

Are there separate circatidal and circadian clocks in the shore crab *Carcinus maenas*?

D. G. Reid, E. Naylor

School of Animal Biology, University College of North Wales, Bangor, Gwynedd LL57 2UW, United Kingdom

ABSTRACT: Shore crabs *Carcinus maenas* collected in winter normally exhibit circadian but not circatidal rhythmicity. When introduced into 20 ‰ seawater (7 ppt), a circatidal rhythmic activity pattern is induced phased to the time of introduction. There is no apparent change in the phase of the extant circadian rhythm which, after treatment, acts to modulate the expression of the circatidal rhythm, the peaks of which are greatest during 'expected' night. These findings suggest that there are separate mechanisms for the control of circadian and circatidal rhythmicity in *C. maenas*. They permit a new appraisal of a key question in rhythm biology as to whether circatidal and circadian rhythmicity can be considered as expressions of the same physiological mechanism.

INTRODUCTION

Circatidal rhythms of behavioural activity and other physiological processes, and the environmental context of such biological cycles, are well documented for marine animals (DeCoursey 1983, Naylor 1976, 1985). Typical of many of these animals, the shore crab *Carcinus maenas* (Leach) also displays a circadian modulation of the circatidal pattern of activity (Naylor 1958), with greater amplitude of tidal activity at the times of expected night time high tides than at day time high tides. The nature of this type of modulation has for some time been the subject of debate in the literature and several hypotheses have been advanced to explain the phenomenon.

One hypothesis is that circatidal or combined circatidal and circadian rhythmicity is driven by a single bimodal circadian oscillator with 2 peaks per cycle (Enright 1976a, b) as occurs in dawn/dusk (crepuscular) activity patterns (Daan & Berde 1978, Pittendrigh 1981). Enright's (1976a, b) conclusion is based on the derivation of a phase response curve (PRC) for the isopod *Excirolana chiltoni* which was bimodal on a circadian time base.

A different hypothesis proposes that tidal rhythms may be controlled by circalunadian (lunar day) clocks (Webb 1983). It has been suggested that circatidal rhythmicity in the crab *Helice crassa* may be controlled by 2 such circalunadian oscillators loosely coupled in antiphase (Palmer & Williams 1986).

Neumann (1981) and Naylor (1982) argued the case

for a third hypothesis, that true endogenous circatidal rhythmicity exists in some coastal species. Experimental evidence to support this hypothesis was presented by Naylor & Williams (1984a, b). These authors demonstrated a PRC on a tidal (12.4 h) time-base in the crab *Hemigrapsus edwardsii* and suggested that the hypothesis of a 'bimodal-circadian' PRC for *Excirolana* (Enright 1976a, b) might be more economically regarded as circatidal. Other authors have also demonstrated PRCs on a tidal time-base in number of other coastal invertebrates (Petpiroon & Morgan 1983, Holmstrom & Morgan 1984, Reid 1986), which provide further support for the autonomous nature of the oscillators driving circatidal rhythms in some animals. However, as pointed out by Naylor (1985), stronger support for the occurrence of truly circatidal rhythmicity would be provided if it were possible to demonstrate rephasing of the circatidal rhythm without any concomitant phase changes in the circadian rhythm in the same individual.

The experimental protocol devised here to test the possibility of separate phase-shifting of circatidal and circadian rhythms derives from the observation that the shore crab *Carcinus maenas*, which normally does not display overt circatidal rhythmicity in winter (Atkinson & Parsons 1973), will do so if exposed to continuous low salinity (Bolt & Naylor 1985). Preliminary observations in the present study suggested that the phasing of this induced rhythmic activity was in fact determined by the time of day of transfer to the low salinity seawater, here defined as 'hypo-osmotic shock', analogous to an earlier reported cold shock effect, some physiological

implications of which are discussed by Naylor (1963). However, whereas cold shock rephases both circatidal and circadian rhythmicity, hypo-osmotic shock appeared to affect only the circatidal rhythm. We therefore set out to investigate, with *C. maenas*, whether hypo-osmotic shock applied at different times of the diel cycle could reset circatidal rhythmicity without also affecting the phase of a crab's circadian oscillator.

MATERIALS AND METHODS

Fresh *Carcinus maenas* were collected in baited traps subtidally in the Menai Strait, North Wales, between January and April 1987. Only adult male crabs of between 45 and 65 mm carapace width, and in intermolt, were used for the experiments. Also, since in recent unpublished work we have shown physiological and behavioural differences between individual *C. maenas* in relation to carapace colour, which may be green or red, only green *C. maenas* (the more common) were used here. Crabs were acclimated to laboratory conditions (34 ppt, 10°C, nLD) for 2 d before experiments were carried out.

After acclimation, groups of 10 to 12 crabs were placed into individual wheel actographs (Bolt & Naylor 1985) filled with 20% seawater (7 ppt), in which they were submerged. Transfer to the actographs from the holding facilities deliberately involved minimal temperature change ($\pm 2^\circ\text{C}$) as substantial temperature changes are known to rephase activity in *Carcinus maenas* (Naylor 1963). Activity, the turning of the wheels, was recorded with a BBC 'B' Microcomputer using magnets attached to the wheels and reed switches connected to the computer. Recordings were continued for a maximum of 4 d, in constant darkness (D:D), after which most crabs (>95%) survived well on return to full seawater. In separate experiments crabs were placed in the actographs at 4 different times of day; 06:00, 12:00, 18:00 and 24:00 h. In addition, each type of experiment was repeated on several different days with different diel timings of the tidal cycle. This protocol was arranged to distinguish clearly whether hypo-osmotic shock induced phase-shifts in the circatidal rhythm without affecting the phase of the circadian rhythm. Results are presented as percentages of the greatest number of events recorded in any 1 h period, or as mean events per hour

RESULTS

The activity records presented in Figs. 1 and 2 show the pattern of hourly locomotor activity recorded for individual *Carcinus maenas* after transfer from 100%

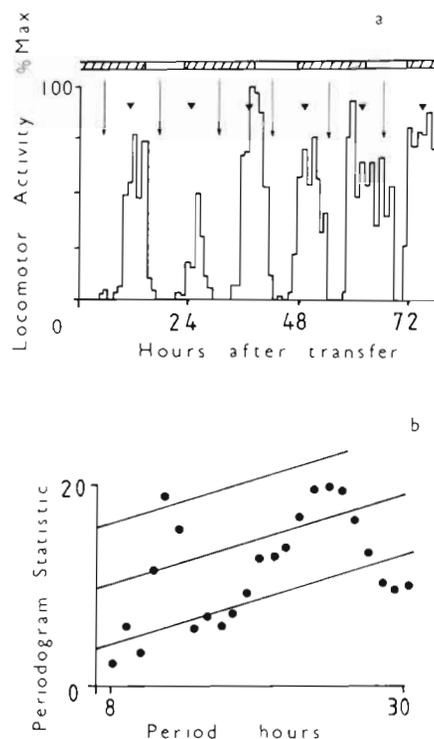


Fig. 1. *Carcinus maenas*. (a) Hourly locomotor activity records for a single, freshly caught crab in constant conditions after introduction into 20% seawater (7 ppt) at 18:00 h (dusk). Triangles are at 12.4 h (tidal) intervals after the start of the experiment, all of which occurred during 'expected' darkness, indicated by the shaded areas in the bar at the top of the figure. Arrows indicate the time of 'expected' high tide on the shore. (b) Periodogram analysis of the data presented in Fig. 1a above, derived as in Bolt & Naylor (1985). The oblique lines represent the regression line ($\pm 95\%$ CI) derived from randomization of the original data

(=34 ppt) to 20% seawater at various times throughout the diel cycle. The record in Fig. 1a is for a crab transferred at 18:00 h and then maintained in 20% seawater for a further 78 h. The activity pattern is apparently circatidal with peaks of locomotor activity recurring at approximately tidal frequency after the start of the experiment. Circatidal rhythmicity is confirmed by the periodogram analysis shown in Fig 1b, in which the most significant period, extending above the upper confidence limit, is around 12 h. Similar experiments were started on 5 separate days, each with different times of expected high tides, with up to 12 individuals on each day. As is usually the case with recordings of activity from individual animals, some (25%) showed no activity at all, while others (25%) displayed random activity, defined as any trace in which no significant peaks were evident in the periodograms. All such individuals were eliminated from the study. In all cases where activity was rhythmic it was apparently circatidal with the peaks of locomotor

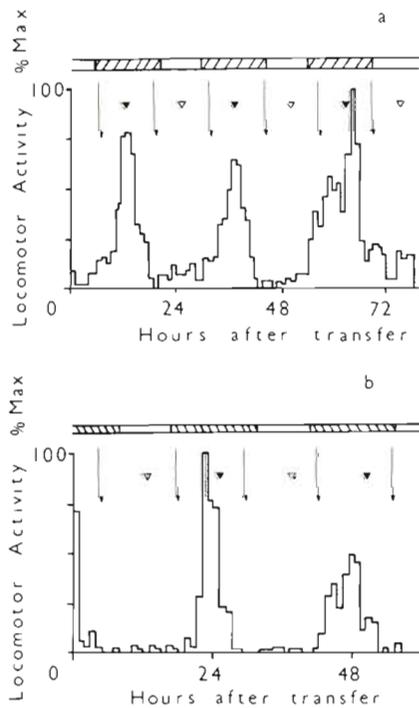


Fig. 2. *Carcinus maenas*. Hourly locomotor activity for single freshly caught crabs in constant conditions after introduction into 20% seawater at (a) 12:00 h and (b) 24:00 h. Triangles are at 12.4 h intervals after the start of the experiment; unshaded occurred in 'expected' daytime, shaded in 'expected' night-time. Arrows as in Fig. 1

activity in the pooled data occurring at approximately tidal intervals after the start of the experiment (see Fig. 3a). It is clear that the activity rhythm shown is phased

to the timing of introduction into 20% seawater and not to the timing of experienced high tides on the shore. In 6 similar experiments crabs were transferred into 20% seawater at 06:00 h, again on days with different expected times of high tide on the shore where the crabs were collected. All individuals showed similar circatidal locomotor activity patterns in response to hypo-osmotic shock to that in Fig. 1a and the activity was again clearly phased to the time of introduction into the 20% seawater. The circatidal pattern in these results is confirmed by the form estimate in Fig. 3b.

In crabs transferred into 20% seawater at 12:00 h or at 24:00 h, the activity patterns recorded are apparently circadian in periodicity (Fig. 2a, b), unlike the results in Fig. 1. However the patterns, each of which was confirmed in several repeat experiments (Fig. 3c, d for pooled data), are also different from each other. When crabs were transferred at 12:00 h (Fig. 2a) the first peak of locomotor activity occurred approximately one tidal wavelength after the start of the experiment, as in Fig. 1a. Subsequent peaks occurred at about twice tidal intervals thereafter, all during 'expected' night (Figs. 2a and 3c). Such a pattern could be explained if the rhythm induced by the hypo-osmotic shock was circatidal (as in Fig. 1) and each alternate, daytime, peak was suppressed by an underlying circadian oscillator which remains undisturbed.

This interpretation is confirmed by the results when hypo-osmotic shock was applied at midnight (Figs. 2b and 3d). The induced rhythm is again apparently circadian or twice-tidal in periodicity. However, it is phased differently, in relation to the start of the experiment,

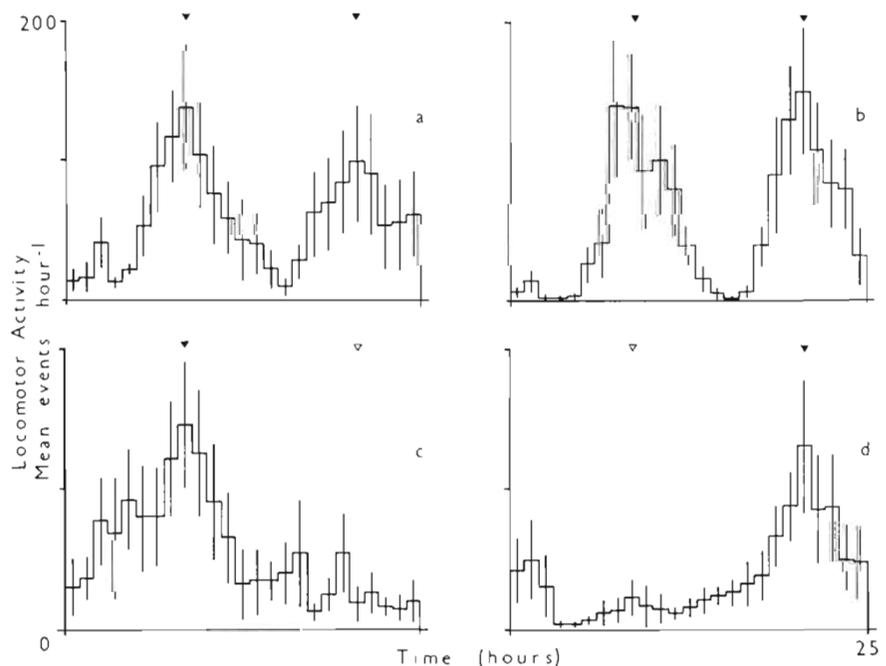


Fig. 3. *Carcinus maenas*. Mean 25 h form-estimates for n groups of up to 12 crabs introduced into 20% seawater at (a) 18:00 h (dusk) ($n=5$), (b) 06:00 h (dawn) ($n=6$), (c) 12:00 h ($n=10$) and (d) 24:00 h ($n=6$) and maintained in constant conditions for up to 78 h in each case. The figures presented show the mean form-estimate derived from the individual form-estimates for each group of crabs in each trial. Each hourly mean (\pm SE) is thus based on up to 10 group values. Data are meaned around the 12.4 h (tidal) anniversaries of the time of transfer into 20% seawater at the start of the experiments, the shaded triangles occurring in 'expected' night-time and the unshaded during 'expected' daytime

from that shown in Fig. 2a. The first activity peak occurs repeatedly ca 24 h after transfer (Fig. 3d). The activity peaks observed in both Figs. 2a and 2b thus occur during expected night, as if the expected daytime circatidal peaks have been largely suppressed by the underlying circadian rhythm. It is important to note that despite the timing in the day of the hypo-osmotic shock which re-sets the circatidal rhythm, the circadian modulation remains in the correct phase with the natural variation on the shore where they were collected. This confirms that while hypo-osmotic shock appears to restart or reset the circatidal activity rhythm in the new phase, an underlying, circadian oscillator appears to be unaffected and continues to modulate the expression of the circatidal rhythm without any phase change.

DISCUSSION

It is clear from the present investigation that a consistent pattern of rhythmic locomotor activity is apparent when overwintering *Carcinus maenas* are transferred from full to 20% seawater at various times of the diel cycle. The effect of this hypo-osmotic shock is to initiate overt circatidal locomotor rhythmicity in the crabs. It has previously been shown that during winter (January to April inclusive) *C. maenas* normally exhibit only circadian rhythmicity, if any, which persists in unaltered phase (Atkinson & Parsons 1973), but that they also display circatidal rhythmicity if introduced into dilute seawater (Bolt & Naylor 1985). Present results confirm that the circatidal locomotor rhythmicity is in fact induced by transfer from full to dilute seawater (hypo-osmotic shock) and show that, in every case, such rhythmicity is phased to the time of that shock. Previous studies (Naylor 1963, Gibson 1967, Fincham 1970) have shown that exposure to low temperature shock rephases both circatidal and circadian rhythmicity, in a number of coastal animals. Present results using *C. maenas* suggest that hypo-osmotic shock affects only circatidal rhythmicity, without affecting circadian rhythmicity in the crabs.

This effect in *Carcinus maenas* appears, so far, to be unique and cannot be readily explained by the type of bimodal circadian rhythmicity which has been described in the isopod *Excirrolana chiltoni* (Enright 1976a, b). If such rhythmicity were restarted by hypo-osmotic shock in a completely new phase, one would expect both the circatidal and circadian components to be equally phase shifted. It is also unlikely that exposure to a single stimulus of hypo-osmotic shock could completely rephase an already free-running (bimodal) circadian oscillator, let alone generate the variety of locomotor rhythmic patterns described. Similarly one

can question whether free-running locomotor rhythmicity in *C. maenas* could, on present evidence, be controlled by two circalunadian oscillators operating in antiphase, as proposed for the crab *Helice crassa* (Palmer & Williams 1986). Once again such a rhythm would be expected to restart with the same wave-form regardless of the time of day hypo-osmotic shock was applied, since each oscillator would be expected to be equally responsive to the environmental perturbation.

The most economical hypothesis to explain the present results is that free-running locomotor rhythmicity in *Carcinus maenas* is controlled by 2 separate oscillators, one circadian (Atkinson & Parsons 1973, Bolt & Naylor 1986) and one of circatidal periodicity which can be started up by exposure to hypo-osmotic shock. The second oscillator would generate activity peaks every 12.4 h, and these peaks would be partially suppressed or exaggerated by the circadian oscillator depending upon whether they occurred during the hours of expected day or night respectively.

This hypothesis does not exclude the possibility that circatidal rhythmicity, in this and other species, may have evolved from a bimodal circadian rhythm (Gibson 1970, Rodriguez & Naylor 1972, Naylor 1976) or from 2 mutually coupled circalunadian oscillators (Palmer & Williams 1986). However it does propose that locomotor rhythmicity in *Carcinus maenas* is not controlled by a single oscillator, whether circadian, circalunadian or circatidal, but must be under the control of at least 2 independent oscillators, one circadian, the other, functionally, circatidal. This view is supported by consideration of the entrainment process of circatidal rhythmicity.

Salinity variation is well known to affect the circatidal locomotor activity of *Carcinus maenas*. Immersion in dilute seawater was shown to induce increased locomotor activity (Thomas et al. 1981). Also, tidally varying salinity cycles are able to entrain free-running circatidal activity rhythms in this species (Taylor & Naylor 1977, Bolt & Naylor 1985, 1986). It is clear therefore that salinity variation is closely involved in the control of circatidal activity patterns. There is, however, no evidence that salinity changes are in any way involved in the control of circadian rhythmicity in this species. Salinity changes experienced on the shore by *C. maenas* vary only on a tidal time base and it would seem highly unlikely that salinity would be an entraining factor for circadian rhythmicity. On these grounds alone it might be expected that coastal animals in some localities would possess separate circatidal and circadian oscillators, the former with the necessary physiological transduction mechanisms to use salinity, and other tidal variables, as synchronising factors (Naylor & Williams 1984a).

Whatever the exact nature of their underlying oscil-

lators mechanisms, circatidal behavioural rhythms are substantially different from behavioural rhythms controlled by circadian oscillators. The principal zeitgeber in circadian systems is the light:dark cycle (Pittendrigh 1981) but light has been shown to be ineffective in entraining circatidal rhythms (Palmer & Round 1967, Webb 1971, Palmer 1974). The range of effective zeitgebers found in circatidal locomotor activity is considerable and includes cycles of turbulence (Jones & Naylor 1970, Neumann 1978), hydrostatic pressure (Naylor & Atkinson 1972), salinity (Taylor & Naylor 1977, Bolt & Naylor 1985) and immersion (Petpiroon & Morgan 1983, Harris & Morgan 1984). Temperature cycles act as synchronisers of both circatidal (Williams & Naylor 1969, Bolt & Naylor 1986) and circadian behavioural rhythms (Zimmerman et al. 1968, Lindberg & Hayden 1974), but entrainment of circadian rhythms to temperature cycles is usually secondary and supplementary to L:D cycles (Pittendrigh 1981).

Further evidence against the 'bimodal circadian' hypothesis is also found in the form of the phase response curves (PRCs) of circatidal rhythms in some marine species (Enright 1976a, b, Petpiroon & Morgan 1983, Harris & Morgan 1984, Naylor & Williams 1984a, b, Reid 1986). With the exception of the PRC derived for the sand-beach isopod *Excirrolana chiltoni* (Enright 1976a, b) all the above are on a clearly circatidal time base. The PRC of *E. chiltoni* was plotted on a circadian time base (Enright 1976a), but as it is symmetrically bimodal, it could also be interpreted as varying on a circatidal time base (Naylor & Williams 1984a, b). In addition all the PRC's derived so far for coastal animals show very small phase changes, usually of less than 2 h, whereas circadian PRCs commonly have phase shifts of up to 8 h or more dependent upon species and stimulus strength (Pittendrigh 1981). This difference may be of adaptive value by providing a greater 'stability' to circatidal rhythms, preventing excessive responses to the normal, weather-driven fluctuations in timing of the tidal rise and fall (Naylor & Williams 1984a, b).

It is important to note that the selection pressure for 'circatidal' rhythmicity, whatever its exact nature, will probably vary geographically according to whether local tides are semidiurnally equal, unequal, or even diel in form. Animals such as *Carcinus maenas* on UK shores, which commonly experience more or less equal semidiurnal tides, might be expected to have been exposed to a greater selection pressure for 'true' circatidal rhythmicity than organisms such as *Excirrolana chiltoni* in California, where tides show marked diurnal inequalities (Klapow 1972).

In conclusion, therefore, there is strong evidence in the shore crab *Carcinus maenas* for separate evolution of true circatidal rhythmicity distinct from circadian rhythmicity, and for which there are clearly separate

zeitgeber and transduction mechanisms. In this species and possibly also in some other coastal animals from localities with similar tidal regimes, it seems reasonable to hypothesise that circatidal and circadian oscillators may have evolved in response to different selective pressures and, though possibly of common origin, are now functionally quite distinct. Not all tidal rhythms appear to be under the control of bimodal circadian, or of alternating circalunadian oscillators; some appear to be truly circatidal.

Acknowledgements. We are grateful to the NERC for financial support of this study.

LITERATURE CITED

- Atkinson, R. J. A., Parsons, A. J. (1973). Seasonal patterns of migration and locomotor rhythmicity in populations of *Carcinus*. *Neth. J. Sea. Res.* 7: 81–93
- Bolt, S. R. L., Naylor, E. (1985). Interaction of endogenous and exogenous factors controlling the activity rhythms in *Carcinus* exposed to tidal salinity cycles. *J. exp. mar. Biol. Ecol.* 85: 47–56
- Bolt, S. R. L., Naylor, E. (1986). Entrainability by salinity cycles of rhythmic locomotor activity in normal and eyestalk ablated *Carcinus maenas* (L.). *Mar. Behav. Physiol.* 12: 257–267
- Daan, S., Berde, C. (1978). Two coupled oscillators: simulations of the circadian pacemaker in mammalian activity rhythms. *J. theor. Biol.* 70: 297–313
- DeCoursey, P. J. (1983). Biological timing. In: Vernberg, F. J., Vernberg, W. B. (eds.) *The biology of the Crustacea*, Vol. 17, Behaviour and ecology. Academic Press, New York, p. 107–162
- Enright, J. T. (1976a). Resetting a tidal clock – a phase response curve for *Excirrolana*. In: DeCoursey, D. J. (ed.) *Biological rhythms in the marine environment*. Univ. of S. Carolina Press, Columbia, p. 103–114
- Enright, J. T. (1976b). Plasticity in an isopod's clockworks: shaking shapes form and affects phase and frequency. *J. comp. Physiol.* 107: 13–37
- Fincham, A. A. (1970). Rhythmic behaviour of the intertidal amphipod *Bathyporeia pelagica*. *J. mar. biol. Ass. U.K.* 50: 1057–1068
- Gibson, R. N. (1967). Experiments on the tidal rhythm of *Blennius pholis* L. *J. mar. biol. Ass. U.K.* 47: 97–111
- Gibson, R. N. (1970). The tidal rhythm of activity of *Coryphoblennius galerita* L. (Teleostei). *Anim. Behav.* 18: 539–543
- Harris, G. J., Morgan, E. (1984). The effects of salinity changes on the endogenous circatidal rhythm of the amphipod *Corophium volutator* (Pallas). *Mar. Behav. Physiol.* 10: 199–217
- Holmstrom, W. F., Morgan, E. (1984). The effects of low temperature pulses in rephasing the endogenous activity rhythm of *Corophium volutator* (Pallas). *J. mar. biol. Ass. U.K.* 63: 851–860
- Jones, D. A., Naylor, E. (1970). The swimming rhythm of the sand beach isopod *Eurydice pulchra*. *J. exp. mar. Biol. Ecol.* 4: 188–199
- Klapow, L. A. (1972). Natural and artificial rephasing of a tidal rhythm. *J. comp. Physiol.* 79: 233–258
- Lindberg, R. G., Hayden, P. (1974). Thermoperiodic entrainment of arousal from torpor in the little pocket mouse *Perognathus longimembris*. *Chronobiologia* 1: 356–361

- Naylor, E. (1958). Tidal and diurnal rhythms of locomotor activity in *Carcinus maenas* (L.). *J. exp. Biol.* 35: 602-610
- Naylor, E. (1963). Temperature relationships of the locomotor rhythm of *Carcinus*. *J. exp. Biol.* 40: 669-679
- Naylor, E. (1976). Rhythmic behaviour and reproduction in marine animals. In: Newell, R. C. (ed.) *Adaptation to environment: essays on the physiology of marine animals*. Butterworths, London, p. 393-429
- Naylor, E. (1982). Tidal and lunar rhythms in animals and plants. In: Brady, J. (ed.) *Biological timekeeping*. Soc. exp. Biol. Seminar Series 14, p. 33-48
- Naylor, E. (1985). Tidally rhythmic behaviour of marine animals. *Symp. Soc. exp. Biol.* 39: 63-93
- Naylor, E., Atkinson, R. J. A. (1972). Pressure and the rhythmic behaviour of inshore animals. *Symp. Soc. exp. Biol.* 26: 395-415
- Naylor, E., Williams, B. G. (1984a). Environmental entrainment of tidally rhythmic behaviour in marine animals. *Zool. J. Linn. Soc.* 80: 201-208
- Naylor, E., Williams, B. G. (1984b). Phase responsiveness of the circatidal locomotor activity rhythm of *Hemigrapsus edwardsi* (Hilgendorf) to simulated high tide. *J. mar. biol. Ass. U.K.* 64: 81-90
- Neumann, D. (1978). Entrainment of a semilunar rhythm by simulated tidal cycles of mechanical disturbance. *J. exp. mar. Biol. Ecol.* 35: 67-79
- Neumann, D. (1981). Tidal and Lunar rhythms. In: Aschoff, J. (ed.) *Handbook of behavioural neurobiology*, Vol 4, Biological rhythms. Plenum Press, New York, p. 351-380
- Palmer, J. D. (1974). *Biological clocks in marine organisms*. Wiley InterScience, New York
- Palmer, J. D., Round, F. E. (1967). Persistent, vertical migration rhythms in benthic microflora. VI. The tidal and diurnal nature of the rhythm in the diatom *Hantzschia virgata*. *Biol. Bull. mar. biol. Lab., Woods Hole* 132: 44-55
- Palmer, J. D., Williams, B. G. (1986). Comparative studies of tidal rhythms. II. The dual clock control of the locomotor rhythms of two decapod crustaceans. *Mar. Behav. Physiol.* 12: 269-278
- Petpiroon, S., Morgan, E. (1983). Observations on the tidal activity rhythm of the periwinkle *Littorina nigrolineata* (Gray). *Mar. Behav. Physiol.* 9: 171-192
- Pittendrigh, C. S. (1981). Circadian systems: entrainment. In: Aschoff, J. (ed.) *Handbook of behavioural neurobiology*. Vol. 4, Biological rhythms. Plenum Press, New York, p. 95-124
- Reid, D. G. (1986). The rhythmic behaviour of a marine isopod crustacean. Ph. D. thesis, University of Wales
- Rodriguez, G., Naylor, E. (1972). Behavioural rhythms in littoral prawns. *J. mar. biol. Ass. U.K.* 44: 163-175
- Taylor, A. C., Naylor, E. (1977). Entrainment of the locomotor rhythm of *Carcinus maenas* by cycles of salinity change. *J. mar. biol. Ass. U.K.* 57: 273-277
- Thomas, N. J., Lasiak, T. A., Naylor, E. (1981). Salinity preference behaviour in *Carcinus*. *Mar. Behav. Physiol.* 7: 277-283
- Webb, H. M. (1971). Effects of artificial 24-hour cycles on the tidal rhythm of activity in the fiddler crab, *Uca pugnax*. *J. interdiscip. Cycle Res.* 2: 191-216
- Webb, H. M. (1983). Persistent rhythms of decapod crustaceans. In: Rebach, S., Dunham, D. (eds.) *The behaviour of the higher Crustacea*. John Wiley and Sons, New York, p. 197-198
- Williams, B. G., Naylor, E. (1969). Synchronization of the locomotor tidal rhythm of *Carcinus maenas*. *J. exp. Biol.* 51: 715-725
- Zimmerman, W., Pittendrigh, C. S., Pavlidis, T. (1968). Temperature compensation of the circadian oscillation in *Drosophila pseudoobscura* and its entrainment by temperature cycles. *J. Insect Physiol.* 14: 669-684

This article was submitted to the editor

Manuscript received: September 27, 1988

Revised version accepted: December 6, 1988