CHAPTER 6: CROSS-SHELF CIRCULATION, DISPERSAL

AND MAINTENANCE OF EUPHAUSIIDS

6.1. INTRODUCTION

The cool waters of the Benguela Current are bounded in the south by the warm Agulhas retroflexion area (35°S) and in the north by the southward flowing sub-tropical Angolan Current (17°S). The general flow of the Benguela is considered to be topographically steered (Nelson and Hutchings, 1983) and the narrowing of the shelf at various localities coincides with areas of enhanced upwelling activity (Shannon, 1985a). Of these areas the perennial Lüderitz upwelling zone (26°S) has been considered as the environmental boundary between the northern and southern Benguela (Agenbag and Shannon, 1988). The physical and biological processes of the southern Benguela system have received considerable attention in the past decade (Andrews and Hutchings, 1980; Chapman and Shannon, 1985; Shannon, 1985a; Shannon and Pillar, 1986). However, until recently, comparatively little was known of these processes in the northern Benguela. Such works by Boyd (1987), Boyd et al. (1987a) and Salat et al. (in press) have provided a good understanding of the physical oceanography of the region and research on biological processes has been the focus of several studies on phytoplankton and zooplankton dynamics (Estrada and Marrase, 1987; Le Clus and Kruger, 1982; Kruger and Boyd, 1984; Fearon et al., 1986; Olivar and Barange, 1990, chapter 3) and fish distribution (Mas-Riera et al., 1990).

In the Benguela system Nyctiphanes capensis, Euphausia lucens and its larger congener Euphausia hanseni, are the principal members of the euphausiid community and form one of the major prey items for the commercially important anchovy (James, 1987) and Cape hakes (Payne et al., 1987b; Macpherson and Roel, 1987; Roel and Macpherson, 1988). E.lucens is the dominant species in the shelf region of the southern Benguela (Pillar and Stuart, 1988) while, in the northern Benguela, N.capensis occurs predominantly in the coastal zone and E.hanseni in the outer shelf region with both species accounting for 90% of the euphausiid community (Olivar and

Barange, 1990, chapter 3; Barange and Stuart, 1991, chapter 4).
All three species share some common features such as displaying
continuous breeding throughout the year and having an adult
lifespan of approximately six months (Stuart and Pillar, 1988;
Barange and Stuart, 1991, chapter 4). Despite seasonal differences
in upwelling intensities in the Benguela system, their horizontal
distribution patterns remain fairly constant throughout the year
(Pillar, 1986; Barange and Stuart, 1991, chapter 4) suggesting that
they display maintenance strategies in order to remain in their
preferred habitat. Pillar et al. (1989) provided a discussion of
the role of vertical migration and ontogenetic layering of E.lucens
in relation to the horizontal and vertical current circulation
system and proposed a one celled cross-shelf circulation model as
a means to explain how E. lucens can remain and develop high
concentrations within the southern Benguela shelf region. They
observed different patterns of cross-shelf distributions of various
stages of E.lucens which reflected their offshore and onshore
transport during different phases of the upwelling cycle.

Since N.capensis is restricted to the coastal zone it is to be
expected that this species experiences different current regimes
than E.hanseni, which predominantly occurs in the outer shelf and
slope regions. It may then be suggested that, in order to maintain
such patterns, a complex cross-shelf circulation scheme may exist
in the northern Benguela in order to explain the inshore-offshore
segregation in the distribution patterns of N.capensis and
E.hanseni. This study attempts to provide a circulation model that
would best explain the distribution patterns of the euphausiid
community in the northern Benguela upwelling system. This is
achieved by examining the horizontal and vertical cross-shelf
distribution of euphausiid developmental stages and the advective
consequences under contrasting oceanographic regimes.

6.2. MATERIAL AND METHODS

The data presented were drawn from two sources, the SWAPELS (South West Africa Eggs and Larvae Surveys) and SNEC (Spanish Namibian Environmental Cruises) collections. The SWAPELS collections comprise approximately 350 samples taken during five cruises between January and November 1983. The sampling grid consisted of transects every half a degree of latitude from 17°30'S to 26°S, although some surveys extended only to 24°S (figure 6.1). Stations were located at 5, 15, 25, 35, 45, 55 and 65 n. miles from the coast. At each station surface temperature and salinity measurements were taken. Temperature and salinity depth profiles were obtained along transects at every degree of latitude. Zooplankton samples were collected at each station by means of Bongo nets fitted with 300μm and 500μm mesh nets and towed from 50m to surface or from 5 m above the bottom at shallower stations. In the present study only samples taken by the 300μm mesh nets were used. Detailed descriptions of the sampling methodology can be found in Le Clus and Kruger (1982) and Kruger and Boyd (1984). All adult euphausiids were counted, sexed and classified to species level. Abundant samples were split using a Folsom splitter until at least 50 individuals per species and sex were counted. The presence of spermatophores in the thelycum of female E.hanseni, or brood pouches in N.capensis females, were recorded. Only night-time sampled stations were considered due to the vertical migratory behaviour of euphausiids (Barange, 1990, chapter 5).

The SNEC data were obtained during SNEC I (active upwelling, September 1985) and SNEC II (abated upwelling, April 1986). The sampling grid consisted of 5 (SNEC I) and 4 (SNEC II) transects from 20°S to 26°S and from 17°30'S to 26°S, respectively (figure 6.1). Stations were located at 5, 15, 35, 55, 75, 105 and 135 n. miles from the coast. Zooplankton samples were collected with a multiple opening-closing RMT 1x6 net, giving five (SNEC I) and four (SNEC II, due to net failure) depth sample intervals from 200 m to the surface, or 5 m above the bottom at shallower stations. These were selected according to the hydrographical structure of the
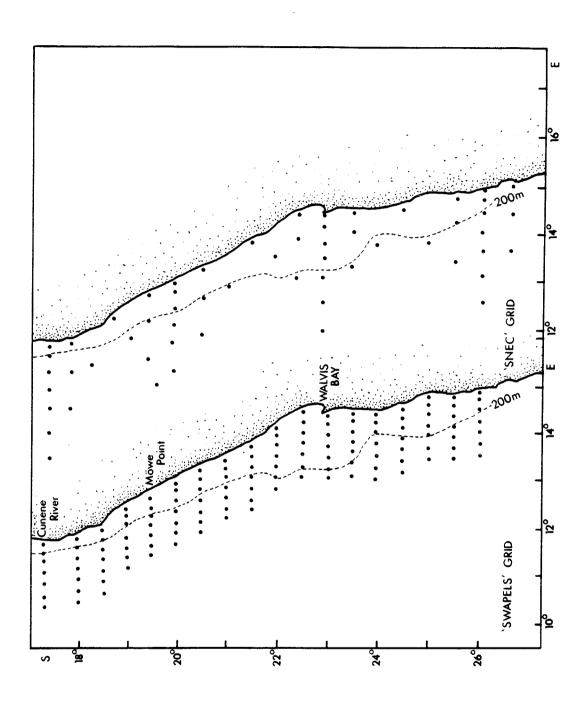
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Figure 6.1. Map of the study area showing location of transects sampled during the SWAPELS and SNEC cruises.

water column. Temperature and salinity profiles were taken at each station by means of CTD casts using a Neil Brown Mark III depth probe. A rosette of 10 Niskin bottles attached to the CTD was used to collect water for nutrients and chlorophyll $\underline{a}$ measurements. Detailed descriptions of the methodology can be found in Estrada and Marrase (1987) and Olivar and Barange (1990, chapter 3). All adult euphausiids were enumerated, and the eggs and larval stages of <u>Euphausia hanseni</u> and <u>Nyctiphanes capensis</u> were counted using the same procedure as described above. Data from both type of samples were standardized to indiv.m^{-3} and indiv.m^{-2} on the basis of the volume of water filtered by the nets and the sampling depth.

6.3. RESULTS

Figures 6.2 and 6.3 show different patterns in cross-shelf distributions of adult <u>N.capensis</u> and <u>E.hanseni</u>. Maximum occurrence of <u>N.capensis</u> was within 35 n. miles from the coast, while <u>E.hanseni</u> resided further offshore and peaking just offshore of the shelf-break. It appears that males and females (both fertilized and non- fertilized) of <u>E.hanseni</u> peak at similar distances from the coast. Female <u>N.capensis</u> bearing brood pouches tended to spread all over the shelf region, while males and females lacking brood pouches consistently peak at 25 miles from the coast. Although this fact could reflect a cross-shelf transport of fertilized females for spawning purposes no definite conclusions can be drawn at this stage. Slight inshore displacement in the distribution patterns are evident in both species during active upwelling.

Average monthly surface temperatures along the transects are presented in figure 6.4. The figure depicts the late winter-spring maximum (lower surface water temperature, September and November) and summer minimum (higher surface water temperature, January-March) in upwelling activity in the northern Benguela (Shannon, 1985a). It is interesting to note that similar inshore-offshore
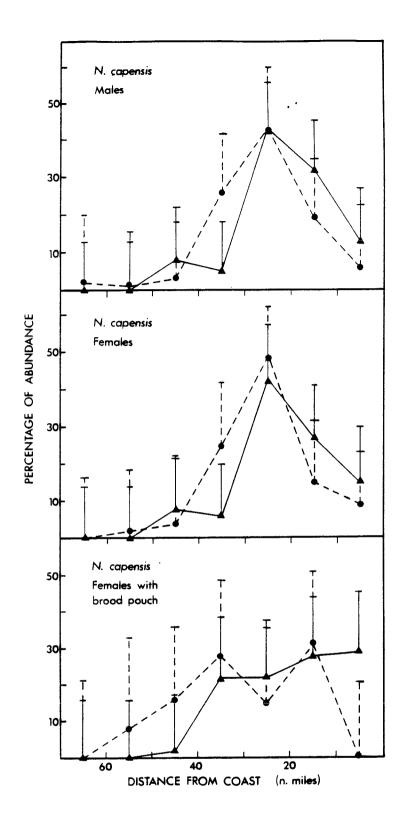
Figure 6.2. Cross-shelf distribution patterns of adult *Nyctiphanes capensis* during active (solid line) and quiescent (dashed line) upwelling conditions. The figure was constructed using data from five SWAPELS surveys.
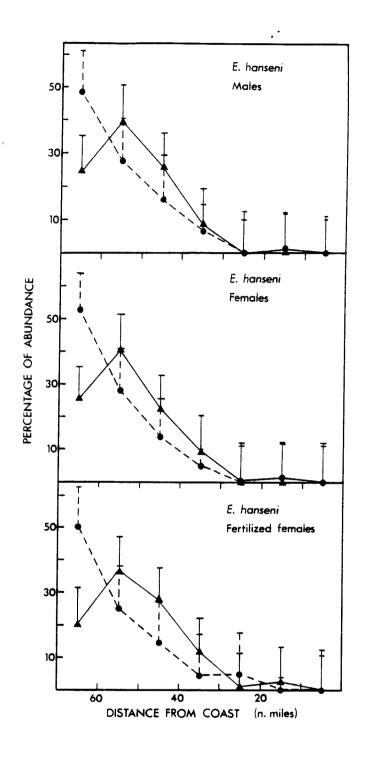
Figure 6.3. Cross-shelf distribution patterns of adult Euphausia hanseni during active (solid line) and quiescent (dashed line) upwelling conditions. The figure was constructed using data from five SWAPELS surveys.
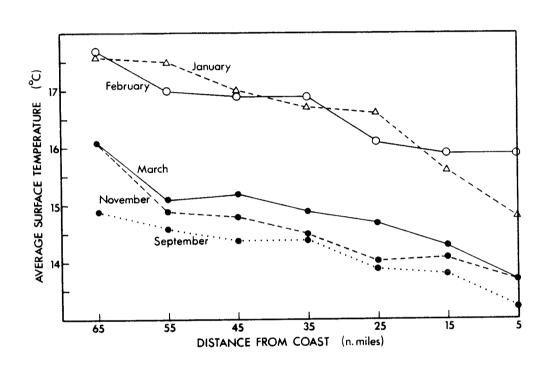
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Figure 6.4. Average monthly surface temperatures (°C) in the area covered during the 1983 SWAPELS collections.

gradients were observed regardless of the upwelling activity, reflecting the onshore displacement of oceanic waters during quiescent upwelling periods.

In order to provide insight into the maintenance mechanisms of N. capensis and E. hanseni, their vertical and ontogenetic distribution patterns were studied. Transects from the SNEC cruises were selected to illustrate the influence of contrasting phases of the upwelling cycle on the horizontal cross-shelf displacement of different developmental stages. Sampling in September 1985 was during active upwelling all along the Namibian coast (Masó and Manriquez, 1986), while more abated conditions were encountered in April 1986 (Masó, 1987) which permitted analysis of cross-shelf circulation during different upwelling situations.

6.3.1. Nearshore species, Nyctiphanes capensis.

In figure 6.5 horizontal and vertical distribution of N.capensis adults and larval stages during active upwelling is presented. More than 90% of the nauplii and larval stages were found at the innermost station (5 n. miles from the coast), while adults and juveniles were distributed within 35 miles from the coast. Nauplii, larval stages and adults were generally concentrated below 20 m depth, and thus below the expected surface Ekman layer (ca 0-20m, Brink, 1983).

During quiescent upwelling conditions (figure 6.6) N.capensis larval stages occupied a more offshore distribution than during active upwelling. However, densities were markedly reduced at the shelf-break front (35-55 n.miles from coast). Adults and juveniles remained close to the coast, with few being recorded over the shelf break at depth. Larval stages extended further over the shelf region than adults and juveniles. At the innermost station the vertical distribution of larvae and adults was similar than that observed during active upwelling conditions (figure 6.5).
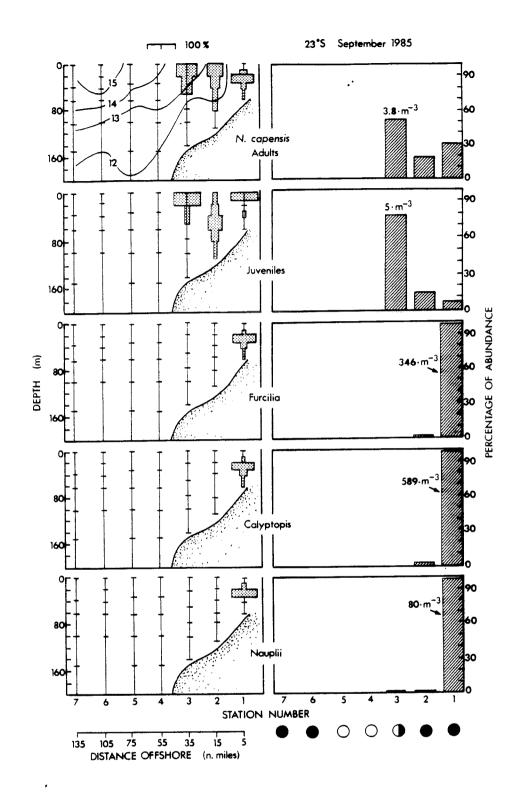
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Figure 6.5. Horizontal and vertical distribution of Nyctiphanes capensis adults and larval stages in the Walvis Bay line (23°S) in September 1985 and concomitant temperature (°C) profiles. Data are presented as percentage of the total densities. Actual densities at prominent stations are also presented. Symbols at the bottom of the right panel reflect day, night and dusk stations.

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Figure 6.6. Horizontal and vertical distribution of Nyctiphanes capensis adults and larval stages in the Möwe Point line (20°S) in April 1986 and concomitant temperature (°C) profiles. Data are presented as percentage of the total densities. Actual densities at prominent stations are also presented. Symbols at the bottom of the right panel reflect day, night and dusk stations.
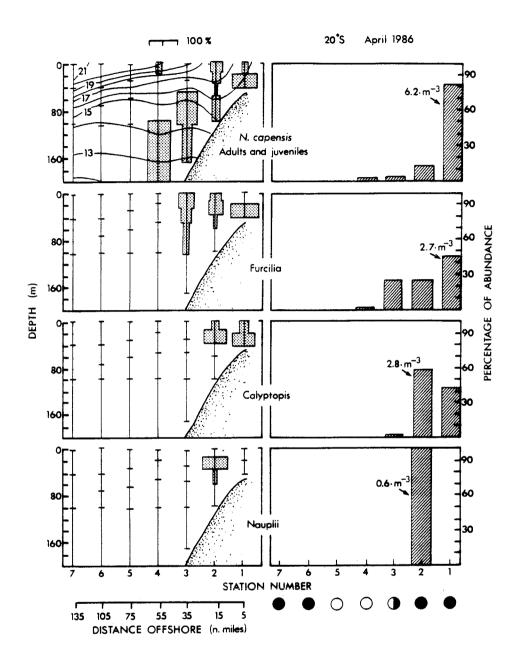
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Figure 6.7. Horizontal distribution of different stages of <u>Euphausia hanseni</u> during different phases of the upwelling cycle and concomitant temperature (°C) profiles. Left panel, active upwelling, Lüderitz line (26°S), April 1986. Right panel, quiescent upwelling, Möwe Point line (20°S), April 1986. Data are presented as percentage of the total densities. Actual densities at prominent stations are also presented. Symbols at the bottom of the right panel reflect day, night and dusk stations.
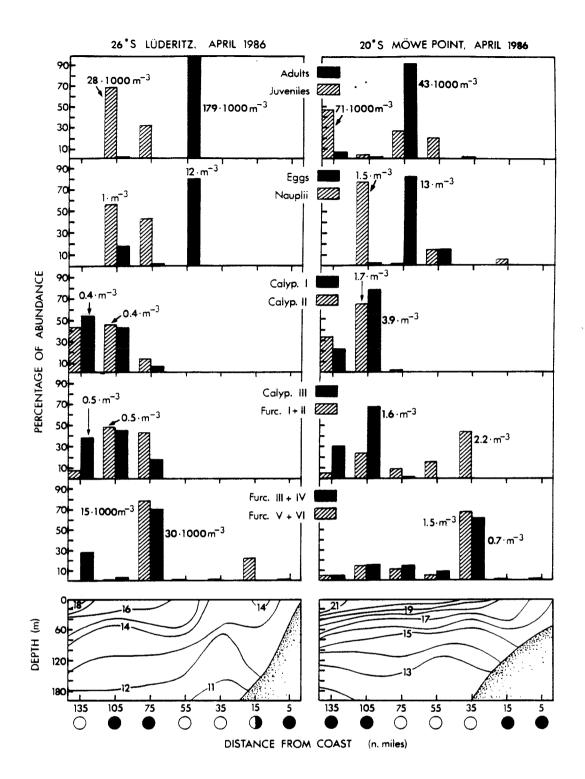
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6.3.2. Offshore group, Euphausia hanseni..

Figure 6.7 illustrates the horizontal distribution of the different developmental stages of E.hanseni along the transects during the two phases of the upwelling cycle. It is interesting to note that a secondary uplift of the temperature isolines can be observed at the shelf break (as was the case in figure 6.5). Adults and eggs were concentrated in the vicinity of the shelf-break (55 n. miles), while the nauplii peaked further offshore, at distances up to 50 miles from the adult population. Early calyptopes larvae occurred further offshore than the eggs and nauplii, suggesting offshore transport of the early larvae. Strong ontogenetic diel migratory behaviour was demonstrated for E.hanseni by Barange (1990, chapter 5), with furcilia III being the first migratory stage. Onshore displacement of furcilia larvae (especially stages FIII+IV and FV+VI) was observed which suggests that these stages may have been entrained in the onshore deep upwelling flow during the day.

During quiescent upwelling conditions eggs and adult E.hanseni were recorded over the shelf break. Nauplii and early calyptopes peaked 30 n. miles offshore than adults and larvae. Furcilia larvae showed a widespread distribution over the shelf and slope.

6.4. DISCUSSION

The evidence presented in this paper demonstrates that N.capensis and E.hanseni complete their entire life cycle within discrete zones across the shelf and slope regions. During both active and quiescent upwelling events all developmental stages of N.capensis consistently occupied the inner shelf region while E.hanseni remained and reproduced within the outer shelf and slope regions. The distribution patterns are consistent along their distributional range in the northern Benguela shelf zone where N.capensis biomass is an order of magnitude greater than that of E.hanseni (Barange

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and Stuart, 1991, chapter 4). N.capensis larvae are seldom found further offshore than 15 n. miles from the coast, which implies that during active upwelling offshore advection does not affect the distribution of these developmental stages. N.capensis appears to avoid the surface layers, and the upper limit of the vertical distribution of the metanauplii is below the Ekman layer (ca 0-20 m, Brink, 1983), which would prevent them from being advected offshore. The genus Nyctiphanes hold their developing young in brood pouches until they are liberated as metanauplii and field data has shown that the metanauplii moult into the first calyptopis stage "within a matter of hours" after being liberated (Williams and Frangopoulu, 1985). D'Arcangues (1977) found that adults and larvae of N.capensis were both concentrated in two layers, one near the surface and a second deeper. The present results suggest that by avoiding the surface layers part of the population would be able to maintain their young within the coastal zone. E.hanseni, on the other hand, release eggs in the surface layer (Barange, 1990, chapter 5) and the cross-shelf distribution observed during active upwelling (figure 6.7) shows offshore transport as a consequence of this spawning behaviour. A similar spawning strategy is adopted by E.lucens in the southern Benguela region where their eggs and early larvae are advected offshore, and tend to congregate at the thermal front which acts as a barrier to further offshore displacement (Pillar et al., 1989).

Because of the ontogenetic shift in the vertical migration pattern of E.hanseni (Barange, 1990, chapter 5), the currents acting on early larval stages would be different from those acting on the older larvae. Changes in the cross-shelf distribution of the developmental stages of E.hanseni during active and quiescent phases of the upwelling is observed as a consequence of their vertical migration pattern (figure 6.7). During active upwelling the late furcilia stages, which migrate extensively (Barange, 1990, chapter 5), experienced less cross-shelf dispersal than the less migratory younger larvae. These deeper dwelling larval stages would

thus be more susceptible to onshore drift during the quiescent phase as evidenced in figure 6.7.

The existence of two abundant euphausiid species in the northern Benguela, one occurring over the shelf and the other occupying neritic areas, suggests different processes governing dispersal in these regions relative to the southern Benguela where a single species, E.lucens, occupies both habitats. The maintenance mechanisms proposed for E.lucens by Pillar et al. (1989) are based on a one-celled circulation model in an area characterised by a narrow shelf. This circulation model, however, does not explain the observed cross-shelf patterns of N.capensis and E.hanseni in the northern Benguela. The observed uplift of isolines near the shelf-break (figures 6.5 and 6.7), implies that a topographically induced secondary upwelling at the shelf-break may exist. Nelson and Hutchings (1983) considered that north of Cape Columbine (32°S) upwelling takes place both in a narrow coastal strip and at the shelf-break and that frontal features become less definite. Although the presence of such features in the northern Benguela is still in debate, several authors have argued in favour of shelf-break upwelling. Hart and Currie (1960) proposed a two-cell structure over a wide continental shelf, with inshore and shelf-break upwelling and sinking inshore of the shelf-break front. Strong shelf-break upwelling was detected by Latun (1962). Bang (1971) observed wave like features over the shelf and shelf-break, forming what he called an offshore divergence belt between 31-34°S. An "S" shaped band of elevated chlorophyll was suggested to be associated with a semi-permanent shelf-break divergence zone by Shannon et al. (1984). The broad shelf in the area 20°-32°S (figure 6.8) could develop secondary upwelling at the shelf-break, as opposed to upwelling in inshore areas only north and south (figure 6.8) of that area (Hutchings et al., 1986), where the shelf is narrow and steep.

A cross-shelf circulation model based on a two-celled structure is
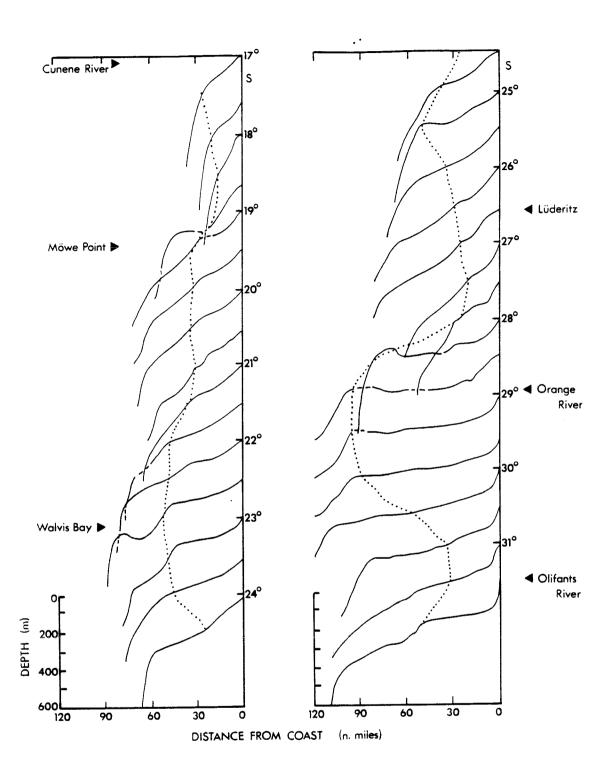
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Figure 6.8. Bathymetric sections of the southern African shelf between 17°S and 31°30'S (redrawn from Boyd, 1987). Dotted line indicates the 200 m isobath.

presented in figure 6.9. Upwelling off Namibia is perennial with a spring-summer maximum and autumn minimum.as far north as 25°S and a late winter-spring maximum and summer minimum north of this latitude (Hart and Currie, 1960; Stander, 1964; Parrish et al., 1983; Nelson and Hutchings, 1983; Shannon, 1985a). The model depicted is not intended to be valid for the whole Namibian coastline, but rather to provide a model to support and explain the distribution patterns presented in this study. Active upwelling conditions are characterized by advection near the coast and over the shelf-break with offshore flow in both cells following the isolines of the frontal area. A strong jet-like equatorward current over the shelf break, such as has been observed in the southern Benguela (Bang and Andrews, 1974; Shannon, 1985a) could explain the marked cross-shelf segregation between N.capensis and E.hanseni (figures 6.2 and 6.3). Recent data suggest that this jet in the southern Benguela may be active throughout the water column at a core speed of up to 40 cm.s^{-1} (G. Nelson, SFRI, pers. comm. 1990). The existence of such a current would effectively act as a major barrier to the cross-shelf displacement of shelf and slope zooplankton populations. Shelf-break upwelled water, whose upwelling may be originated from instabilities in the jet current, may not reach the surface, but rather become trapped by the subsurface onshore flow and become weakened. This feature has been observed in Northwest Africa by Huntsman and Barber (1977). A third frontal zone (oceanic front) is proposed as a consequence of strong temperature gradients observed between 100-140 miles from the coast. Bailey (1979) found that the upwelling events off Lüderitz, the most powerful upwelling centre in the area, are of long duration (>2 weeks) and suggested that during prolonged periods both upwelling cells may merge. As wind stress decreases cross-shelf currents would be weak and directed onshore near the surface, becoming weak and adirectional during relaxed upwelling (as in Hutchings et al., 1986).

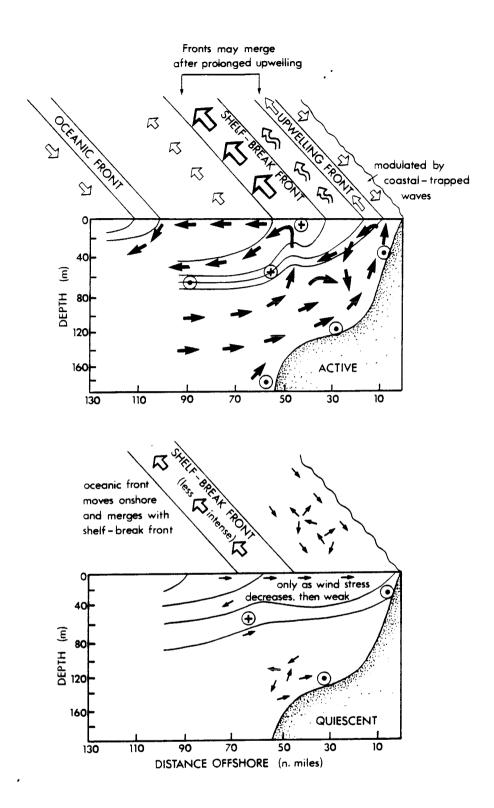Alongshore currents may play a significant role in maintaining the

Figure 6.9. A conceptual three-dimensional model of cross-shelf circulation during active and quiescent upwelling in the northern Benguela upwelling area.

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horizontal segregation of N.capensis and E.hanseni during periods of relaxed upwelling or when both upwelling and shelf-break fronts merge after intense and prolonged upwelling. A poleward undercurrent is present all along the west coast of southern Africa (Hart and Currie, 1960; De Decker, 1970; Bailey, 1979; Nelson,1989) and such features have been observed in the northern Benguela shelf region at 50-100 m depth (Bailey, 1979). The strong, alongshore, jet-like equatorward current may be a compensation for the poleward undercurrent (Shannon, 1985a). These currents over the shelf and shelf-break probably transport zooplankton populations north when living in surface or mid-depth layers, and south when residing near the sea-bed, thus acting as a major dispersal mechanism of zooplankton components along the Benguela area.

During active upwelling the nearshore cell of the circulation scheme is characterized by offshore advection of surface water causing cold water to well up in replacement. Seaward transport of surface-dwelling early larval stages of N.capensis would be influenced by the upwelling front where, by sinking and following isopycnals at depth, would be able to return to the inshore zone. This shoreward transport mechanism would govern the distribution of deeper-dwelling late developmental stages of N.capensis. During the quiescent phase of upwelling there is a net shoreward surface flow with an offshore drift at depth. This mechanism would account for the more widespread distribution observed for N.capensis during the quiescent phase compared to the patterns observed during upwelling phase.

The proposed offshore cell requires a mechanism whereby, by spawning at the shelf-break, E.hanseni can remain and develop in the offshore region. Eggs are laid in surface layers and, unlike true oceanic euphausiid species, the developmental cycle from egg to the beginning of the adolescence takes place within the upper layers of the water column (Barange, 1990, chapter 5). This

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spawning behaviour would result in nauplii and early larvae being displaced offshore, and the extent of this transport would be dictated by the oceanic front. Downward migration of maturing individuals would reduce advective losses from the population, and the increased inshore flow at depth, resulting from secondary upwelling, would facilitate their return to the vicinity of the shelf-break front.

As a result of the interaction of biological processes, especially ontogenetic vertical migration, with the physical features and processes during active and quiescent upwelling, N.capensis and E.hanseni have different probabilities of cross-shelf and alongshore transport. It is concluded that the proposed two-cell circulation model seems the most likely mechanism whereby these species can remain spatially segregated and develop high concentrations within the northern Benguela upwelling system.