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Phenotypic plasticity in larval swimming behavior in estuarine and coastal crab populations

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ABSTRACT

The timing of vertical migrations by newly-hatched larvae determines the extent of transport away from adult populations and exposure to predatory fishes, but it is largely unknown whether larval swimming behavior is a fixed trait or changes adaptively in response to different ocean conditions that are encountered between habitats. We determined whether larvae of the shore crab, *Pachygrapsus crassipes*, hatched in the San Francisco Estuary and those hatched nearby on the outer coast undertake tidal and diel vertical migrations. Vertical swimming of larvae that were released by females collected from the two locations were recorded in the laboratory for up to four days in constant darkness without a tidal cycle to detect the presence of endogenous tidal and diel vertical migrations. *P. crassipes* larvae from the outer coast population did not exhibit rhythmic vertical migrations, remaining near the surface throughout the day, whereas larvae from the estuarine population did undertake complex vertical migrations relative to tidal and diel cycles. Although current patterns differ on the open coast and in the estuary, remaining in surface waters at both locations would favor seaward transport of larvae to offshore nursery areas. However, undertaking tidal vertical migrations in estuaries would expedite seaward transport while increasing the risk of fish predation during the daytime. The differences in behaviors are likely phenotypic, because larvae came from neighboring populations and intermingle in offshore larval nursery areas. This spatial variation in larval swimming behavior among habitats enhances transport to offshore nursery areas.

1. Introduction

Newly hatched larvae of coastal invertebrates are released into a dangerous environment of suspension feeders, planktivorous fishes, and turbulent currents (Morgan, 1995). Though many larvae complete the majority of their development in deeper nearshore or offshore waters, they run a hazardous gauntlet to reach those safer nursery areas, which can have a critical effect on their survival (Morgan, 1990; Morgan and Anastasia, 2008; Strathmann et al., 2002). Larvae released in different habitats, such as estuaries and the outer coast, contend with diverse obstacles to reaching nursery habitats. How larvae that are released into these different habitats reach safer offshore nursery areas while avoiding the dangers of their natal environment is poorly understood.

Larvae of many marine invertebrates exhibit complex behaviors that help direct their transport (Cowen et al., 2006; Kingsford et al., 2002; Queiroga et al., 2007). Many larvae exploit vertically stratified water columns by moving upward and downward between currents that flow at different speeds or in opposite directions, thereby regulating their dispersal distance in response to external cues that are associated with the tidal cycle (Bennett et al., 2002; Forward and Tankersley, 2001; Queiroga and Blanton, 2005). This type of swimming behavior is known as selective tidal stream transport (STST), and has been particularly well documented for crustaceans in Atlantic tidal estuaries, where it aids the departure of newly released larvae from an estuary, and the arrival of postlarvae returning from the ocean to adult habitat (e.g., Cronin and Forward, 1979; Forward et al., 2003; Lopez-Duarte and Tankersley, 2007b; Olaguer-Feliu et al., 2010; Queiroga et al., 1997). One type of STST is reverse tidal vertical migration (RTVM), where larvae swim toward the fast-moving surface waters during ebb tides and toward the slow-moving bottom waters during flood tide, which expedites transport from estuaries to the open ocean (see Gibson, 2003 for review). STST can be modified when larvae also undertake diel vertical migrations whereby they descend into darker portions of the water column during the day to avoid visually feeding fishes and return to the surface to feed at night (DeRobertis et al., 2000).

While estuarine crab larvae frequently exhibit complex swimming behaviors that aid their departure from estuaries, species from the outer coast may have simpler behaviors (Lopez-Duarte and Tankersley, 2007a; Lopez-Duarte et al., 2011; Miller and Morgan, 2013). No study, however, has compared larval swimming behaviors between different populations of the same species from estuarine and outer coast habitats to determine whether the behaviors are phenotypically

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plastic. Numerous crustacean species live in both outer coast and estuarine habitats in the northeastern Pacific Ocean (e.g., *Cancer antennarius*, *Hemigrapsus nudus*, *Pachygrapsus crassipes*), and larvae in different habitats might exhibit different swimming behaviors. Larvae from coastal populations are spawned much closer to offshore nurseries and have to contend with a different set of factors influencing their immediate transport (e.g., weaker tides, stronger winds) than those experienced by larvae from estuarine populations (e.g., lower salinities, higher predation), which could lead to different swimming behaviors among populations (Hovel and Morgan, 1997; Lopez-Duarte et al., 2011; Miller and Morgan, 2013; Morgan, 1990).

Differences in larval behavior among populations could be the result of differences in abiotic and biotic factors in each habitat. Abiotic factors (e.g., light, temperature, pressure, and salinity) and biotic factors (e.g., food and predators; Queiroga and Blanton, 2005; Sulkin, 1984; Young, 1995) can cue changes in larval swimming activity and direction that lead to changes in vertical position. Tidal vertical migrations can be timed exogenously or endogenously by cues that oscillate over the tidal cycle (e.g., salinity and temperature), whereas diel vertical migrations typically are cued exogenously by daylight (Lopez-Duarte, 2008; Morgan and Anastasia, 2008; Palmer and Williams, 1993). Exogenous cues, such as salinity, and biotic cues, such as predators, can differ dramatically between habitats, resulting in different larval behaviors. Comparing the swimming behaviors of newly released conspecific larvae from different environments will provide new insights into the mechanisms regulating larval transport and add to the growing body of knowledge about where larvae go and how they get there.

We compared the timing of vertical swimming by newly released larvae of the lined shore crab *Pachygrapsus crassipes* from estuarine and outer coast populations. These larvae develop on the middle of the continental shelf before returning to adult habitats in cobble fields or mudflats as postlarvae (Morgan and Fisher, 2010; Morgan et al., 2009a). We expected that larvae hatched in San Francisco Bay would exhibit reverse tidal vertical migrations and diel vertical migrations that expedite transport under the cover of darkness from low salinity waters with high densities of planktivorous fishes (DiBacco et al., 2001). In contrast, we expected that larvae hatched on the outer coast in saline waters with lower densities of planktivorous fishes would not exhibit these rhythmic swimming behaviors (Miller and Morgan, 2013).

2. Materials and methods

We collected ovigerous *Pachygrapsus crassipes* Randall, 1840 from the outer coast at Bodega Harbor (38° 20.129 N, 123° 03.566 W) and the estuary at Stege Marsh in San Francisco Bay (37° 54.458 N, 122° 19.734 W), California (Fig. 1). Bodega Harbor is a small embayment with slight freshwater input in winter and spring, and it is almost entirely flushed during each tidal cycle. In contrast, San Francisco Bay is one of the largest estuaries on the Pacific coast of North America and receives freshwater input year round. In San Francisco Bay, these fresher waters flow offshore at the surface, even during strong flood tides (Fram et al., 2007; Martin, 2006; Martin et al., 2007), and the constricted mouth of the bay results in strong offshore flows during ebb tides. Northern California experiences a mixed semidiurnal tidal regime, which usually consists of two tides that differ in amplitude and shift relative to the phasing of the diel cycle. During our study period in late summer, tidal amplitudes were roughly equal at both sites, ranging from +1.8 m to −0.3 m (Fig. 2). Maximum ebb tides occurred primarily at night, and not all tidal states occurred in both light and dark conditions (Fig. 3). Conducting the study during a time of year when all tidal stages occurred during both day and night would have been ideal, but our study species does not release larvae during the time of year when this occurs.

Crabs of similar size (carapace width 18–21 mm) were collected by hand every 3 d during maximum amplitude low tides in August 2010 (Fig. 2), and embryos were staged to within 2 d of hatching. Crabs were maintained in individual containers at Bodega Marine Laboratory, California for up to 48 h before releasing larvae. Larvae were released at night, and 50 newly released larvae from a single mother were transferred within 8 h of hatching to acrylic columns (180 cm tall by 7.5 cm

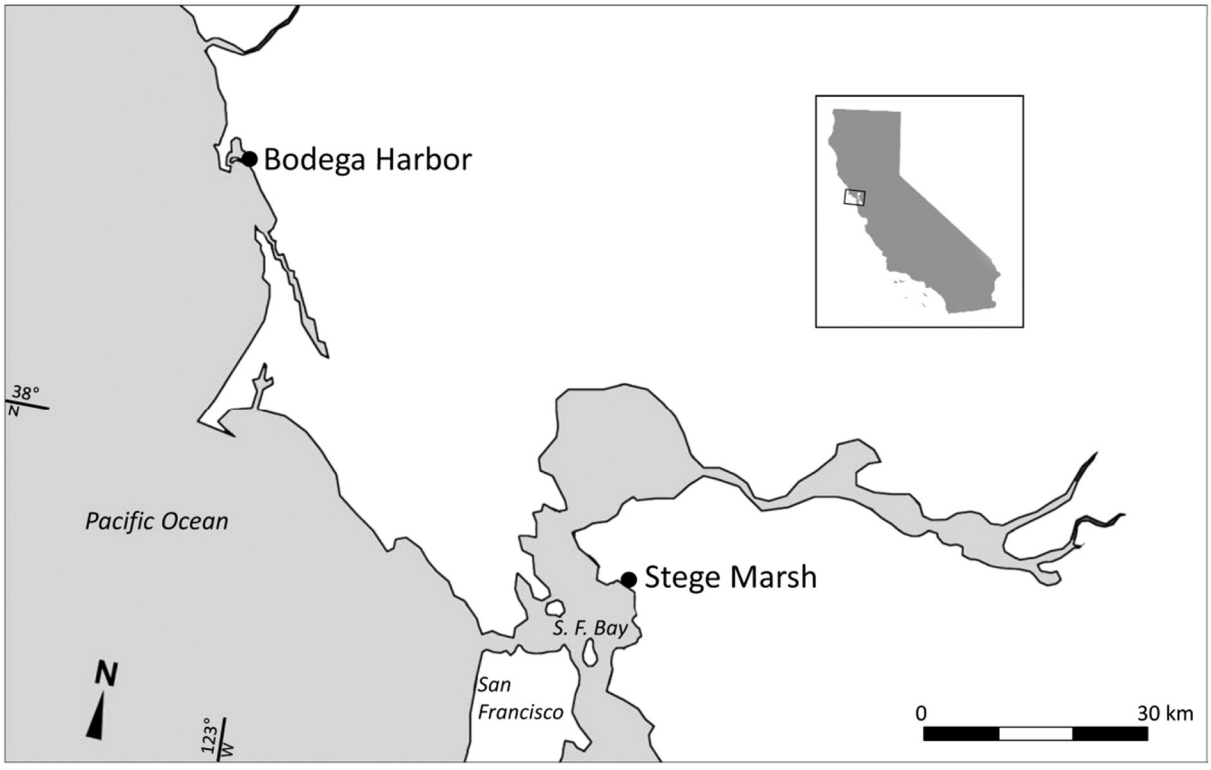

Fig. 1. Map of study region showing outer coast (Bodega Harbor) and estuarine (Stege Marsh) collection sites.

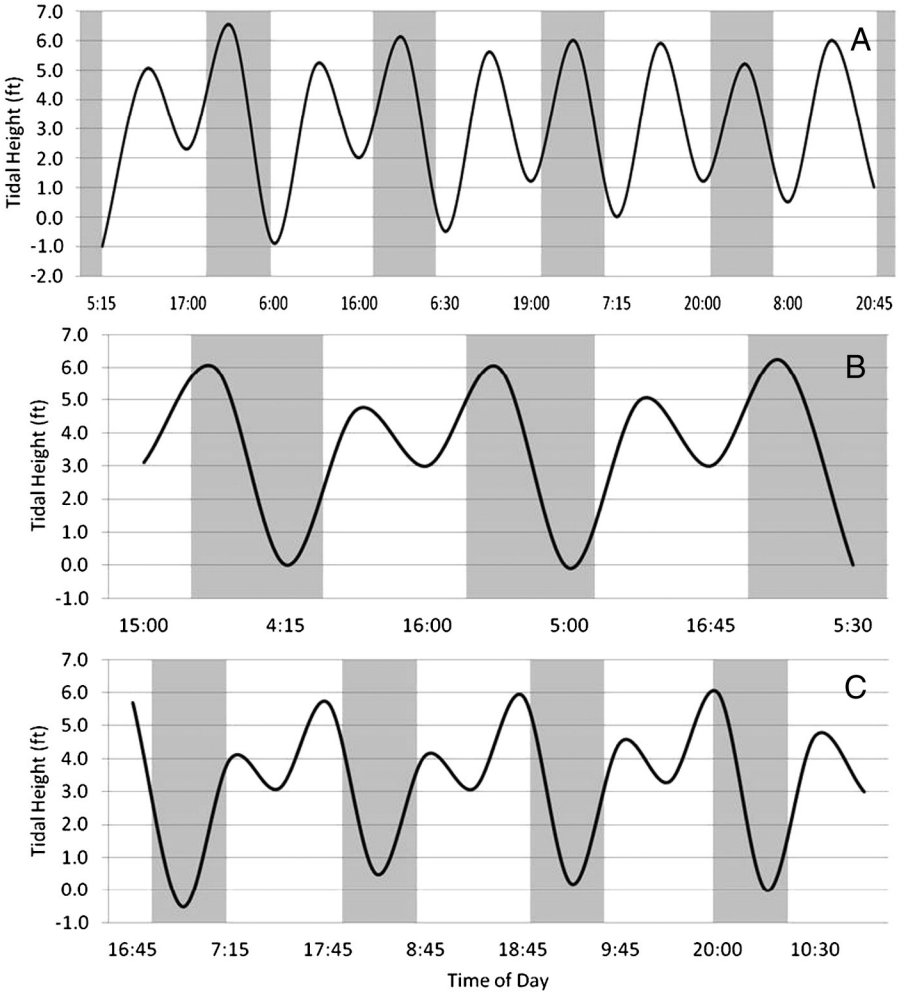

Fig. 2. Predicted tidal height (NOAA tide tables, solid line) and periods of darkness (gray shading) that larvae would have experienced in the field during each of our trials. Trials with coastal larvae took place from August 9 to 13, 2010 (A), and trials with estuarine larvae occurred from August 19 to 21, 2010 (B) and August 31 to September 4, 2010 (C).

diameter) that were filled with seawater from the outer coast (salinity approximately 33) and kept in darkness for the duration of the trial. Larvae were not fed. To maintain constant conditions and focus our study on endogenous rhythms, we did not provide estuarine larvae with the range of salinities or temperatures they might encounter in the field, though we recognize that doing so could yield focused insights into how larvae respond to the range of physical conditions they could encounter during their pelagic durations.

Larvae were recorded using an infrared light and infrared video camera (Swann Security C510R) in a 10-cm segment of the tube that was located approximately 10 cm below the surface of the water column. We restricted observations to the top of the water column because our previous study with *P. crassipes* larvae from the outer coast indicated that larvae remained there regardless of tidal stage (Miller and Morgan, 2013). We also conducted two trials with larvae from the outer coast during this study to ensure that our video system accurately recorded larval distributions at the surface of the column. Observations of the entire water column at the beginning and end of each trial indicated that larvae were not evenly distributed throughout the water column. Larvae were counted in one video frame every 15 min. The duration of trials varied from 39 to 96 h, but most trials lasted at least 72 h; shorter trials were the result of logistical constraints and the requirement that we start each trial with newly released larvae. Five trials were conducted with larvae released by crabs from San Francisco Bay.

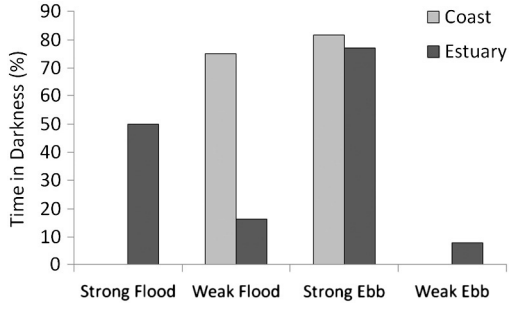

Fig. 3. Percent time larvae would have spent in darkness during each tidal stage in the estuary and on the outer coast for the duration of our study. Time in darkness differed among tidal stages (contingency analysis: $p < 0.0001$), with weak ebb tides occurring almost exclusively during daylight and strong ebb tides occurring primarily at night.

Larval counts were related to the phasing of tidal and diel cycles that larvae would have encountered in the field at that time. Because all trials would have to last for at least 72 h to conduct time series analysis, and endogenous tidal rhythms decay over time, data were classified for univariate analysis. Data were classified relative to the most and least change in tidal amplitude over ebb and flood tides: strong ebb, weak ebb, strong flood and weak flood. Each tidal phase lasted for 6 h, starting 1 h after the predicted time of the tide to one hour after the predicted time of the next tide, to account for residual tidal flows. For example, periods of strong ebb were classified as occurring during the period of greatest change in tidal amplitude from 1 h after high tide until 1 h after low tide. Data also were classified relative to the natural photoperiod (14L:10D).

We analyzed the change in larval counts over the diel cycle using *t*-tests and over the tidal cycle using an analysis of variance (ANOVA). An ANOVA including both tidal stage and diel cycle as factors was not possible because all tidal stages did not occur during both light and dark. Though our data lacked homogeneity of variances, initial single-factor Welch's ANOVAs showed our results to be highly significant (Welch's $p < 0.0001$) and thus robust to unequal variances. When our ANOVA was significant for a population, we used a Student's *t*-test to investigate differences in larval counts among tidal stages.

We also performed a contingency analysis to determine if the amount of time each tidal stage occurred in darkness differed throughout the study and to establish whether diel swimming behaviors might be influenced by tidal stage. Though it would have been ideal to conduct trials for a long time and test all possible combinations of tide and light, the limited reproductive season of our study species and its release of larvae only during maximum amplitude tides constrained our study. Additionally, trials with larvae from each location were run sequentially due to equipment limitations and collection logistics. Concurrent trials are usually not practicable to conduct, so studies testing the larval behaviors of multiple populations or species use sequential trials (Cronin and Forward, 1983; Forward et al., 2003; Lopez-Duarte and Tankersley, 2007a,b; Lopez-Duarte et al., 2011; Zeng and Naylor, 1996). All analyses were conducted using the JMP 9 statistical software package (SAS Institute, Cary, NC).

3. Results

Estuarine larvae showed persistent swimming behaviors relative to tidal and diel cycles, whereas larvae from the outer coast showed no evidence of vertical migration during the study. Over twice as many estuarine larvae occurred, on average, in surface waters during periods when they would have experienced strong flood tides than during times they would have experienced weak flood tides (Fig. 4; ANOVA: $F_{3,1264} = 13.36$, $p < 0.0001$). Estuarine larvae also remained high in the water column during periods of ebb tides (Fig. 4). Larvae from the outer coast showed no difference in swimming behavior among tidal stages (Fig. 4; ANOVA: $F_{3,745} = 69.81$, $p = 0.4489$); the mean number of coastal larvae in the surface waters varied by less than one across tidal stages.

Counts of estuarine larvae near the surface also increased during times larvae would have experienced dark rather than light conditions in the field (Fig. 5; *t*-test $p < 0.0001$), largely because the weak flood tide occurred almost exclusively during daylight (Fig. 3). Outer coast larvae showed no pattern of diel vertical swimming, occurring in surface waters in roughly equal numbers during times that larvae would have experienced light and dark conditions in the field (Fig. 5; *t*-test $p = 0.2713$). The tidal and diel cycles were phased such that weak flood and strong ebb tides occurred primarily in darkness at coastal sites during our study, whereas only strong ebb tides occurred during darkness more than half the time at our estuarine site (Fig. 3; contingency analysis $p < 0.0001$).

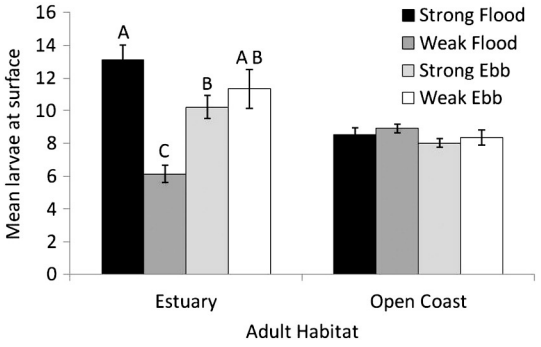

Fig. 4. Mean number of larvae (±1 S.E.) in the surface waters of the column during times that they would have experienced different tidal stages in the field. Larvae from the outer coast showed no differences based on tide (ANOVA: $F_{3,745} = 69.81$, $p = 0.4489$), while the number of larvae from the estuarine population differed among tidal stages (ANOVA: $F_{3,1264} = 13.36$, $p < 0.0001$). Columns connected by the same letter are not significantly different from each other.

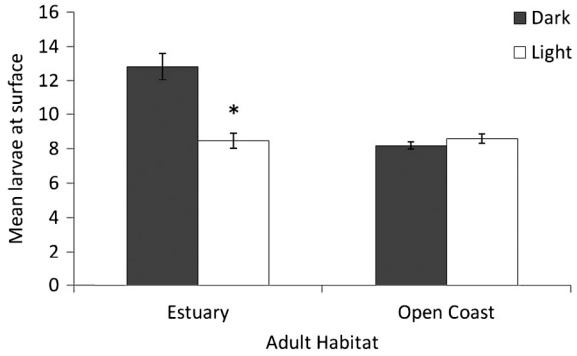

Fig. 5. Mean number of larvae (±1 S.E.) in surface waters during times that they would have experienced light or dark conditions in the field (all trials were conducted in darkness in the laboratory). Fewer larvae from the estuarine population occurred in surface waters during daytime than nighttime (*t*-test: $p < 0.0001$). Larvae from the outer coast population showed no difference in abundance based on field conditions (*t*-test: $p = 0.2713$). The asterisk denotes a significant difference.

4. Discussion

Pachygrapsus crassipes larvae showed clear differences in swimming rhythms based on their natal environment. Larvae from the outer coast showed no repetitive vertical swimming behavior, remaining near the surface regardless of tidal stage, whereas estuarine larvae showed patterns of vertical migrations. Surprisingly, the estuarine larvae did not exhibit a simple RTVM (swimming up on the ebb tide and down on the flood tide), which is a common swimming behavior in Atlantic species (e.g. Lopez-Duarte and Tankersley, 2007b; Queiroga et al., 1997; Zeng and Naylor, 1996) and has been shown for *P. crassipes* larvae in low-inflow Pacific estuaries such as San Diego Bay (DiBacco et al., 2001). Instead, larvae from San Francisco Bay exhibited a complex swimming pattern, moving down on the weak flood tide (but not the strong flood tide) and staying up during daylight hours during the weak ebb tide (but not the weak flood tide). This unusual pattern occurs because the difference in amplitudes between the two flood tides each day, combined with the relatively high freshwater inflow of San Francisco Bay, creates a complicated mosaic of currents much different than those in the low-inflow estuaries of southern California or the estuaries of the eastern United States, which usually experience tides of equal amplitudes.

In Pacific coast estuaries that receive high freshwater inflow, such as San Francisco Bay, remaining in seaward-flowing surface waters over the entire tidal cycle would be the fastest way to exit the estuary. Seaward flow near the surface is fastest during ebb tides. During flood tides, ocean waters rush into estuaries through constricted mouths, and larvae in bottom waters would travel upstream, especially during strong flood tides. Because only fresher surface waters flow offshore or most slowly upstream during strong flood tides in San Francisco Bay (Fram et al., 2007; Martin, 2006; Martin et al., 2007), larvae that remain at the surface at this time would be transported to sea most expeditiously (Fig. 4).

Larvae in the estuary did not remain at the surface during weak flood tides, which primarily occurred during the daytime when they would have been more visible to predatory fishes. During weak flood tides, bottom waters flow weakly into the bay and surface waters flow weakly out of the bay, creating a situation where larvae could enter darker bottom waters without substantially impeding offshore transport. Larvae occupied surface waters during ebb tides, where offshore transport would be expedited, even during weak ebb tides that largely occurred

during the daytime when larvae would have been visible to predatory fishes.

This tradeoff between fast transport and exposure to predation was also found by Morgan and Anastasia (2008) for a species of fiddler crab that spans tidal regimes along the Atlantic and Gulf coasts of the USA. In their study, vertical swimming rhythms matched local tidal regimes, even where nocturnal ebb tides were absent during the reproductive season, necessitating that larvae ascend during daytime ebbs to expedite seaward transport while increasing visibility to predatory fishes. Thus, speeding transport to the nursery grounds was more important than minimizing visibility to predators, and larvae in San Francisco Bay seem to be exhibiting behaviors that result in the same outcome. Studies of vertical swimming rhythms largely have been conducted in predominant semidiurnal tidal regimes, but working in mixed or diurnal tidal regimes where the timing of tidal and diel cycles does not remain in phase provides new insights into the relative importance of these environmental cycles in regulating behavior.

In contrast to their estuarine conspecifics, *Pachygrapsus crassipes* larvae spawned from populations on the outer coast did not exhibit repetitive vertical swimming relative to tidal or diel cycles (Figs. 4 and 5). Instead, they simply remain near the surface where seaward flow transports then offshore (Ekman transport) to nursery areas (Miller and Morgan, 2013; Morgan and Fisher, 2010; Morgan et al., 2009b). In the absence of low salinity, larvae on the outer coast may not be cued to undertake reverse tidal vertical migrations. Selective pressure for STST also may not be as great in coastal populations where salinity stress (Brodie et al., 2007), fish predation (Hovel and Morgan, 1997) and the distance to offshore nursery areas (Lopez-Duarte et al., 2011) are reduced.

The plasticity in larval swimming behavior that we observed in the laboratory has been documented for fiddler crabs from different tidal regimes (Morgan and Anastasia, 2008), and for the estuarine crab *Rhithropanopeus harrisii* that were field-caught or raised in the laboratory in the absence of external cues (Cronin and Forward, 1979, 1983), indicating that these differences could be phenotypic. Additionally, previous work in San Francisco Bay showed that fish larvae can exhibit different vertical migratory behaviors based on interannual changes in river flow, indicating that the behaviors are phenotypically plastic (Bennett et al., 2002). Alternatively, other studies have shown that estuarine larvae lack tidal swimming behaviors when hatched in estuaries with negligible tides (Queiroga et al., 2002), and different species living in different habitats (e.g., estuaries and the outer coast) can exhibit diverse larval swimming behaviors (Lopez-Duarte, 2008; Lopez-Duarte and Tankersley, 2007b; Lopez-Duarte et al., 2011; Miller and Morgan, 2013), which would indicate a genetic component to these swimming behaviors.

While we cannot conclusively determine whether the observed differences in larval behaviors in our study resulted from differences in genotypes or phenotypes without conducting reciprocal transplant experiments, we hypothesize that there were phenotypic differences created either by the abiotic conditions experienced by the developing embryos, such as salinity, or by differences in maternal behaviors, such as abdomen flapping (Barnwell, 1968; Lopez-Duarte and Tankersley, 2007a; Morgan, 1996). If the swimming behaviors were instead the result of differences between two genetically isolated populations, it would require that larvae hatched in each location spend six months together in a common offshore nursery area and then return to settle near their natal site, or else exhibit behaviors that are unsuitable to their new habitat (Barnwell, 1976; Thurman, 2004). This type of extremely specific site affinity seems highly unlikely, particularly given *Pachygrapsus crassipes*' long pelagic larval duration and occurrence over thousands of kilometers of the coast of North America. Additionally, a large-scale study of *P. crassipes* genetics indicated that populations along the coast were relatively well mixed (Cassone and Boulding, 2006).

In addition to reciprocal translocations, future fine-scale genetic analyses of coastal and estuarine populations and tracking larval cohorts would allow researchers to definitively determine if these populations are genetically isolated or if these larval behaviors are indeed plastic and based on habitat, as we propose. Additional investigations using multiple salinity treatments in the laboratory or over multiple summers and locations along the coast also would help further our understanding of how these larvae behave in variable estuarine environments. Our research is the first to show that larval swimming behaviors can vary naturally among populations of the same species in the same tidal regime based on habitat differences, indicating that phenotypic plasticity in larval behavior based on local conditions could be a key component of the population persistence of conspecifics in diverse environments. Phenotypic plasticity may be widespread in the sea where larvae are released into diverse hydrodynamic conditions across species' ranges (Morgan and Anastasia, 2008).

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References

Barnwell, F.H., 1968. The role of rhythmic systems in the adaptation of fiddler crabs to the intertidal zone. Am. Zool. 8, 569–583.
Barnwell, F.H., 1976. Variation in the form of the tide and some problems it poses for biological timing systems. In: De Coursey, P.J. (Ed.), Biological Rhythms in the Marine Environment. University of South Carolina Press, Columbia, SC, pp. 161–187.
Bennett, W.A., Kimmerer, W.J., Burau, J.R., 2002. Plasticity in vertical migration by native and exotic estuarine fishes in a dynamic low-salinity zone. Limnol. Oceanogr. 47 (5), 1496–1507.
Brodie, R.J., Styles, R., Borgianini, S., Godley, J., Butler, K., 2007. Larval mortality during export to the sea in fiddler crab *Uca minax*. Mar. Biol. 152, 1283–1291.
Cassone, B.J., Boulding, E.G., 2006. Genetic structure and phyogeography of the lined shore crab, *Pachygrapsus crassipes*, along the northeastern and western Pacific coasts. Mar. Biol. 149, 213–226.
Cowen, R.K., Paris, C.B., Srinivasan, A., 2006. Scaling of connectivity in marine populations. Science 311, 522–527.
Cronin, T.W., Forward, R.B., 1979. Tidal vertical migration: an endogenous rhythm in estuarine crab larvae. Science 205 (4410), 1020–1022.
Cronin, T.W., Forward, R.B., 1983. Vertical migration rhythms of newly hatched larvae of the estuarine crab, *Rhithropanopeus harrisii*. Biol. Bull. 165, 139–153.
DeRobertis, A., Jaffe, J.S., Ohman, M.D., 2000. Size-dependent visual predation risk and the timing of vertical migration in zooplankton. Limnol. Oceanogr. 45 (8), 1838–1844.
DiBacco, C., Sutton, D., McConnico, L., 2001. Vertical migration behavior and horizontal distribution of brachyuran larvae in a low-inflow estuary: implications for bay-ocean exchange. Mar. Ecol. Prog. Ser. 217, 191–206.
Forward, R.B., Tankersley, R.A., 2001. Selective tidal-stream transport of marine animals. Oceanogr. Mar. Biol. Annu. Rev. 39, 305–353.
Forward, R.B., Tankersley, R.A., Welch, J.M., 2003. Selective tidal-stream transport of the blue crab *Callinectes sapidus*: an overview. Bull. Mar. Sci. 72 (2), 347–365.
Fram, J.P., Martin, M.A., Stacey, M.T., 2007. Dispersive fluxes between the coastal ocean and a semienclosed estuarine basin. J. Phys. Oceanogr. 37, 1645–1660.
Gibson, R.N., 2003. Go with the flow: tidal migration in marine animals. Hydrobiologia 503, 153–161.
Hovel, K.A., Morgan, S.G., 1997. Planktivory as a selective force for reproductive synchrony and larval migration. Mar. Ecol. Prog. Ser. 157, 79–95.
Kingsford, M.J., Leis, J.M., Shanks, A.L., Lindeman, K.C., Morgan, S.G., Pineda, J., 2002. Sensory environments, larval abilities and local self-recruitment. Bull. Mar. Sci. 70 (1 Supplement), 309–340.
Lopez-Duarte, P.C., 2008. Selective tidal-stream transport behavior of fiddler crab (*Uca* spp.) larvae: comparisons among species and different tidal regimes. Florida Institute of Technology, Melbourne, FL 173.
Lopez-Duarte, P.C., Tankersley, R.A., 2007a. Circatidal swimming behaviors of fiddler crab *Uca pugilator* larvae from different tidal regimes. Mar. Ecol. Prog. Ser. 343, 207–220.
Lopez-Duarte, P.C., Tankersley, R.A., 2007b. Circatidal swimming behavior of brachyuran crab zoea larvae: implications for ebb-tide transport. Mar. Biol. 151, 2037–2051.
Lopez-Duarte, P.C., Christy, J.H., Tankersley, R.A., 2011. A behavioral mechanism for dispersal in fiddler crab larvae (genus *Uca*) varies with adult habitat, not phylogeny. Limnol. Oceanogr. 56 (5), 1879–1892.
Martin, M.A., 2006. Chlorophyll and suspended sediment exchange between central San Francisco Bay and the coastal Pacific Ocean. University of California, Berkeley, Berkeley, CA 131.
Martin, M.A., Fram, J.P., Stacey, M.T., 2007. Seasonal chlorophyll *a* fluxes between the coastal Pacific Ocean and San Francisco Bay. Mar. Ecol. Prog. Ser. 337, 51–61.

Miller, S.H., Morgan, S.G., 2013. Interspecific differences in depth preference: regulation of larval transport in an upwelling system. Mar. Ecol. Prog. Ser. 476, 301–306.
Morgan, S.G., 1990. Impact of planktivorous fishes on dispersal, hatching, and morphology of estuarine crab larvae. Ecology 71 (5), 1639–1652.
Morgan, S.G., 1995. Life and death in the plankton: larval mortality and adaptation. In: McEdward, L. (Ed.), Ecology of Marine Invertebrate Larvae. CRC Press, Boca Raton, Florida, pp. 279–322.
Morgan, S.G., 1996. Plasticity in reproductive timing by crabs in adjacent tidal regimes. Mar. Ecol. Prog. Ser. 139, 105–118.
Morgan, S.G., Anastasia, J.R., 2008. Behavioral tradeoff in estuarine larvae favors seaward migration over minimizing visibility to predators. Proc. Natl. Acad. Sci. 105 (1), 222–227.
Morgan, S.G., Fisher, J.L., 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, S.G., Fisher, J.L., Mace, A.J., 2009a. Larval recruitment in a region of strong, persistent upwelling and recruitment limitation. Mar. Ecol. Prog. Ser. 394, 79–99.
Morgan, S.G., Fisher, J.L., Miller, S.H., McAfee, S.T., Largier, J.L., 2009b. Nearshore larval retention in a region of strong upwelling and recruitment limitation. Ecology 90 (12), 3489–3502.
Olaguer-Feliu, A.O., Flores, A.A.V., Queiroga, H., Gonzalez-Gordillo, J.I., 2010. Shelf and estuarine transport mechanisms affecting the supply of competent larvae in a suite of brachyuran crabs with different life histories. Mar. Ecol. Prog. Ser. 410, 125–141.
Palmer, J.D., Williams, B.G., 1993. Comparative studies of tidal rhythms. XII. Persistent photoaccumulation and locomotor rhythms in the crab, *Cyclograpsus lavauxi*. Mar. Freshw. Behav. Physiol. 22 (2), 119–129.
Queiroga, H., Blanton, J., 2005. Interactions between behaviour and physical forcing in the control of horizontal transport of decapod crustacean larvae. Adv. Mar. Biol. 47, 107–214.
Queiroga, H., Costlow, J.D., Moreira, M.H., 1997. Vertical migration of the crab *Carcinus maenas* first zoea in an estuary: implications for tidal stream transport. Mar. Ecol. Prog. Ser. 149, 121–132.
Queiroga, H., Moksnes, P.-O., Meireles, S., 2002. Vertical migration behaviour in the larvae of the shore crab *Carcinus maenas* from a microtidal system (Gullmarsfjord, Sweden). Mar. Ecol. Prog. Ser. 237, 195–207.
Queiroga, H., Cruz, T., Santos, A.d., Dubert, J., Gonzalez-Gordillo, J.I., Paula, J., Peliz, A., Santos, A.M.P., 2007. Oceanographic and behavioural processes affecting invertebrate larval dispersal and supply in the western Iberia upwelling ecosystem. Prog. Oceanogr. 74, 174–191.
Strathmann, R.R., Hughes, T.P., Kuris, A.M., Lindeman, K.C., Morgan, S.G., Pandolfi, J.M., Warner, R.R., 2002. Evolution of local recruitment and its consequences for marine populations. Bull. Mar. Sci. 70 (1 Supplement), 377–396.
Sulkin, S.D., 1984. Behavioral basis of depth regulation in the larvae of brachyuran crabs. Mar. Ecol. Prog. Ser. 15 (1–2), 181–205.
Thurman, C.L., 2004. Unravelling the ecological significance of endogenous rhythms in intertidal crabs. Biol. Rhythm. Res. 35, 43–67.
Young, C.M., 1995. Behavior and locomotion during the dispersal phase of larval life. In: McEdward, L. (Ed.), Ecology of Marine Invertebrate Larvae. CRC Press, Boca Raton, Florida, pp. 249–278.
Zeng, C., Naylor, E., 1996. Endogenous tidal rhythms of vertical migration in field collected zoea-1 larvae of the shore crab *Carcinus maenas*: implications for ebb tide offshore dispersal. Mar. Ecol. Prog. Ser. 132, 71–82.