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**Research Article**

# Environmental factors influencing the dynamics of Chinese mitten crab zoeae in the San Francisco Bay-Delta

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## Abstract

The Chinese mitten crab is an invasive catadromous species that has populated many European estuaries. However, despite repeated 'introductions', the only known established North American population is in the San Francisco Bay Delta, along with recent populations discovered in Chesapeake Bay and the Hudson River. In established populations, adult mitten crab numbers oscillate dramatically, and large numbers of crabs can have severe environmental impacts. Extremely little is known about the biology and ecology of juvenile stages, but understanding the factors behind new cohort survival is crucial for understanding the dynamics of newly-established populations. In this study, we use the only known long-term life-history data set to assess the relative importance of reproductive potential and environmental factors in regulating mitten crab population dynamics in San Francisco Bay. Both exploratory regression tree and bivariate data analyses support the hypotheses that concentrations of planktonic zoeae are strongly influenced by interactions between the number of breeding female crabs, the timing of reproduction, and water temperature. Additional studies are needed in other estuaries invaded by mitten crabs to test the generalities of these relationships and further evaluate the potential of these relationships to inform predictions about the extent and magnitude of mitten crab populations.

**Key words:** mitten crab, *Eriocheir sinensis*, invasive species, San Francisco Bay, zoea

## Introduction

The Chinese mitten crab, *Eriocheir sinensis* (H. Milne-Edwards, 1853), a catadromous brachyuran crab native to eastern China, has become widely established as an invasive species throughout Europe, in San Francisco Bay, USA since 1992 (Rudnick et al. 2000), and more recently in the Chesapeake Bay and Hudson River in the eastern USA (Ruiz et al. 2006; Schmidt et al. 2009). Invasive populations of mitten crabs threaten native species and their habitats, cause bank erosion and collapse in association with burrowing habits (Panning 1939; Dutton and Conroy 1998; Rudnick et al. 2005), and impact commercial and recreational fishing through bait stealing and gear entanglement (Panning 1939; Rudnick and Resh 2002). The mass migration of adult mitten crabs to their breeding grounds in San Francisco Bay has interfered with irrigation pumping systems

and the protection and recovery of endangered and threatened fish species at fish recovery facilities (Siegfried 1999; Rudnick et al. 2000; Rudnick et al. 2005).

These impacts are exacerbated by the complex life history and highly variable population dynamics of the mitten crab. Mitten crabs use several types of aquatic habitats throughout their life: they spend their planktonic larval period in an estuary, settle out as benthic juveniles at the mouths and lower regions of freshwater rivers, and can move up to hundreds of miles upstream into a river system during their juvenile stage before returning to the estuary to reproduce and die. Invasive mitten crab populations have undergone boom-and-bust variations in abundance that occur over periods of less than a decade (Gollasch 1999; Rudnick et al. 2003) and are not well understood. The mitten crab's complex catadromous life history makes it difficult to determine which aspects of the life

cycle have the most influence on this species' population dynamics.

For invading crustaceans with complex life histories such as mitten crabs, the planktonic larval phase is critical for the establishment and persistence of new populations (Anger 2006). Larval supply plays an important role in shaping the population dynamics of marine invertebrates (McConaugha 1992; Todd 1998; Palma et al. 1999). Zoeal abundance may be the best metric for predicting adult mitten crab abundances in future years, given a lack of correspondence in interannual environmental conditions or adult populations due to semelparous reproduction (Panning 1939). Environmental conditions including salinity and temperature may affect the development and survival of crustacean larvae including the Chinese mitten crab, and sensitivity to variation in these conditions can vary over the course of larval development (Dawirs 1985, Charmantier et al. 2002, Rudnick et al. 2005, Anger 1991, 2003, 2006). Low salinities and temperatures have been shown in laboratory studies to adversely affect mitten crab larval growth rate and survival (Anger 1991; Rice 2006; Cieluch et al. 2007). Abundances of planktonic crab larvae in estuaries may be reduced by periods of elevated freshwater discharge (Atrill and Thomas 1996; Queiroga and Blanton 2004).

Therefore, the extent to which environmental conditions match the requirements of the larval stage of this introduced crustacean may be an important determinant of their potential success in a new ecosystem (Bravo et al. 2007; Fowler et al. 2010).

The biology of crustacean larvae is much less understood compared to that of juvenile and adult life history stages (Anger 2006); this is particularly true for mitten crabs, despite their importance as an invasive species (Dittel and Epifaunio 2009). We are not aware of any published studies that provide long-term data on mitten crab zoeae, adults, and the environmental conditions for recruitment to test these theories of larval supply and adult abundance.

In this paper, we use a unique eight-year data set from San Francisco Bay to test for relationships between mitten crab zoeal density and environmental variables that may influence larval survival and population dynamics of this important invasive species. We specifically focus on variation in the abundance of ovigerous adult females (the source of mitten crab zoeae), and

potential agents of zoeal mortality including freshwater discharge, predation, low salinity and temperature. Our objective is to identify environmental variables that are significantly related to and likely influence densities of larval mitten crabs in San Francisco Bay. These relationships may serve to understand how larval supply in turn might shape the population dynamics and impacts of this important invasive species in other invaded and uninvaded estuaries to improve predictions of estuaries capable of sustaining invasive mitten crab populations.

## Methods

### Study area

The San Francisco Bay estuary (N 37°45', W 122°26') is the largest estuary on the U.S. Pacific coast. The Sacramento and San Joaquin Rivers provide the majority of the water inputs to San Francisco Bay. These two rivers drain into a series of downstream bays: Suisun, San Pablo, and finally San Francisco (Figure 1). In this study, we focus on relationships among mitten crab and environmental parameters in San Pablo Bay, for which the most data was available. San Pablo Bay is a large (272 km$^2$), shallow bay characterized by expansive tidal mudflats bisected by a deep channel (10–20m) that is maintained by dredging for ship navigation. Between 1997–2005, during the breeding season for mitten crabs which occurs between November and June, average monthly salinity (in PSU) was 20.8 (range 4.5–29.1), discharge was 1,103 m$^3$/s (range 174–7,350 m$^3$/s), and upper water column temperature 13.6 °C (range 9.5 °C – 19.5 °C).

### Study organism

The Chinese mitten crab was first reported in San Francisco Bay in 1992 and quickly became abundant in the San Francisco Bay system and its tributaries (Rudnick et al. 2003). This catadromous species hatches from brooded eggs in winter or spring in the estuarine waters of San Francisco Bay. Juveniles migrate into freshwater streams in spring and summer. After mitten crabs have reached sexual maturity, estimated at 2–5 years of age and at least 30 mm carapace width, they congregate in the lower portions of freshwater streams and migrate rapidly to San Francisco Bay waters in fall to reproduce (Rudnick et al. 2005). A single female may produce between 250,000 and a million eggs;

**Figure 1.** The San Francisco Bay-Delta which includes San Pablo and Suisun Bays. Individual letters designate sampling sites of: Zoeae (Z1) and (Z2), Discharge (D), Temperature (T), and Salinity (S). Trawls for adult mitten crabs and planktivorous fishes were across open water transects (area of light blue shading) in San Pablo and Suisun Bays. Map source: San Francisco Estuary Institute.
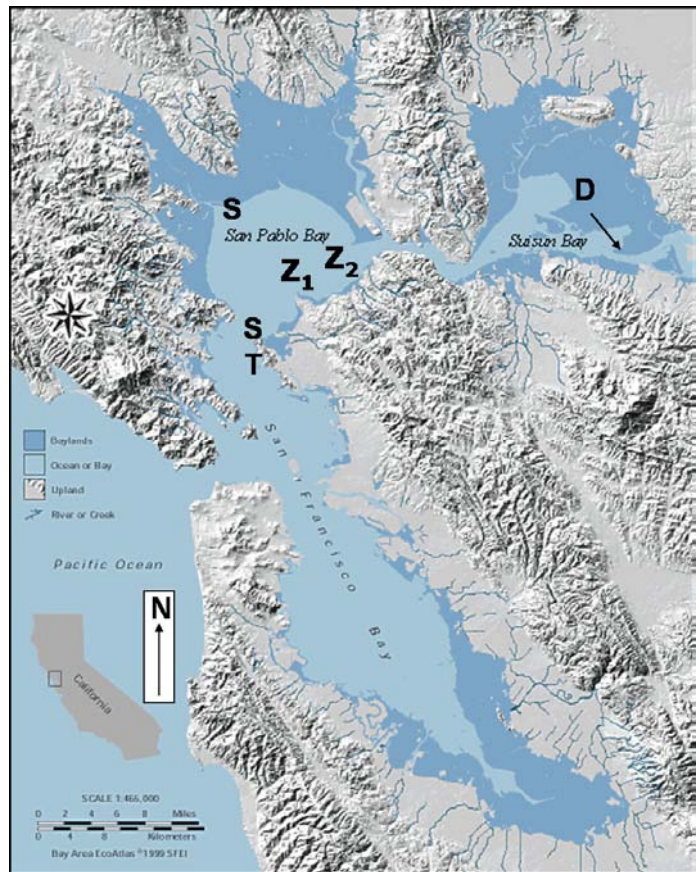
adults are believed to die soon after reproduction (Panning 1939; Hymanson et al. 1999).

In San Francisco Bay, gravid females are first collected in November. Zoeae appear from December through early June, when the last gravid females are generally collected (Rudnick et al. 2003). In this paper, we use the period of December – June to define a reproductive year, or cohort, for breeding adult and larval mitten crabs. Since cohorts span the end and beginning of consecutive calendar years, we refer to cohorts by the year in which they first appear; e.g., a cohort which spans December 1998 – June 1999 is referred to as the "1998 cohort".

### Data sources

This study is based on larval and adult mitten crab abundance and environmental data from San Pablo Bay from 1997 through early 2005. The data sets used in this study vary in observation frequency, ranging from every 15 minutes for fixed automated sampling of temperature and

salinity, to monthly or seasonal sampling for animals (mitten crab life history stages and planktivorous fish). Monthly units were therefore used to standardize comparisons among environmental variables and mitten crab abundance data.

### Zoeal data

Mitten crab zoeae were obtained from monthly November through July zooplankton samples taken by the California Department of Fish and Game (CDFG) at two San Pablo Bay stations (Figure 1) from autumn 1996 through spring 2005. Preliminary data indicated that no *E. sinensis* zoeae occurred from July to October, and in only one November sample. Samples prior to 1996 were not available due to either a prior lack of CDFG sampling in San Pablo Bay or the condition of archived samples. Zooplankton were collected with a net with 154 μm mesh nylon cloth (No.10 mesh), a length of 73 cm, and a mouth diameter of 10 cm which tapered to 4.5

cm to a stainless steel collection bottle with a screened opening. The net was towed for 10 minutes from bottom to surface in a stepwise oblique tow. Volume of water filtered was calculated by the product of the net mouth area and water flow through the net, measured by a flow meter on the side of the boat. Captured zooplankton was preserved in 10% formalin with Rose Bengal dye added to aid in sorting. Because mitten crab zoeal densities are sparse compared to other zooplankton, entire samples were examined for mitten crab zoeae using a Leica MZ7.5 dissecting microscope and Leica KL 750 light source. Mitten crab zoeae were distinguished from other decapod zoeae with a dichotomous key produced by two of the authors for this purpose (Rice and Tsukimura 2007). Mitten crab zoeae densities (# $\times$ L$^{-1}$) were calculated by dividing total counts of Stage I–V zoeae in samples by the volume of water strained by the net. Densities were averaged from the two sampling stations.

*Adult mitten crab data*

Adult female mitten crab abundance data were obtained by CDFG otter trawls from 1997 through early 2005. CDFG otter trawls are conducted monthly from central San Francisco Bay up into the San Joaquin Delta using an otter trawl towed on the bottom against the current for five minutes, then retrieved. For this study we used data primarily from stations in San Pablo Bay, with several comparisons to Suisun Bay (Figure 1). The area swept by the trawl was calculated by the product of the net mouth area assuming a 70% door spread of 3.4m and the distance traveled, measured by Loran-C (Orsi 1999).

Estimates of mitten crab abundance were based on a relative catch per unit effort (CPUE; #/tow) for gravid females from San Pablo Bay. The gravid female CPUE was selected as a metric for estimating the reproductive output of a given year class of mitten crabs and the potential abundance of the following year class of crabs.

*Environmental variables: temperature, salinity, discharge, and planktivores*

We analyzed variables in San Francisco Bay including temperature, salinity, discharge, and abundance of planktivorous fish, relative to

densities of zoeal mitten crabs. The availability of these data are the best spatial and temporal match to the mitten crab data, and are particularly relevant to larval survival. While gravid adults provide the source and numbers of zoeae, temperature and salinity can affect survival of larvae and juvenile crabs, and discharge and planktivorous fish represent losses of larvae from the estuary respectively through export and predation.

Water temperature and salinity data were obtained from US Geological Survey from a continuously recording (15 minute interval) gauge at Point San Pablo (PSP) (lat. 37°57'53", long. 122°25'42") in San Pablo Bay (http://sfbay. wr.usgs.gov/cgi-bin/sfbay/Fixed_sta/SSP-main.cgi) (Figure 1). We used data from the upper water column data recorder, which is set between 1.1 and 2.7 m below Mean Lower Low Water (MLLW). We first compared upper and lower water column temperature sensor data at each gauge and found that gauge temperatures were within 1 °C of each other for the majority of the time. The only substantial differences between upper and lower temperatures were during the fall and winter of 1998. During most of this period lower depth temperatures were substantially warmer than those in upper depths, but were colder than upper depth temperatures for several winter months; this was probably related to the high discharge (up to 3300 cms; ~Feb.–June) of fresh water associated with the El Niño event in that year.

Temperature and salinity data were averaged for calendar months. Salinity data from the PSP upper gauge was unavailable for several months, and we interpolated missing data with monthly averages from gauge GM9 (lat 38°05'19", long 122°26'29"; depth = 2m below MLLW) in northeast San Pablo Bay (Figure 1). Inter-site salinity differences were calculated based on the relationship PSP salinity = 0.937 (GM9 salinity) + 6.880 (r=0.914, $P_{2,17}$<0.01). Because the slope of this relationship did not significantly differ from 1.0 ($t_{1,17}$ =-0.623; P>0.25), the salinity adjustment used was the salinity difference between the two stations (y-intercept = 6.880). Monthly discharge data were obtained from the Interagency Ecological Program (IEP) Dayflow Program website (http://www.water.ca.gov/ dayflow/output/). The IEP measures freshwater discharge from the Delta at Chipps Island (Figure 1) in cubic feet per second (cfs) which we converted to m$^3$/s.

Planktivorous fish abundance data were estimated from mid-water and otter trawls conducted monthly by CDFG from 1995 through early 2005. The fish collected were from the same trawls as described in the adult mitten crab methodology (Section 2.3.2 above). Planktivore CPUE was derived from total fish CPUE (based on individuals/tow volume) by eliminating individual fish >220 mm (K Hieb, CDFG, pers. comm.).

*Data analyses*

Differences in abundance of both zoeal and gravid adult female mitten crabs between months and years were examined with one-way ANOVA. Normal distribution of data and homogeneity of variances were tested respectively with Levene's test and a Kolmogorov-Smirnov standardized test. Data were log(x) or log(x+1) transformed as appropriate to meet these requirements for ANOVA. Adult mitten crab abundance data did not conform to assumptions of parametric ANOVA and were analyzed with a non-parametric Kruskal-Wallis test. Independence of mitten crab abundance across months and years was examined by tests of autocorrelation.

Relationships of log-transformed mitten crab zoeal density with other variables (salinity, temperature, discharge, adult female crab CPUE, and planktivore CPUE) were examined with a regression tree procedure (Breiman et al. 1984; De'ath and Fabricus 2000). Sample months that did not have a value for each parameter in the regression tree model were not included in the analysis; for example, some of the variables that relied on remotely sensed data (such as temperature and salinity) created missing months of complete data. A regression tree is a subset of classification and regression trees (CART) which are used for data exploration, modeling, and prediction. The procedure is useful in under-standing which independent variables account for variation in a dependent variable, similar to stepwise regression. In contrast to stepwise regression, a regression tree is a non-parametric and non-linear recursive fitting procedure that has many advantages over parametric-based multivariate regression procedures, such as no a priori assumption of the quantitative relationship between the dependent and each of the independent variables (Breimen et al. 1984).

The fit of a model in the regression tree procedure is based on a goodness-of-fit statistic which is equivalent to the multiple $r^2$ in more standard regression procedures (Wilkinson 2000). Although the regression tree procedure can account for the amount of sum of squares explained in the model, it is not associated with probability-based hypothesis testing. The regression tree analysis was run with both a least squares and a trimmed mean loss function. The least squares loss function results in binary tree splits at nodes based on producing two 'branches' with the smallest within-group sum of squares about the predicted mean. The trimmed mean loss function also classifies cases in order to minimize within-group sum of squares, but reduces the effects of outliers on the predicted means by eliminating the upper and lower 10% of values prior to calculating means and sums of squares. Splits and nodes were based on a minimum improvement in proportional error reduction of 0.05. A minimum of five observations in the ends of the tree was used as a stop criterion. All analyses were run with SYSTAT Ver. 10 (Wilkinson 2000). Based on regression tree results more specific relationships were examined directly with correlation and residual error analyses.

**Results**

*Zoeal densities*

Stage I zoea were the most common stage in our samples (84%), while individuals in the final zoael stage (V) were quite rare (0.5%). Mean monthly densities of zoeae varied significantly between months ($F_{6,46} = 3.118$; $P = 0.012$; Figure 2A) and years ($F_{8,44} = 2.30$; $P = 0.037$; Figure 2B). Variation within year-classes or cohorts is reflected in the order of magnitude range of mean densities (0.60 – 11.99 zoeae $L^{-1}$) over the December-June period. Monthly densities were regarded as independent, as these data were not auto-correlated within years (Pearson Correlation $r > 0.456$ for each of the seasons analyzed). Average yearly densities were variable (0.60 – 9.18 zoeae $\times$ $L^{-1}$), with little consistency in mean cohort densities from year to year (auto-correlation among consecutive years $P = 0.922$).

*Adult female mitten crab abundance*

Monthly average CPUE of adult female crabs in San Pablo Bay differed among months (Kruskal-Wallis $H = 16.00$; $P = 0.025$; Figure 3A), but only marginally so for Suisun Bay (Kruskal-
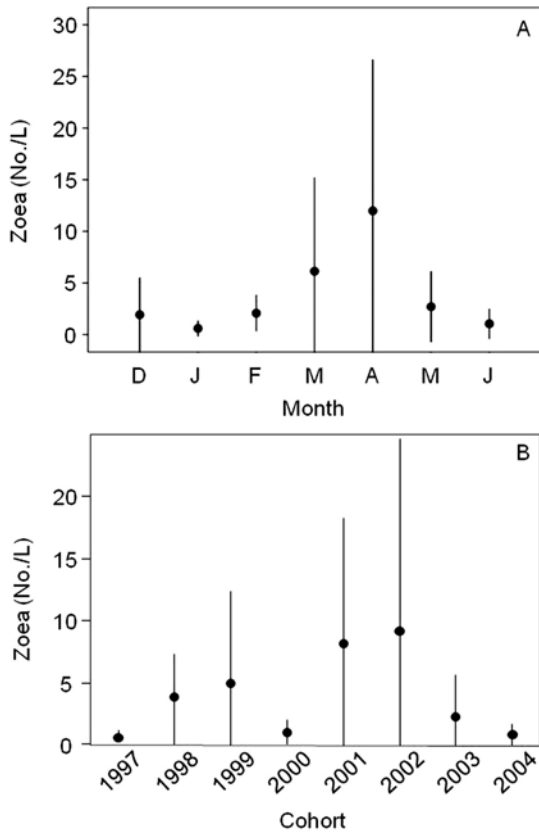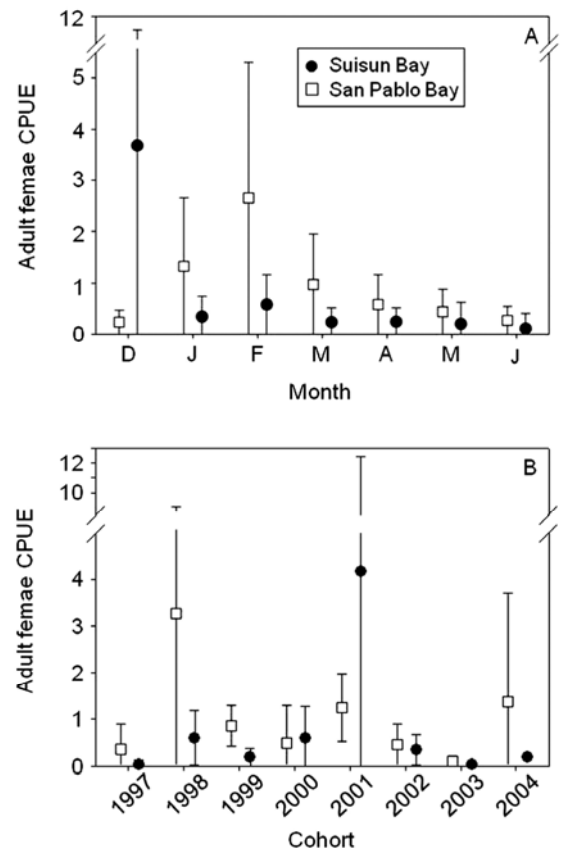
**Figure 2.** Mean mitten crab zoeae densities (± SD.) across (A) months (December-June) and (B) for cohort years. Cohort years start late in a calendar year and extend into the next year. Densities differed among months ($F_{6,46} = 3.118$; $P = 0.012$) and cohort years ($F_{8,44} = 2.30$; $P = 0.037$). Adjustment of the experimentwise error rate for all pairwise comparisons precluded detection of significant pairwise differences among years.



**Figure 3.** Mean adult ovigerous female mitten crab CPUE (± SD) across (A) months (December-June) and (B) cohort years from Suisun and San Pablo Bays. The latter is seaward. CPUE differed among months (Kruskal-Wallis H = 16.00; P = 0.025) and cohort years (Kruskal-Wallis H = 25.08; P = 0.002).

Wallis $H = 12.09$; $P = 0.060$). Adult female CPUE was highest during February in San Pablo Bay and December for Suisun Bay (Figure 3A). The abundance and duration of adult female mitten crabs in both bays were variable across years (Figure 3B). CPUE was significantly different among years in both San Pablo Bay (Kruskal-Wallis $H = 25.08$; $P = 0.002$) and Suisun Bay (Kruskal-Wallis $H = 37.61$; $P < 0.001$). Adult female crab CPUE in San Pablo Bay was highest during the 1998–1999 breeding season, and the next two highest abundances occurred in 2001 and 2004 (Figure 3B).

*Environmental variables: temperature, salinity, discharge, and planktivores*

Mean monthly water temperatures during the mitten crab breeding season of November- June

ranged from a low of 10.6 °C in January to a high of 17.5 °C in June (Figure 4A). Annual average temperatures ranged from 12.2°C during the 1998 cohort year to 13.9 °C for the 2002 cohort year.

Salinity in San Francisco Bay is seasonally variable and is driven by freshwater discharge primarily delivered by the Sacramento and San Joaquin Rivers (Monismith et al. 2002). Monthly average discharge ($log_{10}$ transformed) into San Pablo Bay was negatively correlated with salinity ($r_{1,52} = -0.903$, $P<0.001$) and temperature ($r_{1,61} = -0.465$, $P < 0.001$). Average monthly salinity was lowest in February (mean = 16.7 and highest in November (mean = 26.4 ) (Figure 4B). Interannual variation in salinity was also substantial, with the lowest monthly averages during the mitten crab breeding season in 1997–
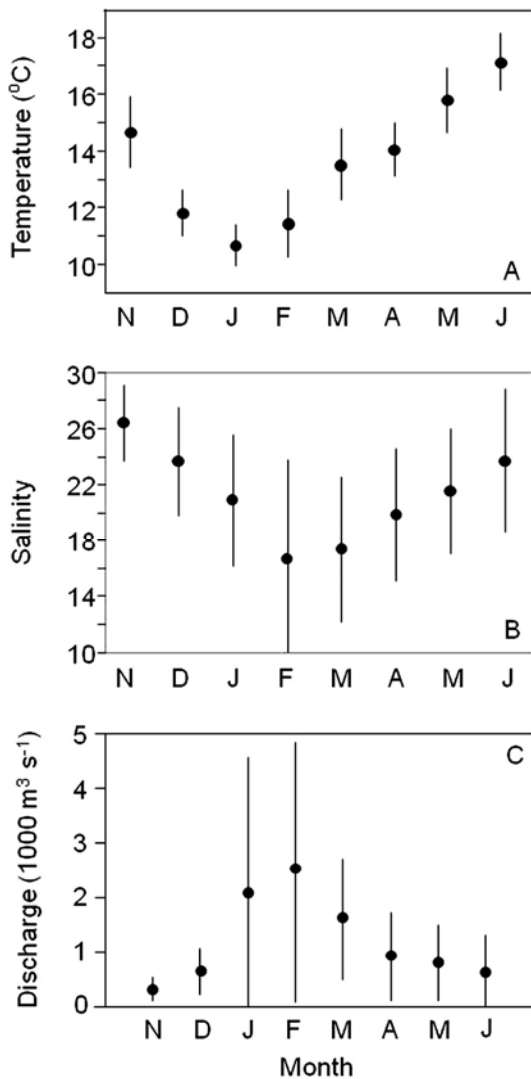
**Figure 4.** Monthly means (± SD) of (**A**) water temperatures, (**B**) salinity, and (**C**) discharge in San Pablo Bay. Temperature and salinty data were obtained from continuous 15 minute recordings from USGS sensors set between 1-3m below MLLW. Discharge data are from a station approximately 40 km landward from stations for other variables used in this study.

**Table 1.** Results parameters for the regression tree based on (log10 (x+1) transformed) mitten crab zoeae (# × L$^{-1}$) as the dependent variable with independent variable inputs of adult female mitten crab CPUE, discharge (m$^3$/s), planktivorous fish CPUE, salinity, and temperature (°C). The fit of the model based on each split is equal to the coefficient of determination (r$^2$).

| Split variable | Node | Fit |
|---|---|---|
| Adult female CPUE | 0.983 | 0.301 |
| Temperature (°C) | 11.8 | 0.633 |
| Discharge (CMS) | 45187 | 0.269 |
| Salinity | 23.2 | 0.501 |

1998 (13.5) and highest during the lowest discharge season of 2000–2001 (26.0). Eight months of our study period included >1 day (range 2–26 d) of salinity <10, which included a 26 day period of very low salinity (mean = 3.78) during February 1998.
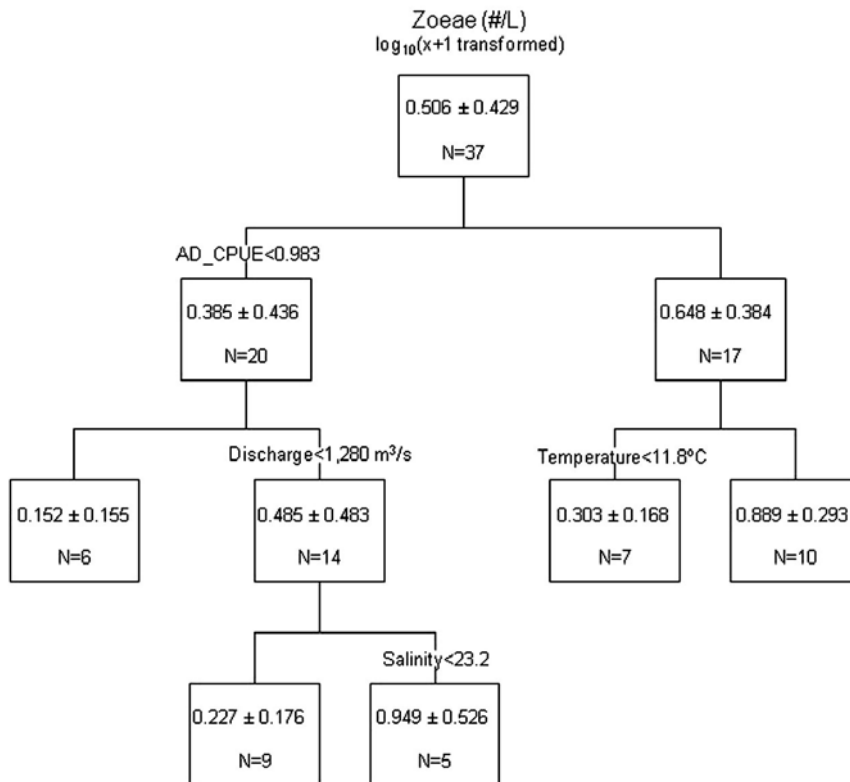
The highest average monthly discharge over the years of this study (1997–2005) occurred in February (2,232 m$^3$/s), and the lowest average discharge occurred in November (354 m$^3$/s) (Figure 4C), which is just prior to the appearance of mitten crab zoeae in San Pablo Bay plankton samples. Inter-annual variation in discharge during the mitten crab breeding season was high, ranging from 2,340 m$^3$/s (1997–1998) down to 379 m$^3$/s (2000–2001).

Mean monthly CPUE of planktivorous fish in San Pablo Bay early in the mitten crab breeding season (January–March) was < 0.6, but rose to monthly means of 2.0 and 3.9 in May and June respectively. Ten fish species make up 98.9% of the planktivore catch (Hieb and Flemming 1996) in San Pablo Bay. Of these ten species, Northern anchovy, *Engraulis mordax* Girard, 1854, are the most common, accounting for 73.2% of the total catch (Jones and Stokes 2004).

*Relationships of mitten crab zoeae densities with adult female crab abundance and environmental variables*

A regression tree with the trimmed mean loss function produced a better fit to the data than the model with the least squares loss function. Planktivore CPUE was not able to explain more than 0.05 of the variation in total zoeal density at any point in the tree and was therefore not included in the model. The first split in the tree was determined by the CPUE of mitten crab adult females, which produced a fit of 0.301 (Figure 5 and Table 1). Densities of zoeae were higher when adult crab CPUE exceeded the split node of 0.98. The terminal split resulting from the higher adult abundance and zoeal density were discriminated by a temperature node of 11.8 °C, with zoeal density higher above this temperature. These splits resulted in the highest fit with zoeal density (0.633) among all produced by the model.

Below the 0.98 adult CPUE node, zoeal densities were best discriminated by successive splits based on discharge, and then by salinity. The terminal split in this branch was distinguished by a salinity node of 23.2, which resulted in a model fit of 0.501. Independent t-

Zoeae (#/L)
$\log_{10}$(x+1 transformed)

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                        0.506 ± 0.429
                            N=37

        AD_CPUE<0.983
        0.385 ± 0.436                    0.648 ± 0.384
            N=20                             N=17

                Discharge<1,280 m³/s      Temperature<11.8°C
  0.152 ± 0.155   0.485 ± 0.483      0.303 ± 0.168   0.889 ± 0.293
      N=6            N=14                N=7            N=10

                    Salinity<23.2
          0.227 ± 0.176   0.949 ± 0.526
              N=9            N=5
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**Figure 5.** Regression tree result based on (log10 (x+1) transformed) mitten crab zoeae (#$\times$ L$^{-1}$) as the dependent variable with independent variable inputs of adult female mitten crab CPUE, discharge (cubic meter per second), planktivorous fish CPUE, salinity, and temperature (°C). Result parameters are summarized in Table 1. The base of the tree is represented by the lone box labeled with the dependent variable. Successive 'branches' or splits above and below split nodes of this data are based on which independent variable and value produces splits (tree branches) which minimize within-group variance. For example, the first split is based on adult female CPUE and divides the dependent variable (zoeae density) into two groups distinguished by the calculated node CPUE of 0.983. Splitting ceases when branches reach five observations or a minimum improvement of 0.05 proportional reduction in error, similar to stepwise multiple regression.

tests suggest that the nodes produced by the salinity split were much less distinct ($t$ = 2.42) compared to the more distinguishable nodes ($t$ = 5.21) resulting from the temperature split associated with higher adult CPUE. The regression tree analysis results suggested the need for further examination of the relationships between zoeae density, adult female CPUE, and water temperature.

On an annual basis, densities of inter-year class zoeae increased with adult female crab CPUE (n = 9; $r$ = 0.706; $P$ = 0.033). Monthly zoeal density and adult female crab CPUE (both $\log_{10}$ (x+1) transformed) were significantly correlated ($r_{1,36}$ = 0.488; $P$ = 0.002) for the months when both adults and zoeae were regularly present in San Pablo Bay (Figure 6). The relationship was not improved by lagging

zoeal density one month or more behind adult CPUE across all study years. Zoeal density was also positively correlated with temperature (Figure 6B; $r_{1,38}$ = 0.473; $P$ = 0.002)
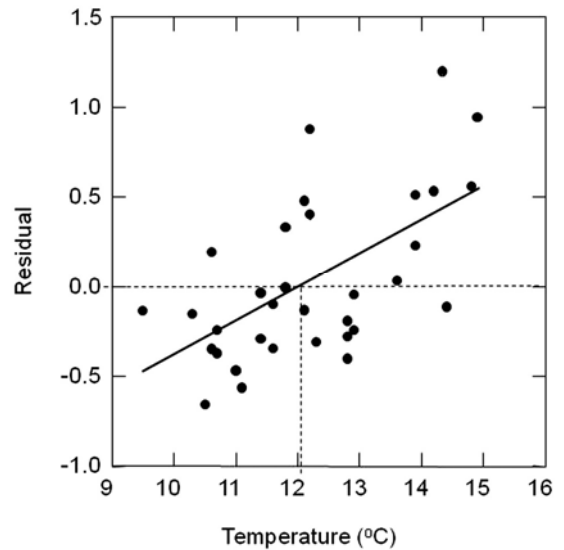
The residuals of the correlation between zoeae density – adult female crab CPUE were positively correlated with temperature ($r$ = 0.60; $P$ < 0.001) (Figure 7). A non-significant relationship would indicate that temperature does not account for a significant amount of the variation in the observed adult female-zoeae points from those predicted by the best-fit line. Rather, the residuals show that for a given number of females, there are fewer zoeae per adult female than expected at cold temperatures (residual <0) and more than expected (residual >0) during warmer temperatures during these months. The x-intercept at Y=0 is 12.1 °C. This value is
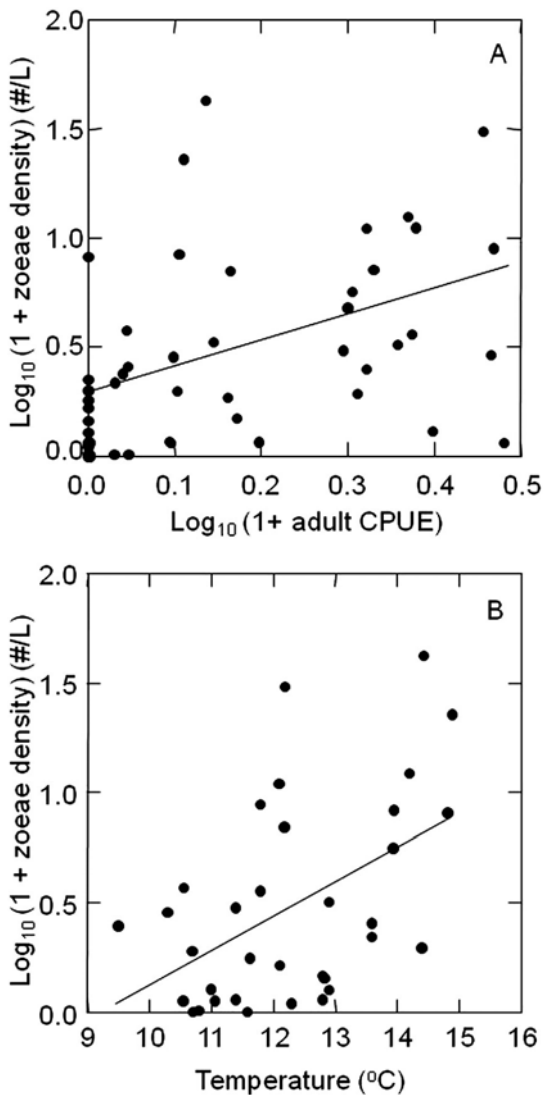
**Figure 6.** Relationships of (a) adult female mitten crab CPUE ($r_{1,36} = 0.49$; $P = 0.002$) and (b) monthly mean water temperature ($r_{1,38} = 0.47$; $P = 0.002$) with zoeae density for peak reproductive season months (December-April).



**Figure 7.** Relationship of the residuals from the correlation of zoeae densities versus adult female CPUE against temperatures for December-April ($r_{1,36} = 0.60$; $P < 0.001$). Dashed lines illustrate the intersection of the 0.0 residual level and the best-fit linear relationship between the two variables.

## Discussion

Temperature and salinity are known to affect development and survival of brachyuran larvae (Dawirs 1985; Dawirs et al. 1986; Anger 1991; Nagaraj 1993; Giménez and Anger 2003), and have also been shown to influence the distribution, hatching, and density of zooplankton throughout San Francisco Bay specifically (Ambler et al. 1985). Our study suggests that temperature and specifically a temperature threshold at or near 11.8 °C is related to densities of mitten crab zoeae in San Francisco Bay. Other variables including freshwater discharge, salinity, and abundance of planktivorous fish had less influence on zoeal densities in our study.

Within their endemic range in China, stage I mitten crab zoeae have historically appeared in the Yangtze River from April 15 – May 15 when water temperatures range from 18 to 24 °C (Zhang et al. 2002). The development of zoeae is completed in about one month under these conditions (Y. Cheng - Shanghai Ocean University and J. Wang - East China Sea Environmental Monitoring Center, Shanghai, pers. comm.).

extremely close to the regression tree node of 11.8 °C. At 11.8 °C, the predicted residual ($\hat{y}_i$) and its 95% confidence interval are -0.058 ± 0.662. This confidence interval encloses Y=0 and supports the regression tree temperature node of 11.8 °C.

Likewise, optimal culture conditions for zoea in the Yangtze delta region are 18–25 °C and 20–25 salinity, which results in development to megalopae in approximately 24 days. San Pablo Bay temperatures and salinities are variable but often lower during the early spring and for the breeding season as a whole than in the Yangtze delta. Rice (2006) used temperature and salinity-specific development times from Anger (1991) to calculate that zoeal development time given the observed temperatures and salinities in our study area and years would result in zoeal development times of ~45–60 days. However, we observed few zoea in late zoeal stages (84% of zoea found were Stage 1, 1% were Stage V), despite the thorough temporal and spatial coverage of the larval monitoring study that provided the zoea for this research, suggesting high mortality of early zoeal stages rather than prolonged development times compared to aquaculture conditions. High rates of mortality during early life stages is consistent with what is generally understood of the dispersive stages of many marine invertebrates including brachyurans, which are numerous, small and vulnerable to a wide range of predators (Underwood and Fairweather 1989; Rumrill 1990).

The reason for these life history differences is based on fundamentally different seasonal climates; whereas Chinese and northern European estuaries have temperate climates with summer rain resulting in increased water flow and lower water temperatures, the hydrology of San Francisco Bay is driven by winter rains and spring snowmelt from the Sierra Nevada mountains. Therefore, low temperatures and salinities occur in San Francisco Bay when zoeae are present in the mitten crab life cycle. These conditions may border on lethal or sub-lethal conditions for mitten crab zoeae. Threshold temperature conditions that are not experienced by endemic or some invasive European populations may exist for mitten crab larvae in San Francisco Bay, and these conditions could substantially influence the life history and overall success of the San Francisco Bay population of mitten crabs.

Laboratory studies of the physiological tolerances of Chinese mitten crabs are consistent with our findings. For example, in laboratory tests on zoeae from the invasive German population of mitten crabs, most mitten crab zoea failed to survive through all stages at 12 °C, and none survive past zoeae stage I at 9 °C

(Anger 1991). More recent laboratory experiments on zoeae from San Francisco Bay mitten crab females evaluated the rate of development and survival at 10 °C, 11.7 °C, and 15 °C at a constant salinity of 20 (Rice 2006). Complete mortality occurred within 15 days at 10 °C. At 11.7 °C, 34% of the zoeae survived to stage II after 15 days. Zoeae at 15 °C demonstrated the best performance, with 68% surviving to stage II and 50 % surviving to stage III (Rice 2006). These laboratory results support the results of the regression tree analysis, as well as the observed variation in zoeae densities in San Pablo Bay. For example, San Pablo Bay water temperature averaged 10.6 °C in January, when zoeae were limited to stage I individuals and were least abundant compared to other months. These multiple lines of evidence suggest a threshold for zoeal survival and development between 10 and 12 °C.

Our results suggest that zoeal density is not strongly influenced by salinity under the current hydrologic regime in San Francisco Bay. The regression tree produced a node at 23.2 salinity, which is within the optimal range (20–25) for larval survival and development in both culture conditions in China as well as in laboratory experiments (Anger 1991). Stage I mitten crab zoeae are euryhaline, demonstrating tolerance to salinities above 10 at temperatures greater than 12 °C (Anger 1991; Cieluch et al. 2007). Subsequent zoeal stages become less tolerant of low salinity, requiring 15 or greater to survive in laboratory experiments (Anger 1991). Although our San Pablo Bay daily salinity data displays episodic mesohaline events (22 % of all months in the study across years averaged <15 salinity), half of these months were restricted to the 1997 cohort year. Very high discharges in 1996–1997 lead to a mean salinity of 13.5 for December-June, and 155 of 212 total days (December - June) with salinity < 15.

There were only 140 such days among the other seven years of the study. In these seven years, salinity averaged 21.2, well above the minimum salinity tolerance of all mitten crab zoeal stages (Anger 1991; Rudnick et al. 2005; Cieluch et al. 2007).

Salinity in recent years in San Francisco Bay has been higher than historical averages. Anthropogenic reduction of natural freshwater delivery to the San Francisco Bay over the past 50 years has contributed to a general increase in Bay-wide salinities and is a serious concern for

the ability of the Bay to provide mesohaline and low salinity habitats. In response, state and federal regulatory activities are targeting reduction of salt loading and enhanced freshwater discharge in order to reduce salinity to levels consistent with historical natural conditions (SWRCB 2006; Service 2007). Successfully decreasing salinities might provide an additional benefit of diminishing optimal conditions for mitten crab zoeal development.

The weak model fit (0.269) in the regression tree node suggests that discharge does not have a strong influence on densities of mitten crab zoeae. Average discharge in this study was negatively correlated with salinity and temperature in San Pablo Bay, making it difficult to isolate the effect of this variable. Overall, little is known about the effects of increased freshwater discharge on the retention of zooplankton in San Francisco Bay (Kimmerer 2002). Mortality of the post-larval megalopa stage may also be a significant source of mortality in the population. An investigation of megalopae dynamics and relationships with environmental variables in San Pablo Bay is underway in order to build on our broader study of mitten crab life history and population dynamics of this invasion.

Species with life histories which include planktonic larval stages are also at risk of predation by planktivorous fishes (Anger 2006). Our results showed that planktivorous fish abundance was the only variable that was not retained in the regression tree analysis. Two possibilities for this outcome are that: 1) planktivorous fish abundance has co-linearity (redundancy) with salinity and discharge, or 2) that planktivorous fish do not affect survival of mitten crab zoeae because planktivorous fish return to the bay once mitten crab zoeae have developed to benthic life history stages.

Planktivorous fish in San Francisco Bay migrate seaward to warmer, more saline estuarine areas with high spring delivery of fresh water and migrate back to the upper Bay when freshwater discharge declines in late spring and summer (Armor and Herrgesell 1985; Kimmerer 2002). Planktivorous fish abundance in San Pablo Bay is lowest early in the mitten crab breeding season, and high abundances occur in May and June at a time when mitten crab larval densities are decreasing. This co-occurrence leads to the question of whether decreasing densities of mitten crab zoeae in late spring and summer are a result of increasing planktivory. There are several reasons arguing against this direct relationship. From March to April across years, the median zoeae density increased by 2.7 × and the planktivorous fish abundance remained nearly unchanged. Increasing San Pablo Bay temperatures and salinities during May and June are optimal for rapid zoeal development to the juvenile benthic stage (Anger 1991; Y. Cheng - Shanghai Fisheries Univ., pers. comm.). The continuous five month decline in abundance of gravid female mitten crabs in San Francisco Bay from February to June supports a waning of the mitten crab breeding season during this period. Also, we found no significant linear or non-linear relationship between zoeae density and planktivorous fish abundance, even when restricting the analysis to the months of planktivore returns to San Pablo Bay (March - June). In general, mitten crab zoeae are a minor part of the zooplankton by number, and their proportional abundance in the zooplankton has declined even further relative to increasing abundances of invasive copepods (Winder and Jassby 2010). In addition, decapod larvae were a minor component of planktivore diets prior to the mitten crab invasion (Kimmerer, unpub. data).

With respect to the rigidity of physiological tolerances such as the temperature threshold identified in our work, it is important to note that mitten crabs, like many successful invasive species, display substantial plasticity and range in osmoregulatory and life history traits. Ojaveer et al. (2007) identified low salinity as a potential limitation for mitten crab larval development in the Baltic Sea; the sustained presence of mitten crabs in low salinity regions of the Baltic suggests that mitten crabs must migrate very long distances (ca.1500 km) from breeding areas and/or have developed zoeal tolerances to low salinity over approximately 80 years since establishment. This study also suggests that different populations may adapt to regional environmental conditions, such as tolerance to low salinity. Physiological plasticity has been demonstrated for other brachyurans, including *Carcinus maenas*, a highly successful invasive species (Klassen and Locke 2007). Gimenez and Anger (2003) and Gimenez (2003) found that early life history stages of *Chasmagnathus granulata* may exhibit physiological plasticity with respect to osmoregulation. The possibility for such adaptations in mitten crab is supported

by the high degree of life history variation among native and invasive populations (Dittel and Epifanio 2009).

Thresholds identified by this study for the San Francisco Bay population of mitten crabs may or may not be appropriate to apply to other invaded or invadable systems, and even within this population, tolerance thresholds may not be static. Tolerance thresholds may be linked to the genetics of the particular source population for these mitten crabs, or these thresholds may be modified over time as the population adapts to its new environment. In addition, the door remains open for ongoing propagule pressure from crabs that may be transported by vectors including international shipping and illegal transport of mitten crabs; additional intro - ductions could inject genetic variability into the invasive population that may change physiological limits or life history characteristics of this mitten crab population. Finally, minimum temperature thresholds could become less relevant as a limiting factor for mitten crab success in the face of expected rises in sea temperatures, particularly winter temperatures for coastal systems, resulting from global climate change processes (USCCSP 2000).

## Conclusions

The results of this study support that certain environmental conditions, particularly low temperatures, influence mitten crab year-class strength. The physiological requirements of mitten crab larval development suggests that a likely mechanism for this influence is reduced larval survival under suboptimal environmental conditions. When coupled with information about the timing of arrival of larvae in the estuary and propagule pressure, environmental data can assist in evaluating which estuarine systems may have conditions amenable to the establishment of invasive mitten crabs (Herborg et al. 2007a, b; Jerde and Lewis 2007; Hanson and Systsma 2008); it could also assist in the evaluation of probabilities of establishment of areas suspected to be in early stages of invasion (e.g., Chesapeake Bay, Hudson River). Additional research on population variance in thermal and osmotic tolerances of mitten crab zoeae is needed in order to improve the accuracy of these predictions.

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