Vertical distribution and diel vertical migration of *Calanoides carinatus* (Krøyer, 1849) developmental stages in the southern Benguela upwelling region

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**Abstract:** Diel vertical distribution patterns of the copepodite and adult stages of *Calanoides carinatus* were analysed using a 10-day time series of observations under contrasting upwelling conditions at an Anchor Station in St Helena Bay, South Africa. The diel vertical migratory behaviour of *C. carinatus* is probably controlled by both exogenous and endogenous factors. Changes in the food assemblage associated with upwelling significantly modified the vertical distribution and migration of *C. carinatus* from nonmigratory behaviour under nonsatiating feeding conditions (microflagellates) to marked diel vertical migrations in an upwelling-induced, improved feeding environment (small diatoms). Intrinsic factors such as age, sex and state of ovary maturity also play an important role in the vertical habitat partitioning of *C. carinatus* in St Helena Bay. Such differential migratory strategies are believed to be adaptations for optimal food utilisation and population maintenance through age-specific depth partitioning. Other adaptive advantages are maximization of reproductive success by copulating at depth at night, and rapid egg development and maximal survival of the first-feeding nauplii by spawning near the surface.

**Key words:** *Calanoides carinatus*; Diel vertical migration; Food availability; Female maturity; Ontogenetic; Sexual differentiation

**INTRODUCTION**

Many zooplankters undergo vertical movements whereby the animals usually occupy greater depths during daytime and ascend into near-surface waters at night. Such diel migrations thus allow zooplankters to regulate their spatial and temporal distribution to some extent. A wide array of physico-chemical and biological environmental parameters as well as endogenous and intrinsic factors influence vertical migrations (Hutchinson, 1967; Kerfoot, 1980; Rankin, 1985; Bayly, 1986; Forward, 1988). This diel migration behaviour, which is characteristic of many coastal calanoid copepods, has been explained in many ways (see Longhurst, 1976; Enright, 1977; Forward, 1988; Longhurst & Harrison, 1989, for general reviews). It would seem that diel vertical
movements are a function of food utilization (e.g., Vidal, 1980; Huntley & Brooks, 1982) with the light cycle as a synchronizer (Pearre, 1979), and a strategy of avoiding visual predators (e.g., Zaret & Suffern, 1976; Ohman, 1990). In upwelling areas where offshore transport of surface waters prevails, vertical migration and ontogenetic layering have been explained as mechanisms of maintaining large zooplankton populations within the relatively narrow, productive coastal zone (e.g., Binet & Suisse de Sainte Claire, 1975; Peterson et al., 1979; Pillar et al., 1989; Verheye et al., 1991).

During a 27-day Anchor Station time series study in March–April 1987 in the southern Benguela upwelling region, Verheye (1991) observed distinct ontogenetic layering of the dominant copepod *Calanoides carinatus* during daylight hours. The present study is aimed at providing evidence of diel fluctuations in this vertical distribution pattern and examining differences in migratory behaviour among developmental stages. If diel movements of zooplankton are primarily mediated by hunger (e.g., Pearre, 1979; Huntley & Brooks, 1982), then feeding behaviour is expected to be somehow reflected in migratory behaviour. Also, since differential cross-shelf distribution of *C. carinatus* life cycle stages has been observed under different phases of the upwelling cycle in the southern Benguela region (Verheye, 1989; Verheye et al., 1991), significant differences in migration behaviour are likely to exist between stages. To test these hypotheses, day and night vertical distribution patterns of juvenile and adult *C. carinatus* were analysed using data collected during the last 10 days of the Anchor Station study, when upwelling-related processes caused major changes in the copepod's potential feeding environment (Mitchell-Innes & Walker, 1991; Pitcher et al., 1991; Armstrong et al., 1991).

**MATERIALS AND METHODS**

Details on the position of the Anchor Station study site (32° 33' 2" S, 18° 05' 3" E) in St Helena Bay (Fig. 1) and its physico–chemical conditions during the study are described by Bailey & Chapman (1991). Zooplankton samples were collected twice daily at 1200 and 2000 SAST (1000 and 1800 GMT) from 6 to 15 April 1987 with a plankton pump and a 7.6-cm inner diameter hose. Depth and temperature at the suction end were monitored with an electronic bathythermograph. 2.5-m³ samples were pumped from five or six discrete depths between the surface and 45 m in a 47-m water column. Pump flow rate was 0.25 m³·min⁻¹. Approximately twice the dead volume of the pumping system was flushed through before filtration onto a 200-μm Nitex mesh commenced at a particular depth. In addition, 20-l water samples were collected from the filtrate onto a 37-μm Nitex screen for enumeration of *Calanoides carinatus* eggs. From nighttime on 12 April until and including nighttime of the following day, when the pump failed to operate, samples were collected using a Magnum Rosette sampler of six 20-l bottles. Sampling procedure, sample processing and enumeration techniques used for the evaluation of stage abundance of *C. carinatus* are described by Verheye (1991).
Among the adults, males (M), ripe (F_r), unripe (F_u), and spermatophore-bearing females (F_{sp}) were distinguished in the counts. In this study, "unripe" and "ripe" females refer, respectively, to the categories ("immature" + "medium" + "spent") and ("semi-ripe" + "ripe") described for *Calanus finmarchicus* by Marshall & Orr (1972). Abundances of *C. carinatus* eggs were evaluated from replicate subsampling of the > 200-μm samples and analysis of the entire 37–200-μm samples.
Daily variations in the surface temperature, recorded during pump sampling, and in a stratification index, calculated as the vertical density gradient over the upper 30 m, were used as indicators of upwelling and associated processes.

Interpretation of diel vertical migration of C. carinatus was based on differences in the day and night weighed mean depth (WMD) of the life cycle stages. The WMD was calculated according to Roe et al. (1984):

\[
WMD = \frac{\sum (n_i \cdot z_i)}{\sum n_i},
\]

where \( n_i \) is abundance (\( n \cdot m^{-3} \)) of animals at depth \( z_i \).

**Results**

**Environmental Conditions**

Upwelling-favourable southerly winds were experienced at the Cape Columbine upwelling centre to the south-west of the Anchor Station (Fig. 1), advecting cold recently upwelled surface water to the study site on 10–11 and 14–15 April (Bailey & Chapman, 1991). The first advection event was preceded by a period of relaxation, with a well-stratified water column. Surface temperature during that period was in excess of 16 °C (Fig. 2a) and the stratification index was high, > 0.040 σ-t units · m⁻¹ (Fig. 2b). Increased mixing accompanied the advection of recently upwelled water on 10–11 April, as indicated by a sudden drop in both the surface temperature to 15.2 °C (Fig. 2a) and the stratification index to 0.037 σ-t units · m⁻¹ (Fig. 2b). Surface temperature and stratification index then gradually decreased until the second advection event on 14 April when they declined sharply again, reaching their lowest values of 13.1 °C and 0.022 σ-t units · m⁻¹, respectively, on 15 April (Fig. 2a,b). A thick well-mixed bottom layer of 9.5 °C was present throughout the study, while increasing levels of inorganic nutrients were noted during the advection period (Bailey & Chapman, 1991).

The temporal variability of the phytoplankton parameters has been described by Mitchell-Innes & Walker (1991) and Pitcher et al. (1991) and is schematically summarized in Fig. 3. During the relaxation period, surface Chl a concentrations were low (< 2 mg · m⁻³) but increased rapidly with the advection of newly upwelled water on 10 April, reaching highest values of > 15 mg · m⁻³ on 13 April (Fig. 3a). The phytoplankton community was initially composed of high microflagellate concentrations in the near-surface layers while a decaying Coscinodiscus gigas bloom was evident at 30–40 m depth (Fig. 3b), coincident with a subsurface chlorophyll maximum (Fig. 3a). Following the influx of cool upwelled water, this community was replaced by high concentrations of small diatoms (Fig. 3b), characteristic of cold, well-mixed surface waters. Productivity indices \( (P : B) \) were low (< 2 mg C · Chl⁻¹ · h⁻¹) in the subsurface chlorophyll maximum layer associated with the decaying C. gigas bloom (Fig. 3c). In contrast,
vertical migration of calanoides stages

Fig. 2. Time series of (a) surface temperature and (b) a stratification index calculated as vertical density gradient over upper 30 m, during 6–15 April 1987 at Anchor Station in St Helena Bay. Black horizontal bar indicates period of advection.

substantially higher $P:B$ ratios ($> 6$ mg C : Chl$^{-1} \cdot$ h$^{-1}$) were evident in the upper layers throughout the study period, rising slightly during the small diatom bloom (Fig. 3c).

abundance and vertical distribution of C. carinatus

Mean abundances of the life cycle stages of $C$. carinatus were calculated for the period prior to the first introduction of recently upwelled water into the study area (i.e., relaxation period) and after that event (i.e., advection period), and differences between the two periods were tested using a Mann–Whitney $U$ test (Zar, 1984) (Table I). A
Fig. 3. Vertical sections of daily variation in: (a) Chl a; (b) major phytoplankton groups and their dominant taxa; and (c) phytoplankton P : B values during study period (after Mitchell-Innes & Walker, 1991; Pitcher et al., 1991). Black bars as in Fig. 2.
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Mean abundance \((n \cdot m^{-2})\) of life cycle stages of \(C.\ carinatus\) during relaxation period (6 April to 10 April, (day) and advection period (10 April, night to 15 April at Anchor Station in St Helena Bay. M, males; F, females; F\(_r\), ripe females; F\(_u\), unripe females; F\(_sp\), spermatophore-bearing females. Results of Mann-Whitney \(U\) test are also given: *, significant \((P < 0.05)\); NS, not significant \((P > 0.05)\).

<table>
<thead>
<tr>
<th>Stage</th>
<th>Relaxation period ((n = 8))</th>
<th>Advection period ((n = 10))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total population</td>
<td>35 735.4</td>
<td>15 084.0 *</td>
</tr>
<tr>
<td>C1</td>
<td>2424.1</td>
<td>293.2</td>
</tr>
<tr>
<td>C2</td>
<td>5485.3</td>
<td>1687.6 *</td>
</tr>
<tr>
<td>C3</td>
<td>4077.8</td>
<td>1294.9 *</td>
</tr>
<tr>
<td>C4</td>
<td>8438.1</td>
<td>1640.1 *</td>
</tr>
<tr>
<td>C5</td>
<td>10 980.8</td>
<td>2508.5 *</td>
</tr>
<tr>
<td>Adults</td>
<td>4329.3</td>
<td>7659.7 NS</td>
</tr>
<tr>
<td>M</td>
<td>766.3</td>
<td>726.6 NS</td>
</tr>
<tr>
<td>F(_{\text{total}})</td>
<td>3563.0</td>
<td>6933.1 NS</td>
</tr>
<tr>
<td>F(_r)</td>
<td>478.1</td>
<td>2251.2 *</td>
</tr>
<tr>
<td>F(_u)</td>
<td>2980.6</td>
<td>4514.1 NS</td>
</tr>
<tr>
<td>F(_{sp})</td>
<td>104.3</td>
<td>167.8 NS</td>
</tr>
</tbody>
</table>

significant reduction in population size due to significant decreases in abundance of all copepodites was evident during the advection period. Adults, however, increased in abundance, particularly ripe females which showed a significant, five-fold increase in their numbers after 10 April.

Diel changes in the abundance of \(C.\ carinatus\) life cycle stages during the study period were evident and were tested using the Mann–Whitney \(U\) test (Table II). Significantly more individuals were caught at night than during daytime, owing to a significant increase at night of females. This can be attributed to their migrating downward to near

<table>
<thead>
<tr>
<th>Stage</th>
<th>Daytime ((n = 9))</th>
<th>Nighttime ((n = 9))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total population</td>
<td>17 260.3</td>
<td>31 264.6 *</td>
</tr>
<tr>
<td>C1</td>
<td>842.8</td>
<td>1637.8 NS</td>
</tr>
<tr>
<td>C2</td>
<td>2451.5</td>
<td>4299.4 NS</td>
</tr>
<tr>
<td>C3</td>
<td>1909.6</td>
<td>3153.9 NS</td>
</tr>
<tr>
<td>C4</td>
<td>4067.1</td>
<td>5255.8 NS</td>
</tr>
<tr>
<td>C5</td>
<td>4483.1</td>
<td>8064.7 NS</td>
</tr>
<tr>
<td>Adults</td>
<td>3506.1</td>
<td>8853.0 *</td>
</tr>
<tr>
<td>M</td>
<td>571.8</td>
<td>916.7 NS</td>
</tr>
<tr>
<td>F(_{\text{total}})</td>
<td>2934.3</td>
<td>7936.3 *</td>
</tr>
<tr>
<td>F(_r)</td>
<td>660.4</td>
<td>2265.9 *</td>
</tr>
<tr>
<td>F(_u)</td>
<td>2211.3</td>
<td>5453.8 *</td>
</tr>
<tr>
<td>F(_{sp})</td>
<td>62.7</td>
<td>216.6 *</td>
</tr>
</tbody>
</table>
Fig. 4. Diel variations in abundance ($n \cdot m^{-3}$) and vertical distribution of *C. carinatus* copepodite stage (a) CI, (b) CII, (c) CIII, (d) CIV, (e) CV, and (f) adults (males and females pooled) during study period. *WMD* s occupied by animal are also plotted (broken lines). Black bars as in Fig. 2.
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Fig. 4.
the bottom during the day, beyond the normal sampling depth of the pump, as suggested by the presence of large numbers of females near the bottom, e.g., on 13 and 15 April (see Fig. 4f). However, avoidance responses to the pump system during daytime sampling may also be important with regard to diel variation in the catches (see Pillar, 1984).

Fig. 5. Daytime and nighttime WMDs for each developmental stage of C. carinatus during (a) relaxation period (6–9 April) and (b) advection period (10–15 April) at Anchor Station in St Helena Bay. M, males; F, females; F$_s$, ripe females; F$_u$, unripe females; F$_s$, spermatophore-bearing females. Values shown are overall means for each period, error bars are 95% CI. Time (h) is SAST.
Time series of the diel vertical distribution of juvenile and adult *C. carinatus* are shown in Fig. 4. Also plotted are the *WMDs* of the stages at each sampling time. Distinct ontogenetic layering was evident day and night, and the animals occupied shallower depths at night than during the day. As the stages were older, they exploited a wider depth range in the water column during the day–night cycle. Of particular interest, however, is the sudden proliferation in migration range of all stages after the advection of recently upwelled water on 10 April, as indicated by the increased amplitude of the oscillating *WMDs* in Fig. 4 (a–f).

To examine differences in vertical migratory behaviour of *C. carinatus* between the relaxation and advection periods, the daytime and the nighttime *WMDs* of each stage were, respectively, pooled for the periods 6–9 and 10–15 April and their $\bar{x}$ and 95% CL values calculated (Fig. 5). During the relaxation period (Fig. 5a), there was no evidence of marked diel vertical migration in the copepodite stages, their centre of abundance remaining within the upper 15 m. However, considerable day–night differences existed in the *WMD* of adults, but not in that of ripe and spermatophore-bearing females. Adults were also found to occur markedly deeper than juveniles, both during day and night. Females tended to be distributed deeper than males during daytime but not at night.

![Fig. 6](image-url)

**Fig. 6.** Mean amplitudes of vertical migration calculated for each developmental stage of *C. carinatus* during relaxation period (6–9 April) and advection period (10–15 April). Abbreviations as in Fig. 5. Error bars are 95% CL.
when both sexes were concentrated at $\approx 15$ m. During the advection period, pronounced diel vertical migration was evident, and all but the males and spermatophore-bearing females showed considerable day–night differences in their $WMD$ (Fig. 5b). With the exception of copepodite stage C1 all life cycle stages of $C.\ carinatus$ migrated below 15 m during the day and ascended into the upper 15 m at night. Only males and spermatophore-bearing females remained below the 20-m depth day and night.

Nocturnal $WMD$ values of each $C.\ carinatus$ stage were much the same during both periods but daytime $WMD$s were considerably greater during the advection period than during the relaxation period. The mean migration amplitude of each stage, calculated from the difference between day and night $WMD$s of consecutive samplings, increased with age during both periods (Fig. 6). Mean migration amplitudes ranged from 2 (C1) to 9.5 m (adults) during relaxation, and from 7 (C1) to 18.5 m (adults) during the advection period. Of the adult population ripe females migrated most extensively, particularly during the advection period when their mean migration amplitude was 24.3 m. Males and spermatophore-bearing females showed comparatively little evidence of extensive diel vertical movements, irrespective of the state of the environment.

**Discussion**

Marked differences were evident in the diel vertical migration (DVM) patterns of $C.\ carinatus$, both among the developmental stages and between the periods of contrasting environmental conditions. It is highly unlikely that a single ultimate cause exists for the phenomenon of vertical migration in zooplankton. Therefore, it has often been suggested in the literature that there is a trade-off between several factors counteracting one another (e.g., Harding et al., 1986; Vuorinen, 1987). Both external and intrinsic factors can be distinguished as being responsible for the observed differences in migratory behaviour of $C.\ carinatus$.

**Exogenous Factors**

If DVMs are primarily feeding migrations, then these movements are implicitly expected to mirror the state of feeding of migrant zooplankters. Assuming that light conditions and the exposure to predators (with reduced predation risk at night) were consistent throughout the study, our results suggest that food limitation played a fundamental role in controlling DVM of $C.\ carinatus$. Migrations were extensive during the advection period when food (Chl $a$) was plentiful near the surface, but DVM was suppressed at low surface chl levels during the relaxation period. Changes in food availability have been suggested to mediate vertical migration of zooplankton (Pearre, 1979; Huntley & Brooks, 1982; Dagg, 1985; Lampert, 1989). Satiation is reached during all-night foraging in food-rich surface waters so that negative stimuli such as increased light intensity (Forward, 1988) or the presence of visual predators (e.g., Zaret
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& Suffern, 1976) induce daytime descent. Conversely, at low food densities the animals need to spend more time in the surface layer to reach satiation, thus "instinctively" trading off food intake against predation risk (Huntley & Brooks, 1982; Johnsen & Jakobsen, 1987).

Our study indicates that, despite the presence of a potential subsurface food maximum (= Coscinodiscus gigas bloom) during the relaxation period, C. carinatus stages appeared to avoid it day and night (Fig. 3a). This is in contrast with observations by Scrope-Howe & Jones (1986) who noted that, when discrete subsurface chlorophyll maxima (SCM) form, DVM ceases and the grazers aggregate within these food maxima. Other studies have shown, however, that there is no consistent relationship between food availability and DVM (see Forward, 1988). As Mullin & Brooks (1976) emphasized, phytoplankton should not be regarded as a single functional element of the ecosystem with a homogeneous size composition. Many grazers are capable of differential particle selection from mixtures (e.g., Paffenhofer & Van Sant, 1985), selecting for the largest available cells (e.g., Frost, 1977). However, the size of C. gigas cells (200–300 μm diameter, 40 μm height) is well above the optimum range (2–5% of prosome length; Berggreen et al., 1988) for particle capture by C. carinatus stages (prosome length = 614 μm [CI], 2041 μm [adult female]; Verheye, 1991). Also, the C. gigas bloom was in a state of senescence and decay (Mitchell-Innes & Walker, 1991) and thus not likely to be palatable. Alternatively, it seems paradoxical that during this period C. carinatus aggregated in the chlorophyll-poor near-surface layer. However, Napp et al. (1988) draw attention to the importance of the location in the water column of the most nutritious plant cells. They suggested that, if nutritional value is a function of growth rate, then phytoplankton growth rate, or P: B, is a better indicator of nutritional value than primary production or biomass. Ingestion rates of copepods such as A. tonsa (Kiorboe, 1989) and C. carinatus (Peterson, unpubl. data) have been found to be positively correlated with phytoplankton growth rate. So it is not surprising to find C. carinatus stages aggregating near the surface where phytoplankton P: B rate, hence nutritional value, was higher than at subsurface levels. Since this near-surface food assemblage was dominated by <6-μm microflagellates (Pitcher et al., 1991), which are of suboptimum size for particle capture by C. carinatus stages (see Berggreen et al., 1988), the animals required more foraging time before reaching satiation.

In contrast to the relaxation period, C. carinatus exhibited extensive DVM during the advection period. This indicates that the characteristics of the near-surface food environment, viz., higher phytoplankton biomass, increased nutritional value (P: B) and nearer-optimum cell size, favoured optimal feeding conditions for the copepods. In a natural Daphnia longispina population, Johnsen & Jakobsen (1987) experimentally demonstrated that the introduction of ingestion-rate saturating food levels caused a change from a nonmigratory behaviour (under food-depleted conditions) to diel vertical migrations. The improvement of feeding conditions during our study not only affected the copepod’s DVM behaviour, but was also mirrored in its population dynamics, as evidenced by the appearance of increased numbers of ripe females (Table I) and their enhanced reproductive output (Armstrong et al., 1991).
ENDOGENOUS FACTORS

With respect to the stage-specific DVM of *C. carinatus*, the data are in agreement with the general observations that migration amplitude increases with age, as has been discussed by Huntley & Brooks (1982). Sekiguchi (1977; cited in Davis, 1984) contended that ontogenetic migrations are characteristic of herbivorous cold-water species, in which the young gain advantage by remaining in the food-rich upper layers of the water column. One such benefit would be of a metabolic nature, i.e., early copepodites optimize individual growth rate and food utilisation at higher (i.e., near-surface) temperatures, whereas older stages are likely to do so only in colder (i.e., subsurface) environments (Vidal, 1980). One of the consequences of such ontogenetically based differential behaviour is that it may serve as a mechanism of maintaining zooplankton populations within areas to which they are specially adapted (Bayly, 1986), e.g., upwelling regions (Pillar et al., 1989; Verheye et al., 1991). With the advection of upwelled water on 10 April, differential exploitation of different depth strata by copepodite and adult *C. carinatus* possibly resulted in offshore Ekman transport of surface-dwelling copepodites, reducing their numbers (Table I). In contrast, since adults occupied greater daytime depths, they spent comparatively less time in the Ekman layer and thus largely avoided surface transport. In fact, their numbers increased (Table II), possibly owing to re-seeding of the near-shore stock with deep-living individuals in the upwelled water (Verheye, 1991; Verheye et al., 1991).

Results of this study suggest sexual differentiation of DVM of *C. carinatus*, with more extensive migration amplitudes of females than males which remained at depth. These observations corroborate earlier reports on DVM of this species in the northern (Coetzee, 1974) and southern Benguela regions (Hutchings, 1985), as well as off West Africa (Binet & Suisse de Sainte Claire, 1975). Similar sexually differentiated DVM has also been observed in other calanoid copepods, e.g., *Calanus finmarchicus* (Nicholls, 1933; Marshall & Orr, 1960) and *C. helgolandicus* (Williams & Conway, 1984), and may result from differential photosensitivity with males being more reactive to light than females (Forward, 1976; Moore & Sander, 1983). Also, as in many species, adult male *C. carinatus* have rudimentary mouthparts (Schnack, 1982), hence feeding in males is likely to be weak or inefficient. As a consequence, males would benefit bioenergetically by remaining at greater depths throughout the diel cycle without performing extensive vertical movements.

The significantly higher incidence of spermatophore-bearing female *C. carinatus* at night than during the day (Table II), their persistent residence at depth (Fig. 5) and the lack of their migrating extensively (Fig. 6) may suggest that copulation occurs at depth during nighttime. Surprisingly little is known about the mating behaviour of copepods (e.g., Blades, 1977; Blades & Youngbluth, 1979, 1980). Fertilisation usually occurs shortly after the imaginal moult and Marshall & Orr (1972) found that female *Calanus finmarchicus* usually lost their spermatophore with 24 h. One benefit to nocturnal mating behaviour at depth would be that copulating pairs are less conspicuous for visual
predators. Certainly, further investigations are needed to elucidate the adaptive significance of such behaviour, and its effect on diel migration.

Female *C. carinatus* were segregated with depth depending on the state of ovary maturity. Ripe females tended to migrate more extensively into shallower depth strata at night than immature and spent females, particularly during the advection period (Fig. 5b). Marshall & Orr (1960, 1972) found a positive relationship between DVM and the degree of ripeness of female *Calanus finmarchicus*. Ripe females ascended earlier and more extensively, and remained closer to the surface than immature females. This tendency may be expected if DVMs are spawning migrations. In our study, WMDs of *C. carinatus* eggs varied between 3 and 7.1 m at night and between 5.2 and 17.5 m during daytime (Fig. 7). Since peak spawning in *C. carinatus* occurs at night (Armstrong et al., 1991), the greater daytime WMDs of eggs in our study are likely to result from sinking of eggs spawned near the surface at night. The adaptive value of nocturnal spawning in near-surface waters would be speeding up of the rate of egg development at higher ambient temperatures which prevail in surface waters. Also, since naupliar stage NI is the first-feeding stage in *C. carinatus* (Borchers & Hutchings, 1986), spawning in the food-rich upper layers of the water column would ensure sufficient food for the swimming nauplii upon hatching.

The observed patterns of vertical distribution and migratory behaviour of *C. carinatus* reflect the copepod’s ability to rapidly respond to fluctuations in its environment. Their ability to regulate their vertical distribution according to foraging opportunities and through age-, sex- and maturity-dependent nonmigrating and migrating patterns confers
several adaptive advantages. These are population maintenance, optimal food utilization, energy conservation, reduction of encounters with predators, promotion of mating behaviour and ensuring rapid egg development. Such behavioural strategies are ultimately aimed at successful proliferation and survival of the species in this very dynamic upwelling system.

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