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Weak synchrony in the timing of larval release in upwelling regimes

Steven G. Morgan[1,2,*], J. Wilson White[1,5], Skyli T. McAfee[1,6], Steven D. Gaines[3,4], Russell J. Schmitt[3,5]

[1]Bodega Marine Laboratory, University of California Davis, 2099 Westside Drive, Bodega Bay, California 94923-0247, USA

[2]Department of Environmental Science and Policy, University of California Davis, 1 Shields Avenue, Davis, California 93510, USA

[3]Department of Ecology, Evolution and Marine Biology, University of California Santa Barbara, California 93106, USA

[4]Bren School of Environmental Science and Management, University of California Santa Barbara, California 93106, USA

[5]*Present address:* Department of Biology and Marine Biology, University of North Carolina, 601 South College Road, Wilmington, North Carolina 28403-5915, USA

[6]*Present address:* California Ocean Science Trust, 1330 Broadway, Suite 1135, Oakland, California 94612, USA

ABSTRACT: Intertidal crabs in diverse habitats worldwide release larvae synchronously during nocturnal spring high tides. This expedites seaward transport of the larvae to beyond high density areas of predatory fishes under the cover of darkness. We found that 4 species of intertidal crabs along the west coast of the USA shared this reproductive timing pattern. As in other mixed semidiurnal tidal regimes, biweekly patterns of larval release were more closely synchronized with the tidal amplitude cycle than the lunar cycle, and some crabs released larvae in daylight. However, unlike other places in the world, larval release was weakly synchronized to environmental cycles regardless of interspecific differences in vertical distributions on the shore. We provide evidence that weak synchrony in the timing of larval release in upwelling regimes can result from exposure to environmental variation over long incubation periods of externally brooded embryos. According to the prevailing paradigm, weaker synchrony in the timing of larval release will increase predation by planktivorous fishes in upwelling regimes. Weak synchrony in the timing of larval release should increase larval mortality in a wide array of animals that brood embryos in the intertidal zone, regardless of the selective force operating, and it could contribute to recruitment limitation in upwelling regimes.

KEY WORDS: Larval release · Hatching · Endogenous rhythms · Upwelling · Fish predation · Larvae

INTRODUCTION

Synchronous bursts of reproduction typically punctuate the lives of plants and animals in response to predictable variation in survival of offspring during environmental cycles (Ims 1990). Seasonal and interannual synchrony have received considerable attention, including spectacular examples of masting by trees, 17 yr cycles of cicadas and mass spawning by corals (Rathcke & Lacey 1985, Babcock et al. 1986, Taylor & Karban 1986). Seasonal variation in reproductive synchrony usually places offspring in favorable environmental conditions, such as desirable levels of temperature, light, rainfall or food (Rathcke & Lacey 1985, Giese & Kanatani 1987). Intraseasonal variation in reproductive synchrony relative to the daily cycle of sunlight (24 h) and monthly cycle of moonlight (29.6 d) is most commonly attributed to avoiding or swamping predators (Johannes 1978, Ims 1990).

In addition to synchronizing with diel and lunar cycles, larval release by coastal marine organisms is timed to different phases of the tides, including semi-

*Email: sgmorgan@ucdavis.edu

daily (12.4 h) or daily (24.8 h) cycles of tidal height and the biweekly cycle of tidal amplitude (14.8 d; Korringa 1947, Giese & Kanatani 1987, Saigusa et al. 2003, Skov et al. 2005, Morgan 2007). Coastal organisms display a diverse array of timing patterns and synchronize reproduction to coincide with different phases of one or more of these environmental cycles (Forward 1987, Robertson et al. 1990, Morgan 1995, 2007, Palmer 1995, Schmitt & Holbrook 1999).

Despite considerable differences in life histories, a common paradigm has emerged for the adaptive significance of reproductive synchrony by coral reef fishes and intertidal crabs. Predation by planktivorous fishes is a strong selective pressure on larvae (Morgan 1987a, 1989, 1992, Morgan & Christy 1996, Morgan & Anastasia 2008), and many species release most gametes or larvae during nocturnal maximum-amplitude high tides (Johannes 1978, Christy 1982, Robertson et al. 1990, Morgan 1995, Thurman 2004). This common timing pattern occurs even in regions where the tidal amplitude and lunar cycles do not coincide, indicating that most crabs track cues that are associated with the tides rather than moonlight (Morgan & Christy 1994, Morgan 1995, 1996a,b, Kellmeyer & Salmon 2001). During this narrow window, adults, embryos or larvae are least likely to be seen by predatory fishes because they are rapidly transported away from nearshore coastal areas that generally harbor more predators than do offshore waters (Johannes 1978, Christy 1982, Morgan 1990, Morgan & Christy 1995, Hovel & Morgan 1997). Intertidal crabs remain near burrows to release larvae, and consequently, species that live high on the shore are constrained to release larvae when they are inundated by maximum amplitude tides. However, many species that live low on the shore and are inundated every day also release larvae during maximum-amplitude high tides (Christy 1986, Morgan & Christy 1995, Morgan 1995, 1996a, Thurman 2004). The few species that do not release larvae at the safest time, during nocturnal maximum-amplitude high tides, are pigmented so they are inconspicuous and less vulnerable to planktivorous fishes (Morgan 1995, Morgan & Christy 1995, 1997, Gove & Mambonhe 2000, Hsueh 2002). Larvae also recruit to adult habitats during a safe period during nocturnal spring flood tides (Christy & Morgan 1998, Paula et al. 2004). Thus, a wide variety of coastal crabs from tropical and temperate regions synchronize larval release and recruitment to occur during safe periods of diminished fish predation.

There is little information on the timing of larval release from strong upwelling regions along the western margins of continents (Morgan 1995, Christy 2003, Thurman 2004). The timing of peak reproduction around the safe period should be maintained there, provided that predatory fishes are as strong a selective force as they are elsewhere in the world. However, reproductive synchrony by intertidal crabs could be much weaker in upwelling regions, thus increasing the risk of fish predation (Christy 2003). Reproductive seasons are protracted in upwelling regimes (Morris et al. 1980), and intraseasonal synchrony in the timing of larval release also may be much less pronounced. Development times for externally brooded embryos of intertidal crabs are typically <2 wk in warm regions of the world (e.g. DeCoursey 1983, Morgan & Christy 1995, Morgan 1996b), whereas they probably are much longer in upwelling regimes. Upwelled water and fog keep water and air temperatures cold year-round, which lengthens embryonic development times. Long incubation times increase potential exposure to a wide range of temperatures, especially during low tide, which could result in higher variance in development time and thus weaker synchrony in the timing of larval release. Female crabs in warm upwelling regions appear to adjust the timing of fertilization, regulate their depth in burrows and choose the width of burrows during courtship to compensate for variation in development rates of embryos arising from small changes in temperature (Christy et al. 2001, Reaney & Backwell 2007). However, these compensatory behaviors may be less effective when cold temperatures lengthen incubation periods, especially for species that live in depressions under rocks rather than in burrows (Christy 2003). Weaker synchrony in larval release also may result from large waves obscuring tidal cycles along rocky shores (Flores & Paula 2002). Weak synchrony around the safe period in upwelling regions should reduce fitness by increasing fish predation.

Variation in the strength and persistence of upwelling along the coast may also affect the degree of reproductive synchrony around the safe period. Along the coast of California, upwelling is stronger and more persistent north of San Francisco Bay than farther south. This spatial variability already has been found to affect the evolution of seasonal patterns of reproductive timing by fishes and crabs in the region (Parrish et al. 1981, Shanks & Eckert 2005). The colder temperatures in the strong, persistent upwelling regions of northern California could result in weaker synchrony and greater predation than observed in southern California by increasing exposure to variable air and water temperatures over longer incubation periods.

The purpose of this study was to determine the degree and timing of intraspecific reproductive synchrony by 4 common species of intertidal crabs that reside in a mixed semidiurnal tidal regime (usually 2 but sometimes 1 tide per day) along the upwelling coast of California. Our specific objectives were to

determine whether the synchrony and timing of larval release were (1) similar to patterns described elsewhere in the world, (2) affected by variation in upwelling intensity along the coast and (3) influenced by variable water and air temperatures during long incubation periods. We expected that the timing of larval release would be synchronized with nocturnal maximum spring tides to avoid planktivory, but that larval release would be more weakly synchronized than in tropical and other temperate regions. In addition, we expected incubation periods to be longer and reproductive synchrony to be weaker in northern than in southern and central California, where waters are warmer. Determining the extent of variation in the synchrony and timing of larval release relative to the safe period is the first step in evaluating the likely fitness consequences in upwelling regimes.

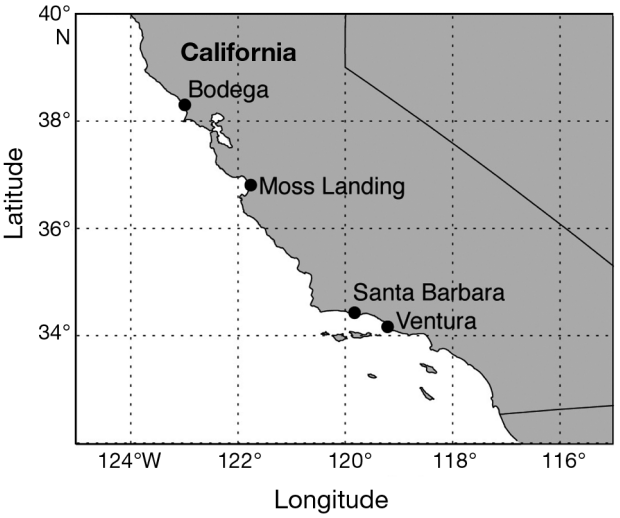

Fig. 1. The 4 crab collection sites along the coast of California

MATERIALS AND METHODS

Determining the timing and synchrony of larval release. The lined shore crab *Pachygrapsus crassipes* occurs in the high intertidal zone of rocky shores and salt marshes, the purple shore crab *Hemigrapsus nudus* and porcelain crab *Petrolisthes cinctipes* both occur in the midintertidal zone of rocky shores and the yellow shore crab *Hemigrapsus oregonensis* occurs from the lower intertidal to the subtidal zone in estuaries. We collected all ovigerous crabs in northern California from the rocky shores of Bodega Harbor or the adjacent open coast, and we collected ovigers from several locations in southern and central California (Fig. 1). *P. cinctipes* was collected from boulder fields and mussel beds between Ventura and Santa Barbara (southern California), *P. crassipes* was collected from the jetty at the Channel Islands Harbor entrance (southern California) and *H. nudus* and *H. oregonensis* were collected from Elkhorn Slough near the entrance to Moss Landing Harbor (central California). All crabs were collected during low tides either from underneath overturned stones during the daytime or with the use of a flashlight at night to immobilize them. Time periods, numbers of ovigerous crabs and numbers of days that crabs were observed are presented in Table 1.

Because all intertidal crabs release larvae during high tide while they are inundated (Forward 1987, Morgan 1995, Thurman 2004), we focused on determining the timing of larval release relative to the other 3 environmental cycles (diel, tidal amplitude, lunar) by means of a method that is conducive to long-term monitoring. Ovigerous females that were collected in northern California were held in uncov-

Table 1. Locations, time period, numbers of ovigerous crabs observed and numbers of days that crabs were observed in determining the timing of larval release relative to tidal amplitude (TA), lunar and diel cycles for 4 species from along the coast of California in 1997, 2000 and 2001. The timing of larval release relative to the diel cycle was determined for subsets of crabs used to determine biweekly periodicities

Species	Family	Location	Observation period	Days		Crabs	
				TA/lunar	Diel	Collections	No.
Petrolisthes cinctipes	Porcellanidae	Bodega Bay	6 Mar–8 Aug 2001	157	152	3	365
		Ventura–Santa Barbara	18 Mar–10 May 1997	54	10	2	82
		Ventura–Santa Barbara	26 Jun–28 Jul 1997	32	1	1	75
Hemigrapsus oregonensis	Grapsidae	Bodega Bay	11 Dec 2000–21 May 2001	162	162	4	256
		Elkhorn Slough	16 Mar–25 May 1997	71	39	1	97
Hemigrapsus nudus	Grapsidae	Bodega Bay	7 Mar–5 Jul 2001	121	121	4	101
		Elkhorn Slough	8 Jul–4 Aug 1997	28	10	1	60
Pachygrapsus crassipes	Grapsidae	Bodega Bay	13 Jul–5 Sep 2001	55	34	1	54
		Ventura	26 Jun–22 Jul 1997	27	1	1	38

ered, outdoor, flow-through seawater tables at Bodega Marine Laboratory (BML), and those from southern California were held in covered, flow-through seawater tables at the Marine Science Institute (MSI) in Santa Barbara. Plastic mesh covered the tanks at BML to shade crabs from direct sunlight by ~25% because these species typically remain under rocks during the daytime. We determined the timing of larval release by all species by holding ovigerous females individually at ambient seawater and light conditions. Large crabs were held in culture dishes (14.0 or 22.9 cm diameter), and small crabs were held in the compartments (4.5 × 4 × 4 cm) of plastic trays. Crabs were checked daily for larval release when seawater in the containers was changed. Females infrequently released larvae on 2 consecutive days, and these females were scored as releasing larvae on the first day. Females that released larvae were returned to the collection site and were occasionally replenished with newly collected ovigerous females.

This method yields accurate estimates of hatching patterns relative to lunar and tidal amplitude cycles, because the date of larval release is established once embryos are spawned as long as crabs are maintained at ambient temperatures. The efficacy of this method has been demonstrated previously for many crab species in a range of tidal and upwelling regimes by comparing hatching patterns in trays to those determined *in situ* (Salmon et al. 1986, Morgan & Christy 1994, 1995, Morgan 1996a). Crabs often were checked shortly after sunrise and before sunset to determine whether they released larvae during the day or night.

The duration of the incubation period for each species was estimated by determining the maximum time that crabs brooded embryos under ambient conditions. Estimates of the incubation periods improved when large numbers of crabs were collected because the probability of capturing females bearing newly spawned embryos increased.

Data analysis. ***Synchrony relative to environmental cycles:*** The predicted difference between the maximum range between a high and low tide was calculated for each day of the observation period by means of NOAA tide tables for each crab collection site. Rayleigh's test was used to detect peaks in timing of larval release relative to both lunar and tidal amplitude cycles. Data were divided into 14 d periods to determine the timing of larval release relative to the tidal amplitude cycle and 15 d periods for the semilunar cycle. Values of Rayleigh's test depend on sample size and are not comparable among different observation periods. Instead, this test detected the degree of synchrony in larval release and the timing relative to tidal amplitude and lunar cycles. A higher r-value and lower magnitude for one environmental cycle relative to the other between observation periods indicated the relative importance of the 2 cycles for the timing of larval release.

Time series analysis of synchrony relative to the tidal amplitude cycle: Cross-correlation and cross-Fourier analyses were used to determine the timing of larval release for time series ≥2 mo long (5 of the 8 observation periods). Hatching data were log transformed for this analysis. Autocorrelations of 1 to 3 d were evident in some of these data and were removed before analysis; seasonal trends were not evident. In cross-correlations, the time series of larval release was lagged relative to that of the tidal amplitude, which was held stationary. Only lags of 10 to 20% of the time series were considered to be valid (Emery & Thomson 1997).

Effects of environmental factors on synchrony and timing: We examined the potential influence of 3 environmental variables on the synchrony and timing of larval release by *Hemigrapsus oregonensis* and *Petrolisthes cinctipes* near Bodega Bay, the 2 longest data sets. We used time-series analysis to compare the temporal pattern of hatching to daily records of sea surface temperature (SST) and air temperature (monitored near BML) and tidal amplitude (from tide tables) from the same time period. We assumed that the probability of hatching on a given day was likely to reflect environmental conditions over several preceding days. Therefore, we constructed statistical models in which the proportion of available broods hatched on Day t was a function of the mean environmental conditions over the previous week (Days $t-1$ to $t-7$). Because hatching also may occur in response to recent changes in the environment, we also constructed models with terms for the rate of change in an environmental parameter, defined as the mean of the variable over the preceding 3 d (Days $t-1$ to $t-3$) minus the mean of the variable on the 3 d preceding that interval (Days $t-4$ to $t-7$). This approach captures smooth trends in each variable rather than daily fluctuations. We limited our analysis to the week preceding hatching to minimize the loss of hatching observations at the beginning of the time series, since physical observations were not available before the onset of hatching data collection.

We considered linear models with terms for both the mean and rate of change in SST, tidal amplitude and air temperature, as well as interactions between those 6 factors. We then compared the suite of models generated for each species using Akaike's Information Criterion (AIC). Models were fitted with generalized least squares (GLS) with an error covariance matrix that accounted for the autocorrelation structure of the data sets (see supplement at www.int-res.com/articles/suppl/m425p103_supp.pdf for details).

RESULTS

Timing and synchrony of larval release

The 4 species of crabs generally released larvae near spring tides at night, regardless of where they were collected along the coast (Fig. 2, Table 2). Near Bodega Bay in northern California, all 4 species released larvae during or 1 d before spring tides, except the pattern was not significant for *Pachygrapsus crassipes* according to Rayleigh's test (Figs. 2 & 3, Table 2). In central and southern California, Rayleigh's test indicated that 3 species released larvae during or 2 d before spring tides, and *P. crassipes* released larvae 4 d before spring tides in a brief time series (Fig. 2, Table 2). A brief second trial for 1 of the 3 species (*Petrolisthes cinctipes*) did not show a significant pattern (Table 2). Cross-correlations for all species again showed that larval release peaked near spring tides in central and southern California (Fig. 3, Table 2). The coupling of larval release to the tidal amplitude cycle was similar for species that reside high (*P. crassipes*, *Hemigrapsus nudus*) or low (*P. cinctipes*, *H. oregonensis*) in the intertidal zone. Similar percentages of larvae were released at night by the 4 species in northern California (86 to 100%) and central and southern California (90 to 100%).

The timing of larval release was not as tightly related to the lunar as to the tidal amplitude cycle

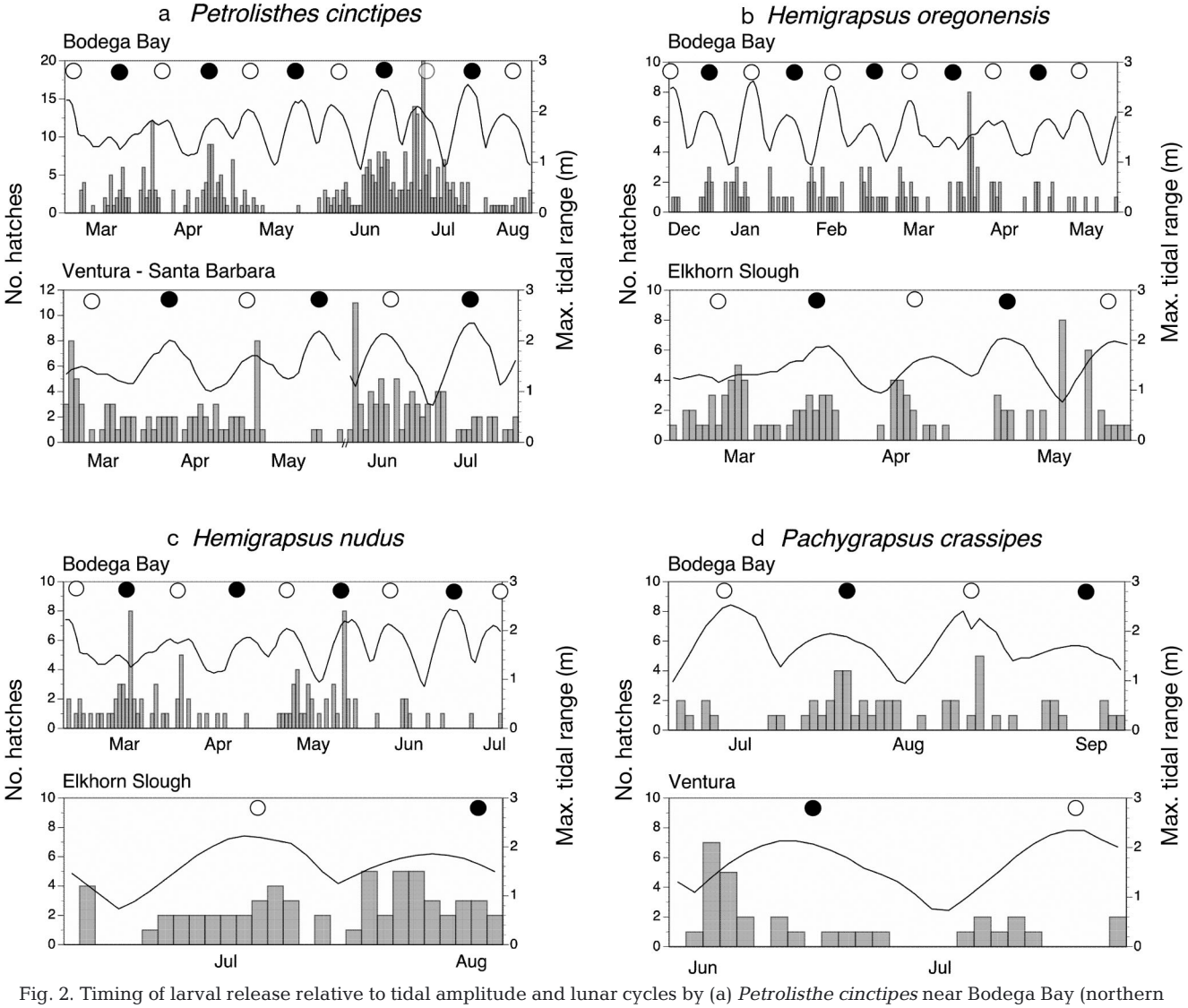

Fig. 2. Timing of larval release relative to tidal amplitude and lunar cycles by (a) *Petrolisthe cinctipes* near Bodega Bay (northern California) from 6 March to 8 August 2001 and between Ventura and Santa Barbara (southern California) from 18 March to 10 May and 26 June to 28 July 1997, (b) *Hemigrapsus oregonensis* near Bodega Bay from 11 December 2000 to 21 May 2001 and in Elkhorn Slough (central California) from 16 March to 25 May 1997, (c) *H. nudus* near Bodega Bay from 7 March to 5 July 2001 and in Elkhorn Slough from 8 July to 4 August 1997 and (d) *Pachygrapsus crassipes* near Bodega Bay from 13 July to 5 September 2001 and at Ventura from 26 June to 22 July 1997. Full moons are indicated by open circles and new moons are indicated by filled circles

Table 2. Timing of larval release relative to tidal amplitude and lunar and diel cycles of 4 crab species along the coast of California. SB: Santa Barbara. Larval release for the tidal amplitude and lunar cycles is shown as the number of days (d) relative to maximum amplitude tides (MAT) and new and full moons. Larval release relative to the diel cycle is reported as the percent hatching at night. The maximum number of days that crabs brooded embryos before releasing larvae is also reported (brood). $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$ for Rayleigh's test, cross-correlations and spectral analysis (Fisher's Kappa). ns: spectral analysis was not significant; na: test was not performed owing to the short time series. See Table 1 for sample sizes

Species	Location	Study period	Rayleigh's test				Cross-correlations	Spectral day	Night %	Brood days
			Tide	r	Moon	r				
Petrolisthes cinctipes	Bodega	Mar–Aug 2001	0 d	0.32***	–1 d	0.16***	0–4 d < MAT*	ns	89	65
	Ventura–SB	Mar–May 1997	0 d	0.29***	–2 d	0.14	0–2 d < MAT*	ns	100	53
	Ventura–SB	Jun–Jul 1997	–5 d	0.14	–6 d	0.20*	na	na	100	33
Hemigrapsus oregonensis	Bodega	Dec 2000–May 2001	–1 d	0.24**	–4 d	0.12	1–3 d < MAT*	ns	80	78
	Elkhorn	Mar–May 1997	0 d	0.24**	0 d	0.30***	0–2 d < MAT*	14.2**	100	71
Hemigrapsus nudus	Bodega	Mar–Jul 2001	0 d	0.41***	0 d	0.29***	1–3 d < MAT*	ns	86	53
	Elkhorn	Jul–Aug 1997	–2 d	0.28*	–1 d	0.25*	na	na	90	29
Pachygrapsus crassipes	Bodega	Jul–Sep 2001	–1 d	0.14	2 d	0.24	0–1 d < MAT*	ns	100	55
	Ventura	Mar–May 1997	–4 d	0.57**	–6 d	0.56***	na	na	100	26

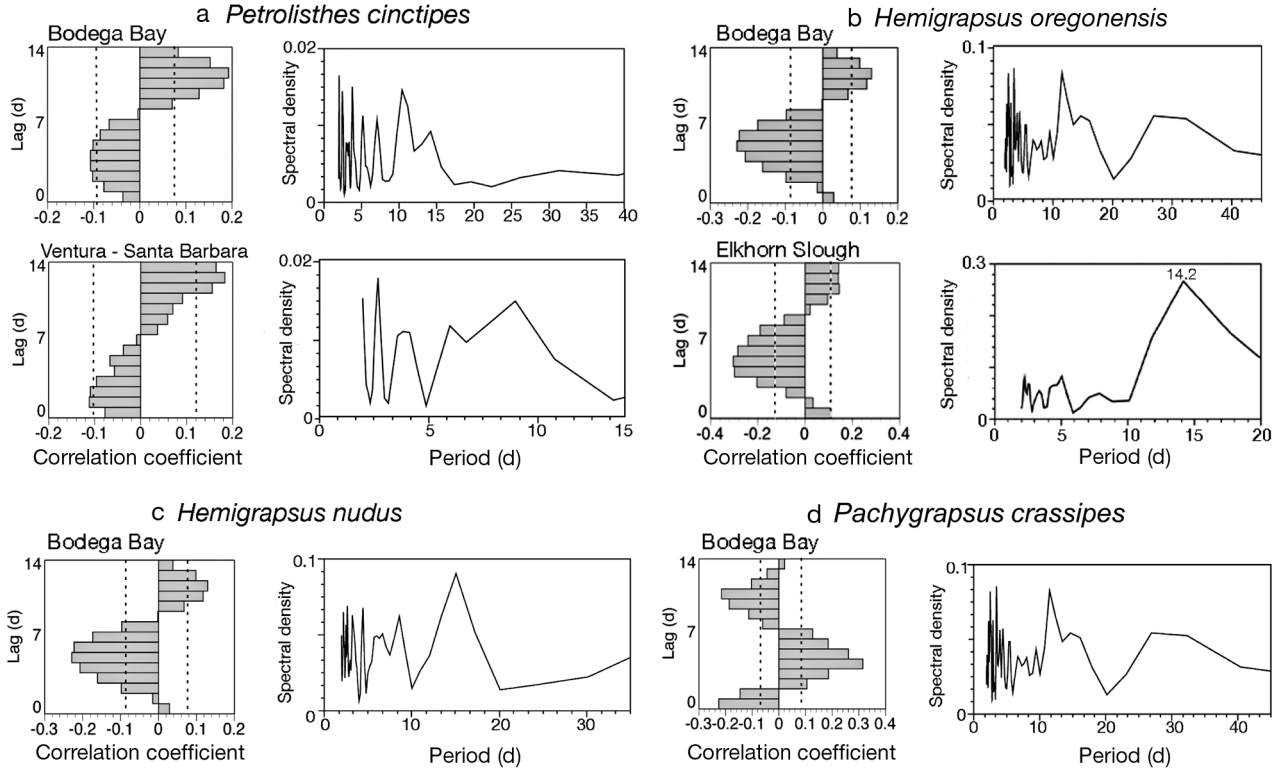

Fig. 3. Cross-correlation (left panels) and spectral analyses (right panels) of the timing of larval release relative to the tidal amplitude cycle by (a) *Petrolisthes cinctipes* near Bodega Bay and between Ventura and Santa Barbara, (b) *Hemigrapsus oregonensis* near Bodega Bay and in Elkhorn Slough, (c) *H. nudus* near Bodega Bay and (d) *Pachygrapsus crassipes* near Bodega Bay. Lags are relative to peak tidal amplitude within a biweekly cycle with 0 and 14 d corresponding to spring tides and 7 d corresponding to neap tides. Dashed lines indicate $p < 0.05$ on cross-correlation plots, and the one significant periodicity is labeled on spectral plots

(Fig. 2, Table 2). Only 2 species in northern California released larvae during or 1 d before new and full moons (*Petrolisthes cinctipes*, *Hemigrapsus nudus*). In central and southern California, peak release by only 2 species occurred during or 1 d before new and full moons (*H. oregonensis*, *H. nudus*). The other 2 species (*P. cinctipes*, *Pachygrapsus crassipes*) released larvae 6 d before new and full moons (i.e. on quarter moons), and the longest trial for one of them was not related to lunar phase (*P. cinctipes*).

Peaks in larval release were neither pronounced nor closely coupled with the biweekly tidal amplitude

cycle indicating that synchrony was weak (Fig. 3, Table 2). Periodicities in 5 of 6 cases with long time series were not significant; a biweekly periodicity was found only for *Hemigrapsus oregonensis* at Elkorn Slough. Maximum incubation times by the 4 species were longer in northern (53 to 78 d) than in southern or central California (26 to 53 d).

Effects of environmental factors on synchrony and timing

For *Hemigrapsus oregonensis*, the lagged mean tidal amplitude and the rates of change in tidal amplitude and SST were the only factors with statistically significant ($p < 0.05$) coefficients in univariate GLS models (Fig. S1 in the supplement at www.int-res.com/articles/suppl/m425p103_supp.pdf). Given the evidence that those 3 variables had better predictive power than did the others, we then considered a full set of models including interactions among those 3 variables (Table S1a). The most parsimonious model (AIC weight $w = 0.89$) had terms for the rate of change in SST, tidal amplitude and their interaction (Table S1a). In this model, the proportion of broods hatching increased on a rising tide or when SST was increasing; when both SST and tidal amplitude were increasing the total effect was slightly less than additive (Table S1b). This model explained 12.5% of the variance in the data and afforded a reasonable fit to the hatching time series, capturing the presence, though not the magnitude, of most of the peaks and valleys in hatching (Fig. 4). The fit was poorest in regions near the beginning of the time series, for which SST data were missing and had been interpolated. For *Petrolisthes cinctipes*, the lagged mean tidal amplitude and air temperature were the only factors with coefficients that were significantly different from zero in univariate GLS models, but no model that included environmental factors was more parsimonious than an intercept-only model (in the supplement at www.int-res.com/articles/suppl/m425p103_supp.pdf).

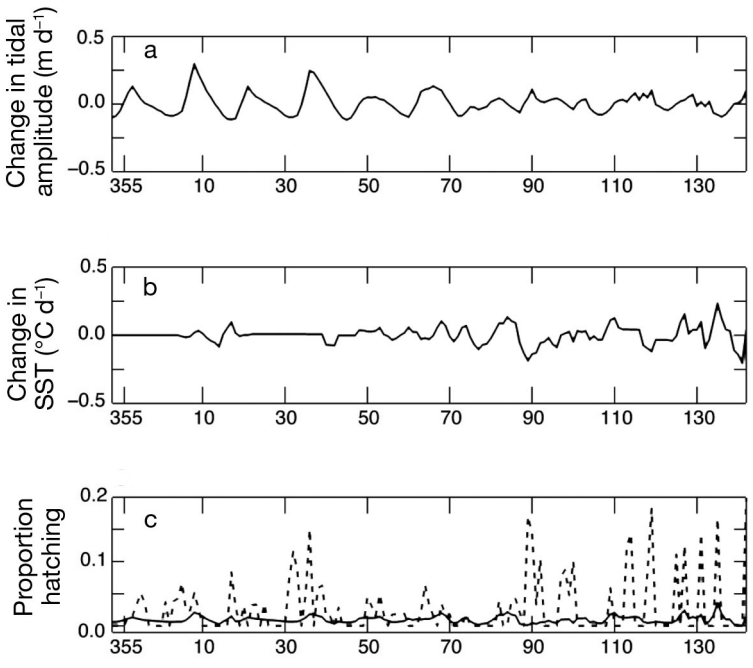

Fig. 4. *Hemigrapsus oregonensis*. Best-fit GLS models for the time series collected near Bodega Bay. Panels show the rates of change in (a) tidal amplitude and (b) sea surface temperature (SST) over 1 wk before hatching and (c) proportion of ovigerous females hatching (dashed line) relative to the most parsimonious model fit (solid line), including the effects of the rate of change in tidal amplitude, SST and their interaction

DISCUSSION

Larval release by the 4 species of crabs peaked near spring tides at night in an upwelling regime as it does for many intertidal species elsewhere in the world (Forward 1987, Morgan 1995, Thurman 2004). The timing patterns also were characteristic of other mixed semidiurnal tidal regimes, where peak larval release generally is more closely related to the tidal amplitude than the lunar cycle and larvae sometimes are released in daylight (Morgan & Christy 1994, Morgan 1996a, Kellmeyer & Salmon 2001, Weaver and Salmon 2002). Because the tidal amplitude and lunar cycles do not always coincide in mixed semidiurnal tidal regimes, crabs must time larval release according to only one of the 2 environmental cycles, and they typically timed it by the tides rather than moonlight with the exception of one semiterrestrial species (Saigusa 1988). Crabs sometimes released larvae in daylight because high tides do not always peak at night in mixed semidiurnal tidal regimes (Morgan & Christy 1994, Morgan 1995, 1996a,b, Thurman 2004).

The timing of larval release was similar along the coast of California despite differences in the intensity and persistence of upwelling (Hickey 1998). The different timing pattern by one species (4 d before spring tides by *Pachygrapsus crassipes*) and nonsignificant results (second brief trial for *Petrolisthes cinctipes*) are to be expected for weakly synchronous timing patterns in the shorter time series obtained for southern and central California.

Larval release was less synchronous than that observed in nonupwelling regimes. The strong, regular peaks of biweekly or monthly larval release that are

characteristic of intertidal crabs elsewhere in the world were not evident along our upwelling coast. Nor was larval release more synchronous by species that live higher in the intertidal zone, even though females in natural populations are constrained to release larvae on maximum amplitude tides while they are inundated (Salmon et al. 1986, Morgan 1995, Morgan & Christy 1995). Although larval release by all 4 species coincided with spring tides in most trials, peaks of larval release were neither well defined nor highly periodic. The weak synchrony raises the possibility that females that are not inundated by high tides every day commonly walk to the water line to release larvae rather than releasing larvae from the safety of their refuges, which would increase the risk of predation on females, embryos and newly released larvae (Morgan & Christy 1995).

The weak synchrony in the timing of larval release probably arose from the cumulative effect of environmental variation during long incubation times in cold water and air temperatures. This relationship was found for 1 of the 2 crabs tested (*Hemigrapsus oregonensis* from Bodega Bay), and the amount of variation in reproductive synchrony explained by temperature might even have been greater if a complete temperature record had been available. Although less plausible, selection for synchronous release may have been relaxed if newly released larvae encountered fewer planktivorous fishes in upwelling regimes. Juvenile fishes that are exclusively zooplanktivorous regardless of their dietary preferences as adults (Morgan 1990) are most abundant in estuaries and kelp forests, both of which are patchy in space along the California coast. However, larval release by many intertidal crabs is quite synchronous in the weaker upwelling regimes off the Pacific Coast of Panama (Christy 1986, Morgan & Christy 1994, 1995, 1997) and Portugal (Paula 1989, Pereira et al. 2000), suggesting that fish predation on newly released larvae can be high in warmer upwelling regions. Large waves obscuring tidal cycles were not responsible for the weak synchrony (Flores & Paula 2002), because crabs were collected in sheltered habitats (except for *Pachygrapsus crassipes* near Bodega Bay).

Follow-up studies should be conducted with intertidal crabs across upwelling regimes to determine (1) the degree of synchrony in the timing of larval release in the field, (2) whether females of mid- and high intertidal species walk to the shore to release larvae and (3) whether fish predation on newly hatched larvae increases in upwelling regimes. We recommend using a precise, labor-intensive method to determine incubation periods and the timing of larval release in the field. This method involves placing a bottomless, well-ventilated box with a translucent cover over a natural population, and frequently pumping water and any newly hatched larvae while crabs are inundated during high tide (Morgan & Christy 1994, Morgan 1996a). Surveying ovigerous females at the waterline with a flashlight over consecutive nocturnal high tides would determine whether larvae are released from the safety of their refuges (DeCoursey 1983). Comparing the density of fish and numbers of larvae eaten by fish (Morgan 1990, Hovel & Morgan 1997) between cold upwelling and warm coasts would be a first step toward determining whether there was a cost to poorly synchronized larval release.

In conclusion, larval release by intertidal crabs appears to be weakly synchronized in cold upwelling regimes. This result stands in stark contrast to well-known examples of strong synchrony in other coastal regions. Given the intense selective pressures leading to synchrony in those regions, our results suggest two possible interpretations. Either planktivory is lower in this upwelling region, which we find unlikely, or environmental constraints preclude strong synchrony. Females may be unable to compensate for the cumulative variation in temperature experienced by developing embryos during long incubation periods in cold upwelled waters. Weak synchrony has important implications for the reproductive success of all intertidal species that brood their offspring by exposing newly released larvae to a greater risk of fish predation. The survival of newly hatched larvae has been linked to peaks in settlement for crabs and fishes (Christy & Stancyk 1982, Robertson et al. 1988, Morgan 1990, Tilburg et al. 2008), and increased fish predation resulting from weak synchrony could contribute to recruitment limitation in upwelling regimes (Gaines & Roughgarden 1987). The timing of larval release by a diverse array of taxa can be affected by other selective factors (Salmon et al. 1986, Anger et al. 1994, Morgan 1987b, 1995, Brodie et al. 2007), but weaker synchrony should still result in reduced reproductive success relative to other regions.

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