

# Endogenous tidal rhythms of vertical migration in field collected zoea-1 larvae of the shore crab *Carcinus maenas*: implications for ebb tide offshore dispersal

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**ABSTRACT:** Employing a highly sensitive infra-red light actography system, circatidal rhythms of vertical migration were recorded in first stage zoea larvae of the common shore crab *Carcinus maenas* (L.), freshly collected from coastal waters. The rhythms persisted in constant conditions in the laboratory for several days, ascent occurring at the times of expected ebb tides at collection sites, and descent during expected flood tides. Timing was identical in larvae sampled at different stage of spring/neap cycle and from sites where different hydrodynamic conditions prevail. These experiments, supported by repeated surface plankton samples which confirmed that zoea-1 larvae of *C. maenas* were most abundant at the surface during ebb tides, suggest that the vertical migration behaviour might be linked with avoidance of stranding and offshore dispersal of newly released larvae. The fact that tidal migration rhythm was exhibited by larvae collected from different sites implies that the behaviour is probably widespread for the species. So far, endogenous tidal rhythms of vertical migration in plankton have been demonstrated solely in a few estuarine forms, and have been interpreted only as estuarine retention or reinvasion mechanisms. Present results appear to be the first to demonstrate that endogenous tidal rhythms also exist in the planktonic larvae of a coastal invertebrate and suggest that these larvae may have an adaptive mechanism to avoid stranding and enhance offshore dispersal in the open sea.

**KEY WORDS:** *Carcinus maenas* · Zoea-1 · Tidal vertical migration · Endogenous · Timing · Surface abundance · Dispersal · Avoidance of stranding

## INTRODUCTION

Diel vertical migration in plankton has been recognized for more than a century (Longhurst 1976), but it is only relatively recently that plankton vertical migration over tidal timescales has been reported. The latter has been typically reported in the context of retention and reinvasion mechanisms for the larvae of species which as adults occur in estuaries. Field surveys in estuaries have reported such behaviour in the larvae of molluscs (Carriker 1951, 1961, Wood & Hargis 1971), crab zoeae (DeCoursey 1976, Cronin & Forward 1982), crab megalopae (Epifanio et al. 1984, Brookins & Epi-

fanio 1985, Mense & Wenner 1989, Dittel & Epifanio 1990, Little & Epifanio 1991, De Vries et al. 1994, Olmi 1994, Queiroga et al. 1994), penaeid postlarvae (Young & Carpenter 1977, Rothlisberg et al. 1995) and planktonic copepods (Wooldridge & Erasmus 1980, Hough & Naylor 1991). However, no attention appears to have been paid to the possible occurrence of tidal vertical migration in the larvae of open coast species.

Theoretically, if a coastal planktonic organism exhibits vertical migration rhythms that are exactly synchronized with the tidal period in tidal currents, a particularly efficient unidirectional transport mechanism results. Moreover, depending on the phase of the vertical migration, the direction of transport could be with either the flood tide or the ebb tide direction of flows (Hill 1991a, b, 1995). This suggests that tidal vertical

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migration is worthy of investigation in planktonic larvae of coastal invertebrates as a possible mechanism for assisting dispersal or recruitment.

The biology and ecology of juveniles and adults of the shore crab *Carcinus maenas*, commonly found on coasts and estuaries of Northwest Europe and North-east America (Crothers 1968, Berril 1982), are well documented (Broekhuysen 1936, Naylor 1962, Crothers 1968, Klein-Breteler 1975, 1976, Thiel & Darnedde 1994). However, whilst larval dispersal and recruitment in other crab species have attracted much attention in recent years (Johnson & Gonor 1982, Provenzano et al. 1983, Johnson 1985, Shanks 1985, Epifanio 1988a, b, McConaughy 1988, 1992, Little & Epifanio 1991, Hobbs & Botsford 1992, Hobbs et al. 1992, McConaughy et al. 1992, De Vries et al. 1994, Olmi 1994, Tankersley & Forward 1994), these processes have been largely ignored in *C. maenas*, except for a recent field study concerning larval dynamics of the species in an estuary (Queiroga et al. 1994).

The present work aimed to investigate the vertical migration behaviour of newly released larvae of *Carcinus maenas* from coastal waters. Our preliminary observations revealed that these larvae are dispersed seawards, as was also shown by Queiroga et al. (1994) in a Portuguese estuary. We also sought by laboratory experiments to ascertain whether any vertical migration rhythms exhibited by *C. maenas* were endogenous. Harris (1963) and Enright & Hamner (1967) have published evidence for endogenous control of diel vertical migration in open sea plankton and Cronin & Forward (1979), Hough & Naylor (1992) and Tankersley & Forward (1994) reported endogenous control of tidal migration rhythms of estuarine plankton species. However, there are, so far, no reports of endogenous circatidal rhythms in an open sea plankton species.

## MATERIALS AND METHODS

**Laboratory studies of larval tidal vertical migration rhythms. Collection of crab larvae:** The first stage zoea larvae of *Carcinus maenas* were collected from 3 different sites along the Menai Strait and Cardigan Bay, North Wales, UK, during May to July 1994. Site 1 is located between Menai Bridge and Beaumaris in the Menai Strait ( $53^{\circ}13'N$ ,  $04^{\circ}09'W$ ), close to the north-east end of the Strait. At this site, a series of collections was taken at different stages of semilunar (spring/neap) cycles. Additional collections were taken at 2 other sites, one (Site 2) at Traeth Malynog ( $53^{\circ}09'N$ ,  $04^{\circ}19'W$ ), at the opposite southwest end of the Menai Strait where high tides occur roughly 1 h earlier than that at Site 1, and another (Site 3) near Pwllheli ( $52^{\circ}50'N$ ,  $04^{\circ}25'W$ ) on the coast of Cardigan Bay

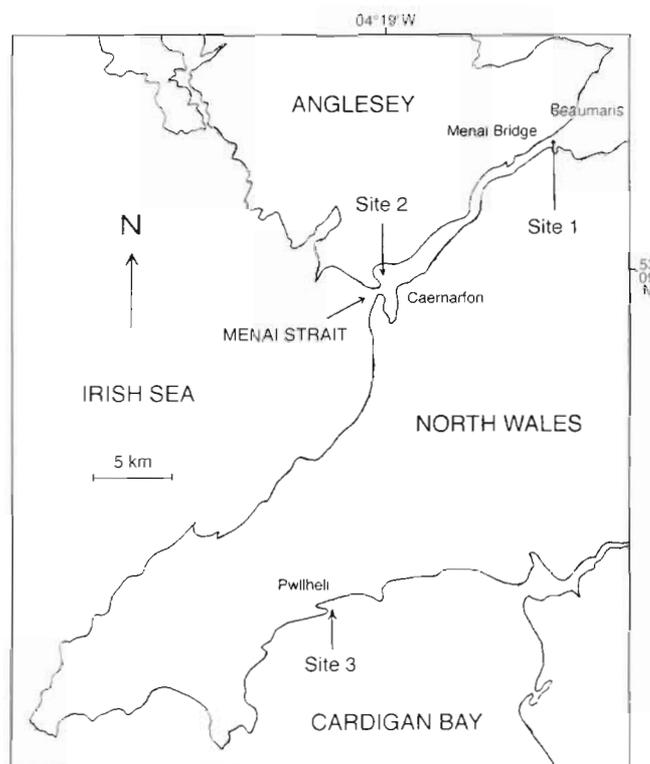


Fig. 1 Menai Strait and Cardigan Bay coasts of North Wales, UK, showing sampling sites

(Fig. 1). These locations were chosen to determine whether the timing of the tidal migration varies spatially and if the behaviour is associated with local hydrodynamic conditions such as the strong residual current in the Menai Strait (Harvey 1968, Sherwin 1992). The tides in the Menai Strait and Cardigan Bay are typically semidiurnal with a period of approximately 12.4 h. Details of the height and time of the tides were obtained from *Menai Strait Tidal Tables 1994* and from the *Laver Liverpool Tide Table 1994*.

The zoea larvae of *Carcinus maenas* were collected in plankton tows (50 cm diam. nets, 0.2 mm mesh size) conducted from a small boat. In order to obtain sufficient numbers of larvae for an actograph experiment, sampling was normally carried out for 2 to 3 h. However, the duration of each tow was limited to no more than 15 min to minimize possible damage to the larvae. Samples were immediately transferred to the laboratory and the zoea-1 larvae of *C. maenas* separated out and identified, following the descriptions of Williamson (1903) and Rice & Ingle (1975). Indeed in the sampling areas, during the summer peak breeding season, most of zoea larvae in the samples were stage 1 zoeae of *C. maenas*, reflecting the abundance of the crab in the area. No attempt was made to determine the moult stage of the first zoeae, but it was noted that generally no more than 10% of larva had moulted to zoea-2 by

the end of the experiments. Separation of appropriate larvae was time-consuming but no more than 12 h elapsed between the collections and the start of an experiment. Effort was made to minimize the temperature changes during the transfer and sorting and these were generally less than 6°C, a difference which was shown in preliminary experiments not to affect the phase of zoea vertical migration rhythms.

**Recording of migration rhythm:** After sorting, larvae in batches of several hundreds were placed in an infra-red light actograph similar to that described by Hough & Naylor (1992). This consisted of a chamber containing seawater with 2 sets of 4 infra-red transmitters and receivers in an array on each side of the chamber. The chamber was constructed of 6 mm transparent Perspex with interior dimensions 40 cm high, 15 cm wide and 5 cm from front to back. Two sets of 4 infra-red transmitters and receivers, operating from front to back across the narrowest dimension of the chamber, were so arranged that one set of the transmitters and receivers was placed just below the water surface and the other just above the bottom. In this way, larval swimming activity on the top and bottom of the chamber was monitored simultaneously.

During the experiments, an event was recorded each time an infra-red light beam was interrupted by larvae swimming across it. All infra-light channels were monitored by a BBC model B microcomputer and, every 15 min, the cumulative sum of beam interruptions in each channel was loaded to a cassette recorder and recorded on tape. A header-tank with a pipe of 1.0 mm diameter inner bore provided very slow, drop by drop fresh seawater supply (approx. 150 ml h<sup>-1</sup>) into one end of the chamber, and an outflow pipe was placed at the other end, protected by a mesh panel of 0.2 mm aperture to prevent loss of larvae. The fresh seawater supply not only maintained water quality, but also stabilized the water level in the chamber, avoiding loss by evaporation. Control experiments showed that the slow water flow did not affect larval migration behaviour.

All experiments were carried out in constant darkness, allowing a 1 to 2 h acclimation period before recording began. Once an experiment started, the whole system was left undisturbed whilst recordings were made and larvae were not fed during the experiments. Survival rate of larvae varied between experiments, but normally, if an experiment was run for less than 4 d, more than half of the larvae survived. During all experiments, water temperature in the experimental chamber was maintained at 16 ± 1°C and salinity varied between 32 and 34‰. At the sampling sites during the period of the experiments, field seawater temperature and salinity normally varied between 12 and 17°C and between 30 and 34‰, respectively.

**Data treatment:** Generally, the pattern of records was consistent between the 4 channels in each block of sensors. Therefore, unless there was an obvious malfunction in a single channel, records of the 4 channels in a same block were summed and plotted as 'swimming activity in top channels' and 'swimming activity in bottom channels' against elapsed time. Data plots are of original data and of periodogram analyses based on repeated 'Buys-ballot' form-estimates. Calculations are made of the variance of raw data points grouped in standard units over each period length being tested for. A function of this variance (usually standard deviation) is then plotted against period length to produce a graphical periodogram. High values of the periodogram statistic occur when the period under investigation approximates to the periodicity inherent in the raw data. Significant periodicity is assumed when the periodogram statistic of raw data for a given period is greater than the upper 95% confidence limit of a 'periodogram' (a regression line for which hyperbolic confidence intervals can be plotted) derived after randomizing the original data. Full details of periodogram procedure are given in Williams & Naylor (1978).

**Surface plankton sampling.** Repeated surface plankton samples were taken at Site 2, Traeth Malynog, by towing a plankton net of 50 cm diameter, 0.2 mm mesh size at a constant speed (approximate 2.5 knots) at a depth of no more than 1 m for 15 min across the sheltered south facing bay, using a small boat. The samples were taken at different stages of the tide over a tidal cycle at different semilunar and diel phases during May to July 1994. Temperature and salinity were also recorded. The time interval between samples was not uniform but generally it was no more than 2 h.

Plankton samples were fixed in 4% formalin immediately upon collection. Entire samples were searched for zoea-1 larvae of *Carcinus maenas* and numbers counted in the laboratory.

## RESULTS

### Larval tidal vertical migration rhythms in the laboratory

Clear circatidal vertical migration rhythms were present in all experiments using freshly collected zoea-1 larvae of *Carcinus maenas* kept in constant conditions in the laboratory. Peaks of swimming activity recurred at approximately 12.4 h intervals in records of both top and bottom channels in any one experiment. Moreover, the peaks and troughs were always reciprocal between the records at the surface and bottom of the test chamber, indicating that larvae moved up and down periodically in the chamber. Figs. 2A to 6A show examples of the results. Periodogram analysis con-

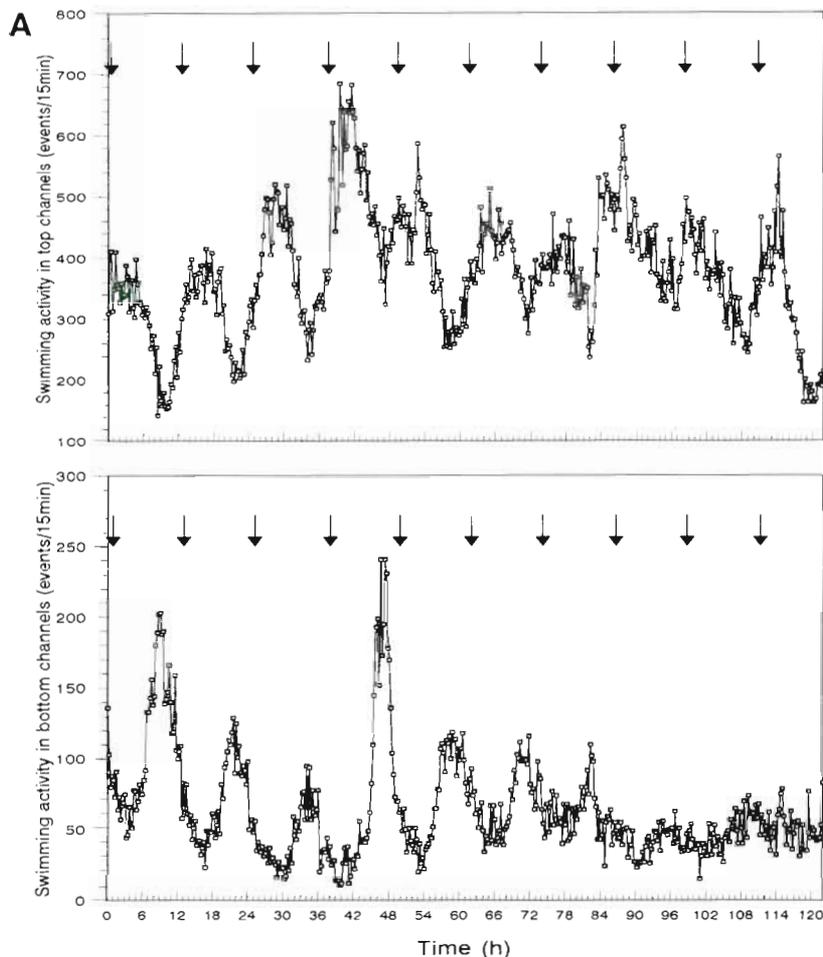
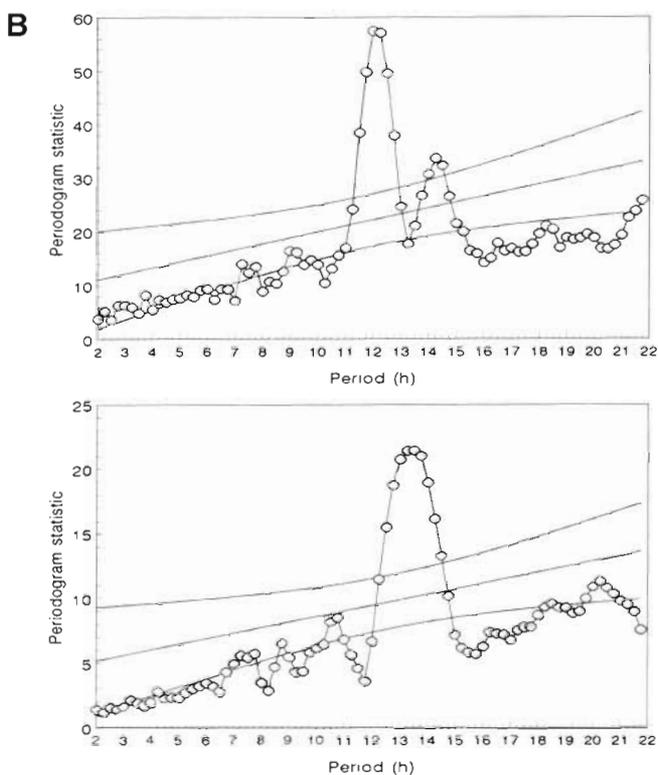


Fig. 2. *Carcinus maenas*. (A) Swimming activity records of field-caught zoea-1 larvae showing tidal vertical migration rhythms in constant laboratory conditions. Upper and lower part of the graph represent records near the surface and near the bottom of a vertical chamber, respectively. Arrows show times of expected high tides at the collection site. The experiment started at 1:00 h, 14 June 1994, with an initial number of 800 freshly collected zoea-1 larvae. The larvae were collected from Site 1, at the northeast end of the Menai Strait during a spring tide, and 745 larvae survived when the experiment stopped 5 d later. (B) Periodogram analysis of each of the data sets presented in A, with 95% confidence limits derived after randomization of the original data



firming that the rhythms in all experiments were circatidal (Figs. 2B to 6B).

Though most of the experiments were terminated after 5 or 6 tidal cycles, Fig. 2A shows a prolonged experiment in which, even though the larvae were starved throughout, the rhythm persisted for 10 tidal cycles without excessive damping. None of the records showed any indication of circadian modulation of the endogenous circatidal rhythms (Figs. 2A to 6A).

In all experiments, peaks of abundance at the top of the vertical test chamber consistently occurred soon after expected high tides, i.e. during expected ebbing phases. Reciprocally, abundance at the bottom of the chamber always occurred during expected flood tides. The phase relationship between the timing of the vertical migration and the local tidal cycle was the same in larvae sampled at different stages of the spring/neap cycle and from sites where the tidal phase and residual flows are different. For example, Figs. 2A to 4A demonstrate that this was so in larvae collected from Site 1 (Fig. 1) at a spring tide, after springs and after neaps. Similar results are illustrated in Figs. 5A & 6A using larvae collected from Site 2 after neaps and from Site 3 (Fig. 1) at a neap tide.

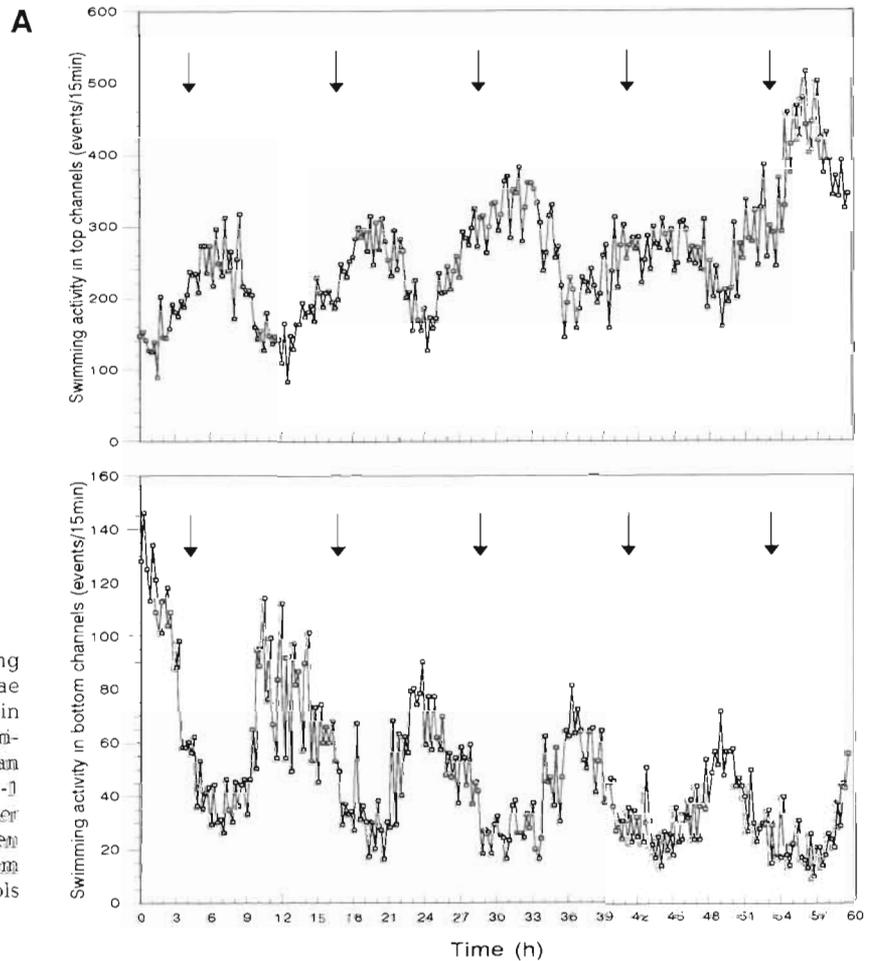
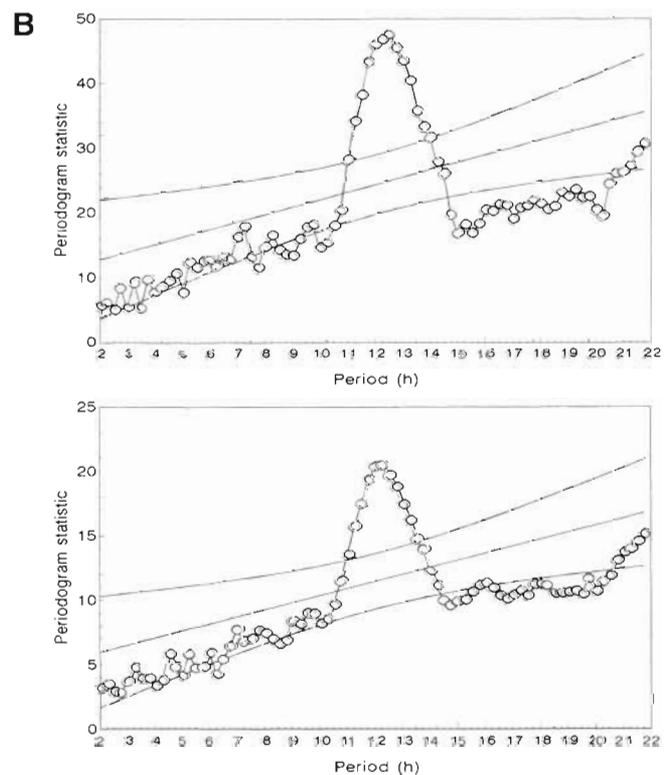


Fig. 3. *Carcinus maenas*. (A) Swimming activity records of field-caught zoea-1 larvae showing tidal vertical migration rhythms in constant laboratory conditions. The experiment started at 0:00 h, 17 May 1994, with an initial number of 600 freshly collected zoea-1 larvae. They were collected from Site 1 after spring tides and 469 larvae survived when the experiment stopped. (B) Periodogram analysis of the data presented in A. Symbols and further details as in Fig. 2 legend

#### Larval abundance in coastal surface waters

Fig. 7A–E shows abundance of first stage zoeae of *Carcinus maenas* in surface plankton tows over the tidal cycle at Site 2 during April to July 1994. The samples were taken over approximately 1 tidal cycle (12 h) at different stages of the semilunar and diel cycles to eliminate any bias due to spring/neap or day/night differences. Fig. 7A, D shows results of sampling during daytime neap tides, Fig. 7B during a nighttime neap tide, Fig. 7C during a nighttime spring tide and Fig. 7E after springs at nighttime. Clearly, in most cases, significantly fewer zoea-1 larvae were caught around low tides, but numbers increased just before high tide and reached a peak after that time. The pattern appears consistent regardless of the sampling date and the stage of spring/neap and diel cycle (Fig. 7A–E), and is summarized from pooled data in Fig. 8. This observed pattern in field catches fits well with laboratory records of vertical migration in the actograph (see Figs. 2A to 6A), providing evidence that tidal vertical migration exists in the field and that larvae ascend to surface most abundantly at the early phase of ebb tides.



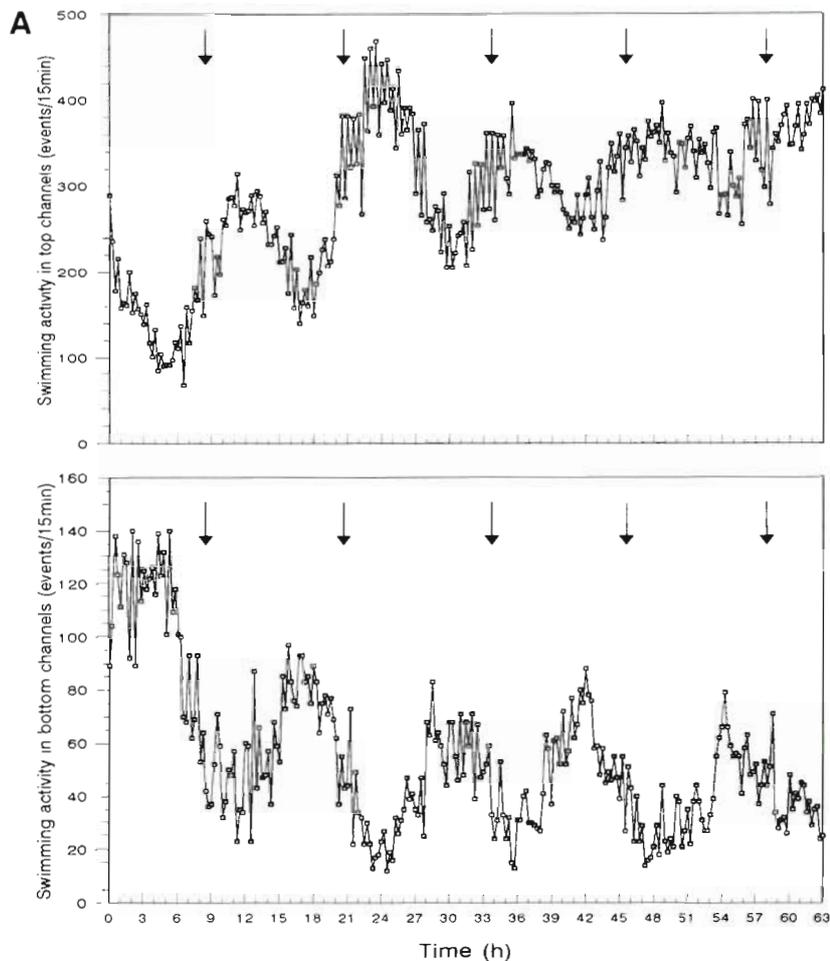
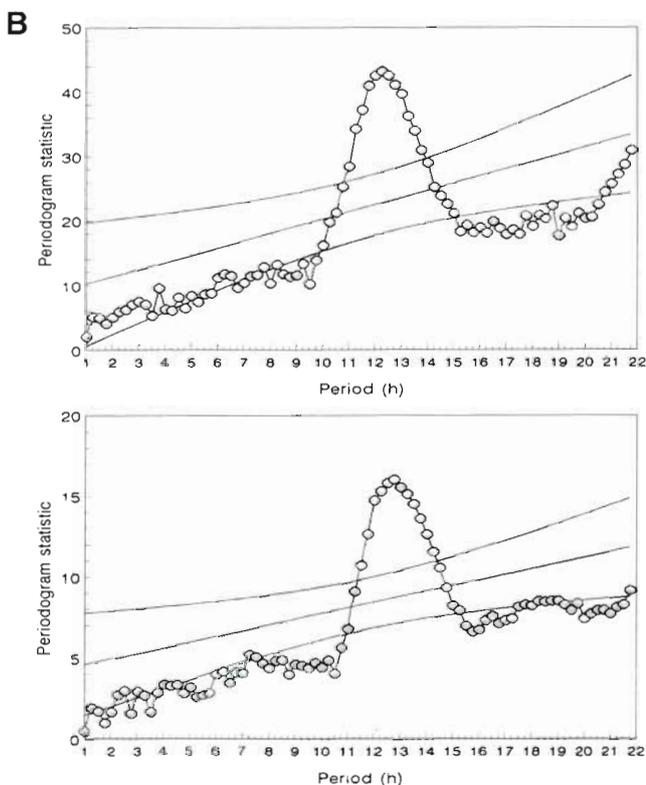


Fig. 4. *Carcinus maenas*. (A) Swimming activity records of field-caught zoea-1 larvae showing tidal vertical migration rhythms in constant laboratory conditions. The experiment started at 1:00 h, 24 May 1994, with an initial number of 825 freshly collected zoea-1 larvae. They were collected from Site 1 after neap tides and 700 larvae survived when the experiment stopped. (B) Periodogram analysis of the data presented in A. Symbols and further details as in Fig. 2 legend



DISCUSSION

Present laboratory and field results together suggest that, in the field, newly released zoea larvae of *Carcinus maenas* undergo endogenously controlled tidal vertical migration, whereby they rise to the surface during early ebbing tides and remain deeper at low tide and the flood tides, regardless of semilunar and diel state. In shallow coastal seas, the predominant movement of water is often due to the tide (Hill 1995) and UK shelf seas, including the study area, are characterized by this feature (Prandle 1991, Tomczak & Godfrey 1994). As the velocity of tidal currents decreases with depth and sharply decreases to zero within a few meters to the sea bed, interaction with such oscillatory tidal flows by vertical migration which is specifically synchronized with tide period could lead to unidirectional transport of the migrants (Hill 1991a, b, 1995). In the present locality, since slack water occurs about or slightly earlier than the time of high tide in the study areas (Sherwin 1992), it seems reasonable to postulate that the larvae which repeatedly rise to the surface after predicted high waters experience ebb

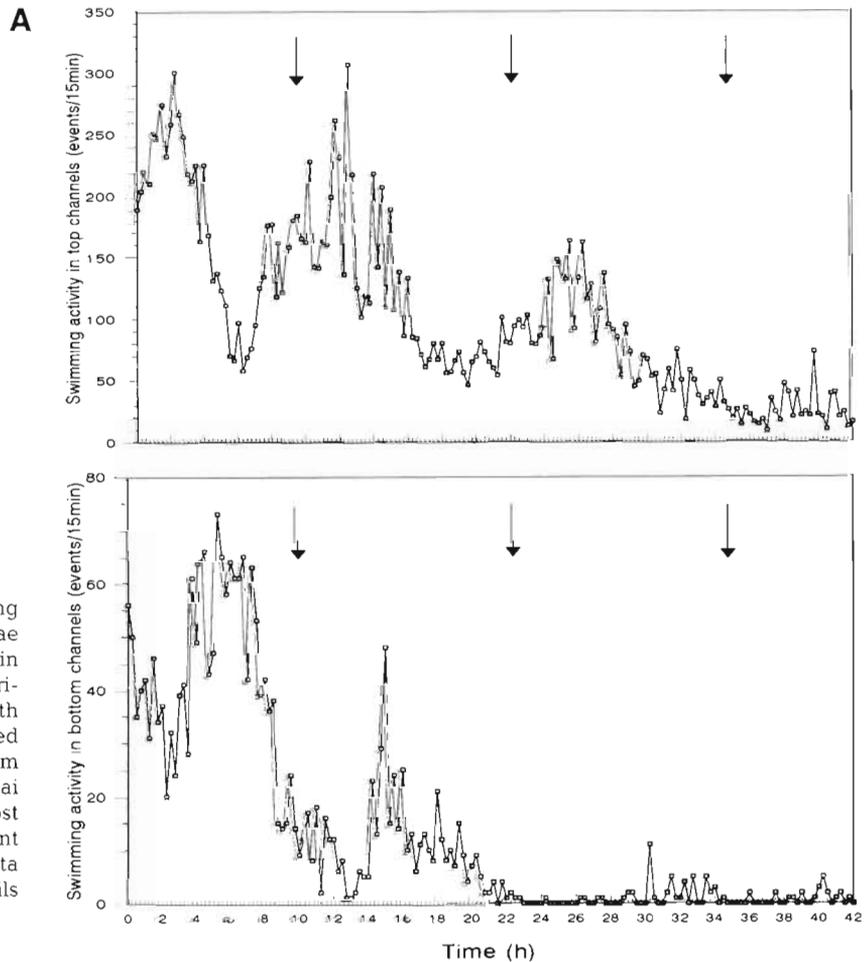
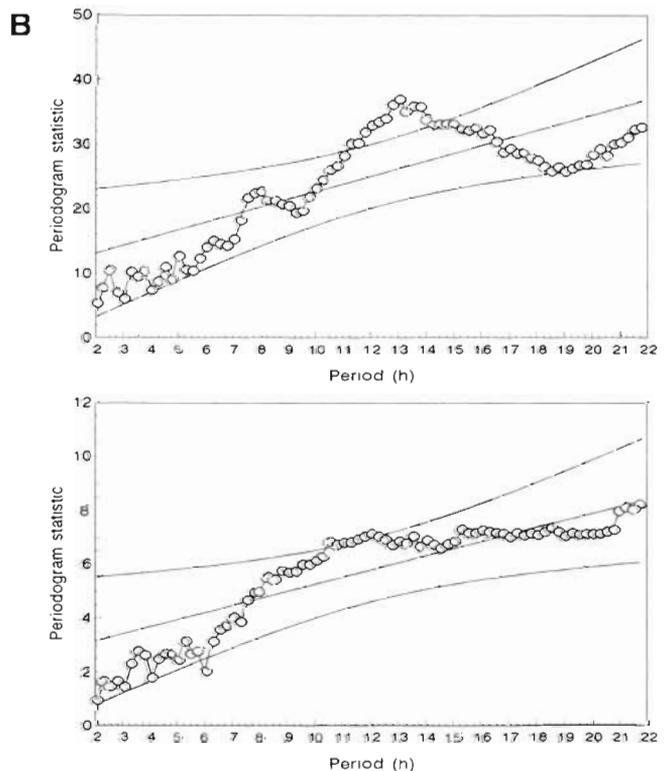


Fig. 5. *Carcinus maenas*. (A) Swimming activity records of field-caught zoea-1 larvae showing tidal vertical migration rhythms in constant laboratory conditions. The experiment started at 23:30 h, 23 June 1994, with an initial number of 480 freshly collected zoea-1 larvae. They were collected from Site 2, at the southwest end of the Menai Strait after neaps. Due to water fouling, most larvae were dead when the experiment stopped. (B) Periodogram analysis of the data presented in A. Symbols and further details as in Fig. 2 legend

tide flows and are preferentially transported seaward by the across-shelf component of the ebb flows. Indeed, since ebb-phased upward swimming occurred in newly released *Carcinus* zoeae from all localities studied, the inherited pattern of vertical migration behaviour (Zeng & Naylor 1994) is considered to be adaptive to general tidal conditions in coastal waters rather than to specific hydrodynamic conditions in a particular area. Such a hypothesis could certainly be tested by further detailed distributional studies of such larvae in Menai Straits and adjacent open coasts. However, whether or not that hypothesis is validated in a particular area, the observed vertical migration behaviour should prevent potential stranding of zoea larvae in inshore areas by maintaining larvae near the surface as the tide falls. The latter interpretation would certainly be generalizable, consistent with the widespread distribution of adult *C. maenas* on shores of various hydrodynamical types in Northwest Europe.

In *Carcinus maenas*, though the biology and ecology of adults have been extensively studied (Broekhuysen 1936, Naylor 1962, Crothers 1968, Klein-Breteler 1975, 1976, Thiel & Darnedde 1994), field investigations of



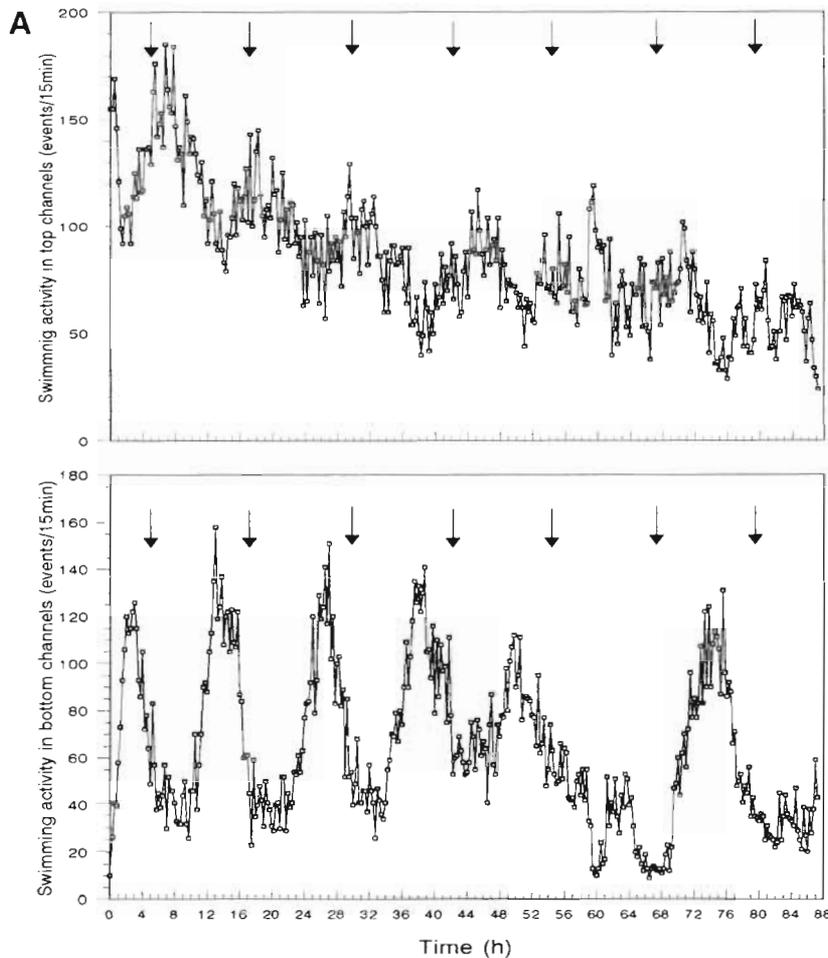
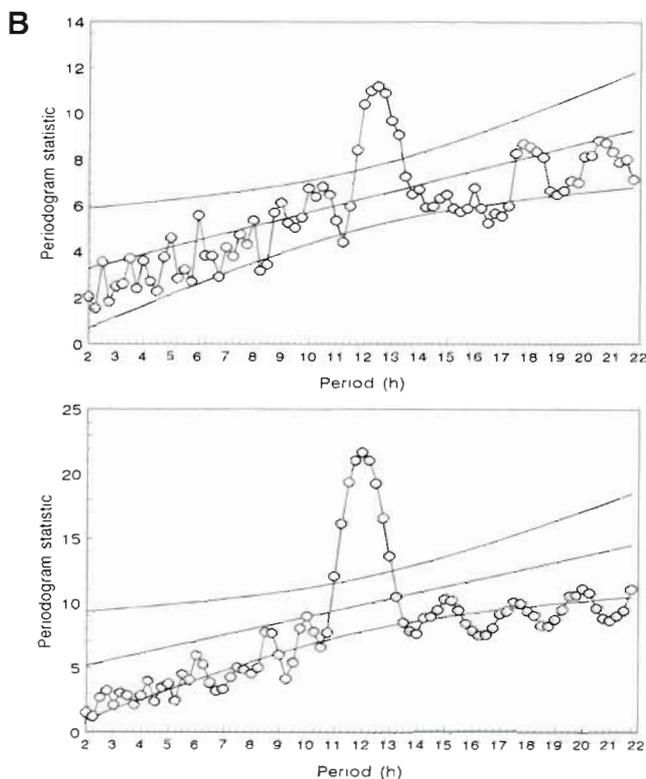


Fig. 6. *Carcinus maenas*. (A) Swimming activity records of field-caught zoea-1 larvae showing tidal vertical migration rhythms in constant laboratory conditions. The experiment started at 2:00 h, 7 July 1994, with an initial number of 800 freshly collected zoea-1 larvae. They were collected from Site 3, Pwllheli in Cardigan Bay, during a neap tide and 450 larvae survived when the experiment stopped. (B) Periodogram analysis of the data presented in A. Symbols and further details as in Fig. 2 legend



larval dynamics are rare. Here we present evidence to suggest that the newly released larvae are dispersed offshore, as was reported in an estuary (Queiroga et al. 1994).

During present field sampling in nearshore coastal waters in the breeding season, mainly first stage zoeae and megalopae were collected, but intermediate stages were rare. In addition, all megalopae in the present study from nearshore coastal waters were found very close to metamorphosis to crab stage. Among thousands of megalopa larvae collected on different dates and months, nearly 60% metamorphosed in 2 d, more than 95% in 4 d and all in 7 d (Zeng & Naylor in press). Since the average development time for megalopae of *Carcinus maenas* is reported to be 13 d at similar temperatures to those recorded in the present study (Dawirs 1985), it is evident that only late megalopae return and occur in coastal areas when the time of metamorphosis approaches.

Studies of hatching rhythms of *Carcinus maenas* also suggest offshore dispersal of the newly released larvae. We have unpublished data (Zeng & Naylor unpubl.) which show that females of *C. maenas* exhibit an endogenously controlled hatching rhythm with

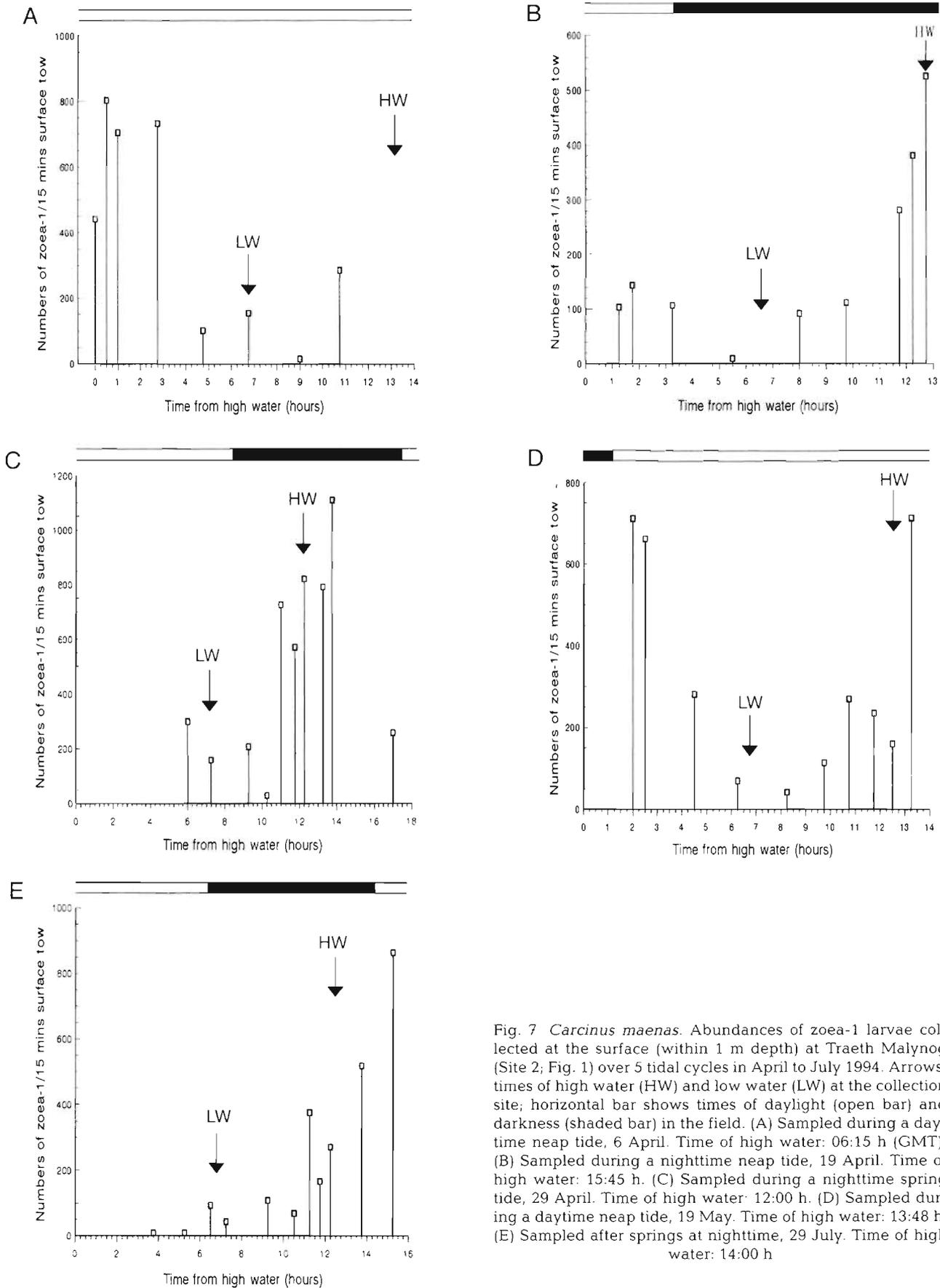


Fig. 7 *Carcinus maenas*. Abundances of zoea-1 larvae collected at the surface (within 1 m depth) at Traeth Malynog (Site 2; Fig. 1) over 5 tidal cycles in April to July 1994. Arrows: times of high water (HW) and low water (LW) at the collection site; horizontal bar shows times of daylight (open bar) and darkness (shaded bar) in the field. (A) Sampled during a daytime neap tide, 6 April. Time of high water: 06:15 h (GMT). (B) Sampled during a nighttime neap tide, 19 April. Time of high water: 15:45 h. (C) Sampled during a nighttime spring tide, 29 April. Time of high water: 12:00 h. (D) Sampled during a daytime neap tide, 19 May. Time of high water: 13:48 h. (E) Sampled after springs at nighttime, 29 July. Time of high water: 14:00 h

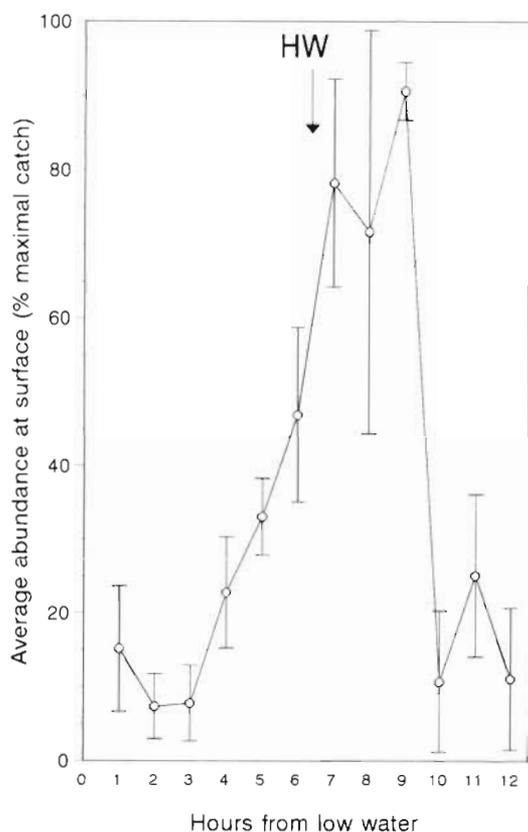


Fig. 8. *Carcinus maenas*. Average abundance of zoea-1 larvae near the surface (within 1 m depth) in relation to the tidal cycle. Error bars indicate  $\pm$ SD. All samples from Fig. 7 were pooled regardless of time and date of the collection and spring/neap cycle. Because of variations in absolute numbers of larvae caught in different samples, all data have been transformed to relative values by dividing by the maximum catch during the same sampling period before pooling. Samples were rounded up to the nearest hour

hatching taking place mainly at nocturnal high tide. Apparently, high tide hatching enhances offshore dispersal of the larvae. In addition, in a study of effects of salinity and temperature on larval survival and development of *C. maenas*, Nagaraj (1993) reported that for first stage zoeae from the Isle of Man, close to present study areas, the highest survival rates were in full strength seawater (35‰). Thus, all available evidence suggests that the newly released zoea larvae of *C. maenas* undertake offshore transport and that development takes place away from the coastal zone, to which the megalopae return a few days before metamorphosis to the crab stage. The tidal vertical migration rhythms of ascent during ebbing tides reported in the present study would reduce the risk of inshore stranding and thus enhance the process of offshore dispersal of the newly released larvae.

Although larval release around nocturnal high tides may account for increased zoea abundance near the sur-

face just after nighttime high tide (Fig. 7A, B, C), it is clear that abundance near the surface also increased during daytime ebbing tides (Fig. 7D, E), leading to the conclusion that larval abundance patterns observed in the field do reflect larval endogenous migration rhythms.

Compared to open coast populations, larval movements of estuarine *Carcinus maenas* are better understood. Queiroga et al. (1994) concluded that zoeae of *C. maenas* in a Portuguese estuary were flushed seaward soon after hatching, consistent with the findings of Nagaraj (1993) that low salinity typically encountered in estuaries could be fatal to *Carcinus* zoea larvae. Therefore, export of newly released larvae and re-invasion of postlarvae or juveniles is suggested as a general mechanism of recruitment by this species in estuaries (Nagaraj 1993, Queiroga et al. 1994). Whether newly released zoeae of estuarine *C. maenas* exhibit tidal rhythms of vertical migration is not known, but upward swimming at the tidal ebb, as reported here, would certainly enhance export of larvae from an estuary.

The phase of endogenous tidal vertical migration in zoeae of *Carcinus maenas* is opposite to that reported in zoeae of *Rhithropanopeus harrisi* for facilitating estuary retention (Cronin & Forward 1979). However, the migration phase in each case remained constant over the spring/neap cycle (Cronin & Forward 1979, 1982). For *R. harrisi* larvae, this is correlated well with the field observations that larvae of all zoea stages of the crab are normally retained in the upper reaches of estuaries (Williams 1971, Sandifer 1973, 1975, Cronin 1982). In contrast, flexibility in phasing of the time of endogenous peak activity over the semilunar cycle and with position along the estuary has been demonstrated for the estuarine copepod *Eurytemora affinis* (Hough & Naylor 1992). These authors reported that copepods collected during spring tides of increasing amplitude showed peak activity during the expected flood tide, while those sampled on spring tides of decreasing amplitude or towards the limit of tidal influence displayed peak activity during the expected ebb tide. The phase-lability was attributed to fine-tuning of behaviour correlated with the field observed concentration of this copepod in middle reaches of an estuary which varies only by a shift upstream at spring tides and downstream at neaps (Hough & Naylor 1991, 1992). In the present study of *Carcinus* zoea larvae, consistent timing of vertical migration over the semilunar cycle is also in agreement with the hypothesis that the behaviour is adaptive for avoidance of stranding inshore and hence enhancement of offshore dispersal of the larvae.

In the crab *Rhithropanopeus harrisi*, it was found that first stage zoeae from an estuary with strong semi-diurnal tides exhibited tidal vertical migration rhythms, whilst in larvae from an estuary with aperiodic tides, no clear migration rhythm was expressed

(Cronin & Forward 1983). In contrast, there were no differences in the rhythmic behaviour of first stage zoeae of *Carcinus maenas* in the present study related to local differences in tidal timing or residual flows. Again, the consistency of behaviour irrespective of locality supports the hypothesis that the behaviour is generally adaptive for facilitating offshore dispersal of the larvae and suggests that the behaviour is likely not to be a local phenomenon, but is widespread in this crab species.

The synchronization process of circatidal rhythms in intertidal animals is well documented (for reviews see Palmer 1974, Enright 1975, DeCoursey 1983, Naylor 1985). In adult *Carcinus maenas*, it has been demonstrated that tidal locomotor rhythms can be entrained by various synchronizers, including changes in hydrostatic pressure, salinity, temperature and immersion/emersion (Naylor & Atkinson 1972, Taylor & Naylor 1977, Naylor & Williams 1984, Bolt & Naylor 1985, Reid et al. 1993, Warman & Naylor 1995). However, for planktonic organisms which remain in the water column, some of the environmental variables that are effective zeitgebers for benthic intertidal animals may have little influence. In studies related to present work, we have shown that if detached eggs of *C. maenas* were subjected to periodic water agitation in the laboratory, tidal rhythms can be entrained in subsequently hatched larvae (Zeng & Naylor 1994). This suggests that the larval tidal clocks are probably set in phase with local tides before zoeae are released, ensuring quick transport of larvae offshore. However, the pattern, strength and synchrony of the tidal migration rhythms are likely to be further entrained by environmental factors in the water column after release.

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