



FEATURE ARTICLE

Influence of vertical migration pattern on retention of crab larvae in a seasonal upwelling system

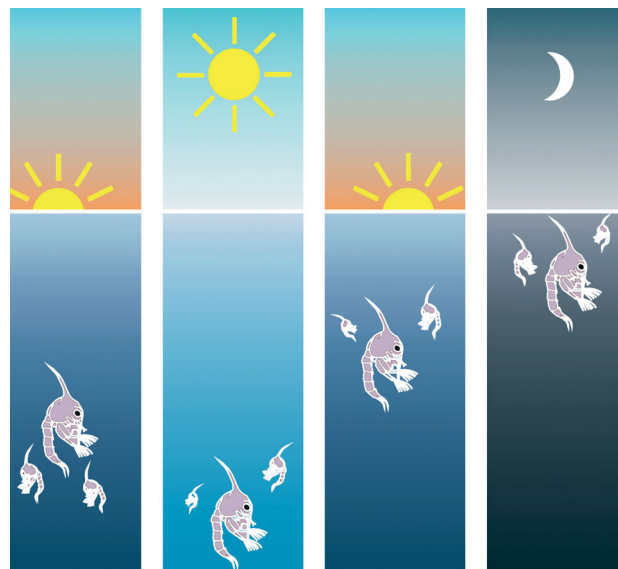
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ABSTRACT: Coasts subjected to upwelling are very advective environments where zooplanktonic organisms face forcible removal from the system. Partition of time between a surface layer, which is under the direct influence of the wind, and a deeper layer, dominated by the compensation counterflow, has been proposed as a mechanism that could enhance retention over the shelf. We used a 3-dimensional numerical model to examine the hypothesis that diel vertical migration (DVM) is able to retain larvae of the littoral crab *Carcinus maenas* over the shelf of the northwestern Iberian upwelling system. Simulations contrasted 2 different wind regimes typical of winter (non-upwelling) and spring (upwelling), and 4 scenarios of vertical distribution: 2 with nocturnal DVM and 2 without DVM. Larvae were simulated as particles released in the model during neap tides at semilunar intervals, to simulate the hatching behaviour of the species, and were followed for 5 wk, which approximates the average larval development time of the species. The particles from the different migration scenarios showed very different responses to wind forcing. Particles without DVM were more sensitive to wind-driven surface currents and were often advected seaward of the shelf break, even during winter when upwelling events were less frequent and of short duration. Particles with DVM were consistently distributed over the shelf, and were very frequently found in the inner shelf region during upwelling. This was accomplished by a larger proportion of time spent in the onshore underflow, which dragged the particles shorewards, than at the surface. The results of the simulations show that, for larvae of littoral species exhibiting DVM over a large expanse of the water column, upwelling may actually be a mechanism that enhances retention over the shelf.

KEY WORDS: Diel vertical migration · Larvae · Recruitment · *Carcinus maenas* · Upwelling

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Crab larvae perform vertical migrations in synchrony with the day cycle. During upwelling events, they migrate between a surface water layer with a seaward flow and a deeper layer with a landward flow. A modelling study indicates that this behavior enhances retention in nearshore waters, increasing the likelihood of onshore and up-estuary transport by a variety of bio-physical processes.

Illustration by Henrique Queiroga

INTRODUCTION

Temperate coasts subjected to upwelling are very productive systems where mero- and holoplanktonic organisms find abundant food and moderate temperatures that favour growth and reproduction. These systems are also very advective environments, where planktonic organisms face a particular problem: how

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can they avoid being swept out of the system by the prevailing seaward circulation at the surface? Several purely physical processes can explain the retention of zooplankton in shelf waters, like the action of eddies (Chiswell & Booth 1999, Nishimoto & Washburn 2002), Taylor columns (Kloppmann et al. 2001), frontal zones (Werner et al. 1996), and Ekman convergence/divergence (Lee et al. 1992, Freeland 1994). Vertical displacement, either in the form of diel migrations or ontogenetic migrations, has been cited as a behavioural mechanism that improves retention of zooplankton in upwelling systems (Peterson 1998). During upwelling the surface waters move offshore due to Ekman transport, while a compensating onshore flow develops in deeper waters. Therefore, any behaviour of planktonic organisms that partitions time between the surface and the deeper layers reduces seaward advection and wastage from the system. The existence of behavioural mechanisms of this kind would constitute a selective advantage for these organisms. The purely physical mechanisms identified above depend to a great extent on local topographic conditions, whereas some kind of vertical migration would provide a general mechanism to increase retention on shelf waters independently of local topographic singularities.

In this study we used a modelling approach to test the hypothesis that diel vertical migration (DVM) may constitute a mechanism for retention of larvae of littoral invertebrate species in the northwest Iberian upwelling system. Our model was a 3-dimensional numerical model of the circulation in the region, and was forced by air-ocean bulk fluxes. Particles that were introduced into this model simulated several traits of the larval phase of the portunid crab *Carcinus maenas*. Nocturnal DVM is a widespread behaviour in larvae of decapod crustaceans, and these larvae have swimming abilities that allow them to cross vertical distances in the order of several 10s of m during the course of the migrations (reviewed by Queiroga & Blanton 2004). The extent of the vertical distribution is also known to change during larval ontogeny, and in some cases the last stage is mostly neustonic (e.g. Zeldis & Jillett 1982, Shanks 1986, 1995). In order to account for uncertainties concerning the vertical migration behaviour of *C. maenas* larvae, several vertical migration scenarios were imposed on the particles. Moreover, series of runs were performed using wind time series typical of non-upwelling and upwelling regimes, in order to contrast the outcome of the different migration scenarios between different wind-forcing conditions.

The Portuguese coast extends approximately south-north along the longitude 9° W and has no significant irregularities in the northern region. The shelf width is about 40 km and the slope is steep (Fig. 1). The region

of study was the shelf adjacent to the estuary of the Ria de Aveiro, northwest Portugal. Ria de Aveiro is a shallow lagoon that harbours a commercially important population of *Carcinus maenas*. It is located in the middle of a sandy coast with a single narrow inlet of 400 m width that connects to the sea. Tidal heights in the northern Iberian Peninsula coastal region are dominated by the semi-diurnal tidal components M_2 and S_2 , which give rise to clear spring-neap cycles modulated by other constituents. Tidal amplitude varies between 0.5 and 1 m during neap tides, and 1 m and 2 m during spring tides at the Ria de Aveiro inlet. The wind regime along the Portuguese coast is dependent on the dynamics of the Azores anticyclone, whose centre migrates from 27° N in the winter to 33° N in the summer (Fiúza et al. 1982). This condition originates weak westerly winds during the winter and northerly winds during the spring and summer. Due to the south-north orientation of the Portuguese coast, the northerly winds give rise to upwelling (Wooster et al. 1976, Peliz et al. 2002). Based on observed winds, Huthnance et al. (2002) have computed upwelling indices for the west Iberian coast that show average positive values from March to September, with higher values from June to August. Even though these calculations have shown that the variability of northerly winds outside the

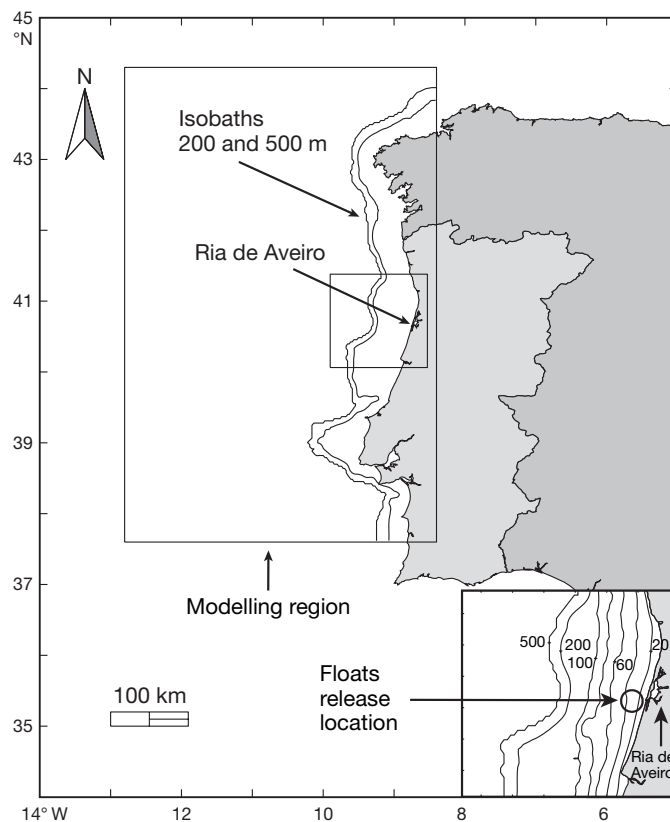


Fig. 1. Study area (NW Portugal) with modelling region and release location

period June to August is large, the data indicate that winds that favour upwelling are a recurrent feature of the Portuguese coastal ocean during a protracted period of the year.

Our model species was the littoral portunid crab *Carcinus maenas*. This is the most common crab in northwest Iberia and in coastal waters of the Palaearctic Atlantic, and it forms large populations in estuaries and rocky shores throughout a native range that extends from Norway and Iceland to Mauritania (d'Udekem d'Acoz 1999). This species had become a global invader during the last century, having established successful populations in the east and west coasts of the USA (Almaça 1962), South Africa (Le Roux et al. 1990), and Australia (Thresher et al. 2003). The life cycle of *C. maenas* includes a larval phase composed of 4 zoeal and 1 megalopa planktotrophic stages (Rice & Ingle 1975). The megalopa is the stage that accomplishes the transition between the planktonic and the benthic phases. Hatching of larvae occurs in estuaries or shallow bays, and first stage *C. maenas* zoeae rapidly abandon the release areas and spread into coastal shelf waters where they develop through the next zoeal stages and the megalopa. The megalopa must then find appropriate littoral habitats for settlement, metamorphosis and successful juvenile development.

The mechanisms by which *Carcinus maenas* leave and reenter the estuaries in northwest Iberia have been studied in recent years, and were found to be associated mainly with environmental processes that occur at tidal, diel, and semi-lunar periodicities. In northwest Portugal larval release occurs during night ebb tides. This combination of phase of tide and phase of day takes place during neap tides following the quarter moons, and thus has a semi-lunar periodicity. A rapid export of the first zoea to shelf waters then follows immediately (Queiroga et al. 1997, Pereira et al. 2000). Once in shelf waters, development up to the megalopa stage takes about 4 to 6 wk depending on water temperature (Darwirs 1985, Mohamedeen & Hartnoll 1989). The migration from shelf waters to the estuarine habitat is thought to occur in 2 steps: (1) the shoreward transport (Shanks 1995, Queiroga & Blanton 2004), and (2) passage through the estuarine inlet and upstream transport until an appropriate settlement environment is found. The mechanisms responsible for step (1) are not clear, but supply of megalopae to estuaries in northern Portugal has been related to episodes of relaxation/inversion of northerly winds (Almeida & Queiroga 2003, Queiroga 2003, Queiroga et al. 2006, this volume). Step (2) is accomplished by selective tidal stream transport that takes place during night flood tides (Queiroga 1998, Forward & Tankersley 2001). The vertical migration behaviour of *C. maenas* larvae

over the shelf is not clearly described, but megalopae of this species are known to migrate to the neuston layer during the night in the British Isles (Zeng & Naylor 1996). Moreover, a recent literature review (Queiroga & Blanton 2004) indicated that nocturnal DVM is a very common behaviour in crustacean decapod larvae in shelf waters.

The objective of this work was to investigate the consequences of active DVM under different wind forcing conditions for the retention and recruitment of larvae in regions without prominent coastal or bathymetric features. The absence of topographic singularities excludes *a priori* retention of larvae caused by possible stable and persistent circulations related to topography. Given the life-cycle characteristics of the species, the available knowledge on critical aspects of its larval biology, and its widespread occurrence, we believe *Carcinus maenas* provides a good model to test the retention hypothesis, and that the results of the present work may be important to elucidate aspects of recruitment processes of littoral invertebrates in coastal upwelling areas.

METHODS

Model setup. The influence of the pattern of vertical distribution of larvae on their dispersion and retention over the shelf was studied with a 3-dimensional hydrodynamical model that simulated the shelf water dynamics with realistic forcings and stratification. The domain of the model spanned from 37.6 to 44.3° N and 12.8 to 8.4° W, which corresponded to 360 km in the longitudinal and 740 km in the latitudinal directions (Fig. 1). The model used was the Regional Ocean Modeling System (ROMS) (Haidvogel et al. 2000) and it was forced by wind and heat fluxes from the National Centers for Environmental Prediction (NCEP) reanalysis database, which were interpolated for the simulation grid.

Useful prediction of oceanographic circulation and advection based on the use of numerical models depend on a proper validation of the models. The model used in this study was validated by comparing observations, obtained during the 'ProRecruit' project cruise conducted over the shelf in front of Ria de Aveiro during May 2002, with model simulations for the same period (M. Marta-Almeida unpubl. data). Fig. 2 shows a typical result obtained when current measurements made at 35 m, off the Ria de Aveiro, were compared with model simulations. The simulated instantaneous velocities have a lower variance than the observed values, both for the zonal (across-shore) and longitudinal (along-shore) components. This results from the fact that NCEP winds do not represent

real winds with high accuracy in the studied region, as revealed by comparison with data from coastal meteorological stations: observed winds have systematic higher values than NCEP winds. However, simulated residual currents at weekly and longer time scales were similar to the observations. Therefore, the model appeared to realistically reproduce transport integrated over the time scales of larval development.

Two simulations were performed, one for the late winter and the other for the spring, covering the months of February to April and April to June 2002, respectively. These periods were chosen because they show contrasting wind regimes between non-upwelling and upwelling season. Fig. 3 shows the wind for the winter and spring simulations at the release location, off the Ria de Aveiro. The wind was more variable in winter than in spring. In February it was southerly during the 1st week and northerly until 25 February. There was 1 episode of northerly wind between 4 and 10 March, and then southerly wind persisted until 23 March. During the rest of the month the wind was weaker and more variable, but originated mainly from the north. In contrast with this situation,

the wind during the spring simulation was almost always northerly with a westerly component. The exceptions were between 4 and 10 April and between 12 and 24 May. The southerly wind during these periods was weaker than the average northerly wind during the rest of the spring simulation. The north-westerly wind during the months of April and May is typical of the Portuguese west coast in spring and summer, and drives coastal upwelling in this region.

Tidal forcing was not used in the present study, but preliminary simulations including tides and vertical migration were carried out in order to inspect the sensitivity of the model to interactions between DVM and tidal currents. The results of those simulations showed that significant net horizontal transport was not observed. Hill (1991a,b, 1995) described a series of situations where planktonic organisms migrating vertically in the water column on a background of tidal currents would experience considerable horizontal transport, provided that the period of migration is a multiple, or close to a multiple, of the tidal period. Since there is no evidence to suspect that *Carcinus maenas* larvae would retain a migration behaviour synchronised with

the lunar semi-diurnal tide in shelf waters, horizontal transport by the M_2 tide (lunar semi-diurnal, period of 12.42 h) would not be expected. The 24 h period of the diel migration would interact with the S_2 tide (solar semi-diurnal, period of 12.00 h). However, in the area of study, this constituent is of minor importance relative to the principal lunar M_2 . A systematic interaction between tidal currents and vertical migration is expected in places where tides are the main driving mechanism; this contrasts with the shelf region of northern Portugal, where wind appears to be the main ocean forcing mechanism (Vitorino et al. 2002, Peliz et al. 2003).

Simulation of larvae behaviours. Larvae were simulated by inserting drifters in the model. The drifters had lagrangian movement in the horizontal, i.e. they had a passive behaviour in terms of horizontal transport. In order to examine the influence of vertical migration pattern on dispersal, 4 patterns of distribution were implemented. These were chosen in order to contrast 2 scenarios with active DVM with 2 scenarios without vertical migration. The patterns of vertical movement and the number of particles released each day were as follows. A set of 500 particles was dropped at the surface and constrained to remain there. Another set of 500 particles was released with a uniform distribution between the surface and the bottom and left to vary vertical position according to

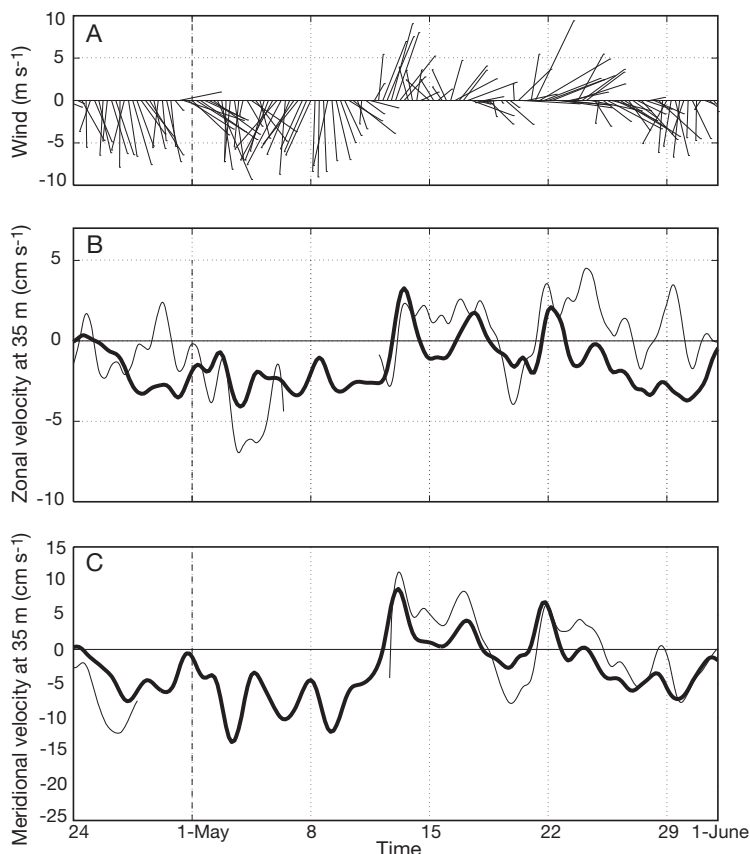


Fig. 2. (A) Wind and (B,C) simulated (thick lines) and observed (thin lines) currents at the 'ProRecruit' project mooring site off the Ria de Aveiro. In (A) positive values on the y-axis refer to southerly wind. (B) Across-shelf and (C) along-shore currents are shown at 35 m depth

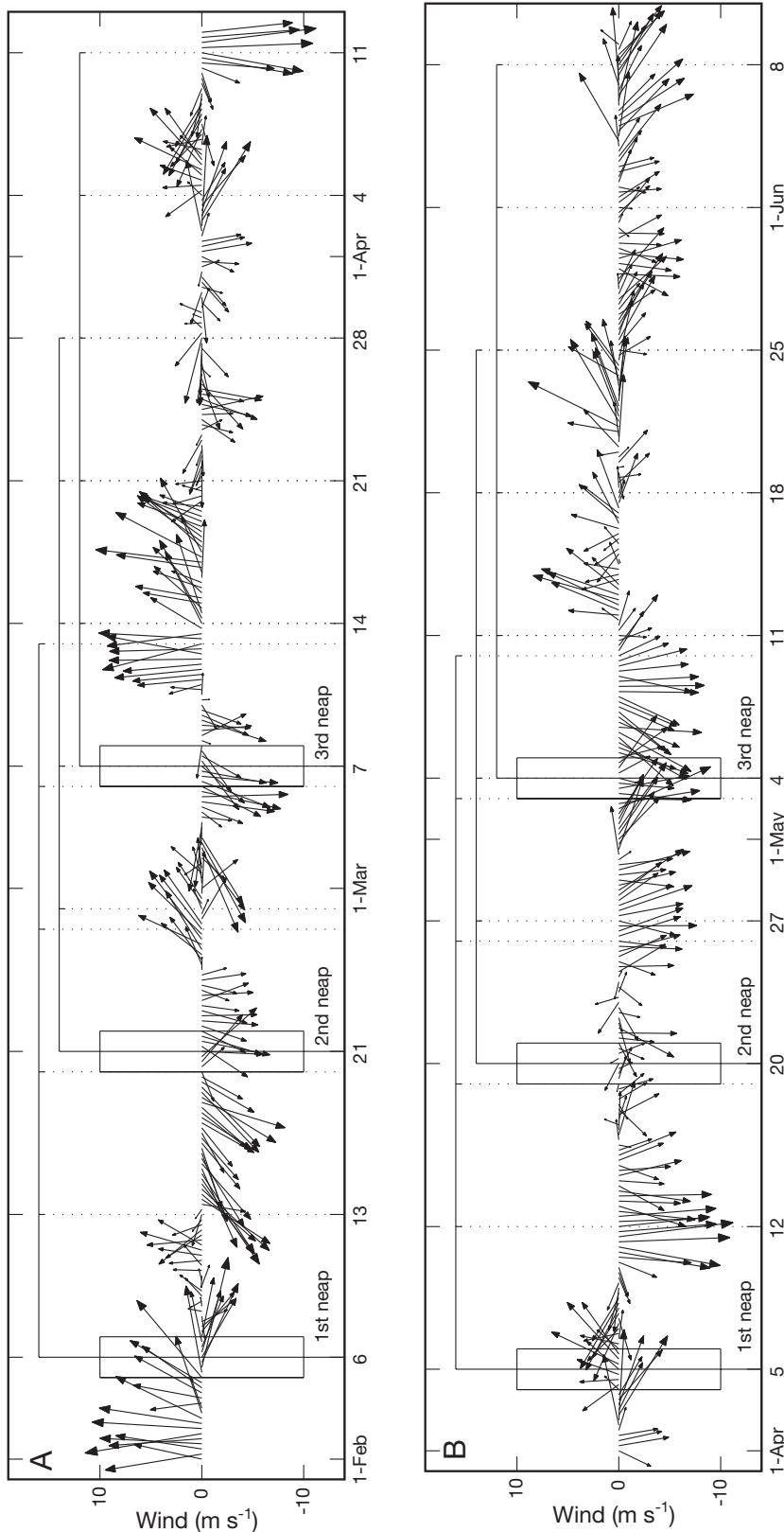


Fig. 3. Wind near Ria de Aveiro during (A) winter (February to March) and (B) spring (April to May) simulation periods. Vertical rectangles: 3 release days within each neap tide period; dotted lines: 5 wk after each release

the vertical velocities in the model. In a third set of 500 particles, nocturnal vertical migration was imposed by forcing them to migrate daily between a surface and bottom layer, which were arbitrarily set with thicknesses of 5 m and 10 m, respectively. Finally, 1000 particles were released with a more complex pattern of nocturnal vertical migration between an upper and lower layer, which is detailed in Fig. 4. In order to force this pattern, the water column was divided into 6 levels. The surface and the bottom levels were always 5 m and 10 m thick, respectively. The intermediate levels were equal but their thickness depended on the total depth. During the day, 80% of the drifters were in the bottom level and 10% were in each of the next 2 levels. During the night, half of the particles in the bottom level (i.e. 40% of the total number) remained there. The other 40% plus the 20% in the 2 levels above the bottom layer moved upwards, reaching a final distribution with 10% in each intermediate level and 20% in the surface level. This last scheme was based on recent observations on the vertical distribution of decapod larval stages made during a cruise conducted in coastal waters off the Ria de Aveiro (A. dos Santos unpubl. data). These observations described a very clear nocturnal upward migration of crab larvae during the night that extended along much of a water column of height 60 m, and is consistent with swimming velocities of decapod zoea and megalopae in the order of 1 cm s^{-1} (Chia et al. 1984).

In the 2 scenarios with vertical migration, the particles remained in the deeper levels between 06:00 h and 20:00 h. Then they began the upward movement reaching the shallower levels at 22:00 h, where they remained until 04:00 h. At this moment they started a downward movement at a rate that took them back to the deeper levels by 06:00 h (Fig. 5). To facilitate further reference, the 4 migration scenarios were coded NS for no migration and surface distribution, NU for no migration and uniform distribution, SB for nocturnal DVM between surface

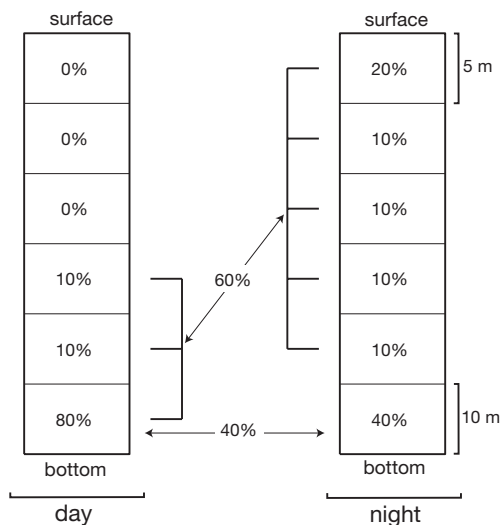


Fig. 4. Vertical distribution of particles in the nocturnal DVM scenario between surface and bottom layers

and bottom, and UL for nocturnal DVM between upper and lower layers.

Initiation of the particles in the model was programmed to simulate the hatching pattern of *Carcinus maenas*. Larval hatching takes place during nocturnal neap ebb tides which recur in the Portuguese coast with a basic semi-lunar periodicity (see 'Introduction'). Therefore, drifters were released into the model for 3 consecutive days around the lowest amplitude tide, during 3 consecutive neap tide periods (Fig. 6). All drifters were released at 00:00 h. Tables 1 & 2 summarise the drifters' release date and the number of drifters used per release day. For the winter simulation (February and March), the release days were 5 to 7 February (1st neap tide), 20 to 22 February (2nd neap tide), and 6 to 8 March (3rd neap tide). The release days in the spring simulation were 5 to 7 April (1st

neap tide), 20 to 22 April (2nd neap tide), and 6 to 8 May (3rd neap tide). By releasing larvae at several consecutive neap tides, we hoped to explore possible responses of the larval pool to different wind regimes at the time of initial appearance of larvae on the shelf. The particles were released in random positions inside a circle of radius 5 km near the Ria de Aveiro inlet (Fig. 1). This is considered to be a good approximation of the estuarine plume and, therefore, of the larval distribution immediately after they left the estuary (carried by the ebb current). The number of particles used in each of the 2 simulations was 2500 d⁻¹, during 3 days per neap tide period, for 3 neap tides, which summed to a total of 45 000 analysed drifters' trajectories.

Analysis of dispersal patterns. The analysis of the results was based on 4 descriptors: (1) the cross-shelf distribution of the particles, (2) the percentage of the particles on the inner shelf, (3) the latitudinal distribution of the particles over the inner shelf, and (4) the dispersion pattern of the particles. The cross-shelf distribution of particles was calculated until the end of the 5th week, at weekly intervals starting 1 wk after the release (using the 2nd day of release as a reference). The period of 5 wk was chosen because it corresponds to the average development time of *Carcinus maenas* larvae in the temperature range usually found in Portuguese coastal waters during winter and spring (Darwirs 1985, Mohamedeen & Hartnoll 1989). The percentage of particles on the inner shelf was calculated weekly as the proportion of those within 5 km from the coast, and was chosen in order to obtain a measure of the size of the larval pool available for recruitment to littoral habitats. The latitudinal distribution of these particles was also calculated at weekly intervals. With the aim of measuring the dispersion pattern of the particles, the region of the model was

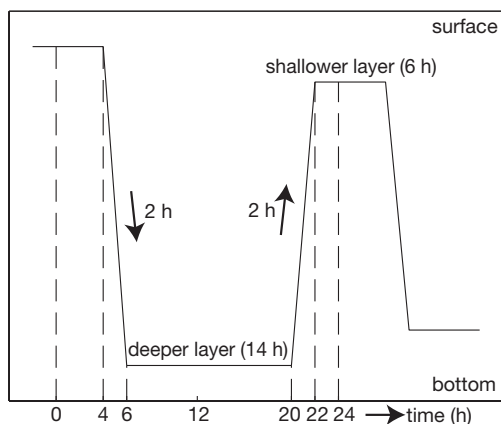


Fig. 5. Timing of vertical movements imposed in scenarios with DVM between surface and bottom (SB) and with DVM between upper and lower layers (UL). Actual depth of shallower and deeper layers dependent on migration scenario

Table 1. Date of particle release for winter and spring simulation

Neap tide	Winter	Spring
1st	5 to 7 February	4 to 6 April
2nd	20 to 22 February	19 to 21 April
3rd	6 to 8 March	3 to 5 May

Table 2. Vertical migration scenarios imposed on particles, and the number of particles released d⁻¹

Drifters d ⁻¹	Migration scenario
500	None, surface (NS)
500	None, uniform (NU)
500	Surface ↔ bottom (SB)
1000	Upper layer ↔ lower layer (UL)

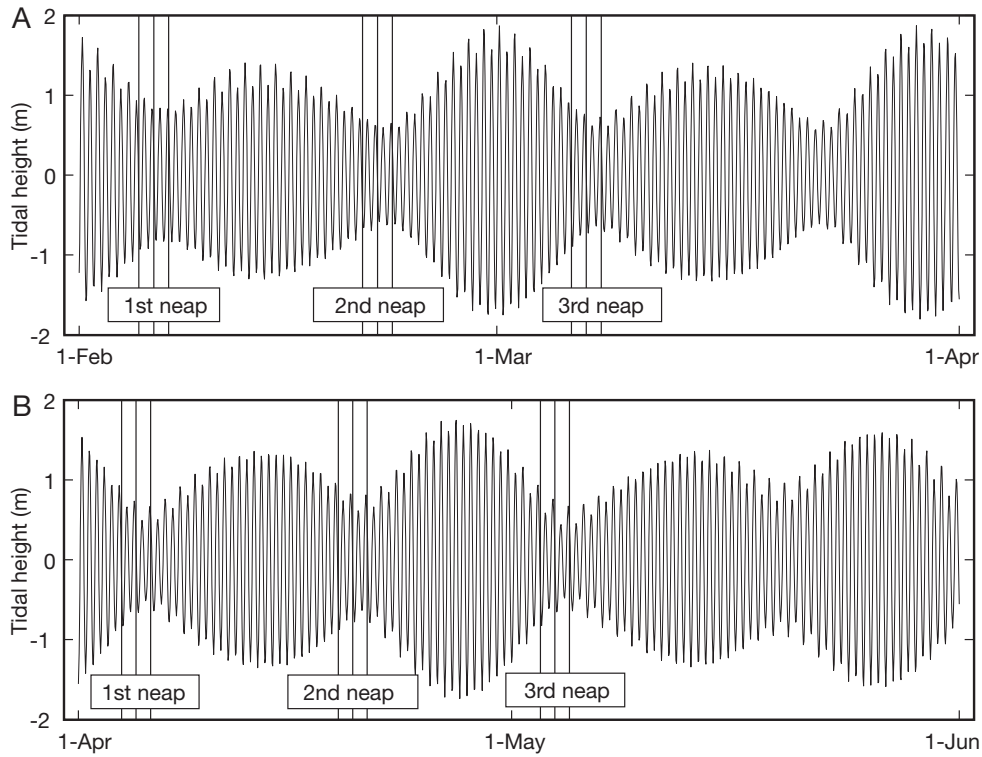


Fig. 6. Tidal amplitude near Ria de Aveiro inlet during (A) winter (February to March) and (B) spring (April to May) simulation periods. Vertical lines: 3 release days within each neap tide period

divided into 100×200 boxes (longitudinally $\times$ latitudinally) of equal size, and the variance of the resulting matrix of the number of particles was calculated. Since the total number of drifters does not change with time and the boxes were of equal size, the variance $\sum_{i=1}^b (n_i - \bar{n})^2 / b$ (in ind.²) is a measure of the particles' horizontal dispersion. Because this variance depended on the total number of particles and the UL migration scenario used twice as many larvae as other scenarios, the variance was normalised by $(N/b)^2(b-1)$, which is the maximum variance when all particles are inside a single box, i.e. $\sum_{i=2}^b (0 - \bar{n})^2 / b + (N - \bar{n})^2 / b$. In these formulae, b is the number of boxes used, n_i is the number of particles in box i , N is the total number of drifters, and $\bar{n}$ is the average number of drifters per box, N/b . Therefore, high values of the normalised variance corresponded to higher aggregations. The calculation of the variance was performed after the 3rd day of release, every day, until the end of the 5th week, separately for each of the 4 migration scenarios and for each of the 3 release periods. Mortality of the larvae was set to 0.

RESULTS

Movements of the particles depended on the interaction between their vertical position in the water col-

umn and the forcing factors. Since observed winds were the main driving force of the circulation, it was expected that trajectories of the particles depended on the migration scenario and on the day of release into the model domain.

Fig. 7 shows the normalised variance of the particles for all migration scenarios and for the 3 release periods in the winter and spring simulations. Figs. 8 to 13 show the longitudinal distribution of the particles in the inner shelf, expressed as the percentage of particles at a distance less than 5 km from the coast (Figs. 8A to 13A), and the cross shelf distribution of the particles (Figs. 8B to 13B), calculated at weekly intervals, for the 3 release periods in the winter (Figs. 8 to 10) and spring (Figs. 11 to 13) simulations. To facilitate analysis and cross-referencing, all these figures are organised into matrices where rows correspond to the 4 migration scenarios.

Winter simulation

The normalised variance of the NS scenario in winter showed large fluctuations over time, in contrast to the other 3 vertical migration scenarios (Fig. 7). As is shown below, large variances in the NS scenario were always associated with situations when particles hit the coast and remained concentrated there. In the NU,

SB and UL scenarios, the variance decreased over 5 wk for each of 3 release periods, to levels consistently below 0.03 at the 5th week. Of these, the NU particles showed the lowest variance.

For all scenarios, the particles released in the first neap tide of the winter simulation moved southwards and offshore (Fig. 8) on to the middle shelf. Most of the net displacement took place during the first 3 wk, corresponding to a period of strong northeasterly wind (Fig. 3). For all migration scenarios, retention in the inner shelf was usually below 5% from the 4th week onwards (Fig. 8A).

In the 2nd winter neap tide release (Fig. 9) there were larger differences in the trajectory and dispersal of the particles among the different larval migration scenarios than in the first release. This was caused by higher variability of the wind in the weeks after the 2nd release (Fig. 3), which led to different responses of particles from different migration schemes. While NS particles move southwards during the first 2 wk and then northwards, all others particles were subjected to very little southward transport before also moving northward after the 2nd week (Fig. 9A). Two maxima were found in the variance of particles in the NS scenario (Fig. 7), one after the 1st week and the other around the 4th week. These maxima were

caused by the interception of the northward trajectory of the particles with the coast, southward (1st maximum) and northward (2nd maximum) of the release location (Fig. 9). In all other scenarios, particles moved seawards with time until they reached the outer shelf in the 5th week, with concentration maxima at 20 to 40 km from the coast (Fig. 9B). The contrast between the NS and the other scenarios is evident when the percentage of the particles in the inner shelf region is compared (Fig. 9A). The values were over 60% for the NS particles until the 4th week. The decrease to 0.1% in the 5th week was due to the onset of northerly and easterly wind after the 4th week (Fig. 3). The percentage of particles in the inner shelf region was always below 5% in all other scenarios.

The particles of the 3rd winter release (Fig. 10) were subjected to strong southerly wind during the first ~2 wk, and then low and variable wind with an easterly component around the 3rd week (Fig. 3). The movement of the particles was thus basically northwards (Fig. 10A) and seawards to the middle and outer shelf (Fig. 10B). A maximum in variance of the particles occurred 2 wk after release in the NS scenario (Fig. 7) and was again caused by convergence at the coast. While propagating northwards, the particles met the coast to the right and remained concentrated there

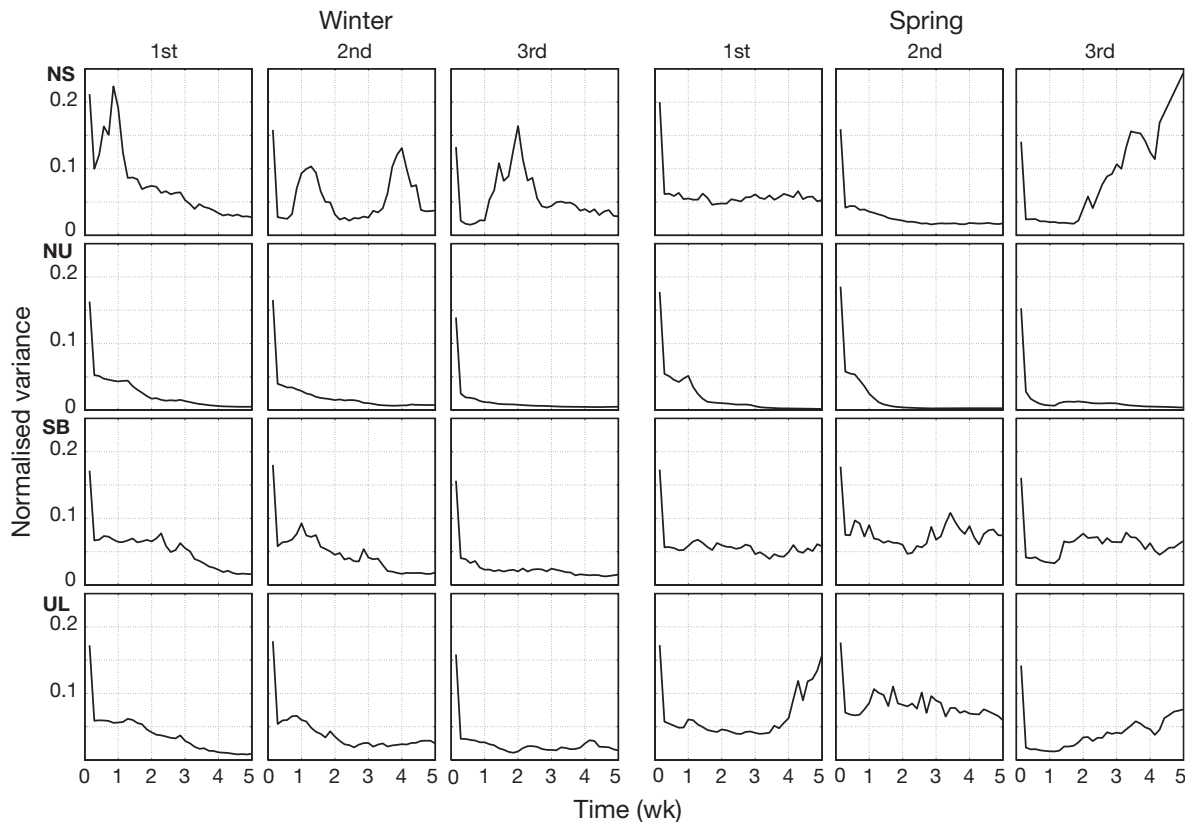


Fig. 7. Variance of particles during the first 5 wk after 3 releases in winter and spring. Migration scenarios—NS: none, surface; NU: none, uniform; SB: surface ↔ bottom; UL: upper layer ↔ lower layer

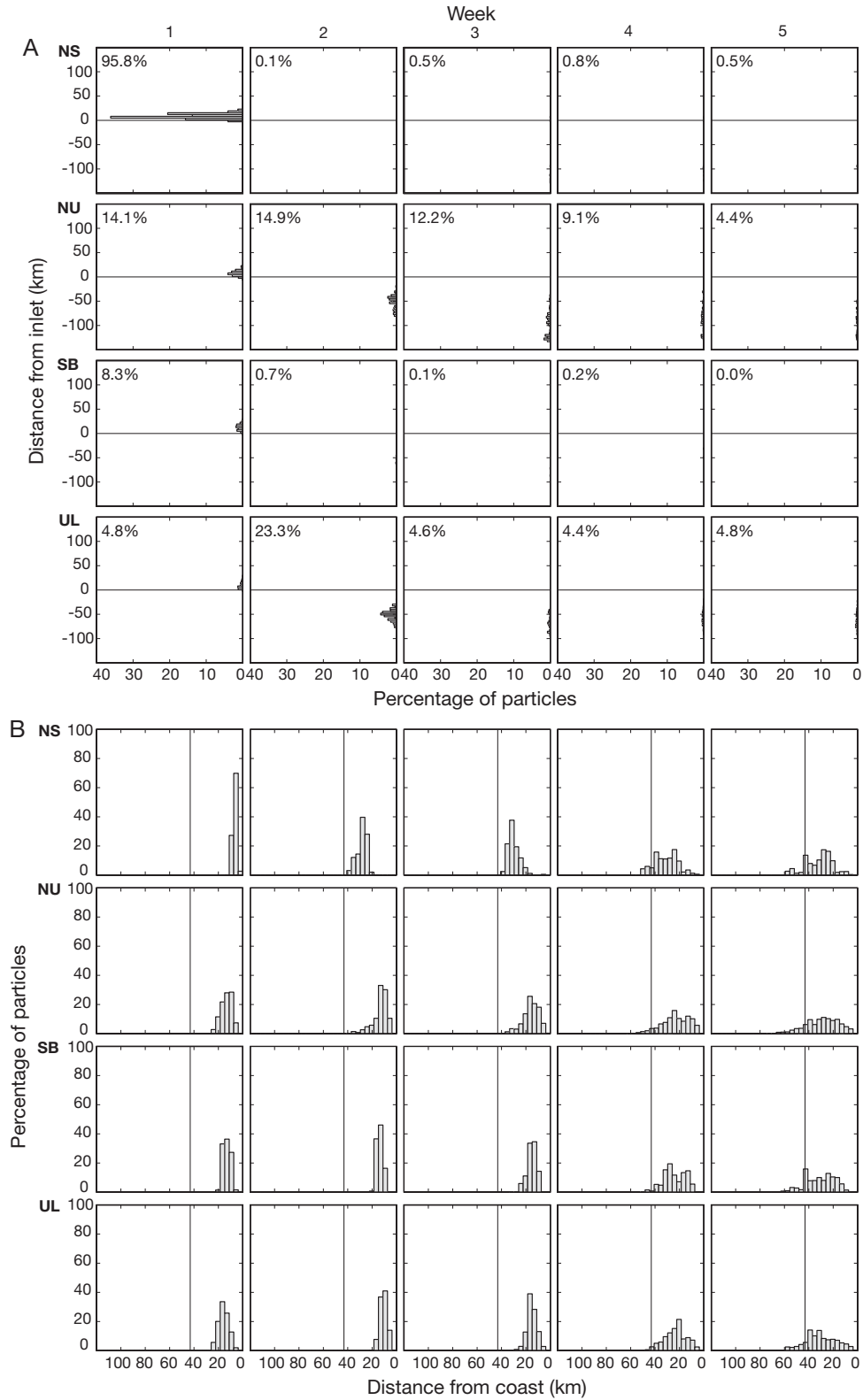


Fig. 8. Winter simulation, 1st release. (A) Latitudinal distribution and percentage (inset value) of particles within 5 km of the coast, and (B) cross-shelf distribution of total number of particles. Five columns represent 1 to 5 wk after release. (A) Release point located at 0 km on y-axis; positive values are particles located north of inlet. (B) Coast located at 0 km on x-axis. Vertical line at 43.1 km: average position of shelf break calculated over a 300 km stretch of shelf centred on release location. Migration scenario—NS: none, surface; NU: none, uniform; SB: surface ↔ bottom; UL: upper layer ↔ lower layer

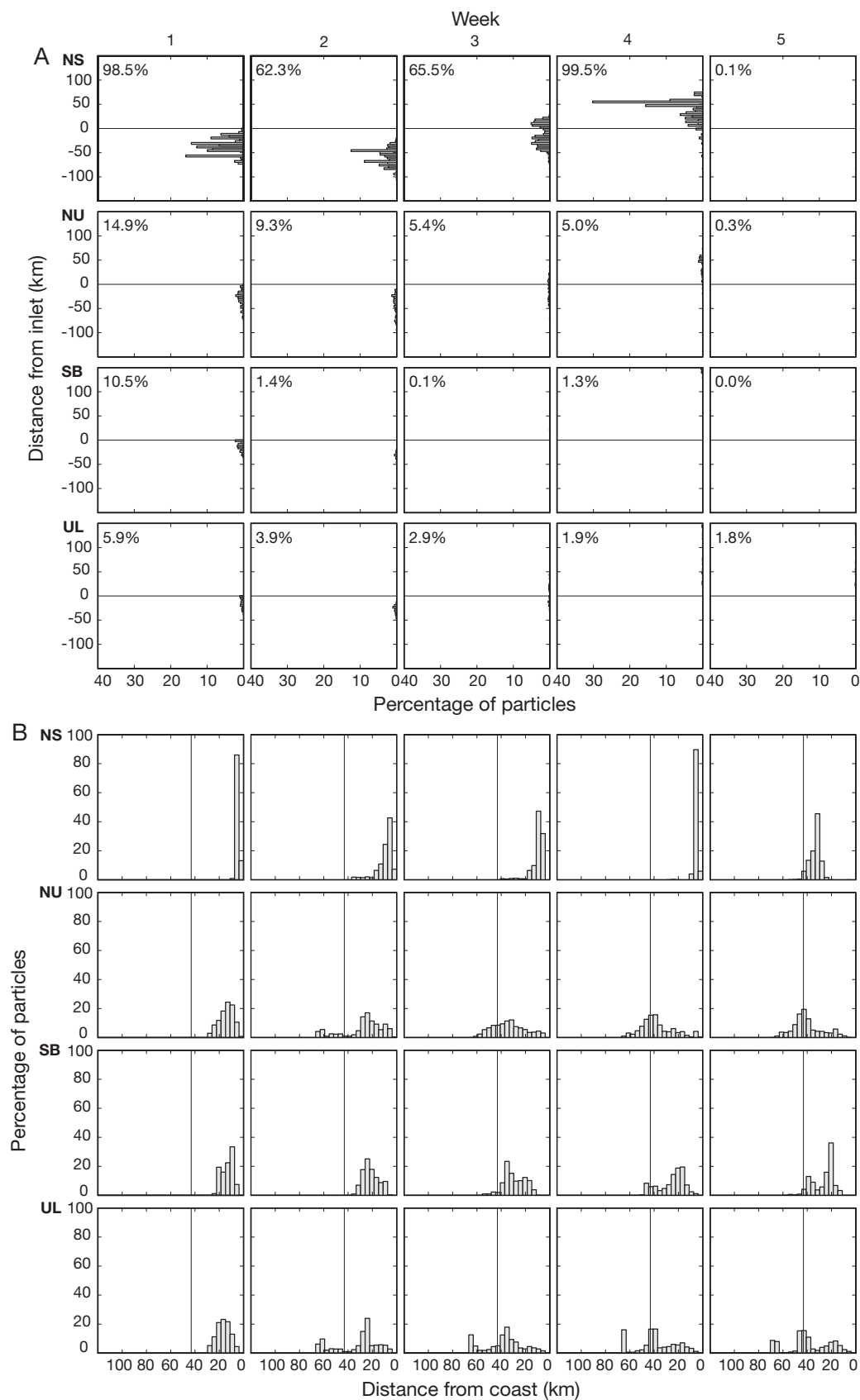


Fig. 9. Winter simulation, 2nd release. See Fig. 8 for details

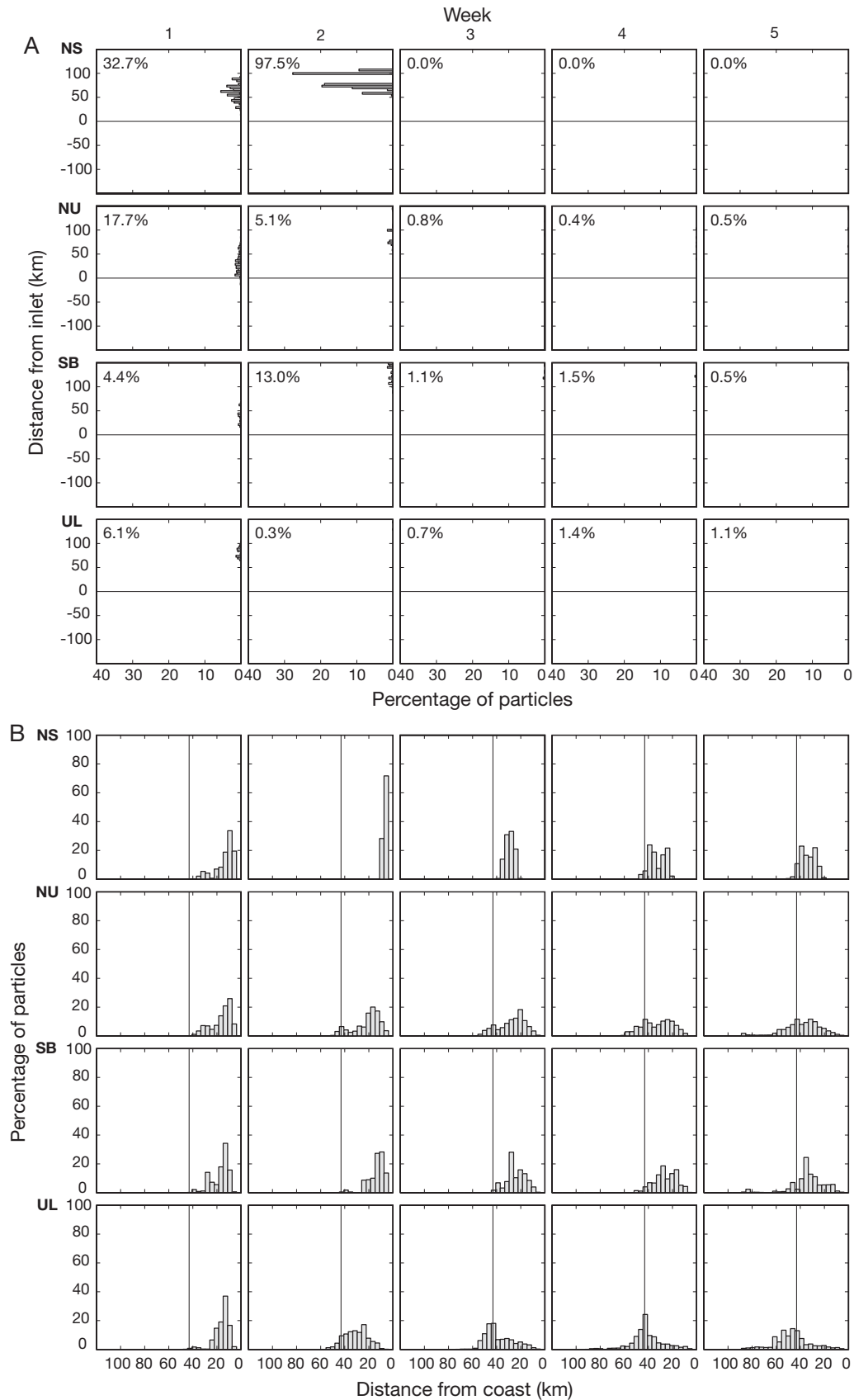


Fig. 10. Winter simulation, 3rd release. See Fig. 8 for details

due to a small westerly wind component. This was shown by a peak in concentration near the coast in Fig. 10B in Week 2 of this scenario. Particles other than those in the NS scenario were spread over the shelf with concentration maximum around the middle and outer shelf (Fig. 10B). Except for the very high peak in the percentage of NS particles in the inner shelf region, caused by interception of particle trajectories with the coast, the values were low and mostly below 2% for the other scenarios after the 2nd week (Fig. 10A).

Spring simulation

In spring, the normalised variance of particles in the SB and UL scenarios, both with DVM, usually remained bound within intermediate levels from 0.05 and 0.15 over the 5 wk, for all 3 releases (Fig. 7). This contrasted with the same scenarios in the winter simulation, where variance decreased to lower values. It also contrasted with the NS and NU scenarios, both in winter and spring. In the NU scenario, similar to what had occurred in the winter simulation, the variance decreased to levels below 0.01. In the NS scenario the pattern of change in variance with time differed across the 3 releases, with intermediate and low values for the 1st and 2nd release, and very high values of variance in the 3rd. Again, the increase in the variance in the NS scenario was associated with the interaction of the shoreward flow with coastal topography.

A few days after the 1st spring release (Fig. 11) the wind turned northerly (Fig. 3). Thereafter, a southward and offshore transport was expected for the NS and NU particles, as did actually occur. After the 3rd week the NS particles were southward of the release point, had moved off the shelf, and kept moving seaward with little subsequent dispersal (Fig. 11B). The NU particles were subjected to less offshore transport and were dispersed over the outer shelf and off the break by the 5th week. This dispersal and offshore transport occurred because the particles (originally with a uniform distribution between the surface and the bottom) became more concentrated in layers close to the surface due to the upwelling internal return current, which led to an upward transport of the particles. The SB and UL particles also moved southward (Fig. 11A) but were not advected offshore by the upwelling currents. Instead, they remained over the inner shelf throughout the 5 wk period (Fig. 11B). Because of the migration schemes imposed upon them, these SB and UL particles spent more time in the lower layers of the water column, where currents were onshore, than in the upper layers. The particles followed an oscillatory trajectory: they were transported offshore in the upper layers but onshore in the lower layers, despite weaker currents at

depth. Accordingly, the percentage of particles close to shore was higher in the SB and UL scenarios than in the other 2 scenarios, with proportions that reached over 70% after the 2nd week in the UL scenario (Fig. 11A).

After the 2nd release (Fig. 12) the particles were subjected to wind conditions similar to those of the 1st spring release (Fig. 3), and they behaved very similarly. The main differences were related to (1) the northeasterly wind event at the end of the 2nd week and beginning of the 3rd (1 to 4 May); and (2) the wind inversion during the 4th and 5th weeks after the release that brought the NS and NU particles—which had moved offshore during the first 2 wk—back into a shoreward direction (Fig. 12B), reaching the shelf break (NS particles) and middle shelf (NU particles). The percentage of particles in the inner shelf region was also similar to that of the previous release, except for higher values for SB particles that, now like the UL particles, were retained close to the coast during most of the 5 wk (Fig. 12A).

The particles released in the 3rd neap tide (Fig. 13) showed quite different behaviour from particles in the 1st and 2nd releases. The wind was northerly during the 1st, 4th and 5th weeks. After the middle of the 2nd week the wind had a strong westerly component. Because of these events, particles never left the shelf. The NS and NU particles were advected by the upwelling currents only in the 1st week and moved southwards (Fig. 13A) until they reached the middle shelf (Fig. 13B). The southwesterly wind then carried the particles onshore, and in the following weeks the NS particles remained attached to the coast while the NU particles dispersed over the inner and middle shelf. The SB and UL particles behaved as in the previous releases, remaining in the inner shelf during the entire simulation period (Fig. 13B), and only exhibiting a small degree of southward transport in comparison with particles from the 1st and 2nd release (Fig. 13A). The proportion of particles in the inner shelf region was the highest of all releases in both winter and spring simulations, and for all the migration scenarios (Fig. 13A). However, this occurred not because the particles returned to the region near the coast, but because they never left that region at any time during the simulation period. In the case of NU particles, variance values were very small (as expected) due to the large degree of dispersion; for NS particles, variance increased with time as a consequence of shoreward movement and collision with the coast (Fig. 7).

DISCUSSION AND CONCLUSIONS

This study used 4 different vertical migration scenarios that were kept constant over the duration of expected planktonic development of the larvae. This

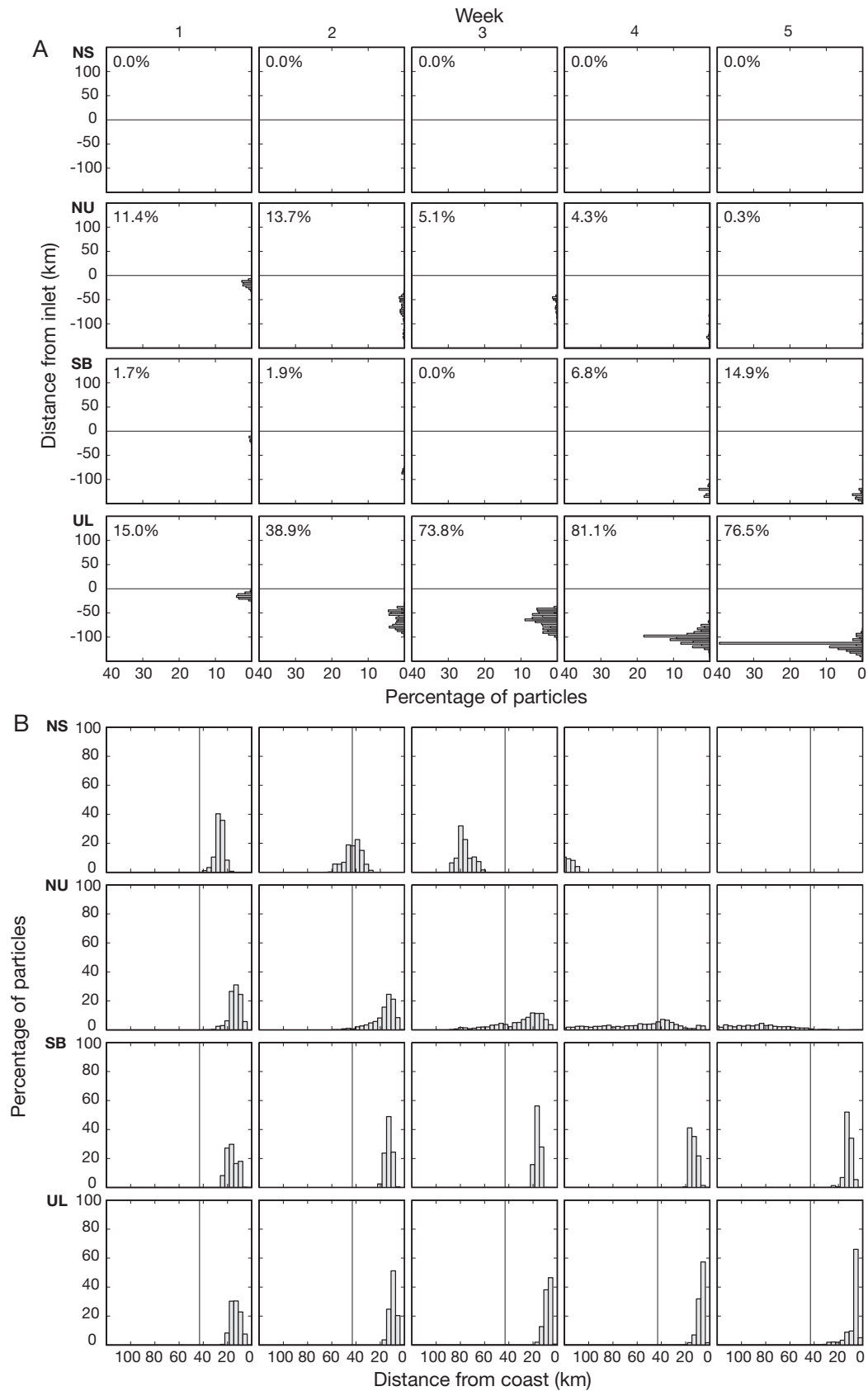


Fig. 11. Spring simulation, 1st release. See Fig. 8 for details

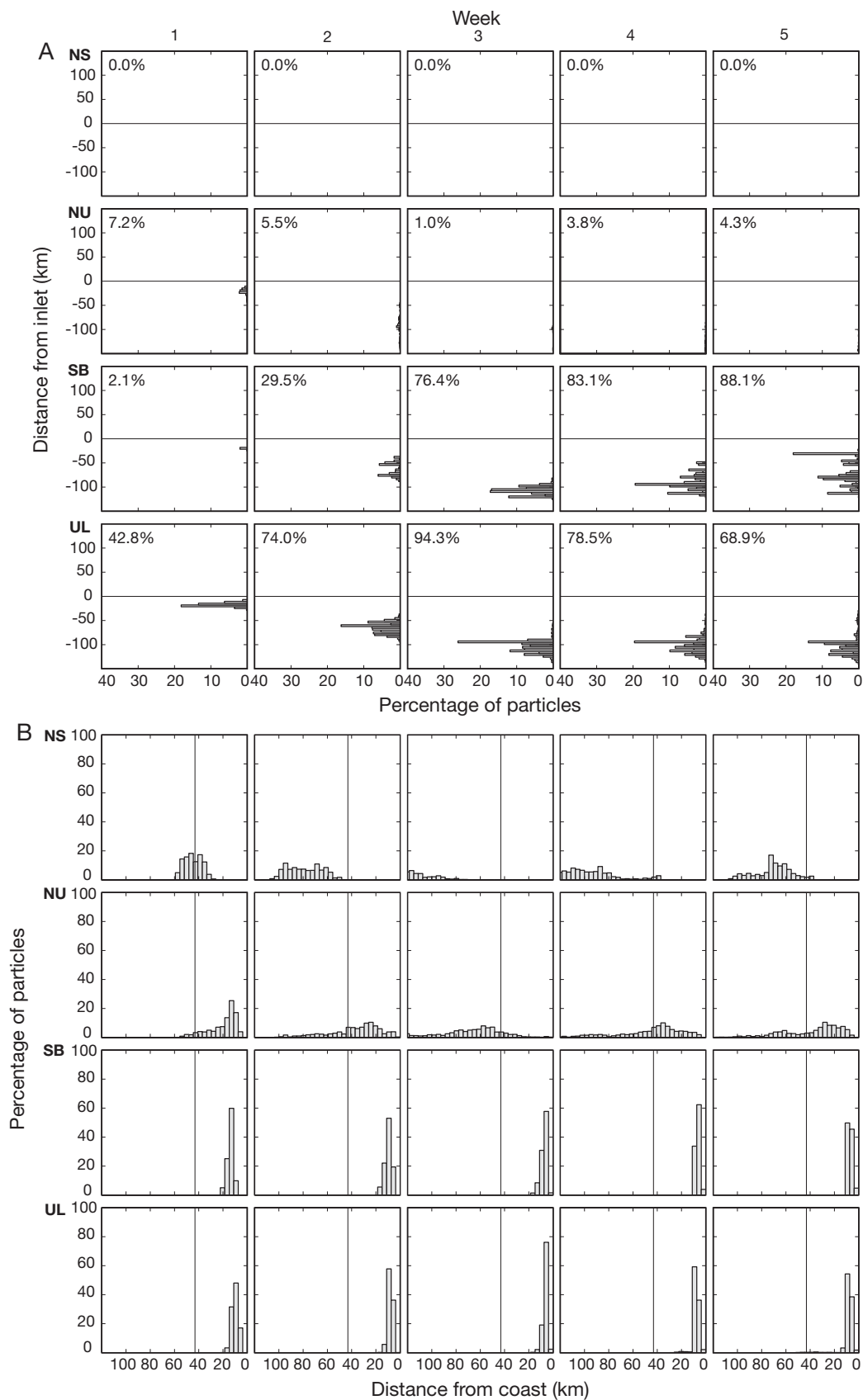


Fig. 12. Spring simulation, 2nd release. See Fig. 8 for details

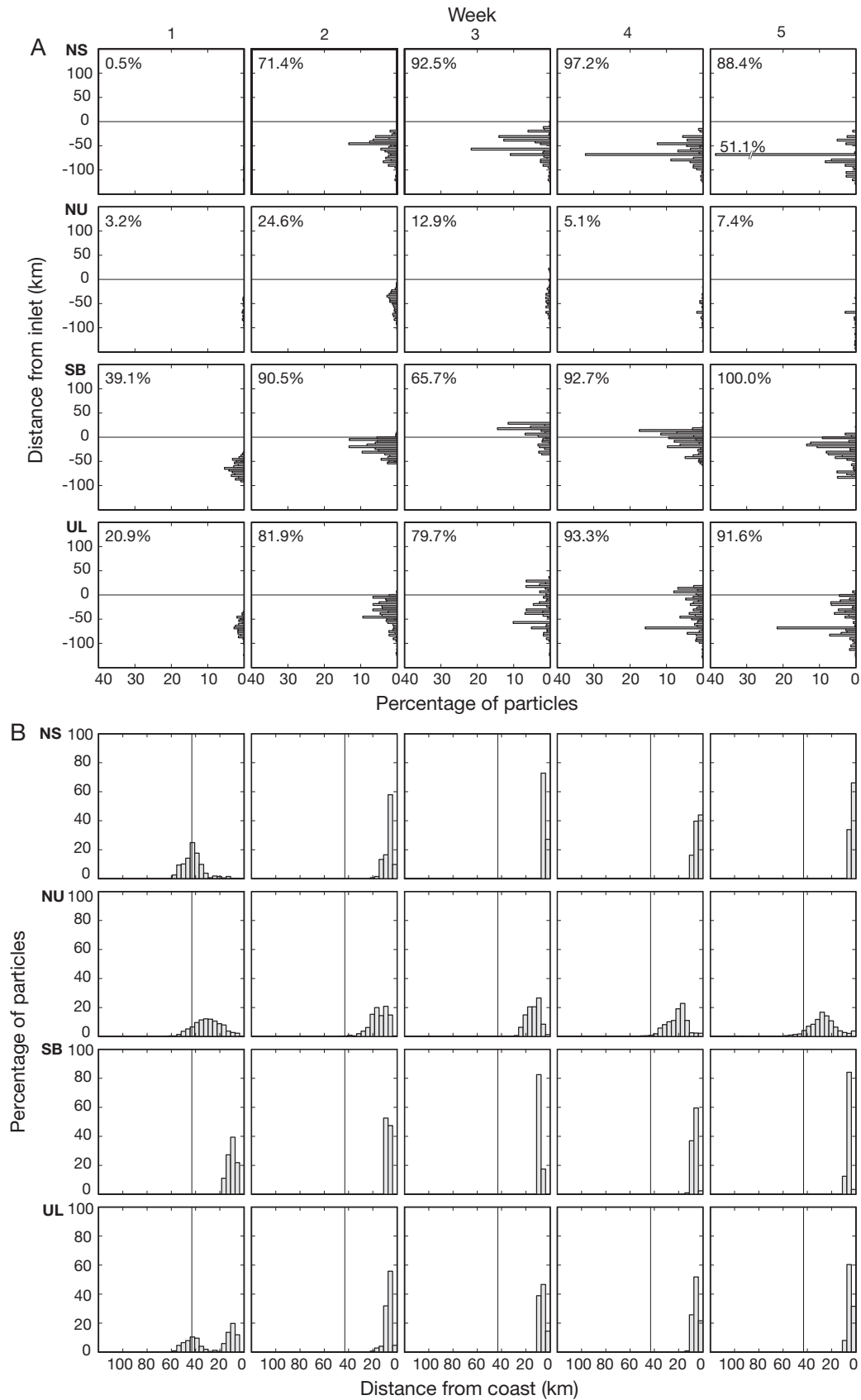


Fig. 13. Spring simulation, 3rd release. See Fig. 8 for details

option was taken due to the lack of detailed information that would be necessary to simulate ontogenetic shifts in distribution of *Carcinus maenas*. However, this is an unrealistic situation because in most cases behavioural reactions of decapod larvae change throughout larval ontogeny, leading to variations in the average depth of distribution with age (Sulkin 1984, Queiroga & Blanton 2004). Ontogenetic migrations are likely to also affect advection patterns in this species, as suggested for other invertebrate groups (Peterson 1998). A second simplification of the model was that mortality was set to 0. Estimates for decapods indicate that larval mortality may often exceed 90% over the full planktonic period (Morgan 1995). Based on data on abundance of first and last stage larvae found inside the Ria de Aveiro (Queiroga 1995), and assuming that larvae that do not return to the estuary will die, it is possible to estimate an overall mortality value of 99% for *C. maenas*: first zoea produced inside the estuary were 100 times more abundant than the megalopae that recruited into it. Little is known about how these high mortality values are distributed among age classes of larvae, or about the variability of mortality over space (e.g. concentrations of predators might be higher closer to the coast). Setting a constant mortality with time or space was a simplification that would not change the pattern of distribution, but only decrease the number of drifters returning or retained close to the coast. In our opinion, these imperfections in the model do not impinge on the interpretation of the very clear and distinctive patterns of dispersal produced by the simulations, which depended on the type of migration and on its interaction with wind regimes.

The first pattern that emerged from the simulations was that particles with DVM were retained to a greater extent in the inner shelf region during upwelling than in any other combination of migration scenario and wind regime. This arose from the bottom Ekman coastward current characteristic of the upwelling circulation that contrasts with the downwelling regime (Fig. 14). Both DVM scenarios (SB and UL) resulted in a longer period of time spent in deeper layers than at the surface, which agreed with observations made for several species (Shanks 1986, Jamieson & Philips 1988, Abelló & Guerao 1999). Therefore, coastward advection during the day overcompensated the surface offshore transport during the night. A second pattern was that dispersal was highest and retention lowest for particles that were not subjected to DVM and released with a uniform vertical distribution (NU). The lowest aggregations resulted from particles at different levels being subjected to different instantaneous currents, thereby becoming separated from each other. In this scenario, the size of the larval pool in the inner shelf region after 5 wk was typically below 4% independently of the

wind regime, while retention under the other scenarios often rose above 50%. Surface particles (NS) generated a third pattern. These particles were more sensitive to the wind, and responded more quickly and extensively to wind variations. In this scenario, aggregation near the coast occurred both with non-upwelling and upwelling regimes, and was associated with westerly winds and the resulting convergence of the surface layer with the coast.

The main conclusion of this study is that upwelling conditions do not necessarily lead to offshore transport of larvae. Upwelling can lead to the offshore transport of larvae that do not display vertical migration behaviour and either remain at the surface or become passively redistributed throughout the water column by the vertical component of the currents. However, decapod larvae seldom, if ever, show these characteristics. In fact, given that nocturnal DVM is the general condition exhibited by these organisms, it may be that retention in the inner shelf region and recruitment to littoral habitats is enhanced during the upwelling season. In the coast of northwest Iberia, which lacks topographic irregularities that may generate concentration and retention areas, nocturnal migration may constitute an important mechanism necessary to avoid seaward dispersal of the larvae.

Two aspects of the biology of *Carcinus maenas* along the Portuguese coast are consistent with the retention of larvae in the inner shelf region due to DVM. A study of the distribution of larvae off the Aveiro coast during April (Queiroga 1996) showed that maximum abundance of all larval stages was located over the middle shelf, and that larvae were not collected beyond the shelf break. The results of the simulations in this study showed that scenarios without DVM resulted in particle distributions that often extended well beyond the shelf break, in sharp contrast to scenarios with DVM

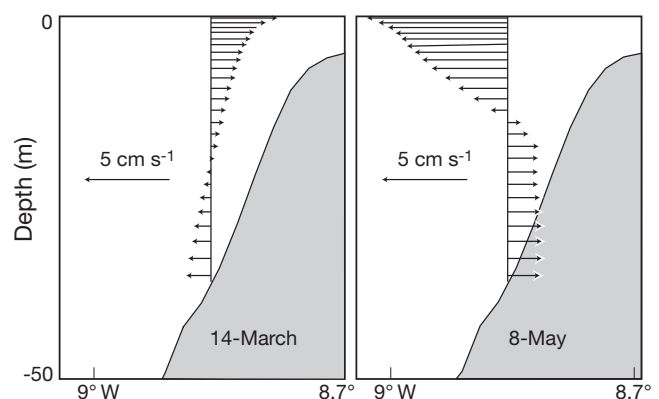


Fig. 14. Vertical profile of velocity in front of Ria de Aveiro inlet during 1 downwelling (left) and upwelling (right) event. Currents averaged over inertial period on 14 March and 8 May, respectively

(Figs. 8B to 13B). The other aspect is a temporal mismatch between the initiation of larval production and subsequent recruitment. Along the Portuguese coast, large numbers of first zoeae of *C. maenas* can be found from November to July (Gonçalves 1991, Paula 1993, Queiroga 1995, Sprung 2001), but major recruitment events in estuaries only take place from April onwards (Queiroga 1993, Sprung 2001, Almeida & Queiroga 2003). Larval development time cannot account for this delay of several months between production of larvae and recruitment, because *C. maenas* larvae take at most 6 wk to develop from hatching to the megalopae stage within temperatures commonly found in Portugal during winter and early spring. This mismatch between larval production and recruitment (Sprung 2001) could partly be explained if the onset of the upwelling season aids in the retention of vertical migrating crab larvae in shelf waters. Climatological upwelling indices calculated for the Portuguese coast (Huthnance et al. 2002) indicate that persistent upwelling events may start as early as March to May, and these could set the conditions for successful recruitment of the species.

Several studies on recruitment of invertebrate larvae in relation to upwelling/downwelling circulation (e.g. Flores et al. 2002, Johnson et al. 1986, McConnaughey et al. 1995, Wing et al. 1995) emphasized that the patterns of dispersal depend on the nature of the interactions between physical forcing and larval behaviours, including those that affect the position of the larvae along the water column. In a recent and timely paper on vertical distribution and horizontal advection, Shanks & Brink (2005) demonstrate that slow-swimming bivalve larvae (swimming velocities $<0.1 \text{ cm s}^{-1}$) may be retained in nearshore waters ($<5 \text{ km}$ from the coast) despite upwelling and downwelling; they proposed a conceptual model based on a depth-keeping mechanism that may explain retention within a narrow coastal strip. Despite differences in the biological models (depth-keeping mechanism in slow-swimming bivalve larvae; nocturnal DVM in strong-swimming decapod larvae), the present study and the study by Shanks & Brink indicate that larvae of littoral invertebrates may be retained in inshore waters in an environment dominated by strong upwelling and downwelling currents. The existence of a pool of larvae in nearshore waters increases the likelihood of successful onshore and up-estuary transport by a variety of bio-physical mechanisms (e.g. Queiroga et al. 2006).

Our results regarding the scales of along-shore transport may also be relevant to an understanding of other aspects of the dynamics of *Carcinus maenas* populations in the region. The west coast of northern Iberia has several estuaries and rias separated by dis-

tances of 20 to 60 km, which all harbour populations of the species. The along-shore distribution of the particles retained in the inner shelf region showed maxima located predominantly to the north of the inlet of the Ria de Aveiro in winter, and to the south in spring (Figs. 8A to 13A). The direction of transport was consistent with the winter and summer oceanographic regimes in the region (Wooster et al. 1976, Mazé et al. 1997, Huthnance et al. 2002, Peliz et al. 2005). During the simulated period, which lasted 5 consecutive weeks, the maxima were typically located at distances of 50 to 100 km from the release point. This radius of dispersal is enough to account for the exchange of larvae between adjacent systems, indicating that these populations likely exchange individuals on a regular basis.

Another result of this simulation study that is applicable to mechanisms of across-shore transport of larvae is that onshore wind events were responsible for downwind advection of neustonic larvae towards the coast. Correlations between onshore winds and recruitment have been found in several studies of invertebrate larvae (e.g. Hawkins & Hartnoll 1982, Olmi 1995), and a recent study showed that surface drifters are advected onshore by sea-breezes (Tapia et al. 2004). Since megalopae of decapods may occupy the neuston layer for extended periods of time, these larvae may use occasional or persistent onshore winds for return to littoral habitats (Shanks 1995).

As in other modelling studies, the predicted patterns of along- and across-shore dispersal are speculative because of the uncertainties regarding (1) the ability of the model to realistically represent the main aspects of oceanography in the area, and (2) details of the behaviour of the larvae. However, the results of the model assisted in the formulation of hypotheses that can be experimentally addressed in the future. One hypothesis is that the delay between production and recruitment of larvae depends on the onset of the upwelling season. The other is that there is a regular exchange of larvae between adjacent populations of *Carcinus maenas* along the west coast of northern Iberia. These hypotheses can be tested using observational programs to monitor the supply of larvae into estuaries and recruitment from winter to early summer, and with the use of high resolution genetic markers that can describe the genetic structure of populations along the coast.

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