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Influence of tidal variation on reproductive timing

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Abstract

Tidal variation may cause the timing of activities by coastal organisms to vary geographically. This was demonstrated by determining the timing of larval release by the same or closely related species in diurnal and mixed semidiurnal tidal regimes along the northeastern Gulf of Mexico and by contrasting hatching patterns with those previously documented in a semidiurnal tidal regime along the Atlantic coast of the USA. Five species of crabs primarily released larvae during nocturnal maximum amplitude high tides near new and full moons along the Atlantic coast. In contrast, larval release by the same or closely related species on the Gulf coast peaked either when maximum amplitude high tides occurred during the daytime or several days away when submaximal amplitude high tides occurred near dawn. This variation in reproductive timing arose because maximum high tides do not occur at night along the Gulf coast during most of the reproductive season. Reproductive timing also differed for two species pairs along the Gulf coast due to changes in the phasing of the tides and light–dark cycle. Species-specific hierarchies of rhythms regulating reproductive timing were revealed by the degree to which larval release kept phase with lunar, tidal amplitude and light–dark cycles. These hierarchies enabled crabs to track phase shifts of cycles in variable tidal environments and may enhance reproductive success across tidal regimes.

Keywords: Larvae; Hatching; Rhythms; Tides; Diel; Lunar; Predation; Crabs

1. Introduction

The periodic rise and fall of tides profoundly affect the lives of coastal marine animals (see Palmer, 1974, 1990; Barnwell, 1976; DeCoursey, 1983; Morgan, 1995 for reviews). Distributions, abundances, reproduction and activities of these animals may fluctuate

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with tidal and tidal amplitude cycles. The tidal cycle refers to the semidaily or daily cycle of high and low tides, and the tidal amplitude cycle is the biweekly cycle of daily differences in the height of high and low tides that is usually synonymous with the spring-neap cycle. Animals often track these changes in tides endogenously thereby enabling them to anticipate and reliably time reproduction and other activities (Palmer, 1974, 1990; DeCoursey, 1983; Forward, 1987; Giese, 1987; Morgan, 1995). Tidal and tidal amplitude rhythms are entrained by cues that are associated with tides, such as salinity, temperature, hydrostatic pressure and vibrations. Moonlight also may entrain biweekly rhythms (Saigusa, 1988). Furthermore, coastal animals also commonly track changes in the light–dark cycle (Palmer, 1974, 1990; DeCoursey, 1983; Forward, 1987; Giese, 1987; Morgan, 1995). Thus, circatidal (usually 12.4 h but sometimes 24.8 h), circadian (24 h) and circasemilunar (14.8 days) rhythms in reproduction and behavior often are entrained by tidal, light–dark, tidal amplitude and lunar cycles.

A wide variety of timing patterns is possible because activities may be synchronized by several of these environmental cycles and by different phases of each cycle. However, species may commonly converge on the same timing pattern. Intertidal spawning fishes, coral reef fishes and crabs release eggs or larvae on nocturnal maximum amplitude high tides near new and full moons (Clark, 1925, Johannes, 1978; DeCoursey, 1983; Morgan, 1995). This may be adaptive because eggs and larvae would be swept rapidly by nocturnal ebb currents away from reefs and shallow coastal waters where diurnally-foraging planktivorous fishes abound (Johannes, 1978; Morgan and Christy, 1995). In addition, predation on female crabs and their embryos, which are attached to abdomens, also may be reduced by releasing larvae at this time (Morgan and Christy, 1995). Intertidal crabs that live high on the shore may release larvae near refuges by waiting until they are inundated by maximum amplitude high tides. Exposure to predators would be increased if females walked to the waterline to release larvae during other tidal phases. Species that live low on the shore or subtidally have greater flexibility in the timing of larval release relative to the tides, because refuges are inundated more often.

If synchronizing reproduction by the tides and other environmental cycles is adaptive, then deviations from timing patterns may alter fitness. Such deviations may be widespread because coastal marine species often range across tidal environments. Species may occur in as many as four tidal regimes along the Atlantic and Gulf coasts of the USA and would encounter considerable variation in the number, phasing and range of tides (see Barnwell, 1976, for review). Along the Atlantic coast, semidiurnal (two tidal cycles per day) tides prevail, and along the Gulf of Mexico mixed semidiurnal (usually two, but sometimes one tidal cycle per day), diurnal (one tidal cycle per day) mixed diurnal (usually one, but sometimes two tidal cycles per day) tides occur. In the semidiurnal tidal regime, the phase relationship between the tides and the light–dark cycle varies with a predictable semilunar period throughout the year. Large amplitude tides peak near dusk on new and full moons year-round. In the diurnal and mixed tidal regimes, maximum amplitude high tides primarily occur in daylight during summer months, and they coincide with new and full moons during some months and quarter moons during other months (Fig. 1). This occurs because tidal amplitude along the Gulf coast is controlled more by the declination of the moon than planetary alignment, which

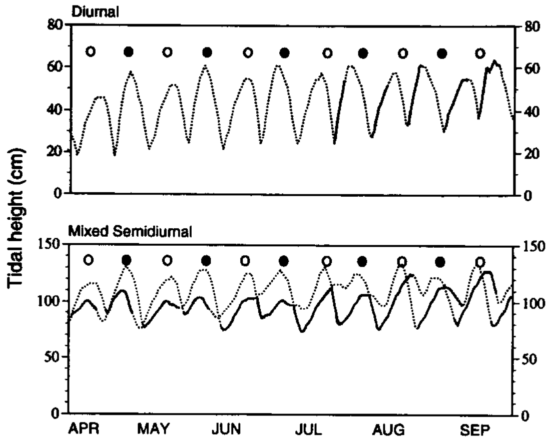

Fig. 1. Daily nocturnal (—) and diurnal (- - - -) predicted high tide relative to lunar phase (solid and open circles represent new and full moons, respectively) in the diurnal tidal regime at Mobile Bay, Alabama, and the mixed semidiurnal tidal regime at Florida State Marine Laboratory at Turkey Point, Florida, during 1989. Maximum amplitude high tides occurred during the day in both tidal regimes. Nocturnal high tides primarily occurred near minimum amplitude tides during most of the study period in the diurnal tidal regime, and they occurred during larger amplitude tides in the mixed semidiurnal tidal regime. See Fig. 2 for location of study sites.

gives rise to the semilunar cycle of new and full moons. Finally, tidal amplitudes range from about 1–4 m along the Atlantic coast but are only about 0.5 to 1 m along much of the Gulf coast.

The changing relationships of tides to light–dark and lunar cycles along shorelines may result in spatial and temporal variation in the timing of activities by coastal animals. The time of larval release by the same or sibling species of crabs differed in Pacific semidiurnal and Caribbean mixed semidiurnal tidal regimes along the coasts of Panama (Morgan and Christy, 1994). The spatial differences in reproductive timing may be genetically predetermined or phenotypically plastic. Animals along the Pacific and Caribbean coasts have been isolated since the isthmus of Panama last emerged two million years ago (Keigwin, 1982), perhaps providing sufficient time for crabs to adapt genetically to different tidal conditions. However, intraspecific variation in reproductive timing clearly occurred in the Caribbean, where the phasing of entraining environmental cycles changed during the year. A hierarchical arrangement of endogenous rhythms was proposed that enabled crabs to track complex changes in phase relationships among environmental cycles. Hierarchies of rhythms were revealed by the degree to which larval release remained in phase with each environmental cycle. Caribbean species that tracked tides throughout the year, necessarily released larvae at different times of the light–dark and lunar cycles. Conversely, species that kept phase with the light–dark cycle released larvae at different phases of the tidal and tidal amplitude cycles. This flexible timing system would enable crabs to synchronize reproduction as well as possible across a range of tidal environments, although reproductive success may vary.

The effect of tidal variation on biological timing largely remains unexplored primarily because semidiurnal tidal regimes prevail throughout much of the world (Barnwell, 1976). The purpose of this study was to determine whether or not changes in reproductive timing occur in three contiguous tidal regimes along the Atlantic and Gulf coasts of the USA. Reproductive synchrony by crabs has been well studied in semidiurnal tidal environments of the Atlantic coast, where the timing of larval release varies little among populations (see Morgan, 1995, for review). Although reproductive timing by crabs on the Gulf coast is poorly known, it should differ from that documented for crabs on the Atlantic coast. For instance, species that share the common pattern of releasing larvae on evening maximum amplitude high slack tides near new and full moons along the Atlantic coast (see Morgan, 1995, for review) should release larvae at other times on the Gulf coast. On the Gulf coast, maximum amplitude tides do not occur at night during most of the reproductive season and they are not always phased with new and full moons. Therefore, reproductive timing by crabs must change relative to at least one of the entraining environmental cycles. Larval release should either occur during maximum amplitude high tides in the daytime (light–dark phase shift) or during submaximal high tides before dawn (biweekly phase shift). Larval release also must keep phase with either the tidal amplitude or the lunar cycle. Variation in the timing of larval release relative to several entraining environmental cycles may indicate the relative dominance of rhythms controlling reproductive timing.

To determine whether reproductive timing varies among tidal regimes, the timing of larval release relative to tidal amplitude, lunar and light–dark cycles was examined for seven species of intertidal and shallow subtidal crabs occurring in adjacent diurnal or mixed semidiurnal tidal regimes along the northeastern Gulf of Mexico. Reproductive timing could be compared for three species or closely related species that occurred in both Gulf coast tidal regimes. Comparisons were also possible for five species pairs on the Gulf and Atlantic coasts.

2. Methods and materials

2.1. Field sites and collections

The timing of larval release was determined for six species of crabs that were collected from diurnal tidal environments in Mobile Bay, Alabama, and St. Joseph Bay (SJB), Florida (Fig. 2). *Eurypanopeus depressus* (Smith 1869), *Sesarma reticulatum* (Say 1817), *Sesarma cinereum* (Bosc 1802) and *Panopeus obesus* (Smith 1869) were collected from lower Mobile Bay in 1990. *Dyspanopeus texana* (Smith 1869) and *Dissodactylus mellitae* (Rathbun 1900) were collected at SJB in 1989. The timing of larval release also was determined for three species of crabs, *Eurypanopeus depressus*, *S. cinereum* and *Panopeus simpsoni* (Rathbun 1930), that were collected from a mixed semidiurnal tidal regime at Florida State Marine Laboratory (FSU) in 1989 (Fig. 2).

Eurypanopeus depressus was collected by overturning stones and oyster shells at Cedar Point and at Airport Marsh on Dauphin Island, Alabama, and at FSU. *Sesarma reticulatum* was collected by digging burrows in marshes of Fowl River, Alabama. *Sesarma cinereum* was collected at night from seawalls and rocks on Dauphin Island and

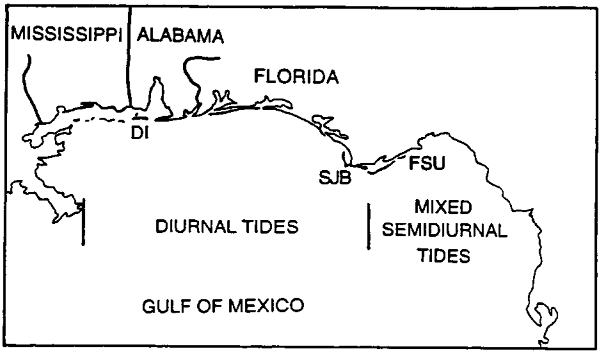

Fig. 2. Locations of study sites in diurnal and mixed semidiurnal tidal regimes along the northeastern Gulf of Mexico: Dauphin Island (DI), Alabama, St. Joseph Bay (SJB), Florida, and Florida State Marine Laboratory (FSU) at Turkey Point, Florida.

from *Spartina alterniflora* marshes at FSU. *Panopeus obesus* was collected by digging burrows that were situated beneath oysters along seaward edges of salt marshes on Dauphin Island and Little Dauphin Island. *Dyspanopeus texana* was collected from beneath rocks, oysters and ascidians in seagrass meadows at SJB State Park. *Dissodactylus mellitae* was collected from sand dollars, *Mellita quinquiesperforata*, that were captured from shallow, subtidal sand flats at SJB State Park. *Panopeus simpsoni* was collected by overturning oyster shells and stones during daytime low tides at FSU.

Sesarma cinereum was collected near nocturnal high tides and *D. mellitae* was collected during the daytime regardless of tides. All other species were collected during daytime low tides.

2.2. Determination of the timing of larval release

Females that were collected in Alabama were held in seawater tables at the Dauphin Island Sea Laboratory, and those from Florida were held in seawater tables at FSU. The timing of larval release by all species was determined by holding ovigerous females individually in the compartments (4.5 × 4 × 4 cm) of plastic trays at ambient seawater and light conditions, and crabs were checked daily for larval release. Seawater in trays was changed daily, and ovigers were not fed. Females infrequently released larvae on two consecutive days, and these females were scored as releasing larvae on the first day. This method yields accurate estimates of hatching patterns relative to lunar and tidal amplitude cycles as long as crabs are maintained at ambient conditions, because the date of larval release is determined once eggs are spawned (Christy, 1982, 1986; DeCoursey, 1983, Salmon et al., 1986; Morgan and Christy, 1994, 1995). Numbers of collecting trips, numbers of crabs collected, numbers of days that crabs were observed and months that crabs were observed are presented in Table 1.

To determine whether crabs released larvae during the day or night, trays were checked for larvae shortly after sunrise and before sunset until eggs of all females hatched. The timing of larval release relative to the light–dark cycle was determined for

Table 1
Numbers of collections made, numbers of ovigerous crabs collected, numbers of days that crabs were observed and months that crabs were observed in determining the timing of larval release relative to tidal amplitude, lunar and light–dark cycles for six species from diurnal and mixed semidiurnal tidal regimes along the northeastern Gulf of Mexico during summers of 1989 and 1990

Species	Family	Tidal amplitude/lunar cycles				Light–dark cycle			
		Collections	Crabs	Days	Months	Collections	Crabs	Days	Months
(a) Diurnal tidal regime									
Eurypanopeus depressus	Xanthidae	8	276	74	Jun–Sep	3	167	30	Jun–Aug
Sesarma reticulatum	Grapsidae	4	109	57	Jun–Sep	3	78	41	Jun–Aug
Dyspanopeus texana	Xanthidae	3	96	30	May–Jun	3	94	22	May–Jun
Dissodactylus mellitae	Pinnotheridae	3	92	33	May–Jun	2	91	22	May–Jun
Sesarma cinereum	Grapsidae	5	120	58	Jun–Aug	4	97	40	Jun–Aug
Panopeus obesus	Xanthidae	2	37	20	Jun, Sep	2	32	16	Jun, Sep
(b) Mixed semidiurnal tidal regime									
Eurypanopeus depressus	Xanthidae	5	309	50	Jul–Sep	2	96	17	Jul
Sesarma cinereum	Grapsidae	1	67	12	Aug	1	14	12	Aug
Panopeus simpsoni	Xanthidae	5	95	53	Jun–Sep	2	15	19	Jul

The timing of larval release relative to the light–dark cycle was determined for subsets of crabs used to determine biweekly periodicities.

subsets of crabs used to determine biweekly periodicities (Table 1), because time constraints precluded checking for larval release twice each day during the lengthy study. The timing of larval release relative to the tidal cycle was not determined because this is best done in situ where tides reinforce rhythms (Christy, 1986; Salmon et al., 1986; Morgan and Christy, 1994, 1995).

2.3. Data analysis

Along the Gulf coast, tidal amplitude cycles with the declination of the moon twice each tropical month (27.32 days), and new and full moons occur each lunar month (29.53 days) (Barnwell, 1976). Therefore, data were divided into 14 and 15 d periods before Rayleigh's *r*-statistic was used to detect peaks in timing of larval release relative to lunar and tidal amplitude cycles (Zar, 1974). This test is appropriate for analysis of biological rhythms when periods of cycles are predetermined. The test compared the magnitude of the *r*-statistic, which is a measure of the temporal concentration of release times ranging from 0 to 1, to that expected if crabs released larvae uniformly during a given physical cycle. If the *r*-statistic was significantly large, then the mean angle and angular deviation of the distribution identified the peak time and dispersion of larval release (reported as $d \pm 1$ SD in Table 2). The chi-square test determined whether most females released larvae during day or night.

The timing of larval release by *E. depressus, S. cinereum* and a congeneric pair of species, *P. obesus* and *P. simpsoni*, in diurnal and mixed semidiurnal tidal regimes was compared to determine whether or not reproductive timing differed in the two tidal regimes. The nonparametric Watson–Williams test was used to detect differences in the timing of larval release relative to tidal amplitude and lunar cycles in the two tidal regimes (Zar, 1974). The number of days separating the time of peak larval release from maximum amplitude tides and new and full moons in these tidal regimes indicated whether larval release was better synchronized with the tidal amplitude or lunar cycle. The *G*-test determined whether the number of females releasing larvae during daylight and darkness differed between tidal regimes (Sokal and Rohlf, 1981).

3. Results

Two patterns of larval release were evident for crabs from diurnal tidal regimes. Larval release by four species, *S. reticulatum, E. depressus, D. texana* and *D. mellitae,* peaked biweekly on maximum amplitude tropic tides and within 2 days of new and full moons (Fig. 3, Table 2). These species commonly released larvae during the daytime and nighttime (Fig. 4, Table 2). Two species, *S. cinereum* and *P. obesus,* primarily released larvae near minimum amplitude equatorial tides (Fig. 3, Table 2) at night (Fig. 4, Table 2). *Sesarma cinereum* released larvae asynchronously relative to the lunar cycle, and *P. obesus* mostly released larvae midway between quarter moons and new/full moons (Fig. 3, Table 2).

In the mixed semidiurnal tidal regime, larval release by *Eurypanopeus depressus* peaked 2 days after new and full moons, when maximum amplitude tides occurred

Table 2
Timing of larval release relative to tidal amplitude (day ± 1 SD), lunar (day ± 1 SD) and light–dark cycles of six species of crabs from a diurnal tidal regime and three species from a mixed semidiurnal tidal regime in the northeastern Gulf of Mexico

		Tidal amplitude cycle			Lunar cycle			Light–dark cycle	
Species		Timing	SD	r	Timing	SD	r	Timing	χ^2
(a) Diurnal tidal regime									
Eurypanopeus depressus		MAT	4.6	0.12*	1d < O	3.6	0.32***	Day–Night	1.01^{ns}
Sesarma reticulatum		MAT	2.6	0.51***	2d < O	3.2	0.40***	Day–Night	3.00^{ns}
Dyspanopeus texana		MAT	2.7	0.49***	O < 2day	2.6	0.56***	Day–Night	1.53^{ns}
Dissodactylus mellitae		MAT	2.7	0.47***	O < 2day	2.7	0.54***	Day–Night	1.86^{ns}
Sesarma cinereum		6day < MAT	3.7	0.25***	Asynchronous	5.0	0.11^{ns}	Night	61.12***
Panopeus obesus		5day < MAT	2.0	0.66***	4day < O	1.7	0.77***	Night	18.00***
(b) Mixed semidiurnal tidal regime									
Eurypanopeus depressus	Day	MAT	2.9	0.42***	O < 2days	3.3	0.38***	Day–Night	0.04^{ns}
	Night	4day < LAT	2.9	0.43***					
Sesarma cinereum	Day	MAT < 5day	3.9	0.24***	O < 6days	3.7	0.30***	Night	11.27***
	Night	1day < LAT	3.9	0.24***					
Panopeus simpsoni	Day	MAT < 2day	2.7	0.50***	O < 3days	2.9	0.47***	Night	10.29**
	Night	1day < LAT	2.8	0.48***					

Larval release in the diurnal tidal regime was shown relative to maximum amplitude high tide (MAT), which usually occurred during the daytime. In the mixed semidiurnal tidal regime, larval release was shown relative to daytime maximum amplitude high tides (Day MAT) and the largest amplitude nocturnal high tides (Night LAT) (See Fig. 1). O = new and full moons; ns = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$ for Rayleigh's r and chi-square statistics. See Table 1 for sample sizes.

Table 3
Timing of larval release relative to tidal amplitude, lunar, tidal and light–dark cycles by *the same species or closely related species of crabs in a semidiurnal tidal* regime along the Atlantic coast and in mixed semidiurnal and diurnal tidal regimes along the northeastern Gulf coast of the USA

Species	Tidal regime	Timing of larval release				References
		Tidal amplitude	Lunar	Tidal	Light–dark	
Group 1: Biweekly rhythms dominant						
Eurypanopeus depressus	Semidiurnal	MAT	O	High	Night	Christy and Stancyk, 1982
	Mixed semidiurnal	MAT	O < 2 d	–	Day–Night	
	Diurnal	MAT	1d < O	–	Day–Night	
Sesarma reticulatum	Semidiurnal	MAT	O	High	Night	Seiple, 1979; Christy and Stancyk, 1982
	Diurnal	MAT	2d < O	–	Day–Night	Hovel, 1995
Dyspanopeus sayi	Semidiurnal	MAT	O	High	Night	Salmon et al., 1986; De Vries and Forward, 1989
Dyspanopeus texana	Diurnal	MAT	O < 2 d	–	Day–Night	Hovel, 1995
Group 2: Circadian rhythms dominant						
Sesarma cinereum	Semidiurnal	MAT	O	High	Night	Seiple, 1979; Dollard, 1980; Christy and Stancyk, 1982
	Mixed semidiurnal	LAT (intermediate)	O < 6 d	–	Night (Day)	De Vries and Forward, 1989
	Diurnal	LAT (minimum)	Asynchronous	–	Night (Day)	
Panopeus herbstii	Semidiurnal	MAT	O	High	Night	Christy and Stancyk, 1982; Salmon et al., 1986
Panopeus simpsoni	Mixed semidiurnal	LAT (intermediate)	3 d < O	–	Night (Day)	
Panopeus obesus	Diurnal	LAT (minimum)	4 d < O	–	Night (Day)	

Species are grouped by the relative dominance of biweekly (tidal amplitude = 13.7 days, lunar = 14.8 d) and circadian (24 h) rhythms regulating the timing of larval release. MAT = maximum amplitude tide; LAT = largest amplitude nocturnal high tide, which is of minimal and intermediate amplitude in diurnal and mixed semidiurnal tidal regimes, respectively; O = new and full moons; (Day) = uncommon release during the daytime. Published references document reproductive timing in the semidiurnal tidal regime. Biweekly periodicity recently was documented for *Dyspanopeus sayi* by Hovel (1995), but see Salmon et al. (1986) and De Vries and Forward (1989).

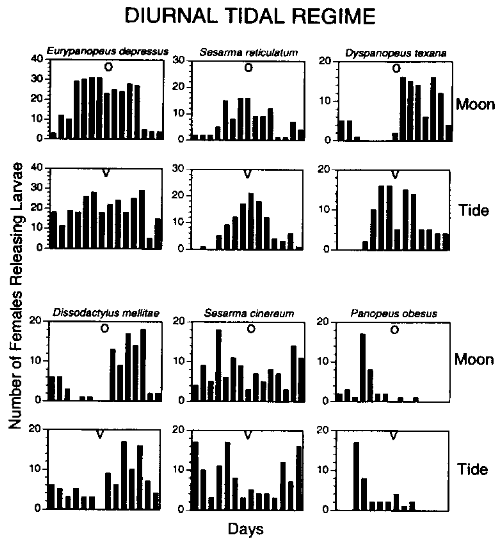

Fig. 3. Timing of larval release relative to predicted lunar and tidal amplitude cycles by six species of crabs in a diurnal tidal regime. *Eurypanopeus depressus*, *Sesarma reticulatum*, *Sesarma cinereum* and *Panopeus obesus* were collected from Mobile Bay, Alabama and were observed from June through September 1990. *Dyspanopeus texana* and *Dissodactylus mellitae* were collected near Florida State Marine Laboratory and were studied from mid-May through June 1989. See Table 1 for numbers of collecting trips, numbers of crabs collected, numbers of days that crabs were observed and months that crabs were observed. New and full moons (circle) and large amplitude tides (inverted triangle) occur at the midpoints of 15 d lunar and 14 d tidal cycles, respectively.

during the daytime and smaller amplitude tides occurred at night (Fig. 5, Table 2). *E. depressus* often released larvae during the daytime and nighttime (Fig. 4, Table 2). The timing of larval release relative to the lunar cycle differed significantly in diurnal and mixed semidiurnal tidal regimes ($F = 56.82$; df $= 1, 583$; $P < 0.001$), but it did not differ relative to the time of maximum amplitude tide ($F = 3.38$; df $= 1, 583$; $P > 0.05$). Similar numbers of females released larvae during daytime and nighttime in the two tidal regimes ($G = 0.30$; df $= 1, 1$; $P > 0.05$).

Larval release by *S. cinereum* and *P. simpsoni* in the mixed semidiurnal tidal regime peaked one day before the largest amplitude nocturnal tides (Fig. 5, Table 2). The timing of larval release relative to maximum amplitude daytime tides and lunar phase differed for the two species (Table 2), which were observed during different months. Larval release relative to maximum amplitude tides and lunar phase also differed significantly between tidal regimes for both *S. cinereum* (maximum amplitude tides: $F = 20.71$; df $= 1, 185$; $P < 0.001$; lunar phase: $F = 78.85$; df $= 1, 185$; $P < 0.001$) and *P. simpsoni* (maximum amplitude tides: $F = 222.75$; df $= 1, 130$; $P < 0.001$; lunar phase: $F = 300.07$; df $= 1, 130$; $P < 0.001$). Both species primarily released larvae at night (Fig. 4, Table 2), and the frequency of nocturnal release was similar in the two tidal regimes for both *S. cinereum* ($G = 0.13$; df $= 1, 1$; $P > 0.05$) and *P. simpsoni* ($G = 0.35$; df $= 1, 1$; $P > 0.05$).

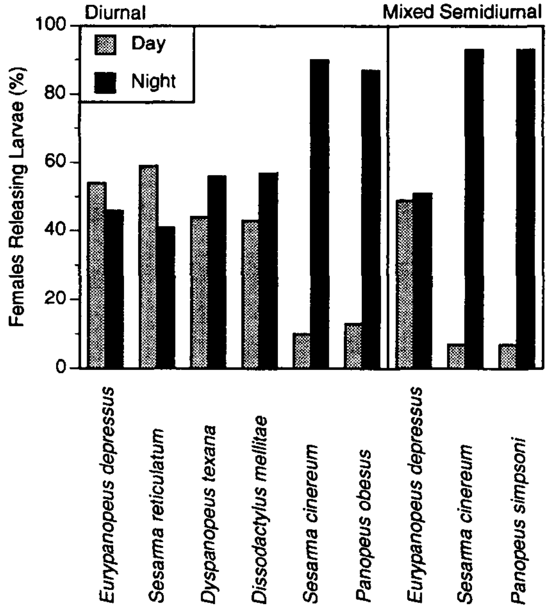

Fig. 4. Percentage of females releasing larvae during daytime and nighttime for six species of crabs from a diurnal tidal regime and three species from a mixed semidiurnal tidal regime along the coasts of Alabama and northwestern Florida. See Table 1 for numbers of collecting trips, numbers of crabs collected, numbers of days that crabs were observed and months that crabs were observed.

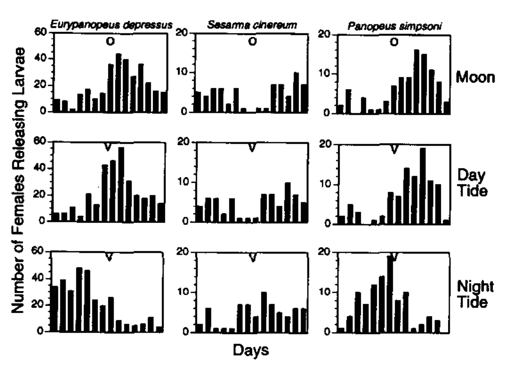

Fig. 5. Timing of larval release relative to predicted lunar and tidal amplitude cycles by three species of crabs from a mixed semidiurnal tidal regime at Florida State Marine Laboratory from June through mid-September 1989. See Table 1 for numbers of collecting trips, numbers of crabs collected, numbers of days that crabs were observed and months that crabs were observed. New and full moons (circle) and large amplitude tides (inverted triangle) occur at the midpoints of 15 d lunar and 14 d tidal cycles, respectively. Larval release is shown relative to daytime maximum amplitude high tides (Day MAT) and the largest amplitude nocturnal high tides (Night LAT) (See Fig. 1).

4. Discussion

The timing of larval release by crabs varied considerably between the Atlantic and Gulf coasts of the USA. In the semidiurnal tidal regime along the Atlantic coast, peak larval release by five species occurred during nocturnal maximum amplitude high tides near new and full moons (Table 3). The same species or closely related species in diurnal and mixed semidiurnal tidal regimes along the Gulf coast released larvae at other times (Table 3). All Gulf coast crabs released larvae during the daytime, and several species (*E. depressus, S. reticulatum, D. texana*) did so often. In addition, peak larval release by several species (*S. cinereum, P. simpsoni, P. obesus*) along the Gulf coast occurred at different phases of the lunar and tidal amplitude cycles.

The variation in reproductive timing between Atlantic and Gulf coast crabs arose because nocturnal maximum amplitude high tides do not occur along the Gulf coast during most of the summer (Fig. 1). In the diurnal and mixed semidiurnal tidal regimes, crabs either released larvae near maximum amplitude tides during the daytime or submaximal tides at night. Larval release by four species (*E. depressus, S. reticulatum, D. texana, D. mellitae*) peaked during maximum amplitude tides, and larval release by three species (*S. cinereum, P. simpsoni, P. obesus*) peaked near the largest amplitude nocturnal tides. The first group of crabs often may have released larvae in daylight, because high tides primarily occurred after dawn on those days. These species, like all other crabs studied worldwide (see Morgan, 1995 for review), probably released larvae during high tide. Larval release by the second group occurred primarily in darkness when the largest amplitude nocturnal high tides occurred near dawn. Thus, the first group of species released larvae on maximum amplitude tides and forsaked releasing larvae only at night, and the second group primarily released larvae at night and forsaked releasing larvae on maximum amplitude tides.

The timing of larval release by *E. depressus* changed little between the two Gulf coast tidal regimes (Table 3), because maximum amplitude high tides occurred during the daytime and lower amplitude tides occurred at night in both tidal regimes (Fig. 1). In contrast, the timing of larval release relative to the tidal amplitude, lunar and perhaps the tidal cycle by several other species (*S. cinereum, P. simpsoni, P. obesus*) differed in the two tidal regimes (Table 3), because the time of the largest amplitude high tides changed relative to the light–dark cycle (Fig. 1). Peak larval release occurred near minimum amplitude tides in the diurnal tidal regime and during larger amplitude tides in the mixed semidiurnal tidal regime. These differences arose because nocturnal high slack tides occurred near minimum amplitude tides during most of the reproductive season in the diurnal tidal regime, but they occurred everyday in the mixed semidiurnal tidal regime enabling larvae to be released during large amplitude tides. Reproductive timing also may have differed relative to the tidal cycle. Before mid-July in the diurnal tidal regime, high slack tides occurred soon after dawn on the days following minimum amplitude tides. Because larvae were commonly released in darkness on these days, they probably were released during late flood tides just before dawn. Finally, the timing of larval release relative to lunar phase differed geographically for *S. cinereum*, because the largest amplitude nocturnal high tides occurred at different phases of the moon in the two tidal regimes. The similar timing of larval release relative to the lunar cycle by *P.*

simpsoni and *P. obesus* in these regimes was coincidental, because *P. obesus* was observed only briefly (Table 1).

All of the species examined in two or more tidal regimes released larvae on the largest amplitude tides available, depending on the relative dominance of circadian and biweekly rhythms (Table 3). All crabs belonging to the first group (*E. depressus, S. reticulatum, D. sayi, D. texana*) released larvae on maximum amplitude tides in the three tidal regimes, and all crabs in the second group (*S. cinereum, P. herbstii, P. simpsoni, P. obesus*) released larvae near the largest amplitude tides occurring in darkness. Therefore, reproductive timing by all species was related to the tidal amplitude cycle. In contrast, the timing of larval release relative to the lunar cycle by the second group of crabs changed (Table 3) suggesting that lunar phase did not entrain biweekly rhythms in reproduction. The timing of larval release relative to lunar phase did not change for the first group of crabs, because maximum amplitude tides coincided with new and full moons during the study period. Cues associated with the tidal amplitude cycle also most likely entrain biweekly rhythms in reproduction by several other intertidal and subtidal species of crabs (Morgan and Christy, 1994) and killifish, *Fundulus grandis* (Hsiao and Meier, 1989). Biweekly rhythms may be entrained by moonlight for semiterrestrial species that live above the tide line (Saigusa, 1988).

Thus, variation in the timing of larval release revealed different hierarchies of rhythms regulating reproductive timing. The first group kept phase with the tidal amplitude cycle regardless of the light–dark cycle, and the second group tracked the light–dark cycle over the tidal amplitude cycle. At least some species in both groups did not appear to time biweekly rhythms in reproduction by lunar phase. Hence, the relative importance, in descending order, of environmental cycles for the timing of larval release by the first group appeared to be: tidal amplitude, light–dark and lunar cycles. The relative importance of physical cycles for the second group appeared to be: light–dark, tidal amplitude and lunar cycles.

Temporal changes in reproductive timing may have occurred because the phasing of entraining environmental cycles shifted during the summer (Morgan and Christy, 1994). In the diurnal tidal regime, maximum amplitude high tides occurred during the daytime in June and at night in September (Fig. 1). Therefore, all species studied were able to release larvae during nocturnal maximum amplitude high tides late in the reproductive season, as they do all summer long on the Atlantic coast (Table 3). Temporal changes were not detected primarily due to insufficient sampling in September, but they were observed for *Uca pugilator* on the Gulf coast (Morgan, 1996).

Variable winds did not appear to alter the timing of larval release relative to the tides. Winds generally were light and blew onshore, which forced water higher on the shore than when the wind switched direction and blew offshore (Morgan et al., 1996). Despite the unpredictable fluctuations in water level, the timing of larval release remained in phase with small amplitude tides in both the Gulf and Caribbean (Morgan and Christy, 1994).

If releasing larvae on maximum amplitude high tides at night along the Atlantic coast reduces predation (see Morgan and Christy, 1995), then predation may be greater along the Gulf coast. On the Gulf coast, larvae may be released either under the cover of darkness or when intertidal refuges are inundated and tides rapidly transport larvae from shorelines. The dominant circadian rhythms of species in Group 2 may ensure that larvae are released under the cover of darkness in all tidal environments, and the dominant tidal amplitude rhythms of species in Group 1 ensure that larvae are released near refuges by high intertidal species and are swept rapidly away from shorelines. This adaptive scenario correctly predicted the dominance of tidal amplitude rhythms for *S. reticulatum*, which released larvae near burrows high on the shore. Other species may release larvae during lower amplitude tides, because they either released larvae lower on the shore or walked from burrows above the tide line to release larvae in water (*S. cinereum*). The paradigm also predicts that highly conspicuous larvae in clear tropical waters should be released only under the cover of darkness, and therefore circadian rhythms should dominate over tidal amplitude rhythms in such species (Morgan and Christy, 1994, 1995). However, morphological defenses are important in turbid temperate waters (Morgan, 1987, 1989, 1990), and predicting whether circadian or tidal amplitude rhythms should dominate based on larval traits currently is too tenuous for Gulf coast species.

In conclusion, crabs previously had been found to release larvae only at night because they primarily were studied in temperate semidiurnal tidal environments (see Morgan, 1995, for review). Recent studies in other tidal environments (see also Christy, 1986; Morgan and Christy, 1994, 1995) have shown that 12 of 46 species are now known to release larvae in daylight (see, Morgan, 1995, for review). The lunar cycle formerly was believed to entrain biweekly peaks in reproduction, but the tidal amplitude cycle has entrained rhythms by all five species of intertidal and subtidal crabs studied in two or more tidal regimes (see also Morgan and Christy, 1994). Furthermore, reproductive timing by all species of crabs studied across tidal regimes changed relative to one or more environmental cycles, and the timing of other activities by coastal animals also may vary. Thus, studying organisms in several tidal environments may reveal intraspecific variation in the timing of activities, proximate and ultimate causes of the timing, and the nature of biological timing systems in marine organisms.

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