

ABSTRACT

THE POPULATION DYNAMICS OF MITTEN CRAB LARVAE IN THE SAN FRANCISCO BAY

The Chinese mitten crab, *Eriocheir sinensis*, has a history of invasions in numerous countries. In 1992, the Chinese mitten crab was introduced to the San Francisco Bay/Delta system. Since its invasion in the San Francisco Bay, it has become an aquatic nuisance species. Little is known about the population dynamics of the megalopa stage of the Chinese mitten crab in the San Francisco Bay estuary, particularly the megalopa stage. Light traps are often used to sample marine larvae and can provide measures for relative abundance of larvae between sampling locations. As part of an ongoing study to monitor mitten crab larvae in the San Francisco Bay, light trap and plankton tow samples were analyzed for mitten crab megalopae and zoeae. In order to implement low cost sampling devices for mitten crab megalopae such as light traps, it is necessary to be able to identify their larvae in collected samples. Thus, the main objective of this work was to develop a means to distinguish mitten crab megalopae from other native and invasive brachyuran megalopae inhabiting the San Francisco Bay Estuary. The minimal amount of mitten crab megalopae found in light trap samples may be linked to the recent decline of mitten crab zoeae in San Pablo Bay.

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THE POPULATION DYNAMICS OF MITTEN CRAB LARVAE
IN THE SAN FRANCISCO BAY

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INTRODUCTION

The opportunity for non-native species to disperse to new habitats has greatly increased as humans have become more and more mobile. Many invasive species have been introduced to different environments because of human activities. In the past, geographic barriers, such as oceans, deserts, and mountains, made it difficult for species to colonize new habitats. However, the transoceanic movement of humans has helped to facilitate the invasion of many species to novel habitats (Bright, 1999; McNeely, 2006). The consequences of such invasions often are negative (Vitousek et al, 1997; Sanders et al., 2003).

Aquatic habitats are among the most invaded environments (Ruiz et al., 1999). This is probably due to commercial shipping, fishing, and recreational activity that occur in these habitats (LeMaitre et al., 2004; McNeely, 2006). Although unsuccessful invasions go unnoticed, aquatic invaders that are successful in establishing populations can have dramatic affects on the structure and function of the ecosystem that they invade (Miehls et al., 2009; Pejchar and Mooney, 2009). Once a nuisance species has been established, control efforts can be extremely costly (Pimetel et al., 2001; Pimetel et al., 2005). Some introduced species can even act as vectors for disease, and thus pose risks to native species and in some cases human populations (Prenter et al., 2004; Cohen, 2003).

One aquatic ecosystem that has been heavily invaded is the San Francisco Bay Estuary (Cohen and Carlton, 1998). The Chinese mitten crab, *Eriocheir sinensis*, is a problematic invader in the San Francisco Bay (Veldhuizen, 1997; Veldhuizen and Stanish, 1999; Rudnick et al. 2000; Rudnick et al., 2003). In 1992, the Chinese mitten crab was first discovered in the San Francisco Bay/Delta

system in California. Since its invasion in the San Francisco Bay, Chinese mitten crab abundance has fluctuated greatly, with population explosions occurring in 1999 and 2002 (Rice, 2006).

Chinese Mitten Crab Life History Stages

The Chinese mitten crab is a catadromous species, spending much of its adult life in freshwater and requiring saline water for reproduction. In San Francisco Bay, the reproductive period of the mitten crab is from December through June (Rudnick et al., 2005). The mitten crab zoeae hatch in saline water and undergo five stages before metamorphosing into a post-larval megalopa stage (Figure 1). The first zoeal stage of the mitten crab has been found as early as December in San Francisco Bay (Rice, 2006). However, previous studies suggest minimal zoeae survivorship until March (Rice, 2006). Stage five zoeae have been found as late as June (Rice, 2006). The megalopae are thought to use currents to migrate to less saline areas (Panning, 1939; Anger, 1991). It is unclear whether megalopae use environmental cues to migrate to appropriate habitats for metamorphosis, or if their transport to freshwater habitats is completely passive. However, in laboratory experiments, megalopae were found to tolerate low salinities (Anger, 1991). This indicates the megalopae stage may be the stage that migrates to less saline environments. Once megalopae make their way to these environments they metamorphose into benthic juveniles. In San Francisco Bay, early juvenile crabs are found in brackish water ranging from salinities of 1 to 20 parts per thousand (Rudnick et al., 2003). The juveniles make long journeys to freshwater rivers and streams, where they grow and mature into adult crabs. This is thought to take more than two years for the San Francisco Bay population (Rudnick et al., 2005). Once they become reproductively mature, adult mitten

crabs then migrate back downstream to more saline environments (Rudnick et al., 2005). Reports of downstream migrations occurring as fast as 18 kilometers per day indicate these migrations can occur very rapidly (Herborg et al., 2003). Once in saline environments, adult mitten crabs will mate and reproduce (Rudnick et al., 2005). In San Francisco Bay, the mitten crab lifecycle is thought to be completed in about three years (Rudnick et al., 2005).

Chinese Mitten Crab Invasion History

The Chinese mitten crab (*Eriocheir sinensis*) has a history of invasions in numerous countries (Panning, 1939; Clark et al., 1998; Cabral and Costa, 1999; Normant et al, 2000). In 1912, the Chinese mitten crab was reported in the Aller river of Germany. This was the first report of a Chinese mitten crab sighting outside its native range in Asia (Panning, 1939). By the 1940s, the species could be found in other parts of Europe including the United Kingdom, Denmark, the Netherlands, Belgium and France, and now there are reports of crab sightings in areas of the Baltic Sea as far as Russia and Finland (Panning, 1939; Herborg, 2003).

The mitten crab was first introduced into the United Kingdom in the 1930s (Ingle, 1986). However, it did not become established in this area until the early 1970s (Ingle, 1986, Rainbow et al., 2003). Mitten crabs were found in the Tagus river in Portugal in the early 1980s but the population did not become established until the 1990s (Cabral and Costa, 1999). By 1997, the mitten crab had become established in Spain (Cuesta et al., 2004). More recently, the mitten crab has been found in two countries in western Asia (Clark et al., 2006; Robbins et al., 2006). In northern Iran a specimen was discovered in the Tazeh Bekandeh River in 2002

(Robbins et al., 2006). In Iraq one mitten crab was found in a canal that dumps into the Persian Gulf in 2005 (Clark et al., 2006).

Mitten crabs have been captured in several places in North America including the Great Lakes in the United States, the St. Lawrence River in Canada, and the Chesapeake Bay in the United States (Nepszy and Leach, 1973; de Lafontaine, 2005; Ruiz et al., 2006). However, the San Francisco Bay Delta system is the only region in North America with an established population of Chinese mitten crabs (Rudnick et al., 2003). The Chinese mitten crab was first found in San Francisco Bay, California in 1992 (Veldhuizen and Stanish, 1999). Since its invasion to the San Francisco Bay, the mitten crab has become a nuisance species with negative ecological and economic effects. Many of these effects are due to massive population explosions (Veldhuizen and Stanish, 1999). Some negative effects caused by the mitten crab invasion include stream bank and levee erosion through burrowing behavior and interference with commercial fisheries through gear destruction and bait stealing (Veldhuizen and Stanish, 1999). During times of adult population explosion, the mitten crabs interfere with the water diversion at fish salvage facilities. In 1998, almost 1 million crabs were captured in holding tanks at the Tracy Fish Collection Facility. The vast numbers of crabs captured in holding tanks severely hinders fish salvage operations (Veldhuizen and Stanish, 1999).

Explosions in juvenile and adult populations may also negatively affect the ecology of the area through predation of smaller invertebrate species and competition with native species (Veldhuizen and Stanish, 1999). The Chinese mitten crab is known to be omnivorous (Rogers, 2000; Rudnick and Resh, 2005). Previous studies have shown omnivorous crustaceans are capable of influencing food webs through trophic interactions (Lodge, et al., 1994; Charlebois and

Lamberti, 1996). During years of great abundance, it is possible mitten crab juveniles, through predation, crabs could reduce populations of other invertebrates in San Francisco Bay. This ultimately may change the structure of the estuary's benthic communities, especially in intertidal zones where large crustacean predators are not as common (Rudnick and Resh, 2005). Still, there has been no research done to determine whether the mitten crab is negatively affecting the native species in the region. However, Rudnick et al. (2000) investigated the interactions between mitten crabs and two co-existing invasive crayfish species in the area and found that the presence of the mitten crab was not correlated with the absence of the red swamp crayfish. However, the crayfish was observed backing away from approaching mitten crabs, suggesting the mitten crabs are the more dominant species in the region (Rudnick et al., 2000). In laboratory experiments no difference between the number of aggressive actions initiated between the mitten crab and the commercially important signal crayfish were reported. Although, the mitten crabs were able to gain possession of shelters when placed in the same enclosure as the signal crayfish (Rudnick et al., 2000). Together, these studies suggest the mitten crab is more aggressive than the co-existing crayfish species in San Francisco Bay. During times when food and shelter are scarce, it is possible the mitten crab would outcompete these two species.

Environmental Factors Influencing Growth and Survival of Brachyuran Megalopae

Several studies have showed that temperature and salinity can affect the survival and development of brachyuran zoeae and megalopae (Anger, 1996; Forward et al., 2001; Anger et al., 2008). Previous studies that have focused on the zoeal stages of the Chinese mitten crab have shown temperature thresholds for successful development of the larval stages to be around 11.8°C for the San

Francisco Bay population (Rice, 2006; Blumenshine et al., in review). Another study showed that the laboratory raised megalopa stage of *E. sinensis* is influenced by temperature and salinity (Anger, 1991). This study reported a reduced ability of the megalopa to develop into juveniles at temperatures below 12°C. Temperatures below 12°C were shown to increase mortality of experimental megalopae. The optimal salinities for megalopae development are between 15‰ and 25‰, while the zoeae had shorter development times in salinities between 25‰ and 32‰, (Anger, 1991). This suggests that the megalopa stage has an increased tolerance to brackish water.

Other studies have investigated the relationship between osmotic stress and recruitment for the megalopae of the freshwater crab, *Armases robertii* (Torres et al., 2006). These studies found megalopae were able to metamorphose properly when allowed to acclimatize to salinities of less than 3‰, suggesting that the megalopae is the life stage that transitions to from saline to freshwater environments (Torres et al., 2006). Similar studies showed other brachyuran megalopae are able to cope with changes in salinity (Diele and Simith, 2006; Mingkid et al. 2006). *Eriocheir sinensis* megalopae also show a remarkable ability to cope with decreasing salinity, provided the change from highly brackish water to less saline water is gradual (Anger, 1991). The megalopae of the mitten crab may be the stage in its life history that returns to freshwater habitats (Panning, 1939; Anger, 1991).

Research Objectives

Like many other brachyuran crabs, *Eriocheir sinensis* possess a type III survivorship in which much of the population's mortality occurs at the larval stages. Therefore, the high mortality of zoeae may decouple the relationship

between zoeae and adult abundances, making it difficult to use zoeae densities to predict when ensuing adult densities will be high. It is possible megalopae abundances will have a strong correlation with adult abundances as the time interval between these two life history stages is very short. Currently, little is known about the environmental factors and cues that influence mitten crab megalopae settlement, distribution and abundance. Post-larval megalopae recruitment may have an effect on adult population dynamics. If a link can be found between megalopae abundance and adult mitten crab abundance then megalopae numbers may be used as predictors of when adult populations will be high. If population explosions can be predicted, preparations can be made for the negative effects caused by the downstream migration of mitten crab adults. One aim of this study was to investigate possible locations of mitten crab megalopae settlement in San Pablo Bay and determine environmental factors that may influence megalopae distribution and settlement. In addition, this work will also examine trends in mitten crab zoeae abundance over an eleven year period. A key for the brachyuran zoeae found in San Francisco Bay was previously created so that zoeae from plankton samples could be analyzed (Rice and Tsukimura, 2007). However, the study of mitten crab megalopae inhabiting the region is hindered by the lack of a means to identify this post-larval stage. Therefore, the main objective of this work was to create a dichotomous key of the brachyuran megalopae of the San Francisco Bay and estuary that includes both native and non-native species.

MATERIALS AND METHODS

Megalopae Dichotomous Key

A dichotomous key for the brachyuran megalopae inhabiting San Francisco Bay was developed to identify megalopae found in light traps and plankton tows. A list of brachyuran species found in San Francisco Bay was generated using the species identified in plankton tow sampling done by researchers studying the Bay (Mooi et al., 2007; Rice and Tsukimura, 2007) and the invertebrate collection catalog of the California Academy of Sciences (California Academy of Sciences, 2008). Post-larval descriptions and illustrations were obtained for both native and non-native species of brachyuran crabs known to inhabit the San Francisco Bay Estuary. The key was created using morphological characteristics for the megalopae of brachyurans found in San Francisco Bay. Illustrations adapted from published literature and drawn from captured specimens are provided to identify species and characteristics used in the key. A short species description is provided for all megalopae included in the key. Along with the family Pinnotheridae, the brachyuran megalopae included are: *Cancer productus*; *Carcinus maenas*; *Eriocheir sinensis*; *Hemigrapsus nudus*; *Hemigrapsus oregonensis*; *Lophopanopeus bellus*; *Lophopanopeus leucomanus*; *Metacarcinus (Cancer) anthonyi*; *Metacarcinus (Cancer) gracilis*; *Metacarcinus (Cancer) magister*; *Pachygrapsus crassipes*; *Pyromaia tuberculata*; *Rhithropanopeus harrisii*; and *Romalaeon (Cancer) antennarius*. Appendix C, Table 1 shows literature used for descriptions and illustrations of megalopae.

Illustrations of megalopae for *M. gracilis*, *E. sinensis*, and the family Pinnotheridae were drawn from specimens found in light traps and zooplankton

samples taken from the region. Other species illustrations used in this key were adapted from illustrations in published literature (Appendix C, Table 1). Light trap samples were provided by our collaborators at the Smithsonian Environmental Research Center (Tiburon, CA). Zooplankton samples were obtained from the California Department of Fish and Game *Neomysis* and Clarke-Bumpus Zooplankton Survey. In order to view morphological characteristics clearly, specimens were preserved in 10% formalin and subsequently dyed using Rose bengal dye.

Several species of Pinnotheridae are thought to inhabit San Francisco Bay, including *Pinnixa franciscana*, *P. littoralis*, *P. schmitti*, *P. occidentalis*, *P. longipes*, and *Scleroplax granulata*. Because little literature exists on the larval or post-larval description of pinnotherid crabs in the region, all the pinnotherid species were grouped together in the key using one morphological trait that has been described in published literature (Lough, 1974). This feature has been used in previous dichotomous keys to group species in the family Pinnotheridae (Shanks, 2001).

Overall, conspicuous morphological characteristics were chosen for couplets of the dichotomous key. However, in cases where species are almost identical, less obvious morphological features were used to separate species. For example, the number of setae on the mandibular palp was one characteristic that was used to separate the species *Metacarcinus gracilis* and *Metacarcinus anthonyi*. Illustrations were provided to make differences between species easier to detect.

Megalopae Distribution

Previously, areas in southern San Francisco Bay were analyzed for mitten crab megalopae and zoeae using light traps. However, no mitten crab megalopae or zoeae were found in these areas. Previous studies found the highest abundance of mitten crab zoeae at station California Department of Fish and Game station D41 in San Pablo Bay (Rice, 2006). Consequently, the distribution of mitten crab megalopae was assessed using light trap samples taken from areas in San Pablo Bay (N 37°45', W 122°26') including Point San Pablo, McNear's Beach, and Point Pinole Regional Shoreline during March through June (Appendix B, Figure 2). These areas were sampled biweekly for the months of March, April, May, and June during 2007 and 2008 using light traps. Four traps were deployed at each site and left over night. The light trap samples were taken by the Smithsonian Environmental Research Center at Tiburon, CA. All samples were dyed using Rose Bengal Dye to make organisms in the samples easy to identify. Mitten crab megalopae were identified in samples using a Leica MZ7.5 dissecting microscope and Leica KL 750 light source and preserved in vials with a 10% formalin solution. A key for the brachyuran megalopae inhabiting San Francisco Bay Estuary was created so that mitten crab megalopae could be identified in light trap samples. Other sympatric brachyuran megalopae were also collected and identified.

Zoeae Identification and Abundance

Brachyuran zoeae were identified and recorded from California Department of Fish and Game (DFG) Clarke-Bumpus plankton tow samples taken monthly from station D41 in San Pablo Bay. These monthly plankton tow samples were analyzed to determine the species composition and temporal abundance of brachyuran zoeae at this station. Previous studies found *E. sinensis* zoeae

abundance to be the highest at DFG station D41 (Rice, 2006) and this site was used for spatial consistency of the data. Data on zoeae abundance for the months of December- July from 1998-2005 was used from an earlier study (Rice, 2006). Rice's work focused on the population dynamics of mitten crab zoeae and only analyzed plankton tow samples taken during months when mitten crab zoeae would be found (Rice, 2006). For the present study, Clarke-Bumpus plankton tows samples for the months of August-November from 1998-2005 were analyzed to account for the zoeae abundance of every brachyuran species found at this station. In addition, Clarke-Bumpus plankton tow samples taken from DFG station D41 (Appendix B, Figure 2) during the years of 2006-2008 were analyzed for brachyuran larvae in order to gain a better understanding of the species composition of brachyuran zoeae in San Francisco Bay and to continue to monitor invasive species such as the mitten crab. The monthly catch per unit effort (CPUE) was calculated for every species in every year. The relative abundance for every species was also calculated. The analysis of these samples provided eleven years of zoeae abundance data for every brachyuran species in San Francisco Bay. A Pearson's Correlation was used to determine relationships between *E. sinensis* zoeae density and other native brachyuran zoeae density.

Plankton samples were preserved in 10% formalin and dyed using Rose Bengal dye. Zoeae were identified in Clark-Bumpus plankton tow samples using a Leica MZ7.5 dissecting microscope and Leica KL 750 light source. Brachyuran zoeae were keyed to species with the use of a dichotomous key (Rice and Tsukimura, 2007) and specimens were stored in separate vials so that they could be counted and recorded.

Environmental Parameters

Temperature and salinity data used in this research was obtained from the United States Geological Survey (USGS) continuous monitoring gauge, PSP, located in San Pablo bay (T/S1) (Appendix B, Figure 2) and a National Estuarine Research Reserve System (NERRS) monitoring gauge located at China Camp also in San Pablo Bay (T/S2) (Appendix B, Figure 2). Temperature and salinity data were used from gauge PSP when available. However, data from USGS monitoring gauge PSP are unavailable after July of 2006. Temperature and Salinity data are obtained from a monitoring gauge at China Camp in San Pablo Bay for August of 2007 through December of 2008. A correlative analysis was used to compare temperature and salinity readings from the two monitoring sites and found that there was a high correlation between the temperature and salinity data sets ($R^2=0.98$; $R^2=0.96$). Environmental data from the China Camp monitoring site was calibrated to be more comparable to the PSP monitoring site. Monthly temperature and salinity averages were used for correlation analysis for both monitoring gauges. A Pearson's Correlation was used to evaluate the relationship between temperature and salinity with *E. sinensis* zoeae density. Data for adult mitten crab abundance used in this study was collected by CDFG otter trawls from 1998-2008.

The catch per unit effort (CPUE) was used to measure zoeae abundance. CPUE was calculated by dividing the total number of zoeae found in each sample by the tow volume of that sample (m^3) and multiplying the product by 100. Relative abundance of the zoeae of each brachyuran species in the San Francisco Bay was calculated by dividing total CPUE of each species from 1998-2008 by the total CPUE of every species from 1998-2008. The product of this calculation was

then multiplied by 100. Linear regression was used to compare temperature and salinity data from continuous monitoring gauges in San Pablo Bay.

RESULTS

Introduction

The following section presents a dichotomous key of the native and invasive brachyuran megalopae in San Francisco Bay. The figures that accompany the key below can be found in Appendix A.

A Key to Brachyuran Megalopae of the San Francisco Bay Estuary System

- 1A. Rostrum pointed or with rostral spine (Fig. 1, arrow A) 2
- 1B. Rostrum blunt or flat (Fig. 11A, arrow A) 9
- 2A. Carapace with dorsal spine (Fig. 1, arrow B) Cancridae 3
- 2B. Carapace without dorsal spine (Fig. 6, arrow A) 7
- 3A. Carapace with reduced lateral spines (Fig. 1, arrow C) 4
- 3B. Carapace without lateral spines (Fig. 3, arrow A) 5
- 4A. Telson subquadrate with indentation on terminal portion (Fig. 1, arrow D).
..... *Cancer productus* Randall, 1839. (Fig. 1).
Carapace with rostral and dorsal spines. Lateral spines on carapace greatly reduced. Carapace length about 3.6 mm. Antenna of 11 segments with proximal to distal setal arrangement of five, four, four, zero, zero, three, two, three, one, three and five, respectively. Mandible with 12 setae on palp. First Maxilliped: endopod with 38 to 40 spines on basal end and nine setae on distal end; exopod with six plumose setae on distal end. Second Maxilliped: exopod with five plumose setae. Third Maxilliped: endopod of four segments with many spines; exopod with six plumose setae. Pleon of six pleomeres plus a telson (Lough 1974; Trask, 1970).

4B. Telson flat, without indentation on terminal portion (Fig. 2, arrow A)
 *Romalaeon antennarius* (Stimpson, 1856) (= *Cancer antennarius*) (Fig. 2).

Carapace with rostral, dorsal, and greatly reduced lateral spines. Carapace length about 2.4 mm. Antenna with 11 segments, proximal to distal setal arrangement of four, two, four, zero, zero, four, zero, five, zero, four and four, respectively.

Mandible two-segmented palp with nine terminal spines. First Maxilliped: endopod of two segments. Distal segment of endopod with three subterminal plumose setae and two terminal spines; exopod of two segments with three plumose setae on proximal segment and four plumose setae on distal segment.

Second Maxilliped: endopod of three segments with spine arrangement of zero, seven and eight, respectively; exopod with four plumose setae on distal segment.

Third Maxilliped: endopod of four segments with spine arrangement of ten, six, eight and seven, respectively; exopod with five plumose setae on distal segment.

Pleon of six pleomeres. Posterior edge of telson smooth (Lough, 1974; Roesijadi, 1976).

5A. Carapace length about 6.8 mm
 *Metacarcinus magister* (Dana, 1852) (= *Cancer magister*) (Fig. 3).

Carapace with rostral and dorsal spines. Antenna of 11 segments, proximal to distal setal arrangement of 11, 11, eight, zero, two, seven, six, two, five and five, respectively. Mandible palp with 18 spines. First Maxilliped: endopod basal end with many spines and distal end with eight to nine setae; exopod with seven terminal setae. Second Maxilliped: endopod of four segments with spine arrangement of seven, six, 20 and 14, respectively; exopod with six natatory setae on the terminal portion. Third Maxilliped: endopod of four segments with many setae on all segments. Pleon of five pleomeres plus a telson (Lough, 1974; Poole, 1966).

5B. Carapace length between 1.5 to 2.5 mm 6

6A. Antenna of 11 (occasionally ten) segments, proximal to distal setal arrangement of five, two (occasionally three), four (occasionally three), zero, zero, four (occasionally three and five), zero, five, zero (occasionally one), four and five (Fig. 4A) and Mandibular palp with eight (sometimes seven or nine) setae on terminal segment *Metacarcinus gracilis*

..... (Dana, 1852) (= *Cancer gracilis*) (Fig. 4B).

Carapace with rostral and dorsal spines. Mandible three-segmented palp with setal arrangement of zero, zero and eight, respectively. First Maxilliped: endopod flattened process with four setae; exopod of two segments with two to four plumose setae on distal portion of proximal segment and five plumose setae on terminal portion of distal segment. Second Maxilliped: endopod of five segments with setal arrangement of one, one (occasionally zero), one, six to seven (occasionally five) and nine, respectively; exopod of two segments with five plumose setae on distal segment. Third Maxilliped: endopod of five segments with setal arrangement of 23 to 27, 13 (occasionally 12), ten to 12, ten to 13 and nine, respectively; exopod of two segments with two to four setae on proximal segment and five plumose setae on second segment. Telson flat, posterior margin rounded (Ally, 1975).

6B. Antenna of 11 segments, proximal to distal setal arrangement of five, two, three, zero, zero, four, zero, five, zero, five, and five (Fig. 5A) and Mandibular palp with 13 setae on terminal segment *Metacarcinus anthonyi*

..... (Rathbun, 1897) (= *Cancer anthonyi*) (Fig. 5B).

Carapace with rostral and dorsal spines. Total length about 3.2 mm. First Maxilliped: endopod with 20 spines on basal portion and 15 on distal portion; exopod with five long setae on terminal portion. Second Maxilliped: endopod of

four segments with spinal arrangement of two, one, seven and ten, respectively; exopod with five long setae on terminal portion. Third Maxilliped: endopod of four segments with a setal arrangement of 14, 12, 13, and ten, respectively; exopod with 15 hair-like setae along surface and six setae on terminal portion. Pleon of six pleomeres plus a telson (Anderson, 1978).

7A. Telson with no terminal setae (Fig. 6, arrow B)
 *Carcinus maenas* (Linnaeus, 1758) (Fig. 6).

Carapace with rostral spine. Carapace length about 1.26 to 1.4 mm. Antenna of ten segments. Mandible two-segmented palp with six terminal setae. First Maxilliped: endopod with four to five setae; exopod of two segments with setal arrangement of two, and three to five, respectively. Second Maxilliped: endopod of five segments with no setae on proximal segment; exopod of two segments with four to five setae on terminal portion of distal segment. Third Maxilliped: endopod of five segments with many setae; exopod of two segments with four setae on terminal portion of distal segment. Pleon of six pleomeres plus a posteriorly narrow telson (Crothers, 1966; Rice and Ingle, 1975).

7B. Telson with two or three terminal setae (Fig. 7, arrow A) 8

8A. Front of carapace wide with broad triangular projections on the antero-lateral corners (Fig. 7, arrow B)
 *Lophopanopeus bellus* (Rathbun, 1900) (Fig. 7).

Carapace with wide front, projections on the antero-lateral corners of the carapace. Carapace length about 1.68 mm. Antenna of 11 segments with cluster of setae on segments eight and ten. First Maxilliped: endopod reduced with four setae; exopod of two segments with four plumose setae on terminal portion of distal segment. Second Maxilliped: endopod of four segments with proximal to distal setal arrangement of two, zero, six and six, respectively; exopod of two segments with

four setae on terminal portion of distal segment. Third Maxilliped: exopod of two segments with five setae on terminal portion of distal segment. Pleon of six pleomeres plus a telson with three terminal setae (Knudsen, 1959; Lough, 1974).

8B. Carapace with no triangular projections on the antero-lateral corners of the carapace *Pachygrapsus crassipes* Randall, 1839 (Fig. 8).

Carapace length about 1.96 mm. Last joint of leg with three setae longer than last joint of leg. Telson with terminal two to three setae on posterior margin (Lough, 1974).

9A. Width of carapace greater than length of carapace (Fig. 9). (Lough, 1974).

..... Pinnotheridae

9B. Width of carapace less than length of carapace 10

10A. Antenna with 11 segments 11

10B. Antenna with seven to ten segments 13

11A. Carapace with broad, blunt fronto-lateral projections (Fig. 10A, arrow A).
..... *Lophopanopeus leucomanus* Lockington, 1876. (Fig. 10A).

Carapace with squared rostrum. Antenna of 11 segments with hairs on segments 11 and ten (Fig. 10B). Terminal antenna segment with tuft of hair. First Maxilliped: endopod with three setae at terminal end; exopod of two segments with plumed hairs on terminal end of distal segment. Second Maxilliped: endopod of four segments with proximal to distal setal arrangement of zero, zero, five and seven; exopod of two segments with five plumose hairs on terminal end of distal segment. Third Maxilliped: exopod with five terminal hairs. Pleon of six pleomeres plus a telson with three terminal setae (Knudsen, 1958).

11B. Carapace with no broad, blunt fronto-lateral projections 12

12A. Plumose setae on posterior margin of telson (Fig. 11A, arrow B), total length of megalopae about 3.6 mm

..... *Hemigrapsus nudus* (Dana, 1851). (Fig. 11A).

Carapace with blunt rostrum. Frontal region of carapace slightly depressed.

Carapace length about 1.8 mm. Antenna of 11 segments with long bristle-like setae on last three segments (Fig. 11B). Mandible two-segmented palp with eight to ten short setae on distal segment. First Maxilliped: endopod reduced with no segments; exopod with four plumose setae and two distal setae. Second Maxilliped: endopod of five segments with rigid setae on terminal segments. Third Maxilliped: endopod and exopod well developed. Pleon of six pleomeres. Telson with three to four short plumose setae on rounded distal margin (Hart, 1935).

12B. No plumose setae on posterior margin of telson (Fig. 12, arrow A), total length of megalopae about 2.9 mm

..... *Hemigrapsus oregonensis* (Dana, 1851). (Fig. 12).

Carapace with blunt rostrum. Frontal region of carapace slightly depressed.

Carapace length about 1.5 mm. Antenna of 11 segments with long bristle-like setae on distal three segments (Fig. 11B). Mandible two-segmented palp with eight to ten short setae on distal segment. First Maxilliped: endopod reduced with no segments; exopod with four plumose setae and two distal setae. Second Maxilliped: endopod of five segments with rigid setae on terminal segments. Third Maxilliped: endopod and exopod well developed. Pleon of six pleomeres plus a telson (Hart, 1935).

13A. Antenna with seven segments (Fig. 13A)

..... *Pyromaia tuberculata* (Lockington, 1877). (Fig 13B).

Carapace with blunt rostrum. Carapace with single pair of dorsal lobes. Carapace length about 1.15 mm. Antenna of seven segments with setal arrangement of two,

one, three, zero, zero, three and three, respectively. First Maxilliped: endopod with three setae; exopod of two segments with three plumose setae on distal segment. Second Maxilliped: endopod of four segments with a proximal to distal setal arrangement of zero, one, three and four, respectively; exopod of two segments with a setal arrangement of zero and four, respectively. Third Maxilliped: endopod of five segments with setal arrangement of seven, five, two, four and four, respectively; exopod of two segments with four setae on distal segment. Pleon of six pleomeres. Telson with four terminal setae (Fransozo and Negreiros-Fransozo, 1997; Luppi and Spivak, 2003).

13B. Antenna with nine segments
 *Rhithropanopeus harrisi* (Gould, 1841). (Fig. 14).

Carapace rectangular, rostrum blunt with triangular notch. Carapace length about 1.1 mm. Antenna of nine segments (Connolly, 1925).

13C. Antenna with ten segments (Fig. 15A)
 *Eriocheir sinensis* H. Milne Edwards, 1853. (Fig. 15B).

Carapace with blunt rostrum. Carapace with deep notch in frontal region.

Carapace length about 1.37 to 1.55 mm. Antenna of ten segments with setal arrangement of two, two, two, zero, zero, six, one, three, three and two to three, respectively. Mandible two-segmented palp with setal arrangement of zero, and eight to nine, respectively. First Maxilliped: endopod with 15 setae; exopod of two segments with setal arrangement of one to two, and eight to nine, respectively. Second Maxilliped: endopod of four segments with setal arrangement of four, zero, five and 13, respectively; exopod of two segments with setal arrangement of zero and nine, respectively. Third Maxilliped: endopod of four segments with setal arrangement of 11, six, eight, and seven, respectively; exopod of two segments with setal arrangement of zero and four, respectively. Pleon of six pleomeres with

postero-lateral spines on the second, third and fourth segment. Telson subquadrate with rounded edges (Montu et al., 1996).

Megalopae Distribution

Point San Pablo was the only sampling site of the three areas sampled where *E. sinensis* megalopae were found. A total of six mitten crab megalopae were found in light trap samples during the 2007 and 2008 sampling periods (Appendix B, Figure 3). Four megalopae were found in 2007. Two mitten crab megalopae were found in 2008. With the exception of one megalopae which was found in the month of April, all megalopae were found in the month of May (Appendix B, Figure 3). No conclusions on how environmental parameters effect distribution and settlement of mitten crab megalopae could be determined as the abundance of megalopae was very low.

Zoeae Abundance

The zoeae of ten brachyuran species from seven families were collected. Species collected are as follows: *Cancer productus*, *Carcinus maenas*, *Eriocheir sinensis*, *Hemigrapsus nudus*, *Hemigrapsus oregonensis*, *Lophopanopeus bellus*, *Metacarcinus gracilis*, *Pachygrapsus crassipes*, *Pyromaia tuberculata*, *Rhithropanopeus harrisi*, and specimens from the family Pinnotheridae. Most of the species found in plankton tow samples had very low relative abundance at this station (Appendix C, Table 2). Sampling from station D41 was preselected for its high *E. sinensis* abundance. Other species may appear in higher abundances at other DFG stations. The most abundant species in the region were *E. sinensis*, *M. gracilis*, and *P. tuberculata* (Appendix C, Table 2). The zoeae of *M. gracilis* comprised 19.8% of the zoeae found in plankton tows from 1998-2008 (Appendix C, Table 2). Peak abundance for the zoeae of *M. gracilis* occurred in February of

2001, with a CPUE of 2584. *M. gracilis* was also the most abundant species in 2001 (Appendix C, Table 6). The zoeae of *P. tuberculata* made up 16.1% of the zoeae captured from 1998-2008. The highest abundance of *P. tuberculata* zoeae occurred in September of 2006, with a CPUE of 849. In 2006, *P. tuberculata* was the most abundant species in the region (Appendix C, Table 11). Along with the zoeae of the family Pinnotheridae, the zoeae of *M. gracilis*, *P. tuberculata*, and *E. sinensis* made up 91.3% of the zoeae collected from 1998-2008. *E. sinensis* was the most abundant species from 1998-2000 (Appendix C, Tables 3-5) and 2002-2005 (Appendix C, Tables 7-10). Peak *E. sinensis* abundance occurred in April of 2003 with a CPUE of 4034.7 (Appendix B, Figure 4). While the zoeae of the invasive species, *E. sinensis*, comprised 30.5% of the zoeae caught from 1998-2008 (Appendix C, Table 2), mitten crab zoeae have been less abundant in San Francisco Bay during recent years. *E. sinensis* zoeae had the lowest abundance in 2006 and 2007. In 2006 and 2007, months with peak abundance had a CPUE of 9.8 and 8.1 (Appendix B, Figure 4), respectively. Although *E. sinensis* zoeae have showed a rapid decline after 2003, zoeae could still be found during DFG sampling at station D41 until 2008 (Appendix C, Table, 13; Appendix B, Figure 4). No mitten crab zoeae were found in DFG plankton tows in 2008 (Appendix B, Figure 4).

The zoeae of other invasive species, *C. maenas* and *R. harrisi*, have also been found in DFG plankton tow samples. The zoeae of *R. harrisi* were only found in samples from June of 1999, September of 2003, June of 2008, and August of 2008 with a CPUE for these months of 14.0, 163.5, 18.0, and 25.9, respectively. The zoeae of *R. harrisi* comprised 0.3% of the zoeae captured from 1998-2008. *C. maenas* had the highest monthly zoeae abundance in August of

2002, with a CPUE of 50.2. The zoeae of *C. maenas* comprised 0.4% of the zoeae collected from 1998-2008 (Appendix C, Table 2).

The zoeae of *H. oregonensis*, *C. productus*, *L. bellus*, *H. nudus*, and *P. crassipes* comprised approximately 8% of the zoeae captured from 1998-2008 (Appendix C, Table 2). *H. oregonensis* zoeae abundance peaked in July of 2003, with a CPUE of 243. *H. oregonensis* zoeae comprised 2.9% of the zoeae collected from 1998-2009 (Appendix C, Table 2). The zoeae of *C. productus* was most abundant in February of 1999, with a CPUE of 224. *L. bellus* zoeae comprised 2% of the total zoeae catch from 1998-2008 (Appendix C, Table 2). *L. bellus* zoeae abundance peaked in May of 2004, with a CPUE of 129. *H. nudus* zoeae was ranked low in abundance during 1998-2008 and comprised only 0.2% of the total zoeae captured from 1998-2008 (Appendix C, Table 2). *H. nudus* zoeae abundance peaked in February of 2005, with a CPUE of 34. *P. crassipes* zoeae was least abundant at this station and comprised only 0.1% of the total zoeae collected from 1998-2008 (Appendix C, Table 2). *P. crassipes* zoeae was most abundant during March of 1998 and August of 2000, with a CPUE of 15.

A Pearson's correlation was performed to determine if a relationship exists between *E. sinensis* zoeae density and the zoeae density of native species in the region. Pearson's correlation detected a correlation between the zoeae abundance of *E. sinensis* with *M. gracilis* ($p < 0.000001$, $r = 0.4$) and *C. productus* ($p < 0.0000001$, $r = 0.46$) (Appendix B, Figure 7).

Environmental Parameters

A Pearson's correlation was used to examine the influence of monthly average temperature and salinity on monthly *E. sinensis* zoeae abundance. A correlation was found between *E. sinensis* zoeae density and temperature

($p < 0.0008$, $r = -0.347$) (Appendix B, Figure 5). Pearson's correlation also detected a significant correlation between *E. sinensis* zoeae density and salinity ($p < 0.00002$, $r = -0.375$) (Appendix B, Figure 6). Mitten crab adult CPUE peaked in 1999 (Appendix B, Figure 4). Adult crabs were found in DFG otter trawls in every year from 1998-2005. However, no adult crabs were found in DFG otter trawl sampling in 2006-2008 (Appendix B, Figure 4).

DISCUSSION

Megalopae Dichotomous Key

In order to better understand the life history of the invasive crab species in the San Francisco Bay, it is important to analyze all stages in their life history including the post-larval megalopa stage. One goal of this research project was to ascertain where mitten crab megalopae are settling in San Francisco Bay. Efforts to study these invading organisms are hampered by our inability to identify the brachyuran megalopae of San Francisco Bay. To this end, we constructed a dichotomous key including native brachyuran species and those that had invaded San Francisco Bay by 2007. There are twenty-two brachyuran species found in San Francisco Bay and its estuary (Mooi et al., 2007; Rice and Tsukimura, 2007; California Academy of Sciences, 2008). *Pugettia producta* and *Romalaeon jordani* have been collected in San Francisco Bay and are listed in the invertebrate collection catalog of the California Academy of Sciences (California Academy of Sciences, 2008), however their megalopae are not included in this key as they remain undescribed. Virtually no literature describing the larval and post-larval stages exists for many of the pinnotherid species found in the San Francisco Bay. Pinnotherid species known to inhabit the region are lumped together in this key using one previously described morphological feature (Lough, 1974).

It is possible that the zoeae of other brachyuran species occupying coastal regions near San Francisco Bay (Carlton, 2007 and Wicksten, 2009) could be transported into the Bay and metamorphose into megalopae. These species include: *Callinectes sapidus* Rathbun, 1896; *Cancer branneri* (Rathbun, 1926); *Cancer oregonensis* (Dana, 1852); *Cycloxanthops novemdentatus* (Lockington,

1877); *Herbstia parvifrons* (Randall, 1840); *Heterocrypta occidentalis* (Dana, 1854); *Loxorhynchus crispatus* Stimpson, 1857; *Loxorhynchus grandis* Stimpson, 1857; *Mimulus foliatus* Stimpson, 1860; *Oregonia gracilis* Dana, 1851; *Paraxanthias taylori* (Stimpson, 1860); *Pelia tumida* (Lockington, 1877); *Planes cyaneus* Dana 1852; *Platymera gaudichaudii* (Milne-Edwards, 1837); *Podochela hemphilli* (Lockington, 1877); *Pugettia gracilis* Dana, 1851; *Pugettia richii* Dana, 1851; *Randallia ornata* (Randall, 1840); *Scyra acutifrons* Dana, 1851; *Telmessus cheiragonus* (Tilesius, 1815). Because these species are not found in San Francisco Bay, they are not included in this dichotomous key (Mooi et al., 2007; Rice and Tsukimura, 2007; California Academy of Sciences, 2008). The main objective of this study was to supply a method of identifying the brachyuran megalopae of the San Francisco Bay Estuary system to better understand this life history stage, particularly of *Eriocheir sinensis*.

Megalopae Distribution

It is important to study the population dynamics of each life stage to gain a better understanding of what factors influence adult year-class strength. Thus, an additional objective of this study was to analyze light trap samples for mitten crab megalopae using the dichotomous key for the brachyuran megalopae in San Francisco Bay. The goal was to determine the distribution and abundance of mitten crab megalopae using light traps in order to gain a better understanding of where and when the megalopae settle in the San Francisco Bay. It is possible that the megalopae abundances are more tightly linked to adult survivorship than zoeae abundances, since megalopae occur just before metamorphosis into juveniles. Thus, survivorship of the megalopae may greatly affect adult year-class strength.

Very few megalopae were found in light trap samples during this study. The low numbers of megalopae found may be linked to low adult abundance. Because very few megalopae were collected, this study could not identify a relationship between environmental factors and megalopae distribution and abundance.

Many brachyuran larvae show photopositive responses to light (Shanks, 1995; Webley and Connolly, 2007). The swimming orientation of several brachyuran megalopae species has been investigated (Shanks, 1995). It was hypothesized that the megalopae stage was able to orient toward the shore and make the migration all the way back to shore (Shanks, 1995). The brachyuran larvae of several species belonging to the families Grapsidae, Xanthidae and Cancridae were housed in clear containers under illumination or were allowed to swim in the ocean. This study found that specimens in the clear containers swim in the direction of the sun's bearing. Megalopae that were left free to swim in the ocean also showed a preferred pattern of swimming in the direction of the sun's bearing (Shanks, 1995). The research suggested some megalopae swim in the direction of the sun's bearing at the water's surface (where underwater illumination was brightest) because this behavior may have an adaptive advantage of some kind. One idea is that the currents towards the surface of the water might be used by the megalopae to swim shoreward faster. The megalopae may use photo cues to orient toward the surface of the water (Shanks, 1995).

Another study showed the megalopae of the mud crab *Scylla serrata* displays movement towards surface waters in response to light (Webley and Connolly, 2007). Mud crab megalopae were placed in 1 meter high towers and the patterns of their swimming were recorded. The study found that the megalopae put in illuminated towers swam higher than megalopae that were contained in dark

swimming towers (Webley and Connolly, 2007). Also, if a darkened tower was changed from dark to light, the megalopae would ascend higher in the tower. The authors suggest that the mud crab must use this vertical movement response to light to remain close to the surface of water. Surface water is subject to strong winds causing currents that may move the mud crab megalopae closer to shore (Webley and Connolly, 2007). These studies suggest that *E. sinensis* megalopae, like other brachyuran megalopae, may be attracted to the light. Therefore, light traps may be suitable method to collect mitten crab megalopae in the San Francisco Bay estuary.

However, few mitten crab megalopae were found in light trap samples. It is possible mitten crab megalopae do not possess positive phototaxis and are not attracted to light produced by light traps. Low megalopae abundance doesn't necessarily mean mitten crab megalopae exhibit negative phototaxis. One possible explanation for low megalopae abundance could be related to the recent low abundance of mitten crab zoeae and adults (Appendix B, Figure 4). In the future, phototaxis in *E. sinensis* megalopae should be examined. Of course, it would be best to determine what types of traps should be used to collect *E. sinensis* megalopae by doing experiments with live specimens. Currently, due to the lack of live adults it isn't possible to grow megalopae for these types of experiments. Once the locations of megalopae settlement in San Francisco Bay are detected, future studies can focus on monitoring abundance of the mitten crab post larval stage.

Zoeae Abundance

Another focus of this research was to look at trends in temporal abundance and species composition of brachyuran zoeae in the San Francisco Bay. Past

studies have focused on the zoeae stage of the mitten crab. One study, reports that female adult abundance is closely correlated with zoeae abundance (Blumenshine et al., in review). Although the regression tree analysis done by Blumenshine et al. (in review) suggests adult abundances are highly correlated with zoeae abundances, during times of high adult abundance in 1999 there is low zoeae abundance. Also, when adult abundance is low in 2003 zoeae abundance was very high (Appendix B, Figure 4). This suggests there must be other environmental factors that are important in effecting zoeae abundance such as temperature.

Other studies have shown temperature can directly affect development and survival of the zoeae of other invasive brachyurans, *Rhithropanopeus harrisi* and *Carcinus maenas* (Costlow et al., 1986; Sprung, 2001). Temperature experiments performed on *E. sinensis* larvae in the past have shown that temperatures below 12°C cause increased mortality of the first zoeal stage (Anger, 1991; Rice, 2006). One study found monthly zoeae densities in San Pablo Bay were significantly higher above 11.7°C (Rice, 2006). Rice (2006) suggested 11.7 °C may be a thermal tolerance threshold for mitten crab zoeae. Blumenshine et al. (in review) also showed that a temperature around 11.7 °C was a potential threshold for zoeae mortality. In this study, Pearson's correlation detected a significant correlation between mitten crab zoeae density and temperature ($p < 0.0000856$, $r = -0.347$) (Appendix B, Figure 5).

As the mitten crab is a sub tropical species, we would expect temperatures below the 11.7 °C tolerance threshold to cause an increase in zoeae mortality, and therefore, a decrease in zoeae abundance. In 2003, during the highest peak in zoeae abundance only one month falls below the temperature tolerance threshold of 11.7 °C (Appendix B, Figure 5) and zoeae abundance was high. The higher temperatures during this year may have contributed to the increase in zoeae

survivorship. In 1999, there was a population explosion of adult mitten crabs and we would expect to see a high abundance of zoeae due to the high number of adults. Yet, zoeae abundance was relatively low (Appendix B, Figure 4). This could have been due to the severe dips in temperature in the beginning of winter in 1999, which may have increased zoeae mortality. Mitten crab zoeae abundance was also low in 2006-2008. This may be due to the low water temperatures in the early reproductive months of the mitten crab. Water temperatures below 11.7°C may be responsible for the recent decline in mitten crab zoeae as zoeae have a thermal tolerance of 11.7°C (Blumenshine et al., in review; Rice, 2006). Although zoeae abundance was found from previous studies to be highly correlated with adult abundance, it is possible that temperature is decoupling the correlation between adult and zoeae abundances. During times when we would expect zoeae abundance to be high, low water temperatures may be causing increasing larval mortality. This could lead to a decoupling of adult and zoeae abundances.

Pearson's correlation found a correlation between zoeae density and salinity ($p < 0.0000231$, $r = -0.375$) (Appendix B, Figure 6). Yet, salinity rarely falls below the tolerance threshold for mitten crab zoeae in San Francisco Bay. Salinity was low at the beginning of 1998 and 2006 (Appendix B, Figure 6). While zoeae abundance was also low during these time periods, adult abundance was high only in 1998 (Appendix B, Figure 4). During times of very low salinity it is possible that salinity may also decouple the adult and zoeae density relationship. However, because other factors such as temperature are more highly correlated with zoeae abundance, it may be a questionable parameter to use to explain zoeae abundance. Adult density has been found by other studies to be correlated with zoeae abundances (Blumenshine et al., in review; Rice, 2006). However, temperatures below the tolerance of zoeae can decrease their survivorship. Salinity may also

affect zoeae survivorship, however, salinities recorded in this part of San Pablo Bay rarely fall below the salinity tolerance of 10 parts per thousand. Therefore, other environmental parameters such as temperature may be more useful in explaining zoeae densities.

The sensitivity of this species to environmental parameters such as temperature provides an opportunity to apply ecological niche modeling approaches such as the genetic algorithm for rule-set prediction (GARP). This approach uses environmental and biological data along with measures of propagule pressure to predict areas where a specific invasive species could become successfully established (Herborg et al., 2007a). GARP has been previously used to predict the potential distribution of the mitten crab in areas of Europe and North America (Herborg et al., 2007a; Herborg et al., 2007b). It is possible this approach could be applied to predict the larval distribution of the mitten crab in San Francisco Bay. This would require the collection of environmental measurements from several areas of the region as well as estimates of propagule pressure. Such an approach may help to focus sampling efforts within the San Francisco Bay Estuary to better improve the accuracy of mitten crab population estimates.

Like mitten crab population crashes in other countries, the abundance data from San Francisco Bay may show a temporary decline in what is probably a recurring population cycle of extreme abundance followed by rapid decline (Clark et al., 1998). Other brachyuran populations have also experienced temporary declines (Rome et al., 2005; Zheng and Kruse, 2006). Despite environmental constraints, propagule pressure could be contributing to the success of the mitten crab population in this region. Because San Francisco Bay is a high traffic area for commercial trade, multiple introductions are likely. Populations experiencing

decline during times of environmental stress can be maintained in this way until environmental conditions improve giving a window of opportunity for population resurgence (Lockwood et al., 2005). For this reason, it is important that mitten crab populations continue to be monitored. Although the findings of this work will provide a starting point for the study of the postlarval megalopae stage of the mitten crab in San Francisco Bay, several questions remain unanswered: where do megalopae settle in the San Francisco Bay? What environmental factors affect megalopae distribution and abundance? Do megalopae abundances correlate with adult abundances?

Conclusion

The central focus of this study was to create a means of identifying mitten crab megalopae found during sampling. To this end, a dichotomous key was created for the native and invasive brachyuran megalopae found in the San Francisco Bay Estuary. Another goal of this study was to determine mitten crab megalopae distribution and abundance in San Francisco Bay. However, due to the very low numbers of megalopae caught in light trap samples and relatively low numbers of zoeae and adults, this goal was not accomplished. The low number of mitten crab megalopae caught in light trap samples may be due to the recent decline of mitten crab zoeae and adult populations in this region. It is crucial that more research is done to explore factors that may be influencing larval recruitment and settlement of the mitten crab in San Francisco Bay. The population dynamics of each life stage of the Chinese mitten crab needs to be better understood so that in the future a predictive life history model for the San Francisco Bay mitten crab population can be developed.

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LITERATURE CITED

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APPENDICES

APPENDIX A
MEGALOPAE KEY FIGURES

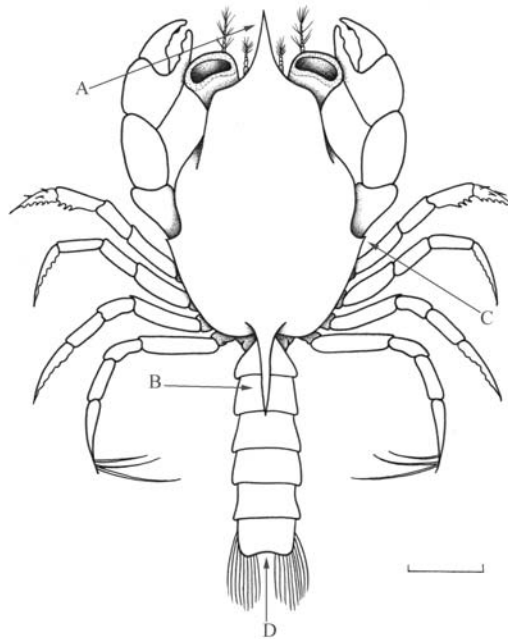


Fig. 1. *Cancer productus* megalopa (after Trask, 1970). Arrow A, Rostral spine; Arrow B, Dorsal spine; Arrow C, Reduced lateral spine; Arrow D, Telson subquadrate with indentation. Scale bar = 1 mm.

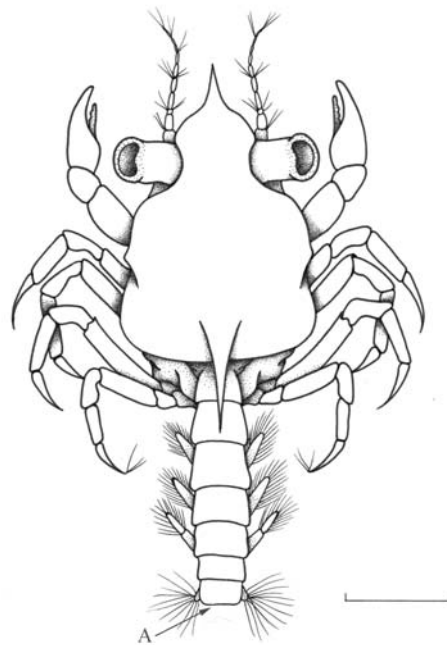


Fig. 2. *Romalaeon antennarius* megalopa (after Roesijadi, 1976). Arrow A, Telson flat without indentation. Scale bar = 1 mm.

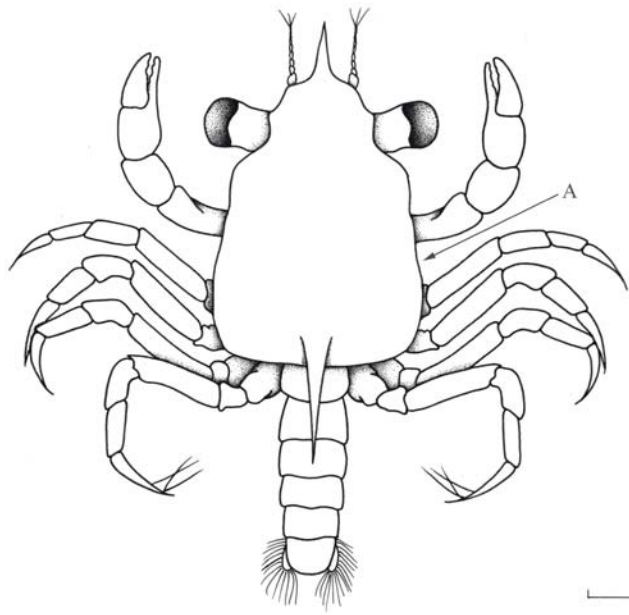


Fig. 3. *Metacarcinus magister* megalopa (after Poole, 1966). Arrow A, Carapace without lateral spine. Scale bar = 1 mm.

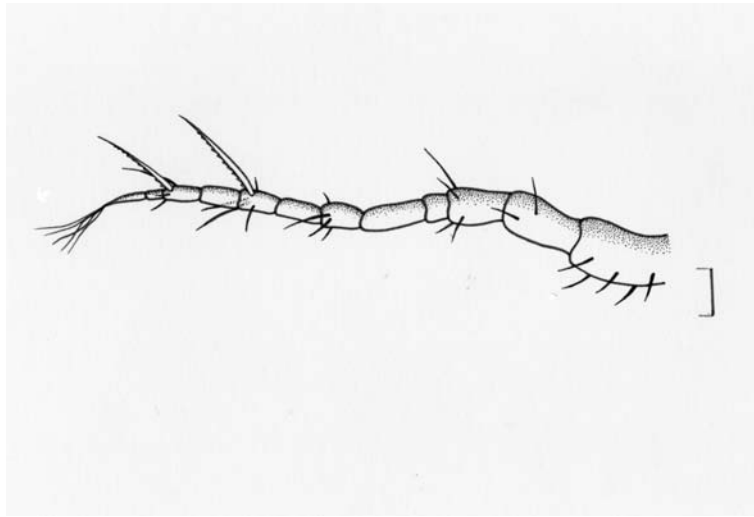


Fig. 4A. *Metacarcinus gracilis* antenna (after Ally, 1975). Scale bar = 0.1

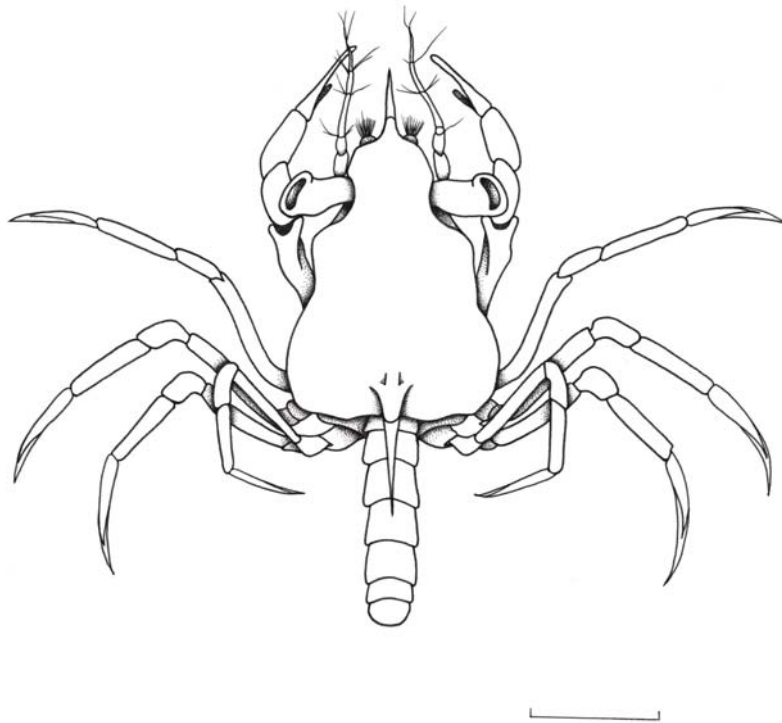


Fig. 4B. *Metacarcinus gracilis* megalopa (original by G. G. Castañeda). (B). Scale bars= 1 mm.

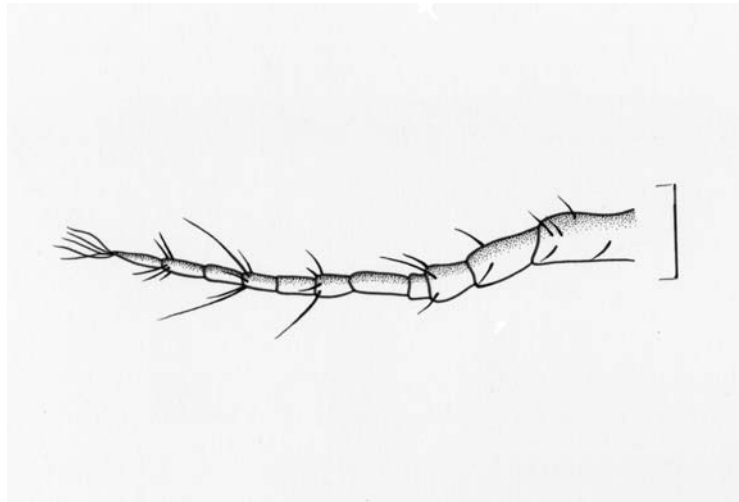


Fig. 5A. *Metacarcinus anthonyi* antenna (after Anderson, 1978). Scale bar= 0.2 mm.

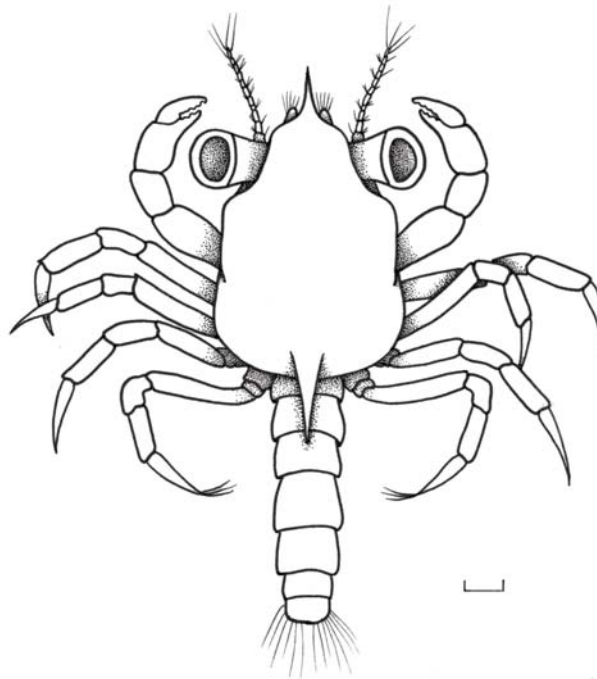


Fig. 5B. *Metacarcinus anthonyi* megalopa (after Anderson, 1978). Scale bar = 1 mm.

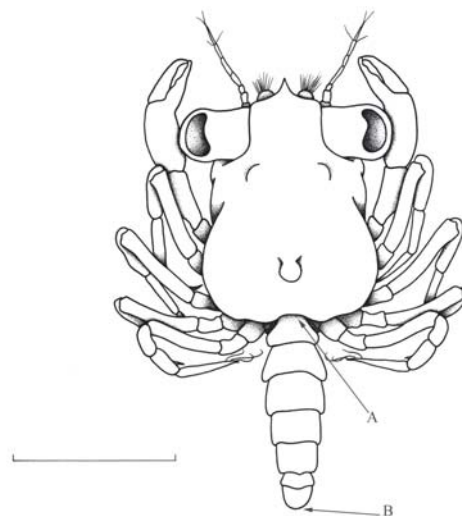


Fig. 6. *Carcinus maenas* megalopa (after Rice and Ingle, 1975). Arrow A, Carapace without dorsal spine; Arrow B, Telson without terminal setae. Scale bar = 1 mm.

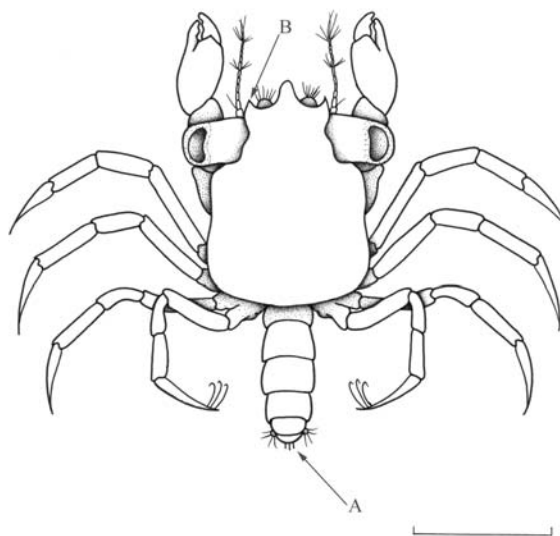


Fig. 7. *Lophopanopeus bellus* megalopa (after Knudsen, 1959). Arrow A, Telson with two or three terminal setae; Arrow B, Carapace with triangular projections. Scale bar = 1 mm.

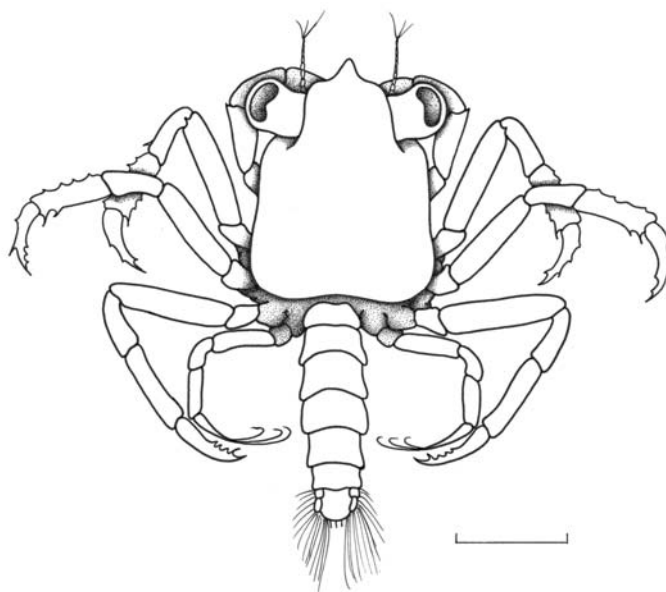


Fig. 8. *Pachygrapsus crassipes megalopa* (after Lough, 1974). Scale bar = 1 mm.

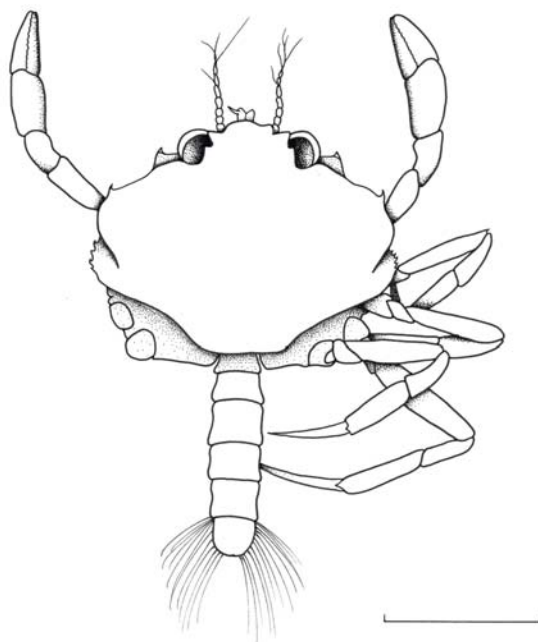


Fig. 9. Pinnotherid megalopa (original by G. G. Castañeda). Scale bar = 1 mm.

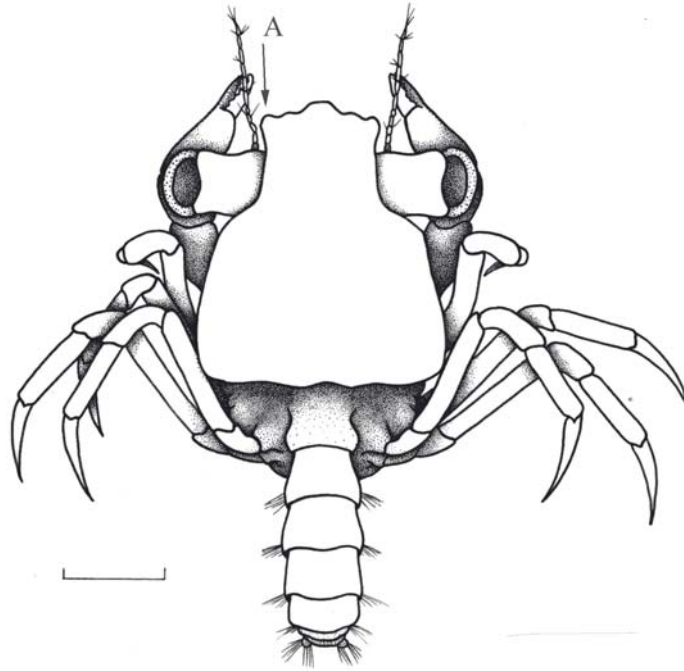


Fig. 10A. *Lophopanopeus leucomanus* megalopa (after Knudsen, 1958). Arrow A, Carapace with blunt fronto-lateral projections. Scale bar = 1 mm.

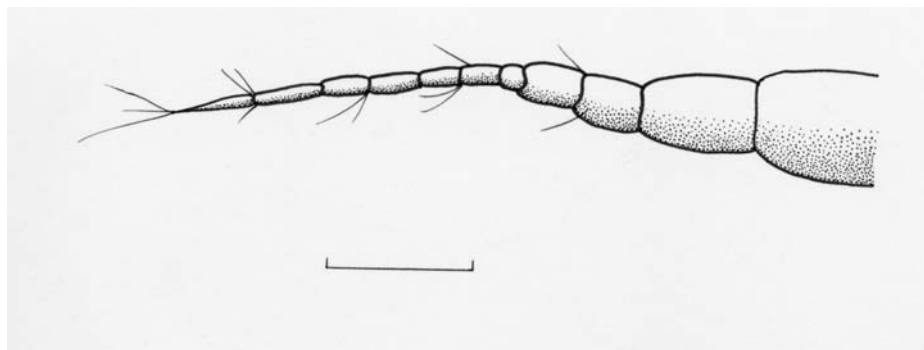


Fig. 10B. *Lophopanopeus leucomanus* antenna (after Knudsen, 1958). Scale bar = 0.2 mm.

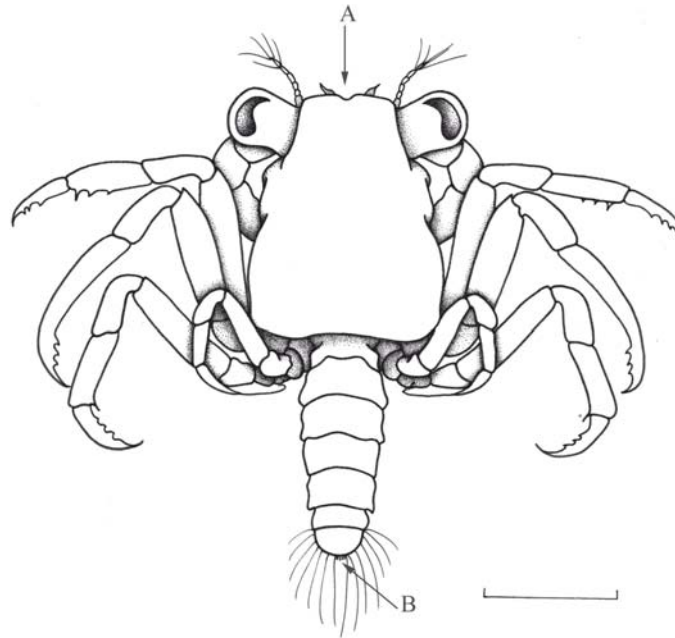


Fig. 11A. *Hemigrapsus nudus* megalopa (after Hart, 1935). Arrow A, Rostrum blunt or flat; Arrow B, Plumose setae on posterior margin of telson. Scale bar = 1 mm.

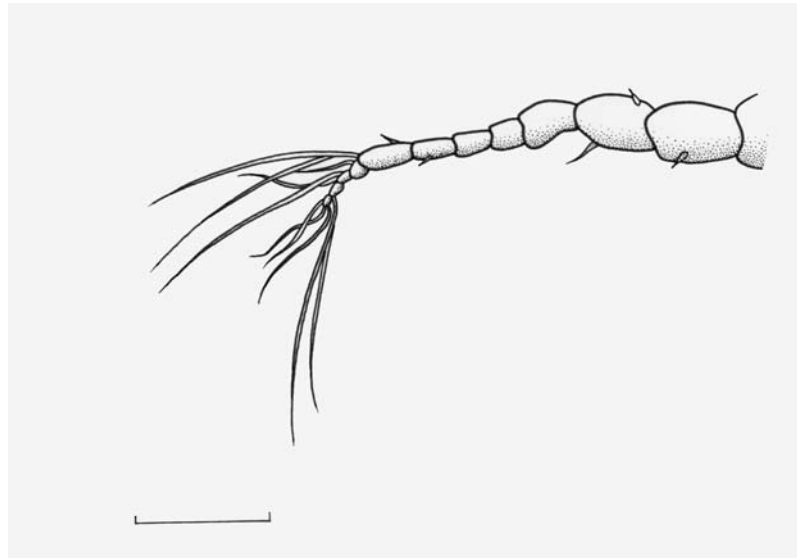


Fig. 11B. *Hemigrapsus nudus* and *Hemigrapsus oregonensis* antenna (after Hart, 1935). Scale bar= 0.175 mm.

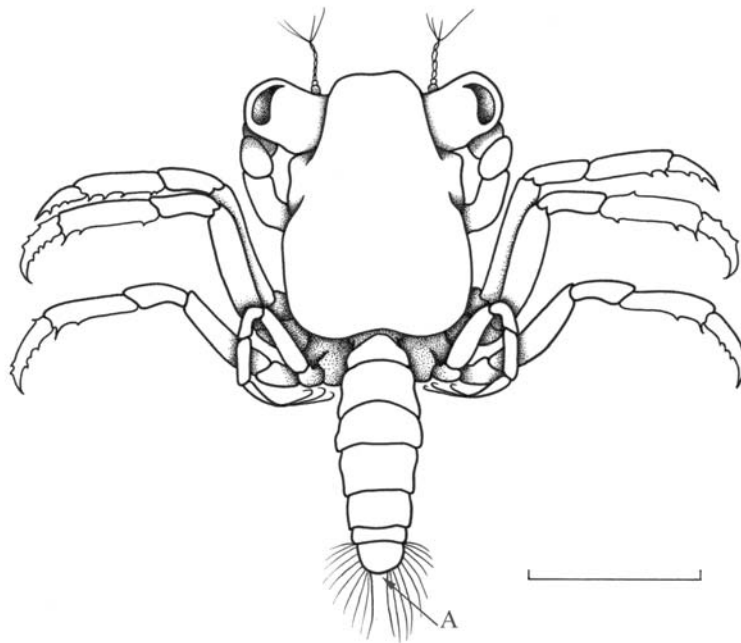


Fig. 12. *Hemigrapsus oregonensis* megalopa (after Hart, 1935). Arrow A, No plumose setae on posterior margin of telson. Scale bar = 1 mm.

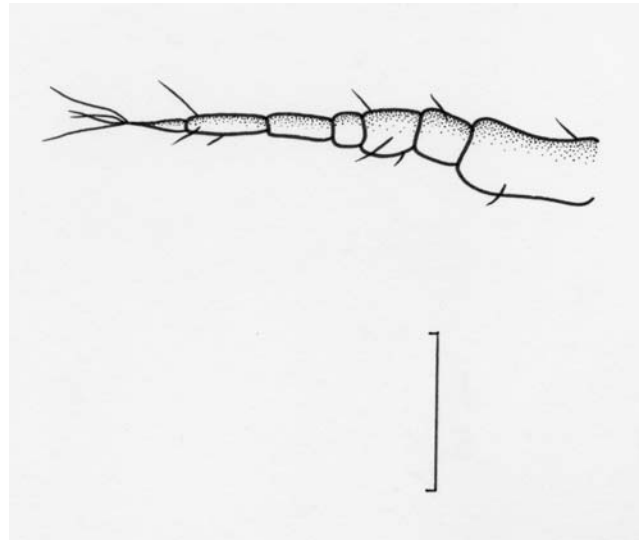


Fig. 13A. *Pyromaia tuberculata* antenna (after Fransozo and Negreiros-Fransozo, 1997). Scale bar= 0.1 mm.

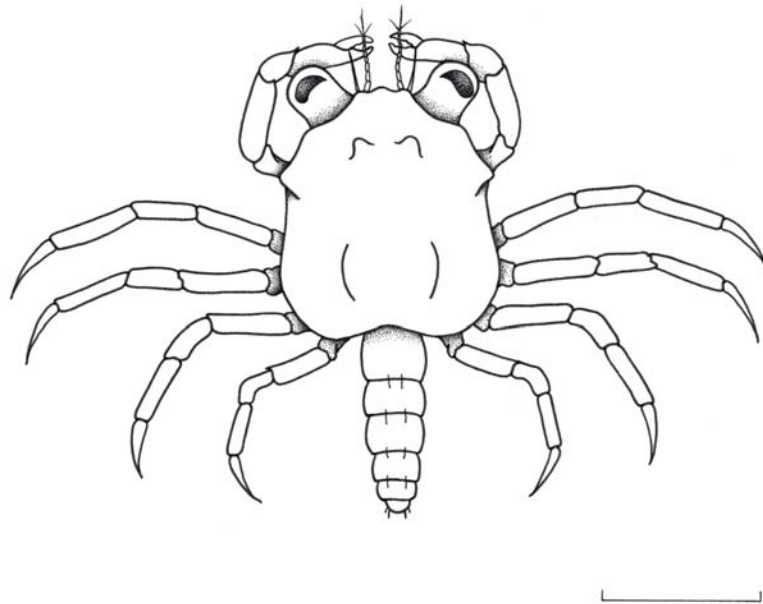


Fig. 13B. *Pyromaia tuberculata* megalopa (after Fransozo and Negreiros-Fransozo, 1997). Scale bar = 1 mm.

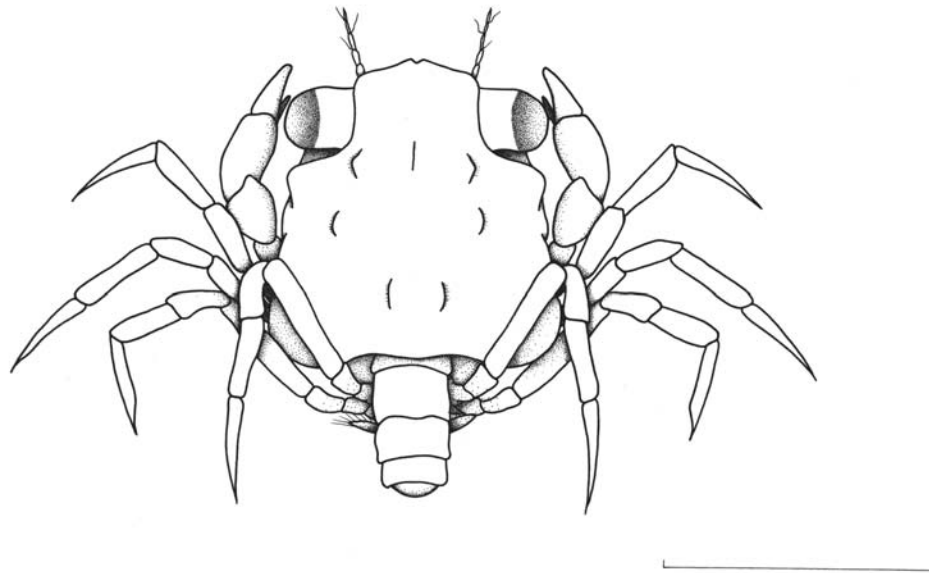


Fig. 14. *Rhithropanopeus harrisii* megalopa (after Connolly, 1925). Scale bar = 1 mm.

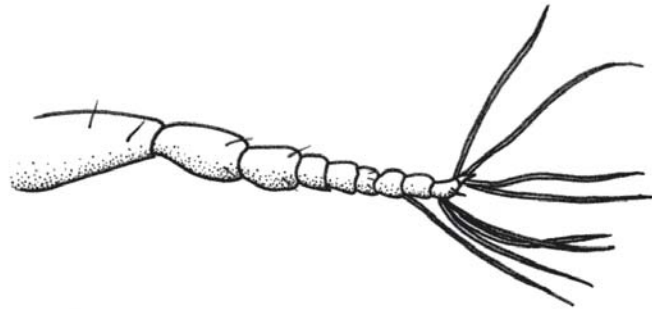


Fig. 15A. *Eriocheir sinensis* antenna (after Montu et al., 1996). Scale bar = 0.2 mm.

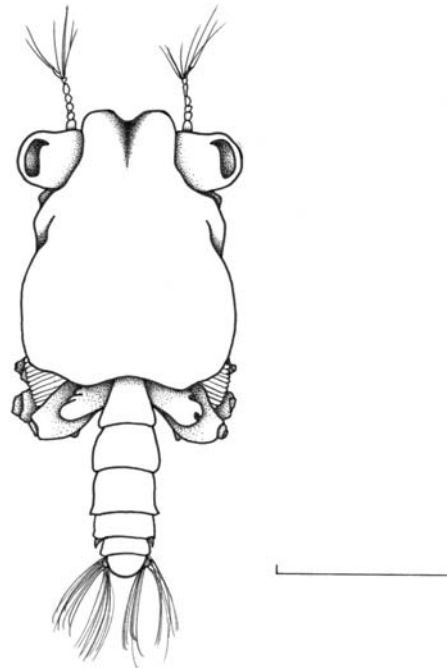


Fig. 15B. *Eriocheir sinensis* megalopa (original by G. G. Castañeda). Scale bar= 1 mm.

APPENDIX B
FIGURES

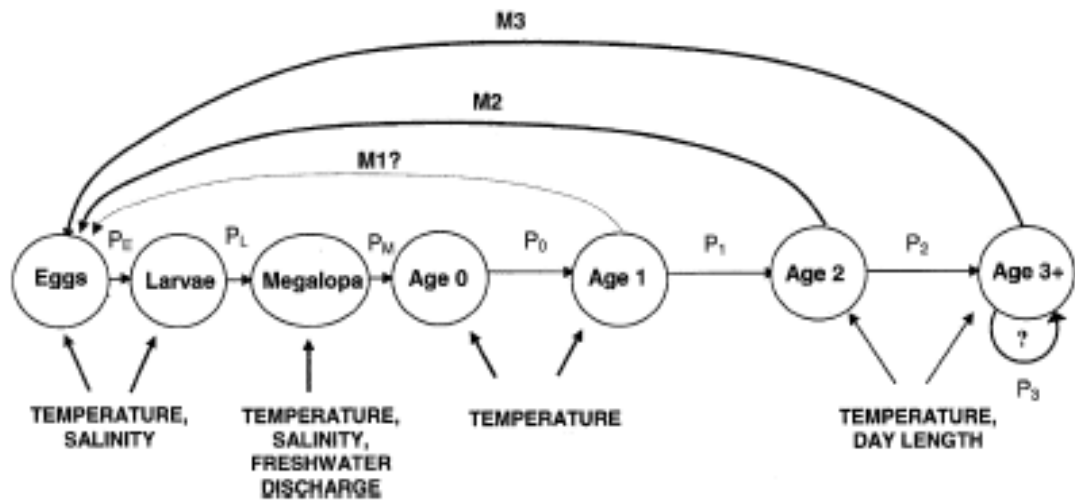


Figure 1. *Eriocheir sinensis* life stages. $P_{(x)}$ is the probability of survival to stage x and $M_{(x)}$ represents the fecundity at age x (Rudnick et al., 2005).



Figure 2. Map of light trap sampling locations in San Pablo Bay, Point San Pablo (PSP), Point Pinole (PP), and McNear's Beach (MB); USGS continuous monitoring gauge (T/S1) and NERRS monitoring gauge (T/S2) provided temperature and salinity data.

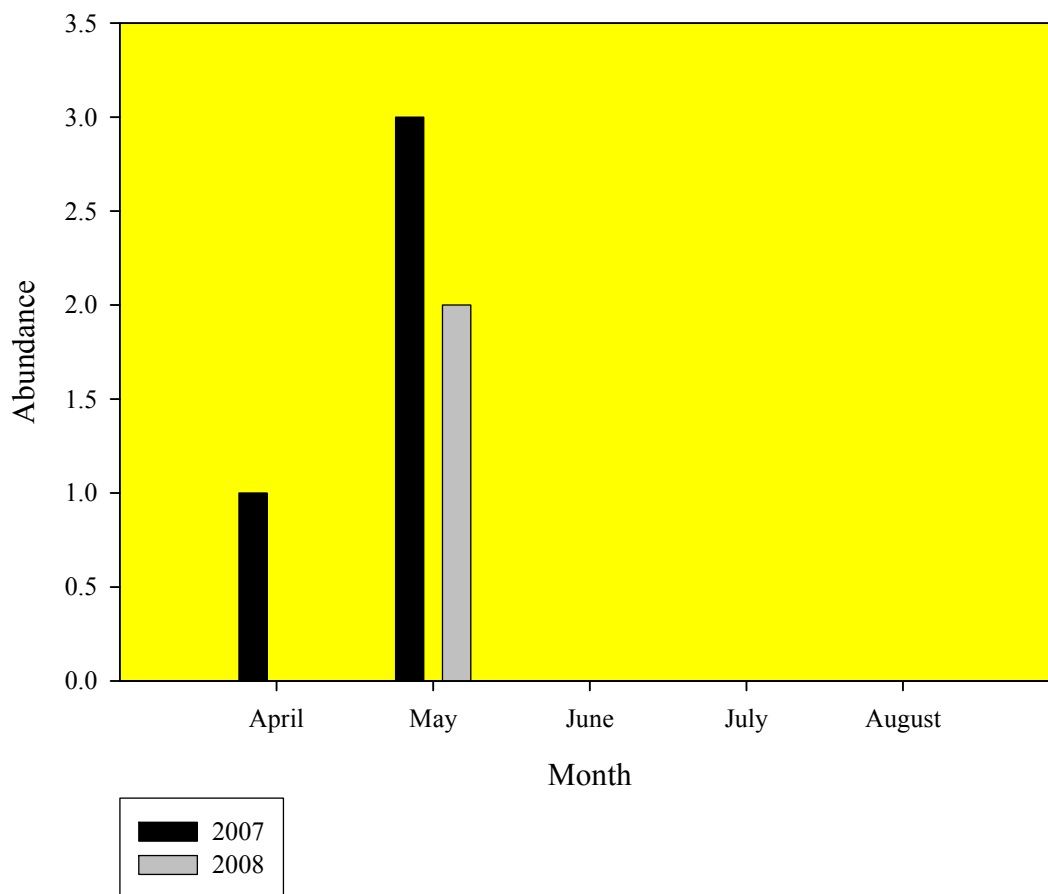


Figure 3. *Eriocheir sinensis* megalopae found in light traps from 2007-2008. All *Eriocheir sinensis* megalopae were found at sample site, Point San Pablo. *E. sinensis* megalopae were identified in light trap samples taken during April and May in 2007 and in May in 2008.

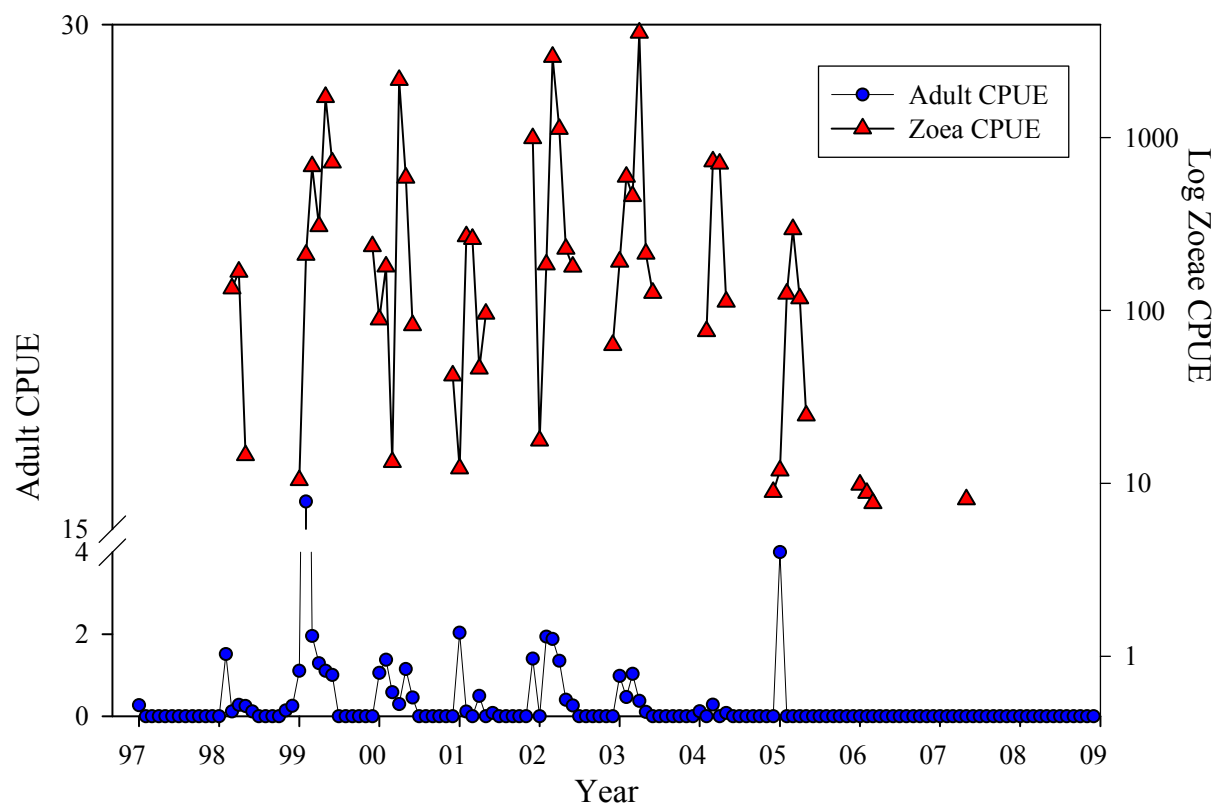


Figure 4. *Eriocheir sinensis* zoeae and adult mitten crab abundances in San Pablo Bay from 1998-2008. Zoaeae abundance is in red. Zoaeae Adult abundance is in blue.

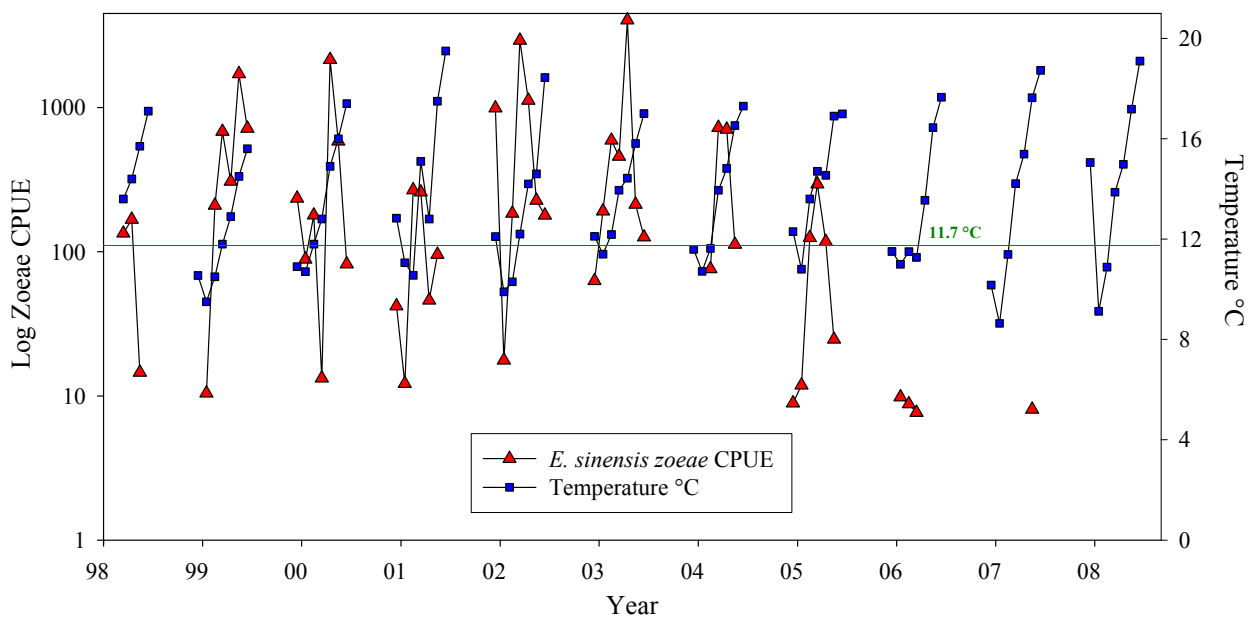


Figure 5. *Eriocheir sinensis* zoeae abundance and temperature in the San Pablo Bay from 1998-2008. Zoeae CPUE in log scale. Temperature in degrees Celsius. Pearson's correlation detected a significant correlation between mitten crab zoeae density and temperature ($p < 0.0000856$, $r = -0.347$). *E. sinensis* zoeae temperature tolerance of 11.7°C shown in green.

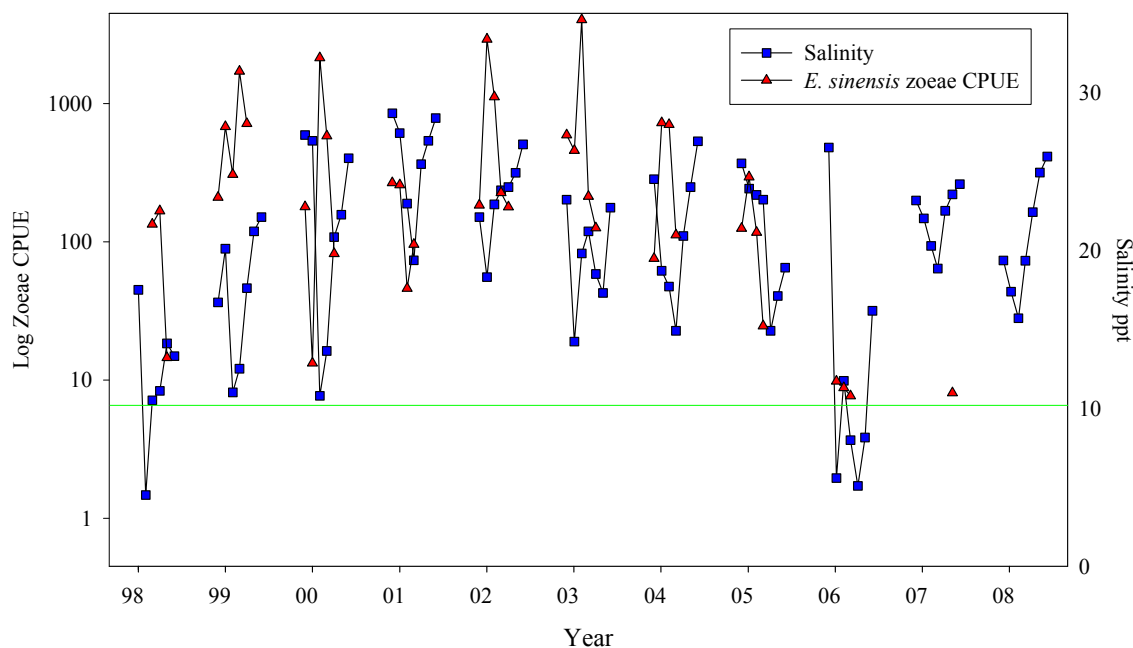


Figure 6. *Eriocheir sinensis* zoeae abundance and salinity in the San Pablo Bay from 1998-2008. Zoeae CPUE in log scale. Salinity in parts per thousand. Pearson's correlation detected a significant correlation between mitten crab zoeae density and salinity ($p < 0.0000231$, $r = -0.375$). *E. sinensis* zoeae salinity tolerance of 10 ppt shown in green.

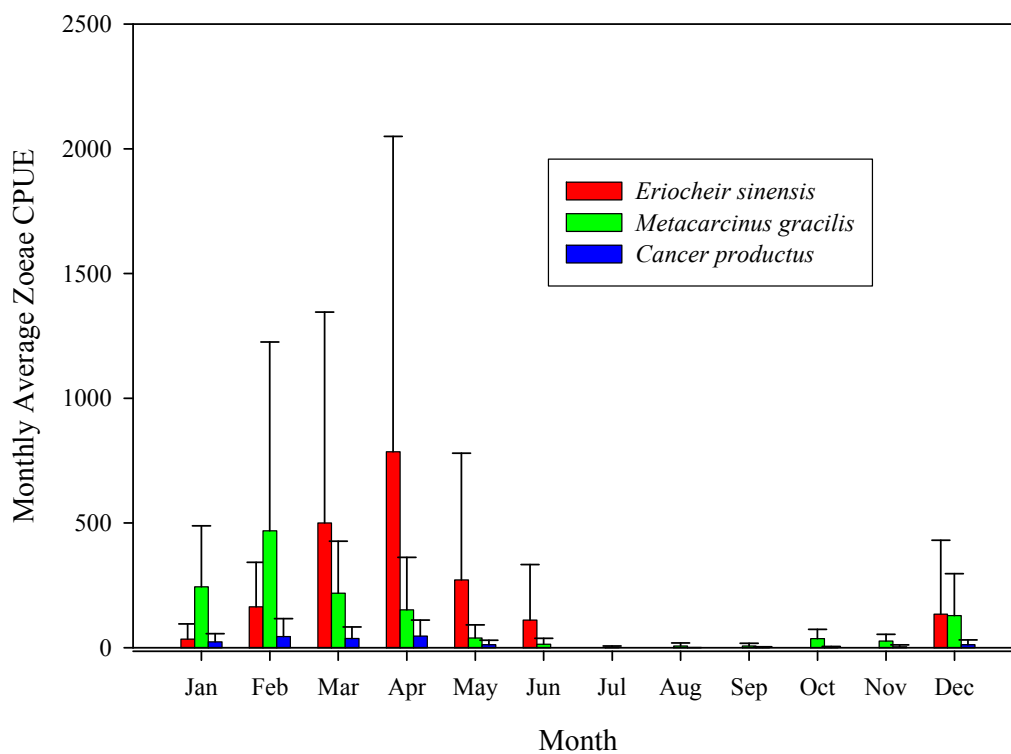


Figure 7. Monthly average zoeae abundance for *E. sinensis*, *M. gracilis*, and *C. productus* from 1998-2008. Pearson's correlation detected a significant correlation between *E. sinensis* zoeae density and *M. gracilis* zoeae density ($p < 0.000001$, $r = 0.4$). A significant correlation was also found between *E. sinensis* zoeae density and *C. productus* zoeae density. ($p < 0.0000001$, $r = 0.43$).

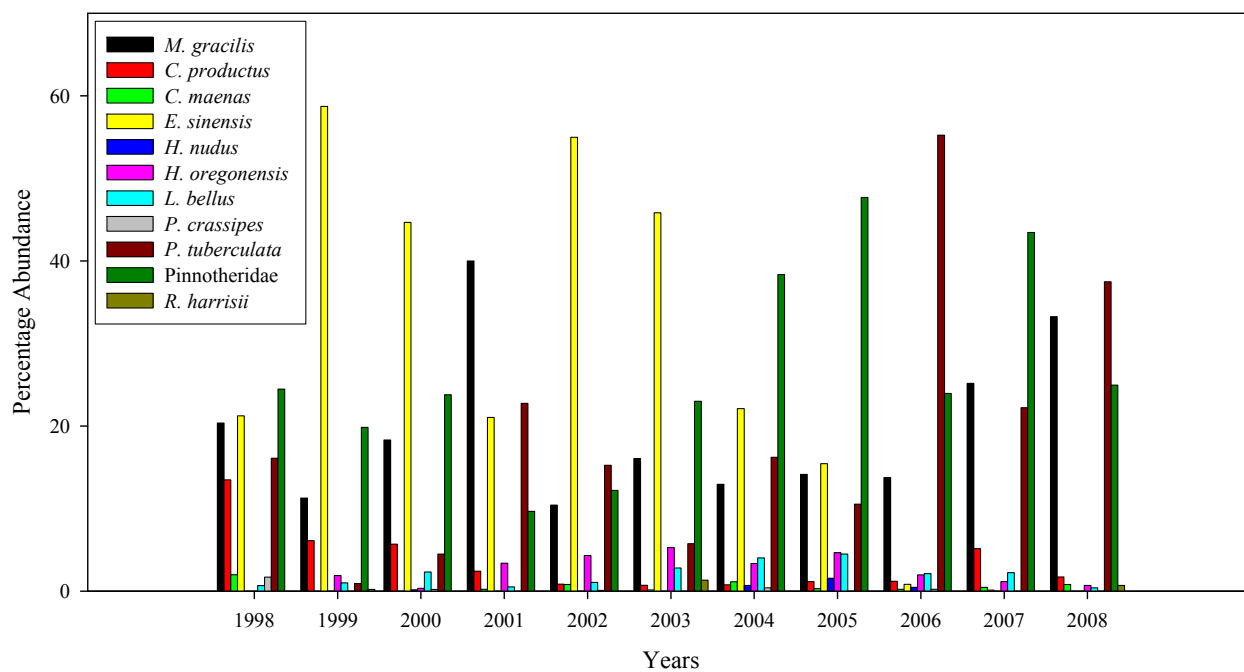


Figure 8. Relative abundance of the species of brachyuran zoeae collected at station D41 for every year from 1998-2008.

APPENDIX C

TABLES

Table 1. Sources of description and illustrations for each species of brachyuran megalopae presented in the dichotomous key.

Species	Authors
<i>Cancer productus</i>	Lough (1974); Trask (1970)
<i>Carcinus maenas</i>	Crothers (1966); Rice and Ingle (1975)
<i>Eriocheir sinensis</i>	Montu et al. (1996)
<i>Hemigrapsus nudus</i>	Hart (1935)
<i>Hemigrapsus oregonensis</i>	Hart (1935)
<i>Lophopanopeus bellus</i>	Knudsen (1959); Lough (1974)
<i>Lophopanopeus leucomanus</i>	Knudsen (1958)
<i>Metacarcinus anthonyi</i>	Anderson (1978)
<i>Metacarcinus gracilis</i>	Ally (1975)
<i>Metacarcinus magister</i>	Poole (1966); Lough (1974)
<i>Pachygrapsus crassipes</i>	Lough (1974)
Pinnotheridae	Lough (1974)
<i>Pyromaia tuberculata</i>	Fransozo and Negreiros-Fransozo (1997); Luppi and Spivak, (2003)
<i>Rhithropanopeus harrisi</i>	Connolly (1925)
<i>Romalaeon antennarius</i>	Lough (1974); Roesijadi (1976)

Table 2. Relative Abundance of the species of brachyuran zoeae collected at station D41 from 1998-2008, ranked by the percentage of the total abundance of all species.

Rank	Species	Percentage Abundance
1	<i>Eriocheir sinensis</i>	30.5
2	Pinnotheridae	24.9
3	<i>Metacarcinus gracilis</i>	19.8
4	<i>Pyromaia tuberculata</i>	16.1
5	<i>Hemigrapsus oregonensis</i>	2.9
6	<i>Cancer productus</i>	2.7
7	<i>Lophopanopeus bellus</i>	2
8	<i>Carcinus maenas</i>	0.4
9	<i>Rhithropanopeus harrisi</i>	0.3
10	<i>Hemigrapsus nudus</i>	0.2
11	<i>Pachygrapsus crassipes</i>	0.1

Table 3. Relative Abundance of the species of brachyuran zoeae collected at station D41 in 1998, ranked by the percentage of the total abundance of all species.

Rank	Species	Percentage Abundance
1	Pinnotheridae	24.47
2	<i>E. sinensis</i>	21.23
3	<i>M. gracilis</i>	20.36
4	<i>P. tuberculata</i>	16.11
5	<i>C. productus</i>	13.48
6	<i>C. maenas</i>	2.00
7	<i>P. crassipes</i>	1.69
8	<i>L. bellus</i>	0.66
9	<i>H. nudus</i>	0.00
10	<i>H. oregonensis</i>	0.00
11	<i>R. harrisi</i>	0.00

Table 4. Relative Abundance of the species of brachyuran zoeae collected at station D41 in 1999, ranked by the percentage of the total abundance of all species.

Rank	Species	Percentage Abundance
1	<i>E. sinensis</i>	58.73
2	Pinnotheridae	19.84
3	<i>M. gracilis</i>	11.28
4	<i>C. productus</i>	6.13
5	<i>H. oregonensis</i>	1.89
6	<i>L. bellus</i>	0.99
7	<i>P. tuberculata</i>	0.92
8	<i>R. harrisii</i>	0.21
9	<i>C. maenas</i>	0.00
10	<i>H. nudus</i>	0.00
11	<i>P. crassipes</i>	0.00

Table 5. Relative Abundance of the species of brachyuran zoeae collected at station D41 in 2000, ranked by the percentage of the total abundance of all species.

Rank	Species	Percentage Abundance
1	<i>E. sinensis</i>	44.66
2	Pinnotheridae	23.81
3	<i>M. gracilis</i>	18.31
4	<i>C. productus</i>	5.70
5	<i>P. tuberculata</i>	4.48
6	<i>L. bellus</i>	2.32
7	<i>H. oregonensis</i>	0.33
8	<i>P. crassipes</i>	0.21
9	<i>H. nudus</i>	0.16
10	<i>C. maenas</i>	0.00
11	<i>R. harrisii</i>	0.00

Table 6. Relative Abundance of the species of brachyuran zoeae collected at station D41 in 2001, ranked by the percentage of the total abundance of all species.

Rank	Species	Percentage Abundance
1	<i>M. gracilis</i>	40.00
2	<i>P. tuberculata</i>	22.75
3	<i>E. sinensis</i>	21.05
4	Pinnotheridae	9.67
5	<i>H. oregonensis</i>	3.38
6	<i>C. productus</i>	2.41
7	<i>L. bellus</i>	0.52
8	<i>C. maenas</i>	0.22
9	<i>H. nudus</i>	0.00
10	<i>P. crassipes</i>	0.00
11	<i>R. harrisii</i>	0.00

Table 7. Relative Abundance of the species of brachyuran zoeae collected at station D41 in 2002, ranked by the percentage of the total abundance of all species.

Rank	Species	Percentage Abundance
1	<i>E. sinensis</i>	54.98
2	<i>P. tuberculata</i>	15.25
3	Pinnotheridae	12.21
4	<i>M. gracilis</i>	10.42
5	<i>H. oregonensis</i>	4.33
6	<i>L. bellus</i>	1.05
7	<i>C. productus</i>	0.85
8	<i>C. maenas</i>	0.81
9	<i>P. crassipes</i>	0.10
10	<i>H. nudus</i>	0.00
11	<i>R. harrisii</i>	0.00

Table 8. Relative Abundance of the species of brachyuran zoeae collected at station D41 in 2003, ranked by the percentage of the total abundance of all species.

Rank	Species	Percentage Abundance
1	<i>E. sinensis</i>	45.83
2	Pinnotheridae	23.00
3	<i>M. gracilis</i>	16.07
4	<i>P. tuberculata</i>	5.74
5	<i>H. oregonensis</i>	5.29
6	<i>L. bellus</i>	2.81
7	<i>R. harrisii</i>	1.33
8	<i>C. productus</i>	0.71
9	<i>C. maenas</i>	0.15
10	<i>P. crassipes</i>	0.07
11	<i>H. nudus</i>	0.00

Table 9. Relative Abundance of the species of brachyuran zoeae collected at station D41 in 2004, ranked by the percentage of the total abundance of all species.

Rank	Species	Percentage Abundance
1	Pinnotheridae	38.34
2	<i>E. sinensis</i>	22.12
3	<i>P. tuberculata</i>	16.23
4	<i>M. gracilis</i>	12.94
5	<i>L. bellus</i>	4.02
6	<i>H. oregonensis</i>	3.34
7	<i>C. maenas</i>	1.14
8	<i>C. productus</i>	0.77
9	<i>H. nudus</i>	0.70
10	<i>P. crassipes</i>	0.40
11	<i>R. harrisii</i>	0.00

Table10. Relative Abundance of the species of brachyuran zoeae collected at station D41 in 2005, ranked by the percentage of the total abundance of all species.

Rank	Species	Percentage Abundance
1	Pinnotheridae	47.70
2	<i>E. sinensis</i>	15.44
3	<i>M. gracilis</i>	14.13
4	<i>P. tuberculata</i>	10.55
5	<i>H. oregonensis</i>	4.67
6	<i>L. bellus</i>	4.50
7	<i>H. nudus</i>	1.56
8	<i>C. productus</i>	1.15
9	<i>C. maenas</i>	0.31
10	<i>P. crassipes</i>	0.00
11	<i>R. harrisii</i>	0.00

Table11. Relative Abundance of the species of brachyuran zoeae collected at station D41 in 2006, ranked by the percentage of the total abundance of all species.

Rank	Species	Percentage Abundance
1	<i>P. tuberculata</i>	55.22
2	Pinnotheridae	23.95
3	<i>M. gracilis</i>	13.76
4	<i>L. bellus</i>	2.12
5	<i>H. oregonensis</i>	1.98
6	<i>C. productus</i>	1.20
7	<i>E. sinensis</i>	0.83
8	<i>H. nudus</i>	0.47
9	<i>C. maenas</i>	0.23
10	<i>P. crassipes</i>	0.23
11	<i>R. harrisii</i>	0.00

Table12. Relative Abundance of the species of brachyuran zoeae collected at station D41 in 2007, ranked by the percentage of the total abundance of all species.

Rank	Species	Percentage Abundance
1	Pinnotheridae	43.45
2	<i>M. gracilis</i>	25.17
3	<i>P. tuberculata</i>	22.22
4	<i>C. productus</i>	5.16
5	<i>L. bellus</i>	2.25
6	<i>H. oregonensis</i>	1.16
7	<i>C. maenas</i>	0.46
8	<i>E. sinensis</i>	0.13
9	<i>H. nudus</i>	0.00
10	<i>P. crassipes</i>	0.00
11	<i>R. harrisii</i>	0.00

Table13. Relative Abundance of the species of brachyuran zoeae collected at station D41 in 2008, ranked by the percentage of the total abundance of all species.

Rank	Species	Percentage Abundance
1	<i>P. tuberculata</i>	37.48
2	<i>M. gracilis</i>	33.26
3	Pinnotheridae	24.96
4	<i>C. productus</i>	1.72
5	<i>C. maenas</i>	0.81
6	<i>H. oregonensis</i>	0.69
7	<i>R. harrisii</i>	0.69
8	<i>L. bellus</i>	0.40
9	<i>E. sinensis</i>	0.00
10	<i>H. nudus</i>	0.00
11	<i>P. crassipes</i>	0.00

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