



SYMPOSIUM

Timing of Hatching and Release of Larvae by Brachyuran Crabs: Patterns, Adaptive Significance and Control

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Synopsis Most semiterrestrial, intertidal and shallow subtidal brachyuran crabs that live in tropical and warm temperate estuaries, bays and protected coasts world-wide release their planktonic larvae near the times of nocturnal high tides on the larger amplitude tides in the biweekly or monthly cycles of tidal amplitude. Crab larvae usually emigrate quickly to the sea where they develop to return as postlarvae to settle in habitats suitable for their survival. Predators of larvae are more abundant where larvae are released than where they develop, suggesting that this migration from estuaries to the sea reduces predation on larvae. Crabs with larvae that are relatively well-protected by spines and cryptic colors do not emigrate and often lack strong reproductive cycles, lending support to this explanation. Adults control the timing of the release of larvae with respect to the biweekly and monthly cycles of tidal amplitude by controlling when they court and mate and females control when development begins by controlling when they ovulate and allow their eggs to be fertilized by stored sperm. By changing the time they breed, fiddler crabs (*Uca terpsichores*) compensate for the effects of spatial and temporal variation in incubation temperature on development rates so that embryos are ready to hatch at the appropriate time. Control of the diel and tidal timing of hatching and of release of larvae varies with where adults live. Females of the more terrestrial species often move from protected incubation sites, sometimes far from water, and they largely control the precise time, both, of hatching and of release of larvae. Females of intertidal species also may influence when embryos begin to hatch. Upon hatching, a chemical cue is released that stimulates the female to pump her abdomen, causing rapid hatching and release of all larvae in her clutch. Embryos, rather than females, largely control hatching in subtidal species, perhaps because females incubate their eggs where they release their larvae. Topics for further study include the mechanism whereby adults regulate the timing of breeding, the mechanisms by which females control development rates of embryos, the nature of communication between females and embryos that leads to precise and synchronous hatching by the number (often thousands) of embryos in a clutch, and the causes of selection for such precision. The timing of hatching and of release of larvae by cold-temperate, Arctic, and Antarctic species and by fully terrestrial and freshwater tropical species has received little attention.

Introduction

Many marine organisms reproduce synchronously. The annual mass spawning by over 100 species of corals on Australia's Great Barrier Reef (Babcock et al. 1986) is perhaps the most dramatic and best-known example. Reproductive cycles with periods shorter than a year are less widely known but also are common (Morgan 1995). Here, I review nonseasonal patterns in the timing of the hatching of embryos and of release of larvae by 81 species of semiterrestrial, intertidal, and shallow-water, subtidal

crabs in the infraorder Brachyura, studied at 108 locations. I briefly discuss the evidence that these patterns are selected by predation on larvae and female crabs (Christy 2003) and I summarize what is known about the control of the timing of hatching and larval release both by embryos and the females that carry them (hereafter “ovigerous females”). New studies since the previous comprehensive reviews (Forward 1987; Morgan 1995) extend the known patterns and provide additional insight into their adaptive significance and control.

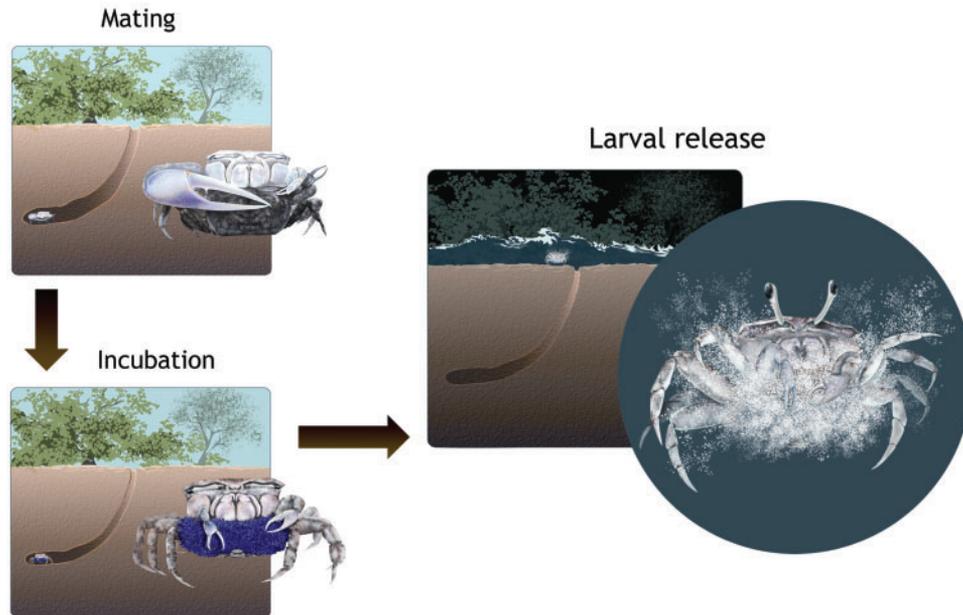


Fig. 1 The breeding sequence of the dancing fiddler crab *Uca terpsichores*. After mating, the male leaves the female in the terminal chamber of his burrow where she incubates her embryos until they are ready to hatch, about 12–15 days after mating. The female releases her larvae at high tide, typically in the early morning before dawn on a large-amplitude tide. She may not fully emerge to the surface to do so. Drawings by Laura Vollset.

Reproductive biology

Hatching of embryos and release of larvae by brachyuran crabs are the final events in the reproductive sequence that begins with courtship and mating (reviewed by Asakura 2009). In many aquatic species, mating occurs soon after the female molts, whereas mating and molting generally are not coincident in intertidal and semiterrestrial species (Fig. 1). In both groups, the male may guard the female at a protected and often socially isolated location until she has ovulated. The eggs are fertilized as they pass out of the female's body, where they adhere to specialized setae on the female's abdominal appendages (Fig. 2). Development begins immediately and development rates increase with increasing temperature (Wear 1974). Most of the warm-temperate and tropical species discussed here breed when the water temperature is $>20^{\circ}\text{C}$ and development typically lasts from just over a week to about a month. Oviparous females actively care for their embryos (Ruiz-Tagle et al. 2002). Eggs that are within a day of hatching consist of an embryo and a small amount of yolk, both of which are surrounded by an inner and an outer membrane (DeVries and Forward 1991a; Saigusa 1992a). When embryos hatch, the outer membrane breaks first, probably by the action of an enzyme from the embryo (DeVries and Forward 1991b). The embryos break out of the egg membranes through expansion of their exoskeletons and, often

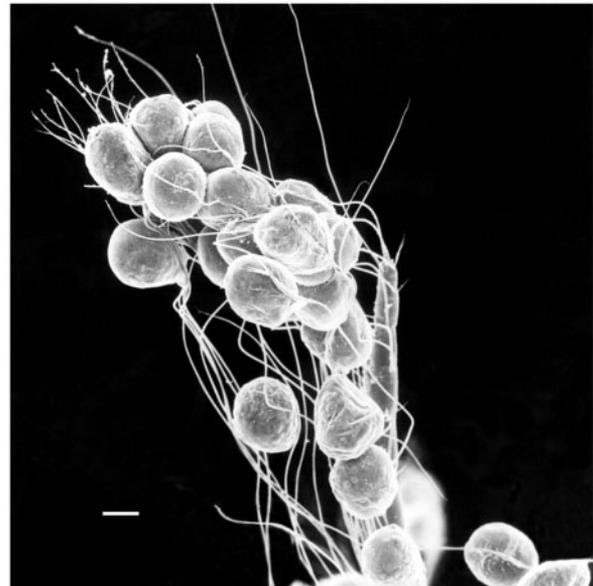


Fig. 2 Eggs of the fiddler crab *Uca pugilator* beginning to adhere to the setae on the female's abdominal appendages. The eggs were ovulated about 20 min before they were preserved. The white bar indicates 100 microns. Photomicrograph taken in 1978 by JM Dumont, Oak Ridge National Laboratory.

with mechanical assistance provided by vigorous abdominal pumping by the female, they enter the water column as swimming aquatic larvae (zoeae). Zoeae of many species use tidal currents both to

Table 1 Timing of release of larvae by 81 species of brachyuran crabs from 3 habitats with respect to the diel, tidal stage, and tidal-amplitude cycles (totals for each kind of cycle can exceed 81 because release of larvae could be equally common across more than one phase of each cycle and some species were studied in 2 or more tidal regimes; see Supplementary Table)

Habitat	Environmental cycle												
	Diel ^a					Tidal stage ^b				Tidal amplitude ^c			
	Day	Evening	Night	Morning	All	Flood	High	Ebb	All	Max	Large	Inter	All
Semiterrestrial	0	10	3	1	0	2	10	0	1	7	6	1	0
Intertidal	11	32	21	22	1	2	51	4	1	45	21	5	3
Subtidal	7	2	10	0	0	0	6	1	8	3	0	1	15
Totals	18	44	34	24	1	4	68	5	10	56	27	7	18

^aDiel: day: during daylight hours; evening: sunset to midnight; night: midnight to 0300; morning: 0300 to dawn; all: anytime.

^bTidal stage: flood: 3–1 h before high tide; high: 1 h before to 1 h after high tide; ebb: 1–3 h after high tide; all: any tide stage.

^cTidal amplitude: max: 1 day before to 1 day after the maximum-amplitude tides; large, 3–1 days before or 1–3 days after the maximum-amplitude tide; inter: tides of intermediate but not lowest amplitude; all: any tidal amplitude.

emigrate from estuaries to the coastal ocean where they develop (Forward and Tankersley 2001) and to immigrate as postlarvae (megalopae) and settle in habitats suitable for growth and survival (Christy and Morgan 1998).

General patterns

The crabs discussed here time when they release their larvae with respect to each of the three physical cycles that produce fluctuations in nearly all biotic and abiotic factors in their intertidal and shallow-water habitats: (1) the diel cycle of alternating daylight and darkness with a 24 h period; (2) the tidal cycle of variation in depth of water with an average period of 12.4 h giving two tides per day each with an average period of 24.8 h period; and (3) the tidal-amplitude cycle, which has an approximately biweekly period of 13.7 or 14.8 days and a monthly period of 27.3 or 29.5 days, corresponding to the half and full tropic and synodic months, respectively. Regional and local coastal geomorphology largely determines whether the tropic or synodic monthly tidal forces prevail at a given location. With one known exception (Saigusa 1988) crabs do not time reproduction with respect to the phases of the moon independently of the effects of the lunar cycle on the timing and amplitudes of the tides. The most common pattern (Table 1 and Supplementary Table) is for hatching to occur at night near the time of high tide on the larger-amplitude tides in the biweekly or monthly cycle of tidal amplitude. Such tides typically occur for several days during each bi-weekly cycle in the amplitude of the tides. However, the temporal distribution of hatching often shows a sharp peak within this interval corresponding to the

day with the nocturnal tide of maximum amplitude (Table 1).

The timing and duration of the interval for hatching in the lunar month vary considerably from coast to coast, across tidal regimes, and, at some locations, from the beginning to the end of a breeding season (Barnwell 1976; Morgan 1995; Thurman 2004). The timing of hatching changes in correspondence with changes in the interval for hatching (discussed below). Here, I recognize three tidal regimes that differ broadly in the time that the preferred interval for hatching occurs during the lunar month and during the solar day, and I give selected examples of crabs that track these changes.

Timing in different tidal regimes

Eighty-one of the 108 studies of the timing of hatching (Supplementary Table) were carried out in the semidiurnal tidal regime, the most common one world-wide. The preferred interval for hatching in this regime occurs over the same range of times in the solar day twice each month during “spring” tides of large amplitude, typically just after the syzygies. The release of larvae on the tides of maximum amplitude is the most common pattern among semiterrestrial (6 of 6 studies, 100%) and intertidal (38 of 60 studies, 63%) crabs that live in this predictable tidal regime (Supplementary Table). The time of high tide during the tides of maximum amplitude varies with location and so too does the time of release of larvae. For example, in North Inlet Estuary on the Atlantic Coast of the USA, seven species of brachyurans in four families that live from the supratidal zone to the shallow subtidal zone released larvae (in 1977 and 1978) just after dusk on the maximum-amplitude nocturnal tides

following the new and full moons and continued for several nights as the amplitude of the tides decreased (Christy and Stancyk 1982). On the Pacific Coast of Panama, the maximum amplitude nocturnal tides typically occur in the early morning just before dawn and several estuarine crabs release their larvae then (Morgan and Christy 1995) on a biweekly cycle.

Monthly cycles of the release of larvae on tides of maximum amplitude also occur in this tidal regime. This pattern is exhibited by a group of eight species that live in the upper intertidal zone in the mangrove forests of Pacific Panama (Morgan and Christy 1995). When only one of the two spring tides reaches their habitat in a month, these species all release larvae predominantly on a single night on the highest morning spring tide in the month. This pattern may be common. A long-term study of six species of brachyurans on the coast of Kenya found that four species that live in the upper intertidal zone released larvae once monthly on the highest spring tides, while two species that live lower on the shore exhibited biweekly cycles (Skov et al. 2005; see also Zucker 1978).

Release of larvae on the tides of maximum amplitude is the most common pattern in the semidiurnal tidal regime. However, 12 of the studies in this regime (Supplementary Table) found that crabs that live in the lower intertidal (e.g., Christy 1986) and subtidal (e.g., Forward et al. 1982) zones released their larvae shortly after dusk on tides that were less than maximum in amplitude. These tides ebb entirely during the night and may be favored because they allow larvae to leave shallow waters when fewer fish that eat plankton are feeding compared to other times (Christy 1986).

Mixed semidiurnal tides are the second most common tidal pattern world-wide. Too few studies (20) have been done in this tidal regime to reveal clear differences in the timing of the release of larvae by crabs that live at different levels on the shore. One or two high tides, typically of unequal height, occur each day in this tidal regime. The time of night at which high tides of larger-amplitude occur varies considerably. The fiddler crab *Uca thayeri* illustrates how crabs time hatching in this variable tidal regime (Kellmeyer and Salmon 2001; Weaver and Salmon 2002; Christopher et al. 2008). *Uca thayeri* lives in a semidiurnal tidal regime on the east coast of Florida, USA and in a mixed semidiurnal regime (usually with two high tides each day) on the west coast of Florida. Crabs on the east coast release larvae on large-amplitude tides in the evening. Crabs on the west coast change the timing of hatching with the season. In the spring (of 1998 and 1999)

the amplitudes of the two daily tides differed little and the crabs released larvae near the time of high tide in the early mornings before dawn, as well as in the afternoons before sunset. As the season progressed, the morning nocturnal tide decreased in amplitude and the crabs released larvae only during daylight on the larger-amplitude afternoon tide. Crabs that were experimentally transferred from the west coast to the east coast adopted the “east-coast” hatching pattern, confirming that the rhythms that regulate timing readily entrain to local tides (Morgan 1996).

Diurnal tides are the least common world-wide and only seven examples of hatching are known from this tidal regime. Diurnal tides occur along the Gulf Coast of the USA and in the Gulf of Tonkin in the South China Sea. In this tidal regime, there is but one high tide each day for most of each month, which may occur during daylight or darkness, and (typically) very low-amplitude semidiurnal tides twice monthly, lasting for a day or two. The timing of the release of larvae in this tidal regime is particularly challenging as a nocturnal interval most favorable for hatching may never occur during the breeding season. The timing of release of larvae by the fiddler crab *Uca pugilator* shows how one species deals flexibly with changes in the tidal regime across its range (Morgan 1996).

In the semidiurnal tidal regime on the east coast of the USA, *U. pugilator* releases larvae just after dusk during nocturnal tides of large amplitude (Bergin 1981; Christy and Stancyk 1982; DeCoursey 1983). In both mixed semidiurnal and diurnal tidal regimes along the Gulf Coast of the USA, crabs released larvae at night near dawn. Release in the mixed tidal regime occurred at high tide on tides of intermediate amplitude. In the diurnal regime early in the season, crabs released larvae on flooding (rather than high) tides of intermediate amplitude. Later in the season when the morning high tide peaked before sunrise and included the maximum-amplitude tides, the crabs released their larvae then. Crabs transferred between tidal regimes changed and released larvae to match local conditions. Thus, in contrast to *U. thayeri*, this species hatched during darkness on tides that usually were of intermediate amplitude rather than on the tides of larger amplitude during the day.

Adaptive significance

Semiterrestrial and intertidal species tend to release larvae on nocturnal high tides of maximum or large amplitude, whereas subtidal species do not (Table 1).

Such timing might be advantageous for the simple reason that it would allow the greatest imprecision in timing with respect to the tidal stage because the intertidal habitat would be inundated for longer periods during tides of larger amplitude. This might allow females to avoid releasing larvae at a given moment if conditions were unfavorable, due, for example, to the presence of a passing predator. However, this does not explain why hatching often precisely coincides with high tide at night, even among terrestrial species that walk long distances to release larvae from cliffs or steep stream banks. Variation in tidal amplitude should have little effect on the ability of these species to shed larvae successfully into the sea. Instead, considerable, albeit indirect, evidence suggests that the timing of larval release by brachyuran crabs is an adaptation that allows ovigerous females at the time of hatching as well as their newly hatched larvae, to avoid their predators; the “predator-avoidance hypothesis” (Christy 2003).

Although the predator-avoidance hypothesis has a long history (e.g., von Hagen 1970), substantial indirect evidence for it first came from studies showing that the timing of release of larvae results in rapid emigration of larvae from estuaries, where predators on larvae abound, to relatively safer coastal waters (Christy and Stancky 1982; Morgan 1990). Emigration is not passive; endogenous rhythms of vertical swimming place crab larvae in currents most favorable for transport out of the estuary to the coastal ocean (Forward and Tankersley 2001; Lopez-Duarte and Tankersley 2007; Morgan and Anastasia 2008). A recent study of 15 species of fiddler crabs found that rhythms of vertical swimming by larvae that promote seaward dispersal are strong in species that live in the upper estuary and weak or absent in species that live in the lower estuary or on the exposed coast (Lopez-Duarte et al. 2011). Nevertheless, all species release larvae on maximum-amplitude nocturnal ebb tides. Hence, both of these traits that promote dispersal and escape from predators are present in species that release larvae relatively far from the sea. In contrast, only precise timing of release of larvae and, consequently, rapid off-shore dispersal over shorter distances is observed in species that live closer to safer, deeper waters. For these species, the benefits of energetically costly vertical swimming may be too small to favor this additional mechanism that promotes dispersal. Other studies showed that crabs with larvae that are protected by spines from predation by fish (Morgan 1989; Hovel and Morgan 1997) or that have colors making them difficult for fish to see (Morgan and Christy 1997) do not time hatching

to coincide with tides of large amplitude (Christy 1986). Indeed, the larvae of some of these well-defended and cryptic species tend to be retained in the estuary rather than emigrate to the sea (Cronin 1982; Hovel and Morgan 1997). Hence, interspecific variation in the vulnerability of crab larvae to predation in shallow water by planktivorous fish may largely explain interspecific variation in the timing of release of larvae relative to the times most favorable for dispersal from shallow water and early larval survival.

Exposure of females to predators at the time they release their larvae also may favor certain times over others for the release of larvae. For example, estuarine species such as *Rhithropanopeus harrisi* (Forward et al. 1982) and *Dyspanopeus (Neopanope) sayi* (DeVries and Forward 1991b) have relatively protected larvae that they release near the time of high tides at night in the early evening. Predation on females when they emerge from incubation sites to release larvae may also select for the release of larvae at certain times. A test of this idea will require making difficult observations of females, larvae and their predators at the moment that larvae are released under natural conditions.

Control

Biweekly and monthly timing

Adults control the timing of release of larvae relative to the biweekly or monthly tidal-amplitude cycles by controlling when they court and mate and when the female ovulates and begins incubation (e.g., Christy 1978). Temperature-dependent timing of courtship and mating by the dancing fiddler crab *U. terpsichores* illustrates the fine control adults have at this temporal scale. Courting males of this tropical species build sand structures called hoods on one edge of the opening of their burrows into which they attract females for mating and where females remain (at about 20 cm depth) until their eggs hatch (Christy et al. 2001; Fig. 1). The daily rate that males with hoods attract mates varies little (mean \pm SEM: $9.0 \pm 2.7\%$) over a 3-fold difference in the number of males that build these structures on a given day (Christy et al. 2001). Hence, the number of hoods built on a given day in a given area (the tide destroys all hoods daily) is a reliable index of the number of females that chose mates that day in that area, and, 1.5 days later (Christy et al. 2001), the number that ovulate and begin incubation. In The Republic of Panama, this species breeds year-round and experiences sea and sediment temperatures of about 28°C most of the year.

However, during cold-water upwelling in January–March, females and their embryos are exposed to sediment temperatures as low as 22–24°C at times during their 2-week incubation period (J. Christy and K. Kerr, unpublished data). These lower temperatures slow embryonic development by about 5 days (from 13–14 days at 28°C to 18–19 days at 23°C). (Christy 2003; K. Kerr, unpublished data). Daily counts of hoods over a 4.5 month period spanning the cool period (December 1999 to mid-April 2000) revealed an advance in phase of ~5 days in the timing of hood building and presumably in the onset of incubation (Christy 2003). The advance in phase at the onset of incubation may have compensated for the longer developmental period at the lower temperatures such that females released larvae on the larger-amplitude nocturnal ebb tides in spite of the lower temperatures. There is no evidence that the cycle of reproduction by one sex either leads or follows the cycle of the other (Christy et al. 2001). Rather, the cycles of reproduction in both sexes may be governed by the same endogenous clocks (Thurman 2004) and may change in concert with changes in temperature.

A comprehensive study now nearing completion (K. Kerr, unpublished thesis research) has verified temperature-dependent changes in reproductive timing by *U. terpsichores*. This study has also found that the timing of courtship and mating varies within seasons between beaches <0.5 km apart that vary in sediment temperature. *Uca terpsichores* is abundant along portions of the tropical eastern Pacific coast that do not experience upwelling (Crane 1975). Hence, the ability of this species to change the times when it courts and mates to compensate for the effects of spatial variation in sediment temperature on timing of release of larvae may be selected across this species' range. Spatially selected flexibility in this timing mechanism may be a fortuitous pre-adaptation to temporal variation in sea temperature, whether driven by seasonal upwelling at some locations in its range or by more wide-spread and longer-term changes in climate.

The mechanisms that regulate the timing of breeding may differ depending on where adults live and the physical cycles they experience. While variation in the amplitudes of the tides could easily be sensed by intertidal and shallow subtidal species, no study has identified the cues that entrain these longer-term rhythms in the species that live in those habitats. In contrast, through an extensive series of experiments, Saigusa (1980; 1988) has demonstrated convincingly that the lunar moonlight cycle sets the phase of the semilunar cycle of release of larvae in the terrestrial

grapsid crab *Sesarma heamotocheir*. This timing mechanism will function well on coasts with semi-diurnal tidal regimes where the times of the large-amplitude nocturnal high tides occur at nearly the same phase of the semilunar cycle each month.

Tidal and diel timing

Reproductive timing by adults establishes the range of phase relationships between the cycles of light and height of the tide that embryos experience when they are competent to hatch. The roles of adults and embryos in controlling the timing of hatching relative to these cycles seems to depend on whether or not females move from their usual habitats or protected incubation sites to where larvae are released; the more terrestrial the species, the more extensive the movement and the greater the contribution by females to the timing of release of larvae at these temporal scales (Forward 1987).

Saigusa has studied in depth the timing of release of larvae and its control in the terrestrial grapsid crab *S. heamotocheir* in Japan. Here, I summarize the main results of that work (Saigusa 1982, 1992b, 1992c, 1993, 2000). This small crab lives on steep wooded hills on the coast above all influence of the tide. Females stay hidden in the forest while they incubate their eggs. When their eggs are ready to hatch, they walk to the edge of streams where they release their larvae on large-amplitude nocturnal high tides that typically peak between sunset and midnight. Eggs hatch before larvae are released (Saigusa 1992a). Females usually stand just at the edge of the water and pump their abdomen vigorously, leading to a burst of release of larvae (as in *Sesarma cinereum*: Dollard 1980). Embryos in clusters (several hundred per cluster) that were removed from females on the day they released their larvae, or 1 day before, hatched on the same night as did the embryos left on the females, but over a span of hours rather than minutes. In contrast, embryos that were removed more than two nights before larvae were released by the females failed to hatch although they remained viable. These results suggested that an interaction between females and their embryos within a 2-day period prior to hatching may be required for embryos to hatch and may increase synchrony of hatching. A series of clever experiments, in which eggs at different stages of development were transferred between ovigerous females, confirmed this model of the control of hatching; females cue a “hatching program” in embryos that leads to their hatching two nights later. The embryos follow that program even when transplanted to females with

embryos that hatch at another time. However, action by the female is required for synchronous release of the emerging larvae into the sea. A substance apparently is released during hatching that helps to detach the now empty egg cases from the seatae on the female's abdominal appendages (Saigusa 1994). Hatching in other terrestrial crabs, which also may be induced by the female, typically occurs slightly before females release their larvae by pumping their abdomen (e.g., Wolcott and Wolcott 1982; Hicks 1985; DeVries and Forward 1991b), by shaking their whole body (Liu and Jeng 2005) or simply by dropping the mass of hatched larvae into the water (Liu and Jeng 2007). Females of these semiterrestrial crabs carefully select the sites at which they release their larvae; such sites may include crevices in cliffs some meters above the water where they are safe from wave surge but where the shed larvae will fall directly into the sea. The control of the timing of release of larvae by females obviously is required if they must first find sites favorable for release.

Female brachyuran crabs that live in the intertidal zone also may largely control hatching. In this habitat, ovigerous females and their embryos often remain hidden in protected incubation sites (e.g., in the terminal chamber of a burrow provided by the female's mate; *U. pugilator*, Christy 1982). However, even females that are hidden in closed burrows may experience cyclic variation in pressure, temperature, salinity, and other factors that vary with the tides. If ovigerous female fiddler crabs *U. pugilator*, *Uca Pugnax*, and *Uca minax* are put into constant conditions early in development, long before embryos have functional organ systems, they release their larvae at the appropriate time with respect to the light and tidal cycles, presumably following an endogenous rhythm(s) in the female (Bergin 1981; Salmon et al. 1986). Embryos that will hatch on a given evening but are removed in the afternoon from ovigerous *U. pugilator* and *S. cinereum*, hatch ~2 h later and over a longer period of time relative to the embryos that remain on females (DeVries and Forward 1991b). When embryos of these and other species begin to hatch, they release a peptide (Rittschof et al. 1985; Forward et al. 1987; DeVries et al. 1991) to which females respond by vigorously pumping their abdomens. This pumping helps synchronized hatching and release of larvae among the typically several thousand embryos in a clutch (Forward and Lohmann 1983). This explains why embryos removed from females usually do not hatch synchronously. This sequence of events is similar to that which controls hatching in *S. heamatocheir* except that hatching immediately stimulates release

of larvae so that the two events nearly coincide. The critical step is the timing of the initiation of the sequence. It is not known which factors cue this early step nor how the female and her embryos communicate at this stage.

Females appear to play a relatively minor role in the timing of hatching in low-intertidal and subtidal brachyurans. The timing of release of larvae by *Rhithropanopeus harrisi* can be entrained to light and tidal cycles in the field (Forward et al. 1982) and to salinity (tidal), light, and hydrostatic pressure cycles in the laboratory (Forward et al. 1986; Forward and Bourla 2008). Embryos of *R. harrisi* removed from females on the night of hatching and placed on a mechanical shaker hatch at about the same time and over the same period as those that remain attached to females (Forward and Lohman 1983). The embryos of *Dyspanopeus (Neopanope) sayi* also will hatch on time when separated from the female (DeVries and Forward 1991b). Hence, unlike the embryos of some semiterrestrial crabs that have been removed from the female, there is no delay in hatching by the embryos of these subtidal species. However, the hatching embryos of both species release proteins that stimulate abdominal pumping by females which, in turn, synchronizes hatching and release of the remaining larvae in the clutch that are able to hatch that night. Hence, the timing of hatching and release of larvae appears to be controlled by endogenous rhythms in embryos that are set by cues present in local physical cycles. Release of larvae via abdominal pumping in another subtidal species *Callinectes sapidus* also has been shown to be stimulated by substances that are released when embryos hatch (Tankersley et al. 2002). In general, however, hatching by subtidal species is less precisely timed and less synchronous, compared to intertidal and semiterrestrial brachyurans (Table 1). For example, hatching in the stone crab *Menippe mercenaria* begins with a pulse of release of larvae but then extends for a median of 20 h; the timing of hatching varies considerably among locations with respect to the diel cycle and especially to the tidal cycles (Krimsky et al. 2009). Females of most subtidal species incubate at locations that are also suitable for release of larvae. Hence, the control of hatching can be invested largely in embryos.

Conclusions and future directions

Gifford (1962) noted, "Whether lunar spawning is rare in crustaceans or whether other forms have not been observed as closely as *C. guanhumii* is unknown, but its occurrence in this species seems

reasonably certain.” Almost 50 years later, over 100 studies using close observations have shown that biweekly or monthly reproductive cycles are common among brachyuran crabs that live in semi-terrestrial, intertidal and shallow subtidal habitats in tropical and warm temperate regions world-wide. In the majority of species, these cycles result in the release of larvae on maximum or large-amplitude nocturnal high tides in the biweekly or monthly tidal-amplitude cycles. Crabs in several families and with diverse ecologies exhibit this general pattern, suggesting that reproductive timing is not driven by tidal schedules of resource consumption and allocation to reproduction by adults (but see Kim and Choe 2003). Instead, there is a strong comparative, but indirect, evidence that predation by fish on newly hatched larvae and perhaps predation on female crabs at the moment of release selects for the timing of all phases of courtship, mating and release of larvae (Christy 2003). Nevertheless, experimental studies comparing predation rates on females and larvae when larvae are released inside (control) and outside (phase-shifted) the interval thought to be most favorable for their survival have yet to be conducted. In addition, relatively little is known about the causes of variation in larval color and spination, traits that affect the vulnerability of larvae to planktivorous fish. Crabs obtain carotenoid pigments from their diet and these are transferred as lipovitellins to the egg and embryo (Cheesman et al. 1967; Ghidalia 1985). Perhaps the red color of the relatively vulnerable larvae of species such as *Cataleptodius taboganus* and *Xanthodius sternberghii* is a consequence of the herbivorous diet of the adults; while the cryptic yellow–green color of the larvae of *Eurypanopeus planus* may reflect the predatory diet of this species. A study of reproductive timing, pigments in adults’ diets and pigments and morphology of newly hatched larvae among species within a diverse genus (*Uca* or *Sesarma*) or family (Xanthidae) would be informative.

Behaviors that increase the precision of the timing of the release of larvae by reducing temporal variation between (or by temporally decoupling) courtship, mating, ovulation, and fertilization have been little studied. The embryos of brachyuran crabs develop external to, but in intimate contact with, the female. By choosing incubation microhabitats and therefore the temperatures that embryos experience, females may be able to control the timing of hatching (K. Kerr, manuscript in preparation). Females use specific and energetically costly behavior (especially so in large species) to care for their embryos, including frequent probing to detect

oxygen conditions in the egg mass and abdominal pumping to aerate their embryos (Fernández et al. 2002). These behaviors no doubt help maintain the health of embryos. They also reduce differences in oxygen concentrations between embryos in the center and periphery of the clutch and thereby help reduce differences in development rate between them (Fernández et al. 2003); this may ensure that most larvae in a clutch of thousands are competent to hatch at the same time. The physical proximity of embryos and females also creates the opportunity for communication between them by chemical cues or signals. Communication at this level may promote precise timing of hatching relative to the diel and tidal cycles (DeVries and Forward 1991a, 1991b; Saigusa 1993). The chemicals that mediate this interaction before hatching have yet to be identified.

The timing patterns I have discussed are exhibited by crabs that live in warm temperate, subtropical, or tropical environments. There is one report of biweekly timing by crabs from cool temperate habitats and none, to my knowledge, of biweekly timing by crabs from cold waters. Morgan et al. (2011) studied the timing of release of larvae by three intertidal grapsid crabs that live on the coast of California, USA. This coast experiences upwelling of cold water and considerable variation in temperatures in the intertidal zone. Consequently, incubation can take 28 days at warmer southern locations and ~78 days at cooler northern sites. The release of larvae by the three species coincided with the biweekly tides of larger amplitude but the crabs exhibited very weak synchrony, which was attributed to variation in temperature during the relatively long incubation periods. It is not surprising that crabs from cold water apparently lack biweekly or monthly cycles of release of larvae. Development at temperatures near 0°C is prolonged and any small proportional change in rate due to a change in temperature can alter hatching dates by months. For example, the embryonic development period of the snow crab *Chionectes opilio* from the eastern Bering Sea at 6°C is about 6 months, extending to 13–14 months at –1°C; hatching occurs over a 7–17 day period, and this species does not time hatching with respect to the tidal-amplitude cycle (Webb et al. 2007). Embryos of this and other cold-water species can exhibit one or more diapauses during development, which may permit timing with respect to slowly changing conditions suitable for larval growth and survival (Webb et al. 2007). Embryonic development in another well-studied crab of commercial importance, the red king crab, *Paralithodes camtschaticus* (an anomuran crab) takes ~1 year. Females release

larvae nightly over about a month, with hatching concentrated in the early evening (Stevens and Swiney 2007). However, hatching by this species also does not appear to be timed with respect to the tidal or tidal-amplitude cycles. The implications of relatively imprecise timing of hatching for survival and dispersal of larvae in cool and cold-water species have yet to be explored.

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Supplementary Data

Supplementary data are available at *ICB* online.

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