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To cite this article: C.G. Quilter & R.D. Lewis (1989) Clock control of foraging in the isopod *Scyphax ornatus* Dana, *New Zealand Journal of Zoology*, 16:3, 373-382, DOI: [10.1080/03014223.1989.10422903](https://doi.org/10.1080/03014223.1989.10422903)

To link to this article: <http://dx.doi.org/10.1080/03014223.1989.10422903>



Published online: 09 Feb 2012.



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Clock control of foraging in the isopod *Scyphax ornatus* Dana

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Abstract The terrestrial sand beach isopod *Scyphax ornatus* Dana exhibits circadian and circa-semilunar activity rhythms when kept in constant conditions in the laboratory. The circadian rhythm restricts activity to the subjective night and can be synchronised to artificial light cycles. The circa-semilunar rhythm is expressed as a cyclic variation in overall activity level, with isopods alternately active on 6–8 consecutive nights and then inactive on the next 6–8 nights. The circa-semilunar rhythm matches a fortnightly cycle in food availability on the isopods' home beach, but does not appear to be causally related to the lunar cycle, the spring/neap tidal cycle, or to moulting. This and other evidence suggests that the ecological role of the endogenous circa-semilunar rhythm is to allow *Scyphax*, within the protection of their burrows, to predict nightly foraging opportunities; a new role for such a long-period rhythm.

Keywords *Scyphax ornatus*; isopod; circadian rhythm; semilunar rhythm; foraging; sand beach

INTRODUCTION

The terrestrial isopod *Scyphax ornatus* lives on exposed beaches of North Island, New Zealand. Field studies at Piha Beach (Quilter 1987) have shown that adult *Scyphax* spend the daytime in

burrows near the high water mark and emerge at night to make lengthy excursions across the middle beach. A lifestyle such as this which involves many hours spent in a refuge isolated from external stimuli, interspersed with regular sorties which are precisely timed, creates an obvious need for an internal timing system; among other intertidal crustaceans some impressive examples of endogenous timing have been reported (e.g., Enright 1972). Both circadian, circatidal, and circa-semilunar clocks, either separately or in combination, may control activity (Naylor 1985). The ecological importance of endogenous timing is suggested by the fact that among shore crustaceans the precision and persistence of free-running activity rhythms is greater in burrowing than in surface-living species (Williams 1983). Other suggested roles for circadian or circatidal clocks in shore animals include controlling the cessation of activity in advance of unfavourable conditions (Atkinson & Naylor 1973), controlling re-emergence after a prolonged quiescent period associated with moult or adverse meteorological conditions, and reducing interspecific competition for food by generating a different foraging time for each species (Williams 1983).

Several species of shore animals have also been found to show activity rhythms of circa-semilunar or circa-lunar periodicities (Naylor 1985). The role of these long-period rhythms is much less clear. In the swimming isopods *Eurydice pulchra* (Alheit & Naylor 1976) and *Excirologa chiltoni* (Enright 1972) peak emergence occurs during spring tides, suggesting that the rhythm which generates this pattern acts to prevent individuals from becoming stranded above high water during neaps. Two species of supralittoral amphipods, *Talitrus saltator* (Williams 1979) and *Talorchestia quoyana* (Benson & Lewis 1976), also show circa-semilunar rhythms in overall activity level, and Williams has demonstrated that, in *Talitrus* at least, the cyclic variation in activity level is associated with an endogenous circa-semilunar moult rhythm in which moulting individuals are inactive for 2 days at times of neap tides.

In this paper we describe laboratory experiments which tested whether or not the locomotor activity of *Scyphax ornatus* is endogenously timed. We then investigated the possible role of endogenous activity rhythms in generating the foraging behaviour previously recorded in the field.

METHODS

Adult *Scyphax* (at least 10 mm overall length and of both sexes) were collected from the surface of the middle beach at night. Most came from Piha Beach (36°57'S, 174°28'E) but some were collected at Garden Bay (36°46'S, 175°08'E) as described later. The animals were placed immediately in actograph tanks filled with moist sand into which they could burrow. The tanks were returned to a constant temperature room at 21±1°C and time allowed for the mass of sand to reach room temperature. Recording commenced at noon on the third day following capture. Walking activity was detected when isopods interrupted an infra-red light beam produced by a light-emitting diode (wavelength at peak emission 930 nm). The beam was projected across the actograph tank just above the level of the sand surface. To prevent burrowing isopods from throwing up a mound of sand into the light path a narrow piece of wood, with sandpaper glued onto its upper surface, was set beneath the beam flush with the sand surface. Interruptions of the light beam were recorded either as spikes on an Esterline Angus Event Recorder or as counts accumulated at 10 min intervals on a microcomputer modified for data collection. Isopods were held either singly in small cylindrical actograph tanks 150 mm diameter and 200 mm deep or in groups of 2–8 in larger rectangular tanks 330 × 140 mm and of the same depth. Artificial light cycles were provided when necessary by tungsten bulbs giving approximately 50 lux at the sand surface.

The isopods were not fed during experiments for three reasons: to avoid disturbance; to inhibit moulting, since starvation discourages moulting in most crustaceans (Passano 1960); and because trial experiments showed that after feeding *Scyphax* remain inactive in their burrows for several days. Survival of unfed isopods was good, with 83% alive after 40 days.

Some preliminary experiments were carried out to investigate whether moulting is related to locomotor activity cycles. Isopods housed individually in actographs were dug up during "lights on" at 4 or 5 day intervals. Their stage in the moult cycle was

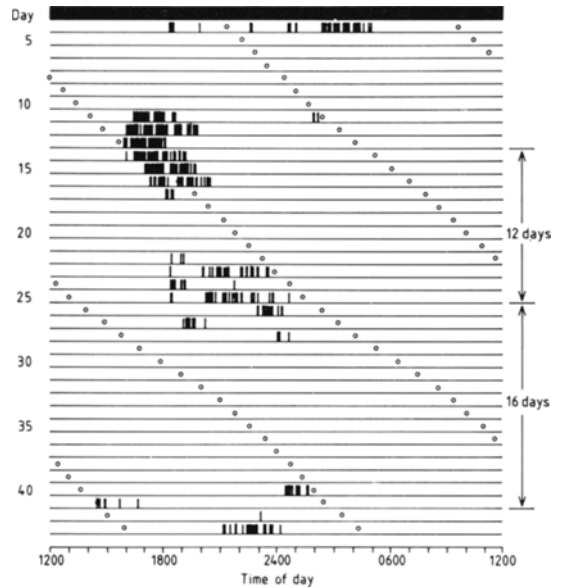


Fig. 1 Free-running unimodal activity rhythm of one isopod from Piha, in constant darkness. The record begins at noon on the third day after collection and continues for a further 40 days. Open circles indicate the time of HW on the home beach. Times of sunrise and sunset on the isopod's home beach were approximately 0720 and 1710 respectively. Intervals between successive semilunar peaks (12 and 16 days) are estimated by eye.

determined using a visual method described by Steel (1982) for *Oniscus asellus*.

RESULTS

Test of the endogenous timing hypothesis: circadian and circa-semilunar rhythms recorded in constant darkness

Sixteen isopods were kept without food in constant darkness (DD) for durations of up to 43 days. Recordings of the locomotor activity of two of these animals are shown in Fig. 1 and 2. Most isopods (12) showed a clear circadian rhythm of activity; the remaining 4 showed little or no activity but were found to be alive 10 days after the start of the experiment.

A striking feature of the activity records from 11 of the 12 rhythmic isopods was that the overall daily activity level showed a rhythmic variation during the course of the experiment. Bursts of activity during which the isopods were active for 6–8 consecutive days were interspersed with 6–8 day

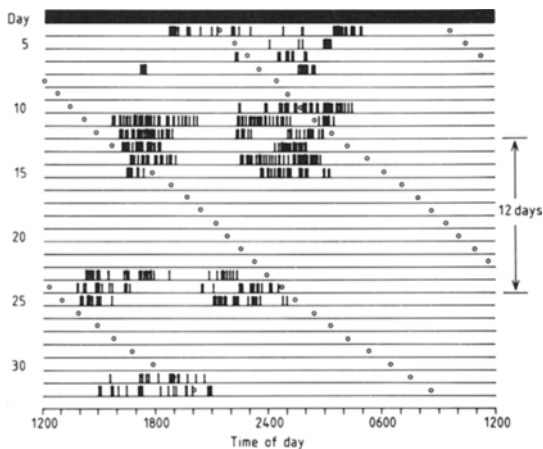


Fig. 2 Free-running bimodal activity rhythm of one isopod from Piha, in constant darkness. The record lasts for 29 days; all other details are as for Fig. 1.

intervals in which little or no activity was recorded (Fig. 1, 2). Thus, periods of high activity level tended to occur at intervals of 12–16 days, and the activity peaks of all 11 isopods were clearly coincident. This fortnightly or circa-semilunar rhythm in overall activity level was investigated in further experiments which we describe later.

The circadian activity rhythm expressed during the circa-semilunar peaks persisted in some animals for 30–40 days with gaps as described. The free-running period is difficult to determine because activity seldom took place on more than 8 consecutive days, and many rhythms showed spontaneous changes in period. In Fig. 2 for example, the period during the circa-semilunar peak on days 10–15 is somewhat greater than 24 h since the isopod commenced activity successively later each day; but from days 16–23 when no activity occurred its circadian clock obviously had a period less than 24 h, as is shown by the start of activity on the first day of the circa-semilunar peak, (Day 23). Taking these difficulties into account, the free-running period for all 12 rhythmic animals lay in the range 23.7–24.2 h.

The pattern of activity during the subjective night was variable. Five isopods showed unimodal peaks of activity, (e.g., Fig. 1), whereas another five were bimodal, (e.g., Fig. 2). The remaining two animals were inconsistent in their activity. We found no evidence of a tidal component in the activity rhythm.

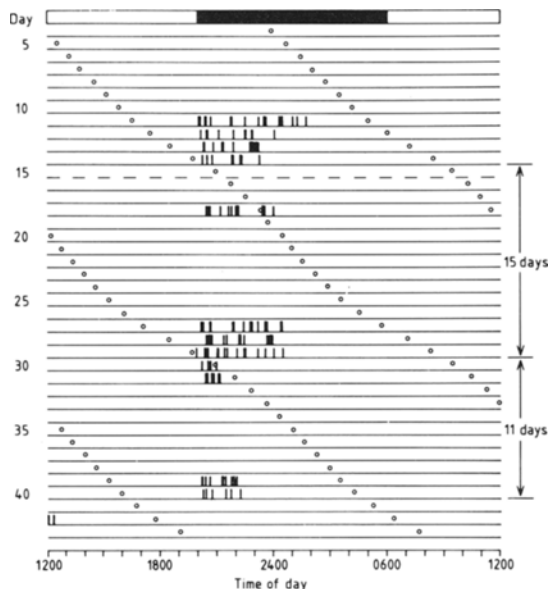


Fig. 3 Activity rhythm of one isopod from Piha, kept in LD 14:10. The record lasts for 40 days; data for day 15 were lost, (because of operator error). Other details are as for Fig. 1.

Response to artificial light cycles

The activity of a total of 32 individual isopods was recorded under light/dark cycles (LD 14:10 or 13:11) over 18–60 days. Most animals, (for example Fig. 3), showed rhythms with activity commencing at lights-off as expected from field observations. The circa-semilunar rhythm in overall activity level observed in DD was clearly expressed in LD also.

Features of the circa-semilunar rhythm

A series of experiments was conducted to determine the form, period, and persistence of the circa-semilunar rhythm in overall activity level. To allow an accurate estimate of period the total daily activity counts of many isopods were combined to produce a “mean daily activity level”. In some instances, the isopods were kept individually in small actographs, (32 animals recorded for 18–60 days as described in the previous section); in other experiments they were kept in groups in larger actographs, (18 groups of 2–16 isopods recorded for 43–49 days).

Fig. 4C shows a typical record in which mean total daily activity of 16 isopods kept individually is plotted against time. Two major peaks of activity are evident, approximately 15 days apart. A third peak

would be expected at about Day 43, but the circa-semilunar rhythm usually decayed after 35–40 days. Examination of the activity records of individual animals showed that this was because of a combination of factors: reduced activity presumably caused by starvation, disappearance of the rhythm in individual animals, and loss of synchrony among individuals.

The peaks of the circa-semilunar rhythm occurred when the moon was in its first and last quarter (Fig. 4A), but field studies (Quilter 1987) did not show any reason why this relationship should be ecologically significant. Similarly, circa-semilunar activity peaks coincided with times when spring tides were changing to neaps (Fig. 4B), but nothing that we know about the ecology of *Scyphax* suggests any significance in this association.

The circa-semilunar rhythm was also unrelated to moulting. One series of 15 *Scyphax* were housed individually in actographs for between 50 and 90 days, and examined every 5 days for evidence of moulting, (the late premoult, moult, and postmoult stages are easily identified and span 7–8 days). Disturbing the isopods had a definite effect on overall activity level, causing a 2 to 3-fold increase on the following night, but despite this, 13 animals showed circa-semilunar rhythms. Of these rhythmic isopods only two moulted. Both did so at a time coinciding with the second circa-semilunar peak and both entirely suppressed this peak, remaining inactive for 5–7 days at a time when their fellows were showing maximal activity. Thus the circa-semilunar rhythm is not caused by a fortnightly moult cycle with low activity during ecdysis, as may occur in *Talitrus* (Williams 1979).

The circa-semilunar rhythm in relation to foraging opportunities

Field studies (Quilter 1987) suggest that the circa-semilunar rhythm recorded in the laboratory may be associated with the foraging strategy of *Scyphax*. These isopods feed mainly on carrion, especially on insects such as honey bees which have been drowned and washed ashore. At Piha Beach, carrion accumulates in a dense, narrow band, (the swash mark), near the water's edge during the flood tide, but it is spread thinly over the middle beach during the ebb. The foraging pattern of adult *Scyphax* corresponds to the availability of carrion. For the first 2 h of a flood tide little foraging occurs because the swash mark is inaccessible, since the isopods cannot walk on the wet surface of the lower beach. For the remaining

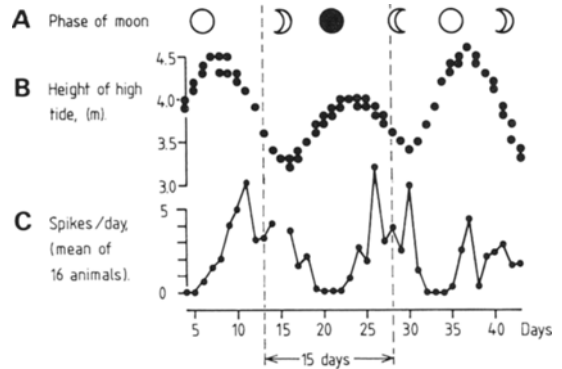


Fig. 4 A circa-semilunar rhythm in mean overall daily activity level of 16 isopods kept individually in LD 14:10 (C), compared with the spring/neap tidal cycle (B) and the lunar cycle (A) which occurred at Piha during the experiment. Peaks of the circa-semilunar rhythm (indicated by vertical dotted lines) are estimated by eye. Data for day 15 were lost (because of operator error).

4 h of the flood, *Scyphax* forage intensively at the swash mark, moving slowly up the beach with the advancing tide. Once the tide begins to ebb, foraging decreases again, presumably because the chance of locating carrion is low. There is a further restriction on foraging; adult *Scyphax* do not emerge from their burrows at the high water mark until 1 h after sunset, and they return to the upper beach to dig new burrows about an hour before sunrise.

In summary, the optimum foraging time for *Scyphax* on exposed shores is the last 4 h of the flood tide between Time of sunset + 1 h and Time of sunrise - 1 h. One can immediately predict that some nights will offer better feeding opportunities than others, depending on the time at which the nighttime high tide occurs. If, for example, high water occurs as the isopods emerge from their burrows about 1 h after sunset then for most of the night the tide will be ebbing and there will be no opportunity for *Scyphax* to forage at the swash mark. On the other hand, if high water occurs at or before the time when the isopods dig new burrows in the early morning, then they will have been able to forage for the maximum 4 h during the flood.

Fig. 5A illustrates the relationship between foraging opportunity and time of high water at Piha Beach during the 40 days when the actograph experiment shown in Fig. 4C was in progress. All of the data used to construct Fig. 5A came from almanac predictions. When the number of hours of foraging time available each night is plotted against date,

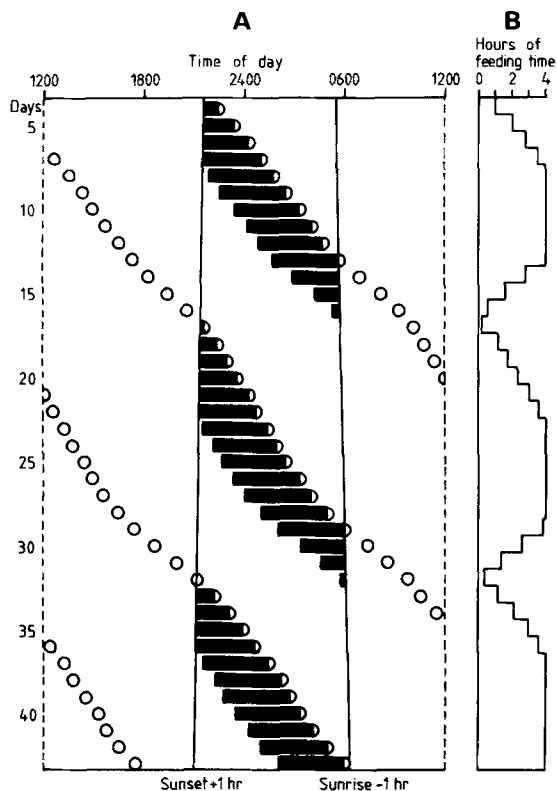


Fig. 5 Model for a fortnightly cycle of nightly foraging opportunities at the swash mark on Piha Beach. In (A), for each of 40 days when the actograph experiment shown in Fig. 4,C was in progress, the times of HW are shown by open circles; the approximate times of emergence (1 h after sunset) and re-burrowing (1 h before sunrise) are indicated by near-vertical lines; and a horizontal black bar indicates any of the last 4 h of each flood tide which fall after the time of emergence and before the time of re-burrowing. In (B) the length of each black bar is re-plotted from a common base-line (zero) showing a semilunar cycle in the number of hours each night during which the flood-tide swash mark is available for feeding.

(Fig. 5B), then the amount of feeding time available each night is seen to follow a semilunar cycle with maximum values of 4 h and minima of almost zero hours. If this cyclic variation in foraging opportunity on the home beach is plotted beside the circa-semilunar rhythm of overall activity level recorded in the laboratory between the same dates, (Fig. 6), a reasonably good fit can be seen.

Groups of *Scyphax* from Piha Beach were recorded for durations of at least 40 days in DD on five further occasions. On three of these, (Fig. 7,8,9),

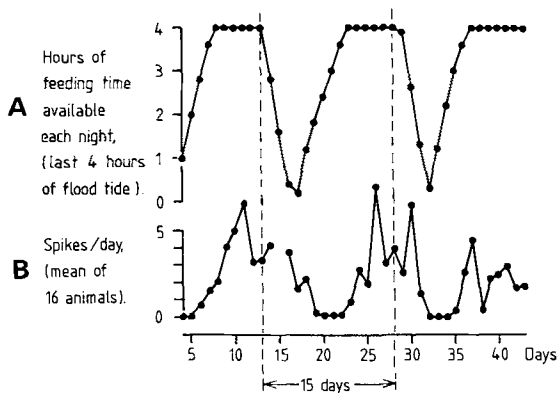


Fig. 6 The phase relationship between a model for the semilunar cycle of nightly foraging opportunities at Piha Beach (A, as derived in Fig. 5), and a circa-semilunar rhythm in mean overall activity level of 16 isopods in LD 14:10 recorded concurrently (B, as in Fig. 4C).

the mean daily activity level for all animals showed a clear circa-semilunar rhythm which seems to be correlated with the semilunar cycle in foraging opportunity on the isopods' home beach. Maximum activity in the laboratory tended to coincide with maximum opportunity on the beach. In two of the five further experiments, the presence of a circa-semilunar rhythm was questionable; but on no occasion was a clear circa-semilunar rhythm recorded which was out of phase with the cycle of foraging opportunity at Piha Beach.

A test of the association between foraging patterns and the endogenous circa-semilunar rhythm

If an ecologically significant relationship exists between foraging habits as observed in the field and the rhythm of overall activity level which is recorded in the laboratory, then a fair test of the association would be to find a beach population of *Scyphax* in which individuals employ a different foraging pattern and see whether the difference is reflected in locomotor activity rhythms recorded in the laboratory. Such a population exists at Garden Bay, a sheltered sandy beach near Auckland (Quilter unpubl. data). These animals show a foraging pattern quite different from that of *Scyphax* at Piha Beach. Instead of feeding intensively during the last 4 h of the flood they forage over the dry middle beach (at a density of c. 0.2–0.5 isopods/m²) during both flood and ebb

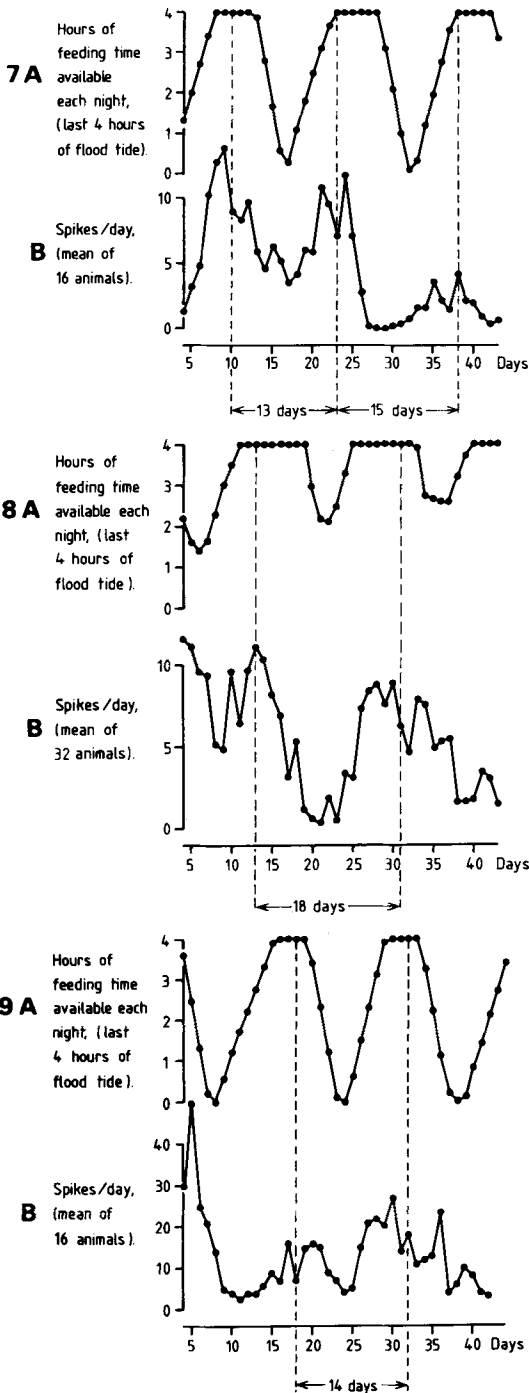


Fig. 7,8,9 Three further tests of the model with isopods from Piha kept in LD 14:10. Each figure shows the phase relationship between the semilunar cycle of nightly foraging opportunities at the beach (A), and a circa-semilunar rhythm in mean overall activity level (B) recorded concurrently in the laboratory. Peaks of the circa-semilunar rhythm are estimated by eye. The breadth of the peaks on the "available feeding time" curves varies from one figure to another because of seasonal changes in the length of the night. **Fig. 7:** 8 actographs each containing 2 animals. **Fig. 8:** 4 actographs each containing 8 animals. **Fig. 9:** 2 actographs each containing 8 animals.

tides. A slight concentration of isopods (density 1/m²) occurs during the first 4 h of the ebb tide when they are found in a broad band above the water's edge, but this is not nearly as marked as the concentrated feeding effort which occurs in a very narrow zone at the flood tide swash mark on Piha Beach.

The unusual foraging pattern employed at Garden Bay allows us to make a prediction about the endogenous circa-semilunar rhythm which might be recorded from these isopods. If there is a significant association between the endogenous rhythm and the foraging pattern, we would expect animals from Garden Bay not to show a circa-semilunar rhythm; or if they do show a rhythm, for it to be in phase with a semilunar cycle of foraging opportunity based on maximal foraging during the first 4 h of the ebb-tide, (rather than the last 4 h of the flood). If however the close fit between endogenous rhythm and feeding pattern seen in *Scyphax* from Piha Beach is merely a chance correlation, then most isopods from Garden Bay should show a circa-semilunar rhythm and the rhythm should phase-match a feeding cycle based on maximal foraging during the last 4 h of the flood.

The locomotor activity of *Scyphax* from Garden Bay was recorded under artificial LD cycles in four experiments each lasting 45–53 days. The first involved 16 isopods recorded individually, whereas in the remainder the animals were recorded in groups of 2–8. Isopods in three of the four experiments showed no sign of a semilunar fluctuation in overall activity level, (Fig. 10,11,12). The fourth group did show some indication of a weak circa-semilunar rhythm (Fig. 13B), and the phasing of the rhythm is of particular interest. The three "semilunar" peaks coincide exactly with peak feeding opportunities at Garden Bay (Fig. 13A), if one assumes that foraging there is most productive during the first 4 h of the ebb tide. The semilunar peaks do not match a cycle of feeding opportunities based on the Piha Beach pattern in which optimal foraging takes place during the last 4 h of the flood, (Fig. 13C).

DISCUSSION

Role of the circadian rhythm

Scyphax spend the daytime in burrows about 20 cm beneath the sand surface. It seems extremely unlikely that any environmental changes occur at that depth which would indicate emergence-time 1 h after sunset. Most burrows, for example, would be dark because they are usually plugged with wind-blown sand or because the mouth of the burrow has collapsed as the surface dries after sunrise. The humidity remains close to saturation (Kensley 1974; Holanov & Hendrickson 1980) and temperature changes are gradual and of low amplitude. Continuous recordings of sand temperature at Garden Bay (Quilter unpubl. data) showed that during one 24 h period a temperature range of 11°C (min. 11°C, max. 22°C) at the sand surface was damped to 4°C (min. 12°C, max 16°C) at a depth of 10 cm, and to 1°C (min 14°C, max 15°C) at a depth of 30 cm.

If no external signals are available to indicate when *Scyphax* should commence activity then the need for an internal circadian clock is self-evident (Enright 1970). Without endogenous timing, the isopods would have to make a series of trialexursions towards the sand surface during the daytime which would be metabolically expensive (Trevor 1978) and perhaps hazardous. Thus, the circadian rhythm of activity shown by *Scyphax* in constant conditions has a clear "ecological role"; it stimulates the isopods in the absence of any external time cues, to dig towards the surface shortly after dusk. Other authors working on burrowing crustaceans of both the supralittoral and intertidal zones have reached a similar conclusion, (e.g., Bregazzi & Naylor 1972; Atkinson & Naylor 1973; Williams 1980), and indeed this circumstance is one of relatively few in which endogenous as opposed to exogenous control of behaviour is clearly essential.

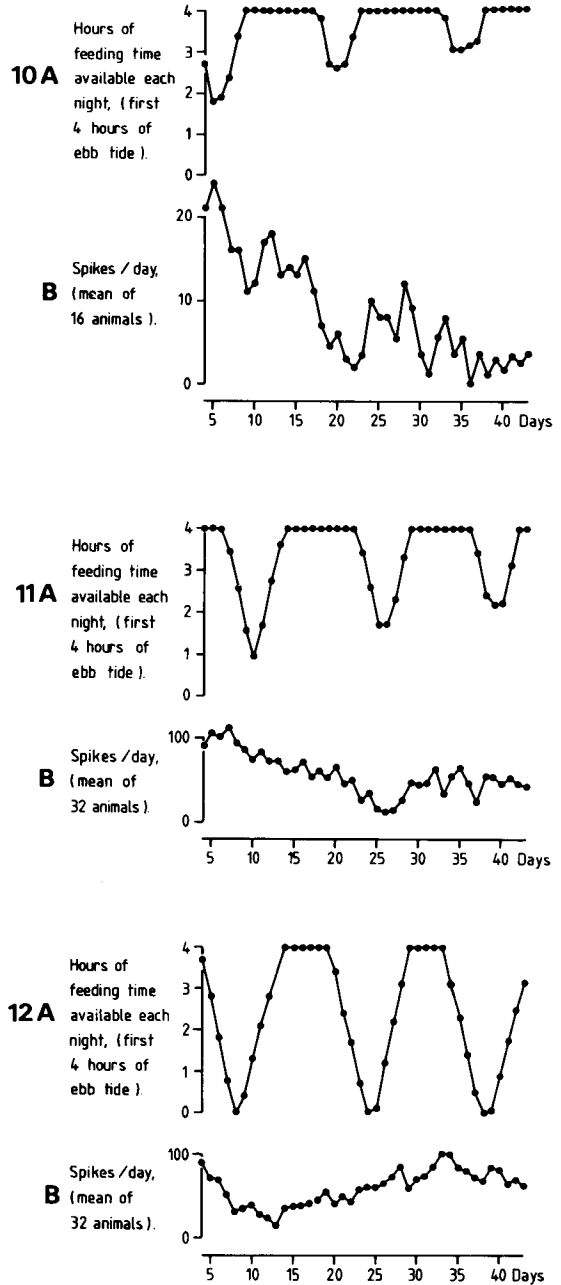


Fig. 10,11,12 Three actograph experiments using isopods from Garden Bay kept in LD 14:10 or 13:11. Each figure compares a possible semilunar cycle of nightly foraging opportunities at the home beach (A, where the cycle is based on maximal foraging during the first 4 h of the ebb tide), with the daily mean overall activity level (B) recorded concurrently in the laboratory. Fig. 10: 16 actographs each containing 1 animal Fig. 11: 4 actographs each containing 8 animals. Fig. 12: 4 actographs each containing 8 animals.

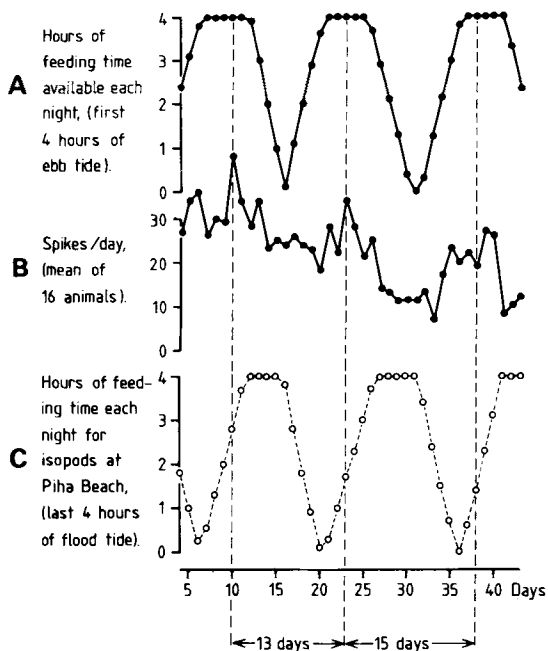


Fig. 13 The daily mean overall activity level of 16 isopods from Garden Bay (8 actographs each containing 2 animals) is shown (B), compared to two possible semilunar cycles of nightly foraging opportunities. The upper cycle (A) is based on maximal foraging during the first 4 h of the ebb tide; the lower cycle (C) is based on maximal foraging during the last 4 h of the flood. Peaks of a low-amplitude circa-semilunar rhythm in (B) are estimated by eye and indicated by vertical dotted lines. Spring tides occurred on Days 8, 21, and 38.

The presence of a circa-semilunar rhythm in activity level makes the need for an internal circadian timer even more obvious. When kept in the laboratory *Scyphax* sometimes do not emerge from their burrows for 6–8 consecutive nights and must rely on the circadian clock to bring them to the surface at dusk on the first day of the next semilunar “peak”. Actograph experiments in DD show that the clock can perform this role with an error of about ± 2.4 h; (assuming the free-running period to lie in the range 23.7–24.2 h, which produces a daily error of about ± 0.3 h accumulated over 8 days of inactivity).

Role of the circa-semilunar rhythm

The correlation observed between overall activity level in actograph experiments and nightly feeding opportunities at Piha Beach suggests that the circa-semilunar rhythm stimulates foraging activity on nights when food is most likely to be available. The

rhythm therefore predicts a biotic cycle (food availability) caused by the interaction of solar (24 h) and tidal (12.4 h) cycles, and although the period of the rhythm is about 15 days it appears to be unrelated to the fortnightly cycle of spring and neap tides.

The different rhythmic behaviour shown in the laboratory by isopods from Garden Bay strengthens the argument. Only one group of isopods from this location showed a circa-semilunar rhythm; in that instance the rhythm caused maximal activity at times when food was most accessible on the home beach even though this meant that the phase relationship between the circa-semilunar rhythm and the spring/neap tidal cycle was different to that shown by *Scyphax* from Piha Beach.

We speculate that the foraging pattern shown by Garden Bay isopods is a response to different physical characteristics of the swash zone there. During a flood tide on exposed shores such as Piha Beach the swash line is moved up the beach in steps of 1–2 m by large waves which arrive some minutes apart. However at Garden Bay the swash line is lifted up the beach in steps of a few centimetres by small ripples which arrive at about 16 s intervals, (mean period measured at mid-flood under moderate weather conditions). Since it takes 5–10 s after each ripple for the sand in the swash zone to become firm enough to walk on, any isopods which attempted to forage at the swash mark during a flood tide would spend 30–60% of their time submerged or unable to move in wet sand. Therefore, although carrion accumulates in the flood-tide swash line at Garden Bay, just as it does at Piha Beach, *Scyphax* apparently cannot exploit it. On a falling tide the problem of frequent inundations does not occur.

The circa-semilunar activity rhythm shown by isopods from Piha Beach means that they spend many days inactive in their burrows. A strategy in which foraging excursions are only made under optimum conditions would be justified if the refuge is safe and the metabolic cost of remaining there is low, if foraging excursions are metabolically expensive and/or hazardous, and if the digestive system is able to utilise large meals at long intervals.

We are unable to compare the risks of remaining in the burrow with that of a foraging excursion. Among adult *Scyphax* the mortality in both situations is probably low. The burrow environment is stable and beyond the reach of shore birds, and no predator was ever seen to take *Scyphax* foraging on the beach surface at night. Kensley (1974) was also unable to find any predators of *Tylos granulatus* on South

African beaches, and Hamner et al. (1969) concluded that mortality among the Californian beach isopod *Tylos punctatus* was "unusually low".

Metabolic costs are unknown for *Scyphax*, but data on respiratory rates have been published for *Tylos granulatus* and *T. punctatus* which occupy a similar niche to *Scyphax*, with the exception that they eat stranded algae as well as carrion. Marsh & Branch (1979) showed that the rate of energy expenditure of active *T. granulatus* was six times greater than that of resting isopods. These authors also cite Hayes (1969) who found that the respiratory rate of experimentally starved *T. punctatus* fell to about 16% of its former level. Assuming that respiration rates of *Scyphax* are similar to those of *Tylos*, it seems likely that a day which includes a night-time foraging excursion is energetically much more costly than a day spent resting in the burrow without emerging at night. The difference becomes even greater if *Scyphax* in the inactive phase of their circa-semilunar rhythm, have basal respiratory rates comparable to the "starved" isopods of Hayes (1969). Given these circumstances it may well be more economical in terms of energy expenditure for *Scyphax* to remain inactive when feeding opportunities are restricted, and to reserve foraging for nights when the metabolic cost of an excursion is likely to be justified. The foraging habits of bees (Renner 1960) provide an analogy; the bees restrict their excursions to times of day when particular flowers are open, employing a circadian clock to time their visits. This is generally accepted (Enright 1970) as providing a clear demonstration of the need for endogenous timing.

If our interpretation of the circa-semilunar activity rhythm is correct, then fortnightly cycles should occur in the abundance of isopods active on Piha Beach at night. Field studies (Quilter 1987) showed that few isopods emerged on nights when high tide occurred near the time of sunset, which is as predicted since these nights occur at fortnightly intervals and correspond to the trough of the circa-semilunar rhythm as recorded under constant conditions in the laboratory. Beyond this, objective data on night-to-night variations in the number of active animals are difficult to obtain. An accurate index of abundance on any one night can only be obtained by the laborious method of averaging hourly counts between sunset and sunrise along transects extending from the high water mark to the water's edge. Moreover *Scyphax* are inhibited from emerging by strong winds or low temperatures so that nightly counts over several

semilunar intervals might be needed to separate irregular climatic effects from an underlying oscillation.

Previous studies on shore crustaceans have demonstrated circa-lunar or circa-semilunar rhythms of locomotor activity, reproduction and moulting (Naylor 1985). However *Scyphax* is the first species in which a circa-semilunar rhythm has been shown to predict the availability of food.

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