CIRCATIDAL RHYTHM OF FREE-ROAMING SUB-TIDAL GREEN CRABS, *CARCINUS MAENAS*, REVEALED BY RADIO-ACOUSTIC POSITIONAL TELEMETRY

BY

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ABSTRACT

Activity patterns of sub-tidal free-roaming green crabs, *Carcinus maenas* (L., 1758), were monitored in real time using radio-acoustic positional telemetry in New Harbour, Nova Scotia, Canada. Activity patterns were monitored relative to time of day and tidal height. Periodogram analysis showed activity was circatidally rhythmic, as activity increased with rising tides and decreased with falling tides. Potential proximate and ultimate causes of observed circatidal rhythmicity in *C. maenas* are discussed. In contrast to other studies, no circadian rhythm was observed in crab activity. This is likely because other studies have been conducted in the intertidal zone, where desiccation and predation stress favour reduced activity during daylight hours. This study provides the first demonstration of circatidal rhythmicity in sub-tidal free-roaming *C. maenas*.

RÉSUMÉ

Les modèles d'activité des crabes verts subtidaux errants, *Carcinus maenas* (L., 1758), ont été déterminés en temps réel, en utilisant la télémétrie radio-acoustique positionnelle à New Harbour, Nouvelle-Ecosse, Canada. Les modèles d'activité étaient suivis par rapport au moment de la journée et à la hauteur de la marée. L'analyse du périodogramme a montré que l'activité était calquée sur le rythme des marées, car l'activité augmentait avec les marées montantes et diminuait avec les marées descendantes. Les causes potentielles directes et indirectes de cette rythmicité circatidale observée chez *C. maenas* sont discutées. Contrairement à d'autres études, aucun rythme circadien n'a été observé dans l'activité du crabe. Ceci s'explique probablement parce que les autres études ont été menées dans la zone intertidale, où le stress dû à la dessiccation et à la prédation favorise une activité réduite pendant la journée. Cette étude fournit la première démonstration de la rythmicité circatidale chez les *C. maenas* subtidaux errants.

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INTRODUCTION

Knowledge of a species' movement and activity patterns can provide useful information regarding its resource utilization, habitat requirements, and predatory and competitive interactions with other species of the community (Turchin, 1998; Pittman & McAlpine, 2001). Numerous studies have investigated movement and/or activity patterns in the European green crab, *Carcinus maenas* (Linnaeus, 1758) (cf. Naylor, 1958, 1960, 1963; Atkinson & Parsons, 1973; Bolt & Naylor, 1985; Reid & Naylor, 1989; McGaw & Naylor, 1992; Styrishave et al., 1999, 2003). These studies have suggested that *C. maenas* displays both circatidal and circadian rhythmicity, being more active when the tide is high than low (Naylor, 1958, 1960, 1963; Atkinson & Parsons, 1973; McGaw & Naylor, 1992; Styrishave et al., 1999, 2003), and at night than during daytime (Naylor, 1958, 1960, 1963; Atkinson & Parsons, 1973; Reid & Naylor, 1989; Aagaard et al., 1995; Styrishave et al., 1999, 2003). Some studies also suggest that *C. maenas* migrates up and down intertidal slopes with rising and falling tides, respectively (Hunter & Naylor, 1993; Rewitz et al., 2004).

Despite the numerous studies that have addressed movement and activity rhythms of *C. maenas*, our understanding of natural movement patterns displayed by free-roaming individuals in nature remains uncertain. Many of the studies conducted to date have been done in the laboratory, and it is known that activity patterns displayed by decapods constrained in unfamiliar or atypical surroundings can be misleading (Atkinson & Naylor, 1973). Some studies have been done in the field, but none of these have involved continuous recording of free-roaming individuals. Instead, these studies have involved capture rates by baited or unbaited traps/dropnets, activity rates inside small cages, or animal counts based on static video observation (Dare & Edwards, 1981; Styrishave et al., 1999, 2003; Aagaard et al., 1995). Furthermore, nearly all field information available pertains to movement and activity of green crabs while in the intertidal zone, and to our knowledge only one study has investigated rhythmicity in movement patterns of green crabs in the subtidal zone (Styrishave et al., 1999). This study suggested locomotor activity of subtidal *C. maenas* is circatidally rhythmic and seemingly positively influenced by temperature and depth and negatively affected by light, but it involved caged individuals and it is unclear how readily these rhythms translate to crabs roaming freely over larger areas. Understanding natural movement patterns of green crabs in the subtidal zone is important considering they are likely to interact with a different suite of species here than in the intertidal zone.

Here we report results of preliminary work involving use of radio-acoustic positional telemetry to investigate the movement and activity patterns of free-roaming sub-tidal green crabs relative to time of day and tidal amplitude.

METHODS

This study was conducted in July 2005, in New Harbour (45°10′37″N 61°27′28″W), Nova Scotia, Canada. Sub-tidal *Carcinus maenas* (N = 6, 3 male, 3 female) measuring 50-81 mm in carapace width were collected by SCUBA divers, brought to the surface, and fitted with Vemco® ultrasonic coded V9 transmitters (pingers) using marine epoxy. Animals were then released into the study area, in the centre of a 3-buoy array described below, where they were allowed to acclimate for 12-24 h. After this acclimation period, crab movements and activity patterns were monitored continuously for 54 hours using a Vemco® radio-acoustic positional telemetry (RAPT) system. This system enables real-time high-resolution tracking (when animals are inside the buoy triangle; see below) while probably causing little if any constraint or disturbance to the animal, as the V9 pinger is small (25 mm long cylinder with 9 mm diameter) and light relative to the size and weight of our tagged animals (tag weighs <15 % of crab blotted body mass).

The three Vemco® receiving buoys of the RAPT system were deployed in a ≈200 m equilateral triangle using ≈45 kg moorings and stretch cord (stretch ratio: 33%). The stretch cord was used to accommodate tidal fluctuation in water level (ca. 1.5 m during the study) and reduce lateral movement of the buoys, which affects precision of position estimates. Each buoy was equipped with a hydrophone, which received information from the Vemco® pingers attached to the crabs, and relayed it to a base station, which was established on shore adjacent to the study site. The base station uses the time of signal reception at each buoy to triangulate the (X, Y) coordinate from which the "ping", or signal, originated; a given signal must be received by the hydrophones on all three buoys for a position to be resolved. Acoustic signals from the pingers are emitted periodically, a minimum of once and a maximum of three times every three minutes, but successful reception of signal by the hydrophone on each buoy is dependent on signal attenuation by background noise, solid objects (e.g., when animals shelter under rocks), and 'collisions' between acoustic signals from different pingers.

We used the number of resolved pings per hour as an indication of crab activity; because *C. maenas* is known to make use of rock and shell cover when inactive low in the intertidal zone (Jensen et al., 2002) and in the shallow subtidal zone (B. R. Lynch, pers. obs.), the number of pings received by the tracking system should be an indicator of crab activity level. Aitken et al. (2005) similarly used number of pings received by a RAPT system to quantify activity of cuttlefish, *Sepia apama* Gray, 1849 in a rocky reef environment. We did not use estimates of distance moved as an indicator of crab activity because of the high positional measurement error for animals outside the buoy triangle (Tremblay et al., 2003), where some of our tagged animals were located.

We also deployed reference pingers in a number of different locations over a period of 54 hours, to evaluate temporal variability in "sensitivity" of the RAPT system, due to signal attenuation (e.g., due to temporal variation in background noise) and buoy position and stability (e.g., due to variation in tidal height). Here we present data for 2 such reference pingers, which best overlap, spatially and temporally, with data obtained from our six animal pingers. One reference pinger was deployed in the centre of the buoy triangle and the other one ≈5 m outside the triangle, towards the shore, where several of our animals were situated. The data from the animal and reference pingers overlapped for 29 of the 54 hours of recordings that we analysed, but the reference data started and ended 24 hours before the crab data. Pings from reference transmitters were received at a much greater frequency than those on crabs, because there was a direct path between these pingers and the receiving buoys at all times; the reference pingers were placed on open substrate and there was probably little if any attenuation of their signals due to solid objects.

ANALYSIS

We used the periodogram analysis proposed by Williams & Naylor (1978) to test for rhythmicity. This analysis consists of breaking the time-series into sub-series, or periods, of various lengths, and then building a modified Buys-Ballot table for each period investigated. For example, for the 8-hour period table of a 35 hour time series, one column would show the activity of crabs during hours 1, 9, 17, 25, and 33 (on separate rows), whereas a second column would show crab activity during hours 2, 10, 18, 26 and 34, and so on. One then computes mean activity values for each column of a given table, and then the standard deviation of these column means. If data are rhythmic at a given period, then activity peaks will tend to be in the same columns and troughs will be in the same columns, which will cause the standard deviation of column means at that particular period to be high. Conversely, if activity does not follow a certain period, high and low activity values will be spread across columns, and hence column means will tend to be more similar and their standard deviation smaller. To assess statistical significance of observed "rhythmicity" of activity patterns, the original data are randomized, reprocessed through the periodogram technique, and a regression line is drawn that depicts the relation between period and standard deviation of the randomized activity data. Significant rhythmicity is indicated when observed standard deviations at a given period exceed the 95% confidence intervals of the regression line of the randomized data. We tested rhythmicity in *C. maenas* activity for periods ranging from 8-30 hours, as this encompasses both circatidal

(ca. 12.4 h) and circadian (ca. 24 h) rhythms, which previous studies have shown to be displayed by decapods (Guerao, 1995; Aguzzi et al., 2003; Chabot et al., 2004; Stillman & Barnwell, 2004), including green crabs (see Introduction).

RESULTS

The tracking system detected an average of 14.2 ± 0.50 (SE) pings per reference pinger over the 54-hour study period, but only 3.12 ± 0.24 pings per green crab pinger. This difference was likely the result of signals from green crab pingers often being blocked by solid objects such as rocks and boulders. Interestingly, the reception of signals from green crab pingers varied considerably over the study period, suggesting that green crab activity and shelter use were not constant over time. In particular, the periodogram analysis indicated that the frequency of signal reception from green crabs followed a 12-14 h cycle (fig. 1c), which is consistent with a circatidal (ca. 12.4 h) rhythm; the activity of the green crabs increased with rising tides and decreased with ebbing tides, being greatest at high tide and least during low tide (fig. 1a). In contrast, the two reference pingers showed no rhythmicity in "activity" over the 5 days they were deployed (fig. 1b and d show data for the 54 hours that best overlapped animal recordings), which indicates that the rhythmicity recorded for green crab pingers was not an artifact of temporal variation in sensitivity of the tracking system.

We recorded greater activity levels of green crabs in the first than in the second day of observation (fig. 1a), which may have been due to variability in crab behaviour, either natural or due to insufficient acclimation time. This difference was unlikely the result of temporal variation in system sensitivity, because reception of signals from reference pingers did not show much daily variation over the 5 days they were deployed. Whatever the cause of this difference, circatidal rhythmicity in green crabs was evident over both days of observation (fig. 1a).

The periodogram analysis provided evidence of a second periodicity in green crab activity of approximately 25-26 hours, although this second peak was not significant at alpha level of 0.05. This pattern does not appear to reflect a circadian rhythm, because green crab activity levels did not show obvious differences between daytime and nighttime (fig. 1a); the mean number of signals detected from tagged green crabs was 3.54 ± 0.36 (SE) pings during daytime and 2.67 ± 0.30 (SE) pings during nighttime. Instead, this apparent second peak in periodicity (fig. 1c) likely results from a doubling of the true ≈ 12.4 hour circatidal periodicity in green crab activity.

Visual inspection of the data from individual crabs suggested that all six individuals displayed circatidal, but not circadian, rhythmicity. We also visually
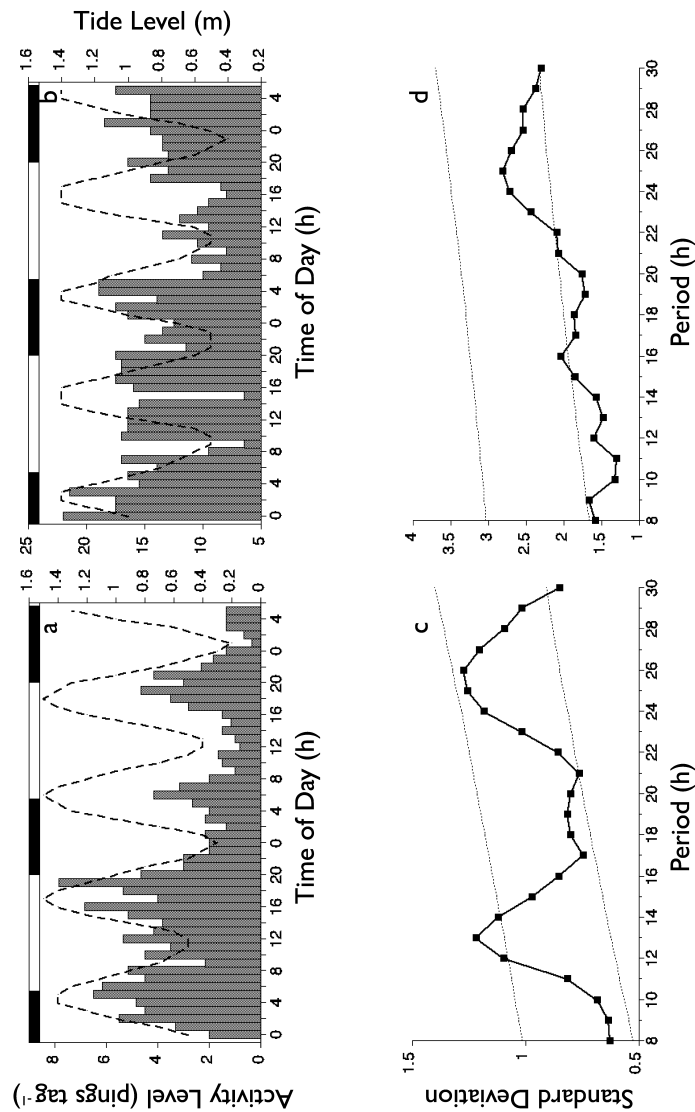
Fig. 1. *Carcinus maenas* (L. 1758). Time series of mean activity level and tidal amplitude recorded in July 2005 for: a, *C. maenas* (n = 6); and, b, stationary reference pingers (n = 2). Black horizontal bars represent nighttime, from sunset to sunrise, and white bars represent daytime. Dashed lines represent tidal amplitude. Below, c and d, are periodograms calculated from the data in (a) and (b), respectively. Dotted lines represent the 95% confidence intervals drawn from a regression line through the randomized data (see Methods). Observed standard deviation values above the upper confidence interval indicate significant rhythmicity in activity patterns at the corresponding period. Note: time series from reference and crab transmitters were not recorded synchronously, see Methods.

inspected data from the crab acclimation period. Though these data were somewhat more variable, the circatidal rhythmicity was also apparent during this period.

DISCUSSION

Our study provides evidence of circatidal rhythmicity of *Carcinus maenas* roaming freely in shallow ($\approx$2-4 m) parts of the subtidal zone. Over the course of the four consecutive tidal cycles, 1.97 times more signals from green crab emitters were detected during the 5-hr period surrounding high- versus low-tide. Because reference pingers showed no cyclical pattern, circatidal rhythmicity of green crab pingers was almost certainly due to green crabs moving more actively over the benthos at high tide, presumably in search of food and/or mates, and spending more time inactive and "sheltered" at low tide. Because several (n = 3/6) of the green crabs were situated outside the buoy triangle, closer to shore, positional data were not reliable, which is why we did not use "distance moved" to test for rhythmicity. It may prove difficult to use this technology to study movement rates of animals in the first 5 meters or so of the subtidal zone, particularly in areas with high tidal ranges. Nevertheless, our study shows that presence/absence data can be used in such shallow-water habitats to describe temporal patterns of activity in animals that utilize shelter when inactive.

Our study provides the first evidence of circatidal rhythmicity for continuously-monitored free-roaming green crabs. Another novel aspect of our study is that it was conducted with green crabs that remained in the subtidal zone throughout the duration of the study; all but one (Styrishave et al., 1999) of the field studies that have reported circatidal rhythmicity in *C. maenas* have involved animals monitored in the intertidal zone (Naylor, 1958, 1960, 1963; Atkinson & Parsons, 1973; Bolt & Naylor, 1985; Reid & Naylor, 1989; McGaw & Naylor, 1992; Styrishave et al., 2003). The proximate control of circatidal rhythms in *C. maenas* is not fully understood, but it has been shown to be endogenous and it can persist in the absence of relevant environmental cues (e.g., temperature, depth, light), though exogenous cues, such as changes in salinity, can override these endogenous rhythms in the short-term (Bolt & Naylor, 1985).

The function of circatidal rhythmicity is probably complex. It has been suggested to allow access to intertidal prey organisms (Rewitz et al., 2004), while at the same time reducing risk of avian predation (Dumas & Witman, 1993; Ellis et al., 2005) and physiological stresses (Rewitz et al., 2004) when the tide is low. One study has shown that intertidal *C. maenas* forage almost exclusively during flood tides (Hunter & Naylor, 1993), presumably because deeper water provides protection from avian and terrestrial predators (cf. Carlton & Hodder, 2003; Ellis

et al., 2005). It is thus likely that reduced activity during low tides decreases the susceptibility of *C. maenas* to predation. Avian predation has also been suggested to affect the vertical distribution of brachyuran crabs in the intertidal zone (Dumas & Witman, 1993; Ellis et al., 2005).

The function of circatidal rhythms for subtidal green crabs is somewhat less clear, as these animals remain submerged even at low tide, but we posit it may be related, either ultimately or proximately, to that just described for intertidal individuals. Because green crabs used in our study were in as little as 2 m of water at times, decreasing movement and seeking shelter in periods of low tide might have contributed to reducing their susceptibility to avian and terrestrial predators, as a number of birds and terrestrial animals are known to feed on *C. maenas* (cf. Dumas & Witman, 1993; Carlton & Hodder, 2003; Ellis et al., 2005). Also, we monitored experimental crabs for only 5-7 days, and it is possible that these "subtidal individuals" occasionally do venture in the intertidal zone. Our tagged green crabs were approximately 100-200 m from the intertidal zone, which is a relatively short distance considering intertidal green crabs have been reported to walk as much as 300-400 m during a single tidal cycle (Dare & Edwards, 1981). Furthermore, shallow-subtidal to low-intertidal migration has been documented in this species (Hunter & Naylor, 1993). It is thus possible that subtidal green crabs become less active and seek shelter at low tide because these behaviours are beneficial when they are in the shallow subtidal or intertidal zone.

Alternatively, the circatidal rhythmicity of subtidal individuals might be maintained because of endogenous (Bolt & Naylor, 1985) and exogenous (e.g., salinity, temperature) proximate controls, even if they are of no immediate benefit when the animals are in the subtidal zone. However, such behaviours probably entail significant lost-opportunity costs (Sih, 1987; Lima & Dill, 1990), and their maintenance in subtidal animals would suggest they are beneficial, or that there are important costs and/or constraints associated with their fine-scale temporal regulation. Longer-term tracking or mark-recapture studies would help document the connectivity between green crabs in subtidal and intertidal habitats, which could help elucidate the proximate and ultimate control of their circatidal rhythms.

Our study did not reveal circadian rhythmicity in *C. maenas* activity patterns, which contrasts with results of several other studies (Naylor, 1958, 1960, 1963; Atkinson & Parsons, 1973; Reid & Naylor, 1989; Aagaard et al., 1995; Styrishave et al., 1999, 2003). One possible explanation for this discrepancy is that studies reporting circadian rhythmicity in *C. maenas* have all been conducted in the intertidal zone, where desiccation stress and increased vulnerability to visual predators likely favour reduced activity during the day as compared to night. Another potential reason why our study failed to reveal circadian rhythmicity is that our observation period was relatively short, only encompassing slightly

more than two days (54 hours). This limited duration reduces our ability to detect more subtle rhythms, especially those acting on lengthier periods, such as a circadian rhythm (ca. 24 hour period). However, our data do not show any evidence of reduced activity during daytime, as signals from tagged crabs were actually somewhat more frequent in day (3.54 ± 0.36) than at night (2.67 ± 0.30). We therefore suspect the short duration of our experiment was not the cause for this lack of circadian periodicity.

Further research is needed to quantify movement rates, home range, and migration patterns of *Carcinus maenas* over broader temporal (and spatial) scales, and to investigate how these activity rhythms affect resource utilization patterns as well as competitive and predatory interactions with other species inhabiting intertidal and shallow-subtidal habitats. Ultrasonic telemetry is a useful tool to help elucidate such activity and movement patterns.

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