



## Vertical migration and selective tidal stream transport in the megalopa of the crab *Carcinus maenas*

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### Abstract

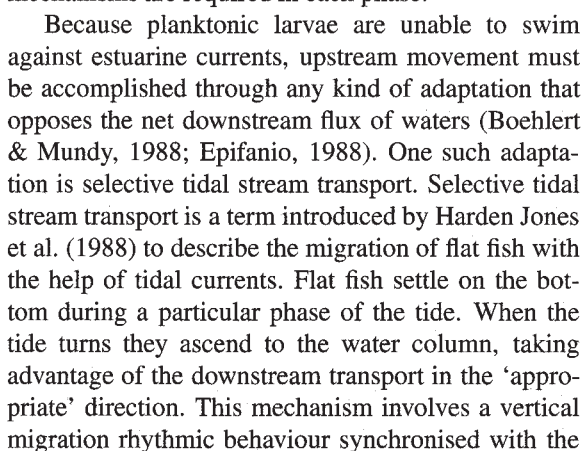
Megalopae of *Carcinus maenas* (L.) were intensively sampled in the Canal de Mira (Ria de Aveiro, Portugal) during the years of 1990 and 1991, with the use of a pump and nets, respectively. Plankton sampling was carried out along 25 h cycles conducted at fixed stations, at pre-determined depths along the water column. In 1990, the average depth of distribution of megalopae throughout the water column was affected by tidal phase: the larvae were closer to the surface during flood than ebb. Stepwise linear regression showed that a shallower distribution of the larvae was also associated with higher salinity. Other hydrological variables did not account well for the vertical distribution of megalopae. Analysis of megalopal instantaneous transport velocity indicated that their horizontal velocity depended on phase-of-tide: during ebb megalopae were transported downstream at a lower velocity than the vertically integrated water column velocity; during flood, the vertically integrated velocity of the larvae and water column were similar. Thus, a shift of vertical position during the tidal cycle controlled the transport velocity of megalopae, which was due to vertical water velocity shear current differences. During the 1991 study, significantly higher densities of megalopae were collected during flood. Main effects of phase-of-day and depth of sampling on density were not significant. However, highest densities during flood were found at mid-water, in both day phases, whereas during ebb megalopae were evenly distributed throughout the water column during the day, with low densities, or showed increasing abundances towards the bottom during the night. These observations are consistent with the hypothesis that megalopae of *C. maenas* undergo active vertical migration synchronised with the tidal cycle, which can be classified as a selective tidal stream transport mechanism to travel up estuaries. A conceptual model for the reinvasion of estuaries by *C. maenas* megalopae is proposed. According to the model, vertical movements between the bottom and the water column are controlled by exogenous factors associated with the tidal cycle.

### Introduction

The portunid crab *Carcinus maenas* (L.) is the commonest European estuarine crab species. It forms a large population in the Ria de Aveiro, a bar-built estuary located on the north-western coast of Portugal (Figure 1). Queiroga et al. (1994, 1997) and Queiroga (1995, 1996) have described several aspects of the species' larval ecology. Synchronous release of first zoeae occurs during night-time ebbing tides. These larvae use selective tidal stream transport to maximise seaward transport, migrating vertically in synchrony with the tidal cycle so that they are closer to the

surface during the span of the ebb. All larval stages are found in shelf waters. Shoreward advection of megalopae seems to occur during periods of relaxed northerly, upwelling-favourable, winds. Inside the estuary, megalopae are significantly more abundant during floods than during ebbs, and at night.

Migration of larvae from the sea to estuarine habitats has been recognised as a 2-step process (Boehlert & Mundy, 1988; Shanks, 1995; Forward et al., 1995): (1) cross-shelf transport of the larvae towards the shore; (2) passage through the inlet and upstream movement until an appropriate environment is found.



tidal cycle. Field investigations concerning fish larvae (Fortier & Legget, 1983; Laprise & Dodson, 1989; Rowe & Epifanio, 1994) and crab zoeae (Queiroga et al., 1997) and megalopae (Olmi, 1994) reported tidally timed vertical movements that can be classified as selective tidal stream transport mechanisms to maximise transport in estuaries, to move both up- and downstream, depending on species and larval stage. In the case of larval fish and crab zoeae the migration is entirely planktonic, and a resting-on-the-bottom phase does not occur. The larvae simply move closer to the bottom where, due to reduced water velocities caused by bottom friction, they experience slower transport velocities in the 'wrong' direction.

Previous studies on *Uca* spp. (Christy, 1982; Dittel & Epifanio, 1990; Little & Epifanio, 1991) *Callinectes sapidus* (Brookins & Epifanio, 1985; Little

& Epifanio, 1991) and *Carcinus maenas* (Queiroga et al., 1994) reported higher megalopal abundances in the water column during night-time flood tides. To explain this pattern the authors postulated that most megalopae passing through the sampling station during flood settled upstream before the turn of the tide. This behaviour would result in a net upstream transport by selective tidal stream transport. However, none of these studies described the actual process of vertical migration of the larvae. The only conclusive evidence that crab megalopae do migrate vertically in synchrony with the tide, when entering estuarine waters, is given by Olmi (1994). His study described vertical migrations of *C. sapidus* megalopae that resulted in distributions of the larvae higher in the water column during flood and at night.

In the present paper I address the temporal patterns of change of the vertical position of the megalopa of *Carcinus maenas* in an estuary, and its consequences to the transport processes of these larvae. I will show that: (i) *C. maenas* megalopae are closer to the surface during flood tide; (ii) the observed shift of vertical position according to phase-of-tide is consistent with the hypothesis that these larvae use selective tidal stream transport to travel up the estuary; (iii) the transport velocity of megalopae depends on their vertical position throughout the water column.

## Materials and methods

The study site was located in the Canal de Mira (Figure 1). Tides in the Ria de Aveiro are semi-diurnal, with a mean tidal range of 2.1 m at the inlet. Circulation in the Canal de Mira can be classified as a two-layer flow with vertical mixing (Bowden, 1967; Queiroga, 1995). Two sampling experiments were carried out, hereafter referred to as the 1990 and 1991 studies. During the 1990 study plankton samples were collected with a pump (see Queiroga et al., 1994, 1997). Plankton nets were used in the 1991 study.

### 1990 study

**Field sampling.** Plankton samples were collected with a pump, fitted to a 500 mm net, during 2 sampling periods: one in the winter (February 12 to March 11) and the other in the spring (May 9 to June 7) of 1990. Each seasonal sampling period was designed as a series of 25 h sampling cycles at fixed stations. Within each 25 h sampling cycle plankton samples were collected

every hour at several depths. In winter, the samples were collected in a quick succession over 1 m depth intervals within each hourly period, starting at 0.2 m. Every time the last sample in the series was collected more than 0.5 m from the bottom, an extra sample was taken at 0.2 m from the bottom. The filtered volume for a pumping time of 2 min at each depth was about 1.0 m<sup>3</sup>. In spring, plankton samples were collected only at three levels: 0.5 m below the surface, at mid water and 0.5 m above the bottom. Pumping time at each depth was increased to 5 min, corresponding to filtered volumes of about 2.2 m<sup>3</sup>. Although the original sampling program was conducted at three stations, very small number of megalopae were collected at two of them. Accordingly, only the sampling cycles carried at Station #2 are analysed.

Hydrological measurements were obtained every hour, at the standard 1 m depth intervals, immediately before the collection of the plankton samples. Salinity and temperature were measured during all 25 h cycles, using a Yellow Springs Instrument Model 33 SCT meter. During some of the 25 h cycles current speed and direction could also be obtained (Table 1) with the use of a Valeport BMF008 current meter. The height of the water column was always measured every hour with a sounding line. Average depth and tidal range at Station #2 were 4.7 and 2.1 m respectively.

**Analysis of hydrological data.** Stratification of the water column was characterised by an index of stratification,  $S_t$ , calculated as:

$$S_t = \frac{\sigma_t \text{ surface} - \sigma_t \text{ bottom}}{Z_t}, \quad (1)$$

where  $t$  is time,  $\sigma$  was derived from the salinity and temperature measurements according to the equation given by Fofonoff and Millard (1983) and  $Z_t$  is the instantaneous depth of the water column.

**Vertical distribution of the larvae.** To inspect temporal patterns of vertical position of *Carcinus maenas* megalopae, the depth specific instantaneous concentration of the larvae,  $C_{zt}$  (ind m<sup>-3</sup>), was first calculated, as a function of discrete depth ( $z$ ) and time ( $t$ ) intervals:

$$C_{zt} = \frac{\text{counts}_{zt}}{\text{filtered volume}_{zt}}. \quad (2)$$

The instantaneous mean depth of the megalopae,  $\overline{D}_t$ , (hereafter referred to as the instantaneous depth of the megalopae), was calculated as the weighted average depth of collection:

Table 1. Data concerning the 25 h fixed station plankton sampling cycles performed in the Canal de Mira

Year	Date	Station #	Number of samples: total (with megalopae)	Number of sampling moments: total (with megalopae)	Water current data?	Salinity and temperature data?
1990 Winter	12 Feb	2	107 (14)	25 (9)	Yes	Yes
	14 Feb	2	119 (9)	25 (7)	Yes	Yes
	16 Feb	2	124 (3)	25 (3)	Yes	Yes
	18 Feb	2	105 (0)	25 (0)	Yes	Yes
	20 Feb	2	128 (1)	25 (1)	Yes	Yes
	22 Feb	2	125 (0)	25 (0)	Yes	Yes
	24 Feb <sup>a</sup>	2	76 (0)	13 (0)	No	Yes
	26 Feb	2	127 (0)	25 (0)	Yes	Yes
	28 Feb	2	123 (0)	25 (0)	No	Yes
	04 Mar	2	126 (1)	25 (1)	Yes	Yes
	06 Mar	2	131 (0)	25 (0)	Yes	Yes
	11 Mar	2	132 (0)	25 (0)	No	Yes
1990 Spring	09 May	2	75 (4)	25 (4)	Yes	Yes
	11 May	2	75 (11)	25 (9)	Yes	Yes
	13 May	2	75 (12)	25 (10)	Yes	Yes
	15 May	2	75 (3)	25 (2)	No	Yes
	19 May	2	75 (2)	25 (1)	Yes	Yes
	23 May	2	75 (1)	25 (1)	No	Yes
	25 May	2	75 (1)	25 (1)	No	Yes
	02 Jun	2	75 (6)	25 (5)	No	Yes
1991	07 Jun	2	75 (1)	25 (1)	No	Yes
	13 Apr	1	39 (13)	13 (6)	No	No
	22 Apr	1	39 (28)	13 (13)	No	No
	06 May	1	39 (13)	13 (10)	No	No
	14 May	1	39 (16)	13 (11)	No	No
	21 May	1	39 (12)	13 (7)	No	No
	28 May	1	39 (3)	13 (2)	No	No
	05 Jun	1	39 (1)	13 (1)	No	No
	12 Jun	1	39 (3)	13 (3)	No	No
	27 Jun	1	39 (11)	13 (6)	No	No

<sup>a</sup> Only the first 13 hours of the series were sampled.

$$\overline{Dl_t} = \frac{\sum_{z=l}^n C_{zt} \times D_{zt}}{\sum_{z=l}^n C_{zt}} \times \frac{1}{Z_t}, \quad (3)$$

where  $D$  is the depth of sampling and  $Z$  is the total height of the water column. In the above equation, data are standardised by dividing the absolute mean depth of the megalopae at the moment of collection by the total height of the water column, yielding an average relative depth where surface has a value of 0 and bottom a value of 1. This transformation is convenient because it enables comparisons of megalopal position along the vertical axis independent of tidal state.

**Horizontal transport.** The influence of the vertical position of megalopae on their net tidal transport was

assessed by first calculating the vertically integrated instantaneous current velocity  $\overline{u_t}$  ( $\text{m s}^{-1}$ ):

$$\overline{u_t} = \frac{\sum_{z=l}^n u_{zt} \times \Delta D_{zt}}{\sum_{z=l}^n \Delta D_{zt}}, \quad (4)$$

where  $u$  is the longitudinal component of velocity,  $\Delta D$  is the height of each stratum and  $\sum_{z=l}^n \Delta D_{zt}$  equals  $Z_t$ , the instantaneous height of the water column. Subsequently, a vertically integrated instantaneous megalopal velocity,  $\overline{u_{lt}}$  ( $\text{m s}^{-1}$ ) was calculated, and designated as the instantaneous megalopal velocity:

$$\overline{u_{lt}} = \frac{\sum_{z=l}^n u_{zt} \times \Delta D_{zt} \times C_{zt}}{\sum_{z=l}^n \Delta D_{zt} \times C_{zt}}, \quad (5)$$

where the different symbols have the meaning explained above. Note that if the megalopae are uni-



formly distributed throughout the water column, the  $C_{zt}$  terms in the above equation are all equal and cancel out to produce a value that is equal to  $\bar{u}_t$  in Equation 4. The larvae are thus transported at a velocity that equals the vertically integrated current velocity. If the larvae do not distribute evenly with depth, then  $\bar{u}_{li}$  does not equal  $\bar{u}_t$ . Since tidal current intensity usually increases with increasing distance from bottom due to a decrease in bottom friction, changes in vertical position result in instantaneous transport velocities of megalopae that differ from the depth integrated current velocity. The concept of larval velocity described above is similar to that reported by Rowe and Epifanio (1994), except that depth integrated larval velocity was calculated for each time interval, rather than time integrated velocity for each depth interval.

#### *1991 study*

During this study, nine 25 h plankton sampling cycles were performed at Station #1, mostly at weekly intervals, between April 13 and June 27 (Table 1). Three different nets were used, all equipped with 500  $\mu\text{m}$  meshes and flowmeters: a neuston net with an opening of  $0.60 \times 0.30$  m; a conic net with a 0.40 m diameter opening which was towed at mid-water; and a similar conical net mounted on a sledge, to sample close to the bottom. Every 2 h the three nets were deployed in a quick succession. Each tow lasted approximately 5 min. The vertical position of the neuston net was adjusted so that the immersed height of its mouth was 0.20 m on average. Assuming this, a filtered volume was calculated for the three nets, and abundances expressed in  $\text{ind m}^{-3}$ . Average filtered volumes were 35.1, 30.7 and 25.3  $\text{m}^3$  for the neuston, plankton and sledge net, respectively. No currents, salinity and temperature data were collected. Average depth and tidal amplitude at Station #1 were 6.5 m and 2.3 m.

#### *Statistical analysis*

For purposes of statistical analysis, samples collected during the 1990 and 1991 studies were classified using the following criteria. Tides covered by a particular 25 h fixed sampling cycle were designated by the starting date of that cycle, even when they overlapped the next calendar day. All samples collected in each sampling moment (=each 1 h period in the 1990 study; each 2 h period in the 1991 study) were classified as ebb or flood samples according to the phase of the tide, defined by high and low water slack times, during which the discrete time interval began. Similarly,

the samples were classified as day time or night time, where the day phase was taken as the period between daily sunrise and sunset and the night phase as the complement of this period. All statistical analysis described below were made using the SPSS package.

*1990 study.* The significance of the effect of phases-of-tide and day, and sampling period, on the vertical position of the megalopae was analysed using a three-way analysis of variance (ANOVA), in which phase-of-tide (ebb, flood), phase-of-day (day, night) and sampling period (winter, spring), each with two levels, constituted the three factors in the analysis. Prior to analysis data were subjected to an angular transformation, which homogenised the variances in all cases. The effects of the phases of tide and day, and of the sampling period on the instantaneous megalopal velocity, were analysed by means of a three-way ANOVA as above, but the instantaneous current velocity was introduced in the analysis as a co-variable. The analysis was performed on the subset of data for which current data were obtained. No transformation was applied to the data because variances were homogeneous.

The effects of environmental variables associated with the tidal cycle on vertical position of megalopae were analysed by stepwise linear regression. The independent variables were average salinity and temperature throughout the water column for each sampling moment, vertically integrated instantaneous current velocity and height of the water. The instantaneous mean depth values were first subjected to an angular transformation. One regression was calculated for the pooled data of winter and spring.

As stated before, during the spring plankton samples were obtained only below the surface, at mid depth and above the bottom, while during the winter period had been taken at 1 m depth intervals. In order to ascertain whether the different resolution that was used to sample the water column influenced the estimates of the instantaneous vertical position and velocity of the larvae, the first 13 sampling hours of the sampling cycles performed at Station #2 on February 16, 20 and 26 and March 4 and 6 were used. These observations were selected because, due to good weather conditions, the depth of sampling could be determined very precisely. The instantaneous depth and velocity of the megalopae were first calculated, for all sampling moments, with equations 3 and 5, using the observations obtained at regular intervals. The same variables were again calculated from a subsample, now using

only the samples collected at 0.2 m, at the depth level closest to mid-height of the water column, and above the bottom. The two series of values were then compared by least squares linear regression. It could be demonstrated that the two methods of sampling did not produce significantly different estimates neither of the instantaneous vertical position nor of the instantaneous velocity of the megalopae. In both cases there was a highly significant linear relation ( $P < 0.001$ ) between the estimates obtained with sampling at surface, mid-water and bottom and at regular intervals. Moreover, the slope of the regression line and the Y-intercept never differed from 1 and 0, respectively ( $t$ -test;  $P > 0.20$ ).

**1991 study.** In order to analyse the effects of depth of sampling, phase-of-tide and phase-of-day on the concentration of megalopae, a three-way ANOVA was used again. However, variances were highly heterogeneous, a feature that was impossible to correct by any of the usual transformations. Accordingly, a non-parametric ANOVA of the ranks of the concentrations, rather than of the concentrations, was employed, following the procedure described by Zar (1984, page 249). Factors in the analysis were depth level (surface, mid-water and bottom), phase-of-tide (ebb, flood) and phase-of-day (day, night).

## Results

### 1990 study

The average concentration of the megalopa was only slightly higher in spring than in winter: 0.028 ind  $m^{-3}$  in winter versus 0.031 ind  $m^{-3}$  in spring (Queiroga et al., 1994). Average concentrations during flood and ebb were, respectively: 0.050 ind  $m^{-3}$  and 0.008 ind  $m^{-3}$  in winter, 0.051 ind  $m^{-3}$  and 0.013 ind  $m^{-3}$  in spring. Megalopae were usually concentrated closer to the surface during flood than ebb (Figure 2). Analysis of the data collected within the sampling periods of winter and spring indicated that tidal phase, phase-of-day and sampling season variably affected the average vertical position of the megalopa (Figure 3). The ANOVA (Table 2) showed that megalopae were significantly closer to the surface during flood and in spring. ( $P < 0.05$  in both cases). No significant effects of phase-of-day or of the interactions were found.

An increase in average salinity (AS) caused a decrease in the relative depth (RD) of distribution of the

larvae ( $\sin^{-1} \sqrt{RD} = 111.4 - 1.731 AS$ ;  $P < 0.01$ ; Figure 4). The other hydrological variables employed in the regression analysis did not account well for the vertical position of the megalopa. As a consequence of rainfall, decreased salinity values recorded during winter at the surface resulted in lower average salinity throughout the water column, as well as in higher stratification values than in spring (Queiroga, 1995; Queiroga et al., 1997). A scatter diagram of the relative depth of the megalopa against the stratification index (Figure 5) shows that for stratification values over 0.2, which were more frequently observed in winter, no megalopae were collected in the upper half of the water column.

Average values of the difference between the instantaneous larval velocity and the instantaneous water velocity revealed several patterns (Figure 6). Results of the ANOVA (Table 3) showed that the effect of the co-variable current velocity was highly significant ( $P < 0.001$ ), meaning that the velocity of the larvae is related to the velocity of the water current. The results further show that the phase of the tide, and the season, have a significant influence on the transport velocity of the megalopae ( $P < 0.001$  and  $P < 0.01$ , respectively).

### 1991 study

Significantly ( $P < 0.05$ ) more megalopae were collected during flood (0.073 ind  $m^{-3}$ ) than during ebb (0.030 ind  $m^{-3}$ ) (Figure 7, Table 4). The main effects of depth level and phase-of-day were not significant. However, proportionally more megalopae were collected during night ebbing than in day ebbing tides, which is reflected in a significant phase-of-tide by phase-of-day interaction ( $P < 0.05$ ). Another noticeable feature of Figure 7 is that the highest abundances during flood were found at mid-water, in both day phases, whereas during ebb the megalopae were uniformly distributed throughout the water column during the day, albeit with very low densities, or showed increasing concentrations towards the bottom during the night. The depth level by phase-of-tide interaction was not statistically significant at the 5% level, although it was very close to statistical significance ( $0.06 > P > 0.05$ ).

## Discussion

During the 1990 study, *Carcinus maenas* megalopae were 5 times more abundant in the Canal de Mira dur-

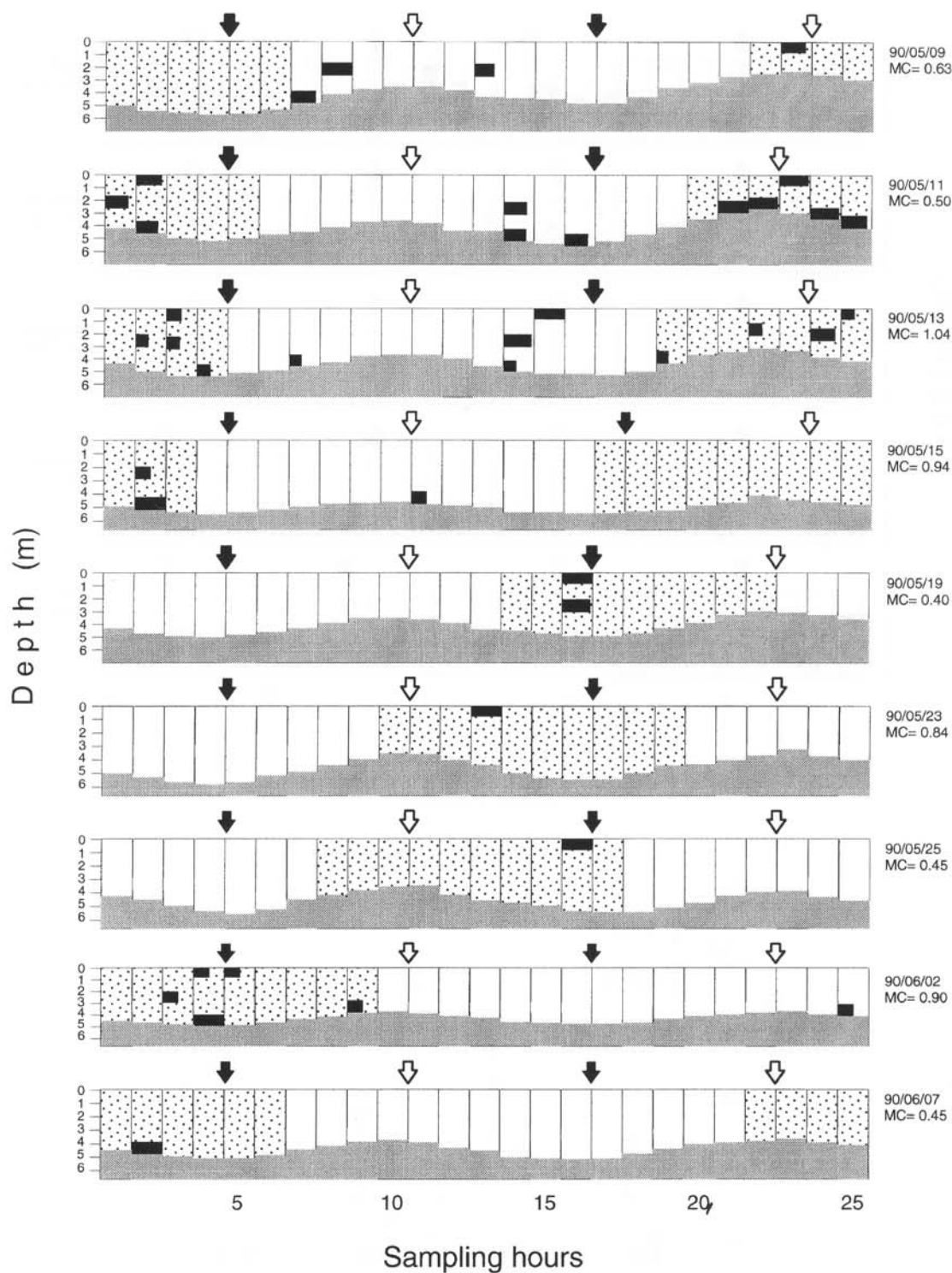


Figure 2. *Carcinus maenas*. Concentration of the megalopa recorded during the 1990 study, at Station #2, in each 25 h plankton sampling series, relative to depth level, tide phase and day phase (only the series where megalopae were collected are shown). Concentrations (larvae  $m^{-3}$ ) are represented by horizontal bars at each depth and time interval and scaled to the maximum concentration (MC) in each 25 h series. Black arrow: high water slack; open arrow: low water slack; dotted areas: night. In each 25 h series surface is set to level 0 m, while bottom, represented by the grey area in the bottom of each series, is seen rising and sinking with the tide.

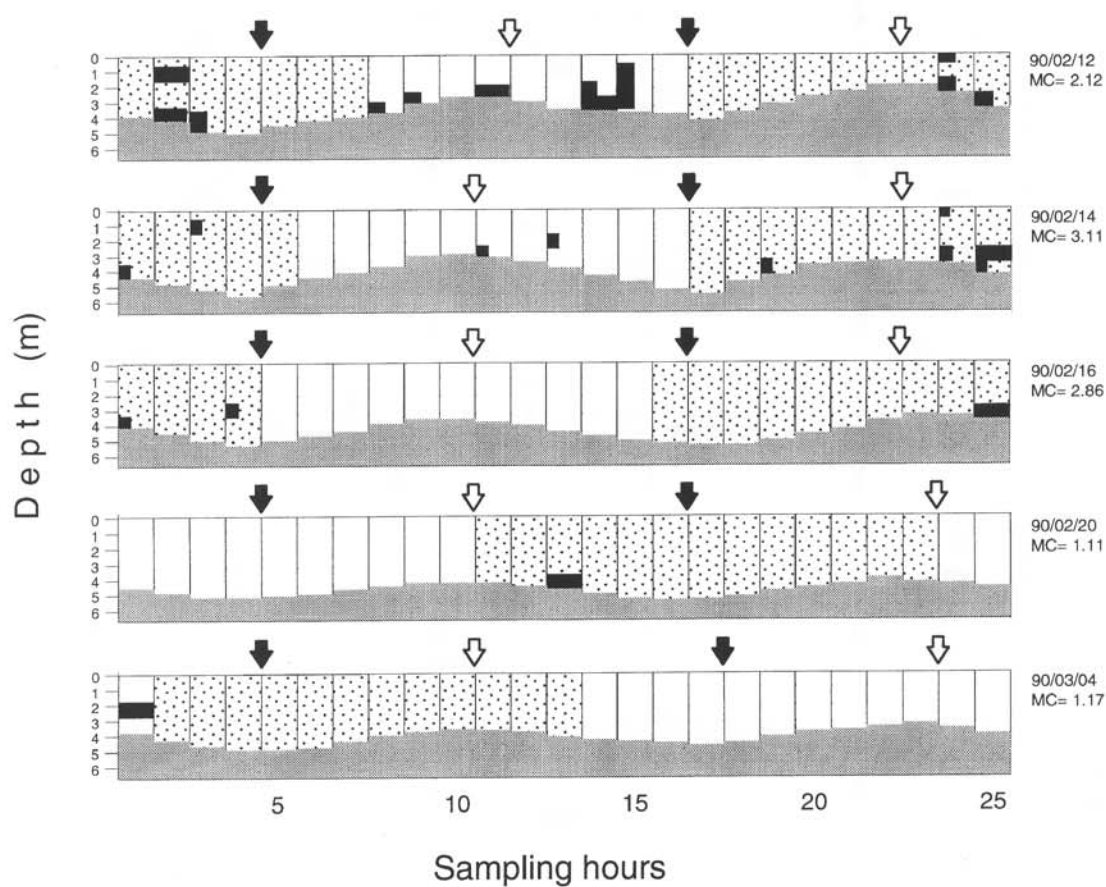


Figure 2. Continued

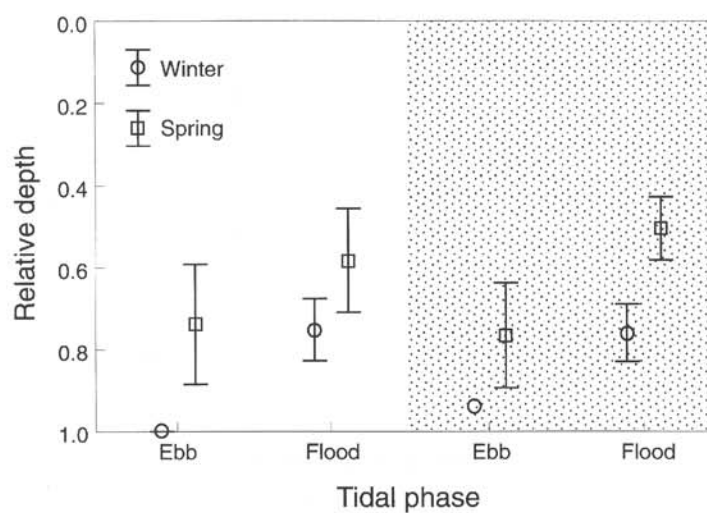
Figure 3. *Carcinus maenas*. Vertical position of the megalopa during the 1990 study at Station #2, according to phase-of-tide, phase-of-day and sampling period. Vertical bars represent 1 standard error. Dotted area: night.



Table 2. Three-way ANOVA of the vertical position of megalopae of *Carcinus maenas* during the 1990 study at Station #2. The null hypotheses are that, when there are megalopae in the water column, their average vertical position does not differ across treatments. df = degrees of freedom; MS = mean square;  $F_s$  =  $F$  test value;  $P$  = probability value

Source of variation	df	MS	$F_s$	$P$
Phase-of-tide	1	1960.69	4.34	$0.05 > P > 0.01$
Phase-of-day	1	586.65	1.30	$P > 0.25$
Sampling period	1	1850.15	4.10	$0.05 > P > 0.01$
Phase-of-tide by Phase-of-day	1	22.52	0.05	$P > 0.75$
Phase-of-tide by Sampling period	1	39.92	0.09	$P > 0.75$
Phase-of-day by Sampling period	1	21.76	0.05	$P > 0.75$
Phase-of-tide by Phase-of-day by Sampling period	1	225.83	0.50	$P > 0.25$
Error	47	451.59		
Total	54	555.43		

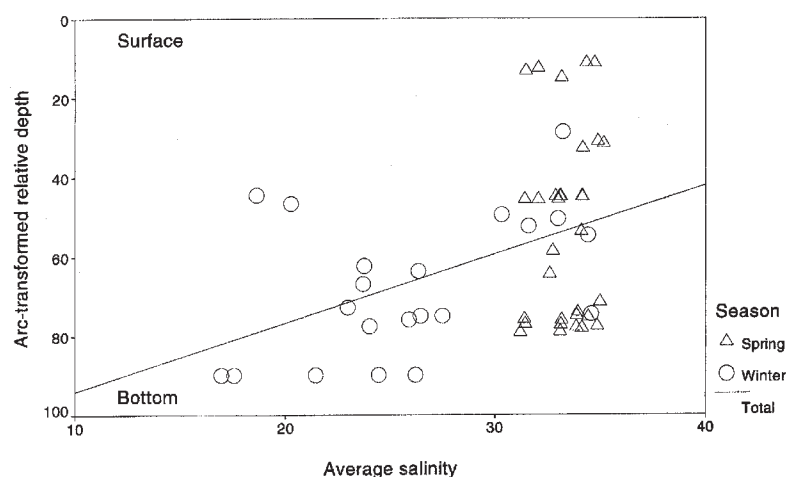


Figure 4. *Carcinus maenas*. Scatter plot of arc-transformed relative depth of the megalopa during the 1990 study at Station #2 as a function of salinity.

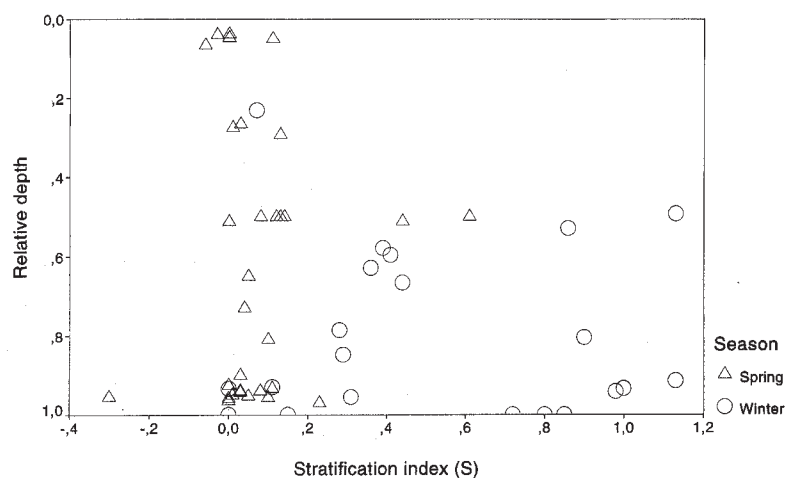


Figure 5. *Carcinus maenas*. Scatter plot of the relative depth of the megalopa during the 1990 study at Station #2 against the instantaneous stratification index.

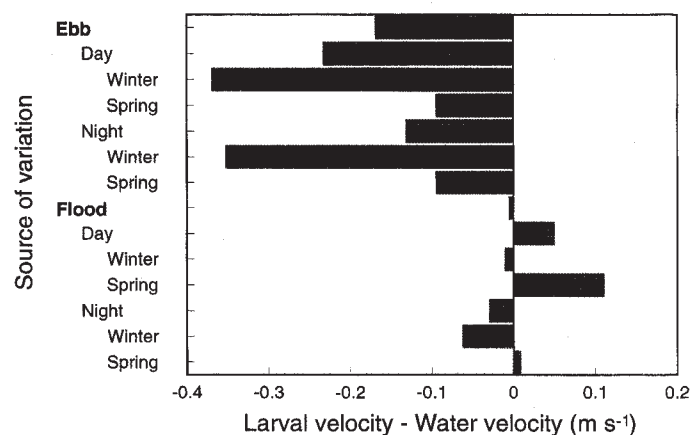


Figure 6. Difference between the instantaneous velocity of *Carcinus maenas* megalopa and the instantaneous velocity of water, recorded during the 1990 study at Station #2, by tidal state, phase-of-day and sampling period. Positive values of the difference indicate that the velocity of the larvae is higher than the current velocity.

Table 3. Three-way ANOVA of the transport velocity of megalopae of *Carcinus maenas* during the 1990 study at Station #2. The null hypotheses are that, when there are megalopae in the water column, their average transport velocity does not differ across treatments. df = degrees of freedom; MS = mean square;  $F_s$  =  $F$  test value;  $P$  = probability value

Source of variation	df	MS	$F_s$	$P$
Co-variable (Current velocity)	1	1.29	99.46	$P < 0.001$
Phase-of-tide	1	0.23	17.83	$P < 0.001$
Phase-of-day	1	0.01	0.65	$P > 0.25$
Sampling period	1	0.12	9.56	$0.01 > P > 0.001$
Phase-of-tide by Phase-of-day	1	0.01	1.15	$P > 0.25$
Phase-of-tide by Sampling period	1	0.03	2.40	$P > 0.10$
Phase-of-day by Sampling period	1	0.00	0.02	$P > 0.75$
Phase-of-tide by Phase-of-day by Sampling period	1	0.00	0.16	$P > 0.50$
Error	43	0.01		
Total	51	0.05		

Table 4. Nonparametric three-way ANOVA of the concentration of megalopae of *Carcinus maenas* during the 1991 study at Station #1. The null hypotheses are that the concentration of the megalopae does not differ across treatments. df = degrees of freedom; SS = sum of squares; MS = mean square;  $H$  = Kruskal-Wallis statistic;  $P$  = probability value

Source of variation	df	SS	MS	$H$	$P$
Depth level	2	9274.8	4637.4	1.420	$P > 0.10$
Phase-of-tide	1	29976.4	29976.4	4.590	$0.05 > P > 0.01$
Phase-of-day	1	11842.6	11842.6	1.813	$P > 0.10$
Depth level by Phase-of-tide	2	37838.4	18919.2	5.794	$P > 0.05$
Depth level by Phase-of-day	2	9805.0	4902.5	1.501	$P > 0.50$
Phase-of-tide by Phase-of-day	1	27209.9	27209.9	4.166	$0.05 > P > 0.01$
Depth level by Phase-of-tide by Phase-of-day	2	1209.1	604.5	0.185	$P > 0.75$
Error	339	2152922.1	6350.8		
Total	350	2285850.0	6531.0		

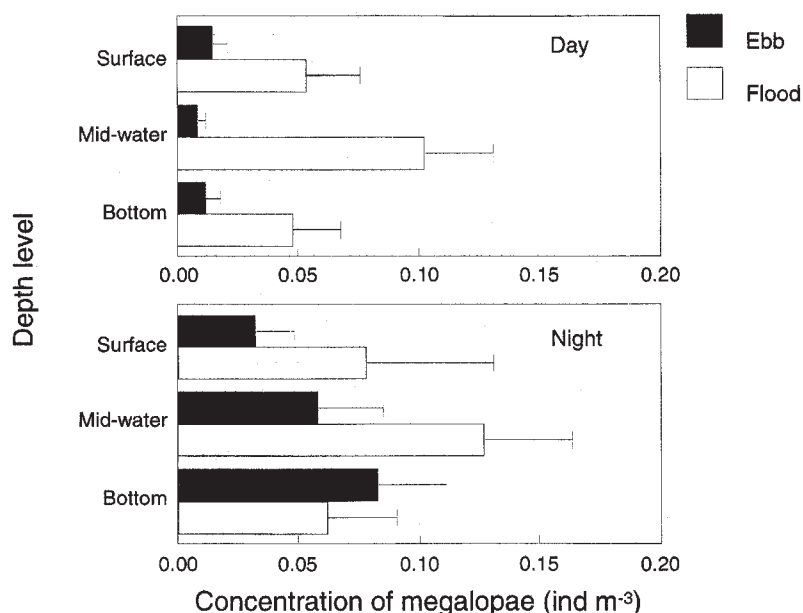


Figure 7. *Carcinus maenas*. Average concentration of megalopae during the 1991 study at Station #1, according to depth level, tidal phase and day phase. Thin bars represent +1 standard error.

ing the flood than ebb tide (see Queiroga et al., 1994). During the 1991 study they were 2.5 times more abundant during the rising tide. This seems to contrast with studies on *Callinectes sapidus* and *Uca* spp. that reported very low abundances during ebb (Christy, 1982; Epifanio et al., 1984; Brookins & Epifanio, 1985; Little & Epifanio, 1991; Olmi, 1994). Nevertheless, the patterns found during the present study imply a net upstream transport of *Carcinus maenas* megalopae in the Canal de Mira. Both the 1990 and 1991 studies produced evidence that megalopae were nearer the surface during flood than during ebb. Taken in conjunction, all these observations are strongly consistent with the hypothesis that *C. maenas* megalopae use selective tidal stream transport to travel up the estuarine environment.

The moment and the nature of the factors that initiate the rhythmic behaviour of crab megalopae invading the estuaries has been addressed recently. Swimming of *Callinectes sapidus* and *Uca* spp. megalopae in estuarine water can be altogether suppressed by high light intensities. This difference in photo-behaviour between estuaries and coastal waters is induced by chemical cues present in the water. The absence or low densities of megalopae observed during the day in estuaries would then result from swimming

inhibition by high light levels, and concurrent sinking to the bottom (Forward & Rittschof, 1994).

Differences between ebb and flood concentrations of *C. sapidus* and *Uca* spp. megalopae cannot be explained by rates of pressure change, because response thresholds obtained in the laboratory were clearly above levels experienced during flood tides in the field (Tankersley et al., 1995). However, in *C. sapidus* the ascent to the water during flood seems to be cued by increasing salinity during the rising tide (De Vries et al., 1995; Forward et al., 1995). In other cases, presence of megalopae in the water is related to rates of change in pressure and current velocity (De Vries et al., 1994). In the case of *Uca* spp. swimming to the water column seems to be caused by an endogenous activity rhythm (Tankersley et al., 1995). Freshly collected *Carcinus maenas* megalopae approaching metamorphosis, kept in the laboratory under constant conditions, showed an endogenous vertical swimming rhythm (Zeng & Naylor, 1996b). The vertical upward movement resulted from active swimming and descent from passive sinking. Surprisingly, however, the larvae moved up during the expected ebb and down during the expected flood tide, exactly like the species' first zoea did (Zeng & Naylor, 1996a). Thus, factors that trigger *C. maenas* megalopal behaviour observed in the field (this study) must be exogenous, because the

endogenous rhythm described from laboratory studies would result in an downstream transport of the larvae.

Queiroga et al. (1994) reported significantly higher densities of *Carcinus maenas* megalopae during the night in the 1990 study. No difference in the depth of distribution of the larvae was detected between day phases (this report). During the 1991 study, however, phase-of-day clearly had an effect not only on the mean density of megalopae, but also on their depth of distribution. This effect depended on phase-of-tide. During the flood, night and day vertical distribution of megalopae were similar. During day ebbing tides, megalopae were uniformly distributed with depth, showing low densities; during night ebbings, concentrations increased clearly towards the bottom. This pattern could be explained assuming a light inhibition of swimming activity during the day, overridden by a reaction to an environmental variable associated with the rising tide that would cause megalopae to ascend during flood.

Temperature, current velocity and height of the water column (which is a measure of the pressure to which a megalopa resting on the bottom is subjected), did not account well for the vertical distribution of *Carcinus maenas* megalopae during the 1990 study. However, an increase in mean salinity of the water column caused a shallower distribution of the larvae. This effect suggests that a salinity increase concurrent with the rising tide might trigger swimming activity, and thus cause an ascent in the water. Previous investigations of the behavioural responses of *C. maenas* megalopae to pressure variation indicated the presence of high barokinesis, with an absolute threshold response of 10 mbar to a pressure increase. Pressure increase resulted always in upward swimming, either in darkness or in light from above, one side or bellow. When subjected to a pressure decrease of unspecified amount, megalopae sank passively (Rice, 1966; Knight-Jones and Morgan, 1966). A pressure difference of 10 mbar corresponds to about 0.10 m of water, which is much less than the water height change associated with an extreme neap tide in the Portuguese coast (ca. 1.0 m). Absolute values like the ones used in the present study, or absolute differences, in environmental variables, however, may not be adequate to describe induced behaviour of the larvae. Rates of change of environmental variables with time (e.g. Forward, 1985; 1989; Forward et al., 1989; Tankersley et al., 1995), as well as the sign of the change (e.g. Rice, 1966), which I did not test, may be of greater biological significance. So, the possibility remains that

increased swimming activity by a *C. maenas* megalopa resting on the bottom could be induced by the rise of the tide, resulting in upward movement. The response to pressure reported by Rice (1966), independent of light level, is also consistent with the large numbers of megalopae collected during day and night flood tides in the 1991 study.

Thus, based on available evidence, I propose the following model for the reinvasion of estuaries by *Carcinus maenas* megalopae. Under the influence of coastal/shelf circulation, megalopae are advected shoreward until they eventually concentrate near estuarine inlets. Chemical substances present in estuarine waters modify phototactic responses of the larvae and inhibit swimming during the day. Megalopae thus settle to the bottom. Pressure and/or salinity increase associated with the rising tide then evoke upward swimming by negative geotaxis, overriding the inhibitory effect of day light levels, causing megalopae to travel with night or day flood currents into, and then up, estuaries. Decreasing salinity during ebb induces passive sinking or swimming to the bottom; this effect may be enhanced by decreasing pressure. During the course of the vertical migrations, water velocity shear current differences further control the amount of horizontal transport during each tidal phase, maximising net upstream transport.

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