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MARCHING TO A DIFFERENT DRUMMER: CRABS SYNCHRONIZE REPRODUCTION TO A 14-MONTH LUNAR-TIDAL CYCLE

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Abstract. Biological rhythms with lunar components are common in nature. In the sea, the moon's gravitational pull on earth is the principal cause of the tides, which normally reach maximum amplitudes every new and full moon. Many populations synchronize spawning to this time. Some choose either the new or the full moon, implying that moonlight is important; but one lunar phase usually has higher tides than the other, and many species select the phase with the higher tide to improve the offshore transport of their progeny. However, tidal dominance by one lunar phase is not constant; it switches between new and full moon every seven months. We tested the influence of this 14-month "syzygy inequality cycle" (SIC) on lunar synchrony by sampling 11 populations of intertidal crabs at two locations in East Africa for 21 months. Eight populations synchronized larval release with the SIC. Tidal cues were more important than moonlight in entraining the reproductive rhythm, although two populations synchronized spawning to the new moon. SIC synchrony increased with population shore level, because only the higher lunar tide permitted top-shore spawning. Top-shore species therefore have a restricted lunar choice. SIC synchrony could be common, given that it occurs in most marine environments.

Key words: crabs; reproductive rhythm; reproductive synchrony; synodic cycle; tidal rhythm; tropics; *Uca*.

INTRODUCTION

Reproductive synchrony with lunar cycles occurs in nature, from metazoans to humans (Harrison et al. 1984, Gabriele et al. 1998). Famous examples include the mass spawnings of corals on a few full moon and last-quarter moon nights per year (Harrison et al. 1984) and the annual spawning of the South Pacific Palolo worm, mainly on a single day near the last quarter of the moon (e.g., Caspers 1984). Lunar rhythms may have evolved because the cycles of the moon offer reliable time cues to which reproductive behavior can be synchronized (Palmer 1995, Morgan 2001). Thus, several polychaete worms use moonlight as a time cue to set their internal reproductive clock (Bentley et al. 2001) and the midge *Clunio marinus* needs only one episode of three full-moon nights to cue its rhythm for the following three lunar cycles (~90 d) (Neumann 1965). But lunar rhythms may also be selected because

there are short windows during the synodic month during which the conditions are optimal for reproduction. Birth during nights without moonlight, for instance, could reduce predation by visual hunters (Johannes 1978) or the light of the full moon might facilitate migration to spawning sites (Colin et al. 1987). Reproductive synchrony in itself has several selective advantages (reviewed by Ims [1990]). Synchronized spawning may increase fertilization success (Olive et al. 2000) or reduce the predation of adults through "safety in numbers" (Johannes 1978), and mass release of young can "swamp" the predator population because there is a limit to the number of prey a predator can catch per unit time (e.g., Karban 1982).

In the sea, the moon's gravitational pull on earth is the principal cause of the tides, and so lunar and tidal biological rhythms are linked. Fortnightly peaks in tidal amplitude, for instance, coincide with the new moon (NM) and the full moon (FM). This makes it difficult to assess whether biological rhythms are entrained by moonlight or by the tide. In crabs, larval release is mainly synchronized with tidal amplitude (Morgan

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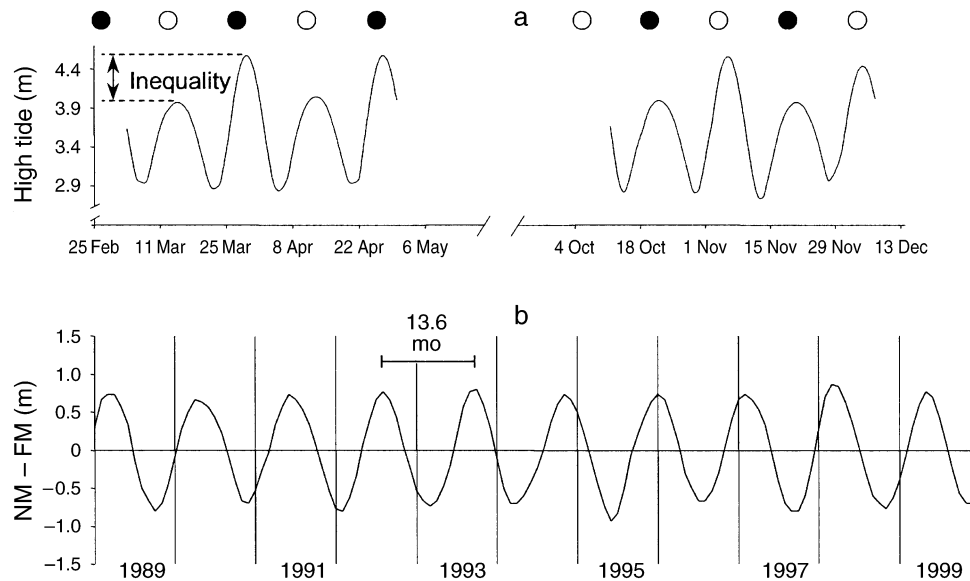


FIG. 1. (a) Inequality between the amplitudes of new moon (NM, black circles) and full moon (FM, white circles) spring high tides at Zanzibar during 1998 and (b) the difference between amplitudes of successive NM and FM spring tides in Zanzibar between 1989 and 1999. Lunar inequality (NM - FM) was calculated per lunar month as amplitude of greatest NM high tide minus amplitude of greatest FM high tide. Positive values indicate predominance of NM spring tides, and negative values indicate FM predominance.

1996a), but moonlight has been shown to entrain spawning in at least one species (Saigusa 1988). Many coastal populations time their reproduction to release planktonic larvae or gametes on nights around NM and/or FM (Palmer 1995). At these two lunar phases the moon and the sun align (a phenomena known as “syzygy”) and their gravitational pulls on earth complement one another. In locations with regular semidiurnal tides (two high and two low tides per day), which is the predominant tidal regime worldwide, this generates two ~5-day periods per lunar (synodic) month, which are characterized by high amplitude “spring tides” (ST) with maxima occurring 1–3 days after NM and FM (Dronkers 1964). The offshore movement of water is strongest during the ebb of spring high tides, and one of the main biological reasons for ST larval release may be to facilitate the speedy offshore transport of larvae away from estuaries and coastal waters, where the density of planktivorous fish and environmental stresses are high (Johannes 1978, Morgan and Christy 1994, 1997). Some populations synchronize spawning with either the NM or the FM, even though spring tides occur at both lunar phases (Johannes 1978, Berry 1986, Palmer 1995). Intuitively, such “preference” for the NM or the FM would imply that moonlight itself is of selective importance. However, succeeding NM and FM spring tides may also have very different amplitudes, as shown in Fig. 1a, and many populations simply spawn at the lunar phase with the greatest spring tides (Berry 1986, Morgan and Christy 1995, Palmer 1995). Disregarding whether it is moonlight or tidal amplitude that has the primary selective importance,

the preference for spawning at one lunar phase may not be constant in space or time: different populations of the same species may display opposite lunar preferences (Ward 1992, Permata et al. 2000), whilst the same population may show interannual or intra-annual switches between NM and FM synchrony (Korringa 1947, Zucker 1978, Hsiao et al. 1994) or switches from lunar (monthly spawning at either NM or FM) to semi-lunar periodicity (biweekly spawning at both NM and FM) (Pearse 1972, Seiple 1979, Hsiao et al. 1994). Although some of these differences have been convincingly explained, the cause of many shifts in lunar preference is still uncertain.

Inequality in the amplitude of consecutive lunar spring tides is often suggested as the selective cause for lunar preference. However, the pattern of lunar dominance in tidal amplitude is not constant; it reverses at regular intervals. An example of this reversal is shown in Fig. 1a using tidal data from one of the present study locations (Zanzibar): NM tides were higher than FM tides early in 1998, but lower than FM ones late in 1998. Fig. 1b shows the difference between the amplitudes of successive FM and NM tides in Zanzibar over a 10-year time period. The majority of coastal locations are subject to this “syzygy inequality cycle” (SIC) (Dronkers 1964). The SIC arises due to the combined effect of two characteristics of the lunar orbit on the moon’s gravitational pull on earth: the anomalist cycle (27.55 d; due to the moon’s elliptic orbit around the earth) and the synodic cycle (29.53 d). The anomalist cycle peaks every 27.55 days when the moon is closest to earth (“perigee”). The synodic cycle peaks

every 14.77 days at syzygy, i.e., at NM and FM. Perigee and syzygy coincide every 207 days (~7 months), and the result is that NM tides are higher than FM ones for ~7 months, after which there is a switch, and the opposite situation occurs. A full SIC lasts on average 13.6 months (414 d) (Fig. 1b). The SIC has long been suspected to be the cause of the periodic shift in lunar preference of some species (Korringa 1947, Pearse 1972, Zucker 1978, Berry 1986). However, its importance has never been tested. Most marine species release planktonic larvae into the sea. Berry (1986) speculated that populations high in the intertidal might be particularly likely to synchronize with the SIC, because only the greatest tides will reach them and permit larval release. Low-shore populations, on the other hand, are copiously flooded by all spring tides and could spawn at any high tide, disregarding the lunar phase and the SIC (Berry 1986). Low-shore species might therefore be less restricted in their lunar choice than high-shore species. Morgan and Christy (1995) also noted that crabs on the mid-shore and below tend to have bi-weekly (semilunar) cycles, while those in the upper zones synchronize reproduction to the larger of the two spring tides. Nevertheless, if population shore level influences the lunar choice, it has not been demonstrated.

This paper demonstrates the effect that this environmental cycle can have on the reproductive rhythms of intertidal animals. We sampled 11 populations of six intertidal crab species over 21 months from two locations in tropical East Africa (Kenya and Zanzibar). The preferred time for larval release was deduced from the developmental stages of embryos carried by females. We examined whether spawning was synchronized with the SIC and whether synchrony with the SIC was more common in high-shore than in low-shore populations. Our species do not migrate to the water's edge to spawn, but depend on tidal flooding reaching them for larval release. Synchrony with the SIC was therefore expected to be more prevalent in populations living high on the shore.

METHODS

Mature-sized female crabs were collected from the mangroves at Mtwapa Creek (Mombasa District, Kenya) and Maruhubi (Zanzibar Island, Tanzania) between November 1997 and July 1999. Six brachyuran crabs were sampled: three fiddler crabs (Ocypodidae), *Uca annulipes* (H. Milne Edwards), *U. inversa* (Hoffmann), and *U. vocans* (Crane); and three sesarimid crabs (Grap-sidae), *Perisesarma guttatum* (A. Milne-Edwards), *Chiromantes ortmanni* (Crosnier), and *Neosarmatium meinerti* (De Man). *Uca vocans* was only sampled in Zanzibar. *Uca* species were excavated, *P. guttatum* and *C. ortmanni* were caught on the forest floor, and *N. meinerti* was taken from burrows. Populations were always collected from the same location, habitat, and shore level. Collection took place throughout the

spring-neap tidal cycle and was most frequent during the months of peak breeding activity. Between 1154 and 6529 females were caught per species, on 49–126 sampling days, averaging >20 females per day per species.

Egg staging

The embryonic incubation of crab larvae has a defined time span during which the embryo passes through a series of development stages (egg stages) and at the end of which the larvae are released. When a population is synchronized to release larvae at specific times (e.g., spring tides), the ripeness of female eggs will peak rhythmically and the preferred time for hatching can be identified through regular sampling (e.g., Brown and Loveland 1985). We classified eggs in five stages: stage 1 (newly laid: yolk even distributed throughout egg), stage 2 (yolk confined to the majority, but not entire egg; no eye spots), stage 3 (pigmented eyespots visible), stage 4 (embryo fully developed, appendages visible), and stage 5 (empty egg cases, larvae hatched).

Statistical analysis

We conducted a preliminary analysis of the egg stage data to ensure that all our species were spring tide spawners. The methods and results of this assessment are shown in the Appendix; the analysis showed that all populations spawned at spring tide.

We next determined with which lunar spring tide (NM or FM) females were synchronized; we calculated a predicted date of larval release (D_r) for each egg stage in a sample and assumed that females were synchronized to the spring tide closest to this date. D_r was calculated by adding the mean time required for the egg stage to reach hatching (T_h , in days) to the date of capture (D_c) (Brown and Loveland, 1985):

$$D_r = D_c + T_h. \quad (1)$$

In our species, T_h takes place on average 12–21 days after stage 1, 8–14 days after stage 2, 3–8 days after stage 3, 2–4 days after stage 4, and 1–2 days before stage 5, depending on species (Skov 2001). From the numbers of NM and FM spawners, we determined the percentage of gravid females per lunar month that released at NM (%_{NM}) and FM (%_{FM}), and from these values we calculated the overall lunar choice of spawning females (LC) per lunar month:

$$LC (\%) = \%_{NM} - \%_{FM}. \quad (2)$$

LC can range between –100%, when all females release at FM, and 100%, when all release at NM. When LC is 0%, equal numbers spawn at NM and FM.

We tested whether females synchronized with the SIC by regressing the LC (Eq. 2) against the difference in maximum NM and FM spring high tides per lunar month (NM – FM, in meters). The influence of shore level on synchrony with the SIC was examined by re-

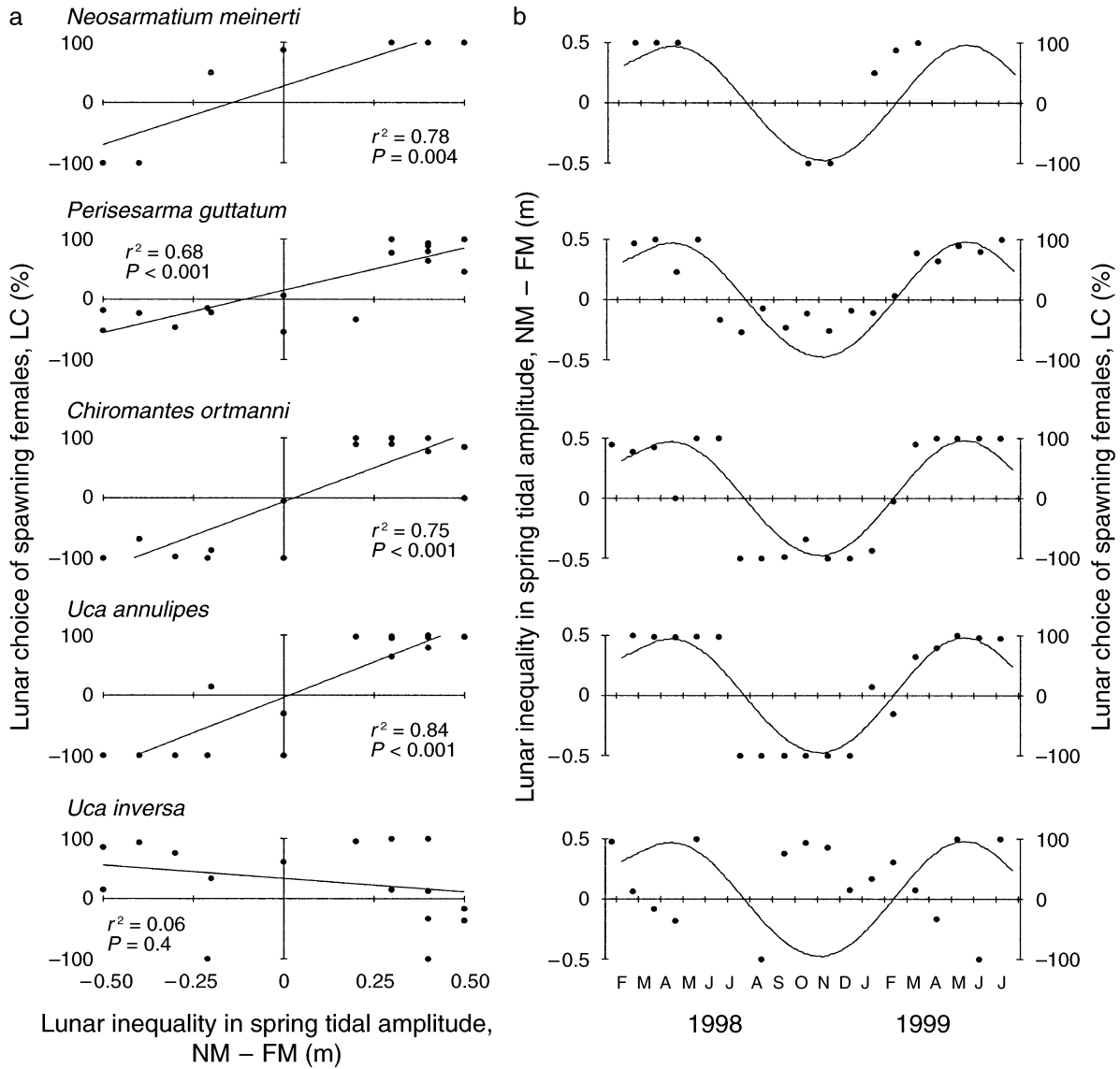


FIG. 2. Lunar choice and lunar inequality in five Kenyan crabs. (a) The lunar choice (LC) of spawning females regressed against the inequality between the maximum amplitudes of new moon (NM) and full moon (FM) spring high tides per lunar month (NM - FM). LC was calculated as the percentage of gravid females per lunar month that spawned at NM minus the percentage that spawned at FM ($\%_{NM} - \%_{FM}$). LC values can range from -100%, when all spawn at FM, to +100%, when all spawn at NM. (b) LC (data points) and lunar inequality (line) plotted against time for the same five crab species. Each data point represents ~68 females. There are fewer data points in panel (a) than in (b) due to data overlap.

gressing the mean percentage of females per population that released at the higher spring tide ($\%_{MAX}$) against the shore level inhabited. We calculated $\%_{MAX}$ for each lunar month (based on the number of NM and FM spawners and knowing which lunar tide had the higher amplitude) and a mean was determined for 8–19 lunar months (depending on population). In order to remove from the regression the effect of the difference in tidal range between Kenya and Zanzibar, shore level (SL) was expressed as a proportion of the mean high water amplitude at spring tide for the location (MHWS; 3.6

m for Kenya and 4.0 m for Zanzibar). For instance, Kenya and Zanzibar populations of *Uca annulipes* both lived 3.4 m above chart datum; their SL were 0.94 (= 3.4/3.6 m) and 0.85 (= 3.4/4.0 m), respectively.

RESULTS

Figs. 2a and 3a show the results of regression analyses between the lunar choice of spawning females (LC) and the lunar inequality in spring tidal amplitude. Regressions were significant in eight populations ($P = 0.03$ to <0.001) and for these the inequality in lunar

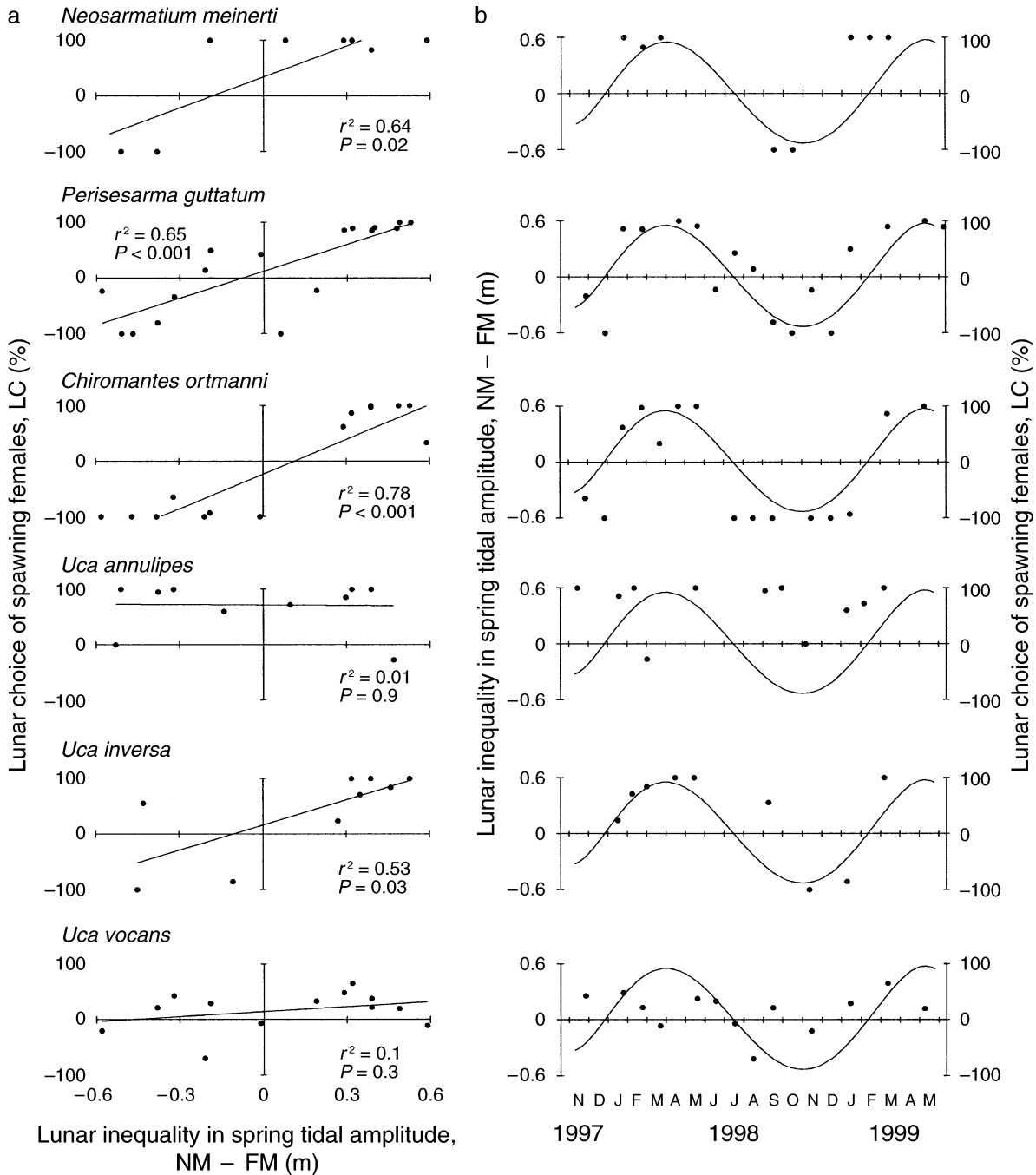


FIG. 3. Lunar choice and lunar inequality in six crabs in Zanzibar (Tanzania). Each data point represents ~ 34 females. Details are as in Fig. 2.

spring tidal amplitude explained between 53% and 84% of the lunar choice (Figs. 2a and 3a: $r^2 = 0.53$ to 0.84). Regressions for Kenya *U. inversa* and Zanzibar *U. annulipes* and *U. vocans* were not significant (Figs. 2a and 3a). Thus eight of the 11 populations synchronized larval release to the SIC. *Neosarmatium meinerti* and *C. ortmanni* alternated between $\sim 100\%$ synchrony with one lunar phase to $\sim 100\%$ synchrony with the

other lunar phase (Figs. 2b and 3b). For Kenyan *C. ortmanni* and *U. annulipes*, the 1998 switches between NM and FM happened from one month to the next, at the same time as the phase-shifts in the SIC. Note that *U. inversa* and *U. annulipes* were synchronized to the syzygy inequality cycle at one location (*U. inversa* in Zanzibar, *U. annulipes* in Kenya), but not the other (Figs. 2 and 3). The populations of *U. inversa* and *U.*

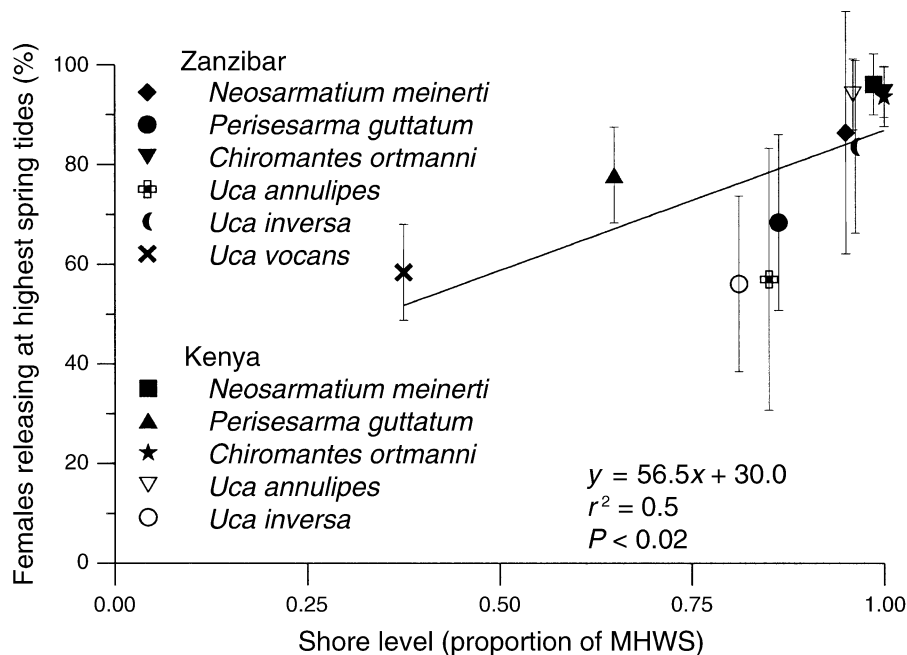


FIG. 4. The percentage of females (mean and 95% CI of 8–19 lunar months) that synchronized their larval release to the higher of the two monthly lunar spring tides, in relation to the inhabited shore level (expressed as a proportion of the mean high water amplitude of spring tides per location [MHWS]; e.g., MHWS was 3.6 m for Kenya; Kenya *Uca annulipes* lived 3.4 m above chart datum; their shore level was: $3.4/3.6 \text{ m} = 0.94$).

annulipes that did not follow the SIC instead showed an overt preference for releasing larvae at NM (Figs. 2 and 3). *Uca vocans* released larvae more at NM (59.8% of females) than at FM, with no apparent link to the SIC (Fig. 3).

A regression analysis (Fig. 4) showed that the higher the position in the intertidal, the significantly greater the population's tendency to release larvae at the higher monthly spring tide. The populations of *U. inversa* and *U. annulipes* that did not synchronize with the SIC lived lower on the shore than those that did.

DISCUSSION

Our data show that the reproductive behavior of intertidal populations can be aligned with the syzygy inequality cycle. Crabs adjusted reproduction so that larvae were released predominantly at the monthly lunar phase with the higher amplitude high tides, disregarding whether this was at new moon or at full moon. In some populations, shifts from 100% synchrony with one lunar spring tide to 100% synchrony with the other happened from one month to the next and was simultaneous with the phase shift in the SIC. Since larval release is the culmination of a process that takes 4–6 weeks to complete (it comprises ovary maturation and embryonic incubation) these females must have initiated a physiological change in lunar association at least one month before the phase-shift in the SIC. This result shows that these populations were precisely phase-aligned with the SIC. Could such precise

alignment be under exogenous control and based purely on the entrainment to cues given every 15 days at spring tide? It seems unlikely: our species reach reproductive maturity within a year, leaving less than one full SIC to precisely imprint its periodicity. Might the capacity to phase-synchronize with the SIC cycle instead be inherited and regulated by a physiological “internal clock”? Rhythms of larval release in crabs generally do appear to be under endogenous control (DeCoursey 1983, Forward 1987), and Morgan (1996b) found that fiddler crabs translocated between a diurnal tidal regime (one high tide per day) and a mixed semi-diurnal tidal regime (usually two, but sometimes one high tide per day) could entrain to the pattern of spring tides on the new home beach within two months. Such relatively quick adjustment might suggest spring tide spawning is endogenously regulated. Long-term biological rhythms are not uncommon; after all, many species adjust reproductive rhythms to the passing of the seasons (Palmer 1995). But lunar rhythms with periodicities more than 30 days (one lunar cycle), such as the SIC, are unusual. Marine polychaete worms are the exception. In this group, several species have moon-related annual rhythms of reproduction, some of which are clock based (Bentley et al. 2001, Naylor 2001).

We do not know which cues associated with the tide keep crabs synchronized with the SIC, but most likely the change in spring tidal amplitude has a major role. Laboratory animals can entrain to environmental rhythms that are related to the tidal cycle, such as pe-

riodical changes in pressure (Abello et al. 1991), substrate wetting (Alifierakis and Berry 1980), turbulence, and noise (Neumann 1978). One month prior to the SIC phase-shift, i.e., when crabs tightly synchronized to the SIC must initiate physiological change in lunar preference, one spring tide is still clearly higher than the other, but a change in the lunar spring tidal dominance has nevertheless started to appear: at our locations the difference between NM and FM spring tidal amplitudes has decreased by 20–30 cm. Do the precisely synchronized crabs cue to this change in relative spring tidal amplitude? The SIC might also be governed by a combination of environmental cues. The annual breeding of the Palolo worm on a few days of the quarter moon is set by a complex interaction of solar and lunar cycles, but the spawning response is cued by the intensity of moonlight (Caspers 1984, Naylor 2001). In most of our populations the shift in lunar preference was less tightly synchronized with the SIC; the shifts were gradual during the 3–4 months surrounding the phase shift in lunar spring tidal dominance, with females then spawning during both lunar phases. It is probable that these populations slowly shifted lunar preference as cued by the gradual change in spring tidal dominance.

The tendency to release larvae on the higher spring tide increased the higher the population lived on the shore. This is not surprising. None of the species sampled here migrate to the water's edge to breed, but release their planktonic larvae during covering high tides from the relative safety of their burrow or preferred shelter. High-shore populations are therefore compelled to release larvae on the higher spring tides, whereas mid- and low-shore populations are well covered by any spring tide and are less restricted in their lunar choice. There are similar records for example in tropical marine snails (Berry 1986), fish (Hsiao et al. 1994), and crabs (Morgan and Christy 1995). The implication is that synchrony with the SIC is imperative for high-shore populations, but not for low-shore populations. Thus, for two species that have a broad shore range, the high-shore populations that we sampled were synchronized to the SIC, whereas the mid-shore populations were not. Tidal cycles have been found to be generally more important than lunar cycles in entraining the biological rhythms of intertidal animals (Palmer 1995, Morgan 1996a), and this was confirmed here: eight of our 11 populations aligned reproduction with the 14-month cycle in tidal amplitude. However, the two mid-shore populations that did not follow the SIC were instead synchronized with the lunar cycle: they released larvae mainly at new moon. The lowest population we sampled also had a tendency for new moon release. Synchrony with moonlight could therefore become more frequent moving down the shore. The preference for larval release at new moon might be because the lack of moonlight reduces the risk of predation by visual hunters (Johannes 1978).

Globally, more than 50% of intertidal environments are subject to the syzygy inequality cycle (Dronkers 1964). It seems intuitive that biological synchrony with such a pervasive environmental cycle should be relatively common, especially in intertidal species for which the difference in spring tidal amplitude has a particular impact. Synchrony with the SIC is likely to be more commonly expressed in regions with a considerable tidal range than in areas where the tides are relatively small. Several previous publications have noted switches between new moon and full moon synchrony, with timing of phase shifts that could correspond to the syzygy inequality cycle, but this was never made explicit on publication. Examples include sea urchins of California (Pearse 1972), crabs on the Pacific coast of Panama (Zucker 1978), intertidal snails in Malaysia (Berry 1986), and Gulf killifish in Florida (Hsiao et al. 1994). Four publications on biological rhythms have noted that lunar spring tidal dominance shifts periodically (Korringa 1947, Pearse 1972, Zucker 1978, Berry 1986), but these did not expand on the subject or provide evidence of biological synchrony. The SIC rhythm may have sometimes escaped notice because biorhythms have been predominantly studied in temperate species, which generally do not have sufficiently long reproductive seasons to demonstrate clearly a shift in lunar preference. The limited tropical studies have rarely been continued over an adequate time scale so that the effect of the SIC could be observed. The results of the present study demonstrate that more interest should be given in the future to this long-term lunar-tidal cycle.

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APPENDIX

A description of the manner in which crab spawning at spring tide was assessed is available in ESA's Electronic Data Archive: *Ecological Archives* E086-063-A1.