

## Mechanisms for emergence from diapause of *Calanoides carinatus* in the Somali current

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### Abstract

We studied mechanisms that might control the emergence of the last juvenile stage of *Calanoides carinatus* from diapause in the Arabian Sea. Diapaused copepods are modeled as Lagrangian particles that include a simplified means for lipid catabolism during diapause. The advective field for the particles, which are released at intermediate and deep layers off the Somali shelf, is determined by a regional version of the Miami isopycnic coordinate model (MICOM). Dormant copepods emerge from diapause in response to either onshore advection (physical upwelling) or depletion of lipid reserves to an assumed critical level (internal biological clock). The majority of the diapaused copepods that successfully complete their life cycle are those retained within the coastal upwelling zone and emerge as a consequence of depletion of the lipid reserves.

Calanoid copepods, with life history strategies that include arrested development (diapause) in late juvenile stages, are observed to drift for a period of time in deep ocean currents. It is generally believed that the mechanism controlling diapause is a combination of internal cues in the form of a timing mechanism, such as endocrine titer levels or critical lipid content, and external cues such as a shift in the light environment (Miller et al. 1991; Hirche 1996). Miller et al. (1991) speculated that light intensity (or possibly daylength) is the critical factor that determines emergence of copepods from diapause. These authors suggested that increased light intensity triggered by physical uplift of the diapausing copepods onto the continental shelf is the primary mechanism terminating diapause in *Calanoides carinatus* off the east and west coasts of Africa.

In this study we use a regional ocean circulation model to demonstrate that the physical mechanism of coastal upwelling can transport individuals from as deep as 1,000 m to shallower depths, thereby allowing exposure to light intensities that may stimulate the termination of diapause. But this external stimulus is superposed upon a presumed internal mechanism: the depletion of lipid reserves that forces the termination of diapause due to the necessity for reproduction from the remaining lipid reserve (gamete production) and the disruption of neutral buoyancy at depth caused by the replacement of wax esters in the body with water (Sargent and Henderson 1986). The extent to which upwelling and lipid depletion contribute to the termination of

diapause has not been documented. It is clear that the diapause mode allows individuals to avoid periods of suboptimal (no food, high temperatures) surface conditions, perhaps to emerge at a later time when environmental conditions are more favorable for growth and reproduction. The combined mechanisms enhance success in variable environments by spreading the emergence period over the span of several months.

### Study area and life history of *Calanoides carinatus*

The Arabian Sea is forced by a unique climatic regime driven by a reversing monsoonal wind system (Smith 1992). Off the coast of Somalia, *Calanoides carinatus* exhibits a life cycle that includes a diapause phase in the last juvenile stage, i.e., fifth copepodite stage (CV) during the winter months. This period is characterized by warm surface waters and low food availability in the Arabian Sea (Fig. 1A,C). During these winter months, known as the Northeast Monsoon (December to February), the prevailing winds are from the northeast, forcing the surface currents of the Arabian Sea to flow to the southwest, causing downwelling along the coasts of the southern Arabian Peninsula and the Horn of Africa (Fig. 1A,C). Active populations that include all developmental stages of *C. carinatus* colonize the surface waters during the summer upwelling season (Southwest Monsoon), which extends from late May into September. During the Southwest Monsoon, alongshore low-level winds known as the Findlater Jet blow from the southwest, forcing eddies and offshore currents at the surface and an upwelling of deep, cold waters rich in nutrients near shore (Fig. 1B,D). At the end of summer, *C. carinatus* CV individuals enter diapause and sink to depths below 200 m until some later period, thus completing the annual life cycle. If the match of the timing of lipid reserve depletion (the intrinsic clock we propose) and the subsequent monsoonal upwelling coincide, then reproduction and growth will be favored.

The vertical distribution of *C. carinatus* CV observed in the Arabian Sea during an annual cycle clearly shows the seasonal ontogenetic migration pattern of summer activity

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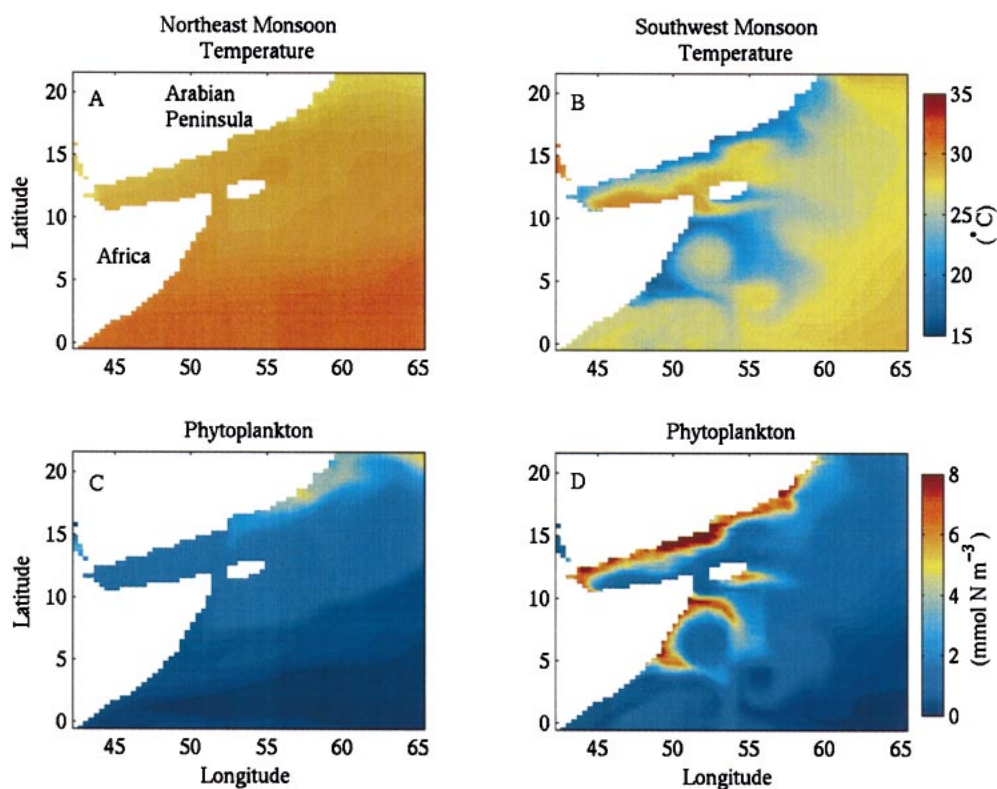


Fig. 1. Seasonal surface fields of temperature and phytoplankton concentrations from the bio-physical model, NPZD-MICOM, during the Northeast Monsoon and the Southwest Monsoon. (A, B) Temperature and (C, D) phytoplankton concentration in the Arabian Sea.

near the surface and winter diapause at depth (Smith et al. 1998; Smith 2001). The majority of individuals off Oman and Somalia usually are found in the surface waters from June to September, but could migrate downward as early as July. From December to April, most of the population that consists of the CV stage was below 400 m when surface temperatures were above 27°C (figure 4 in Smith 2001). In this study, we focus on the deep oceanic transport properties affecting the calanoid copepod *Calanoides carinatus* during the diapause period.

### Model development

To simulate transport of passive individuals in a state of diapause, we used the Miami isopycnic coordinate ocean model (MICOM; Bleck et al. 1989), configured for the Arabian Sea (Esenkov and Olson 2002). For our simulations, MICOM was coupled to a nutrient–phytoplankton–zooplankton–detritus (NPZD) model to create a water column light field with realistic light extinction (Olascoaga et al. in press). The Lagrangian particles were tracked over space and time as they were advected using MICOM isopycnal velocities (Garraffo et al. 2001). The Lagrangian particle and NPZD models were solved on-line, i.e., simultaneously with MICOM at a 15-min time interval. A random component with a joint Markovian algorithm that solves for changes in subgrid position and velocity over the 15-min time interval was added to the particle movement equation. This random

component represents horizontal diffusivity and simulates turbulent flow inherent to oceanic currents (Dutkiewicz et al. 1993). Horizontal diffusivity coefficients calculated for model layers of interest (e.g., layer 10, domain of 1–11°N and 48–54°E:  $K_{xx} = 1.9 \times 10^4 \text{ m}^2 \text{ s}^{-1}$ ,  $K_{yy} = 3.5 \times 10^4 \text{ m}^2 \text{ s}^{-1}$ ) were compared to subsurface floats (approximately 800 m, domain of 0–12°N and 46–60°E:  $K_{xx} = 2.1 \times 10^4 \text{ m}^2 \text{ s}^{-1}$ ,  $K_{yy} = 6.3 \times 10^3 \text{ m}^2 \text{ s}^{-1}$ , R. Davis, Scripps Institution of Oceanography, unpubl. data, World Ocean Circulation Experiment (WOCE—Indian Ocean Program). Small differences in diffusivity coefficients between the observations and model were attributed to interannual variability associated with the floats and the monthly climatological average forcing used to drive MICOM.

Metabolic rates associated with each particle were derived from measurements made on diapausing *C. carinatus* in the Benguela current using electron transport system (ETS) enzyme activity (Arashkevich et al. 1996). ETS enzyme activity is an index of metabolic history that circumvents problems associated with disturbing the animal (Hernández-León and Gómez 1996). These metabolic rates were 20% of active metabolism and were independent of temperature. Metabolism was converted to energy equivalents according to Elliott and Davison (1975) and calculated using lipid as the sole substrate ( $0.037 \pm 0.011 \mu\text{g lipid individual}^{-1} \text{ d}^{-1}$ ; mean  $\pm$  95% confidence interval).

Each particle was assigned a lipid reserve that was used as the sole metabolic substrate during the diapause period.

Initial lipid content for each particle was  $50 \pm 1.8 \mu\text{g}$  (mean  $\pm$  95% confidence interval). Dry weight and total lipid content were determined from 77 specimens of *C. carinatus* CV collected during the Netherlands Indian Ocean Program from 21 to 31 January 1993. These were the best post-Southwest Monsoon lipid data available for use as initial conditions in our model. Samples were collected from aboard the Dutch ship R/V *Tyro* with a Hydrobios Multinet, mesh size of 200  $\mu\text{m}$ , from depths ranging from 500 to 1,000 m (Baars 1994). Specimens were then sorted and analyzed following the methods of Vidal and Whitley (1982) and Smith (1992). In general, approximately 15 specimens each were sorted from fresh plankton samples at sea, rinsed briefly in distilled water, and placed into preweighed aluminum pans. The pans were then dried in a drying oven at about 50°C for at least 24 h. At the end of the cruise the samples were sealed in containers with desiccant for transfer back to the laboratory. The samples were transferred to a drying oven in the lab for several days before reweighing. All weighing was done on a Cahn Model C-30 electrobalance. Each sample was then rinsed several times with a chloroform:methanol (2:1 V:V) solution over heat to extract lipid. The solvent and lipid were pipetted from the pan until the solvent was clear and appeared void of any more lipids (yellowish color). Samples were then dried and reweighed to determine the lipid-free dry weight. Lipid weight was then calculated as the difference between the dry weight and lipid-free dry weight. Individual variability was included in both metabolism and lipid reserve; values corresponding to the range of natural variability were assigned to each particle at the beginning of each simulation.

The simulations were initiated with approximately 38,000 particles (see Table 1 for exact numbers) released in each of three isopycnal layers. Particles were launched off the coast of Somalia at depths ranging from 500 m to 1,200 m. The range of starting depths corresponded to isopycnal layers: layer 8 (intermediate, L8, 500–550 m and density [ $\rho$ ] = 1.0278 g cm<sup>-3</sup>), layer 10 (deep, L10, 790–860 m and  $\rho$  = 1.0282 g cm<sup>-3</sup>), and layer 12 (deep, L12, 1060–1200 m and  $\rho$  = 1.0284 g cm<sup>-3</sup>). These three layers include the depths where diapausing *Calanoides carinatus* CV are located during the winter Northeast Monsoon months within the Arabian Sea (Smith 2001). Particles were released on 1 August, and the simulations continued until 30 June of the following year. The purpose of these simulations was to determine whether currents at the specified depths would retain particles and allow emergence of copepods into regions of phytoplankton blooms. Additionally, we investigated whether the layers carrying particles that represented diapausing *C. carinatus* were forced by the physical mechanism of upwelling into a light field that could stimulate the termination of diapause. The criteria used to determine whether particles successfully emerged from diapause were (1) position of the particle when lipid content reached a critical level (lipid content of 20  $\mu\text{g}$ ) forcing them to emerge due to neutral buoyancy disruption (Sargent and Henderson 1986) into cool waters (temperatures <27°C) with bloom conditions (chlorophyll *a* concentrations >3 mg m<sup>-3</sup>); (2) shoaling of particles must occur after mid-February into cool waters with bloom conditions—mid-February is the time we define

Table 1. Fate of particles simulating diapaused *Calanoides carinatus* CV juveniles released near the coast of Somalia, beginning on 1 August and ending on 30 June of the following year. See text for depths of each layer. All percentages are proportions of the total number of particles released in each year.

Particle properties	Layer 8	Layer 10	Layer 12
Total number of particles released	39,621	39,669	39,667
Particles remaining in the Somali region (%)	49.9	69.1	61.0
Particles ending in the interior of the Arabian Sea (%)	47.6	30.9	36.3
Particles advected to the Omani region (%)	2.5	0.01	2.7
Particles upwelled into favorable conditions off the Somali coast (%)	1.6	0.01	1.1
Particles that swim to the upper layer after lipid depletion encountering favorable conditions off the coast of Somalia (%)	3.1	5.3	4.6
Particles that swim to the upper layer after lipid depletion encountering favorable conditions in the Arabian Sea Interior (%)	3.1	3.5	3.2
Particles that swim to the upper layer after lipid depletion encountering favorable conditions in Omani waters (%)	0.3	0.0	0.3

as the activated phase (Hirche 1996) of the diapause period for *C. carinatus* in the Arabian Sea; and (3) shoaling of particles to 400 m depth or shallower, where light intensity is greater than 100  $\mu\text{W cm}^{-2}$  and where they emerge into cool waters with bloom conditions.

## Results and discussion

Particles initially released in the model domain were intended to cover the upwelling eddy feature off the coast of Somalia known as the Great Whirl, which dominates the circulation during the summer Southwest Monsoon (Fig. 2). All particles were released in Somali waters, defined as being within 200 km of the coast; particles that were transported outside the 200-km Somali region were considered to enter the interior of the Arabian Sea (Table 1). Particles transported to the north and east of Socotra Island were considered to enter Omani waters. Diapaused *Calanoides carinatus* CV juveniles off the Somali coast were mainly present between 500 and 800 m during the Northeast Monsoon (Smith 2001), corresponding to layers 8 and 10 (L8 and L10) in our model. Few diapaused individuals were found at 1,000 m or deeper, which corresponds to layer 12 (L12).

Fate of particles after release depended on how ocean processes acted upon the Lagrangian particles: particles were either retained or dispersed based on ocean currents and turbulent flow in the intermediate and deep isopycnal layers.

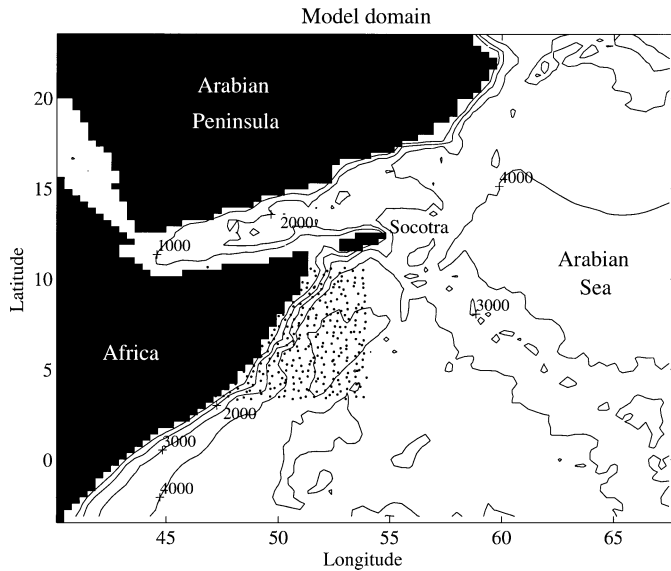


Fig. 2. Model domain within the Arabian Sea, and initial positions of particles for all three layers (small black dots) off Somalia. Lagrangian particle simulations begin on 1 August and end on 30 June of following year. Topography lines are at 1,000 m intervals.

Dispersal away from the original launch region was the dominant mechanism acting on particle movement in L8, where atmospheric forcing at the surface influenced currents deep within the water column off the coast of Somalia (Schott and McCreary 2001). A large proportion of particles were advected eastward to the interior of the Arabian Sea, away from the Somali coast in L8 (47.6%). About 2.5% of the particles were advected northward along the slope of the Somali Basin into Omani waters northeast of the island of Socotra (Table 1; Fig. 3), and slightly more particles were transported into Omani waters in the deeper layer L12 (2.7%; Fig. 3). A similar deep, along-slope transport of diapaused *C. carinatus* CV was observed in the Canary current system in the eastern North Atlantic Ocean (Stöhr et al. 1997). The influence of surface forcing diminished with depth. At L10 (corresponding to approximately 800 m), retention was the dominant fate of particles, allowing 69% of the particles released off Somalia to be retained within the region (Table 1; Fig. 3). The particles in L12 (approximately 1,000 m) were influenced by Red Sea outflow off Somalia between February and April (Schott and McCreary 2001), which has the effect of increasing dispersal through turbulent flow, allowing 36% of the particles to terminate in the interior of the Arabian Sea (Table 1; Fig. 3).

Successful emergence from diapause of *C. carinatus* CV coinciding with the Southwest Monsoon occurred in all three layers (Table 1). In this season, emergence was controlled by two mechanisms. The first mechanism is an internal biological clock driven by lipid reserve depletion to a critical level after which the juvenile copepod emerges and molts into an adult and reproduces. By the second mechanism, the juvenile copepod is physically upwelled along the continental slope, where it is stimulated by an external cue such as a critical light intensity (or rate of change in light intensity)

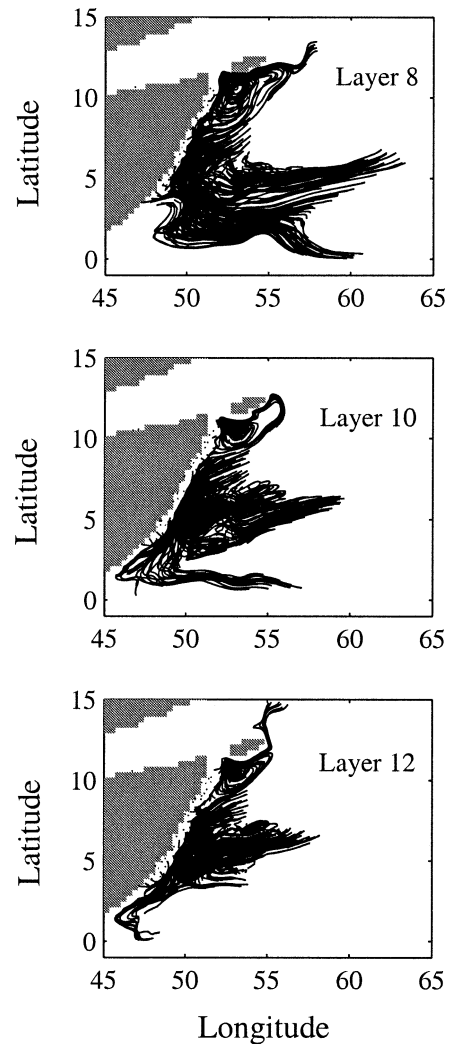


Fig. 3. Trajectories of particles released in layer eight, 39,621 particles (~525 m depth); layer ten, 39,669 particles (~825 m depth); layer twelve, 39,667 particles (~1,130 m depth). Black lines indicate the trajectories of particles from 1 August to 25 January, dark gray lines indicate the trajectories of particles from 1 February to 25 April, and light gray lines indicate the trajectories of particles from 1 May to 30 June.

that will induce arousal from diapause. Emergence due to lipid depletion for juveniles in L8, L10, and L12 is shown in Fig. 4. Note that most of the successful emergence occurred in June as upwelling and phytoplankton bloom conditions became established, increasing the likelihood of emerging in cold, nutrient-rich waters. Regions of successful emergence after lipid depletion include the Somali coast, the interior of the Arabian Sea, and Omani waters northeast of Socotra Island (Fig. 4). Juvenile copepods emerging due to physical upwelling are depicted in Fig. 5. Here the particles were entrained in the deeper portions of the Great Whirl, which may extend down to 1,000 m (Schott and McCreary 2001), eventually being advected onto the Somali shelf (Fig. 5). Particles in L10 that were transported north of Socotra Island eventually circulated back toward the Somali region. Therefore, very few particles managed to enter Omani wa-

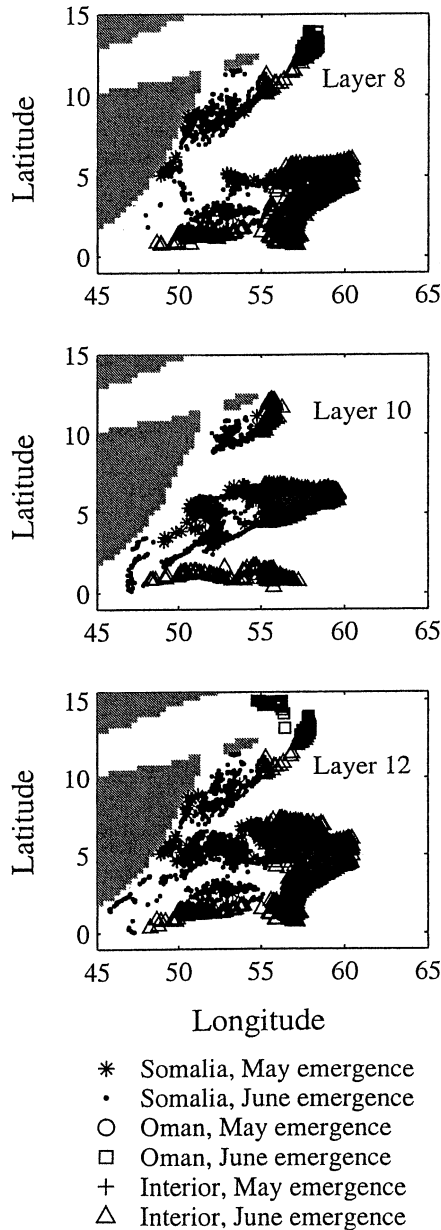


Fig. 4. Positions of particles representing successful emergence due to internal cue determined from lipid content. Layer eight, 2,583 particles; layer ten, 3,501 particles; layer twelve, 3,208 particles.

ters (0.01%), and no particles successfully emerged at the end of the diapause period (Fig. 4). Few particles were upwelled from L10 compared to L8 and L12 (Fig. 5).

The general pattern based on our hypothesized mechanisms for arousal from diapause coupled to physical transport suggests that increased turbulent flow diminishes the capacity for retention and successful emergence into favorable conditions, but higher dispersion allows a greater chance for particles to be physically upwelled onto adjacent shelves. In total, slightly more particles successfully emerge from L10 and L12 (8.8% and 9.1%, respectively) compared to L8 (8.1%). These include both emergence due to the in-

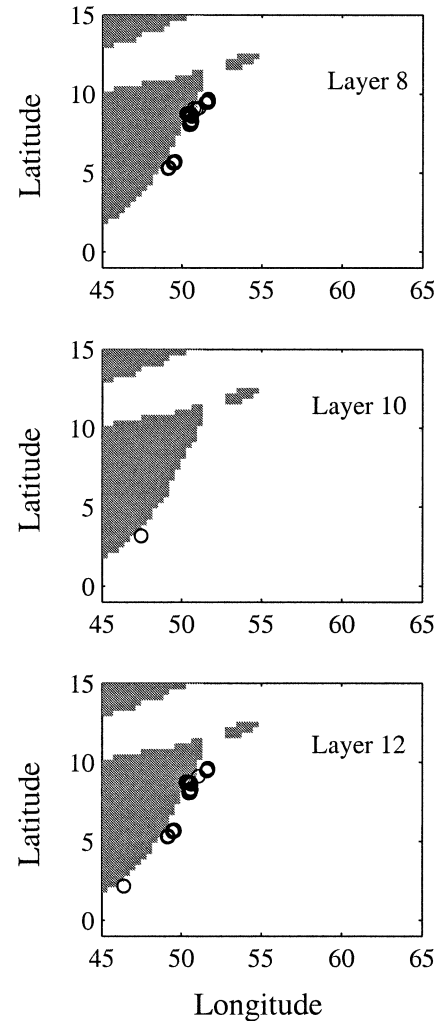


Fig. 5. Positions of particles representing those juvenile copepods being upwelled due to onshore and upslope currents exclusively. Layer eight, 613 particles; layer ten, 5 particles; layer twelve, 417 particles. Circles indicate positions of particles where upwelling occurred to depths shallower than 400 m.

ternal biological clock and physical upwelling, the prevalent arousal mechanism being the internal biological clock (Table 1). Owing to the greater dispersal rates of particles in L8, fewer particles emerged into favorable conditions as lipid reserves were depleted (6.5%; Fig. 4) compared to L10 and L12 (8.8% and 8.1%, respectively; Fig. 4). The remaining particles that were retained and depleted their lipid reserves emerged into unfavorable temperature/food conditions within the upper mixed layer. Alternatively, the higher dispersal rates of particles in L8 and L12 increased the likelihood of physical upwelling onto the shelf (Table 1; Fig. 5). Particles that were most influenced by physical upwelling had a greater chance of emergence into favorable temperature/food conditions since these were entrained in cold, nutrient-rich waters.

Even though the proportional survival and success to emergence of diapaused juvenile *Calanoides carinatus* in our model may seem low, a survival rate of slightly under

10% of the population over the period of 10–11 months is exceptionally successful, especially considering that mortality rates of broadcast spawners is generally upward of 90%. Mortality due to predation is not included in our model because the strategy of diapause in deep waters is specifically thought to be an adaptive response to avoid predation during the winter months (e.g., Hirche 1996; Fiskén 2000). When *C. carinatus* CV enters diapause, individuals undergo physiological changes that allow prolonged periods of inactivity. Accumulation of large lipid reserves prior to diapause and depressed catabolic activity during diapause are key factors that permit successful diapause and emergence at the onset of the following upwelling season (Arashkevich et al. 1996). The simulations in this study revealed that the greatest source of mortality for diapaused individuals appears to be transport offshore from vital upwelling zones. Another source of mortality in our model is early emergence due to insufficient lipid reserves. Because of the small number of individuals initiating the new population, these individuals must emerge in a highly productive upwelling zone to successfully dominate the system during the short productive months. This life history strategy is likely the case for *C. carinatus*, since actively growing populations of this species are found exclusively in upwelling zones (Peterson 1998).

Our model demonstrated that physically mediated biological response in the form of our hypothesized mechanisms for emergence from diapause in *Calanoides carinatus* can be a viable explanation for the success of this species in the Arabian Sea. These hypotheses may also explain emergence mechanisms in other species and other environments as well. Another proposed hypothesis is the seasonal change in day length (Miller et al. 1991; Fiskén 2000), but this hypothesis is unlikely to be the case for *C. carinatus* in the tropical Indian and Atlantic Oceans, where this species is found, because the seasonal change in day length is negligible. Although ocean currents determine the dispersal and fate of the diapaused copepods, the majority of individuals successfully completing their life cycles were those retained within the coastal zone. Furthermore, successful individuals emerged due to an assumed internal mechanism (depletion of lipid reserves). Alternatively, it is possible for diapausing copepods to be physically entrained from intermediate and deep layers to shallow depths by onshore currents.

Variability with respect to vertical distribution and lipid content of diapaused *Calanoides carinatus* is extremely important to the success of the species in response to variability in oceanographic conditions. Those that diapause in the deep ocean layers retained beneath upwelling zones will successfully emerge by means of the internal mechanism when seasonal changes are regular and predictable. Individuals that diapause in highly dispersive layers can be transported onto the slope by physical upwelling regardless of the regularity of seasonal changes, provided the lipid reserves are sufficient for survival until the time of upwelling. Individuals with small lipid reserves that emerge early will be successful if the seasonal upwelling event occurs earlier in the year than usual, while individuals with very large lipid reserves that emerge late will have the advantage if upwelling occurs late. The variability inherent in diapaused individuals may make the species adaptable to different geographical regions (Men-

sah 1974; Verheye et al. 1991; Smith 1992; Stöhr et al. 1997), provided upwelling occurs and growth rates are sufficient to maintain a viable population. Furthermore, it is likely that populations of *C. carinatus* are only observed in upwelling regions because of insufficient food resources in nonupwelling regions to maintain positive growth. The unique climatic conditions in the Arabian Sea in addition to a diapausing life history strategy in a species of copepod illustrate that a persistent population can be maintained in a highly variable tropical environment.

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