



Fish predation after weakly synchronized larval release in a coastal upwelling system

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ABSTRACT: Timing of larval release by many shore crabs is cued by environmental cycles to occur during nocturnal spring ebb tides, when larvae are transported away from high densities of planktivorous fishes in the dark. However, a recent laboratory study indicated that larval release may be weakly synchronized relative to this safe period in upwelling regions, potentially increasing fish predation. We determined the timing of larval release and predation in marshes in an upwelling region by sampling plankton and fishes during flood and ebb tides on either side of high slack tide. Larval release was weakly synchronized, peaking during spring and intermediate ebb tides in twilight and darkness. Almost all larvae (99.8%) were eaten at twilight during peak release, when they likely were more visible than at night. However, larvae comprised only 4.1% of the diets of the 3 fish species that ate them. These fish species were often absent when conditions would make larvae most vulnerable to predation, and they preferred other prey to well-defended larvae. Larvae released outside the safe period were eaten more than those that were released during the safe period, providing selection for the timing of larval release. However, despite the large numbers of larvae present outside of the safe period, predation by fishes was much lower than expected. Thus, the selective effects of fish predation may be relaxed, raising the possibility that the strength of fish predation as a selective force varies among coasts and other selective forces that may affect the timing of larval release.

KEY WORDS: Larval release · Hatching · Reproductive synchrony · Fish predation · Upwelling

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INTRODUCTION

Many organisms throughout the world have synchronous reproductive patterns (Ims 1990, Adamczewska & Morris 2001, Satake & Iwasa 2002). Synchronous reproductive behaviors, ranging from the nocturnal release of offspring to annual large-scale migrations to breeding grounds, are believed to increase the survival of offspring (Limpus et al. 1992, Westneat 1992, Shapiro et al. 1993, Richter & Cumming 2006). In the sea, gametes and larvae are commonly released synchronously relative to diel (light–dark), tidal (high–low), tidal amplitude (spring–neap) and lunar cycles (Korringa 1947, Johannes 1978, Morgan

1995). Although diverse timing patterns have been described, many species time release to occur during nocturnal maximum amplitude tides, when they are rapidly transported under the cover of darkness by strong ebb tides away from high densities of predatory fishes in the nearshore (Johannes 1978, Christy 1982, Morgan 1990, Robertson et al. 1990, Morgan & Christy 1995, Hovel & Morgan 1997). This widespread timing pattern is known as ‘the safe period’ (Morgan et al. 2011), because fishes eat the fewest larvae at this time (Morgan 1990, Hovel & Morgan 1997). Thereafter, suites of larval swimming behaviors determine whether larvae continue to disperse from parental habitats or remain nearby (Morgan

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1995, 2006, Hovel & Morgan 1997, Morgan & Anastasia 2008, Morgan et al. 2009, López-Duarte et al. 2011).

Many sedentary species that live high on the shore release larvae when they are inundated by maximum amplitude tides rather than leaving the safety of refuges to walk to the waterline, but many species that live low on the shore and are inundated daily also release larvae during spring high tides (Christy 1986, Morgan 1995, 1996, Morgan & Christy 1995, Thurman 2004). Species that do not release larvae during the safe period are likely less vulnerable to planktivorous fishes because they are less conspicuous or possess defensive behaviors or long spines, which are effective at deterring predation by juvenile, gape-limited fishes (Morgan 1987, 1989, 1990, Morgan & Christy 1995, 1997, Hovel & Morgan 1997). Many larvae also return to settle in nearshore adult habitats during a safe period on nocturnal spring flood tides (Christy & Morgan 1998, Paula et al. 2004). Thus, rather than releasing larvae synchronously to swamp predators, a wide variety of coastal species from tropical and temperate regions synchronize larval release and recruitment to occur during safe periods of diminished fish predation (Morgan & Christy 1997, Christy & Morgan 1998).

Although many studies have been conducted on the timing of larval release, few have been conducted in highly productive upwelling regions along the western margins of continents. The few studies that have been conducted in upwelling regions indicate that larval release around the safe period may be less synchronous, potentially increasing fish predation on newly hatched larvae (Christy 2003, 2011, Morgan et al. 2011). Cold temperatures from upwelled bottom waters increase development times of crab embryos to about 2 mo compared to about 2 wk in warm-temperate and tropical regions (DeCoursey 1983, Morgan 1995, 1996, Morgan et al. 2011, Kerr et al. 2012). Temperature exposure is more variable during low tide because of the prevalence of both fog and sun and during high tide because of prevailing upwelling-favorable winds, which weaken the warming of water approximately every 3 to 7 d (Morgan et al. 2011). However, some species of crabs thermoregulate embryos, adjusting the timing of hatching to coincide with favorable conditions for hatchlings, as previously described for some species of reptiles and insects (Bernardo 1996, Danks 2002, Shine 2005). Female crabs in warm climates with coastal upwelling can adjust the timing of mating by regulating the depth of their burrows and choosing 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, Christy 2011, Kerr et al. 2012). However, these compensatory behaviors are less effective when cold temperatures lengthen incubation periods, especially for species that live in depressions under rocks rather than in burrows (Christy 2003, Morgan et al. 2011). Decapods cannot hatch at different stages of development to coincide with favorable periods, unlike some fishes and amphibians (Smyder & Martin 2002, Warkentin 2011). Thus, in cold upwelling regimes, the cumulative variance in temperature exposure during long incubation times reduces the probability of synchronizing larval release to closely coincide with the safe period.

Five species of intertidal crabs from the cold upwelled water along the coast of California, USA, were recently shown to have long embryonic durations and weakly synchronized larval release (Morgan et al. 2011). That study was conducted in outdoor seawater tables in the absence of tides, and it is possible that larval release could be more synchronous in natural populations, where tides reinforce endogenous rhythms. Therefore, we conducted a field study in northern California to determine whether (1) larval release by intertidal decapod crustaceans in natural populations is weakly synchronized to the safe period, (2) fishes eat more newly hatched larvae that are released outside the safe period and (3) fishes aggregate to consume the high concentrations of larvae released outside the safe period. We also quantified fish predation on other zooplankters to determine whether they were preferred to decapod larvae.

MATERIALS AND METHODS

Study system

Studies were conducted in 2 small estuaries situated 1.5 km apart near the mouth of Tomales Bay in northern California (Fig. 1A). The primary study site at Tom's Point Estuarine Preserve consists of a 10 m wide channel that was inundated at tide heights >0.5 m. The secondary study site, Walker Creek, consists of a 10 m wide main channel and a 4 m wide side channel. The marshes are inundated during high tide, and broad, expansive mudflats are exposed bayward of the marshes at low tide.

Two grapsid shore crabs are the most conspicuous decapod crustaceans that inhabit marshes along the west coast of California. *Pachygrapsus crassipes*

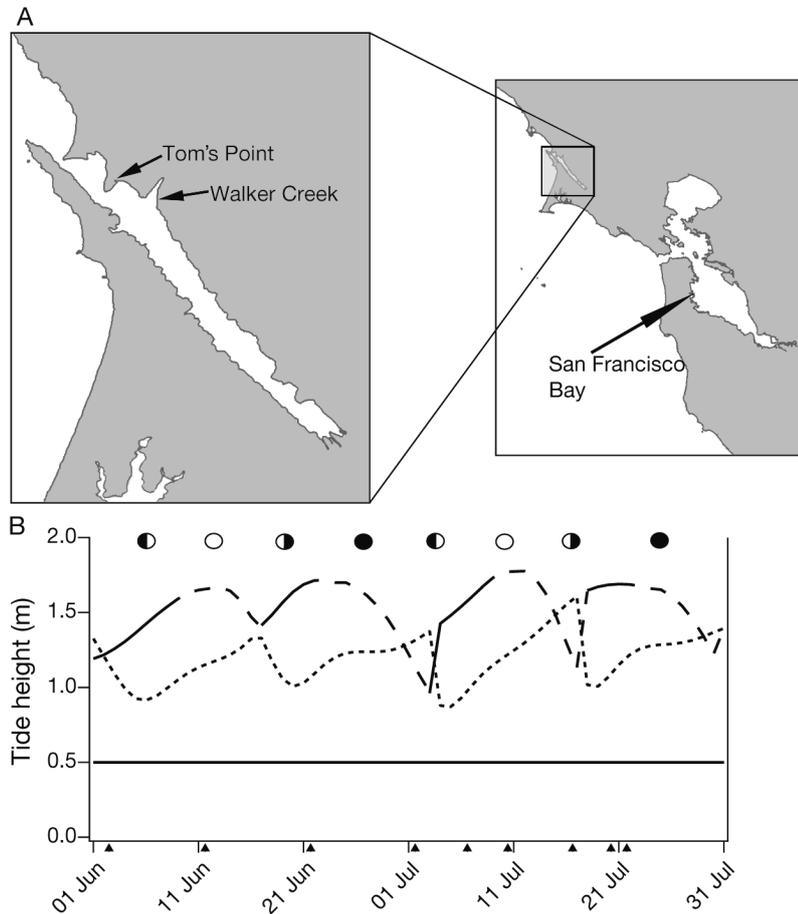


Fig. 1. (A) Locations of the study sites Tom's Point and Walker Creek in Tomales Bay, California, USA. (B) Daily maximum of daytime high tides (dotted line), and both twilight high tides and nighttime high tides (combined dashed-solid line, respectively). The mixed semi-diurnal nature of the tides causes tides to switch between nighttime and twilight high tides; thus a single dashed-solid line denotes these tides. Arrowheads denote sampling dates. Horizontal line represents the tide height at which the marshes began to be inundated by high tides (0.5 m). Half-filled, open and solid circles represent quarter, full and new moons, respectively

ranges from the high to mid intertidal zone, and *Hemigrapsus oregonensis* occurs from the mid to low intertidal zone. Ghost shrimp *Neotrypaea californiensis* and commensal pinnotherid crabs *Scleroplax granulata* and *Pinnixa tubicola* live in burrows on intertidal mudflats. Larval morphologies determine the vulnerabilities of each species to predatory fishes (Fig. S1 in the supplement at www.int-res.com/articles/suppl/m490p185_supp.pdf).

Sampling

The study was conducted in summer (2 June to 22 July 2006) during the peak reproductive season of most coastal nearshore invertebrates and fishes,

when both decapod larvae and juvenile zooplanktivorous fishes were abundant. During our study in this mixed semidiurnal tidal regime (usually 2 tides but sometimes 1 tide per day), spring high tides occurred at night 3 times and at twilight once, whereas neap high tides occurred in daylight (Fig. 1B). We sampled newly hatched larvae and fishes on 9 d: 4 d during spring tides (11 June, 10 July, 20 July and 21 July), 3 d during neap tides (2 June, 1 July and 16 July) and 2 d during intermediate tides (21 June and 6 July) (Fig. 1B). Sampling was conducted during both high tides each day, for a total of 18 sampling trips. We sampled at 30 min intervals from 90 min before high slack tides until water had ebbed from marshes, at most 200 min later, depending on tidal amplitude. This sampling design enabled us to compare larval release and fish predation between 2 consecutive tides with different tidal amplitude and/or light level. Spring tides at night ($n = 2$), spring tides at twilight ($n = 2$), intermediate tides at twilight ($n = 2$) and neap tides during daylight ($n = 3$) were compared to the following daytime tide. (Fig. 1B). Predictions of the timing and height of tides were obtained from Tides & Currents (ver. 2.0, Nobeltec). Predicted light levels were obtained for San Francisco from the US Naval Observatory Astronomical Applications website (<http://aa.usno.navy.mil/>), with twilight being defined as 90 min around sunset and sunrise.

Sampling first stage larvae over tidal, tidal amplitude and diel cycles is one of several effective approaches to determine the timing of larval release (DeCoursey 1983, Christy 1986, Salmon et al. 1986, Morgan 1990, 1995, Hovel & Morgan 1997). Plankton was collected using a net (30 cm diameter, 333 μ m mesh) that was equipped with a flowmeter. The bridle of the net was attached to the end of a pole and walked against the tidal flow along the middle of the tidal creek for 5 min, covering most of the length of the tidal creek at Tom's Point. Three replicate tows were taken during each 30 min interval, for a total of 150 samples. Samples were preserved with 70% ethanol.

Fishes were sampled concurrently with plankton to determine interspecific differences in predation on first stage larvae relative to tidal, tidal amplitude and diel cycles. We collected all fishes in the marshes during high tide by completely spanning the mouth of the tidal creek of each marsh with a beach seine (2.5 mm mesh) during the duration of ebb tide. Metal posts were placed behind the seine for reinforcement, and a heavy chain was attached to the bottom of the net to ensure that fishes did not escape under the net. After the tide had completely ebbed, fishes were stranded in a tidepool upstream from the net and were collected by hand. All fishes were placed in coolers filled with water until they were identified, counted and returned live to the estuary. During each sampling period, about 10 individuals per species, when available, were fixed in formaldehyde for gut content analysis.

In the laboratory, plankton samples were split using a Folsom splitter. Decapod larvae were identified to species and stage, and all other zooplankters were classified into broad taxonomic groups. Only first stage decapod larvae were abundant in plankton samples. Data for amphipods are reported because they were the most common prey of fishes. Standard length was recorded and stomachs were removed for 540 fishes. Only contents of foreguts were analyzed to ensure that prey were recently eaten. Polychaete and oligochaete prey were classified as annelids because we could not differentiate them in gut contents. For the same reason, we combined larvae of *Hemigrapsus nudus* and *Hemigrapsus oregonensis*, although *H. oregonensis* larvae were much more abundant in the plankton.

Data analysis

Plankton data were analyzed with generalized additive models (GAMs) using R (Wood 2006, R Development Core Team 2011) to examine nonlinear relationships between continuous explanatory and response variables with a smooth function (Guisan et al. 2002). Taxa were often absent in plankton tows, causing us to analyze the effects of environmental variables on the presence and absence of larvae. We then modeled the effects of environmental variables on larval abundance after removing the zeros (Barry & Welsh 2002). The presence and absence of larvae of each species were modeled using a binomial distribution. Larval abundance of each species was modeled using a Gaussian distribution on log-transformed data. For both the presence/absence and

abundance models, the set of explanatory variables included in each model was selected according to Akaike's information criterion (AIC). For both steps, models were developed until all factors and continuous variables were significant and the AIC was the smallest. Results for significant continuous smoothers were interpreted visually (Yee & Mitchell 1991, Wood 2006). Tidal amplitude and deviation from high tide were both modeled as smoothed continuous variables, while light level (daytime, twilight and nighttime) was modeled as a categorical factor. The interactions between tidal amplitude and light level and between deviation from high tide and light level were also evaluated. Models were verified to ensure that they met the assumptions of normality and homogeneity.

Temporal variation in fish abundance at Tom's Point marsh was also determined using GAMs in R. Walker Creek marsh was not included in these analyses because it was not possible to completely span the mouth of the marsh with a beach seine. Fish abundance was analyzed relative to the phases of diel and tidal amplitude cycles and the mean number of (1) amphipods, (2) all decapod crustacean larvae and (3) decapod larvae excluding pinnotherids. Amphipods were included because they were omnipresent and a preferred prey item, and pinnotherid larvae were excluded because they were not eaten. All variables except light were modeled as smoothed continuous variables, and light was modeled as a categorical factor. GAMs were generated for each fish species, all planktivorous fishes combined and all fishes combined.

The percent occurrence of prey and feeding preferences is reported for the 11 most abundant species of fishes. Feeding preferences for each species of fish were calculated using Chesson's (1983) index of electivity, with the assumption that there was no depletion in number of planktonic prey. Values range from -1 to 1 , with positive values indicating that prey were preferred, negative values indicating that prey were avoided and 0 indicating that prey types were eaten randomly. The amount of food available to the fishes was determined by calculating the mean abundance of each available prey type collected in the 3 replicate tows while fishes were seined. Feeding preferences of planktivorous fishes were analyzed by ANOVA followed by a Tukey's post-hoc test. Feeding preferences of all species combined were also analyzed by ANOVA. All data met assumptions of the test. Prior to analysis, *Atherinops affinis* was partitioned into 3 size classes (7–39, 40–79 and 80–150 mm).

RESULTS

Timing of larval release

Forty taxa were identified in plankton samples, and 9 taxa of zooplankters accounted for approximately 95% of the zooplankters in the samples (Table S1 in the Supplement at www.int-res.com/articles/suppl/m490p185_supp.pdf). First stage larvae of *Pachygrapsus crassipes* and *Hemigrapsus oregonensis* were the most abundant zooplankters, comprising half of the zooplankters collected, at mean concentrations of 11 210 and 7821 m⁻³, respectively. First stage larvae of *Neotrypaea californiensis* were the sixth most abundant zooplankter, comprising 5.5% of the zooplankton community, and 3 species of pinnotherid crabs (*Pinnixa tubicola*, *Scleroplax granulata* and an unidentified species) comprised only 1.75% of zooplankters. First stage larvae of other decapods were too uncommon for analysis, including 5 species of brachyuran crabs (*Carcinus maenus*, *Hemigrapsus nudus*, *Lophopanepeus bellus*, *Pugettia producta* and a second unidentified pinnotherid), 2 taxa of anomuran crabs (*Pagurus* spp. and *Emerita analoga*) and caridean shrimp. Five common taxa of demersal zooplankters (amphipods, ostracods, cumaceans, harpacticoid copepods and bivalves) comprised 37.3% of zooplankters, whereas calanoid copepods unexpectedly comprised only 3.65% of zooplankters.

Amphipods, like other demersal zooplankters (data not shown), were abundant whenever the marsh was inundated (Fig. S2 in the Supplement). The presence of larvae of each of the 6 most common decapod species (*Pachygrapsus crassipes*, *Hemigrapsus oregonensis*, *Neotrypaea californiensis*, *Pinnixa tubicola*, *Scleroplax granulata* and an unidentified pinnotherid herein referred to as Pinnotherid A) in the plankton was not significantly influenced by any of the 3 environmental cycles analyzed (tidal amplitude, tidal or diel) in the GAMs, because larvae were present during all sampling trips. In contrast, larval abundance of *P. crassipes*, *H. oregonensis* and *N. californiensis* peaked near high slack, spring and intermediate tides during twilight and darkness (Fig. S3 in the Supplement, Table 1). The difference between results with and without zeros in the data arose because larvae collected in the daytime were present near twilight. The following results are for larval abundance including zeros (Figs. S3 & S4 in the Supplement), and model structures and statistical results are for larval abundance excluding zeros (Fig. 2, Table 1).

Visual interpretation of the continuous smoothers generated by the GAMs demonstrated that larval release by *Pachygrapsus crassipes* peaked at twilight during spring tides within 30 min after high slack tide (Fig. 2A–C). The GAMs explained 44.2% of the variation in larval abundance by including the diel and tidal cycles as well as the interaction between tidal amplitude and diel cycles (Fig. 2A–C, Fig. S3 in the Supplement, Table 1). After removing samples in which larvae were absent, the model revealed that larvae were most abundant at night and twilight but were common during the daytime (Table 1). Larval abundance was greatest during spring tides and intermediate tides and was at least 2 orders of magnitude less during neap tides, when the larger of the 2 high tides per day occurred in daylight (Figs. 1B & 2A, Fig. S3 in the Supplement, Table 1). When considering the interaction with the diel cycle, larval abundance peaked at twilight on spring tides, whereas it peaked at night followed by twilight and daytime during intermediate amplitude tides and showed the opposite pattern during neap tides (Fig. S3 in the supplement). Modeled larval abundance increased with tidal amplitude until it peaked at 1.5 m during twilight and darkness; there was no effect of tidal amplitude during daytime (Fig. 2A,B, Table 1). Model results demonstrate that larvae occurred from late flood through late ebb tide but peaked within 30 min after high slack tide, with no effect of diel cycle (Fig. 2C, Fig. S3 in the Supplement, Table 1).

Larval release by *Hemigrapsus oregonensis* was similar to that by *Pachygrapsus crassipes*, peaking 30 to 60 min after high slack tide at intermediate amplitudes in darkness closely followed by maximum amplitude tides in twilight (Fig. 2D–F). The GAMs explained 45.1% of the variation in larval abundance by including the diel and tidal cycles together with the interaction between tidal amplitude and diel cycles (Fig. 2D–F, Fig. S3 in the Supplement, Table 1). Larvae were most abundant at night and twilight and were about 1.5 to 2 orders of magnitude less abundant during the daytime (Fig. S3 in the Supplement, Table 1). Larval abundance was greatest during intermediate tides and spring tides and lowest during neap tides, when the dominant high tide occurred in daylight (Fig. 2D,E, Fig. S3 in the Supplement, Table 1). When considering the interaction with the diel cycle, larval abundance peaked at twilight on spring tides, whereas it peaked at night followed by twilight and daytime during intermediate amplitude tides and showed the opposite pattern during neap tides (Fig. S3 in the Supplement). Mod-

Table 1. Generalized additive model structure describing larval abundance of 6 species of decapod crustaceans. The models presented analyze the abundance of larvae (zeros have been removed); all presence/absence models were insignificant. Parametric coefficients are for light levels, which were modeled as categorical factors. A significant positive difference from the intercept (twilight, Twil) indicates that larval abundance was greatest in the nighttime (Night) or daytime (Day). A significant negative difference from twilight indicates that larvae were more abundant at twilight. Tidal amplitude (TA) and deviation from high tide were both modeled as smoothed continuous variables and interactions between them and with light level are reported. The effective degrees of freedom (edf) for each interaction estimates linearity of the model. % Dev: percent deviations; AIC: Akaike's information criterion

Parametric coefficient				Smooth term (non-parametric)				N	R ² adjusted	% Dev	AIC	
Parameter	Estimate	SE	Z	p	Parameter	edf	F					p
<i>Pachygrapsus crassipes</i>												
Intercept	5.568	0.176	31.568	<0.0001	TA × Twil	1.815	6.786	0.001	111	0.39	44.2	289.32
Day	-1.291	0.284	-4.541	<0.0001	TA × Day	1	1.289	0.26				
Night	-0.675	0.406	-1.662	0.099	TA × Night	1.925	6.613	0.002				
					High Tide	2.664	3.082	0.026				
<i>Hemigrapsus oregonensis</i>												
Intercept	5.444	0.151	35.961	<0.0001	TA × Twil	1.244	13.747	<0.0001	111	0.40	45.1	274.60
Day	-1.172	0.384	-3.055	0.003	TA × Day	1.779	1.646	0.196				
Night	-0.675	0.406	-1.662	0.099	TA × Day	2.265	3.028	0.039				
					High Tide	2.752	5.436	0.001				
<i>Neotrypaea californiensis</i>												
Intercept	5.2	0.146	35.561	<0.0001	TA × Twil	2.06	15.325	<0.0001	86	0.47	53.1	181.74
Day	-1.03	0.308	-3.339	0.001	TA × Day	1.457	0.327	0.693				
Night	-0.456	0.208	-2.189	0.032	TA × Night	2.152	3.569	0.024				
					High Tide	2.09	6.206	0.001				
<i>Scleroplax granulata</i>												
Intercept	4.563	0.105	43.284	<0.0001	NA	NA	NA	NA	96	0.03	5.4	181.08
Day	-0.236	0.148	-1.594	0.114	NA	NA	NA	NA				
Night	-0.345	0.154	-2.241	0.027	NA	NA	NA	NA				
<i>Pinnixa tubicola</i>												
Intercept	4.563	0.105	43.284	<0.0001	TA	1	5.688	0.0194	88	0.31	35.0	132.36
Day	-0.236	0.148	-1.594	0.114	High tide	2.243	3.629	0.0184				
Night	-0.345	0.154	-2.241	0.027								
Pinnotherid A												
Intercept	4.087	0.071	57.45	<0.0001	TA	2.062	4.564	0.01	58	0.15	17.9	98.47

eled larval abundance was greatest during twilight and night, increasing linearly with tidal amplitude to 2.2 m during twilight and peaking about 1.4 m in darkness (Fig. 2D,E, Table 1). Larvae occurred from late flood through late ebb tide but peaked 30 to 60 min after high slack tide, especially during intermediate amplitude tides, with no effect of diel cycle (Fig. 2F, Fig. S3 in the Supplement, Table 1).

Larval release by *Neotrypaea californiensis* was greatest in twilight during maximum and intermediate amplitude tides within 30 to 60 min after high slack tide. The GAMs explained 53.1% of the variation in larval abundance by including the diel and tidal cycles together with the interaction between tidal amplitude and diel cycles (Fig. 2G–I, Fig. S3 in the Supplement, Table 1). Larvae were most abundant during twilight followed by darkness and were 1 order of magnitude less abundant during daylight (Fig. S3 in the Supplement, Table 1). The difference

between results with and without zeros in the data arose because larvae collected at night were present near twilight. Larvae were most abundant during spring and intermediate tides and were least abundant during neap tides, when dominant high tides occurred during the daytime (Fig. 1B, Fig. S3 in the Supplement). When considering the interaction with the diel cycle, larval abundance peaked at twilight followed by night and daytime on spring and intermediate tides, whereas it peaked at night followed by twilight and daytime during neap tides (Fig. S3 in the Supplement). Modeled larval abundance peaked at tidal amplitudes over 1.5 m during twilight and 1.3 m during darkness, with no effect of tidal amplitude during daylight (Fig. 2G,H, Fig. S3 in the Supplement, Table 1). Larvae were abundant from flood tide to 30 to 60 min after high slack tide, when abundance declined (Fig. 2I, Fig. S3 in the Supplement).

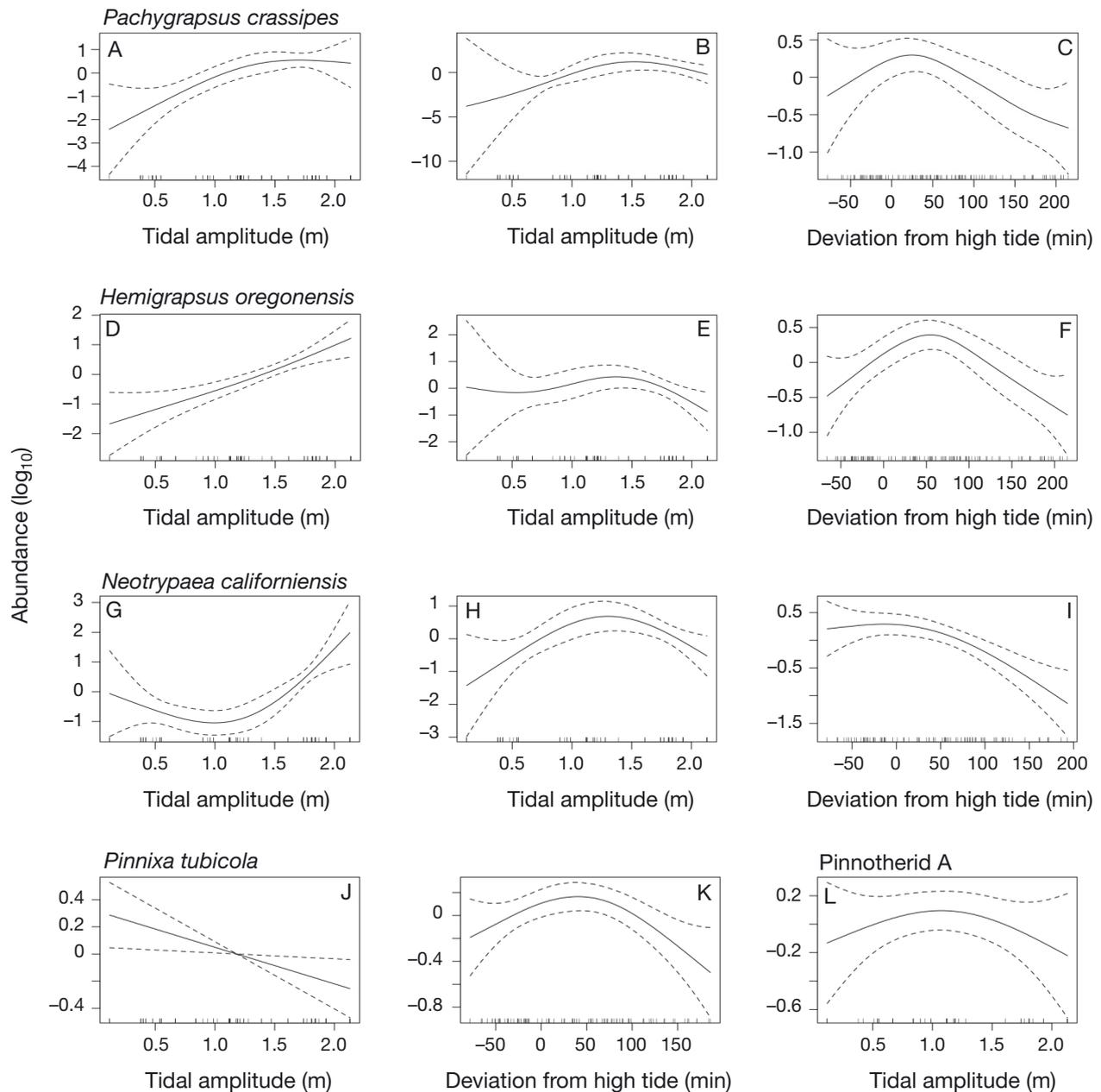


Fig. 2. Generalized additive models for larval abundance (zeros have been removed) of 6 decapod crustaceans in 2 marshes from Tomales Bay, California, USA. Models for (A–C) *Pachygrapsus crassipes*, (D–F) *Hemigrapsus oregonensis* and (G–I) *Neotrypaea californiensis* show the effect of (A,D,G) tidal amplitude at twilight, (B,E,H) tidal amplitude at night and (C,F,I) deviation from high slack tide. Models for *Pinnixa tubicola* show the effect of (J) tidal amplitude (without light level) and (K) deviation from high slack tide. (L) Model for Pinnotherid A shows the effect of tidal amplitude (without light level). Ticks on the horizontal axis represent times that data were collected, and dashed lines represent 95% confidence intervals

Larval abundances of the 3 species of pinnotherid crabs relative to environmental cycles differed from the previous 3 species, appearing to be more abundant during the daytime, during lower amplitude tides and across the tidal cycle; however, the models failed to distinguish many trends observed when

zeros were incorporated into the abundance data (Fig. S4 in the Supplement). Overall, *Scleroplax granulata* larvae tended to be more abundant during spring tides followed by intermediate and neap tides, twilight and daylight rather than darkness and throughout flood and ebb tides (Fig. S4 in the Sup-

plement). After removing samples in which larvae were absent, the model revealed that larvae were most abundant during the daytime and twilight, and there were no significant effects of tidal amplitude or deviation from high tide (Fig. S4 in the Supplement, Table 1). Larvae were abundant throughout tidal and tidal amplitude cycles, with only 5.4% of the variation explained by the 3 environmental cycles in the GAMs (Fig. S4 in the Supplement, Table 1).

Pinnixa tubicola larvae tended to be more abundant during intermediate and neap tides than spring tides, during twilight and daylight rather than darkness and throughout flood and ebb tides (Fig. S4 in the Supplement). After removing samples in which larvae were absent, the model revealed that larvae were most abundant during twilight and daylight, decreased linearly with increasing tidal amplitude and peaked 50 min after high slack tide; there were no significant interactions between light and tidal amplitude or deviation from high tide (Fig. 2J,K, Fig. S4 in the Supplement, Table 1). The 3 environmental cycles explained 35% of the variation in larval abundance (Table 1).

Larvae of Pinnotherid A tended to be most abundant during neap tides at twilight and during flood tides (Fig. S4 in the Supplement). After removing samples in which larvae were absent, the model revealed that larvae peaked at 1 m, which explained 7.9% of the variation in the model (Fig. 2L, Fig. S4 in the Supplement, Table 1).

Fish predation

We collected all fishes that occurred in Tom's Point marsh during high tide. A total of 13 species were caught, and most of them were small planktivorous fishes (Table S2 in the Supplement). Topsmelt *Atherinops affinis* was most common (46.8%), northern anchovy *Engraulis mordax* was second (26.5%) and three-spined stickleback *Gasterosteus aculeatus* was third (9.1%), comprising 82.4% of fishes caught. Fish abundances did not vary consistently with tidal amplitude or diel cycles (Fig. 3), and all model structures (prey abundance, tidal amplitude and light level) for fish abundance were not significant (data not shown). However, most fishes entered the marsh during twilight high tides (61.7%),

and fewer of them were present during nighttime (19.5%) and daytime (18.8%).

The 9 species (and 3 size classes of *Atherinops affinis*) of fishes primarily ate demersal crustaceans (amphipods, harpacticoid copepods and ostracods), and sediment was common in stomachs; few of them ate decapod larvae even though these larvae composed 54.7% of the zooplankton community (Fig. 4, Table S3 in the Supplement). Three fishes ate *Neotrypaea californiensis* larvae, which comprised small percentages of the total number of prey eaten: *Engraulis mordax* (8.7%), small *A. affinis* (2.6%) and *Gasterosteus aculeatus* (2.0%). These fishes preferred demersal crustaceans and strongly avoided eating *N. californiensis* (Table S3 in the Supplement).

In the 3 species of fishes that ate decapod larvae, more prey was consumed during twilight and night than during the day (Fig. 5). *Gasterosteus aculeatus* and *Engraulis mordax* consumed most zooplankton at night followed by twilight and day; *E. mordax* was not even present in the marsh during the daytime. Large and mid size classes of *Atherinops affinis* consumed most prey almost entirely at twilight, and small *A. affinis* ate much more at twilight and night than during the day. The other 6 species also primarily fed during twilight and night, although sample sizes were low (data not shown).

Few larvae were consumed during nocturnal maximum amplitude ebb tides. Most *Neotrypaea californiensis* larvae were eaten during neap and intermediate amplitude tides at twilight, although demersal zooplankton were preferred (Fig. 6A,B). *Gasterosteus aculeatus* consumed 5 *N. californiensis* larvae (0.5% of the diet), and small *Atherinops affinis* consumed 21 larvae (2.7% of the diet). *Engraulis mordax* consumed 554 *N. californiensis* larvae, comprising 32.3% of the diet. Three species of fishes consumed

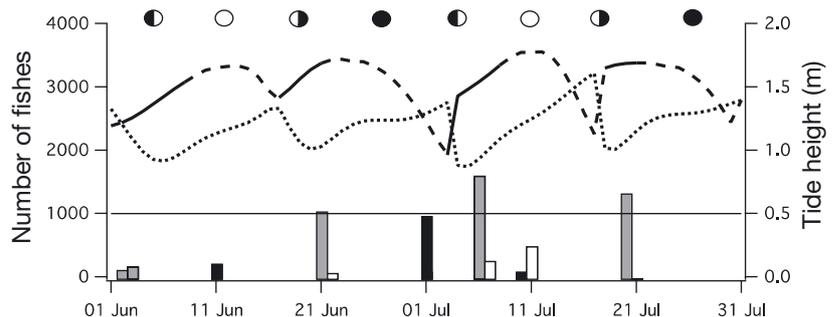


Fig. 3. Number of fishes in Tom's Point marsh in Tomales Bay, California, USA, during daytime (white bars), twilight (gray bars) and nighttime (black bars) high tides. See Fig. 1 for details

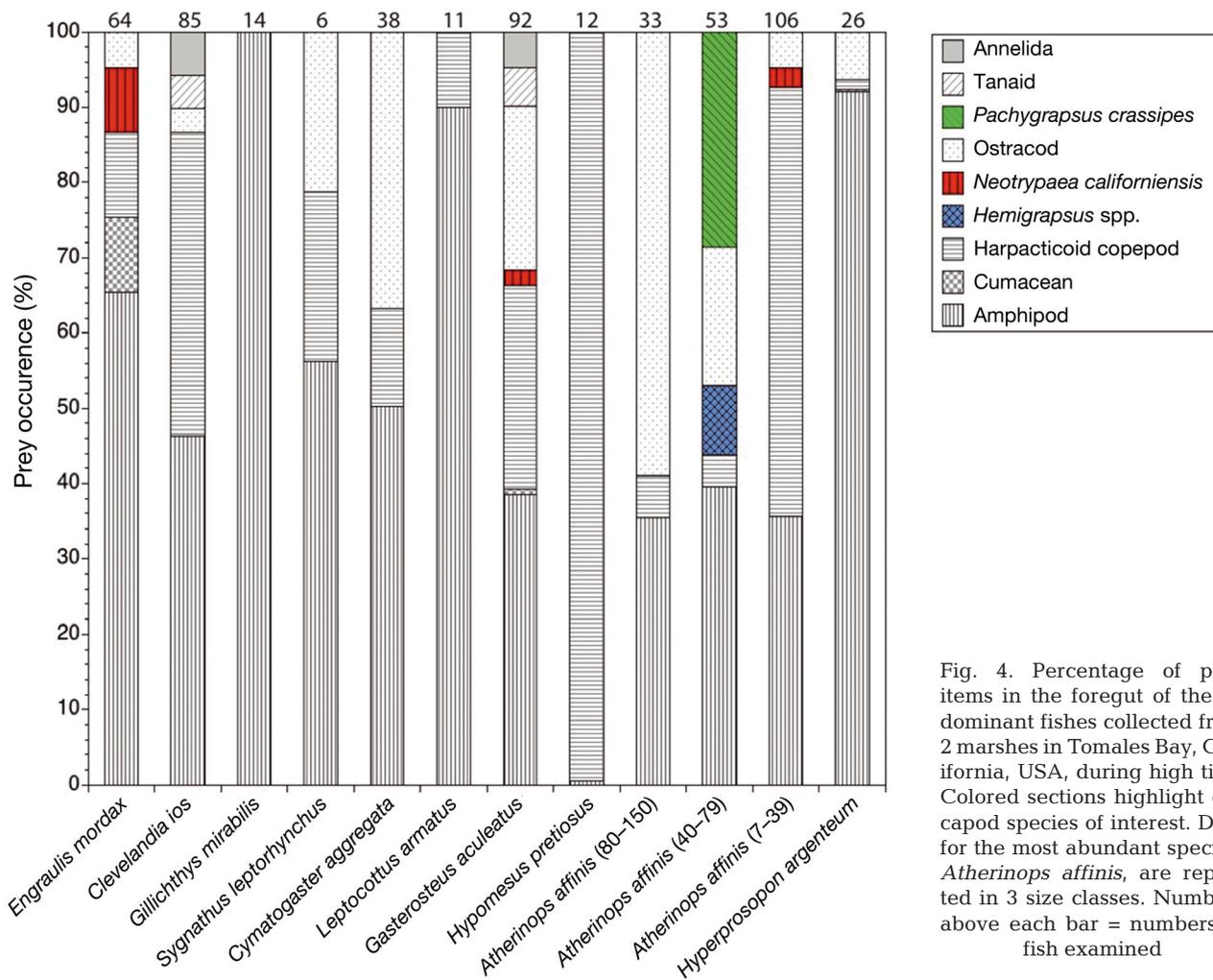


Fig. 4. Percentage of prey items in the foregut of the 10 dominant fishes collected from 2 marshes in Tomales Bay, California, USA, during high tide. Colored sections highlight decapod species of interest. Data for the most abundant species, *Atherinops affinis*, are reported in 3 size classes. Numbers above each bar = numbers of fish examined

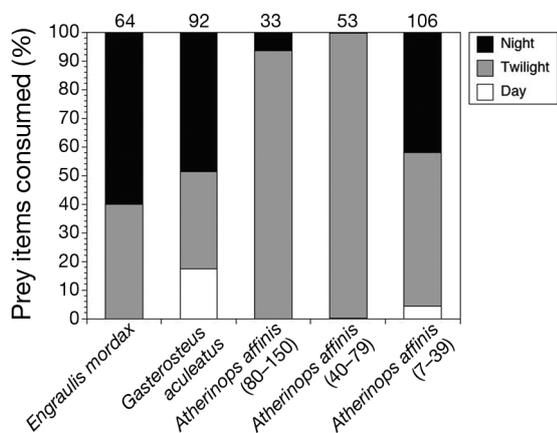


Fig. 5. *Engraulis mordax*, *Gasterosteus aculeatus* and *Atherinops affinis*. Percentage of all prey consumed during daylight, twilight and darkness. Data for the most abundant species, *A. affinis*, are reported in 3 size classes. Numbers above bars are the number of fish that were examined. *E. mordax* and large (80 to 150 mm) *A. affinis* were not present in the marsh during the day

Pachygrapsus crassipes. Only 1 *E. mordax* and 1 large *A. affinis* each ate a single *P. crassipes* larva, but mid-size *A. affinis* ate 909 *P. crassipes* larvae, comprising 28.6% of the diet. Mid-size *A. affinis* also ate 43 *Hemigrapsus* spp. larvae (9.2% of the diet) and were the only fish species to do so. Together, *P. crassipes* and *Hemigrapsus* spp. comprised 37.8% of the diet of mid-size *A. affinis*, and these larvae were eaten only during twilight spring tides when they were preferred (electivity = 0.30) to other prey items ($p = 0.055$); however, fish were not collected during intermediate amplitude tides, twilight neap tides and daytime spring tides (Fig. 6C,D). Pinnotherid larvae were not eaten, but they were uncommon, comprising only 1.75% of zooplankters (Fig. 4, Table S1 in the Supplement). Overall, decapod larvae comprised 4.1% of the diets of 3 of 11 fishes (including all size classes of *A. affinis*), and these fishes avoided eating them (mean electivity for the 3 species = -0.77).

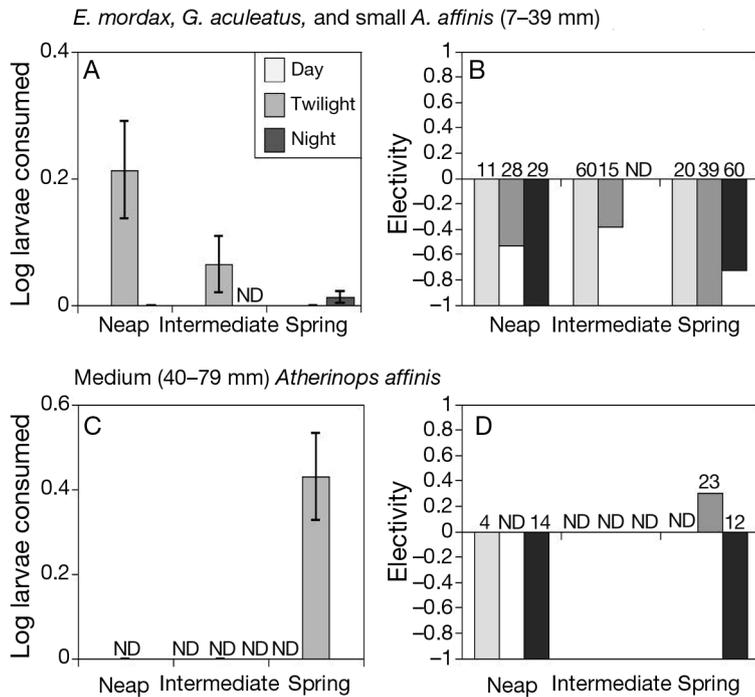


Fig. 6. (A,B) Predation by *Engraulis mordax*, *Gasterosteus aculeatus* and small (7 to 39 mm) *Atherinops affinis* on *Neotrypaea californiensis* larvae during high tides relative to tidal amplitude and diel cycles: (A) mean log number (± 1 SE) eaten and (B) electivities. (C,D) Predation by mid-size (40 to 79 mm) *A. affinis* on *Hemigrapsus oregonensis* and *Pachygrapsus crassipes* larvae during high tides relative to tidal amplitude and diel cycles: (C) mean log number (± 1 SE) eaten and (D) electivities. Positive electivity values indicate preference, negative values indicate avoidance and zero indicates prey items were eaten randomly. ND indicates that fish were not captured. Numbers above each bar = numbers of fish examined

DISCUSSION

Timing of larval release

Larval release by 3 species (*Pachygrapsus crassipes*, *Hemigrapsus oregonensis* and *Neotrypaea californiensis*) in this strong, persistent upwelling region peaked during the safe period (nocturnal maximum amplitude ebb tides) but was weakly synchronous. The 3 environmental cycles (light, tidal amplitude and time from high tide) explained only 44.2 to 53.1% of the variation in the timing of larval release, which most frequently occurred (1) during larger amplitude tides, (2) during low light levels (twilight and darkness) and (3) following high tide. However, analyses could not explain the presence and absence of larvae; larvae were present for all 3 environmental cycles. Larval release outside the safe period is risky because the higher of the 2 high tides each day occurs at twilight during intermediate amplitude

tides and in daylight during neap tides. As expected, larval release by the high intertidal species (*P. crassipes*) coincided most closely with the safe period, peaking during spring tides within 30 min of high slack tides at twilight rather than night. By being inundated more days of the month, the 2 species living lower on the shore were less constrained to release larvae during the safe period, with peak release occurring during intermediate rather than spring tides and 30 min later during ebb tides at twilight rather than night. Thus, peak larval release by the high intertidal species was offset from the safe period by the diel cycle, and it was offset by all 3 environmental cycles for species living lower on the shore, potentially resulting in less effective transport of larvae into deeper waters (where there are fewer fish predators) when larvae are more visible to predatory fishes (Morgan & Christy 1994, Morgan 1996, Hovel & Morgan 1997).

Larval release by the 3 species of pinnotherid crabs in the low intertidal zone was the least synchronous, often occurring during the daytime on lower amplitude tides and flood tides. In contrast to *Pachygrapsus crassipes*, *Hemigrapsus oregonensis* and *Neotrypaea californiensis*, larval abundances of the pinnotherids may not accurately reflect the timing of larval release, because 2 of the 3 low intertidal crabs did not release larvae during ebb tides, as is typical worldwide (Morgan 1995, Thurman 2004). First stage pinnotherid larvae could have been transported back into marshes by flood tides, obscuring larval release patterns. The larvae of pinnotherids are often retained in the estuary because they occur deeper in the water column than larvae of other species, slowing seaward transport and increasing retention in estuaries (Hsueh 2002, Morgan & Fisher 2010). However, we cannot eliminate the possibility that the timing of larval release by these commensal crabs was displaced from the safe period by rhythmic activity of suspension-feeding hosts.

The weak synchrony in cold upwelling regimes may be due to the extended incubation times of externally brooded embryos that were exposed to increased cumulative variance in temperature (Backwell & Passmore 1996, Christy 2003, Morgan et al. 2011), similar to spring in warm-temperate zones, when temperature is more variable (Wheeler 1978,

Dollard 1980, Christy 1982). Crabs were unable to effectively regulate the thermal environment of embryos, as they do in warm upwelling regimes, because cold temperatures greatly increase incubation times, exposing broods to more temperature variation (Christy 2003, Morgan et al. 2011).

The safe period does occur in mixed semidiurnal tidal regimes, and therefore weak synchrony cannot be explained by the absence of time when larvae can be safely released (Morgan & Christy 1994, Morgan 1996, Kellmeyer & Salmon 2001, Weaver & Salmon 2002, Morgan et al. 2011). Nor can it be explained by imprecision introduced by inferring synchrony in hatching from larval abundances in the plankton, because relatively few first stage larvae of species that develop offshore are swept back into marshes during flood tides (Hovel & Morgan 1997). The high intertidal species are rapidly transported from bays and estuaries onto the continental shelf, so that few first stage larvae are present during subsequent flood tides to obscure hatching patterns (Morgan et al. 2009, Morgan & Fisher 2010, Breckenridge & Bollens 2011). Moreover, peak larval release by *Pachygrapsus crassipes* occurred at the same time as it did in a complementary field experiment in which ovigerous crabs were held in a mesocosm near adult populations, and the total amount of hatched larvae were sampled every 30 min during high tides for a month (L. K. Rasmuson et al. unpubl. data). Unlike larvae, demersal zooplankters were abundant throughout the 3 environmental cycles and were consistently available to predatory fishes.

Fish predation

Decapod larvae were expected to be most abundant in fish diets away from the safe period during peak release on intermediate amplitude tides at twilight, when larvae were more visible and less effectively transported from marshes toward the sea. Indeed, larvae were almost entirely eaten (99.8%) at twilight during peak release, when they were more visible than at night. *Atherinops affinis*, *Engraulis mordax* and *Gasterosteus aculeatus* all consumed decapod larvae, and mid-size *A. affinis* ate many of them (37.8% of diet). Even though larvae often were not released at the safest time, they comprised only 4.1% of the diets of these fishes and a far smaller percentage than were available in the plankton (electivity = -0.77). Fishes characteristically preferred demersal zooplankton (Loukashkin 1970, Worgan & FitzGerald 1981, Barry et al. 1996).

We were initially surprised that fishes did not eat many decapod larvae during the daytime, because larvae were present and most visible then. However, on closer inspection, the results make sense because fish predators were frequently absent during daylight tides. *Engraulis mordax* were only present at night, and the only size class of *Atherinops affinis* to eat many decapod larvae usually were also absent during the day. Only 4 mid-size *A. affinis* were caught during the daytime, and they were caught during a neap tide, when the fewest larvae were present. Small *A. affinis* and *Gasterosteus aculeatus* were present during the daytime, but they may simply prefer more abundant demersal zooplankton to well-defended decapod larvae. They did not prey on larvae at all during the daytime, and they strongly avoided them during twilight, when larvae were more abundant. Fishes did not migrate into marshes on flood tides to exploit the high concentrations of decapod larvae released outside the safe period, which is to be expected given that all but mid-size *A. affinis* preferred other prey.

Pinnotherid larvae were not eaten by fishes even though they were most abundant when they would be easily seen. Larvae may have escaped predation because fishes that ate decapod larvae primarily fed at twilight and night. The long pair of posteriolateral spines and being uncommon (only 1.75% of the zooplankton community) also may have contributed to the lack of predation on pinnotherid larvae. We cannot rule out that these larvae were chemically defended. A pinnotherid crab (*Pinnotheres ostrium*) is the only known species of decapod with chemically defended larvae, although chemical defense may substitute for the absence of larval spines in this species (Luckenbach & Orth 1990).

Estuarine fishes outside upwelling regions also mostly consume demersal zooplankton and much prefer them to well-defended decapod larvae (Morgan 1990). On the Atlantic and Gulf coasts of the USA, similar planktivores (*Anchoa mitchilli*, *Menidia menidia* and *Fundulus heteroclitus*) ate numbers of decapod larvae comparable to *Engraulis mordax* and *Atherinops affinis* in our study. Larvae of confamilial shore crabs *Sesarma cinereum* and *S. reticulatum* and shrimp *Palaemonetes pugio* were avoided as much on the Atlantic and Gulf coasts (Kneib 1984, Heck et al. 2001), as were morphologically similar larvae in the present study. On the Atlantic and Gulf coasts, only small fiddler crab *Uca* spp. larvae composed a substantial component of the diets of *A. mitchilli* and *M. menidia*, and they were eaten by all sizes of these fishes (Morgan 1990). Similar larvae

do not occur in our study system for comparison, and, consequently, predation on larvae released outside the safe period was much less than was initially expected. Thus, the vulnerability of morphologically similar decapod larvae is comparable among coasts, even though larvae were released at times that were expected to be riskier on the west coast.

CONCLUSION

Many larvae were released outside the safe period, and fish predation was greater on decapod larvae that were released in twilight than darkness. However, larvae did not comprise a substantial portion of the diets of the 2 dominant species of fishes for 2 reasons. First, *Engraulis mordax* and the only size class of *Atherinops affinis* to prey on larvae in substantial numbers usually were absent from marshes when larvae were most vulnerable to predation. Second, larvae of the decapod species that inhabit marshes are sufficiently well defended that fishes preferred other prey. Additional sampling is required to determine the temporal use and diets of *E. mordax* and *A. affinis* in marshes to determine whether our results are typical. If so, mistiming larval release may not greatly increase predation on larvae of these decapods, possibly explaining why females did not delay larval release in the presence of predatory fishes (L. K. Rasmuson et al. unpubl.). Even so, larvae released outside the safe period would be eaten more than those that were released during the safe period, providing selection for the timing of larval release. Thus, the selective effects of fish predation may be relaxed, raising the possibility that the strength of fish predation as a selective force varies among coasts.

A key difference in marshes on the 3 coasts of the USA is that fishes are much more abundant at twilight than during the daytime or night in marshes on the west coast, whereas they are abundant throughout the day on the east and Gulf coasts (Morgan 1990, Hovel & Morgan 1997, S. T. McAfee & S. G. Morgan unpubl.). Nocturnal and diurnal fish communities may change at twilight, reducing predation, as occurs in kelp forests on the west coast and on coral reefs (Hobson & Chess 1976, 1978, Hobson et al. 1981). Fishes may enter shallow marshes to forage during twilight high tides for the same reason: the assemblage of piscivores fishes (Table S3 in the Supplement) and birds (herons and egrets) in the marsh may turn over at twilight. Moreover, marine and freshwater fishes undertake ontogenetic migra-

tions from vegetated nursery habitats to open waters after they are better able to fend for themselves and escape predators (Weinstein 1979, Werner & Hall 1988). Small juvenile fishes evidently are orders of magnitude more abundant in marshes on the east and Gulf coasts than the west coast, and juvenile fishes are exclusively zooplanktivorous regardless of their dietary preferences as adults (Lazzaro 1987, Morgan 1990). Predatory shrimp and juvenile crabs *Callinectes sapidus* are also much more abundant in marshes on the east and Gulf coasts (Kneib 1984, Heck et al. 2001), and they prey on crab larvae (Morgan 1992, S. G. Morgan & S. T. Miller unpubl.). Fishes and shrimps attain densities over 5000 individuals m^{-2} during low tide (Kneib 1984) and would decimate newly hatched larvae that were not transported to deeper waters during the safe period (Morgan 1990, Morgan & Christy 1995, 1997, Hovel & Morgan 1997). Thus, a much stronger predation gradient occurs on the east and Gulf coasts than the west coast because of different abundances and species compositions of fishes and crustaceans and fundamental differences in the life histories of the dominant planktivorous fishes inhabiting marshes on the 3 coasts, which occur in different families (Gasterosteidae vs. Fundulidae), subfamilies (Atherinopsinae vs. Menidiinae) or genera (*Engraulis* vs. *Anchoa*).

Acknowledgements. We thank J. Couture for her assistance with fieldwork. We thank J. Fisher and S. Miller for their assistance in the development and early analyses of this experiment. L. Peteiro greatly assisted with the development of the GAMs. J. Christy's comments improved the manuscript considerably. Funding was provided by the Murdock Charitable Trust and National Science Foundation (OCE-0326110).

LITERATURE CITED

- Adamczewska AM, Morris S (2001) Ecology and behavior of *Gecarcoidea natalis*, the Christmas Island red crab, during the annual breeding migration. *Biol Bull* 200:305–320
- Backwell PRY, Passmore NI (1996) Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the fiddler crab, *Uca annulipes*. *Behav Ecol Sociobiol* 38:407–416
- Barry SC, Welsh AH (2002) Generalized additive modelling and zero inflated count data. *Ecol Model* 157:179–188
- Barry JP, Yoklavich MM, Cailliet GM, Ambrose DA, Antrim BS (1996) Trophic ecology of the dominant fishes in Elkhorn Slough, California, 1974–1980. *Estuaries Coasts* 19:115–138
- Bernardo J (1996) Maternal effects in animal ecology. *Am Nat* 36:83–105
- Breckenridge JK, Bollens SM (2011) Vertical distribution and migration of decapod larvae in relation to light

- and tides in Willapa Bay, Washington. *Estuaries* 34: 1255–1261
- Chesson J (1983) The estimation and analysis of preference and its relationship to foraging models. *Ecology* 64: 1297–1304
- Christy JH (1982) Adaptive significance of semilunar cycles of larval release in fiddler crabs (genus *Uca*): test of an hypothesis. *Biol Bull* 163:251–263
- Christy JH (1986) Timing of larval release by intertidal crabs on an exposed shore. *Bull Mar Sci* 39:176–191
- Christy JH (2003) Reproductive timing and larval dispersal of intertidal crabs: the predator avoidance hypothesis. *Rev Chil Hist Nat* 76:177–185
- Christy JH (2011) Timing of hatching and release of larvae by brachyuran crabs: patterns, adaptive significance and control. *Integr Comp Biol* 51:62–72
- Christy JH, Morgan SG (1998) Estuarine immigration by crab postlarvae: mechanisms, reliability and adaptive significance. *Mar Ecol Prog Ser* 174:51–65
- Christy JH, Backwell PRY, Goshima S (2001) The design and production of a sexual signal: hoods and hood building by male fiddler crabs *Uca musica*. *Behaviour* 138: 1065–1083
- Danks HV (2002) Modification of adverse conditions by insects. *Oikos* 99:10–24
- DeCoursey PJ (1983) Biological timing. In: Vernberg F, Vernberg W (eds) *The biology of Crustacea*, Vol 7: Behaviour and ecology. Academic Press, New York, NY, p 107–162
- Dollard HA (1980) Larval release patterns in the wharf crab, *Sesarma cinereum*, from North Inlet, South Carolina. MSc thesis, University of South Carolina, Columbia, SC
- Guisan A, Edwards TC Jr, Hastie T (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecol Model* 157: 89–100
- Heck KL Jr, Coen LD, Morgan SG (2001) Pre- and post-settlement factors as determinants of juvenile blue crab *Callinectes sapidus* abundance: results from the north-central Gulf of Mexico. *Mar Ecol Prog Ser* 222:163–176
- Hobson ES, Chess JR (1976) Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. *Fish Bull* 74:567–598
- Hobson ES, Chess JR (1978) Trophic relationships among fishes and plankton in the lagoon at Enewetok Atoll, Marshall Islands. *Fish Bull* 76:133–153
- Hobson ES, McFarland WN, Chess JR (1981) Crepuscular and nocturnal activities of Californian nearshore fishes, with consideration of their scotopic visual pigments and the photic environment. *Fish Bull* 79:1–30
- Hovel KA, Morgan SG (1997) Planktivory as a selective force for reproductive synchrony and larval migration. *Mar Ecol Prog Ser* 157:79–95
- Hsueh PW (2002) Larval release rhythms of four species (family Grapsidae and Ocypodidae) of intertidal crabs on a coastal flat in western central Taiwan. *J Nat Hist* 36: 1341–1349
- Ims RA (1990) The ecology and evolution of reproductive synchrony. *Trends Ecol Evol* 5:135–140
- Johannes RE (1978) Reproductive strategies of coastal marine fishes in the tropics. *Environ Biol Fishes* 3:65–84
- Kellmeyer K, Salmon M (2001) Hatching rhythms of *Uca thayeri* Rathbun: timing in semidiurnal and mixed tidal regimes. *J Exp Mar Biol Ecol* 260:169–183
- Kerr KA, Christy JH, Collin R, Guichard F (2012) Reducing error in reproductive timing caused by temperature variation: interspecific differences in behavioural adjustment by fiddler crabs. *Mar Ecol Prog Ser* 459:1–16
- Kneib RT (1984) Patterns of invertebrate distribution and abundance in the intertidal salt marsh: causes and questions. *Estuaries* 7:392–412
- Korringa P (1947) Relations between the moon and periodicity in the breeding of marine animals. *Ecol Monogr* 17: 347–381
- Lazzaro X (1987) A review of planktivorous fishes: their evolution, feeding behaviours, selectivities, and impacts. *Hydrobiologia* 146:97–167
- Limpus CJ, Miller JD, Paramenter CJ, Reimer D, McLachlan N, Webb R (1992) Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern Australian rookeries. *Wildl Res* 19:347–357
- López-Duarte PC, Christy JH, Tankersley RA (2011) A behavioral mechanism for dispersal in fiddler crab larvae (genus *Uca*) varies with adult habitat, not phylogeny. *Limnol Oceanogr* 56:1879–1892
- Loukashkin AS (1970) On the diet and feeding behavior of the northern anchovy, *Engraulis mordax* (Girard). *Proc Calif Acad Sci* 37:419–458
- Luckenbach MW, Orth RJ (1990) A chemical defense in crustacea? *J Exp Mar Biol Ecol* 137:79–87
- Morgan SG (1987) Morphological and behavioral antipredatory adaptations of decapod zoeae. *Oecologia* 73: 393–400
- Morgan SG (1989) Adaptive significance of spination in estuarine crab zoeae. *Ecology* 70:464–482
- Morgan SG (1990) Impact of planktivorous fishes on dispersal, hatching and morphology of estuarine crab larvae. *Ecology* 71:1639–1652
- Morgan SG (1992) Predation by planktonic and benthic invertebrates on larvae of estuarine crabs. *J Exp Mar Biol Ecol* 163:91–110
- Morgan SG (1995) The timing of larval release. In: McEdward L (ed) *Ecology of marine invertebrate larvae*. CRC Press, Boca Raton, FL, p 157–191
- Morgan SG (1996) Plasticity in reproductive timing by crabs in adjacent tidal regimes. *Mar Ecol Prog Ser* 139:105–118
- Morgan SG (2006) Larval migrations between the Hudson River estuary and New York bight. In: Levinton JS, Waldman JR (eds) *The Hudson River estuary*. Cambridge University Press, New York, NY, p 157–170
- Morgan SG, Anastasia JR (2008) Behavioral tradeoff in estuarine larvae favors seaward migration over minimizing visibility to predators. *Proc Natl Acad Sci USA* 105: 222–227
- Morgan SG, Christy J (1994) Plasticity, constraint, and optimality in reproductive timing. *Ecology* 75:2185–2203
- Morgan SG, Christy J (1995) Adaptive significance of the timing of larval release by crabs. *Am Nat* 145:457–479
- Morgan SG, Christy JH (1997) Planktivorous fishes as selective agents for reproductive synchrony. *J Exp Mar Biol Ecol* 209:89–101
- Morgan SG, Fisher JL (2010) Larval behavior regulates nearshore retention and offshore migration in an upwelling shadow and along the open coast. *Mar Ecol Prog Ser* 404:109–126
- Morgan SG, Fisher JL, Miller SH, McAfee ST, Largier JL (2009) Nearshore larval retention in a region of strong upwelling and recruitment limitation. *Ecology* 90:3489–3502
- Morgan SG, White JW, McAfee ST, Gaines SD, Schmitt RJ (2011) Weak synchrony in the timing of larval release in

- upwelling regimes. *Mar Ecol Prog Ser* 425:103–112
- Paula J, Bartilotti C, Dray T, Macia A, Queiroga H (2004) Patterns of temporal occurrence of brachyuran crab larvae at Saco mangrove creek, Inhaca Island (south Mozambique): implications for flux and recruitment. *J Plankton Res* 26:1163–1174
- R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Reaney LT, Backwell PRY (2007) Temporal constraints and female preference for burrow width in the fiddler crab, *Uca mjoebergi*. *Behav Ecol Sociobiol* 61:1515–1521
- Richter HV, Cumming GS (2006) Food availability and annual migration of the straw-colored fruit bat (*Eidolon helvum*). *J Zool* 268:35–44
- Robertson DR, Petersen CW, Brawn JD (1990) Lunar reproductive cycles of benthic-brooding reef fishes: Reflections of larval biology or adult biology? *Ecol Monogr* 60: 311–329
- Salmon M, Seiple WH, Morgan SG (1986) Hatching rhythms of fiddler crabs and associated species at Beaufort, North Carolina. *J Crustac Biol* 6:24–36
- Satake A, Iwasa Y (2002) The synchronized and intermittent reproduction of forest trees is mediated by the Moran effect, only in association with pollen coupling. *J Ecol* 90: 830–838
- Shapiro DY, Sadovy Y, McGhee MA (1993) Size, composition and spatial structure of the annual spawning aggregation of the red hind, *Epinephelus guttatus* (Pisces: Serranidae). *Copeia* 1993:399–406
- Shine R (2005) Life-history evolution in reptiles. *Annu Rev Ecol Syst* 36:23–46
- Smyder EA, Martin KLM (2002) Temperature effects on eggs survival and hatching during the extended incubation period of California grunion, *Leuresthes tenuis*. *Copeia* 2002:313–320
- Thurman CL (2004) Unravelling the ecological significance of endogenous rhythms in intertidal crabs. *Biol Rhythm Res* 35:43–67
- Warkentin KM (2011) Plasticity of hatching in amphibians: evolution, trade-offs, cues and mechanisms. *Integr Comp Biol* 51:111–127
- Weaver A, Salmon M (2002) Hatching rhythms of *Uca thayeri*: evidence for phenotypic plasticity. *J Crustac Biol* 22: 429–438
- Weinstein MP (1979) Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. *Fish Bull* 77:339–356
- Werner EE, Hall DJ (1988) Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology* 69:1352–1366
- Westneat DF (1992) Nesting synchrony by female red-winged blackbirds: effects on predation and breeding success. *Ecology* 73:2284–2294
- Wheeler DE (1978) Semilunar hatching periodicity in the mud fiddler crab *Uca pugnax* (Smith). *Estuaries* 1: 268–269
- Wood SN (2006) Generalized additive models: an introduction with R. Chapman & Hall/CRC, Boca Raton, FL
- Worgan JP, FitzGerald GJ (1981) Diel activity and diet of three sympatric sticklebacks in tidal salt marsh pools. *Can J Zool* 59:2375–2379
- Yee TW, Mitchell ND (1991) Generalized additive models in plant ecology. *J Veg Sci* 2:587–602

*Editorial responsibility: Paul Snelgrove,
St. John's, Newfoundland and Labrador, Canada*

*Submitted: December 12, 2012; Accepted: June 27, 2013
Proofs received from author(s): September 4, 2013*