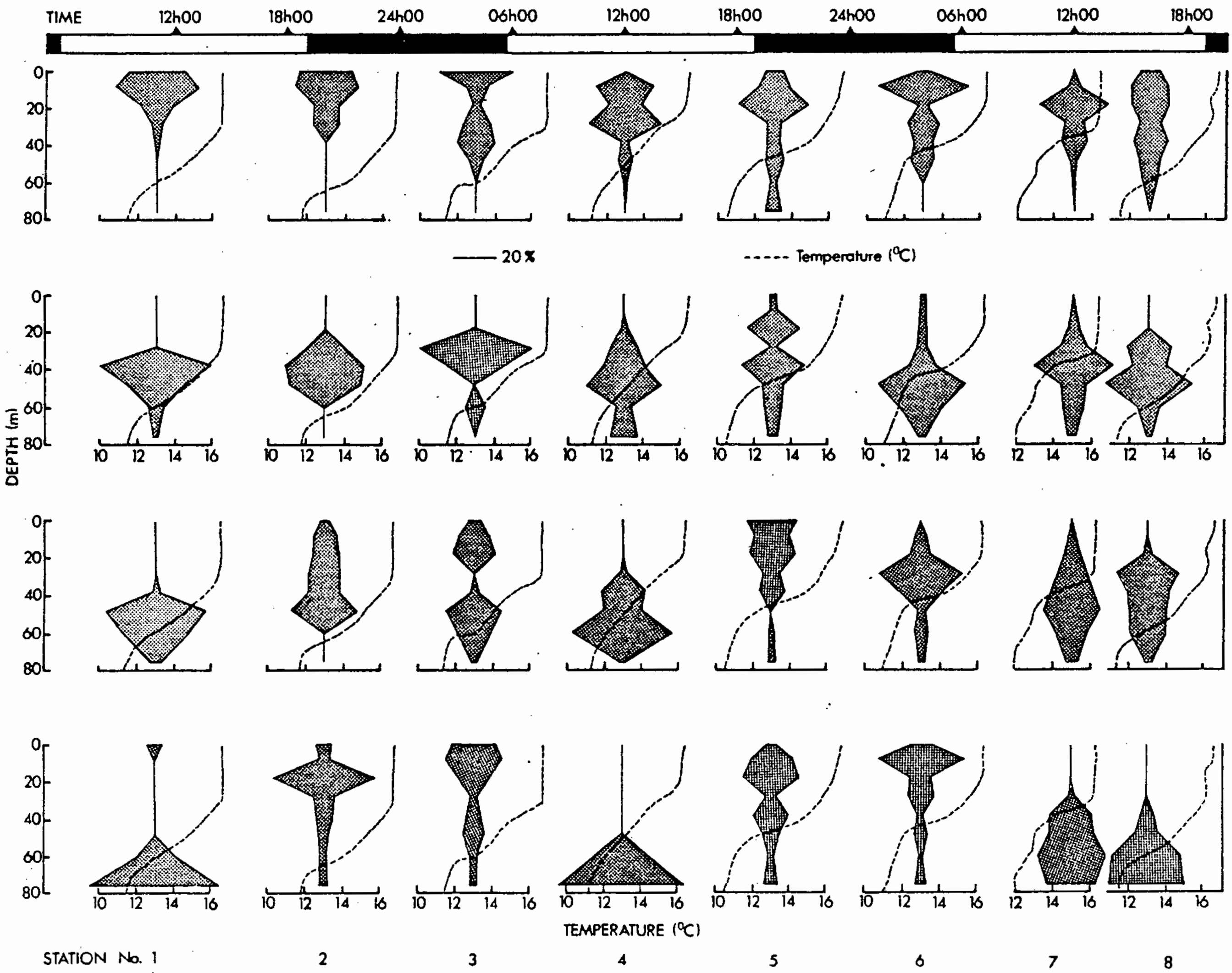

Figure 7.2 Vertical distributions of the egg and larval stages of E.lucens during the Drogue cruise. The values at each depth are expressed as a percentage of the total density (no. m^{-3}) over all sampling depths. Temperature is shown by a broken line

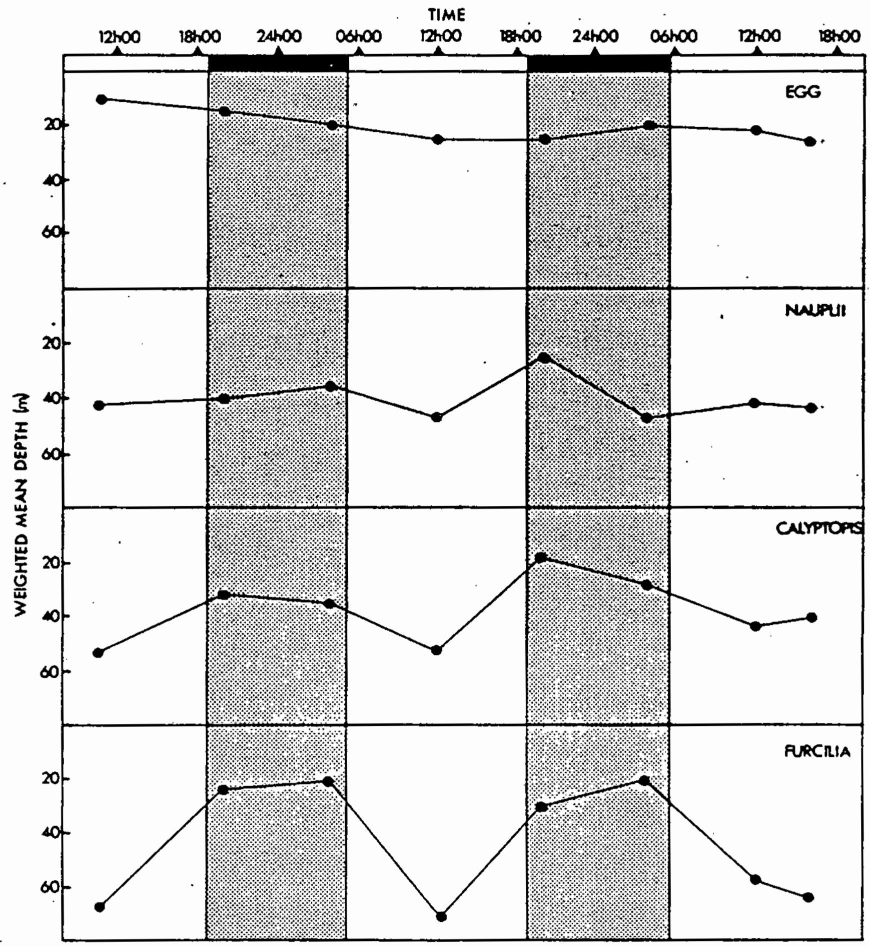

Figure 7.3 Weighted mean depth plots of the egg and larval stages of E.lucens during the Drogue cruise

7.3 RESULTS

7.3.1 Species composition

Euphausia lucens was the dominant euphausiid species in the collections from the three cruises. Other species which occurred infrequently were Nyctiphanes capensis, which formed 0.1 - 0.3% of the euphausiid community during the drogue cruise and time series cruise respectively, and Euphausia recurva and Euphausia similis, which together constituted $<0.1\%$ of the offshore euphausiid community during the frontal zone cruise.

Drogue cruise

The vertical profiles of temperature and relative abundance (percent) at depth of the eggs and larval stages of Euphausia lucens at each station is shown in Figure 7.2. To facilitate tracing the diel movements of each developmental stage, the mean depth occupied by each stage was calculated for each station and is presented in Figure 7.3. This technique was used extensively by Roe et.al. (1984) and termed the 'Weighted Mean Depth' (WMD), which is calculated as follows:

$$WMD = \frac{\sum nidi}{N}$$

where di is the depth of a sample (i) and ni is the number of individuals at that depth. N is the sum of the number of individuals over all sampling depths.

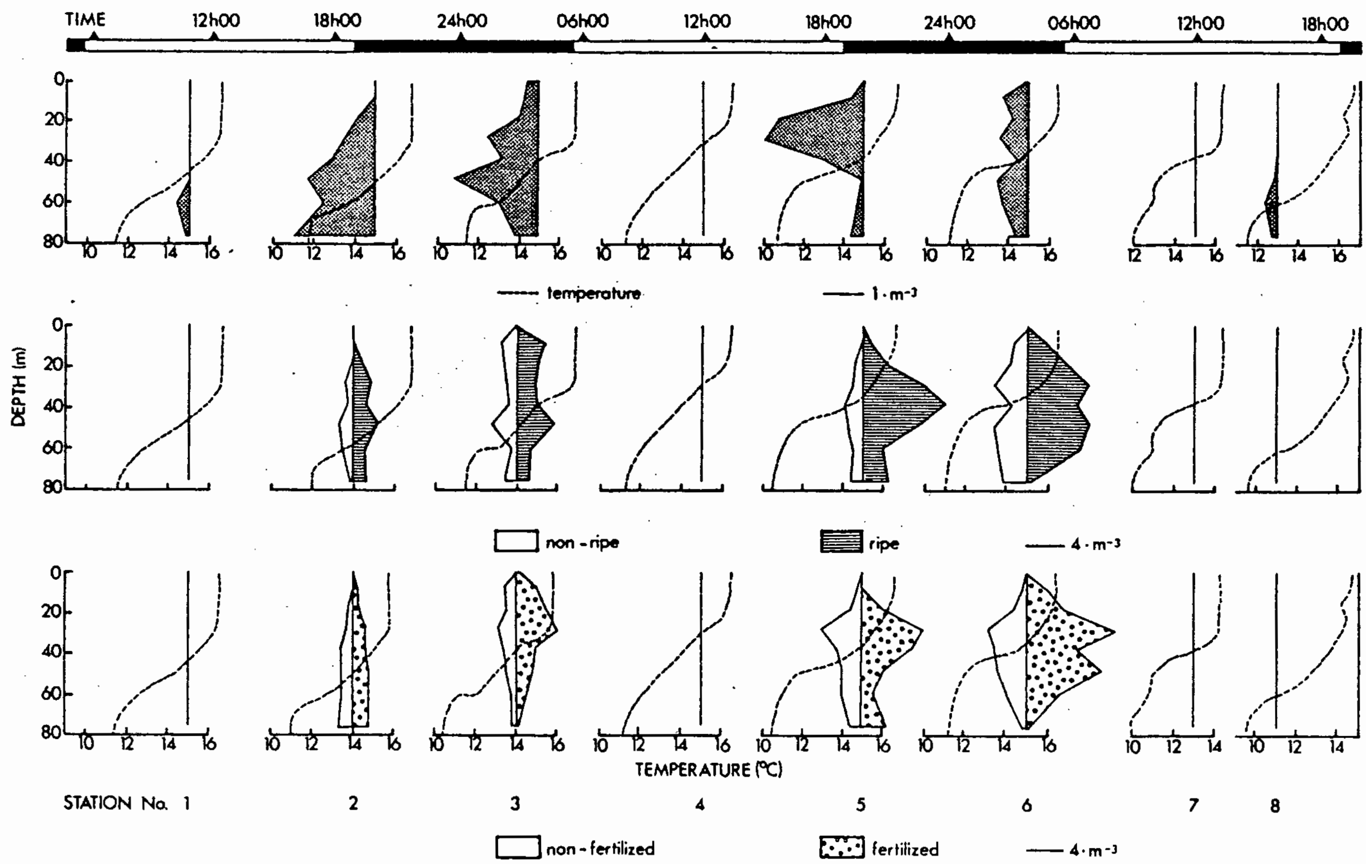

Figure 7.4 Vertical distributions of the juvenile and adult reproductive stages of E.lucens during the Drogue cruise. Temperature is shown by a broken line

Figure 7.3 shows that the eggs occupied a shallower depth range than the nauplii, being concentrated in the upper 30 metres, while the bulk of the nauplii occupied the 20-40 metre depth stratum. Neither of these early stages showed evidence of diel movement. The calyptopis stage showed a limited diel movement, being closer to the surface at night. The furcilia stages migrated more extensively showing a marked nocturnal ascent into the upper 20-30 metres from daytime depths which extended beyond the tracking range of the net (75m). The daytime WMD values for the furcilia stages (Figure 7.3) are considered underestimates, since the lower limits of their vertical distribution was not quantified. This limitation precluded using MWD values for tracing diel movements of the juvenile and adult stages of <u>E.lucens</u>.

The juvenile and adult stages occupied a much wider vertical range than the larval stages as evidence by their near-absence in the daytime collections (Figure 7.4). This observation is not considered to be wholly a result of daytime avoidance and will be discussed later. During the night adults were more numerous than juveniles in the collections, with the population generally centred around the 20-50 metre depth stratum. The vertical distribution of the ripe males and fertilised females appeared similar to the sexually inactive adult population. It should be noted that the paucity of juveniles and adults caught by the surface Miller nets during the nighttime hauls may in part be attributed to the disturbance caused by the ship's movement which, through avoidance, would decrease their availability to the approaching net (Pillar, 1984b).

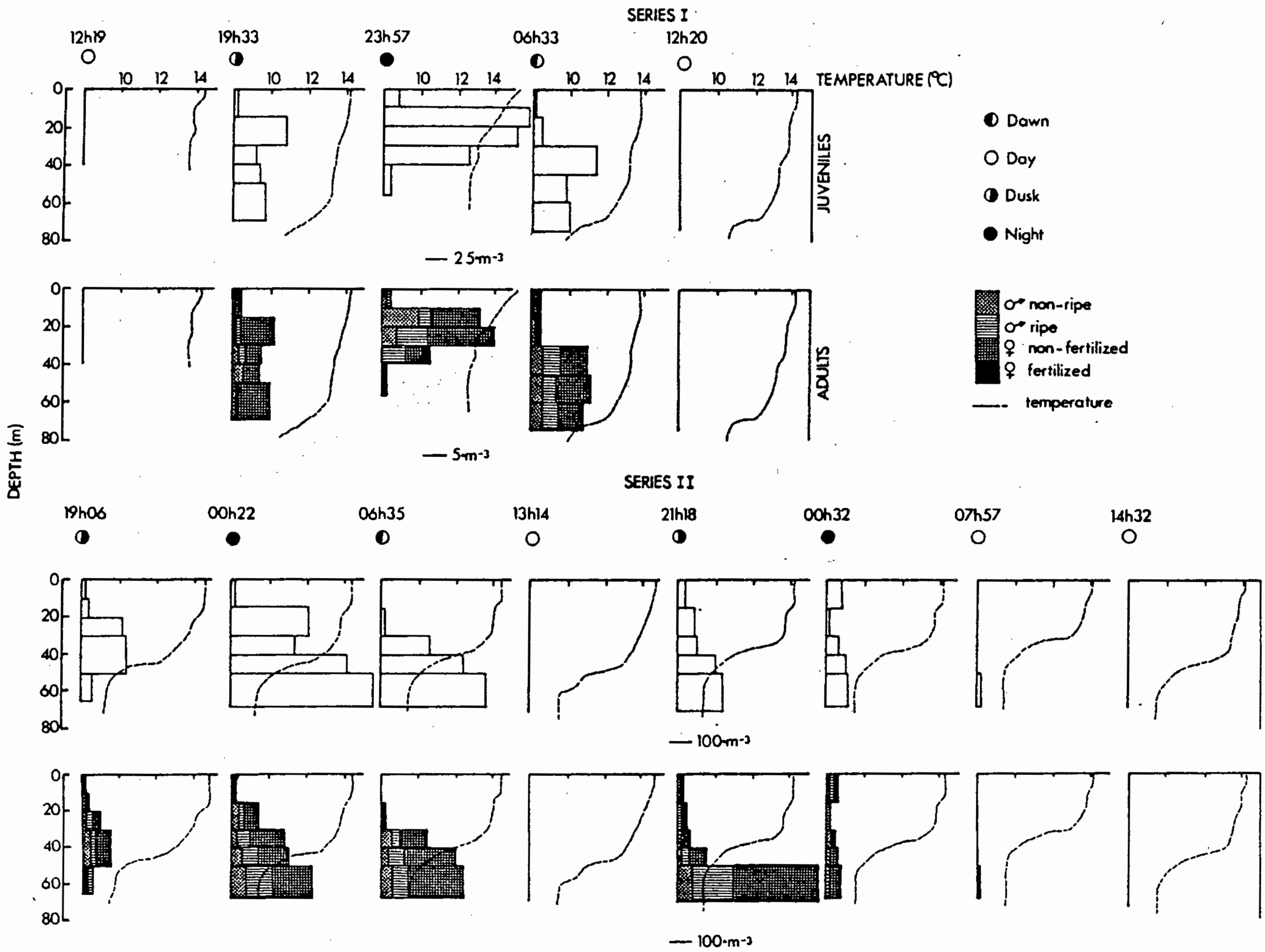

Figure 7.5 Vertical distribution of the juvenile and adult stages of E.lucens during series I and II of the Time series cruise. Temperature is shown by a broken line

The presence of a thermocline did not limit the migratory movement of either the older larvae (Figure 7.2) or the juvenile and adult stages (Figure 7.4). As chlorophyll *a* concentrations were consistently low (1mg.m^{-3}) over all depths, except for an increase (1-3mg.m^{-3}) in the upper layers between the last two stations (Shelton and Hutchings, 1982), it is considered unlikely that phytoplankton concentrations influenced the observed vertical distributions.

7.3.3 Time series cruise

Eggs and larval stages occurred infrequently in the collections and were not in sufficient numbers to allow description of their vertical distributions. Figure 7.5 shows the vertical distribution of the densities of the juvenile and adult stages of *E.lucens* relative to temperature for series I and II of the time series cruise. For comparative purposes sampling times were grouped into dawn, day, dusk, and night.

In series I, highest densities were recorded throughout the water column from dusk until dawn, with negligible densities occurring during the day. The juveniles occupied a similar depth strata to that of the adults. There is evidence of a shift upwards in the population after dusk and a downward shift after dawn. The near-absence of juveniles and adults in the daytime collections should be due to their diel movement into the near-bottom layer and below the tracking range of the net, or due to net avoidance (Brinton, 1967), or a combination of both. During a comparative study in inshore waters, Pillar (1982) showed that juveniles and adults of *E.lucens* were more than an order of magnitude, more dense within a few metres of the bottom than in a layer ranging between 2-14 metres above the bottom during the daytime. Furthermore, he found similar catches of juveniles and adults in both dark- and light-coloured Bongo nets during the day, indicating that visual-associated avoidance was not strongly demonstrated by E.lucens. The present data are perhaps better explained by a daytime distribution in the near-bottom layer with a nocturnal migration into the upper layers, but net avoidance cannot be entirely ruled out.

The scarcity of juveniles and adults during the day is also notable during series II, however there was no nocturnal ascent as evidenced during series I. Although a strong thermocline was present during series II, this feature did not seem to influence the vertical distribution of either the juveniles or adults. A more plausible explanation for these observations is the predatory impact of the anchovy Engraulis capensis, which were present in large and dense shoals in the upper 40 metres during the times and positions of sampling in series II. Stomach analyses of these fish by James (1987) showed that they fed almost exclusively on juvenile and adult E.lucens from dusk until dawn. During the day they were absent in the stomachs, although copepod remains were present. This feeding pattern suggests that the euphausiids were not present in the upper 40 metres during the day, providing additional support to the contention that E.lucens migrated into the bottom layers during the day.

Females formed 59% of the adult population in series I and II, of which 0.1% were fertilised (with attached spermatophores). Mature males formed 56% of the male population. The females and males occupied similar depth

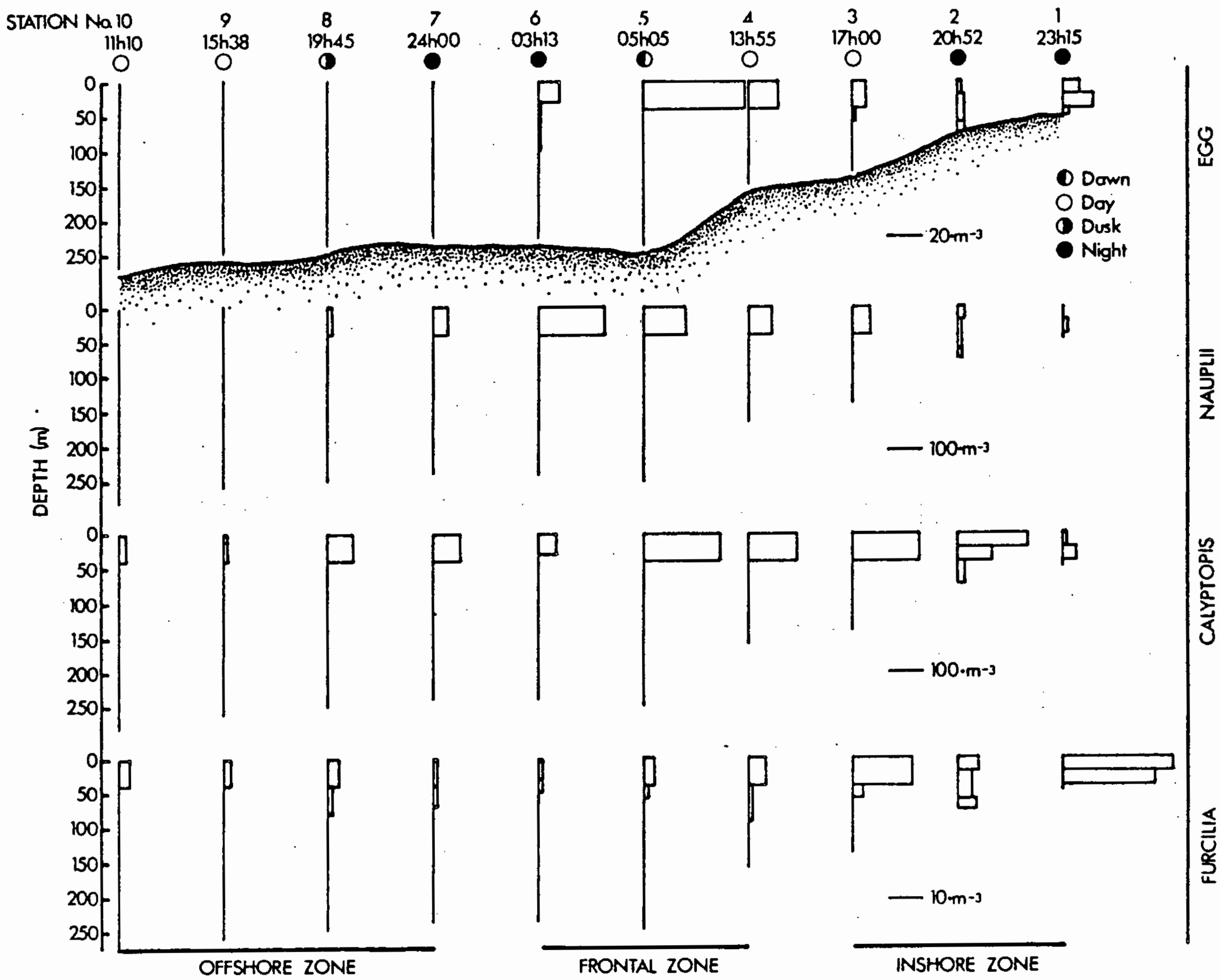

Figure 7.6 Vertical distribution of the eggs and larval stages of E.lucens during the Frontal zone cruise

strata, and there was no evidence to suggest differential migratory behaviour between the immature and mature individuals in the male or female population.

7.3.4 Frontal zone cruise

The samples collected during this cruise give some indication of the depth strata occupied by the different developmental stages of E.lucens in inshore and offshore waters. However, the offshore data should be viewed with some caution when considering that a much greater depth strata was sampled by the bottom nets than the surface nets. Hence when standardised to numbers per m^3, the abundance estimates of the bottom stratum will have artificially lower estimates relative to the shallower depth strata if the animals were not evenly distributed with depth. However, in Figure 7.6, which shows the vertical distribution of the egg and larval stages with distance offshore, several features are apparent which are not masked by the aforementioned bias. Marked changes in the relative abundance and vertical distribution occurred with distance offshore and with depth. The eggs and nauplii were concentrated in the vicinity of the front, while the highest densities of the calyptopis and furcilia larvae were closer inshore. Densities declined markedly in the offshore zone. The eggs and larvae occupied the upper strata during both the day and night offshore, but were distributed throughout the water column at the shallower inshore stations.

The abundance of the juvenile and adult stages of E.lucens was highly variable along the transect as a result of their scarcity in the daytime

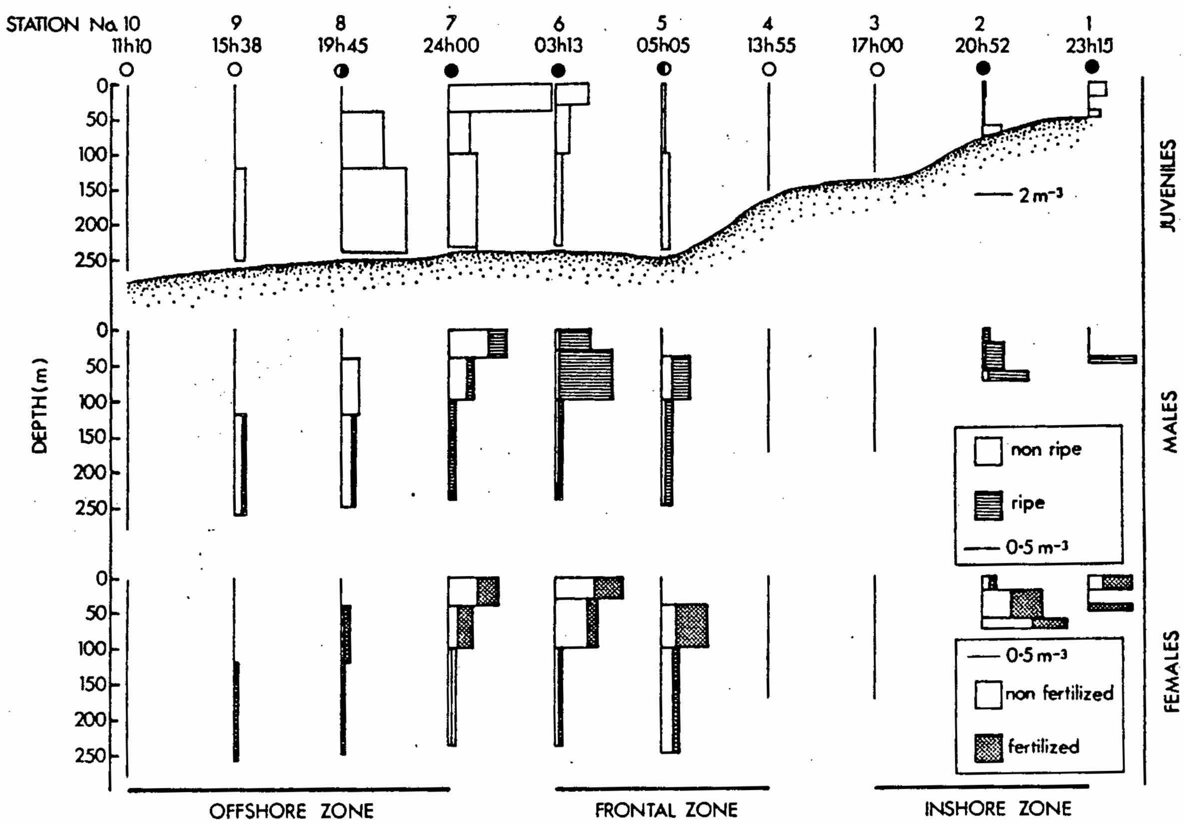

Figure 7.7 Vertical distribution of the juvenile and adult reproductive stages of E.lucens during the Frontal zone cruise

collections (Figure 7.7). They occupied similar depth strata from dusk to dawn within a vertical range more extensive than the younger developmental stages. There is evidence of an upward and downward shift in the population during this period. The presence of a thermocline at depths between 30-40 metres (Armstrong et.al., 1987) did not restrict this diel movement.

Females formed 56% of the adult population, of which 52% were fertilised, while 62% of the male population were in ripe condition. As was observed during the time series cruise, there were no marked differences in the vertical structure between either the males and females or between the sexually active and inactive individuals in the adult population.

7.4 DISCUSSION

7.4.1 Vertical distribution

The eggs of E.lucens were restricted to the near-surface layers, suggesting slower sinking rates than those of oceanic species. Laboratory studies by Marschall (1983) showed that under similar temperature and salinity regimes, eggs of neritic species such as Meganyctiphanes norvegica and Thysanoessa rachii had slower sinking rates than Euphausia superba, a typical oceanic species. Harrington and Thomas (1987) noted that the eggs of Euphausia crystallorophias, a neritic species, were neutrally buoyant and suggested that a proportionately large perivitelline space in the egg would decrease its sinking rate. They calculated that the proportion of the total egg volume occupied by the perivitelline space in E.crystallorophias and other neritic species ranged between 44.7-77.7%, a much larger value than 6.4-13.0 computed for E.superba. In support of their finding they noted that the perivitelline of Thysanoessa longicaudata, an oceanic species, was reported by Williams and Lindley (1982) to be 'very small'. From samples taken from a number of depth strata, the perivitelline space of E.lucens eggs was estimated to be 62.7 ± 4.8% (n = 50), of the total egg volume. This result is supportive of the conclusions of Harrington and Thomas (1987).

The fact that the naupliar stages of E.lucens were concentrated at shallow depths is evidence that the ontogenetic migration of neritic species is different from the classical 'developmenal ascent' characteristic of oceanic species, whereby the eggs sink and hatch at depth and ascend to the surface layers as first-feeding calyptopis larvae (Marr, 1962; Mauchline, 1980; Williams and Lindley, 1982). This difference in ontogenetic behaviour was noted earlier in the Scotia Sea by Makarov (1979) who found nauplii stages of E.crystallorophias in the upper 25 meters, while similar stages of E.superba and Thysanoessa macrura, both oceanic species, were concentrated at depths of between 500-1000 metres. The author related this finding to the hydrology of inshore waters, as well as differences in the spawning behaviour of neritic species.

The observed ontogenetic migrations in E.lucens, with the older furcilia larvae migrating more extensively than the younger calyptopis laravae, is a common feature in most euphausiid species (Mauchline and Fisher, 1969; Mauchline, 1980; Williams and Lindley, 1982; Hirota et.al., 1984). It is evident that the developmental cycle from egg through to the beginning of adolescence of E.lucens takes place within the upper layers, except in shallow waters where turbulence may cause mixing of the water column, as shown during the frontal zone cruise (Armstrong et.al., 1987). There are several advantages to remaining in the upper layers during early development. Firstly, relatively less energy need be invested in the eggs by the adults, as non-feeding nauplii are not required to migrate from the bottom layers to reach the surface layers as first-feeding larvae. Secondly, by remaining in the warmer upper mixed layer, faster egg and naupliar development would result in increased early survival.

It is clear that temperature gradients were not the reason for diel migration as the juvenile and adult stages of E.lucens continued to migrate vertically even in isothermal waters (Figure 34). This finding is not supportive of the hypothesis that migrators gain an energetic and metabolic benefit by remaining in deeper cooler water during the day (McLaren, 1963; Enright, 1977). However, the hypothesis that diel migration is a strategy to avoid predators (Zaret and Suffern, 1976; Stich and Lampert, 1981) may be more applicable in the present study. The concomitant feeding studies of anchovy from collections taken during the time series cruise (James, 1987) showed that juvenile and adult euphausiids were absent in their stomachs during the day, while from dusk to dawn they were feeding almost exclusively on euphausiids. As the anchovies were shown to be opportunistic feeders, being capable of feeding on other crustaceans during the day (James, op.cit.), it may be assumed that the euphausiids migrated beyond the vertical range of the anchovies during the day. Antezana-Jerêz (1978) concluded that the diel migration of *Euphausia mucronata* in the Chile-Peru Current was a strategy to avoid predators rather than an energetic and metabolic advantage. Furthermore, he showed no evidence to suggest changes in the feeding intensity of *E.mucronata* between those caught at the surface at night and those caught at depth during the day, a finding contradictory to the contention that zooplankton entered the upper mixed layer at night to feed. The feeding cycle associated with diel migration of euphausiids has received some attention (e.g. Mauchline, 1980; Simmard *et.al*., 1986; Willason and Cox, 1987); however, feeding rhythms of euphausiids still remain a controversial matter.

7.4.2 Dispersal and transport

The ontogenetic migration of *E.lucens* is extensive enough to carry them to strata of the water column with different current regimes such that currents acting on the eggs and nauplii would be different from those acting on the older larvae and juvenile and adult stages. Nelson and Hutchings (1987) concluded that prevailing currents in the Southern Benguela are of sufficient strength to passively transport pelagic organisms with swimming speeds 30cm.s^{-1}. Also, Brown and Hutchings (1987) showed that newly upwelled near-surface water moved at speeds between 20-40cm.s^{-1} on the shelf. These values are considerably greater than the range 0.6-0.9cm.s^{-1} which was estimated as the mean active swimming speeds for *E.pacifica* (Torres and Childress, 1983) and 6.3 and 9.5cm.s^{-1} which were the maximum swimming speeds recorded from field and laboratory experiments for E.mucronata (Antezana-Jeréz, 1978). Therefore it may be assumed that all stages of E.lucens, especially early larval stages, are subject to passive transport by local currents. However, as cautioned by Nelson and Hutchings (1987), current speeds are variable on time scales of hours and therefore movement against averaged currents may be possible for older stages of E.lucens.

The later winter to early summer spawning of E.lucens places the eggs in the surface layers of the southern Benguela region during the period of the strengthening of the thermal front, resulting from seasonal upwelling during which increased Ekman transport occurs (Shannon, 1985). Although the warmer offshore waters may decrease development time, being transported into warm, plankton poor oceanic waters, might also lead to significant mortality through starvation. The dominance of this offshore transport of the early reproductive stages may be influenced by the thermal front, which seems to exert some control on their offshore displacement (Figure 7.6). The thermal front has been implicated as a barrier to the offshore Ekman transport of shelf water along the west coast (Hutchings et.al., 1986; Shelton, 1986). Off the Cape Peninsula, Armstrong (1987) recorded highest concentrations of euphausiid eggs and nauplii in the upper layers coincident with the thermal front during periods of upwelling, as opposed to during a downwelling event when they were advected inshore. Peaks of copepod eggs, nauplii and copepodite stages have also been recorded in the surface layers adjacent to thermal fronts in the Southern Benguela region (Hutchings et.al., 1986; Armstrong et.al., 1987).

Since older larvae of E.lucens spend proportionately less time in the surface layers than the eggs and nauplii, and migrate to greater depths during the day, they would be less susceptible to offshore transport and more subject to the currents underlying the surface layers. These currents are predominantly longshore. Nelson and Hutchings (1987) reviewed salient features from drogue studies (Shelton and Hutchings, 1982; Nelson and Hutchings, 1983; Holden, 1985; Nelson, 1985) and current meter studies (Nelson, 1983; Holden, 1987; Nelson and Polito, 1987) and proposed a longshore-closure system between the Agulhas Bank and St Helena Bay. This model provides a useful basis for examining some of the mechanisms by which E.lucens could be maintained within the Southern Benguela system. The important features contributing to this current closure system are (1) the northward-flowing jet current which rounds Cape Point from the Agulhas Bank and attenuates north of Cape Columbine, (2) the baroclinic poleward-flowing current which occurs inshore along the west coast, and (3) the cyclonic gyre and associated eddies in the St Helena Bay region where the residence time of the water is substantial and of the order of 25 days (Waldron, 1985).

The resultant effect of offshore displacement coupled with the jet current would facilitate northward movement of young stages (eggs and nauplii) if spawning occurred south of Cape Columbine. Just north of this area there is a divergence zone, partly topographically induced (Shannon, 1985), which provides alternative mechanisms to the northward displacement of material, either into the St Helena Bay area or further north into the Namaqua region. The cyclonic eddy into St Helena Bay has been suggested to be more intensive during summer and the northward component to be more prevalent during winter and spring (Shelton, 1986). This implies that a significant proportion of the early reproductive stages of E.lucens would be transported past St Helena Bay and out of the closure system described by Nelson and Hutchings (1987). Based on drift card recoveries, Shelton (1986) showed little evidence to suggest a return to the inshore zone of near-surface dwelling zooplankton. However, larvae of E.lucens may not necessarily be lost to the Southern Benguela region, as smaller closure systems, suggested by Nelson and Hutchings (1987) to exist further north, might entrain them towards the coast. With the attenuation of the jet current and the broadening of the shelf north of Cape Columbine, the currents would be expected to be more sluggish and therefore permit a longer residence time for larvae to develop deeper vertical migrations. This deeper distribution, coupled with the poleward deep counter-current, would facilitate a return mechanism of E.lucens into the Southern Benguela closure system.

Material transported further north would, in all probability, be lost from the Southern Benguela population. Satellite drogue studies described by Nelson and Hutchings (1983) showed a westward-moving flow off the shelf zone south-west of Luderitz (28°S) into Namibian oceanic waters. It is likely that the Luderitz upwelling zone is the major environmental barrier to the northward extension of E.lucens, as no records of E.lucens have been recorded beyond it in Namibian waters (Boden, 1955; D'Arcangues, 1977).

The importance of the St Helena Bay/Lambert's Bay circulation patterns in accumulating large concentrations of euphausiids inshore and north of Cape Columbine, has been discussed earlier (see Chapter 5). Also, large concentrations of chlorophyll a are frequently encountered in the St Helena Bay and Lambert's Bay area, resulting from the accumulation of phytoplankton production carried downstream from centres of upwelling further south, as well as local production (Hopson, 1983; Shannon et.al., 1984; Shelton, 1986). The ability of the juvenile and adult stages of E.lucens to migrate into the bottom layers during the day and away from near-surface advection, facilitates their maintenance in this consistently high production zone. The southward-flowing current, which is generated further north of St Helena Bay (Holden, 1987), is strongest at depth and therefore might provide a return mechanism out of the Bay past Cape Columbine. Superimposed on this under-current are wavelike motions with periods typically of 6-10 days, producing reversals of flow (Nelson and Polito, 1987). A net poleward movement of sub-surface material therefore occurs over periods longer than weeks.

The eastward penetration of E.lucens past Cape Point and into the Agulhas Bank region would be strongest in winter when the influence of the Agulhas Current is weakest (Shannon, 1985). Eggs resulting from early spawning (August) on the Agulhas Bank may drift eastwards, but later spawning during the spring and summer would increase the possibility of the eggs being transported around Cape Point and up the west coast in the jet current. Work by Talbot (1974) east of the Agulhas Bank suggests this. She found larvae and adult stages of E.lucens as far as Port Elizabeth (34°S, 25°E) during winter (August) collections, but during summer (February-March) and autumn (May), E.lucens was absent from her collections. She concluded that this species was not indicative of the Agulhas Current zooplankton community.

Studies on the basis of vertical migration of E.lucens may therefore have value in contributing towards an understanding of their dispersal and transport. The proposed current-closure scheme, whereby early near-surface dwelling reproductive stages are advected offshore, transported northwards and return southward at depth seems a likely mechanism whereby E.lucens can remain and develop high concentrations within the Southern Benguela upwelling system.

7.5 CONCLUSION

From the present results, several features of the vertical distribution of E.lucens are apparent: (1) larvae migrate vertically while the early reproductive stages (eggs and nauplii) remain in the near-surface layers, (2) the extent of diel migration shifts during the ontogeny of the larvae but their vertical range is restricted to the upper layers, and (3) the juveniles and adults are capable of migrating throughout the entire water column, remaining at depth during the day. These findings show that the ontogenetic migration pattern of E.lucens is different from the developmental ascent which is characteristic of oceanic species. The overall picture of larval dispersal and recruitment suggests that a number of mechanisms are involved in their distribution. Initially, wind-driven Ekman transport advects the early reproductive stages offshore, where the thermal front may present a potential barrier to further offshore transport. Later in the larval cycle, when changed migratory behaviour results in them remaining below the near-surface layer for longer periods, the sub-surface longshore jet current transports the larvae northwards. During the major spawning season (late winter and spring) the Columbine divergence zone may cause loss of larvae to oceanic waters further north. However, more developed, deeper migratory larvae may be entrained into the neritic zone and into the St Helena Bay and Lambert's Bay circulation system, where recruits could remain and develop in the highly productive inshore waters. Southward transport is facilitated by the deep undercurrent, but penetration into the east coast would be constrained by the influence of the Agulhas Current.

The exploitation of differential current regimes between shallow and deep waters seems to be important mechanisms, whereby E.lucens populations can be maintained on the shelf within the Southern Benguela upwelling system. It is possible that to some extent they have evolved behavioural responses which allow them to exploit the physical processes of their environment. However, this is by no means the only benefit hypothesis to explain the diel migratory behaviour in E.lucens in the Southern Benguela system.

CHAPTER 8

GENERAL CONCLUSIONS

8. GENERAL CONCLUSIONS

8.1 Biomass distribution

This study demonstrates that euphausiids are an important component of zooplankton biomass of the southern Benguela system, particularly on the west coast where they constitute between one third and one half of the total dry weight zooplankton biomass collected by a 300 m mesh net. This proportion would be reduced considerably if net escapement by the smaller zooplankton was taken into consideration. However, since anchovy selectively feed on larger organisms of the size range quantitatively sampled by the 300 m mesh Bongo net (Pillar, 1984b; James, 1987), this proportion of euphausiids is a reasonable reflection of the food resource available to pelagic fish. Indeed, ample evidence exists to show the importance of euphausiids as prey items for a variety of local commercially important fish (King and Macleod, 1976; Nepgen, 1979; Botha, 1980; James, 1987; Payne et.al., 1987).

The large zooplankton biomass north of Cape Columbine (Figure 8.1) may be attributed to two main causes. St Helena Bay is an area of more consistent upwelling relative to the Cape Peninsula upwelling area (Taunton-Clarke, 1985) which could enhance primary productivity, provided a better food source and result in increased abundance of zooplankton. Also, mesoscale cyclonic eddies associated with the St Helena Bay area probably play an important role in accumulating biological material carried downstream from centres of upwelling further south. These eddies have been implicated as

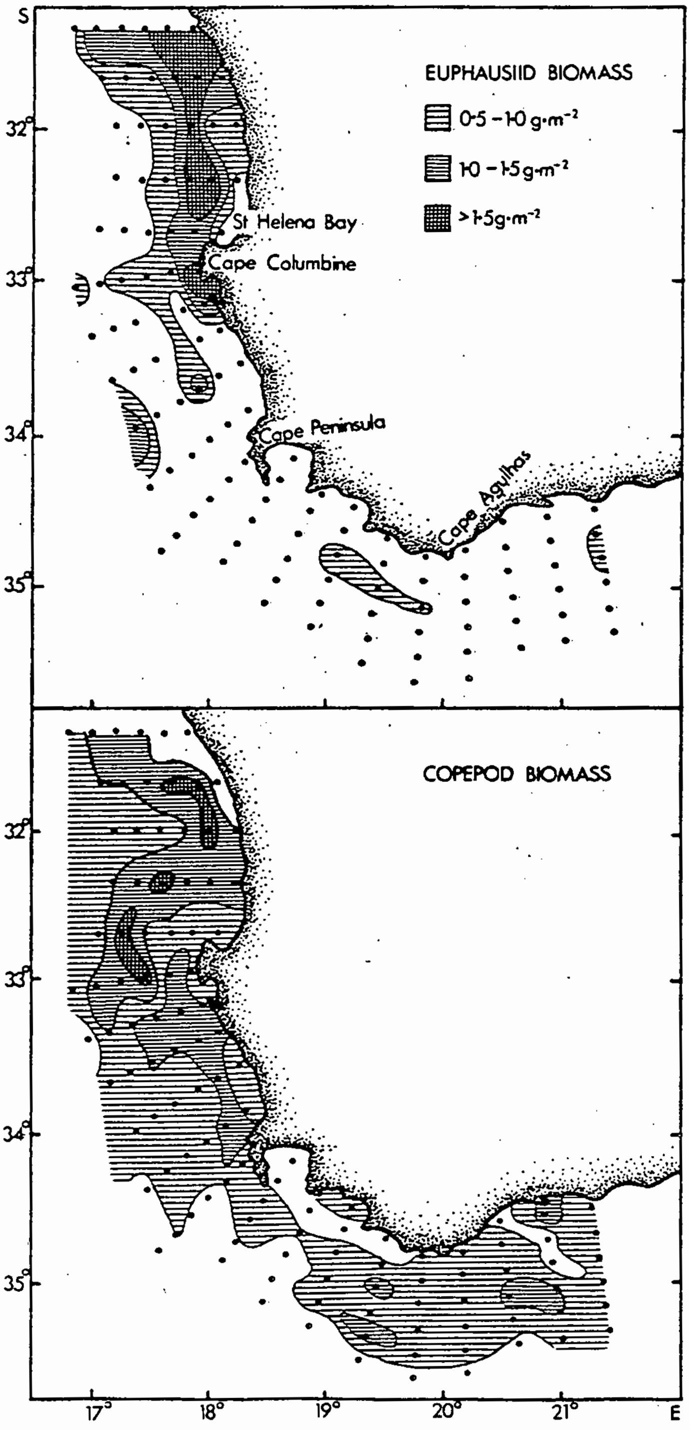

Figure 8.1 Horizontal distribution of euphausiid and copepod biomass over the CELP grid showing the mean monthly abundance between August 1977 and August 1978

mechanisms to facilitate the transport of anchovy larvae into the nursery grounds in the St Helena Bay area and further north (Shelton et.al., 1985). As recruits, they would benefit from this aggregation of plankton in the St Helena Bay/Lambert's Bay region. The importance of patterned circulation such as eddies in concentrating biological material and its ecological importance to higher trophic levels has been emphasised by Owen (1981), Deibel (1985) and Allison and Wishner (1986).

The seasonal and inshore-offshore patterns of zooplankton biomass observed in this study resemble those of other workers in the southern Benguela region. However, since previous studies did not differentiate between sub-regions of the southern Benguela or between major taxa, and no consideration was taken of the effect of diel migration, only a broad outline comparison could be made. From this study no marked seasonal cycle was apparent in euphausiid biomass in either the west coast or the Agulhas Bank, but, there was a summer increase in copepod biomass in the Cape Peninsula area corresponding to the period of maximum upwelling. In the St Helena Bay area, which is characteristically more stable, no seasonality was apparent in the copepod biomass. The offshore displacement of near-surface water which is characteristic of seasonal upwelling events on the west coast was not reflected in the inshore-offshore patterns in the euphausiid biomass but was to some extent in the copepod biomass. The ability of euphausiids to migrate away from the near-surface layers during the day, a behaviour not consistently observed in the copepod community (Pillar, 1984a; Hutchings, 1986), would provide them with a mechanism whereby they could avoid extensive offshore advection.

Euphausiids therefore appear to be less dependent than copepods on seasonal changes in oceanography on the west coast. This finding may in part be a behavioural effect which makes euphausiids less susceptible to environmental fluctuations, or may be due to the limitations of the present data to differentiate critically between a seasonal pattern and noise arising from between-cruise fluctuations. This limitation is compounded by the large variability in euphausiid biomass, relative to copepod biomass (see Figure 3.6), which may make seasonal changes difficult to detect. In spite of these limitations the data adds considerably to our knowledge of the temporal and spatial distribution patterns of euphausiids in the southern Benguela region.

8.2 Population dynamics and production

Since the majority of ovaries examined had more than one stage of developing ova (see Figure 5.4), it appears that the females of E.lucens have multiple spawnings throughout their spawning season. Evidence of multiple spawnings have recently been shown for a few euphausiid species (Ross et.al., 1982; Quetin and Ross, 1983; Hosie and Ritz, 1983) which questions the previous view that euphausiids spawn only once or twice in a spawning season (Mauchline, 1980). The present findings therefore extend the conclusion that multiple spawning may be more common in euphausiid populations that was previously assumed. Also notable in the present study is the scarcity of undeveloped or spent ovaries, indicating that the ovaries of E.lucens do not regress to a resting stage. There are examples in the literature to suggest that ovaries in other euphausiid species regress to a distinct spent stage (Makarov, 1975), or regress to lower ova developmental stages during periods of unfavourable environmental conditions such as low food concentrations (Ross et.al., 1982). It is suggested that sexual development and spawning may be also controlled by temperature (Lindley, 1978). The higher incidence of females in spawning condition (stage IV ova) in the warmer offshore outer-shelf region in the St Helena Bay area (Figures 5.4 and 5.5) may be a response to better feeding conditions. Although chlorophyll levels are higher inshore (Figure 23), E.lucens is omnivorous and adults may benefit from the enhanced secondary production at thermal fronts further offshore. The consistently higher temperatures offshore may also enhance maturation where rapid egg development in the warmer water may result in increased early survival. Upwelling maintains relatively low temperatures in the St Helena Bay area (Shannon, 1985), although sun-warming may elevate surface temperatures during the summer (see Section 5.3.1).

The continuous presence of eggs and early larvae in the collections supports the conclusion that spawning in E.lucens can take place throughout most of the year, although with varying seasonal intensity. Spawning was most intense from August to December (late winter to early summer) which is out of phase with the major upwelling season (October to March) and the associated increase in phytoplankton production in the southern Benguela region (Shannon et.al., 1984). This result is not consistent with the findings in other upwelling areas where intensive spawning in euphausiids coincides with upwelling and the stimulation of phytoplankton production (Smiles and Pearcy, 1971; Brinton, 1976; Antenzana-Jerez, 1978; Ross *et.al.*, 1982). Most larvae recorded in the above studies were in nearshore areas where high primary production prevailed during upwelling, whereas in the St Helena Bay area the larvae were present over the whole shelf region. The spawning strategy adopted by *E.lucens* may rely on the late winter and spring conditions when the food for early larvae is more uniform and widespread (Shannon *et.al.*, 1984; Shelton *et.al.*, 1985; Shelton, 1986). They may also avoid offshore advection of the early reproductive stages by spawning during late winter when offshore Ekman transport is reduced. By spawning during spring the eggs would encounter increasing offshore displacement but not as pronounced as during the summer due to the frequent wind reversals and associated onshore transport of surface water typical of the transition from winter to summer (Shannon, 1985).

The production due to growth of *E.lucens* in the St Helena Bay area was estimated to range between 77-186 mg dry wt.m^{-3}.$year^{-1}$, which is comparable to the value 78.29 mg dry wt.m^{-3}.$year^{-1}$ calculated for *Nyctiphanes australis* in Storm Bay, in south-eastern Tasmania (Ritz and Hosie, 1982). Considerably lower production values were obtained by Lindley (1978, 1980, 1982a and b) for a number of other euphausiid species in the North Atlantic Ocean. However, as Lindley cautioned, the effect of diel migration and the limitations of sampling a single-depth strata (10 metres) using the Continuous Plankton Recorder imposed constraints on the data for comparative purposes.

If the contribution of egg and moult production is considered, the total production varied between 142 and 479 mg dry wt.m^{-3}.$year^{-1}$, the lowest value being obtained in the offshore region. The production due to moulting in E.lucens was 60-281 mg dry wt.m^{-3}, or 6-28g.dry wt.m^{-2}.$year^{-1}$, which is comparable to other temperate and sub-tropical euphausiid species such as E.pacifica (Lasker, 1966; Sameoto, 1976) and N.australis (Hosie and Ritz, 1983). However, E.superba, which lives in much colder Antarctica waters and has a longer intermoult period of 27 days, has a lower moult production of 0.45g.dry wt.m^{-2}.$year^{-1}$ (Ikeda and Dixon, 1982). Since moult production of E.lucens represented approximately six times their mean dry weight biomass and as moults are rapidly colonised by bacteria and ciliates (Stuart, 1986), it suggests that moults may represent a substantial food source in the form of detritus and by rapid decomposition, may play an important role in nutrient regeneration. However, when expressed in terms of carbon, moults become relatively less important as a food resource than would be indicated by dry weight alone.

Production due to reproductive output ranged between 5-12 mg dry wt.m^{-3}.$year^{-1}$, or 2.6-5.6% of the total annual production. These values are comparable to those of Hosie and Ritz (1983), who estimated egg production to be 1.41-4.22mg dry wt.m^{-3}.$year^{-1}$ or 1-3% of total production. To the authors' knowledge there are no other reported values with which to compare the present results.

The annual P/B ratio for flesh production of the E.lucens population varied from 3.92-8.91, the highest ratio being obtained in the offshore region of St Helena Bay. This higher P/B ratio may be attributed to the greater proportion of young larval stages giving faster growth rates and turnover times. However, this result should be treated with caution since a substantial proportion of the larvae offshore would not be of local origin, but could arise from breeding areas downstream of the study area as well as from larvae being advected from further inshore during upwelling events. Nevertheless it is evident that continuous breeding is a characteristic of E.lucens in the southern Benguela region. Comparable high P/B ratios have been reported for other euphausiid species which also have prolonged breeding seasons and have similar short life spans (~1 year) to that of E.lucens. High turnover rates have been associated with areas of high productivity, and also lack of severe winters and relatively warm water throughout the year. Populations of euphausiids in higher latitudes with large seasonal fluctuations, where growth is retarded during the winter months and the breeding season is shorter, have considerably lower P/B ratios than the present values (Lindley, 1980; Allen, 1971; Miller et.al., 1985).

It is concluded that the abundant food supply associated with the St Helena Bay area, the prolonged breeding season, lack of severe winter and relatively mild temperatures throughout the year are all contributing factors to the high production and turnover rates of E.lucens in this region. This high productivity is of major importance for higher trophic levels such as the anchovy (Engraulis capensis) which is a secondary consumer in the southern Benguela (James, 1987), and which recruits to the fishery in the St Helena Bay/Lambert's Bay region (Crawford et.al., 1980; Shelton et.al., 1985).

8.3 Diel vertical migration and population maintenance

Diel migrations are a significant feature of the vertical distribution of E.lucens. It has been demonstrated that while the early reproductive stages (eggs and nauplii) remain in the near-surface layers, progressively deeper levels are occupied by older stages during the day. It is not possible to reach a definite conclusion as to whether the juvenile and adult stages reside close to the bottom during the day since net avoidance may have obscured the daytime distributions presented here. However, concomitant fish stomach analysis by James (1987) suggests that E.lucens was not accessible to anchovy during the day, presumably by migrating below them. Whether residing at depth during the daytime is an adaptive strategy to reduce predation is speculative since benthic fish such as the Cape hakes (Merluccus spp.) which feed copiously on euphausiids (Botha, 1980; Payne et.al., 1987) could take advantage of the high concentrations of E.lucens near the bottom during the day. However, the diel feeding cycle of the Cape hakes has not yet been firmly established and it may be that feeding only takes place during their nocturnal migration to midwater, as suggested by Botha (1980).

As a result of ontogenetic migration, different stages of E.lucens in the southern Benguela have different probabilities of alongshore and cross-shelf transport. By spawning in spring, when the increased frequency of southerly winds initiates the upwelling season, the eggs would be advected offshore across the shelf by wind-generated surface currents, while older larval stages, by remaining at depth during the day, would be more subject to longshore transport. The longshore-closure system postulated by Nelson and Hutchings (1987) has been useful in showing the importance of both the frontal jet current in the entrainment and transportation of material northwards and the mesoscale cyclonic cell north of St Helena Bay where recruits could remain and benefit from the high productivity of that region. The St Helena Bay eddy extends about 50-60km north to as far as Lambert's Bay (Holden, 1985). Further north the shelf narrows and then widens again off the Orange River (29°S) which may facilitate cross-shelf mixing and so 'close' the northern alongshore current system. The southward flowing counter-current, which extends from southern Namibian waters along the entire coast of South Africa (Holden, 1987), would be a mechanism whereby migrating individuals could be returned to the southern Benguela system. The large concentrations of euphausiids in the near-shore zone north of St Helena Bay (Figure 37) implies some control on their cross-shelf position and would allow them to utilise the inshore counter-current.

Although faunistic studies on euphausiids in Namibian waters are rare, there is convincing evidence that a faunal barrier exists at the Luderitz upwelling zone some 600km north of St Helena Bay (SFRI, unpublished data), as north of this region E.lucens is very scarce and Nyctiphanes capensis becomes the dominant euphausiid species (Boden, 1955; D'Arcangues, 1977). This zone has also been implicated as a barrier to the northward extension to several species of chaetognaths (Venter, 1969). As the influence of the Namaqua/Luderitz region (27°-29°S) on the St Helena Bay area appears to be largely restricted to the subsurface countercurrent (Shannon, 1985), it may be suggested that individuals not entrained into this system would be transported further north and off the productive shelf region into oceanic waters where mortality would be high.

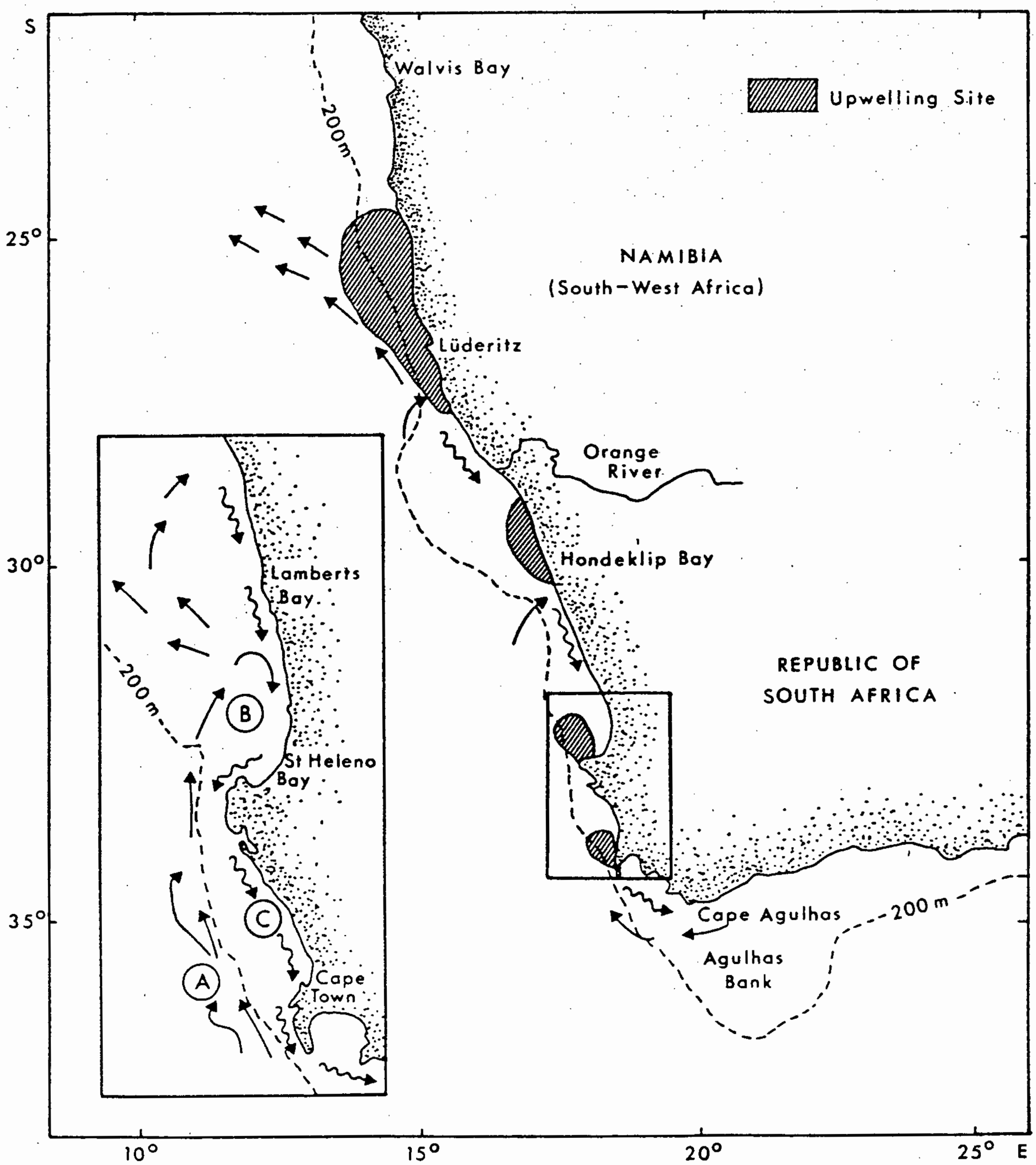

Figure 8.2 Schematic representation of currents between Cape Agulhas and Luderitz. Currents north of Lambert's Bay are assumed from indirect evidence. Key elements are A. the baroclinic jet current, B. the cyclonic gyre and C. the wavelike countercurrent. From Nelson and Hutchings (1983, 1987)

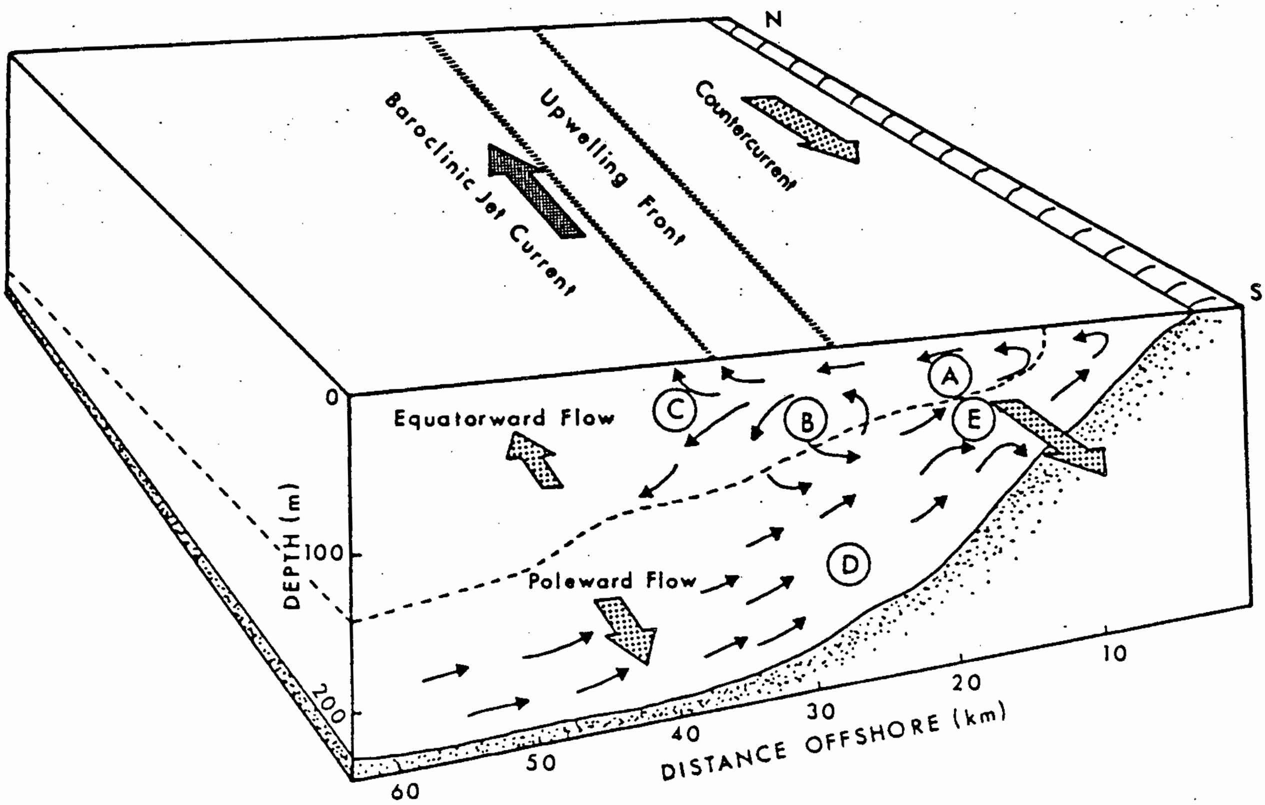

Figure 8.3 Conceptual model of the cross-shelf and alongshore currents between Cape Point and St Helena Bay during fully developed upwelling. Proposed maintenance mechanisms of E.lucens are A. offshore displacement of non-migratory eggs and nauplii, B. sinking at frontal interface, C. entrainment into jet current and northward displacement, D and E. onshore and southward transport of migratory stages (late larvae to adult)

Neither mechanisms of dispersal and transport of E.lucens nor the current regimes are well enough documented, especially north of the St Helena Bay/Lambert's Bay region, to permit more than a preliminary description of population maintenance in the larger region between Cape Agulhas and Luderitz. The general pattern is summarised in the schematic models presented in Figures 8.2 and 8.3. E.lucens spawning takes place in the midshelf region possibly due to optimal combinations of food and temperature. Near-surface dwelling, non-migratory early reproductive stages are subject to wind-induced advection, but offshore displacement is low during the late winter and early spring period due to frequent wind reversals. As summer approaches, the strong frontal gradients and alongshore flow limits dispersal into oligotrophic offshore waters. As vertical migration becomes more developed in later stages, the offshore displacement in near-surface layers is compensated by less directed flow at deeper levels where frequent current reversals allow some southward and onshore movement. Cross-shelf flow of upwelling source water may also enable deeper-dwelling stages to return to the inshore zone. Where the shelf narrows along the west coast, upwelling centres are apparent, for example at Luderitz, Hondeklip Bay, Cape Columbine and the Cape Peninsula, the increased onshore flow at these regions would aid the return of material to the coast. There is very little known of either euphausiid distribution or currents between Lambert's Bay and Luderitz (32°-27°S) so only speculations regarding maintenance mechanisms can be presented at this stage. Nevertheless, it may be assumed that the perennial, powerful upwelling centre at Luderitz and associated strong offshore components of the surface currents would limit the northward extension of E.lucens. If individuals were entrained into the Luderitz upwelling plume they would be displaced offshore, be unable to return to the coastal countercurrent and be lost to the southern Benguela system.

This thesis provides new insight into the question of the ecological significance and the life history adaptations of E.lucens in the southern Benguela region. The large biomass and production in the St Helena Bay/ Lambert's Bay region is a result of a combination of factors such as the perennial abundant food supply of phytoplankton and mesozooplankton, and the prevailing circulation system which favours the accumulation of individuals within the coastal zone. In addition to this mechanism, the ontogenetic vertical distribution patterns interact with the current regime and contribute to the maintenance of the population within the inner shelf region. Several workers have emphasised the key position of euphausiids in the diet of local commercially exploited fishes. James (1987) clearly showed that anchovy, Engraulis capensis, recruits in the St Helena Bay/ Lambert's Bay region rely heavily on euphausiids as a food source, and Wallace-Fincham (1987) estimated that euphausiids comprised 52% by mass in the diet of adult roundherring, Etrumeus whiteheadi. Juvenile Cape hakes, Merluccius spp., have been shown to feed almost exclusively on euphausiids and amphipods (Botha, 1980; Payne et.al., 1987), the annual consumption of euphausiids by hake is estimated to be 119 x 10^3 metric tons (Bergh et.al., 1985). Higher predators such as snoek, Thyrsites atun, consume large quantities of euphausiids (Nepgen, 1979).

Since E.lucens occupies a central position in the food web, being important in the diet of a variety of commercially exploited fishes, these coastal aggregations are of major importance in sustaining high levels of both pelagic and benthic fish stocks. This study also provides for the first time quantitative estimates of the biomass and production of a dominant and ecologically important zooplankton species in the southern Benguela region, and therefore contributes significantly towards understanding the energy flow from phytoplankton through the zooplankton community to the commercial fish stocks and higher predators.

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SUPPORTING PAPERS

(1) PILLAR, S.C. 1984 - Diel variation in the vertical distribution of some common zooplankton species off the west coast of South Africa S. Afr. J. mar. Sci. 2: 71-80

(2) PILLAR, S.C. 1985 - Laboratory studies on the larval growth and development of Nyctiphanes capensis (Euphausiacea). J. Plankt. Res. 7: 223-240

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DIEL VARIATION IN THE VERTICAL DISTRIBUTION OF SOME COMMON ZOOPLANKTON SPECIES OFF THE WEST COAST OF SOUTH AFRICA

*S.C. PILLAR**

The vertical distribution and the diel variation of seven species of copepods and the euphausiid *Euphausia lucens* were examined over a 28-hour period covering 20—21 May 1978 in an area approximately 65 km north-west of Cape Columbine. The majority of the copepod species remained within the sampling depth (0—85 m) and showed no marked diel movement. Those that did migrate (*Nannocalanus minor* and *Metridia lucens*) showed evidence of reverse migratory behaviour. There was ontogenetic layering in the vertical range of *Euphausia lucens*. While the calyptopis larvae remained near the surface and did not migrate, the older stages did, with the juvenile and adults moving through a greater depth range than the younger furcilia stages. The data are discussed with reference to previous depth records from work carried out mainly in the Atlantic Ocean, and specifically to records from local waters.

Die vertikale verspreiding en die daaglikse wisseling van sewe kopepodespesies en die eufausiied *Euphausia lucens* is ondersoek gedurende 'n tydperk van 28 uur wat 20—21 Mei 1978 dek, in 'n gebied ongeveer 65 km noordwes van Kaap Columbine. Die meeste van die kopepodespesies het binne die bemonsteringsdiepte (0—85 m) gebly en geen opvallende beweging tydens die etmaal getoon nie. Die wat wel migreer het (*Nannocalanus minor* en *Metridia lucens*) het tekens van omgekeerde migrasiegedrag getoon. Die verskillende stadiums in die ontogenie het in verskillende lae binne die dieptebestek voorgekom. Terwyl die calyptopis-larwes naby die oppervlak gebly het, het die ouer stadiums wel migreer; die jongstadiums en volwassenes het deur 'n groter dieptebestek as die jonger furcilia-stadiums beweeg. Die gegewens word bespreek met verwysing na vorige diepte-opgawes verkry uit werk wat hoofsaaklik in die Atlantiese Oseaan verrig is, en spesifiek na opgawes afkomstig van plaaslike waters.

Previous research into zooplankton in the southern Benguela region was summarized in a review by Hutchings (1981). Although information on the horizontal distribution of selected zooplankton groups was given in earlier studies, little quantitative data on either vertical distribution or diel movement was provided. Hutchings (1979) discussed the vertical distribution of some copepod species and euphausiid larvae during a period of active upwelling in an area off the Cape Peninsula. His data were drawn from a series of 11 pump collections to a depth of 50 m and he related vertical distribution to depth of the thermocline, chlorophyll *a* concentration and surface temperature. These collections were, however, spread out in time (13 days) in strongly contrasting locations and in an area of great vertical instability. Furthermore, the type of gear he used did not representatively capture the larger, more motile juvenile and adult euphausiids. Working in the same area, Andrews and Hutchings (1980) studied the changes in chlorophyll *a* concentration and zooplankton standing crop at a fixed station over a 24-hour period. This work was restricted to analysis of total zooplankton volume only.

In the present study the vertical distribution and diel movement of seven copepod and one euphausiid species common in the southern Benguela region are examined. The data are discussed with reference to previous depth records from work carried out mainly in the Atlantic Ocean (e.g. Roe 1972a, b), especially the waters of West Africa (e.g. Bainbridge 1972) and southern Africa (e.g. Hutchings 1979). The depth distributions in this study are related only to thermal stratification and times of sampling.

METHODS

The data are derived from samples collected by a pump (Hutchings *et al.* 1970) and Miller nets (Miller 1961) during a comparative study of zooplankton samplers conducted on 20 and 21 May 1978 approximately 65 km north-west of Cape Columbine. The collections were taken at approximately 3-hourly intervals over a period of 28 hours. Time of collection, volume of water filtered and depth range sampled by each sampler are given in Table I. Descriptions of the sampling gear, the cruise strategy and processing of the samples are fully presented by Pillar (1984).

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Table I: Summary of data from the Miller net and the pump

Series	Time	Duration (min)	Volume filtered (m³)†	Maximum depth (m)*
		Miller net		
1	07h50	61	80,9	74
2	12h08	55	77,3	70
3	18h15	54	76,4	72
4	21h24	59	82,5	74
5	00h45	54	75,3	70
6	04h00	57	79,4	73
7	07h30	51	73,5	75
8	10h45	51	72,1	70
		Pump		
1	09h20	55	2,5	85
2	15h45	60	2,5	85
3	19h30	52	2,5	85
4	22h57	56	2,5	85
5	02h26	57	2,5	85
6	05h35	55	2,5	85
7	09h00	61	2,5	85
8	12h05	65	2,5	85

† Integrated volume
* Depth attained by bottom net (for Miller net only)

Oceanic water was chosen because of its relative stability compared to inshore water. Sustained northwesterly winds prior to and during the study suppressed any likely influence of cooler inshore waters and ensured relatively uniform conditions during the cruise. Low chlorophyll *a* levels are generally expected in this area during winter months.

The density estimates of the copepods were standardized to numbers per m³ and the euphausiid stages to number per 100 m³ taking into account the calculated volumes of water filtered at each depth. The density isopleths depicting the vertical distribution of the different species (Figs. 2—8) were plotted by computer by means of the Saclant Graphics Package. The scale used is not consistent for all species because of the variation in the density of the different animals. Superimposed onto the isopleths are the proportions of animals at each sampling depth, expressed as a percentage of the total density of that species in the water column. Where the vertical distribution of a species extended beyond the sampling range, i.e. in the juvenile and adult stages of *Metridia lucens* and *Euphausia lucens*, this procedure was not applied.

GENERAL RESULTS

Temperature profiles at the start, middle and end of the 28-hour series are given in Figure 1. The maximum gradients occurred between 20 and 30 m. Supra-thermocline water between the surface and 20 m had a temperature of 16,5—16,0°C compared with temperatures of 15,0—11,0°C for the subthermocline waters from 30 to 100 m. The data show that the temperature structures of the three profiles were similar, which suggests minimal influences from different water masses during the study period.

Seven species of copepods and one euphausiid were present in sufficient numbers for conclusions to be drawn in respect of their depth distribution and the ranges of any vertical diel migrations. The copepod species represented six families, of which Oithonidae, Paracalanidae and Pseudocalanidae constituted 83 per cent of the catch, followed by Calanidae with 8 per cent, Centropagidae with 6 per cent and Metridiidae with 3 per cent. Copepodite stages of the smaller species (*Oithona* spp., *Paracalanus parvus*, *Clausocalanus* spp. and *Ctenocalanus vanus*) were not identified routinely. The larger species (*Centropages brachiatus*, *Metridia lucens* and *Nannocalanus minor*) were categorized into juvenile and adult stages. One species of euphausiid, *Euphausia lucens*, was dominant in the collections and constituted 96 per cent of the total euphausiid abundance, with *Euphausia similis* making up the remaining 4 per cent.

DIEL PATTERNS

Euphausia lucens Hansen

The calyptopis stages (Fig. 2a) showed no evidence of vertical movement. They remained above the thermocline in the upper 30 m during both day and night, concentrations being maximal near the surface. The furcilia stages (Fig. 2b) showed a distinct vertical movement within the upper 60 m. A marked movement from a daytime density maximum at 20—40 m to a nighttime maximum above 20 m took place at sunset. A counter-movement downwards was seen at dawn when the main concentration of animals reformed again at 20—40 m. The maximum concentration of furcilia moved from a mean daytime position below the thermocline to a position above it during the night (Fig. 2c, d).

The juvenile and adult stages of *Euphausia lucens* (Fig. 3) migrated more extensively than did the larval

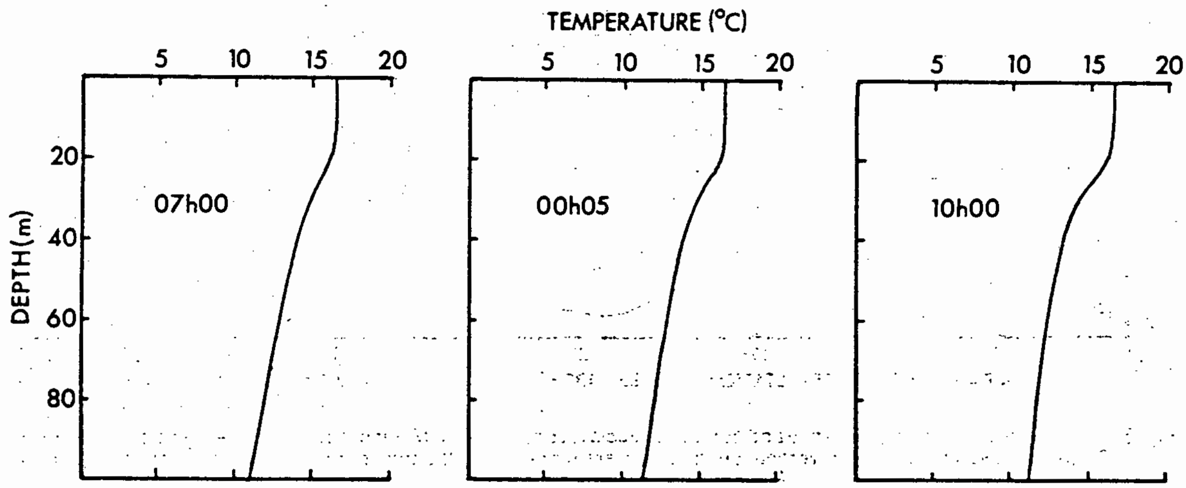

Fig. 1: Temperature profiles from bathythermograph readings — the times approximate the start, middle and end of the 28-hour study

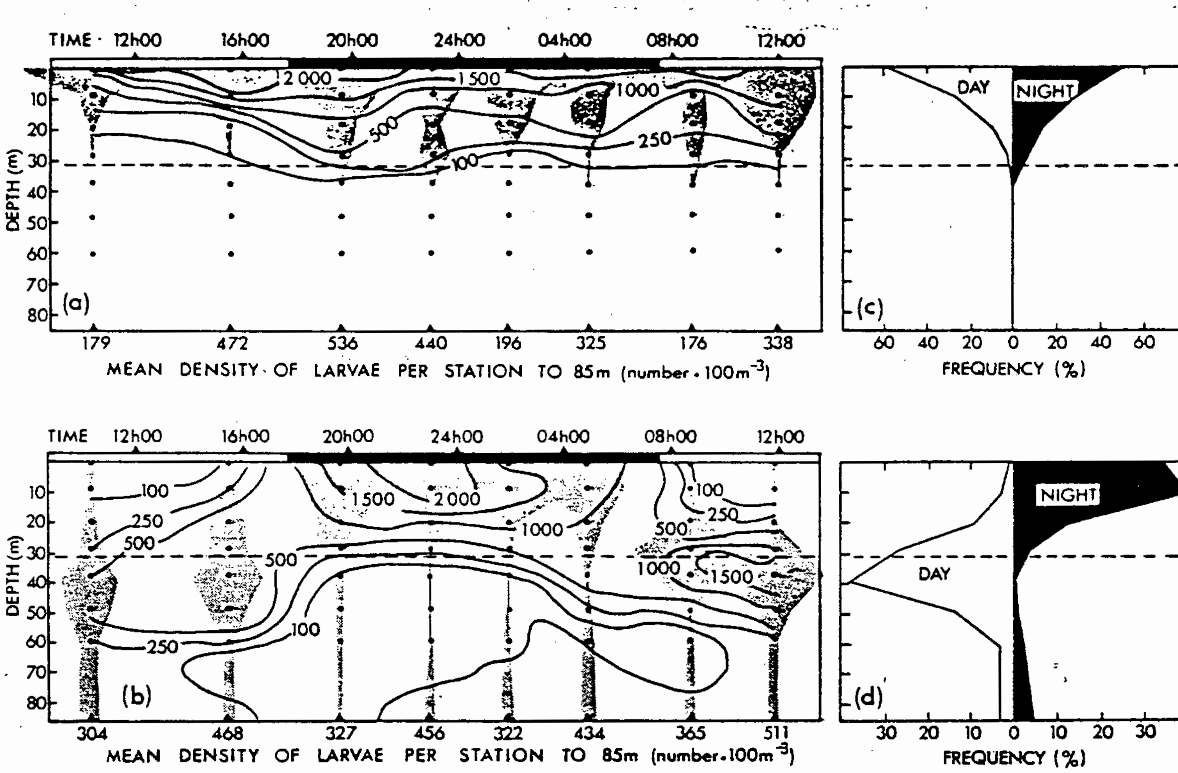

Fig. 2: Vertical distribution of (a) calyptopis and (b) furcilia larvae of *Euphausia lucens*, based on the pump collections. The thermocline is denoted by a broken line, the sampling depths as dots and the proportion of animals at each depth by a shaded area. Day and night vertical distributions are shown for (c) calyptopis and (d) furcilia. The values plotted are the mean proportions at each depth expressed as a percentage of the total mean density of that animal in the water column

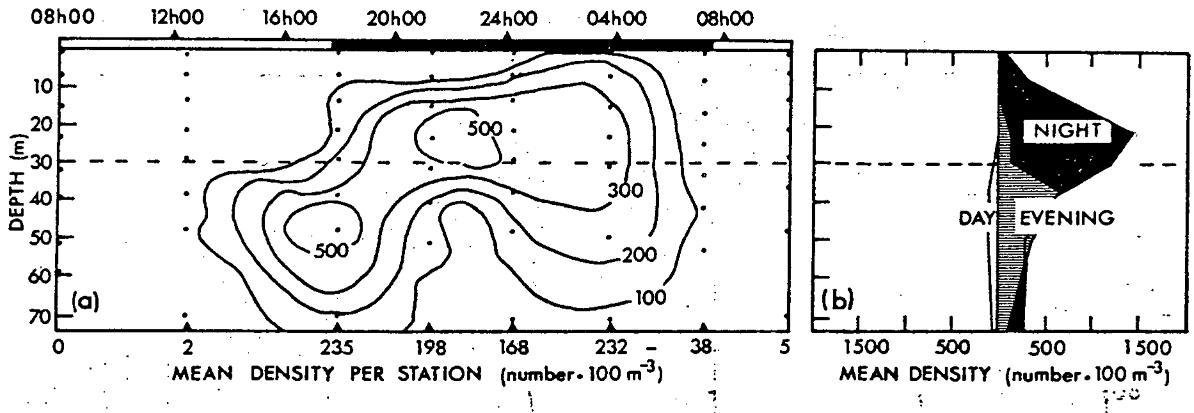

Fig. 3: (a) Vertical distribution of juvenile and adult *Euphausia lucens* based on Miller net collections — symbols as for Figure 2. (b) Day, evening and night vertical distributions are plotted from the total density of the organism at each depth during these periods

stages. During daylight densities were low from all sampling depths, but they increased sharply in the evening. Throughout the night, large numbers were caught in the region of the thermocline. After sunrise, these numbers dropped off sharply.

Few investigators have reported on the vertical distribution of *Euphausia lucens*, but their findings have generally been based on large depth horizons

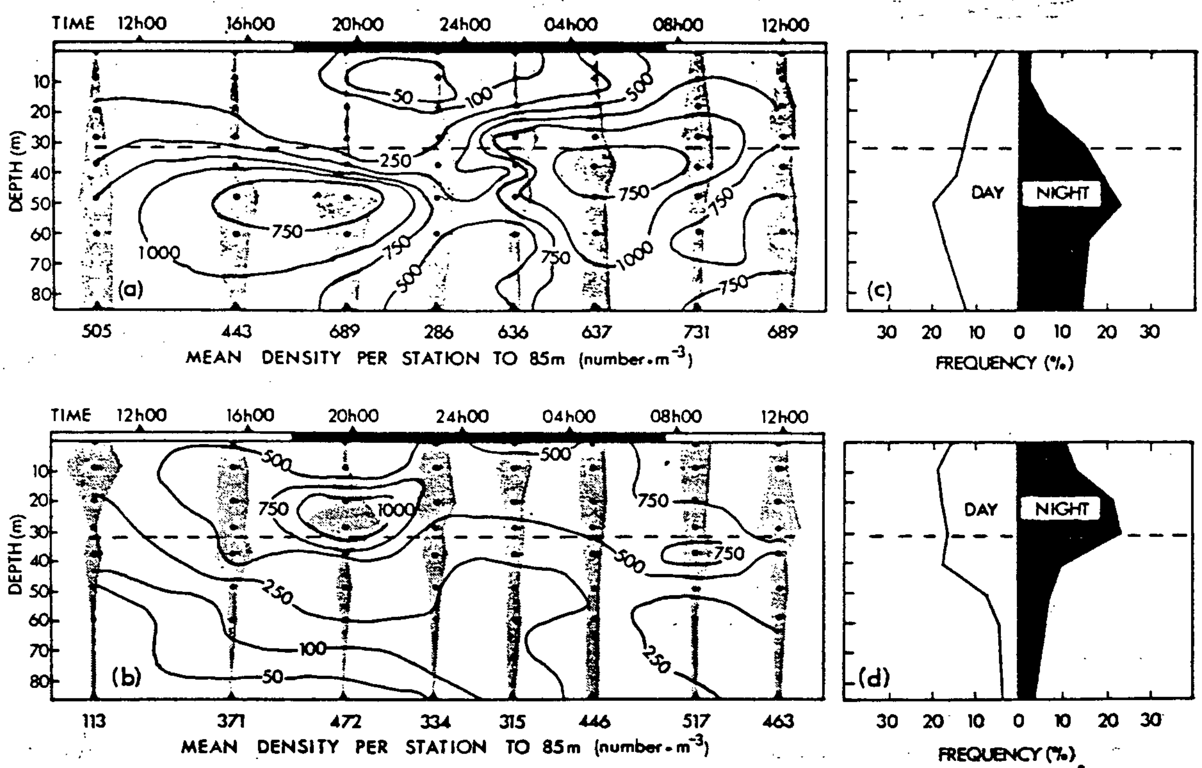

Fig. 4: Vertical distribution of (a) *Oithona* spp. and (b) *Paracalanus parvus*, and (c) and (d) mean day and night distributions for the same species — symbols as for Figure 2

with limited day and night comparisons. In New Zealand waters, Bary (1956) reported a sharp numerical increase of the species in his surface hauls during nighttime, and Bartle (1976), working in the Cook Strait area, reported that most specimens were below 100 m during the day and above 50 m at night. In neither case were the proportions of larvae or adults defined. Talbot (1974), working south of the Cape of Good Hope, found mostly furcilia and small juvenile stages in hauls from 150 m to the surface. As her collections were limited to daylight sampling, it was likely that most of the adults would have been beyond the range of the net.

In support of the present results, Hutchings (1979) found that the calyptopis and furcilia larvae had different depth distributions. While the calyptopis larvae were found mainly above the thermocline, near the surface layer, the furcilia were located in lower depth strata, close to the thermocline (20—30 m). His collections, however, lacked the continuity in time and space to assess the limits of diel movement. Furthermore, the type of gear used (7,6-cm centrifugal pump) did not representatively capture the juvenile and adult stages of this taxon.

Oithona spp.

Oithona was numerically the dominant genus collected. *O. similis* was the most abundant species, constituting approximately 90 per cent of the total for the genus. The main concentrations were located below the thermocline between 30 and 85 m, with maximum densities from 40 to 60 m (Fig. 4a). There was no evidence of vertical migration (Fig. 4c).

Limited data on the vertical distribution of *O. similis* are available. McLaren (1963) described it as an epiplanktonic non-migratory species, and Bogorov (1946) reported no evidence of diurnal migration in *O. similis* in the upper 200 m of the White Sea. Its preference for the upper layers was reported by Boxshall (1977) in the waters off the Cape Verde Islands in the North-East Atlantic, though this conclusion was based on a very small number of specimens. In an area south of Madagascar, De Decker and Mombeck (1965) found *O. similis* in maximum concentrations in the upper 50 m, a finding in direct contrast to that of the present study, where most specimens appeared to prefer the cooler water below the thermocline.

Paracalanus parvus (Claus)

This species was numerically the second commonest species in the series. The majority were collected in the upper 50 m with the maximum being taken in the warmer waters at or above the thermocline during both the day and night (Fig. 4b). There was no evidence of vertical migration (Fig. 4d).

Several authors have reported that *P. parvus* has only a limited tendency to migrate. Bainbridge (1972) working in the Gulf of New Guinea found no evidence of vertical migration, and investigations off the Venezuela coast by Zoppi (1961) have shown the copepod to occur throughout the upper 100 m with no evidence of diel movement. Vilela (1968) and Sequin (1966), working off Portugal and Senegal respectively, found the species to be abundant in the upper 50 m during daylight collections. In local waters, Hutchings (1979) found it in maximum concentrations in the upper 20 m, with little evidence of changes in vertical distribution with time.

Clausocalanus spp.

This genus occurred in maximum concentrations below the thermocline between 40 and 60 m during both day and night (Fig. 5a). There was no evidence of vertical migration (Fig. 5c).

The genus was not identified to specific level although common in the collections. Frost and Fleminger (1968) have reviewed the genus *Clausocalanus* and found that very little agreement existed between their work and the literature as to the identity of several species. De Decker (1962) and Unterüberbacher (1964) reported on two distinct size categories of *C. arcuicornis* as being common off the west coast of southern Africa. These specimens, which were described as forma *minor* (small specimens) and forma *major* (large specimens), were identified by Frost and Fleminger (op. cit.) as *C. parapergens* and *C. ingens* respectively. Adult forms of both these species and *C. furcatus* were observed in the present collections but, because of the preponderance of juvenile stages, no consistent effort was made to identify all specimens to species level.

Because of the inconsistencies in the identification of *Clausocalanus* spp. the literature provides few usable data on their vertical distribution. Frost and Fleminger (1968) found the maximum abundance of all species of this genus in the uppermost 150 m. Roe (1972a) found them to be abundant in his surface hauls (0—50 m) during the day and night and with no evidence of diel migration.

Ctenocalanus vanus Giesbrecht

The occurrence and abundance of *Ctenocalanus vanus* closely resembled those of *Clausocalanus* spp. (Fig. 5b). The numbers above the thermocline tended to increase slightly during the night, though this was

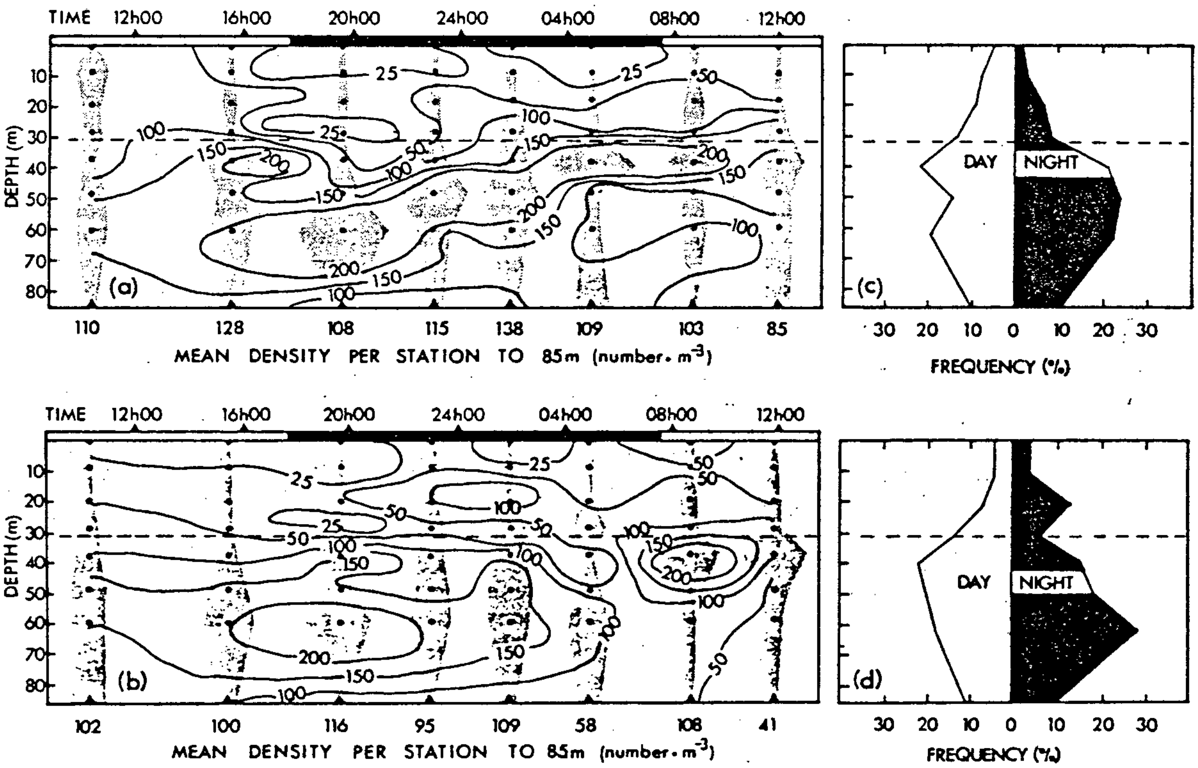

Fig. 5: Vertical distribution of (a) *Clausocalanus* spp. and (b) *Ctenocalanus vanus*, and (c) and (d) mean day and night distributions of the same species — symbols as for Figure 2

not considered to be evidence of vertical migration (Fig. 5d).

Vervoort (1963) implied that *C. vanus* was capable of rapid vertical migration, but he cited no literature to substantiate his implication. In support of the present findings, Hutchings (1979) reported a slight upward shift in *C. vanus* from a daytime position below the thermocline at 20 m to above it at night, but he reported no evidence of diel movement.

Centropages brachiatus (Dana)

The juveniles (Stages III—V) were narrowly stratified between 20 and 50 m with the majority remaining below the thermocline during the day and the night (Fig. 6a). The adults occupied a higher depth stratum (0—30 m) with the maximum above the thermocline throughout the sampling period (Fig. 6b). They showed some evidence of upward movement during the night while the juveniles did not migrate (Fig. 6c, d).

Little information is available on the vertical distribution of *C. brachiatus*. The results of Hutchings (1979) indicated that juveniles preferred cooler waters whereas adults were generally located in the warmer regions above the thermocline in cool, coastal waters. His results gave no evidence of vertical migration. The genus *Centropages* has been considered by other authors to be a non-migrant (e.g. Clarke 1933, Bainbridge 1961).

Metridia lucens Boeck

The adults and the juveniles displayed similar vertical movements with maximum densities below the thermocline at 50—85 m during the day (Fig. 7a, b). During the night both categories appeared to descend below the sampling depths, as is shown by the nocturnal density decrease of both juveniles and adults (Fig. 7c, d). The evidence suggests that *Metridia lucens* may have a reverse migration during the night.

Clarke (1933), working in the Gulf of Maine, found that the upper limits of vertical movements of

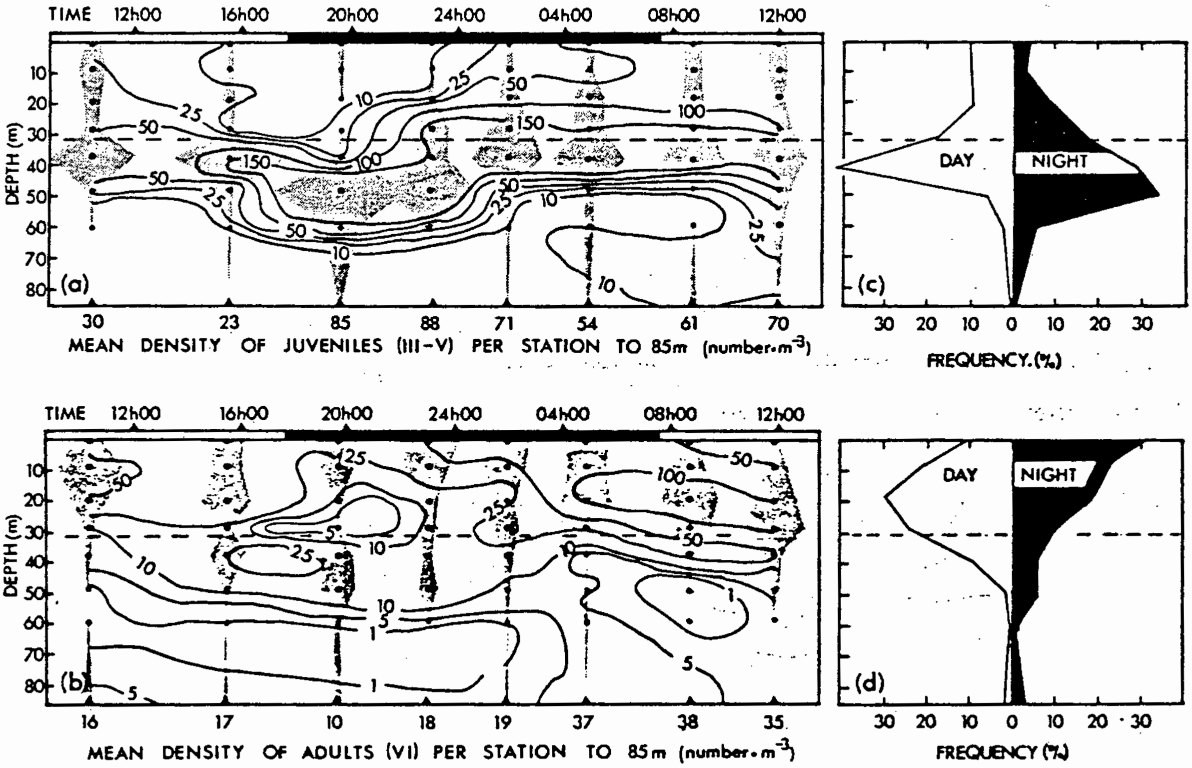

Fig. 6: Vertical distribution of *Centropages brachiatus* (a) juvenile (Stages III—V) and (b) adults (Stage VI), and (c) and (d) mean day and night distributions for the same stages — symbols as for Figure 2

M. lucens corresponded to the beginning of a sharply delineated thermocline. Off the southern coast of Ireland, Farran (1947) observed that this species remained below the thermocline by day and night. In South African waters, De Decker (1964) found *M. lucens* below the thermocline in regions where warm Atlantic water lay near the surface. Hutchings (1979) noted a marked upward movement at night, with very few animals above the thermocline during the day. Numerous authors have confirmed the strong tendency for *M. lucens* to migrate vertically (see reviews by Bainbridge 1961 and Longhurst 1976). To the author's knowledge, there have been no data published to support the anomaly of reverse migration found in this study.

Nannocalanus minor (Claus)

Nannocalanus minor was common in all the collections. The adults and juveniles (Stage V) showed a distinct movement from a density maximum above the thermocline (0—30 m) during the day to a night-time maximum below the thermocline (40—60 m). After sunrise the population ascended through the thermocline to remain in the upper 0—30 m layer (Fig. 8a—d). The evidence suggests that *N. minor* had a reverse migration during the night.

Most specimens of *N. minor* have been recorded in the upper layers. In the North Atlantic, Moore (1949) and Zoppi (1961) found maximum numbers in the upper 100 m. In coastal waters of the Gulf of Guinea, Bainbridge (1972) found maximum numbers of *N. minor* above the thermocline in the upper 0—25 m during the night and below the thermocline between 25 and 30 m during the day. In local waters Hutchings (1979) found no evidence of vertical migration in this species. In support of the present findings, Roe (1972b) found evidence of reverse migration in oceanic waters off the Canary Islands.

DISCUSSION

The validity of the comparisons between the

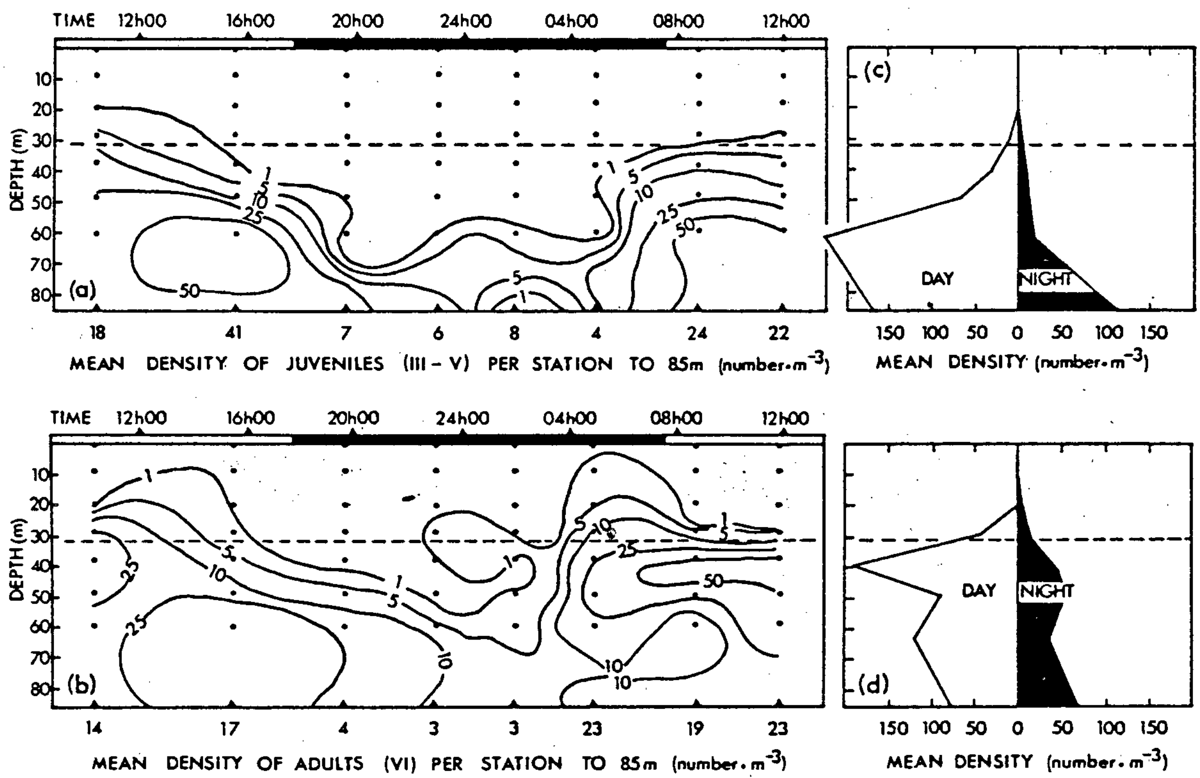

Fig. 7: Vertical distribution of *Metridia lucens* (a) juvenile (Stages III—V) and (b) adults (Stage VI), and (c) and (d) total density by day and night at each depth for the same stages — symbols as for Figure 2

present results and those of other workers depends on a number of factors, of which location and time of sampling are prime variables. Geographical position and seasonal variations in zooplankton numbers and depth have been included in most reviews on vertical distribution and diel migration (e.g. Cushing 1951, Bainbridge 1961, Banse 1964, Mauchline and Fisher 1969, Longhurst 1976). Furthermore, the literature shows that diel migration is by no means regular or predictable.

Despite the difficulties in making valid comparisons, the results presented in this study were broadly similar to those observed in other regions of the Atlantic Ocean. The majority of the copepod community remained within the sampling depth (0—85 m) during both the day and night. The non-migratory behaviour of most of the copepods in the present study is also supported by other work carried out in South African waters. Although the present collections were taken in off-shore water in a non-upwelling season, the vertical distribution and the migratory behaviour of the organisms agree well with the observations made by Hutchings (1979) during a period of active upwelling in coastal waters off the Cape Peninsula.

There is evidence to suggest that the thermocline may be a factor in determining the vertical distribution of some copepod species. The presence of a thermocline did not limit the migratory movement of either the furcilia or juvenile and adult stages of *Euphausia lucens*, but it marked the lower boundary of the depth range of the calyptopis larvae. The ontogenetic stages of *Euphausia lucens* had different migratory depth ranges, with the older stages migrating greater distances than the younger larval forms.

The discrete depth intervals and the continuity in time of sampling in this study have provided finer resolution of the vertical distribution of the more common zooplankton organisms in waters off the west coast of southern Africa. The results lend support to the concept that many zooplankters occupy narrow, though not necessarily the same,

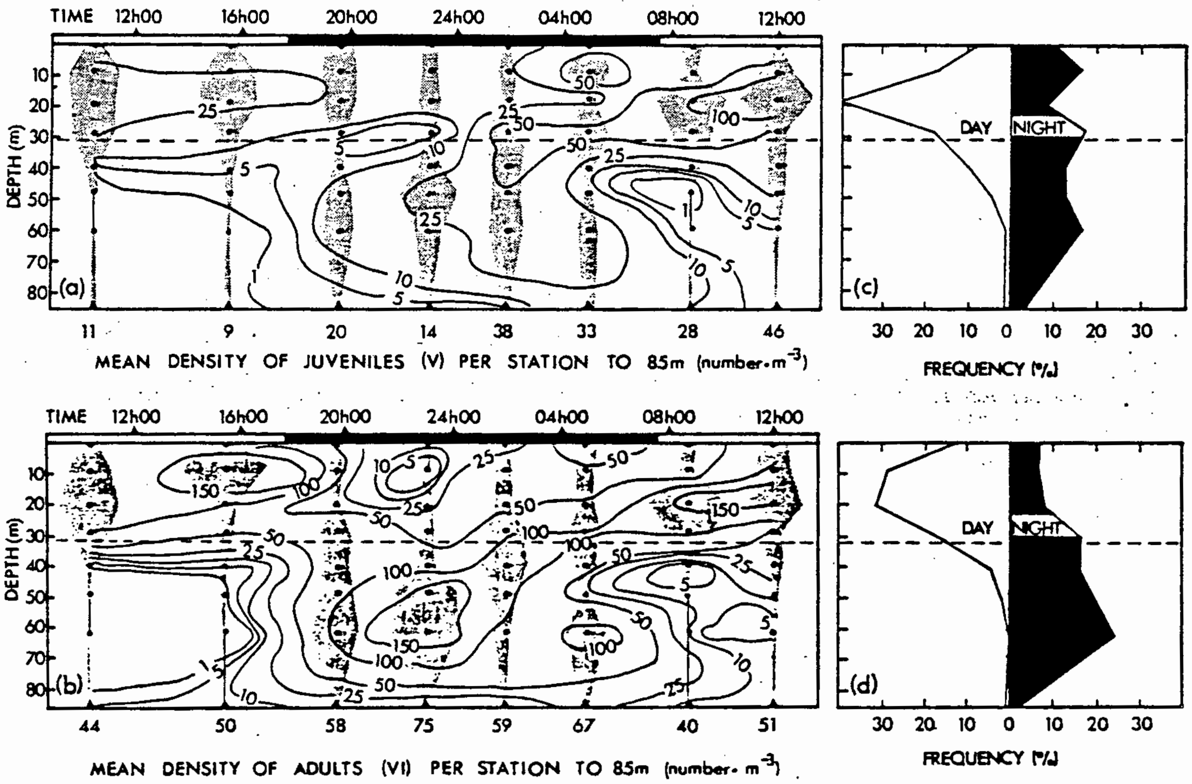

Fig. 8: Vertical distribution of *Nannocalanus minor* (a) juvenile (Stage V) and (b) adult (Stage VI), and (c) and (d) mean day and night distributions for the same stages — symbols as for Figure 2

depth horizons by day and night. It is not within the scope of this study to search for reasons to explain vertical patterns of the organisms under the present conditions. Further research is needed to confirm whether daily migrations by these animals (or their absence) have developed to enhance survival. Several hypotheses regarding the adaptive value of vertical migration, reviewed by Enright (1977), attempt to explain the daytime descent as means of horizontal transport, avoidance of predators or conservation of energy in cooler deeper waters. The nocturnal ascent of zooplankton is generally associated with the availability of food in the warmer mixed layer where production is highest. These adaptive values do not, however, explain the similarity in the day and night depth positions of non-migrant species.

The extent and the importance of vertical distribution and diel migration with regard to the maintenance of zooplankton populations within upwelling zones (Peterson *et al.* 1979, Hutchings 1979) indicate the necessity for more detailed studies on the distribution patterns of zooplankton in the Benguela Current system. In future research, more emphasis and attention should be directed towards laboratory studies together with fieldwork in relation to physico-chemical and biotic factors, such as light intensity, salinity, oxygen, temperature and chlorophyll *a* concentration. Sampling for migrant and non-migrant species should be focussed on small depth intervals where interactions with these parameters are likely to occur, e.g. within discontinuity layers, or regions of subsurface chlorophyll maxima.

ACKNOWLEDGEMENTS

I gratefully acknowledge the critical reviews of Drs L. Hutchings (Sea Fisheries Research Institute) and A.H.B. De Decker (S.A. Museum) and Professor J.R. Grindley (University of Cape Town). The enthusiastic assistance of my colleague Mrs S.M.

Payne in counting some of the material is greatly appreciated.

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Of the euphausiids which occur on the west coast of South Africa, *Euphausia lucens* and *N. capensis* are the most abundant, constituting 76 and 23% respectively of the euphausiid population (Nepgen, 1957). Off South West Africa *N. capensis* has also been responsible for sound-scattering layers (d'Arcangues, 1977). The necessity for identifying and separating developmental stages of these species in field collections has led to laboratory studies on captured animals. In the present study particular attention has been given to the role of diet in determining larval development, growth rates and developmental times of *N. capensis*. Laboratory observations are compared with those obtained from natural populations both from Boden's data and from field collections. Similar rearing studies were also carried out on larvae of *E. lucens* (Pillar, 1984).

Methods and Materials

Larvae of *N. capensis* were collected on 14 April 1982 in the vicinity of Robben Island (Lat. 33°48'S and Long. 18°22'E) with a surface towed 1 metre plankton net. In the laboratory, larvae in calyptopis stage II were sorted from the live material and kept individually in 80 ml crystallizing dishes, each containing 50 ml of filtered sea water (<10 μm). These animals were maintained throughout the study in the dark at a temperature of 12 ± 0.5°C, approximating that of their natural environment.

Table I summarizes the dietary conditions to which the animals were subject during the experiments. The water and food were changed daily at which time each container was checked for the exuvia remains. Both species of algae, *Phaeodactylum tricornutum* and *Tetraselmis chuii*, were grown in Walnes medium under banks of fluorescent lights at ~20°C and cooled to 12°C before use. *Artemia* nauplii were hatched in 2 l of filtered sea water (<10 μm) and fed to the larvae within 24 h of hatching. The estuarine copepod, *Pseudodiaptomus hessei* was mass-cultured in 50 l containers and maintained on a daily diet of mixed algae. To ensure that each ration was of similarly sized animals only copepod stages which passed through a 200 μm mesh and were retained on an 80 μm mesh were used. The developmental stages offered to the larvae ranged from late naupliar stages to early copepodite stages (N4 – CI). The larvae were examined daily and when moulting had occurred the moult was removed and the larva was transferred to a 'welled' slide for measurement and determination of the state of pleopod development. Measurements were taken from the anterior end of the rostrum to the end of the telson including terminal spines, by means of an ocular micrometer. The moults were also examined for number of telson spines.

Additional field material for comparative study was drawn from preserved collections from the South West African Pelagic Egg and Larvae Survey (SWAPELS) (Cram and Visser, 1972) from various regions (between 18 – 24°S) off the south western coast of Africa.

As inconsistencies exist in the literature concerning the nomenclature of larval development it is necessary to explain the terminology used in this study so that valid comparisons can be made with other developmental studies. The furcilia phase was separated into stages on the basis of the condition of the pleopods and the number of terminal telson spines. Within each stage there may be one or more instars termed 'forms'. If several 'forms' exist within a stage the one which is numerically dominant is regarded as being characteristic of that particular 'stage'. In this study 22 'forms' of furcilia were found which represented six stages according to the progressive addition of pleopods and setae and the decrease in numbers of terminal telson spines. These six stages were characterized as follows:

Furcilia 1: five forms with 0 – 4 pairs of non-setose pleopods and seven terminal telson spines.

Furcilia 2: nine forms with 1 – 4 pairs of non-setose pleopods 1 – 4 pairs of setose pleopods and seven terminal telson spines.

Furcilia 3: one form with five pairs of setose pleopods and seven terminal telson spines.

Furcilia 4: three forms with five pairs of setose pleopods and 4 – 6 terminal telson spines.

Furcilia 5: three forms with five pairs of setose pleopods and 2 – 4 terminal telson spines.

Furcilia 6: one form with five pairs of setose pleopods and one terminal telson spine.

The animal was classed as juvenile when the pair of long postero-lateral spines on the telson is lost.

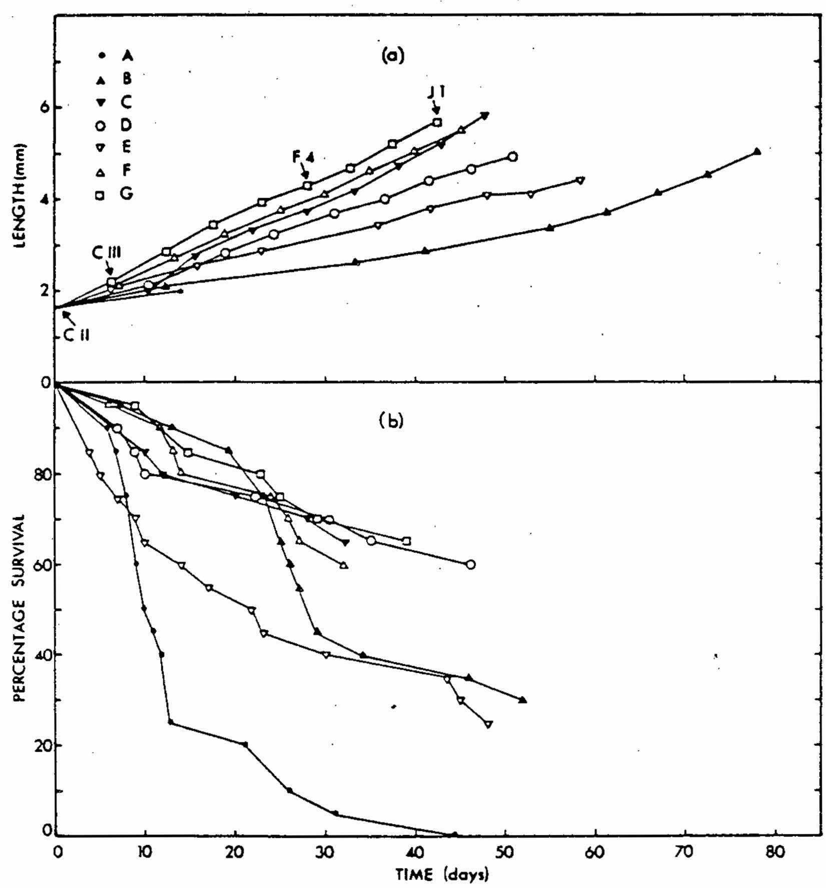

Fig. 1. The effect of the different diets on (a) growth rate based on mean body length per stage and mean intermoult duration per stage and (b) percentage survival of larval *N. capensis* from calyptopis II (CII) to juvenile 1 (J1).

Results

Survival and growth rates

Figure 1 shows the growth rates and percentage survival of the larvae fed under the different dietary conditions presented in Table I. The regression analysis and correlation coefficients for each growth curve are given in Table II together with a comparison of the slopes of the regression lines. The slope of the line (b) expresses in mm the mean daily growth of the larvae.

Those larvae which were deprived of food (A) did not survive to moult into the first

Table I. Type and amount of food offered to the larvae of *N. capensis* during laboratory rearing experiments.

Diet	Food type	Daily ration per 50 ml of filtered sea water	Initial number of larvae
A	Filtered seawater (<10 μm)	–	20
B	*Pseudodiaptomus hessei* nauplii	~200	20
C	*Pseudodiaptomus hessei* nauplii	~200	20
	and *Artemia* nauplii	20	
D	*Artemia* nauplii	20	20
E	*Phaeodactylum tricornutum*	2 ml	20
F	*Tetraselmis chuii*	2 ml	20
G	*Tetraselmis chuii*	2 ml	20
	and *Artemia nauplii*	20	

Table II. (a) Regression analysis of relationship between mean body length per stage in mm (y) and time in days (x) of furcilia of *N. capensis* under the dietary conditions listed in Table I. The slope *b* is equivalent to the mean daily growth rate of the larvae in mm. (b) The slopes are compared statistically with * denoting $p<0.05$, ** denoting $p<0.01$ and n.s. denoting $p>0.05$.

(a) Diet	Regression constants (y = bx + a) a	b	Correlation coefficient (r)
A	–	–	–
B	1.201	0.045	0.971
C	1.141	0.097	0.996
D	1.292	0.076	0.998
E	1.838	0.047	0.995
F	1.518	0.088	0.997
G	1.668	0.093	0.999

(b) Diet	B	C	D	E	F	G
B		**	*	*	**	**
C			**	*	n.s.	n.s.
D				*	*	*
E					**	**
F						n.s.
G						

Table III. Growth factors (%) at the moult from calyptopis III to furcilia 1 and between successive furcilia stages of *N. capsensis* fed on the seven experimental diets. The corresponding regression analysis of log growth factor (y) on body length (x) are given.

Diet	Furcilia stages							Regression constants (log y = bx + a)		Correlation coefficients (r)
	CIII-F1	F1-F2	F2-F3	F3-F4	F4-F5	F5-F6	F6-J1	a	b	
A	–	–	–	–	–	–	–	–	–	–
B	23.8	11.5	17.2	11.8	10.5	4.8	6.8	1.956	−0.247	−0.831
C	33.3	21.4	11.8	10.5	14.3	10.4	11.3	1.745	−0.134	−0.766
D	33.3	14.3	15.6	8.1	10.0	6.8	6.3	2.219	−0.292	−0.918
E	23.8	19.2	12.9	11.4	7.7	2.4	4.7	2.615	−0.442	−0.877
F	28.6	18.5	15.6	10.8	12.2	8.7	10.0	1.818	−0.165	−0.916
G	27.3	14.3	14.7	10.3	9.3	10.6	9.6	1.709	−0.140	−0.860
x	28.4	16.5	14.6	10.5	10.6	7.3	8.1	–	–	–
s.d.	4.3	3.7	2.0	3.2	2.3	3.3	2.6	–	–	–

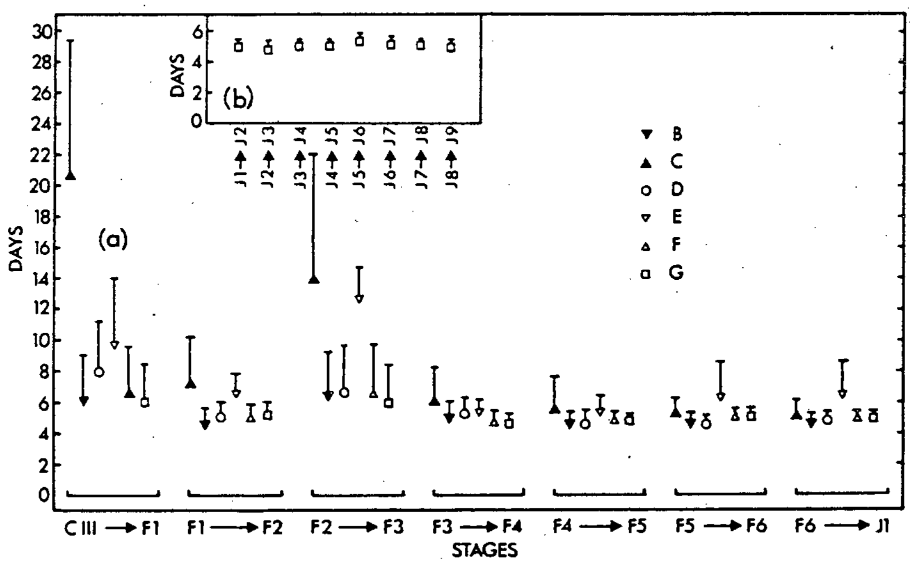

Fig. 2. The effect of the different diets on the mean intermoult period of individual instars (±s.d.) within each stage from (a) the third calyptopis stage (CIII) to the sixth furcilia stage (F6) and (b) the first juvenile stage to late juvenile stage (J1−J8).

furcilia stage, although one larva survived without moulting for 44 days under these conditions. The harshest feeding conditions occurred on diets of *Pseudodiaptomus* nauplii alone (B) and *Phaeodactylum* (E) with survivals of 30 and 25% respectively and mean daily growth rates of 0.045 and 0.047 mm d^{-1} respectively in attaining the first juvenile stage. Higher survival and a significantly higher growth rate occurred on a pure diet of *Artemia* nauplii (D) with a survival of 60% and growth rate of 0.076 mm d^{-1}. Similar larval survival as with those fed on pure *Artemia* nauplii was achieved on diets of *Artemia* nauplii mixed with *Tetraselmis* (G) or *Pseudodiaptomus* nauplii (C) and *Tetraselmis* only (F). However, diets C, F and G yielded statistically higher growth rates, 0.093, 0.097 and 0.088 mm d^{-1} respectively.

A second approach to analysing growth rates is obtained by expressing the increment in body length at each moult as a percentage of the pre-moult length termed a growth factor. Significant linear relationships were demonstrated when the growth factor was logarithmically regressed against the body length of several decapod crustaceans (Mauchline, 1977a) and in studies of growth and moulting of several euphausiid species (Mauchline, 1977b). In the present analysis growth factors of successive stages for each diet are tabulated in Table III. The log of the growth factors were regressed on body length and the corresponding regression analysis and correlation coefficients are also given in Table III.

In all cases the growth factor decreased sharply after the moult into the first furcilia stage (CIII−F1) and continued to decrease throughout successive furcilia stages. This decrease is shown to be a logarithmic function of the body length of the furcilia and is least for the dietary conditions where highest growth note is achieved (i.e., C, F and G).

Table IV. (a) Analysis of variance to test the effect of diet and stages on the mean intermoult period of instars within the furcilia phase. (b) The results of analysis of variance tests to compare the intermoult period of individual instars of all the furcilia stages of the different diets. * denotes $p<0.05$, ** denotes $p<0.01$, n.s. denotes $p>0.05$.

(a)

Source of variation	Degrees of freedom	Sums of squares	Mean squares	Variance ratio (F)
Diet	5	12.01	2.40	20.00**
Stages	6	1.28	0.21	1.75 n.s.
Error	30	3.63	0.12	
Total	41	16.92		

(b)

Diet	B	C	D	E	F	G
B		**	**	*	**	**
C			*	**	n.s.	n.s.
D				**	n.s.	n.s.
E					**	**
F						n.s.
G						

Duration of intermoult period

The mean intermoult period of instars within each stage of larvae fed on the various diets is shown in Figure 2. These data were tested statistically using a two-way analysis of variance (Table IVa). The analysis shows that diet had a significant effect on the mean intermoult period of the larvae ($p<0.0005$) whereas no difference in intermoult period was found between developmental stages ($p>0.05$). This dietary effect was investigated between each diet using a one-way analysis of variance between the intermoult period within each instar for all the developmental stages (Table IVb). It is noted in Figure 2 that the harsher feeding conditions B and E produced longer and more variable intermoult periods between instars within the majority of the stages. These intermoult periods were found to differ significantly when compared to those of the larvae given better feeding conditions (i.e., C, F and G). The most frequent intermoult period for the more healthy individuals ranged from 4 to 6 days with 5 days being the most frequent. The similarity in the intermoult period observed in the furcilia stages was also found in a few individuals which were reared to late juvenile stages (Figure 2b). It was noted that there was a consistent increase in the intermoult period prior to the death of the animal.

Larval development

The dietary effect on the larval pathway of pleopod development from the third calyptopis stage (CIII) to the appearance of five pairs of setose pleopods which characterizes the third furcilia stage (F3) is shown in Table V. Great variability is apparent in both the number of instars and the sequence of pleopod development in attaining the F3 configuration. The number of instars between CIII and F3 ranged from three, with one instar per stage to eight indicating more than one instar per stage. The percentage of

Table V. The effect of the different diets on the sequence of pleopod development of *N. capensis* and the number of moults needed to attain five pairs of setose pleopods. CIII denotes the third calyptopis stage, F denotes furcilia and (′) denotes a pair of setose pleopods (e.g., F3′2 denotes a furcilia larva with three pairs of setose and two pairs of non-setose pleopods).

	Furcilia moults								Diet type and number of larvae							
	I	II	III	IV	V	VI	VII	VIII	A	B	C	D	E	F	G	Total
CIII →	F0 →	F0 →	F0 →	F2 →	F2′2 →	F2′2 →	F5′			1						1
			F2 →	F2′2 →	F5′					1						1
				F3′1 →	F4′1 →	F5′				1			1			2
		F2 →	F2′1 →	F3′2 →	F5′					1						1
			F2′2 →	F4′1 →	F5′					1			1			2
			F2′3 →	F5′											1	1
		F3 →	F3′1 →	F4′1 →	F5′								1	1		2
			F3′2 →	F5′								1		1		2
		F4 →	F4 →	F4′1 →	F5′										1	1
			F4′1 →	F5′								1			1	2
	F1 →	F1 →	F1′1 →	F1′1 →	F2′1 →	F3′1 →	F4′1 →	F5′		1						1
		F1′1 →	F2′1 →	F3′1 →	F4′1 →	F5′					1					1
		F1′3 →	F4′1 →	F5′								1		1		2
	F2 →	F2′1 →	F3′2 →	F5′									1			1
		F2′2 →	F4′1 →	F5′							2	3		4	3	12
		F2′3 →	F4′1 →	F5′							1	1	1			3
			F5′									1		1		2
	F3 →	F3′1 →	F4′1 →	F5′							1			1		2
		F3′2 →	F5′									2		4	5	11
			F4′1 →	F5′									1			1
	F4 →	F2′2 →	F4′1 →	F5′							1					1
		F3′2 →	F5′								1					1
		F4′1 →	F5′								7	3			3	13

Table VI. The dietary effect on the percentage of larvae which pass a given number of instars within each stage from the third calyptopis stage (CIII) through the six furcilia stages (F1 – F6) to the first juvenile stage (J1). n denotes number of larvae.

Diet	B						C			D			E			F			G		
Instars / Stage	1	2	3	4	5	n	1	2	n	1	2	n	1	2	n	1	2	n	1	2	3
CIII-F1	16.7	33.3	33.3	16.7		6	85.7	14.3	14	50.0	50.0	14	50.0	50.0	8	75.0	25.0	12	76.9	23.1	13
F1-F2	83.3	16.7				6	100.0		14	100.0		13	100.0		8	100.0		12	92.3	7.7	13
F2-F3	33.3	50.0			16.7	6	69.2	30.8	13	69.2	30.8	13	100.0		6	75.0	25.0	12	76.9	23.1	13
F3-F4	83.3	16.7				6	100.0		13	91.7	8.3	12	60.0	40.0	5	100.0		12	100.0		13
F4-F5	100.0					6	100.0		13	100.0		12	100.0		5	100.0		12	100.0		13
F5-F6	66.7	33.3				6	100.0		13	91.7	8.3	12	100.0		5	100.0		12	100.0		13
F6-J1	100.0					6	100.0		13	100.0		12	100.0		5	100.0		12	100.0		13

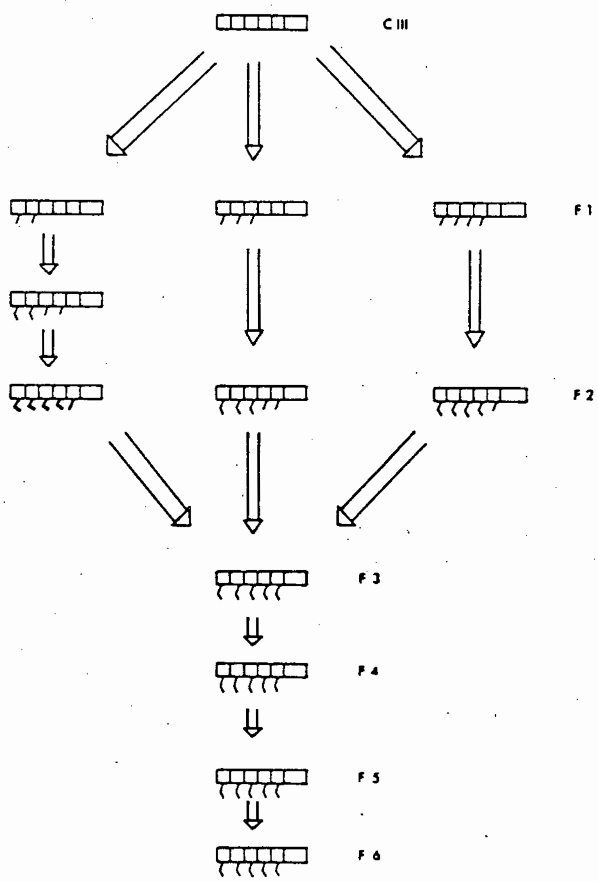

Fig. 3. Dominant pathways of pleopod development from the third calyptopis stage (CIII) to the ~~third~~ sixth furcilia stage (F6) of *N. capensis* reared in the laboratory. Segmented bars denote abdomen with anterior on left side. Single line denotes pair of non-setose pleopods and angled line denotes pair of setose pleopods.

larvae which pass through a given number of instars within each furcilia stage for each diet is shown in Table VI. Those larvae which were subjected to poor dietary conditions (i.e., B, D and E) have relatively higher percentages of two or more instars within the first furcilia stage and in some of the succeeding stages. All diets, however, produced some larvae which passed through two instars during the third furcilia stage. Higher percentages were generally found under poorer dietary conditions.

Three of the 23 developmental pathways exhibited by the larvae (Table V) can be considered dominant. These pathways were relatively shorter than the variant pathways in which there were a greater number of instars and less morphological change between them. In several cases moults took place without any morphological change. The number of larval forms was greatest when the F1 form had either no pleopod buds or one pair of non-setose pleopods. In two of the three dominant pathways of development shown in Figure 3 three moults took place between stage CIII and the final stage of pleopod development. There were four moults in the remaining pathway. In all cases

Table VII. The pathway of terminal telson spine reduction in the late furcilia stages (F3 – F6) for the different diets.

F3	Number of moults: I	II	III	IV	Number of larvae in pathway on diet: B	C	D	E	F	G	Total
7	7	6	3	1	1						1
7	7	5	2	1				1			1
7	7	4	2	1			1	2			3
7	6	4	3	1			1				1
7	6	3	3	1	1						1
7	6	3	2	1	1						1
7	6	3	1			2	2	1	1		6
7	5	4	1			1	1			2	4
7	5	3	1		2	9	6	1	8	8	34
7	5	2	1		1	1	1		2	3	8
7	4	2	1						1		1

F3 ——— F6

a pair of setose pleopods appeared where a pair of non-setose pleopods existed before.

Reduction of the terminal spines of the telson began after the third furcilia stage (F3) when all setose pleopods were present (Table VII). In most cases one moult occurred between each reduction from seven to one spines, with the combination 7 – 5 – 3 – 1 being dominant.

Comparison of laboratory and field data on the furcilia of N. capensis

Data from the trials exhibiting the fastest growth, (i.e., series C, F and G) were combined. The frequency distributions of laboratory-reared larval forms in these data are shown in Figure 4 and are compared to frequency distributions of specimens collected from various areas off South West Africa and from Boden (1955). Although the field data were from different seasons and areas larval forms were fairly similar to those found in the laboratory. At the first furcilia stage, forms with two, three and four pairs of non-setose pleopods were generally dominant over those with one pair or with no pleopods. This sequence differs widely from that described by Boden (1955) where the form with no pleopods far outnumbered the other forms. At the second furcilia stage the dominant forms of the field collections and those from Boden's data are similar. The rank order of decreasing dominance is four pairs of setose with one pair of non-setose pleopods, three pairs of setose with two pairs of non-setose pleopods and two pairs of setose with two pairs of non-setose pleopods. The final stage of pleopod development (i.e., five pairs of setose pleopods) is attained at the third furcilia stage.

The mean body lengths per stage of the larvae reared under favourable laboratory conditions, (i.e., series C, F and G) were compared to those of the *N. capensis* larvae collected form the field and to those from Boden's material (Table VIII). There is little difference in length between reared and wild individuals. However, Boden reported smaller CIII and F1 stages and larger F2 and F3 stages than those observed in the laboratory or the field in this study. Differences between the means decrease as the development advances to the final furcilia stage. The large increase in length between

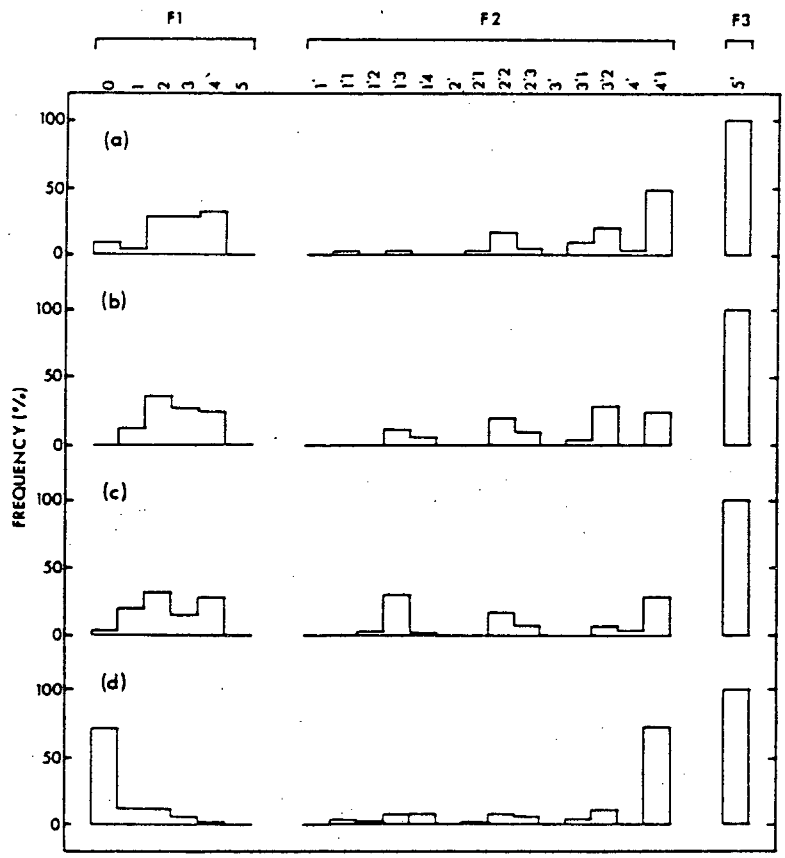

Fig. 4. Frequency distribution of the forms within the first three furcilia stages (F1, F2 and F3) of *N. capensis* from the following sources. (a) reared in the laboratory on diets C, F and G; (b) swarm of larvae located off Henties Bay S.W. Africa; (c) from various positions off S.W. Africa; (d) from Boden (1955). n denotes number of specimens examined.

the F1 and F2 stages in Boden's data (1.4 mm) corresponds to a growth factor of 56% which is over three times the increase attained in field or laboratory animals (i.e., 17 and 18%, respectively).

Discussion

Laboratory studies have shown that environmental factors, such as temperature, food type and food availability can be important in determining the growth rates, moulting frequency and developmental sequences of euphausiids (Lasker, 1966; Le Roux, 1973, 1974; Sameoto, 1976). Studies by Ross (1981) indicated that genetic factors may be important in larval development. Following the development of larvae reared from ovigerous females of *E. pacifica* she concluded that maternal effect probably existed, but felt that further laboratory breeding experiments with known males and females were necessary to distinguish genetic from environmental maternal effects. The present study was not designed to examine temperature or genetic effect on larval develop-

Table VIII. Comparison of the mean body lengths of the larvae reared in the laboratory on diets C, F and G with those from field samples and from Boden (1955). C denotes calyptopis, F denotes furcilia.

Development stages	Laboratory measurements				Field measurements				Boden's measurements			
	Number	Body length (mm)	Range	s.d.	Number	Body length (mm)	Range	s.d.	Number	Body length (mm)	Range	s.d.
CIII	37	2.1	1.9-2.5	0.15	50	2.2	2.0-2.6	0.17	6	1.9	1.8-2.2	.
F1	37	2.8	2.5-3.1	0.18	50	2.9	2.6-3.3	0.23	12	2.5	2.2-2.8	.
F2	36	3.3	3.0-3.7	0.22	50	3.4	3.2-3.7	0.16	19	3.9	3.7-4.1	.
F3	36	3.8	3.4-4.2	0.22	50	3.8	3.5-4.2	0.19	10	4.2	4.0-4.4	.
F4	36	4.2	3.7-4.6	0.24	50	4.3	3.7-4.5	0.23	15	4.4	4.3-4.6	.
F5	36	4.7	4.3-5.3	0.24	50	4.6	4.4-5.6	0.27	13	4.7	4.5-4.9	.
F6	36	5.2	4.7-5.9	0.29	50	5.0	4.6-5.7	0.25	21	5.1	4.8-5.3	.

ment but the results permit evaluation of the role played by diet on the growth, moulting, and ontogeny of the larval stages of *N. capensis*.

Survival and growth rate

Of the various diets offered to the larvae, the flagellate *Tetraselmis* alone or mixed with *Artemia* nauplii and an animal mixture of *Artemia* nauplii and *Pseudodiatomus* nauplii produced the best survival and growth rates. A pure diet of the diatom *Phaeodactylum* was not as favourable to the development of *N. capensis* larvae. This is supported by the results of Le Roux (1973) who found that larvae of *N. couchi* when fed on *Phaeodactylum* grew at about half the rate as those larvae which were fed on pure *Artemia* nauplii. He suggested that the capture of isolated cells of this relatively short diatom posed problems to the furcilia larvae. It is also plausible that the 'spiky' shape of the diatom was less acceptable to the larvae than the smoother form of the flagellate *Tetraselmis* which was a more efficient diet for rearing *N. capensis* larvae.

Le Roux (1973, 1974) found that a pure diet of *Artemia* nauplii was sufficient for proper larval development and growth of both *Nyctiphanes couchi* and *Meganyctiphanes norvegica*. He concluded that the animal component in the diet was important from the early stages of development of these euphausiids. His observations are supported in the present study as regards the efficiency of *Artemia* nauplii in stimulating growth. However, the poor development and growth rates achieved on a diet of pure *Pseudodiaptomus* nauplii casts some doubt on the ability of natural populations of early larval stages of *N. capensis* to utilize copepod nauplii. Nevertheless the apparent increase in growth after the third furcilia stage (Figure 1) indicates a greater efficiency of older larvae in utilizing the copepod nauplii. This is also indicated by the faster growth rate achieved by the larvae fed on a mixture of *Pseudodiaptomus* nauplii and *Artemia* nauplii than by those fed on pure *Artemia* nauplii. There is no evidence in the literature to suggest that euphausiids actively hunt or stalk their prey. Under laboratory conditions, Lasker (1966) and Fowler *et al.* (1971b) showed that *E. pacifica* and *M. norvegica* grazed on *Artemia* nauplii as a passive particle. Berkes (1975) concluded that 'encounter feeding' is probably the mode of carnivorous feeding in euphausiids. It is plausible that the younger *N. capensis* larvae fed on the slower moving *Artemia* nauplii more readily than the *Pseudodiaptomus* nauplii only because they were more easily captured. As the larvae developed, it became easier for them to take the *Pseudodiaptomus* nauplii.

Under similar dietary conditions (i.e., *Artemia* nauplii and algae) the mean daily growth rate in the furcilia phase of *N. capensis* (0.093 mm d^{-1}) is slower than that of *N. couchi* [0.13 mm d^{-1} (Le Roux, 1973)], *M. norvegica* [0.152 mm d^{-1} (Le Roux, 1974)] and *E. lucens* [0.131 mm d^{-1} (Pillar, 1984)] but similar to that of *Nematoscelis difficilis* [0.10 – 0.12 mm d^{-1} (Gopalakrishnan, 1973)]. Growth rates lower than that found on diet G in the present study were recorded in juvenile *E. pacifica* [0.048 mm d^{-1} (Lasker, 1966)] and in juvenile *M. norvegica* [0.050 mm d^{-1} (Fowler *et al.*, 1971a)]. Mauchline (1977b) demonstrated that for euphausiids the percentage growth at successive moults decreased logarithmically. A similar decrease in growth during the furcilia phase was observed in the present study. The rate of this decrease was a function of the dietary conditions with better feeding conditions resulting in a slower decrease in growth. The mean growth increase of 28.4 ± 4.3% for the moult from the calyptopis into the furcilia phase (CIII – F1), compares favourably with that of 26

± 8% which is characteristic of six genera of euphausiids (including *Nyctiphanes*) reviewed by Mauchline (1980). He estimated that this growth factor was equivalent to a doubling of the body weight at this moult.

Intermoult duration

Comparison of the moulting frequency in *N. capensis* larvae reared on the seven dietary regimes indicates that when nutrition is unfavourable the duration of the intermoult period is longer. This is in agreement with the results of Le Roux (1973, 1974) who found that the moulting frequency of the larvae of *N. couchi* and *M. norvegica* was a function of the type of food and its availability. When food was given only on alternate days the intermoult duration of *M. norvegica* lengthened and became more variable. Lasker and Theilacker (1965) noted a longer intermoult duration of adult *E. pacifica* raised on alga than of those raised on *Artemia* nauplii. In the present study the larvae raised on the algae *Phaeodactylum* had longer and more variable intermoult duration than those raised on *Artemia* nauplii, however, the larvae reared on the alga *Tetraselmis* achieved similar moulting frequencies to those raised on *Artemia* nauplii. Contrary to the present study, Fowler *et al.* (1971b) did not observe a lengthening of the intermoult period in adult *M. norvegica* deprived of food, although he also found an increase in the intermoult period prior to the death of his animals.

The 4−6 days intermoult period observed for healthy individuals is common not only to other euphausiid larvae and juveniles but also to adults of other species studied under similar temperature regimes (Mauchline, 1980). Present results suggest that the intermoult period is not age dependent for furcilia or early juvenile stages. This is contradictory to the observations of Mauchline (1977b) who found that intermoult period increased logarithmically at successive moults. This relationship was based on experimental data from Fowler *et al.* (1971b) on adults of *N. couchi*, Le Roux (1973) on furcilia of *N. couchi* and Gopalakrishnan (1973) on larvae and early juvenile of *N. difficilis*. Other studies, however, are in agreement with the present results. Under controlled constant temperature regimes no age or size dependence on intermoult periods were found in larvae and juveniles of *E. mucronata* (Antezana, 1978), of *M. norvegica* (Le Roux, (1974)) and *E. lucens* (Pillar, 1984). It should however, be noted that the size ranges of the euphausiids in the above investigations, including this study, are relatively small and water temperature could not be controlled during microscopy analysis. Any slight change in moulting frequency related to growth could have been masked by changes in temperature which has generally been cited as a major causative factor for changes in the moulting frequency of euphausiids (Mauchline, 1980). The fact that Fowler *et al.* (1971b) observed consistently longer intermoult periods in a single adult *N. couchi* (4−9 days) over a period of 11 months suggests that age dependency may be likely in the post juvenile stages. Studies on other decapod crustaceans have shown that older animals generally have a longer intermoult period than younger members of the same species (Kurata, 1962; Mauchline, 1977a).

Larval development

The variation in the sequence of pleopod development in *N. capensis* has shown that unfavourable trophic conditions can influence the ontogeny of this species. Poor nutrition retards pleopod development and growth and results in a greater number of moults in attaining a particular stage. It has been suggested that environmental factors such as food availability are partly responsible for the variation in ontogenesis of euphausiid larvae observed in the ocean (Einarsson, 1945; Sheard, 1953; Makarov, 1974). This hypothesis has been supported in laboratory studies on *N. couchi* and *M. norvegica* (Le Roux, 1973, 1974) and is further supported in the present study. Similar to Le Roux's observations, the present results show that larvae reared under unfavourable feeding conditions from calyptopis II had fewer pleopod buds in the first instar of furcilia stage I. As a result a greater number of moults and larval forms were required to achieve the final stage of pleopod development (five pairs of setose pleopods). This lends support to the theory proposed by Mauchline and Fisher (1969) that environmental conditions encountered by the larvae prior to the furcilia stage may determine their future developmental pathway.

Comparison of laboratory and field data

The three dominant pathways of development found in healthy reared individuals were consistent with those found in the field. Furthermore there was a close similarity between the mean lengths of larval stages. Antezana (1978) found that in the wild the dominant developmental pathway of furcilia of *E. mucronata* seemed to be shorter and more direct than those reared in the laboratory. The apparent tendency in his reared population to develop through longer pathways was correlated with growth rates lower than those determined from an oceanic population. Smiles and Pearcy (1971) found that the growth rate of *E. pacifica* off Oregon was appreciably faster than laboratory specimens reared by Lasker (1966). On the contrary Gopalakrishnan (1973) found that laboratory reared *N. difficilis* grew as fast as animals in the field. It is highly probable that those differences in larval development and growth rates result from differences between oceanic and laboratory ambient conditions.

Boden (1955) described the dominant form representing the first furcilia stage as having no pleopod buds. This form was encountered in the laboratory principally among the larvae reared on poor diets, however, it was rarely found in the field collections. It is plausible that poor environmental conditions prior to Boden's collections of the first furcilia stage larvae could account for the dominance of this configuration. The high growth increment between the first two furcilia stages described by Boden might be explained by the large difference in complexity between these two forms i.e., from no pleopods to four setose and one non-setose pleopods. It has generally been assumed from field observations and substantiated by laboratory studies, including this study, that a setose pleopod appears only at the site of a non-setose pleopod (Sheard, 1953; Mauchline and Fisher, 1969; Le Roux, 1973, 1974; Antezana, 1978; Pillar, 1984). This strongly suggests that several moults were needed to attain the F2 configuration proposed by Boden.

Boden (1955) first suggested that the large variation in larval development in the genus *Nyctiphanes* was a secondary feature resulting from their invasion of coastal waters and that the genus may have different developmental stages under different conditions. In discussing the significance of dominance in larval forms of euphausiids Makarov (1974) concluded that dominant pathways of development corresponded to optimal environmental conditions for larval growth and ontogenesis while variant forms reflected suboptimal environmental conditions. The present results which relate growth rate, moulting duration and ontogenesis to trophic conditions in the laboratory support this hypothesis. The high degree of plasticity in the larval development of *N. capensis* makes this species well fitted to the highly variable environmental conditions off the west coast of South Africa and South West Africa (Shannon *et al.*, 1984).

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