

Tidal migrations and rhythmic behaviour of sandbeach Crustacea

Migraciones mareales y conducta rítmica de crustáceos de playas arenosas

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ABSTRACT

Examples of tidal migration of sandbeach crustaceans are given for downshore and upshore migrants, and for intertidal infauna which swim at high tide. Field observations are related to laboratory demonstration of endogenous clock control of locomotor activity rhythms and rhythms of responsiveness to environmental variables. Intensive sampling strategies and experimental protocols reveal spatial and ontogenetic differences in rhythmic behaviour of individual species.

Key words: Sand beaches, crustaceans, tidal migration, rhythms.

RESUMEN

Se entregan ejemplos de migraciones mareales en playas arenosas, tanto para organismos que se mueven hacia niveles inferiores y superiores de la playa, como para aquellos que nadan durante la marea alta. Se relacionan observaciones de terreno a experimentos de laboratorio que demuestran control endógeno de los ritmos de actividad y ritmos de respuesta a las variables ambientales. Estrategias intensivas de muestreo y protocolos experimentales revelan diferencias espaciales y ontogenéticas en la conducta rítmica de especies individuales.

Palabras clave: Playas arenosas, crustáceos, migración mareal, ritmos.

INTRODUCTION

On sandy beaches influenced by tidal rise and fall the space and resources of the intertidal zone are exploited by mobile animals in several ways. Some semi-terrestrial species forage downshore at low tide, particularly at night, some infaunal residents emerge to swim and feed at high tide, and other, low shore forms migrate up and downshore with the tide.

Each of these three patterns of migration raises questions concerning the timing and direction of locomotor activity, notably in relation to the tidal and daily rhythmicity of particular behavioural events. In some cases field observations of such migrations are documented, though these are often anecdotal and not based upon extensive sampling. In others field migrations are well understood, but their behavioural basis is uninvestigated,

and only in a few cases have there been intensive field and laboratory studies seeking to explain a full behavioural repertoire. The present paper seeks to review such migrations and their behavioural basis in intertidal crustaceans of sandy beaches.

DOWNSHORE MIGRANTS

Talitrid amphipods are well known to burrow by day to depths of 10-30cm in a 5-10m wide zone near the strandline of sandy beaches just above HWM.

At night field studies by observation and by pitfall traps showed that they emerge to forage above HWM on non-tidal shores (Geppetti & Tongiorgi 1967, Scapini et al. 1992) but downshore on wet sand between tidemarks on some tidal shores (Bregazzi & Naylor 1972, Williams 1983). In *Talitrus*

saltator (Montagu) it has been known for some time that the rhythm of downshore foraging during nocturnal low tides is under the control of an endogenous circadian rhythm of emergence from sand, modulated exogenously by external tidal conditions (Bregazzi & Naylor 1972, Williams & Naylor 1978).

Moreover it has been demonstrated that the navigational ability of *Talitrus saltator* also varies on a circadian time-base under endogenous control. Williamson's (1951) early documentation of upshore migration towards the dune/sky boundary by this species was later shown to occur in constant conditions (Edwards & Naylor 1987), but only during subjective daytime starting just before the time of expected sunrise. This suggests a temporally-varying behavioural mechanism for the control of upshore migration at dawn. During subjective night time when they normally migrate downshore, *Talitrus saltator* was shown to be indifferent to the dune sky boundary, raising the question

as to how the downshore-orientated phase of the migration occurred after dusk (Edwards & Naylor 1987).

Recently this question has been addressed by Mezzetti et al. (1994) who showed that *Talitrus saltator* from a tidal European shore also exhibited an endogenously controlled diel rhythm of phototaxis. The amphipods were shown to exhibit circadian changes from positive phototaxis during the subjective day to negative phototaxis during expected night (Fig. 1). Positive phototaxis on first emergence at night could induce downshore migration towards the bright sea surface (Mezzetti et al. 1994). Thus the complete behavioural repertoire of *Talitrus saltator* in its nocturnal migrations down and up-shore could be explained by a combination of endogenous circadian rhythms of (i) emergence and locomotor activity, (ii) phototaxis and (iii) orientation towards the dune/sky/boundary. It should be noted, however, that, as for Mediterranean species which migrate inland at night, other factors such as

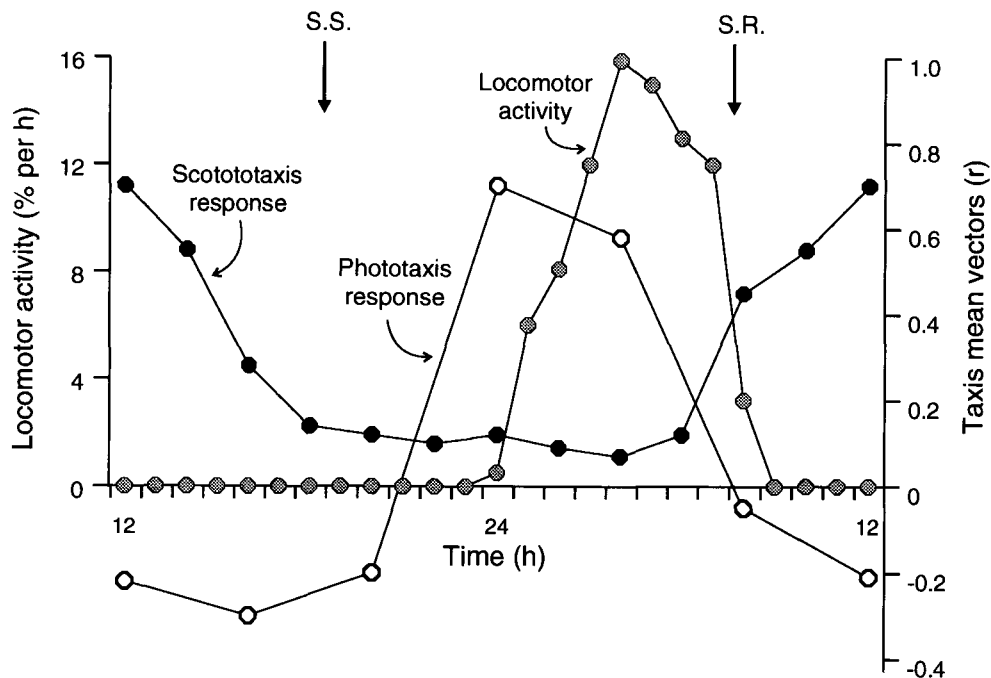


Fig. 1. Endogenous rhythms of locomotor activity, scototaxis responsiveness and phototaxis responsiveness in *Talitrus saltator*: SS - expected sunset, SR - expected sunrise. (After Williams 1980, Edwards & Naylor 1987, and Mezzetti, Naylor & Scapini 1994, respectively).

Ritmos endógenos de actividad locomotriz, respuesta de escototaxia y fototaxia en *Talitrus saltator*: SS - atardecer estimado, SR - amanecer estimado. (Según Williams 1980, Edwards & Naylor 1987, y Mezzetti, Naylor & Scapini 1994, respectivamente).

the earth's magnetic field (Arendse 1980) and solar cues (Ugolini & Cannicci 1991) have also been demonstrated to influence migrations of this species on tidal shores.

INTERTIDAL RESIDENTS WHICH SWIM AT HIGH TIDE

The problem of position maintenance of intertidal sand beach species which burrow at low tide and swim at high tide is well known in literature. The potential role of endogenous and/or exogenous factors controlling emergence and swimming rhythms in such species has been considered with respect to a number of crustaceans, including amphipods (Enright 1963, Morgan 1965, Fincham 1970) and isopods (Jones & Naylor 1970, Fish & Fish 1972, Enright 1972). Detailed studies have been carried out on the

sand-beach isopod crustacean *Eurydice pulchra* (Leach) which is characteristically found at low tide buried to a depth of a few cm on the upper half of a shore. The isopods emerge to swim and feed in the water column during the flood tide and re-burrow in their preferred zone on the beach normally without being transported offshore on the ebb. Position maintenance is partly achieved by an endogenously controlled circatidal rhythm of swimming and burrowing that enables anticipation of tidal ebb (Jones & Naylor 1970). In addition, however, Warman et al (1991) have shown that on the flood tide newly emerged *E. pulchra* occur most abundantly at the surface, exploiting wave-induced upshore currents. In contrast, on the early ebb they aggregate near the bottom in the surf, exploiting the downshore undertow (Fig. 2).

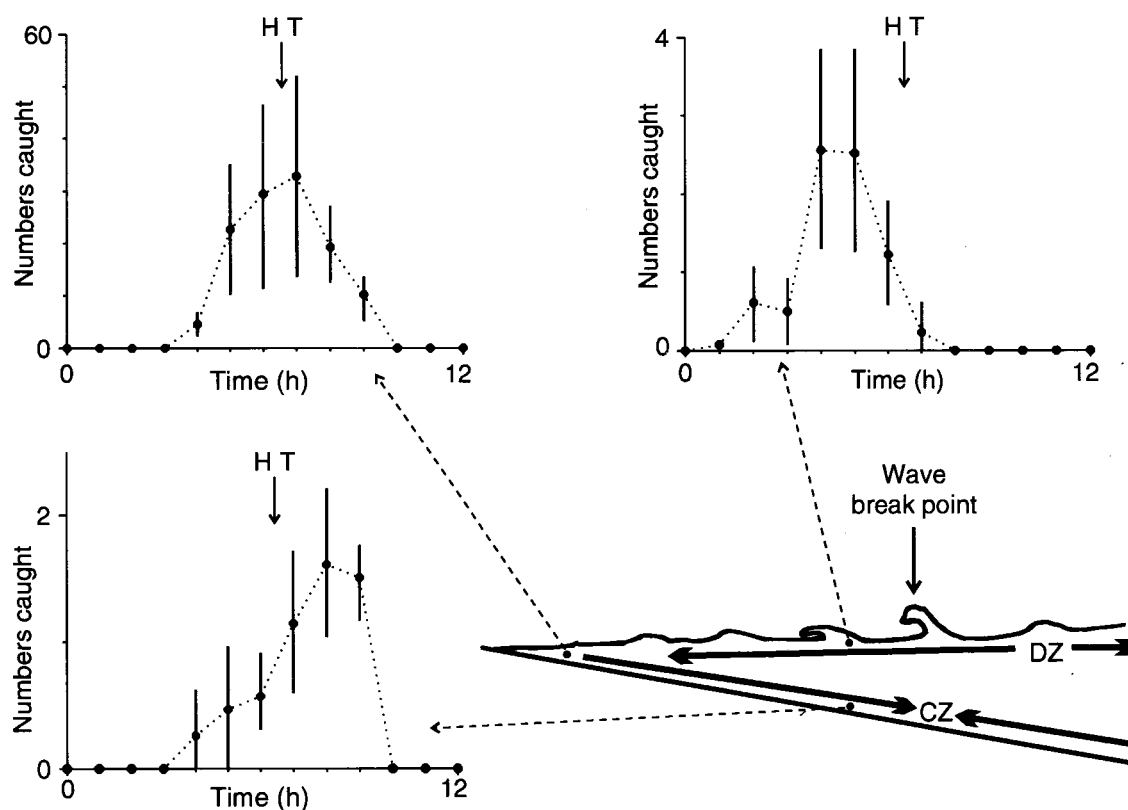


Fig. 2: Field catches (mean \pm s.e. in 5 standard net tows) over a tidal cycle of *Eurydice pulchra* in the surf and in wading depth offshore at the surface and near the bottom: HT- high tide, DZ - divergence zone, CZ - convergence zone. (After Warman, O'Hare & Naylor 1991).

Capturas de terreno a lo largo de un ciclo mareal (promedio \pm e.e. en 5 redes de arrastre estándar) de *Eurydice pulchra* en aguas superficiales y cerca del fondo de la zona de rompiente de las olas y aguas someras: HT- marea alta, DZ - zona de divergencia, CZ - zona de convergencia (según Warman, O'Hare & Naylor 1991).

Differential exploitation of the surface upshore current on the flood and bottom downshore current on the ebb appears to be controlled by an endogenous circatidal rhythm of phototaxis. Spontaneously in constant conditions in the laboratory, *E. pulchra* shows changes from positive phototaxis when it would be emerging during the late flood, to negative phototaxis immediately after subjective high tide (Warman et al 1993a; Fig. 3). Hence, in *Eurydice pulchra*, as in *Talitrus saltator*, endogenous rhythmic responsiveness to directional cues appears to modulate endogenous locomotor activity rhythms in inducing temporal changes of behaviour that control migration on the shore. Intertidal migrations of the intertidal *Synchelidium* may also be controlled, at least in part, through endogenously driven rhythmic changes in responsiveness to light (Forward 1980).

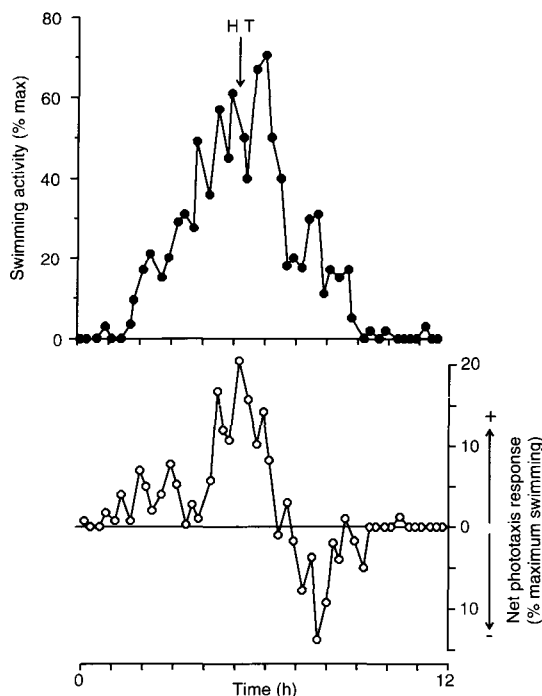


Fig. 3: Endogenous rhythms of locomotor activity (upper) and phototaxis responsiveness (lower) in twelve *Eurydice pulchra*: HT - expected high tide (After Warman, Reid & Naylor 1993a).

Ritmos endógenos de actividad locomotriz (arriba) y respuesta de fototaxis (abajo) en doce especímenes de *Eurydice pulchra*: HT - marea alta estimada (según Warman, Reid & Naylor 1993a).

Further studies reveal that the vertical distribution of *Eurydice pulchra* on the shore at low tide varies with the neaps/springs cycle of tides. The adult population evidently avoids stranding above high tide at neaps by moving downshore during tides of decreasing amplitude just after full spring tides (Alheit & Naylor 1976). Large numbers of the isopods swim spontaneously at high tide during reducing spring tides under the control of an endogenous circasemilunar rhythm of emergence and swimming (Alheit & Naylor 1976) which free-runs in constant conditions (Reid & Naylor 1986). The occurrence of semilunar rhythmicity is not, however, ubiquitous in *Eurydice pulchra* populations. Juveniles exhibit pronounced circatidal swimming at all stages of the springs/neaps cycle, perhaps related to requirements for continuous feeding, thus revealing ontogenetic differences in behavioural control of swimming migrations (Hastings & Naylor 1980). Regional differences in such behaviour patterns are also apparent; a semilunar rhythm occurs in open shore living *Eurydice pulchra* but not in a population from a sheltered estuary (Reid & Naylor 1989). Populations of this isopod in sheltered estuaries may be at greater risk of being carried downshore to unfavourable muddy substrates and low salinity water, than in being stranded at the level of high spring tides.

UPSHORE MIGRANTS

Mobile, epibenthic macrocrustaceans, like fishes, form important components of the fauna of sandy beaches in many parts of the world (Allen 1966; Brown & MacLachlan 1991; Gibson et al 1993). Among the larger forms crabs and shrimps are numerically the most abundant and their occurrence between tidemarks has been well studied over time-scales of seasons and years (Gibson et al 1993). On European shores the crab *Carcinus maenas* (L.) and the brown shrimp *Crangon crangon* (L.) are dominant members of this community in which they are important predators (van de Veer & Bergmann 1987, Pihl 1985). However, few studies have been carried out on such species which migrate up

and downshore from the subtidal by sampling them at various tidal levels at various states of tide, and by carrying out supporting experimental studies of biological clock controlled locomotor activity rhythms and orientational behaviour.

Comparative rhythmic behavioural studies of subtidal and intertidal species of the same genus have been carried out on the isopod genus *Eurydice* (Jones & Hobbins 1985) and the crab genus *Liocarcinus* (Abello et al 1991). In *Eurydice* the near-shore zone sublittoral species *E. spinigera* was shown to exhibit much stronger circadian than circatidal rhythmicity (Jones & Hobbins 1985). While the generally intertidal species *E. pulchra* showed very strong circatidal behavioural rhythmicity (Jones & Naylor 1970). Similarly, the crab *Liocarcinus holsatus* (Fabr.), captured as it migrated into the intertidal zone showed strong circatidal activity rhythms, with maxima at expected times of high tide, synchronized by simulated tidal cycles of hydrostatic pressure (Abello et al 1991). In contrast the predominantly subtidal species *L. depurator* (L.) showed circadian locomotor activity rhythms with peaks during expected night (Abello et al 1991). Such findings suggest that up and downshore migrations of some crustaceans are at least partly controlled by endogenous clock-controlled rhythmic behaviour of tidal periodicity.

Similar endogenous clock-controlled behaviour has been shown partly to control the tidal migrations of the shore crab *Carcinus maenas* (Naylor & Atkinson 1972) and the brown shrimp *Crangon crangon* (Al-Adhub & Naylor 1975). Following the early observations of Hartsuyker (1996) that *Crangon crangon* made up and downshore migrations on each tidal rise and fall in the Wadden Sea, Al-Adhub and Naylor (1975) undertook combined field and laboratory studies of the behaviour of this species. By obtaining push-net sample at the tide edge and beam trawl samples from a small boat on a sandy shore of 6m tidal amplitude, *Crangon* were observed to disperse over the lower half of the shore at times of high tide and to retreat towards low tide level where they buried at low tide. In the laboratory two separate rhythms were shown to occur, emergence

and swimming, both of which, particularly the former, were under endogenous control and persisted with approximately tidal periodicity in constant conditions. Light was shown partially to inhibit emergence and swimming, with day/night cycles in the laboratory modulating the endogenous circatidal rhythm into one of nocturnal periodicity. It was suggested that the flexible behavioural repertoire of *Crangon* is adaptive for the wide range of ecological conditions which it encounters. The endogenous rhythm expressed by shrimps from a tidal locality was considered to be of adaptive value in maintaining zonation beneath sand near low water mark at low tide after movement inshore during high tide (Al-Adhub & Naylor 1975).

Recently the present authors have extended earlier studies on *Crangon crangon* by sampling intensively for 10 months at various tidal levels at different states of tide, using beam trawling at the water's edge from a small boat. These findings (Fig. 4) indicate that there are differences in the behaviour of *Crangon* on the shore dependent upon their size. Large *Crangon* (> 20mm total length) showed a significant reduction in numbers when sampled at MLWM at high tide when compared with samples taken at MTL and at MHWM in samples at high tide, whereas at low tide no *Crangon* larger than 20 mm total length were found in intertidal sand sample, collected at low tide. In contrast small *Crangon* (< 20 mm total length) showed no significant difference in numbers per m² at MLWM between samples taken at low and high tide. Moreover there was no difference in the density of small *Crangon* between MHWM and MLWM in samples taken at high tide, and in sand samples obtained at low tide densities of 12 small shrimp per m² were obtained. Evidently small *Crangon*, unlike larger specimens, do not exhibit up and downshore migrations which would warrant further study.

Similar studies to those reported above for *Crangon* have been carried out on *Carcinus*. In extensive samples over a period of 10 months small (< 35mm carapace width) and large (> 35mm cw) crabs were sampled at the water's edge at LWM at low tide and then at MLWM, MTL and MHWM at high

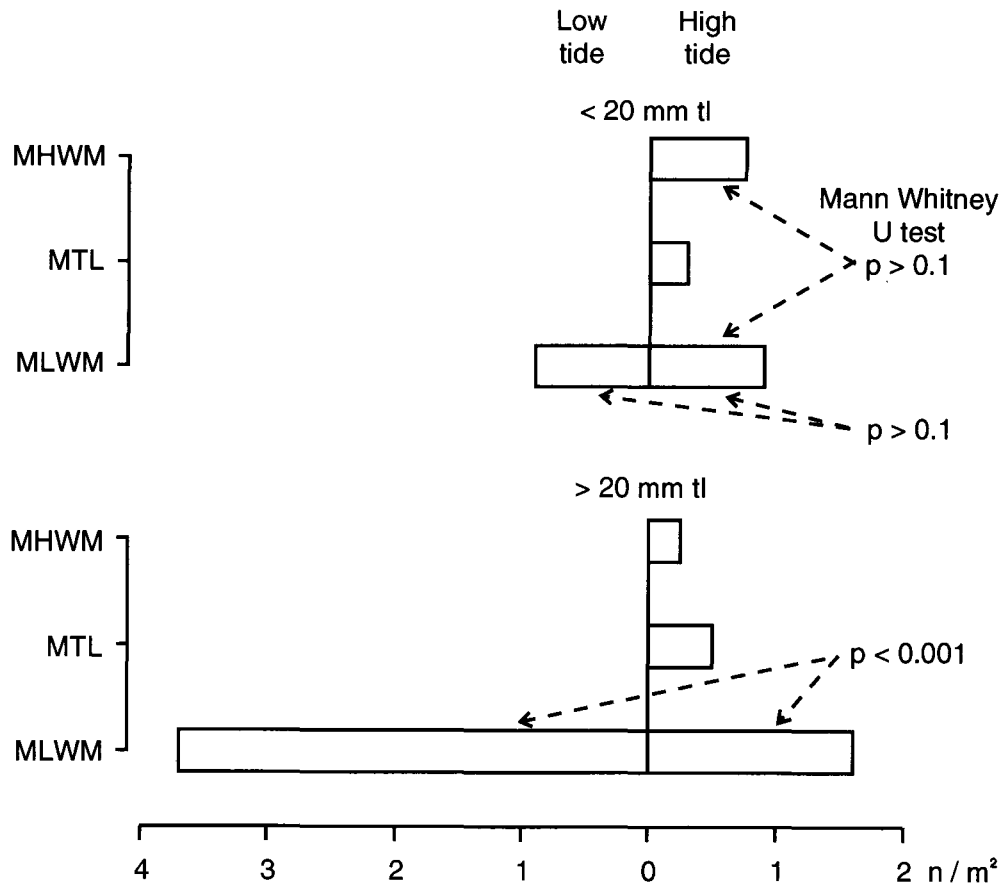


Fig. 4: Densities of *Crangon crangon* taken in beam trawls at MLWM at low tide and at MLWM, MTL and MHWM at high tide. Mean values are shown separately for small (< 20 mm t. l.) and large (> 20 mm t.l.) specimens in 20 samples at each tidal level over a 10 month sampling period (Original).

Densidades de *Crangon crangon* recolectados con redes de arrastre durante marea baja (MLWM) y marea alta (MLWM, MTL y MHWM). Se muestran separadamente los valores promedio para especímenes pequeños (< 20 mm t. l.) y grandes (> 20 mm t.l.) en 20 muestras durante cada ciclo mareal a lo largo de un período de muestreo de 10 meses (Original).

tide. In this species the numbers of both large and small crabs at MLWM fell significantly at high tide, suggesting that both sizes showed some upshore migration (Fig. 5). Low densities of large and small crabs were recorded at MTL and MHWM at high tide confirming some upshore migration, though it should be noted that small crabs of < 35 mm were recorded in sand between tide-marks at low tide in densities of 2 per m^2 . Thus, as in *Crangon*, the behaviour patterns of large and small specimens of *Carcinus* between tidemarks are different. This point is further emphasized in a detailed study of the migratory behaviour of *Carcinus maenas* up and down a boulder-free boat slipway using unbaited directional traps (Hunter & Naylor

1993). This study demonstrated highly orientated migration with significantly more crabs taken in traps facing up- and down-shore tidal flow than in traps set against or at 90° to the tidal flow. The catches in traps set facing tidal flow on rising and falling tides at six tidal levels on the shore are illustrated in Table 1. These data show that upper shore migrants were smaller than lower shore migrants, indicating that on that shore, as on a sandy beach, small crabs, though migratory at high tide, often remain hidden on the shore at low tide, either beneath boulders or buried in sand adjacent to the slipway.

Individual *Carcinus* which perform the most extensive up-and downshore migrations are early-intermoult males (Hunter & Naylor

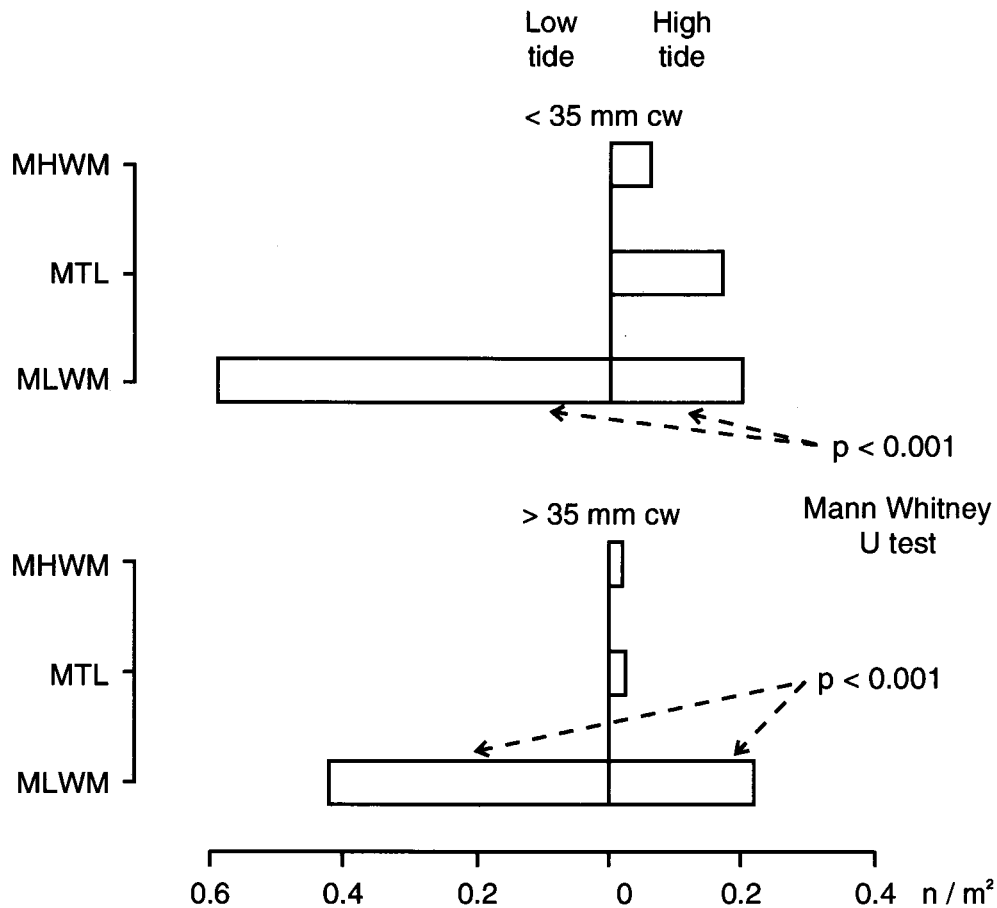


Fig. 5: Densities of *Carcinus maenas* taken in beam trawls at MLWM at low tide and at MLWM, MTL and MHWM at high tide. Mean values are shown separately for small (< 35 mm c. w.) and large (> 35 mm c.w.) specimens in 20 samples at each tidal level over a 10 month sampling period (Original).

Densidades de *Carcinus maenas* recolectados con redes de arrastre durante marea baja (MLWM) y marea alta (MLWM, MTL y MHWM). Se muestran separadamente los valores promedio para especímenes pequeños (< 350 mm c.w.) y grandes (> 35 mm c.w.) en 20 muestras durante cada ciclo mareal a lo largo de un período de muestreo de 10 meses (Original).

1993). It is these individuals amongst the larger crabs (> 35 mm cw) which exhibit the most persistent endogenous circatidal rhythms of locomotor activity (Naylor 1958; Atkinson & Parsons 1973), again confirming that tidal migrations of some species are partially driven by physiological clocks. Certainly direct observations by diving show that such crabs appear to seek shelter or move downshore in anticipation of the ebbing tide, as if under biological clock control (Warman et al 1993b). Moreover, in *Carcinus maenas*, as in *Talitrus saltator* and *Eurydice pulchra*, Warman et al (1993a) have shown that the direction of migration is

determined by endogenously controlled changes in phototaxis. Freshly caught crabs in the laboratory were shown to exhibit spontaneous changes from positive phototaxis before times of expected high tide to negative phototaxis immediately after expected high tide (Fig. 6).

Such photobehaviour, combined with the circatidal rhythms of locomotor activity, appears to provide an endogenous basis for the movement of active male crabs into and away from well-lit areas in shallow water at the edge of the tide on a tidal time-scale. Further comparative studies of such behaviour are necessary over a larger range of

TABLE 1

Size frequency distributions of *Carcinus maenas* collected in standard 6 h samples using unbaited traps set facing tidal flow, upshore and downshore, at various tidal levels. Underlined values are those greater than the mean numbers at each tidal level sampled (After Hunter & Naylor 1993)

Distribución de frecuencias de tamaños de especímenes de *Carcinus maenas* recolectados en muestras estándar de 6 h usando trampas sin carnada y colocadas en contra del flujo marea, en varios niveles mareales. Se subrayan los valores mayores que el promedio de cada nivel marea muestreado (según Hunter & Naylor 1993)

	Station	Carapace width (mm)						
		10-19	20-29	30-39	40-49	50-59	60-69	70-79
Upper shore	1	1	<u>24</u>	<u>47</u>	<u>64</u>	12	1	0
	2	0	<u>12</u>	<u>61</u>	<u>47</u>	9	4	1
Mid shore	3	0	4	<u>39</u>	<u>45</u>	13	6	1
	4	0	5	<u>14</u>	<u>17</u>	9	11	3
Lower shore	5	0	1	7	9	22	<u>10</u>	6
	6	0	3	2	<u>7</u>	<u>17</u>	<u>8</u>	5

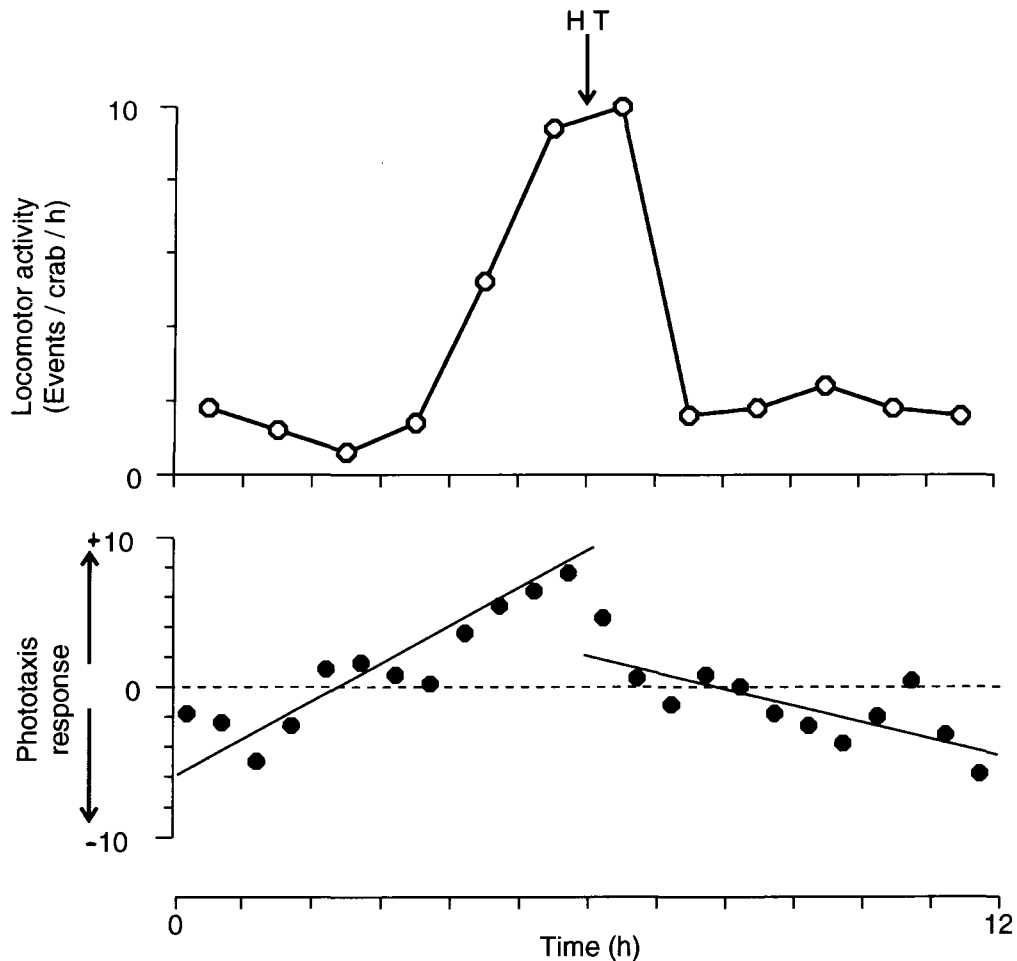


Fig. 6: Endogenous rhythms of locomotor activity and phototaxis responsiveness in *Carcinus maenas*. Upper record - hourly average beam-breaks of 2 crabs; lower record - mean responses of 10 crabs, in each case for 48h in constant conditions. HT - expected high tide (Data from Warman, Reid & Naylor 1993b).

Ritmos endógenos de actividad locomotriz y respuestas de fototaxis en *Carcinus maenas*. Gráfico superior - promedio horario de veces que dos cangrejos interceptan un rayo registrador; gráfico inferior - respuestas promedio de 10 cangrejos, en cada caso por 48 h en condiciones constantes. HT - marea alta estimada (data de Warman, Reid & Naylor 1993b).

sizes and stages of *Carcinus*. Already it is apparent that juvenile crabs (< 35 mm cw), which in many localities are more or less permanently resident between tidemarks, show different rhythmic responses from migratory adults that are less often stranded at low tide. In laboratory experiments it was shown that juveniles (< 35mm cw) would entrain circatidal rhythms of locomotor behaviour to artificial tidal cycles of immersion/emersion (Reid et al 1993) whereas adults (> 35mm cw) would not (Williams & Naylor 1969).

In conclusion, tidal migratory behaviour in a number in a number of high-, mid- and low shore crustaceans has been shown to be at least partly controlled by a combination of endogenous rhythms of both locomotor activity and responsiveness to environmental cues. Some ontogenetic and spatial differences in behaviour associated with ecological differences are also apparent. Future studies of such behaviour should take account of (i) the need for intensive sampling in space and time, (ii) potential differences in behaviour between developmental or moulting stages, and (iii) the role of endogenous rhythms in the control of locomotor activity and of phase-responsiveness to environmental variables.

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