Final Report

Mitten crab (*Eriocheir* spp.) recruitment: Factors that influence larval supply and return to settlement sites.

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Executive Summary

The mitten crab (*E. sinensis*) is a catadromous species that requires high salinities for larval development and a return to freshwater to develop into adult crabs. Even though mitten crab population patterns are dependant upon larval recruitment little, other than salinity and temperature tolerances, is known about the larval stages. This project correlated information on temperature, salinity, and flow to larval vertical and horizontal migration behavior to elucidate the combination of factors that yield high levels of recruitment. The research examined vertical migration behavior of the zoea and megalopae stages and horizontal migration of megalopae and juvenile crabs in response to estuarine and parental habitat cues.

Planktonic larvae in estuaries are subject to a net seaward flow that can export larvae to near ocean waters. Through vertical migration into haloclines or tidal flows, larvae can influence their horizontal position within an estuary. Mitten crab zoea I and III exhibited a diel vertical migration and all stages responded to and occupied the halocline. This vertical positioning likely enhances the retention of mitten crab zoea and permits the zoea to avoid low-salinity seaward flows in periods of strong stratification.

The theory that megalopae actively return to brackish or freshwater conditions was not supported by this study. Megalopae did not respond to horizontal salinity cues, nor did they exhibit vertical migration behavior. Mitten crab megalopae are primarily benthic and are not active swimmers. Megalopae exhibited short-duration swimming activity. Studies that include the effects of turbulence and examine migration over a complete megalopal period would more accurately gauge the potential for migration by megalopae. Given a choice of floating or benthic substrate, the megalopae primarily chose to utilize rocks and submerged seaweed as shelter.

Early crab stages (II and III) responded positively to flow, but only the third molt exhibited an orientation response to salinity. Crab molt I did not respond positively to flow but moved randomly in the flume. Crab molt II responded positively to flow but moved into each arm of the y flume regardless of salinity differences. Crab molt III responded positively to flow and in all trials avoided salinity differences. These results suggest that the mitten crab remains at its settlement site in early development and the upstream migration begins in later molts.

These results combined with a yearly comparison of temperature-based development times and flow events suggest that in most years larvae are slowly pushed out of the San Francisco Bay with a high percentage retained in the lower or south bay. Variability in larval recruitment is correlated with salinity. In high flow events, zoea may behaviorally increase retention through vertical movement into a halocline and away from low salinity surface currents.

Larval recruitment in San Francisco Bay is affected by the combination of temperature, salinity, and flow. The interaction among these factors determines the larval supply to settlement sites. A flow-based salinity regression suggested that high, stable salinity levels in 1994 may have led to the large population of 1999 and that flow can be utilized as a predictive factor for variations in mitten crab populations.

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Introduction

Estuarine species with a planktonic larval form are subjected to the net export of estuarine water. These species have life history strategies to compensate for the continuous flux of larvae away from adult habitat. Three main hypothesis exist for the maintenance of estuarine populations; 1) spawning at estuary mouths and coastal waters with a return migration of late stage larvae or juveniles, 2) spawning and retention of larvae within the estuary, and 3) spawning inside the estuary with export of early larval stages and a return of late larval stages or juveniles (Olmi, 1994). The null hypothesis is that larvae act as passive particles and recruitment is entirely dependant upon estuary circulation. The alternative hypothesis is that behavioral mechanisms exist to increase retention. These behaviors are cued to changes in tidal flows and environmental conditions.

The interaction between estuarine circulation and environmental conditions, life history patterns, and larval developmental requirements determines whether or not a species is able to maintain a population in a specific estuary. Annual and short-term variations in estuarine circulation and environmental conditions have been correlated with population fluctuations in estuarine invertebrate populations (Levins, 1996). Work on benthic invertebrates and coral reef-fish has demonstrated that variation in larval return to appropriate habitat is a common cause of recruitment variability (Levins, 1996). Larval return to settlement sites can be influenced by current patterns, tidal cycles and larval behavior (Eggleston et al., 1995).

The mitten crab (*Eriocheir sinensis*) is a catadromous species that requires high salinities for larval development and a return to freshwater to develop into adult crabs. Little, other than salinity and temperature tolerances are known about the larval stages. Yet, maintenance of mitten crab populations are dependant upon larval recruitment.

A significant characteristic of mitten crab populations is large variations in population size over time (Gollasch, 1999, Clark et al., 1998). The causes of these population fluctuations are not completely understood. Climatic conditions, such as cold springs and variable water years, have been proposed to control population size (Gollasch, 1999, Atrill and Thomas, 1996). These factors have a large influence on the recruitment of larvae whose development is temperature dependent and dispersal is controlled by estuarine circulation.

Many estuarine species have larval stages that migrate vertically (Anger, 2001). Vertical migrations assist in processes such as foraging, predator avoidance, dispersal and recruitment. These migrations are often synchronized to diel or tidal cycles, the most pervasive and predictable short-term environmental cycles in the marine environment (Sulkin, 1984, Queiroga et al., 2002). Studies have documented three types of vertical migration that mediate horizontal transport of larvae: ontogenetic, diel, and tidal. Strong evidence exists in support of ontogenetic (Sandifer, 1975) and tidal (Cronin and Forward, 1979; Dittel and Epifanio, 1982) vertical migrations. The mud crab, *Rithropanopeus harissii*, undergoes a tidally driven vertical migration that increases larval retention in upper estuarine areas and decreases export to near ocean waters (Cronin & Forward, 1982). The blue crab, *Callinectes sapidus*, exhibits a vertical migration cycle that increases the export to near ocean waters and a return in the megalopal stage or as a juvenile crab (McConaugha, 1988). The interaction between larval migration behavior and currents is a key determinant in the dispersal and supply of competent larvae to habitats suitable for settlement and post-larval development.

Vertical migratory behavior can be complicated in an estuary where larvae may encounter vertical salinity gradients, or haloclines, which can be from nearly zero to 15 ppt in just a few meters (Lougee et al., 2002). Larval migration may be stopped, slowed or unaffected by movement through a halocline or into unfavorable salinity conditions. Mitten crab zoea survival generally increases with higher salinity and zoea may actively select to occupy higher salinity layers (Anger 1991). The zoea may also select to remain in the halocline, where there is minimal net horizontal movement allowing the larvae to remain in the estuary.

For many estuarine crab species, the megalopae is the stage responsible for estuary reinvasion. The megalopae is the first stage that is primarily benthic and moves into estuaries through flood tide transport. The megalopae ascend in response to a continuous rate of increase in salinity associated with a flood tide (Christy and Morgan, 1998). Once in the water column, turbulence induces sustained swimming and megalopae settle out of the water column when turbulence declines (Welch et al., 1999). This swimming activity in conjunction with a flood tide moves the megalopae up the estuary where they settle and avoid the ebb tide. Eventually, this activity may result in megalopae being able to migrate through an estuary up to river mouths.

Larval return to adult habitat often involves a directed response to environmental cues. Adult odor, temperature, salinity, and dissolved organic compounds have been suggested as cues by which larvae or early crab stages orientate (Anger, 2001). The return to freshwater is likely accompanied by a response to salinity cues. The mitten crab is not known to complete its development without a return to freshwater and a directed movement toward freshwater from high-salinity estuarine water must occur. The onset of a response to lower salinity probably indicates the developmental point at which migration toward adult habitat occurs.

Understanding the mitten crab life history strategy will elucidate the potential movement of larvae in the estuary and near ocean water and potentially population fluctuations due to annual and short term variability in estuary circulation. A combination of the life history strategy, requirements for larval development and annual variations in the temperature and salinity of the estuary can be utilized to gauge yearly variations in larval survival and supply. This knowledge can allow managers to more aptly gauge the level of effort needed to mitigate future adult populations.

Larval biology

Mitten crab adults migrate to estuaries to breed during the fall and winter. The female maintains the eggs for one to two months before the larvae are released. Egg development is temperature dependant. Laboratory experiments have demonstrated that egg development can occur in salinities as low as seventeen parts per thousand (ppt) (Tullis pers comm., 2004). Females produce 250,000 to 1,000,000 eggs (Panning, 1939; Cohen and Carlton, 1995). Both sexes normally die within several months after reproduction though some crabs produce a second batch of eggs (Hanson, unpublished data 2004). The movement of reproductive adults in estuaries is unknown, though bottom trawls have caught ovigerous females in salinities from 0.1 to 30 ppt

(Rudnick et al., 2003). In some crab species, the ovigerous female moves to the head or mouth of the estuary to release larvae in an effort to increase retention or dispersal.

The planktonic larvae develop through a prezoea, five zoea and one megalopae stage, over a one to four month period (Anger, 1991; Kim and Hwang, 1995). Observations suggest that larvae are present in estuaries from winter through summer (Anger, 1991; Rudnick et al., 2002; Panning, 1939) with inter-annual and range variations likely due to differences in water temperatures. The prezoea is a brief (a few hours) stage followed by the zoea (4 to 15 days per stage), and the megalopae stage (20 to 30 days).

Larval development and survival is temperature and salinity dependant, with survival in a range of salinities from 15 to 32 ppt and temperatures from 12 to 25^{O}C. Optimal survival occurs in temperatures from 18 to 25^{O}C and salinities of 20 to 25 ppt (Anger, 1991; Kim and Hwang, 1995; Huang et al., 2001). The salinity optima of each zoea stage increases through development until the megalopae, which has the ability to survive in a wide range of salinities. Zoea stages IV and V are stenohaline with maximum survival at salinities of 30 ppt, complete mortality at 15 ppt, and minimal survival at 20 ppt (Anger, 1991). The metamorphosis from megalopae to juvenile crab is optimal between 15 and 25 ppt, but can occur in salinities from five to 30 ppt (Anger, 1991). Additionally, Anger (1991) tested temperatures of 9 and 12^{O}C, with complete mortality at 9^{O}C and moderate survival at 12^{O}C.

High mortality in the larval period occurs during the transition from zoea I to zoea II and from zoea V to megalopae (Hanson, unpublished data 2004). Zoea can survive limited periods of stressful conditions outside of the predicted salinity and temperature ranges only to experience mortality days later during the molt. Larvae occasionally do not molt but remain within a zoea stage for an extended period. These larvae often survive for a week or more but are unable to complete development (Hanson, unpublished data 2004). Mortality during the megalopae stage is low. The majority of mortality occurs during the metamorphosis to a juvenile crab (Hanson, unpublished data 2004).

Larval dynamics

The shift in salinity optima and the broad tolerances in the zoea I suggest an ontogenetic horizontal migration of larvae may occur, where larvae are transported from upper low-salinity estuarine waters toward high-salinity, lower estuarine and near-ocean waters as the zoea develop. Early larval stages are tolerant of lower salinities (10 and 15 ppt) that are lethal to later larval stages. Tolerance to lower salinities is finally exhibited in the megalopae stage. Anger (1991) tested the cumulative development and survival of larvae in salinity and temperature combinations, not the survival of individual stages. It is unknown whether zoea that develop to later larval stages in high salinities are able to tolerate and complete development if exposed to lower salinities. After the prezoea stage, the larvae migrate to the surface where currents propel the zoea toward the mouth of the estuary. The zoea is unable to counteract the net seaward currents because of a limited swimming ability. Estuary currents are on the order of 10 to 200 cm/s, while crab larvae swim at a rate of 0.14 to 2.46 cm/s (Anger, 2001). In some estuaries, the larvae may be flushed into coastal ocean waters. The megalopae may return to the adult habitat in onshore-directed near-bottom currents where they settle from spring to mid-summer and develop into benthic juvenile crabs (Anger, 1991; Rudnick et al., 2003). The megalopae is sighted near river mouths in China in May or June and in the Elbe River, Germany, between July and October (Panning, 1939). In cold years, the megalopae appear later and are half the size of those in warm years (Panning, 1939; Gollasch, 1999).

The limited swimming ability, requirement for high salinities, and 20 to 60 days spent in the pelagic zone (as a zoea) suggests that mitten crab populations become established in estuaries with large high-salinity areas and low flushing rates, or where larvae flushed from the estuary would be retained near the estuary mouth. In estuaries with established populations, inter-annual population fluctuations are probably a result of variation in larval recruitment due to either high spring time flows or episodic events that periodically flush the estuary.

The metamorphosis into a juvenile crab typically occurs in brackish and fresh water in the spring and summer (Rudnick et al., 2003), though it can be delayed until fall (Panning, 1939). The early juvenile crab resides in tidally influenced low-salinity areas through the winter (Panning, 1939). The following spring, juvenile crabs migrate upstream to brackish and fresh water rearing areas.

Juvenile crabs

The metamorphosis into a juvenile crab takes place from late spring to fall. Crabs molt approximately every ten to twenty days in the lab. Juvenile crabs in the lab eat aquatic vegetation and fish food. Little field data exists about the early life history of juvenile crabs. It is assumed that juvenile crabs overwinter in brackish to freshwater and then migrate upstream the next spring. Juvenile crabs in the lab have been reared through the first four molts in salinities from zero to twenty-five ppt. Crab molts II through IV have been transferred directly from twenty-five ppt to zero ppt with no apparent affect on growth or mortality rates (Tullis, pers comm. 2005). Low mortality rates are seen in the lab, but predation is likely a significant source of mortality in the wild.

Recruitment cycles

The mitten crab population in the San Francisco Bay-Delta is demographically isolated with no recruitment from other populations. All new cohorts must come from adult crabs that migrate to the San Francisco Bay to spawn. Few studies have demonstrated a clear relationship between the spawning population’s egg and larval production and the subsequent abundance of adults. Most studies have reported strong correspondences between larval supply to settlement sites and abundance of adult invertebrates (Heck et al., 2001).

The interaction between water temperature, salinity and estuarine circulation effects larval supply. Temperature dictates the time frame in which larval survival and development can occur and the length of the larval period from egg to juvenile crab. Salinity is a strong determinant of larval mortality rates. Estuarine circulation influences the level of larval retention within the estuary. Circulation in many estuaries is highly dependant upon freshwater input and episodic storm events. Annual variations in these factors can determine larval supply rates and resultant recruitment.

The ability to predict how freshwater inputs and episodic high flow events affect recruitment is dependant upon knowledge of the physical forces that shape larval supply. Larval supply is also a function of vertical and horizontal migration behavior exhibited by the larvae to enhance or avoid dispersal. Models that incorporate larval circulation patterns and vertical migration behavior can potentially forecast population fluctuations (Roughgarden, 1988).

Estuary circulation

The retention of larvae in estuaries is dependant upon estuary circulation patterns and annual variations. The shape, size and freshwater and ocean inputs create a wide variety of estuary circulation patterns. Many estuaries exhibit a salt-wedge circulation where low salinity water flows seaward on top of a net landward high salinity current. Individual estuaries can exhibit a large range of circulation patterns based on variation in freshwater inputs. Seasonal changes in runoff can change an estuary from slow circulation and high salinity to one of rapid exchange and low salinity.

A measure of estuary circulation is flushing time, which represents the average amount of time a parcel of water spends in the estuary. Flushing times are flow dependant; during periods with high flow rates, the flushing time will be greatly reduced. The rivers and streams in the indigenous range of the mitten crab experience high flows in the summer and low flows in the spring when larvae are likely to be present in the estuary. This increases the likelihood of retention in the native range. West Coast estuaries experience high flows during the period when mitten crab larvae are likely to be in estuaries. This increases the likelihood that mitten crab larvae will be flushed into near ocean waters.

In the San Francisco Bay, flushing times average 80 days (Uncles, 2002). Winter storm events can greatly reduce this time but also complicate flow patterns in the Bay. During high flows, salinity stratification increases and water from the north bay is pushed into the south bay, which creates mixing conditions throughout the south bay (Schemel, 1998). Flow to the bay comes almost exclusively from the Delta and flows into the north bay.

Recruitment Factors

To investigate the importance of larval behavior on recruitment, a series of experiments was conducted on vertical migration and responses to environmental cues. The vertical migration experiments were conducted at the San Francisco State’s Romberg Tiburon Research Center in conjunction with Dr. Steve Bollens. The experiments on megalopae and juvenile crab responses to environmental cues were conducted at USC Hayward in conjunction with Dr. Dick Tullis.

The research encompassed the following hypotheses: 1) vertical migration behavior allows larvae to either maintain a position within the estuary or return to the estuary in later larval stages by movement in and out of tidal currents; 2) larvae behaviorally avoid low salinity net seaward surface layers and maintain a no net movement position within the estuary through utilization of the halocline between surface low salinity net seaward currents and bottom high salinity net landward currents; and 3) that megalopae and early crab stages exhibit a response to freshwater flows that cue individuals to return from lower estuary high salinity conditions to upper estuary brackish areas to settle.

The proposed model of mitten crab larval recruitment is an ontogenetic progression in ability to maintain a horizontal position in an estuary through vertical migration. Early larval stages are expected to exhibit a vertical distribution centered near the surface of the water column. This would transport zoea in surface currents to lower estuarine (high salinity) areas. Later zoea and megalopae stages would exhibit a vertical migration that utilizes bottom salinity currents to return to brackish and freshwater. In response to high flow events that greatly reduce the surface salinity and flushing time, zoea are expected to exhibit vertical migration into haloclines.

Vertical migration

A series of laboratory experiments was conducted to test for the presence of vertical migration behavior in zoea I, III, V and megalopae in response to light cycles and haloclines. Zoea were obtained from ovigerous females caught in trawls conducted by California Fish and Game and from reproductive adults entrained at the Tracy Fish Collection Facility and bred in laboratory conditions. No effort was made to distinguish between the responses of larvae obtained from the field or laboratory females. Zoea were cultured in dishes at densities of 1 larvae per 5 ml, at 18 $\pm$ 1^{O}C and a salinity of 25 ppt. Larvae from seven ovigerous females were utilized in the experiments.

Experiments were run at 18±1^{O}C temperature and light controlled room in four Plexiglass tanks (200 cm tall x 7.6cm wide x 5.1 cm deep). Each column was physically isolated to limit light to a single overhead source that passed through a diffusion panel. Twenty to thirty active larvae were introduced to the apparatus and allowed to acclimate for one hour prior to the start of the experiment. Experiments were run for 50 hours. A scan of each column was recorded hourly with a video camera in near infrared light. The video record was then analyzed at a later date for the depth occupied by each larva. Experiments were performed on zoea I, III, and V with two to four replicates per stage.

Approach

The diel experiment consisted of two control columns with 12:12 light dark cycle (dark from 19:00 to 7:00) and two treatment columns in complete darkness. A light meter was utilized to confirm light levels in both the control and the treatment columns. The columns were randomly assigned to be a treatment or control.

The halocline experiments consisted of two control columns with continuous 25 ppt salinity and two columns with layered salinities of 35, 25, 15 in three depth segments; 15 ppt (0 to 70 cm), 25 ppt (70 to 140cm) and 35 ppt (140 to 200 cm). Larvae were introduced with the 25 ppt layer. Water of 15 ppt was slowly introduced on top of the 25 ppt layer to produce a halocline. The halocline between the 35:25 and 25:15 occurred over a 15 to 20 cm interval and was confirmed through the use of a YSI meter before and after several experiments. All columns were exposed to a 12:12 light cycle.

Analysis

The depth of each larva was recorded in 5 cm depth bins and the depths occupied by zoea each hour between the control and treatment tanks were compared using the non-parametric Kruskal-Wallis ANOVA. Data from duplicate experiments was initially analyzed separately and then combined in the final analysis.

In the diel experiments, a difference in the vertical position of zoea I, III, and V between the treatment and control tanks was only significant in seven, six and three hours out of the 24 hours tested (Table 1). Three, one and two trials with two treatments and two controls were utilized in the analysis for zoea I, III and V respectively. Only the first 24 hours were utilized in the experiments due to high mortality rates experienced in the second 24 hours in some tanks.

Additional experiments were performed with results that agreed with the analysis but were not utilized due to the limited number of zoea in the experiments. The vertical position of the zoea during daylight hours was compared to nighttime hours for tanks with a 12:12 light dark cycle. Results were significant for zoea I and III but not zoea V (Table 2).

The zoea in the halocline experiments exhibited a significant difference in vertical position 23, 17, and 24 times for zoea I, III, and V respectively out of 24 hours tested (Table 1). Three, one and two trials with two treatments and two controls were utilized in the analysis for zoea I, III and V respectively. Only the first 24 hours were utilized in the experiments due to high mortality rates experienced in the second 24 hours in some tanks. Additional experiments were performed with results that agreed with the analysis but were not utilized due to the limited number of zoea in the experiments. The difference between daylight and nighttime hours in the control tanks was significant for zoea I and III but not zoea V (Table 2).

Initial diel experiments on megalopae demonstrated a lack of response. Megalopae were initially introduced to the top of the columns, with their position recorded every half-hour. Several megalopae remained in the water column for four hours but the majority were on the bottom. After four hours, all of the megalopae were on the bottom and no megalopae were observed swimming. Additional experiments were not performed.

Megalopae were tested in additional vertical migration experiments, to examine if swimming behavior could be induced by fluctuations of environmental conditions. To mimic a tidal change, high salinity water was introduced to a shorter tank (50 cm), to test if an increase in salinity and hydrostatic pressure would induce swimming. Megalopae were introduced into the shorter tank with 25 ppt water. Water of 35 ppt was slowly introduced to the top of the water column and swimming events were recorded. Initial experiments did not yield significant results and were not continued.

Table 1: Vertical Migration Results

Kruskal-Wallis ANOVA hourly probabilities													
stage	**experiment**	**1230**	**1330**	**1430**	**1530**	**1630**	**1730**	**1830**	**1930**	**2030**	**2130**	**2230**	**2330**
Z I	salinity	**<0.01**	0.10	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**0.02**
	light	0.52	0.39	0.42	0.50	0.55	0.80	**<0.01**	0.16	0.12	0.95	0.48	0.62
Z III	salinity	**0.04**	**0.06**	**<0.01**	**<0.01**	**0.02**	0.05	**<0.01**	0.44	0.58	0.09	0.07	0.30
	light	**<0.01**	0.53	0.96	0.52	0.07	0.10	0.15	**<0.01**	**<0.01**	**<0.01**	**<0.01**	0.36
Z V	salinity	**0.02**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**
	light	1.00	0.88	0.81	0.12	0.14	**<0.01**	0.91	0.79	0.39	0.95	**0.02**	**0.03**
		30	**130**	**230**	**330**	**430**	**530**	**630**	**730**	**830**	**930**	**1030**	**1130**
Z I	salinity	**0.02**	**0.03**	**<0.01**	**<0.01**	**0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**
	light	0.19	0.18	0.24	0.06	**<0.01**	**0.03**	**<0.01**	**<0.01**	**<0.01**	0.28	0.13	**0.06**
Z III	salinity	0.68	**0.02**	**0.02**	**<0.01**	**<0.01**	**0.03**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**
	light	0.21	**0.02**	0.89	0.74	0.45	0.46	0.15	0.36	0.08	0.86	0.06	0.95
Z V	salinity	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**
	light	0.05	0.09	0.27	0.71	0.66	0.14	0.19	0.56	0.30	0.32	0.55	0.71

Table 2: Diel Migration Results

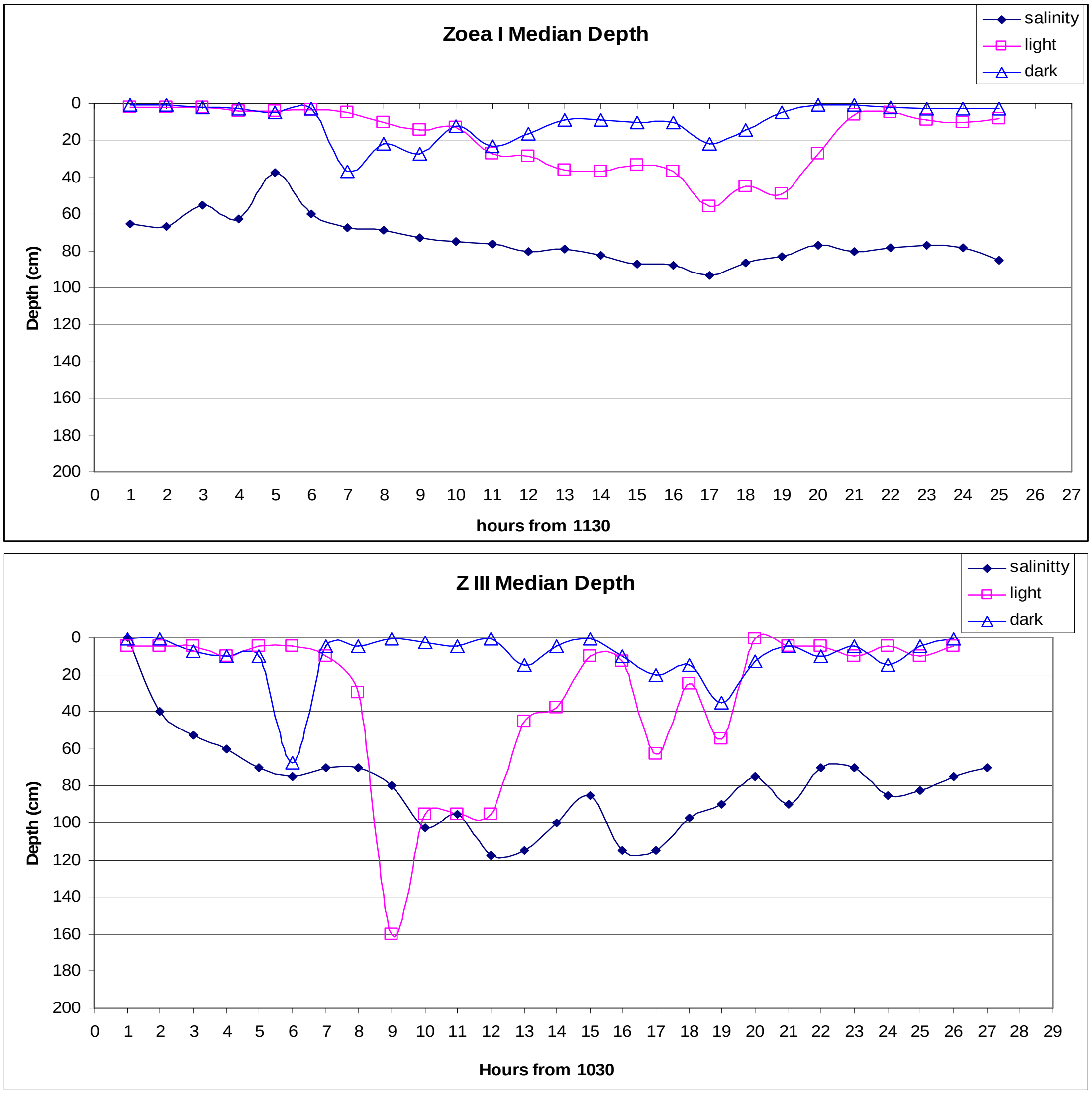
Day versus Night (Kruskal-Wallis ANOVA)	
stage	probabilities
Z I	**<0.0001**
Z III	**<0.0001**
Z V	0.0811

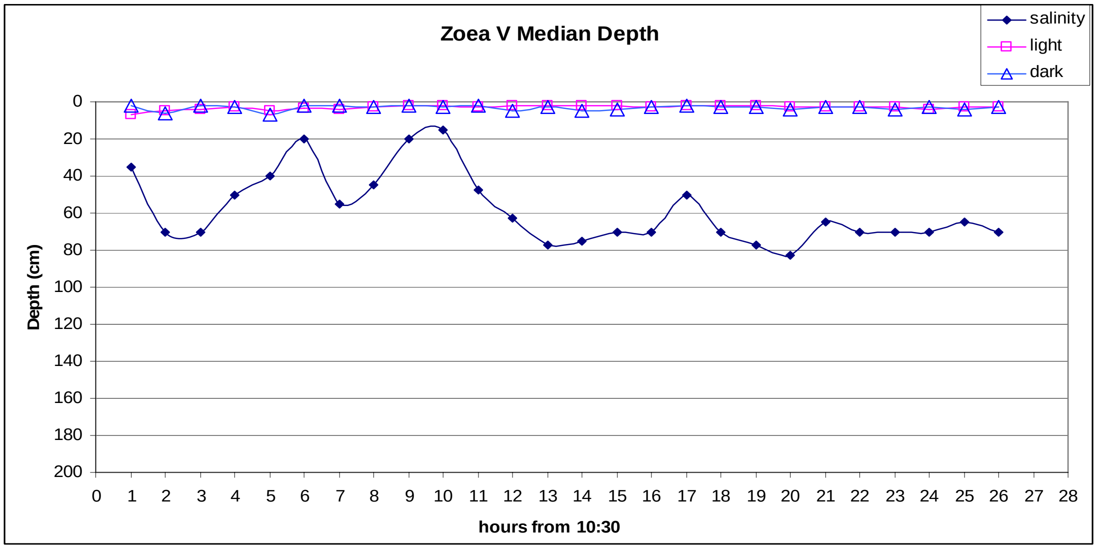
Discussion

The analysis suggests that zoea I and III exhibit a diel vertical migration behavior in response to light. This behavior would increase estuary retention through avoidance of surface estuary flows at night. Zoea V exhibited a strong affinity for the surface layers at all hours; typically the median depth was within five cm of the surface (Figure 1).

All stages exhibited a response to haloclines that became stronger over time. The median depth of zoea in the columns with haloclines was often at or within 10 cm of the 15:25 ppt halocline. In periods of high flow, strong stratification can occur with the majority of outflow occurring in a shallow low salinity layer that occurs on top of a more stationary high salinity layer. The responses of all larval stages to a halocline suggest that they preferentially occupy this layer of no net movement. Additionally, the zoea in the halocline tanks avoided the highest salinity bottom layer. This behavior suggests that these stages do not utilize high salinity bottom layers to move landward. An additional explanation for this behavior could be a response to unfavorable salinity conditions. Zoea development can occur in 15 and 35 ppt but optimal survival rates were seen by Anger (1991) in salinities of 20 to 25 ppt.

Figure 1: Zoea Median Depths





It is unlikely that the halocline effect is due to a potential physical barrier caused by viscosity differences. Salinity has a minor effect on swimming activity and crab larvae are able to migrate vertically in the water column regardless of the degree of stratification (Epifanio, 1988). Sharp haloclines that occur in highly stratified estuaries may slow vertical movement, but they do not prevent it.

The median depth of all stages was in the upper half of the water column, except for a few hours during night by zoea III. This may be an artifact of the experimental design but is likely a characteristic of zoea vertical migration. The persistence of this depth profile in tanks under conditions of continuous darkness is puzzling. All zoea stages are highly attracted to light and the differences between day and night hours demonstrates that zoea stages utilize light as a migratory cue.

The two initial vertical migration experiments on megalopae demonstrated that they are primarily benthic and do not undergo vertical migration in response to light cues. The megalopae swimming in the columns for the first few hours is likely an artifact of the megalopae being introduced to the top of the water column and remaining above the bottom through periodically clinging to port openings.

The swimming response of megalopae varies from species to species, some are active swimmers and utilize light cues (Shanks, 1995), others are primarily benthic and only exhibit swimming behavior in response to salinity, turbulence and hydrostatic pressure indicative of tidal changes.

Initial experiments that attempted to mimic a tidal change did not yield significant results probably due to the inability to mimic the effects of turbulence. Flow and turbulence are primary cues indicative of landward tidal currents.

Migration cues

The Mitten crab returns to freshwater to complete their lifecycle. The megalopae is believed to be the stage that moves from the high salinity water (20 to 25 ppt) necessary for larval development to the brackish to freshwater areas where juvenile crabs are found. After metamorphosis into a juvenile crab in summer or early fall, the mitten crab migrates upstream into freshwater the next spring. Juvenile crabs and megalopae possess the ability to survive in a wide range of salinities from near zero to 25 ppt. Larvae and juvenile crabs that develop in moderate to high salinity waters must possess a means by which to orientate toward freshwater sources to return to freshwater. Cues indicative of freshwater could include lower salinity, dissolved organic and inorganic substances and temperature differences.

While the mitten crab is unique in its use of freshwater habitat, many crab species that utilize estuarine habitat undergo juvenile development in areas where metamorphosis occurred (nursery habitat) and then begin migrations in later instars. Other crab species actively move in the megalopae stage back to adult habitat. A significant cue of estuarine and freshwater habitat is lower salinity. Some crabs species are able to differentiate salinity differences of less than one ppt and orientate toward those signals (McGaw and Naylor, 1991). The hypothesis tested was if mitten crab megalopae and juvenile crabs respond to salinity cues. Orientation in response to salinity differences probably indicates the developmental point at which the migration from estuarine to brackish and freshwater conditions occurs.

Approach

Individual megalopae and juvenile crabs were introduced into a Y flume to test for a response to flow and salinity changes. The Y flume consisted of opaque plexiglass with a four by four cm profile open on top. The arms and straight sections were 40 cm long. The bottom of the maze was treated with a sand impregnated paint to provide traction. Water depth in the Y maze was three cm and was maintained at room temperature ($18 \pm 2^{O}C$).

In trials conducted on megalopae, a cylindrical Y flume with a two inch diameter cross-section and no substrate was used. The initial trials in the Y flume with substrate demonstrated that the megalopae would cling to the substrate and not move, regardless of flow rates and salinity cues.

The same water used to rear megalopae and juvenile crabs (25 ppt) was introduced into one arm of the Y. The treatment consisted of water introduced into the other arm adjusted to higher or lower salinity with Artificial Ocean or tapwater treated to remove chloromines. Flow rates were based on the minimum rate required to create mixing in the straight portion of the Y and constant conditions in each arm. Dye test demonstrated that both solutions introduced from the ends of the arms created uniform conditions in each arm until they reached the central arm where mixing occurred. The current velocity in the Y-maze was not sufficient to carry inactive larvae downstream, except for experiments conducted with megalopae as movement would not occur at low flow levels.

Treatment salinities of 20, 24 and 30 ppt were utilized. Upon introduction and exposure to flow the arm choice and time spent in each portion of the Y was recorded. After each trial, the experimental apparatus was rinsed twice with freshwater and once with control water. The arms used for control and treatment was randomly chosen and switched halfway through trials. Experiments were conducted at night to limit any light mitigated response. A light filtered to near infrared red wavelengths was used to uniformly illuminate the apparatus from directly overhead to minimize any directional cues.

Only uninjured and competent megalopae and juvenile crabs were utilized in the experiments. Five to ten day old megalopae were utilized to avoid any potential effects of the molt cycle. Similarly crabs were utilized between two and six days after each molt. Due to the limited number of juvenile crabs; molt I, II and III experiments were performed on the same set of crabs.

At the start of each trial an individual megalopae or juvenile crab was introduced to the Y-maze on a mesh spatula to the lower third of the middle arm. Individuals were given sixty seconds to acclimatize and then flow was simultaneously started in the two distal arms. Trials were run for five minutes.

Analysis

Twenty trials for each stage and each condition were completed. Results were analyzed using a matched pair test for time spent in each arm (arm choice) and for time in both arms versus straight section (flow response).

Experiments on the megalopae and crab molt I showed no difference in either flow response or arm choice. Data for the megalopae response was from experiments conducted with a y flume that had a cylindrical profile and no substrate. There was a significant difference in the crab molt II in response to flow but not arm choice. For the crab molt III there were significant differences in both arm choice and flow response (Table 3).

Table 3: Y Choice Results

Megalopae

	Experiment 1		Experiment 2		Experiment 3	
salinity (ppt)	*24*	*25*	*20*	*25*	*30*	*25*
Mean	64.37	65.32	52.80	57.65	61.26	59.32
Variance	5078.36	4176.12	1781.33	2815.40	3532.98	2201.45
Observations	19.00	19.00	20.00	20.00	19.00	19.00
df	18.00		19.00		18.00	
t Stat	-0.04		-0.34		0.12	
P(T<=t) two-tail	0.97		0.74		0.91	
t Critical two-tail	2.10		2.09		2.10	
section	*arm*	*straight*	*arm*	*straight*	*arm*	*straight*
Mean	129.68	155.32	110.45	174.55	120.58	164.42
Variance	5460.67	5460.67	5106.47	5106.47	6266.04	6266.04
Observations	19.00	19.00	20.00	20.00	19.00	19.00
df	18.00		19.00		18.00	
t Stat	-0.76		-2.01		-1.21	
P(T<=t) one-tail	0.23		0.03		0.12	
t Critical one-tail	1.73		1.73		1.73	

Juvenile (first molt)

	Experiment 1		Experiment 2		Experiment 3	
salinity (ppt)	*24*	*25*	*20*	*25*	*30*	*25*
Mean	19.30	26.80	49.00	36.65	34.40	39.05
Variance	2718.01	3537.54	5306.21	3857.61	3372.25	4727.21
Observations	20.00	20.00	20.00	20.00	20.00	20.00
df	19.00		19.00		19.00	
t Stat	-0.39		0.52		-0.21	
P(T<=t) two-tail	0.70		0.61		0.84	
t Critical two-tail	2.09		2.09		2.09	
section	*arm*	*straight*	*arm*	*straight*	*arm*	*straight*
Mean	54.24	230.65	95.17	189.83	77.32	207.68
Variance	5666.57	5707.49	7026.26	7026.26	6431.23	6431.23
Observations	17.00	17.00	18.00	18.00	19.00	19.00
df	16.00		17.00		18.00	
t Stat	-4.82		-2.40		-3.54	
P(T<=t) one-tail	0.00		0.01		0.00	
t Critical one-tail	1.75		1.74		1.73	

Juvenile (second molt)

	Experiment 1		Experiment 2		Experiment 3	
salinity (ppt)	*24*	*25*	*20*	*25*	*30*	*25*
Mean	72.85	68.20	85.22	79.06	84.05	80.95
Variance	5479.19	5850.91	4912.65	6749.82	6527.94	4412.83
Observations	20.00	20.00	18.00	18.00	19.00	19.00
df	19.00		17.00		18.00	
t Stat	0.16		0.18		0.10	
P(T<=t) two-tail	0.87		0.86		0.92	
t Critical two-tail	2.09		2.11		2.10	
section	*arm*	*straight*	*arm*	*straight*	*arm*	*straight*
Mean	165.94	113.18	164.28	119.33	165.00	113.95
Variance	2863.43	2464.90	2243.62	2218.00	3534.22	3576.94
Observations	17.00	17.00	18.00	18.00	19.00	19.00
df	16.00		17.00		18.00	
t Stat	2.17		2.02		1.90	
P(T<=t) one-tail	**0.02**		**0.03**		**0.04**	
t Critical one-tail	1.75		1.74		1.73	

Juvenile (third molt)

	Experiment 1		Experiment 2		Experiment 3	
salinity (ppt)	*24*	*25*	*20*	*25*	*30*	*25*
Mean	56.05	148.79	61.79	144.05	67.26	148.26
Variance	4067.61	5996.29	3602.84	6607.83	4581.98	5507.09
Observations	19.00	19.00	19.00	19.00	19.00	19.00
df	18.00		18.00		18.00	
t Stat	-3.41		-2.95		-2.73	
P(T<=t) two-tail	**0.00**		**0.01**		**0.01**	
t Critical two-tail	2.10		2.10		2.10	
section	*arm*	*straight*	*arm*	*straight*	*arm*	*straight*
Mean	204.84	85.00	205.84	89.26	215.53	79.47
Variance	6064.70	6019.44	5676.92	5668.20	3495.60	3495.60
Observations	19.00	19.00	19.00	19.00	19.00	19.00
df	18.00		18.00		18.00	
t Stat	3.39		3.37		5.02	
P(T<=t) one-tail	**0.00**		**0.00**		**0.00**	
t Critical one-tail	1.73		1.73		1.73	

Discussion

The initial trials on megalopae in the y flume with a square cross-section contrasted with the experiments run in a y flume with a cylindrical cross section. In the square y flume, megalopae would cling to the substrate and not move regardless of flow rates and salinity differences. Flow was increased until it exceeded the ability of the megalopae to cling and they were swept downstream. In the cylindrical y flume, there was no substrate for the megalopae to cling to and they had to actively swim regardless of flow rates in order to avoid being swept downstream.

The lack of a response to salinity differences in molt I and II suggests that they cannot detect salinity different or that movement is not a response to salinity differences. The response in molt III to salinity differences suggests that this stage actively maintains its position in nursery habitat and avoids movement into new areas.

The presumed model of mitten crab recruitment suggests that the megalopae returns to low salinity estuary areas and river mouths. Results from our trials suggest that salinity is not a major cue for megalopal migration. A second hypothesis is that settlement and metamorphosis into a juvenile crab occurs throughout the estuary, without a movement toward freshwater in the megalopae stage. As juvenile crabs tolerate a wide range of salinities, it is probable that crabs can develop throughout an estuary and return to lower salinities in later stages.

Habitat selection

In organisms with a planktonic stage, the transition to the benthos (settlement) is a critical period, and can be a major influence on the structure of local populations (Underwood and Fairweather, 1989). Crabs and lobsters settle in a wide variety of habitats with settlement primarily onto structurally complex habitats, such as oyster shells, macroalgae, hydroid, gravel and cobble (Cobb et al., 1997, Booth, 2001). In the laboratory, active habitat selection has been demonstrated by megalopae and juvenile crabs of a number of decapod species (Lee et al., 2004). Bivalve shell middens are the preferred settlement substrate of dungeness crab megalopae

(Fernandez et al., 1993). The choice exhibited by mitten crab megalopae for settlement substrate may determine the habitat type occupied by megalopae and early juvenile crabs.

Approach

Ten gallon glass aquariums were filled 2/3 full with tapwater treated to remove chloromines and adjusted with Instant Ocean to a salinity of 25 ppt. Substrates were taken from San Francisco Bay near Tiburon, CA and rinsed with treated tapwater. Equal volumes of substrates were placed into the corners of each of the aquariums, with the corners randomly selected. Substrates consisted of sand, gravel, shells, submerged macroalgae, floating macroalgae, and floating sticks. Two trials were conducted, the first with two aquariums and the second with four aquariums. The aquariums were held at room temperature(18 ± 2^{O}C) under a 12:12 light cycle. Megalopae were individually introduced using pipets into the center of the aquarium and allowed to select a substrate. Substrate selection was recorded when the megalopae stopped moving for one minute. Subsequent megalopae were then introduced until five megalopae occupied each tank. The substrate choice was recorded for the initial choice and after 24 and 48 hours. Analysis was conducted using a Tukey multiple comparison test on the number of megalopae on each substrate.

Analysis

Initial choice was primarily sand, rock, and seaweed. After 24 and 48 hours primarily rock and seaweed (Figure 2). Results were consistent between tanks and trials.

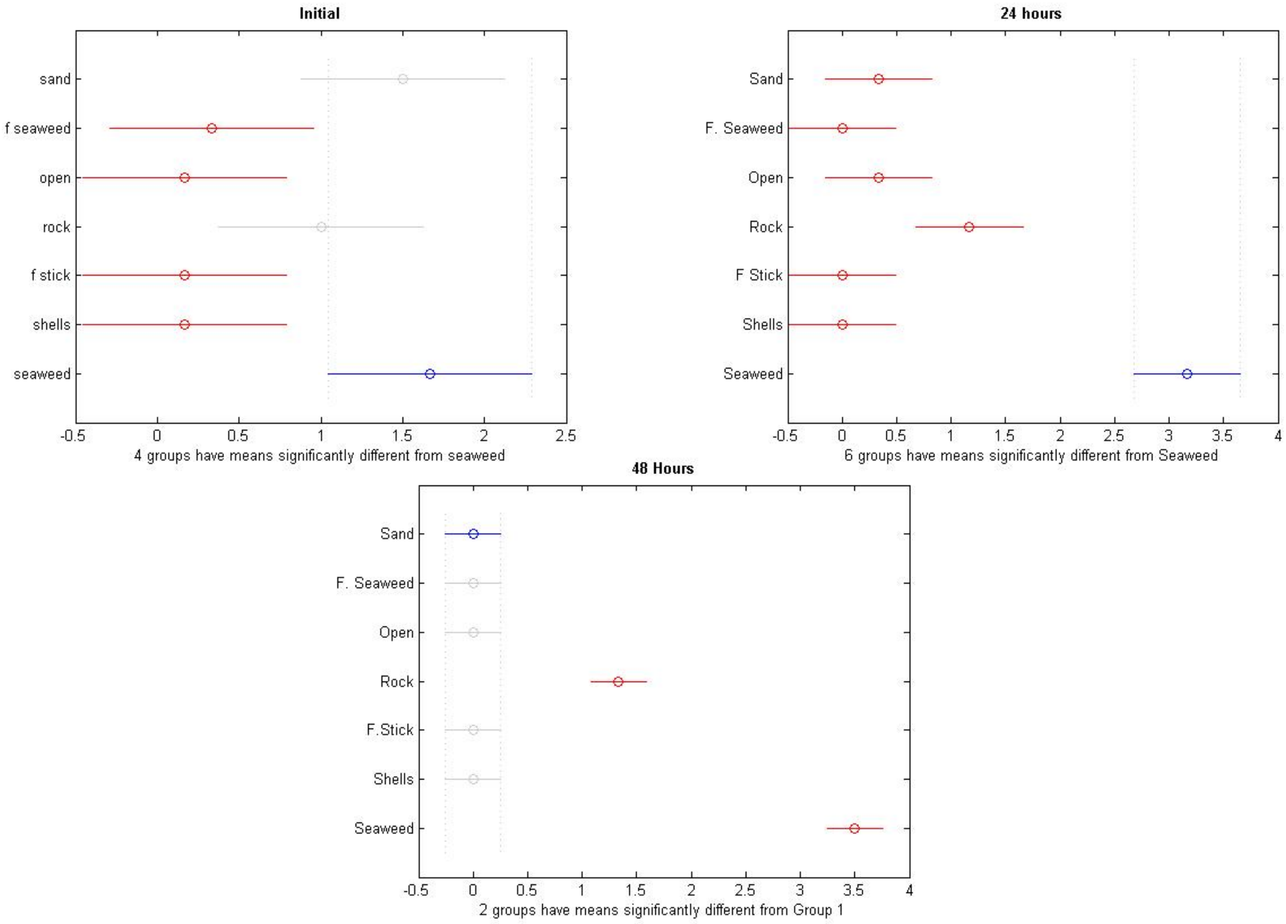


Figure 2: Megalopae Settlement Substrate Choice

Discussion

The megalopae chose benthic structures initially and after 24 hours were primarily on rock and seaweed substrate. These substrates provide shelter and potentially a food resource through grazing on algal growth. Settlement in an unfavorable habitat that provides poor shelter could lead to high predation. Megalopae actively clung to the seaweed and would not release even when removed from the water. If megalopae are the stage that actively migrates toward freshwater, the ability to cling to substrate may decrease the possibility of being displaced by seaward currents.

Larval settlement substrate preference can determine initial juvenile crab distribution (Boudreau et al., 1993). The preference of megalopae for seaweed, suggests that megalopae probably are found in high numbers in seaweed beds or aquatic vegetation in the bay. This choice could be confounded by the fact that megalopae were reared with pieces of seaweed in their dishes.

The difference between the initial substrate choice and the 24 and 48 hour choice is likely to be avoidance of movement in open spaces during daylight. Predation rates are higher during daylight and avoidance of movement during these hours is likely to avoid predation. Mosknes (2003) observed that many megalopae remained in poor habitat until dusk before emigration to higher quality habitat.

Larval Recruitment

Annual variations in estuary conditions probably result in population fluctuations demonstrated by the numbers of adult crabs that return to the San Francisco Bay in subsequent years. Limited data from the Tracy fish collection facility and CAFG trawls exists for estimates of population size in the San Francisco Bay. The data does show that the population peaked in the water year 1999 with moderate populations in 1998, and 2002 and small populations in 2000, 2001 and 2003. The mitten crab reaches sexual maturity in an estimated range of two to five years (Panning 1939). For this study, a crab that hatched in March, 1994 would be considered to be age zero until March, 1995, age one until March, 1996 and finally age five from March, 1998 to March, 1999. This suggests that estuary conditions in 1993, 1994, 1995, or 1996 are correlated with the large population seen in 1999.

The majority of ovigerous females are found in San Francisco Bay from November to March, with fewer numbers seen April to June (Rudnick et al., 2003). Egg development takes a minimum of thirty day at 17^{O}C in the laboratory. Egg development in the Bay is probably longer as temperatures range from 10 to 15^{O}C in this period and egg development is temperature dependant. Ovigerous females found in the bay prior to November probably do not release eggs until December. This suggests that conditions in the estuary from December through June are critical for larval recruitment.

Estuary conditions in the San Francisco Bay are highly dependant upon time of year and freshwater input. The two main estuary conditions critical to larval development and survival are temperature and salinity. Salinity levels determine if larval development can occur and temperature determines the length of the larval period. Freshwater input determines if a sufficient period exists for larval development within the estuary. Variations in these conditions over the period when larvae are in the bay will determine larval supply, the main factor in larval recruitment.

Through vertical migration zoea can increase retention rates. The vertical migration experiments suggest that zoea undergo a limited diel vertical migration and utilize haloclines, which may increase larval retention. Though zoea do undergo a limited vertical diel migration, all stages have a high affinity for the water surface. This suggests that larval recruitment will correspond to surface water conditions that determine larval survival and development.

Approach

The analysis assumed that variations in population sizes is a reflection of estuary conditions three to six years prior, resulting in adult crabs that are two to five years old. The period when larvae are present in the estuary, December through June, was used as the basis for analysis. Year to year variations in salinity and temperature were analyzed using data from NOAA and USGS stations in the North and South bay (Figure 3) (NOAA, 2005, USGS, 2005). Flow data was obtained from DAYFLOW, a model of net delta outflow to the bay, the main source of freshwater input into the bay (IEP, 2005).

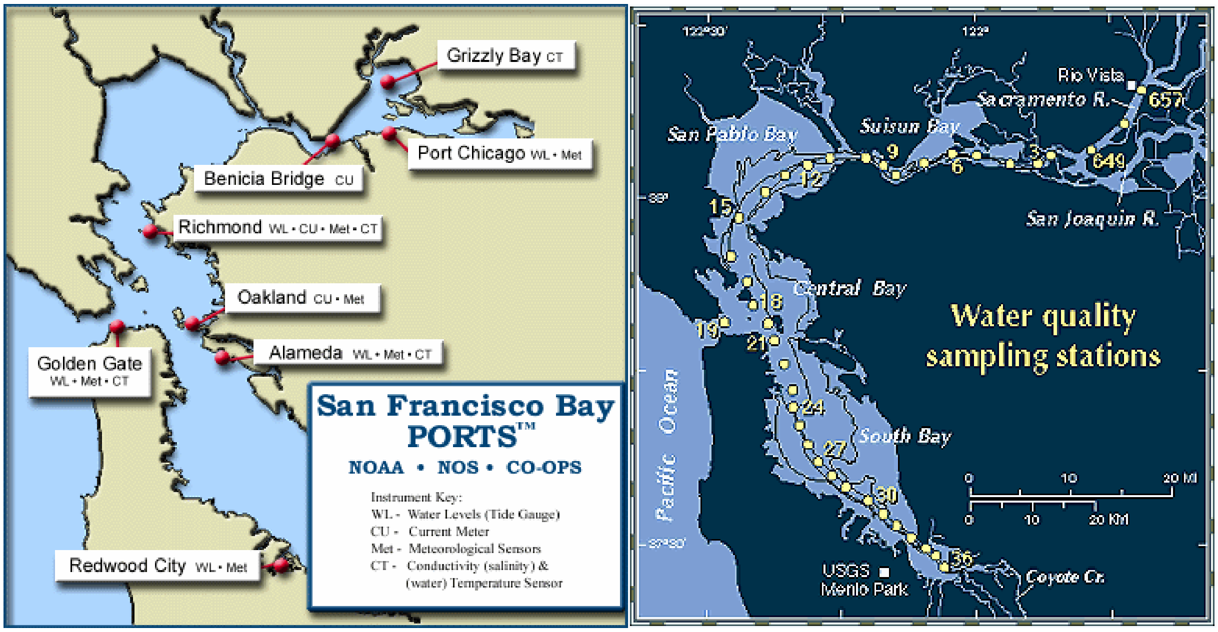


Figure 3: NOAA and USGS Stations

Larval Development

Laboratory rearing times were used by Anger (1991) to develop stage-specific models of development. These stage-specific models were combined to develop a temperature-based regression model of development time for the larval (zoea and megalopae) period (Figure 4). The equation for larval development is

$$D = 393.89e^{-0.123x}$$

where X = water temperature (ºC), and D = development duration in days.

Analysis proceeded on the premise that all temperatures above 9^{O}C permitted development. Limited laboratory data suggests that zoea I can survive at 10^{o}C (Hanson, unpublished data 2005) with complete mortality at 9^{O}C (Anger 1991). Mean daily water temperature was calculated using data from NOAA stations. Temperature data was collected within one meter of the surface and was recorded during the period of 1993 to 2004. These data were used to calculate a daily increment (1/D) in development based upon a daily temperature (X). The (1/D) values were summed until the fractions equaled one and indicated the completion of a larval period. Larval development was assumed to begin on December 1 and continued until June 31, the period when ovigerous females are found in the bay. Larval development periods were calculated in 15 day intervals.

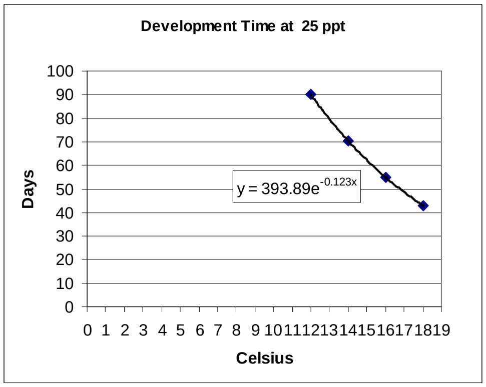


Figure 4: Model of larva development time (data from Anger 1991).

Flow

The San Francisco Bay exhibits a complex circulation pattern that changes with flow rates. This complexity does not permit for a direct correlation between flow rates, flushing time and larval retention. At high flow rates, low salinity north bay water is pushed into the south bay. While a direct measure of larval retention cannot be made, flow rates are correlated with larval retention. Year with high flow rates will result in a decrease of larval supply. Yearly differences in flow rates were analyzed for the periods of December to June and compared to years of mitten crab abundance.

Salinity

Mitten crab zoea can survive in a salinity range from 15 to 32 ppt, with highest survival rates in 20 and 25 ppt. The salinity of San Francisco Bay is a function of Delta flow. Data from USGS water quality sampling in San Pablo Bay (stations 12 to 14) was compared to daily flow rates to develop a regression model of flow based salinity levels in San Pablo Bay (Figure 5). The regression model was used to model the daily surface salinity for the years of 1987 to 2004. The data was analyzed for the number of days from December to June that the calculated salinity was at or greater than 15, 20 and 25 ppt.

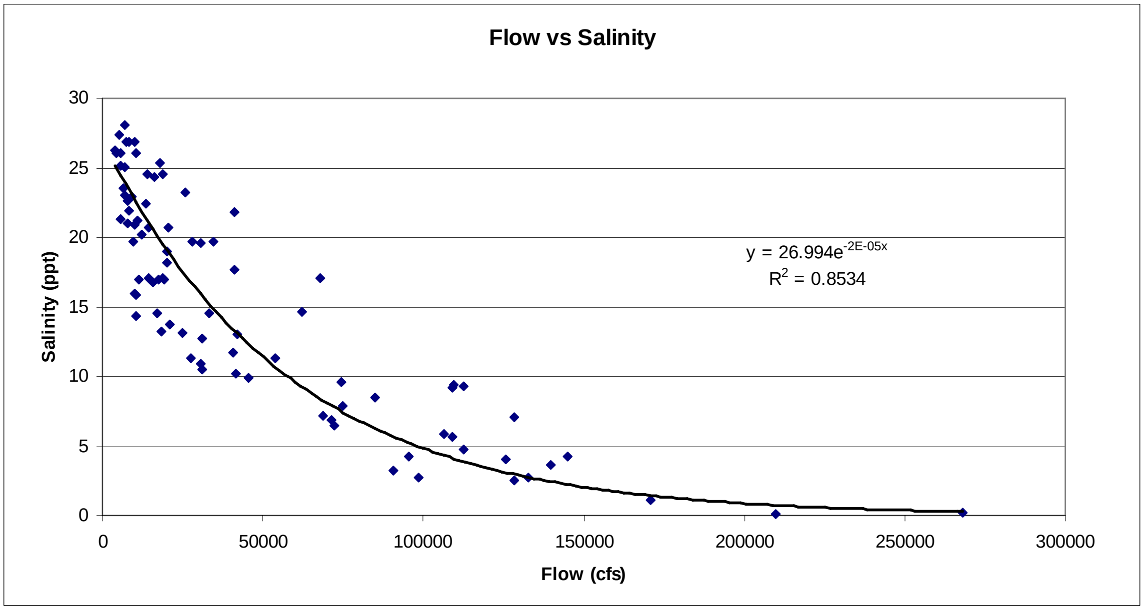


Figure 5: Regression model of Delta outflow based salinity

Analysis

Larval Development

For the December to June period, temperatures were sufficient for larval development (Figure 6 and 7). On average, temperatures did not go below 9^{O}C, and only occasionally during December and January did temperatures drop below 10^{O}C. Larval development times were similar for north and south bay sites. Zoea development time ranges from 16 to 65 days (Table 4).

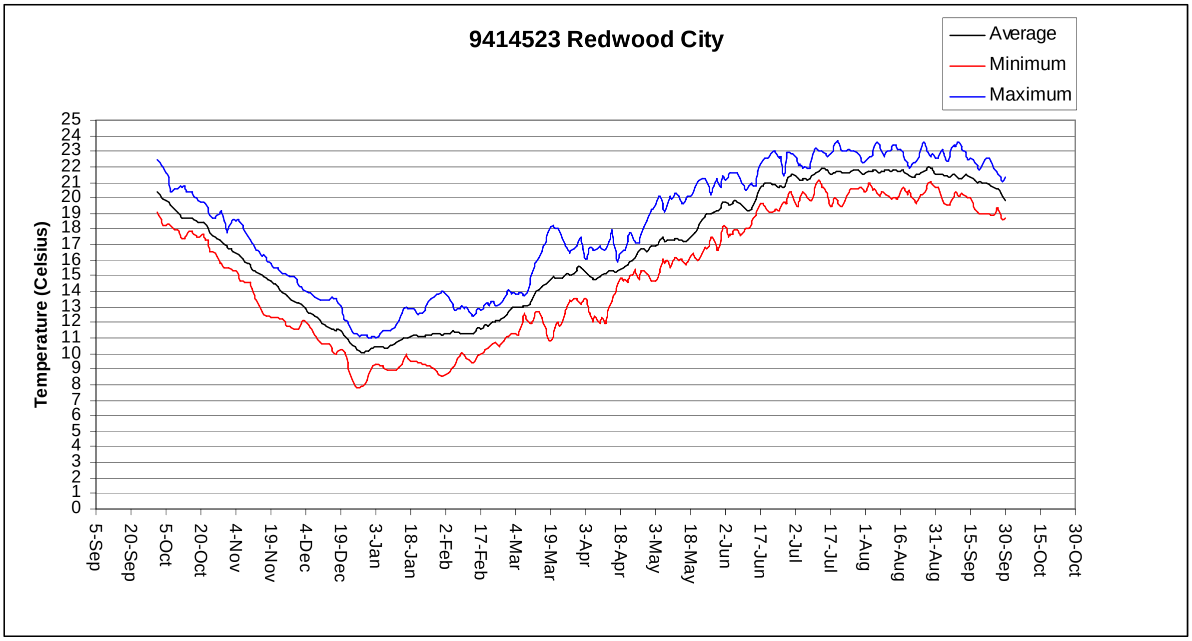


Figure 6: South Bay Water Temperatures

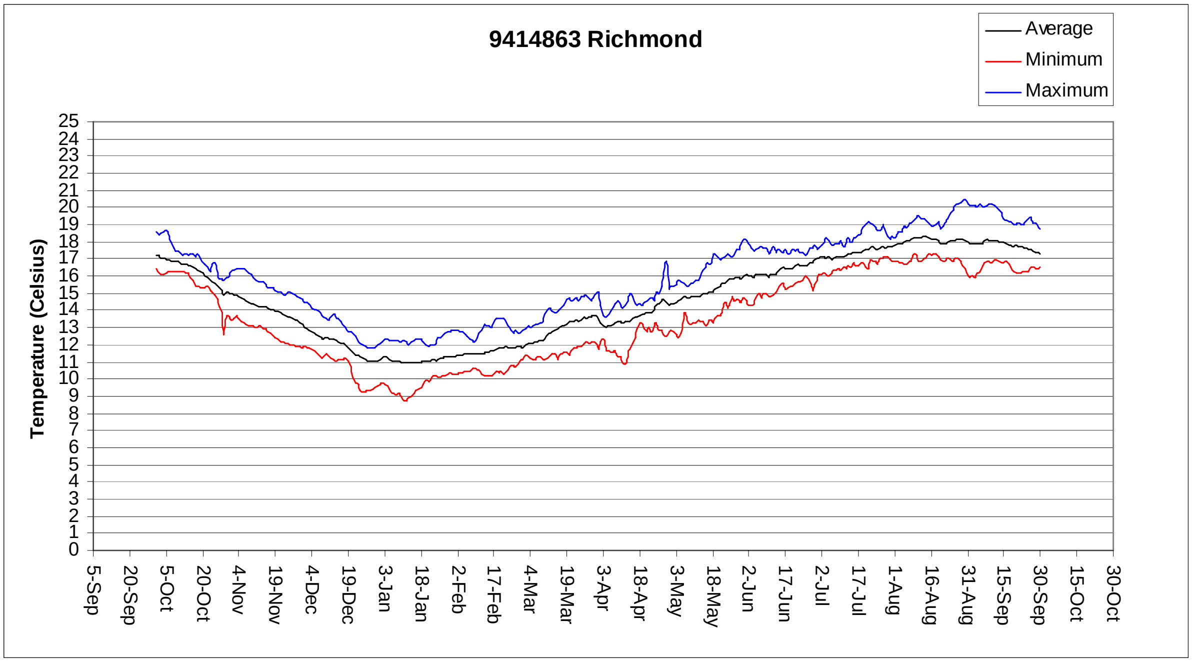


Figure 7: North Bay Water Temperatures

Table 4: Larval Development Times

	St. 9414290 Golden Gate			St. 9414863 Richmond			St. 9414523 Redwood City		
Period	Zoea I to V	Megalopae	Total	Zoea I to V	Megalopae	Total	Zoea I to V	Megalopae	Total
1-Dec	61	32	93	62	33	95	65	32	97
15-Dec	62	31	93	65	30	95	67	27	94
1-Jan	62	30	92	64	27	91	64	24	88
15-Jan	60	30	90	61	27	88	59	22	81
1-Feb	58	30	88	57	26	83	53	22	75
15-Feb	57	29	86	53	26	79	47	22	69
1-Mar	55	29	84	50	25	75	42	21	63
15-Mar	54	28	82	47	24	71	38	20	58
1-Apr	53	26	79	44	22	66	35	18	53
15-Apr	51	26	77	41	21	62	31	16	47
1-May	48	25	73	37	21	58	27	15	42
15-May	46	24	70	34	20	54	23	15	38
1-Jun	44	22	66	32	19	51	20	13	33
15-Jun	41	22	63	30	18	48	17	13	30
1-Jul	38	21	59	28	18	46	16	12	28

Flow

An analysis of the mean flow for the period of December to June shows the years of 1994, 2001 and 2002 as the lowest flow years (Figure 8). Ranks of monthly flow for the year of 1993 to 2004, demonstrate that 1994 and 2000 have the most months with below average ranks followed by 1997 and 2002 (Table 5).

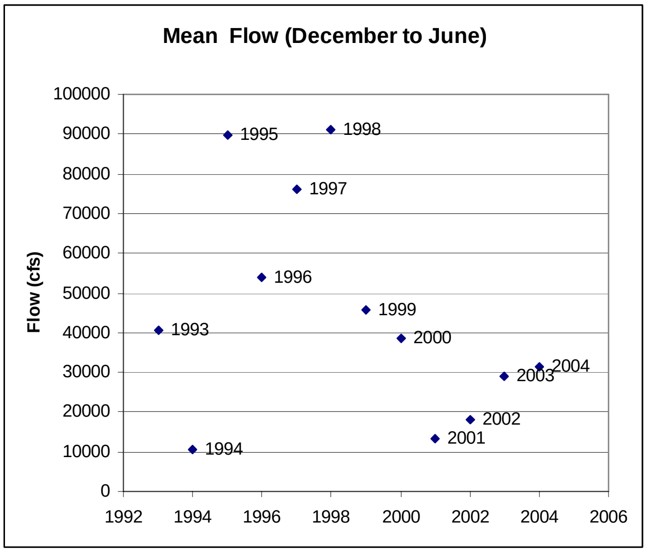


Figure 8: Mean Delta Outflow (December to June)

Table 5: Monthly Delta Outflow

Rank of mean monthly flow							
	Dec	Jan	Feb	Mar	Apr	May	Jun
1993	4	9	5	7	10	8	10
1994	5	1	3	1	1	1	1
1995	2	11	7	12	12	12	11
1996	9	5	11	9	9	10	9
1997	12	12	10	5	4	3	5
1998	6	10	12	11	11	11	12
1999	11	6	9	8	8	6	8
2000	3	3	8	10	7	7	6
2001	1	2	2	4	3	2	4
2002	8	7	1	3	2	5	3
2003	10	8	4	2	5	9	7
2004	7	4	6	6	6	4	2

Salinity

The salinity model demonstrates that the years of 1987 to 1992, 1994, 2001 and 2002 were highly favorable for larval survival (Table 6). In these years, calculated salinity levels were above 20 ppt for more than fifty percent of the December to June period.

Table 6: Yearly Salinity of San Pablo Bay

Yearly number of high salinity days																		
salinity	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
15 ppt	***198***	***205***	***188***	***211***	***203***	***199***	***96***	***206***	34	***74***	***115***	42	***82***	***127***	***192***	***187***	***118***	***148***
20 ppt	***165***	***178***	***168***	***192***	***180***	***174***	27	***166***	31	38	***73***	15	19	***69***	***152***	***120***	61	***72***
25 ppt	***86***	***120***	***96***	***149***	***155***	***111***	12	45	14	0	0	6	0	16	32	7	11	3
Bold cells indicate when the number of days is greater than the maximum zoea development of 65 days																		

The salinity of the north bay is directly influenced by flow. The salinity in the south bay is less directly influenced by flow. Data from 1994 to 1996 from USGS stations in the north bay (12 to 15) and south bay (24 to 27) exhibit similar salinity patterns (Figure 9). The similarity in salinity patterns suggests that year to year variations in salinity conditions due to Delta flow probably can be considered bay wide.

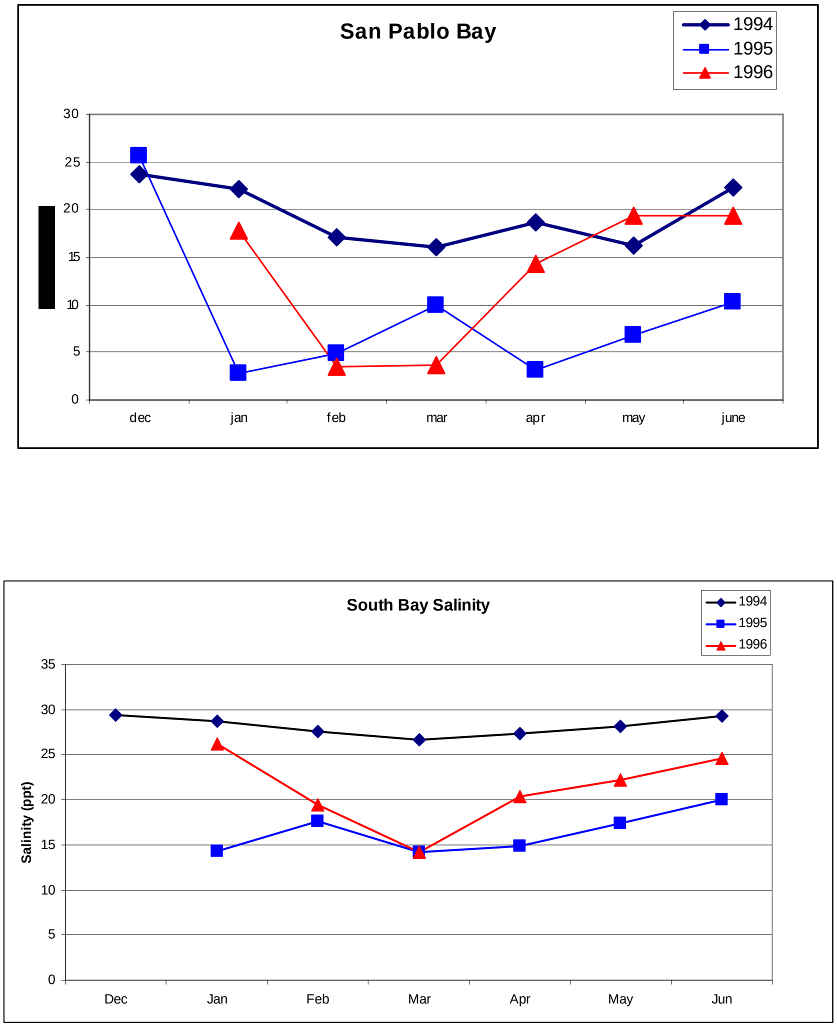


Figure 9: San Pablo and South Bay Salinities

Discussion

Annual variations in estuary conditions are primarily exhibited by Delta flow and salinity levels. A previous analysis determined that temperature would be a major factor for the establishment of mitten crab populations in Pacific Northwest (PNW) estuaries (Hanson and Sytsma, 2005). Wintertime temperatures in San Francisco Bay rarely reach the low temperatures seen in other PNW estuaries. Annual temperature variations are minor and have limited effects on larval development times.

The Delta flow effect is primarily seen in the correlation between flow and salinity. Flow has a great effect on the salinity levels in the bay by decreasing the area where salinity levels are favorable for larval development. Those years with stable low flow rates provide an optimal environment for larval development and retention in the bay.

The stable salinity environment that occurred in 1994 is likely responsible for the large number of adult crabs migrating to the bay in the fall of 1998 and contributed to those seen in the fall of 1997 (water year 1999 and 1998). These crabs would be three and four years old in 1998 and 1999 respectively (Table 7). The salinity environment in 1995 and 1996 was unfavorable with less than forty days above twenty ppt. This suggests a model of larval supply, where flow conditions will influence the adult population four to five years in the future. When salinity is greater than twenty ppt for more than 50% of the December to June period, large increases in population sizes should occur. When salinity is greater than fifteen ppt for more than 50% of the same period, moderate increases in population should occur. This correlation can be seen in Table 7 and suggests that the water years of 2006 and 2007 should see large population increases.

Table 7: Correlation of Salinity to Population

E. sinensis abundance and years of high salinity												
	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
Crab #'s	???	M	H	L	L	M	L	???	???	???	???	???
4 yr old	1992	1993	**1994**	1995	1996	***1997***	1998	1999	***2000***	**2001**	**2002**	**2003**
3 yr old	1993	**1994**	1995	1996	***1997***	1998	1999	***2000***	**2001**	**2002**	**2003**	2004
Red indicates years when salinity was greater than 20 ppt for more than 50% of the period												
Bold indicates years when salinity was greater than 15 ppt for more than 50% of the period												

Conclusions

Mitten crab larval recruitment is primarily a function of flow in the San Francisco Bay. The winter to spring period provides a stable thermal environment for larval development, with very short periods where temperature may limit larval development. Flow rates are highly correlated with salinity levels in the north bay. Even if retention in the north bay can be increased through vertical migration, in periods of moderate to high flow, the salinity environment becomes inhospitable.

The regression of salinity on flow is the first step to determine the yearly variation in salinity conditions and affects on larval survival. The salinity data used in this analysis came from a limited number of stations in the main channel of San Pablo Bay. Given the complexity of circulation patterns in the bay and the variance seen in salinity levels at low flows, more detailed circulation models would provide a better estimate of the salinity conditions. A comparison of the area of high salinity in the bay from year to year should result in a better prediction of population fluctuations.

The data suggest that megalopae may not be the stage that actively migrates toward freshwater. Additional research that incorporates turbulence and examines the whole megalopal period would more accurately explore this hypothesis. Anger's (1991) work on megalopal survival provided an indication that megalopae may not be the stage that reinvades estuaries. When megalopae were exposed to salinities that were lowered stepwise every three days, none of the larvae reached the first juvenile crab stage (Anger, 1991). The megalopae that did survive, were freshly molted megalopae that were gradually acclimatized in five ppt salinity steps every three hours (Anger, 1991). This suggests that megalopal movement only occurs in the first few days of the megalopal stage, which would allow for only limited upstream movement. As the early juvenile crab stages can tolerate a wide range of salinities, it is likely that the reinvasion of low salinity habitats occurs through a combination of movement by megalopae and juvenile crabs.

The model of mitten crab recruitment in San Francisco Bay proposed here suggests that the south bay, with its more constant salinities, provides the majority of habitat for larval development. In low-flow years, with few episodic events, both the south and north bay provide proper larval habitat. Episodic events probably increase the number of zoea in the south bay through the increased movement of north bay water that contains zoea. In years when larval development is confined to the south bay, variability in north bay populations is probably due to movement of juvenile crabs from the bay into brackish and freshwater. Age one juvenile crabs move toward freshwater in the spring, probably using salinity cues. High springtime flows probably increase the low-salinity signals and increase the number of juvenile crabs that migrate toward the delta and favorable freshwater habitat.

The mitten crab was first discovered in the San Francisco Bay in 1992, a population peak occurred in 1999 and then numbers declined. Invasive species typically exhibit wide population fluctuations in the early invasion period. Although many factors influence mitten crab population abundances in the bay, this study suggests that conditions in the estuary, primarily salinity, influence larval recruitment variability and are a major factor in population fluctuations.

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