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ABSTRACT

THE INFLUENCE OF ENVIRONMENTAL PARAMETERS ON ZOEAE RECRUITMENT DYNAMICS OF THE CHINESE MITTEN CRAB, *ERIOCHEIR SINENSIS*, IN SAN FRANCISCO BAY, CALIFORNIA

The Chinese mitten crab, *Eriocheir sinensis*, is an invasive nuisance species that has become established in estuaries around the world. The adult population of mitten crabs oscillates dramatically and population explosions have caused dramatic ecological impacts. Exploring the links between environmental parameters and cohort success is crucial in understanding what drives the dynamics of the North San Francisco Bay population. Temperature and salinity thresholds have been shown to exist at the beginning of the zoeae recruitment period in San Francisco Bay. A model was employed to predict the presence of *E. sinensis* zoeae stages II-V in the field; this model combined long-term mean temperatures from San Pablo Bay with larval development expressed by a temperature and salinity-dependent linear regression function. The analyses suggest that temperature, salinity, and planktivore abundance are three variables that play important roles in driving the recruitment dynamics of *E. sinensis* zoeae.

Ammon Rice
May 2006

THE INFLUENCE OF ENVIRONMENTAL PARAMETERS ON
ZOEAE RECRUITMENT DYNAMICS OF THE CHINESE
MITTEN CRAB, *ERIOCHEIR SINENSIS*, IN
SAN FRANCISCO BAY, CALIFORNIA

by
Ammon Rice

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submitted in partial
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INTRODUCTION

Population dynamics of many r-selected species are influenced by physical factors that affect the vulnerable larval stage. Brachyurans have planktonic larval stages that spend weeks to months in open water before metamorphosing into benthic juveniles. The environmental conditions that the planktonic larvae experience can alter the rate of development and survivorship, and significantly influence the year-class strength of new cohorts.

The Chinese mitten crab, *Eriocheir sinensis* (Crustacea: Decapoda: Grapsoidea), was discovered in San Francisco Bay in 1992, following more than a century of global dispersal. Since the invasion, *E. sinensis* has become one of the most abundant and widely distributed non-native aquatic organisms in the San Francisco Bay (Cohen and Carlton, 1998). The potentially rapid population growth of *E. sinensis* has created ecological concerns. Invasive populations of this catadromous crab in Europe spread hundreds of kilometers into freshwater streams and rivers (Panning, 1939a). Ecological and economic effects include predation on invertebrates of estuarine and freshwater systems (Rudnick and Resh, 2002); burrowing of juveniles can cause stream bank erosion and threaten levee integrity (Veldhuizen, 1997; Rudnick et al., 2000, 2003, 2005b); recreational and commercial fisheries are harmed through gear destruction and bait stealing (Rudnick and Resh, 2002); and mass migrations of adult mitten crabs have led to increased mortality of fish at the South San Francisco Bay Delta fish facilities during salvage operations (Veldhuizen and Stanish, 1999).

Since the San Francisco Bay and Sacramento/San Joaquin Delta system is the only location in North America where the mitten crab has become established,

it can be a good model to identify the patterns and processes associated with biological invasions. The effects that native species and the physical factors of the San Francisco Bay/Delta system have on recruitment dynamics of the mitten crab are largely unknown. This research addresses questions about recruitment dynamics of Chinese mitten crabs in the San Francisco Bay/Delta system, including: 1) what is the monthly supply of zoeae in San Pablo Bay? 2) What is the annual supply of zoeae in San Pablo Bay? 3) What are the environmental parameters that correlate with zoeae abundance? 4) Can the rate of zoeae development be predicted using temperature?

History of Invasions

The Chinese mitten crab is native to the rivers and estuaries along the Yellow Sea in Korea and China (Panning, 1939a). Beginning in the early 1900s, the Chinese mitten crab successfully invaded a large part of Europe, including Germany, Holland, Belgium, France, the Czech Republic, Denmark, Latvia, Russia, Sweden, Finland, and England (Panning, 1939a; Ingle, 1986; Vincent, 1996; Clark et al., 1998; Herborg et al., 2003). Recently, mitten crabs have invaded Portugal and Spain (Cabral and Costa, 1999). These invasions have had a considerable impact; as the following examples indicate, mitten crabs have interfered with fishing efforts by becoming entangled in nets and eating the intended catch (Panning, 1939a), and the burrowing behavior of mitten crabs has caused stream bank erosion and destruction of riparian habitat. For instance, in South San Francisco Bay tributaries the density of juvenile mitten crab burrows reached $30.0 \pm 1.6/\text{m}^2$, which may threaten the integrity of extensive levee systems (Rudnick and Resh, 2002; Rudnick et al., 2003, 2005a).

As a result of the mitten crabs' invasive history, the genus *Eriocheir* was added to the California Department of Fish and Game (CDFG) List of Prohibited Species in 1986 (USFWS, 1989). The means by which the mitten crab was introduced into the San Francisco Bay/Delta system in the winter of 1992 is unknown. Other systems, including the Mississippi, St. Lawrence, and Colombia River estuaries have reported single or limited mitten crab sightings and are considered at high-risk for invasion (Aquatic Nuisance Species Task Force, 2002).

In 1996, CDFG boat trawls in the North San Francisco Bay, and Tracy Fish Collection Facility (TFCF) traps in the tributaries, began to catch mitten crabs migrating downstream. TFCF collected fewer than 100 crabs in the fall of 1996, nearly 20,000 crabs in the fall of 1997, and in the fall of 1998 there was a population explosion, during which an estimated 750,000 crabs were collected (Rudnick et al., 2003). The population declined in 1999, but increased sharply again in 2001, and appears to be following a variable oscillatory pattern similar to other countries where the crab is established (Clark et al., 1998). Although these cyclical dynamics are widely reported, the mechanisms driving the dynamics are poorly understood.

Since invading California, *E. sinensis* has become well established in the San Francisco Bay Estuary. The range of the crab has spread to several thousand km² surrounding the Bay, and is still expanding (Appendix A, Fig. 1 a-d). In their native range, mitten crabs migrate as far as 1,000 km upstream. Current estimates of the crab's distribution in California are likely conservative due to low densities in the upper reaches of tributaries, making detection problematic (Rudnick et al., 2003).

Life History and Biology

To manage an invasive nuisance species such as the mitten crab, it is essential to have a detailed understanding of the life history. A life history model of the Chinese mitten crabs in California was detailed by Rudnick et al. (2005b), which illustrated distribution over space and time and hypothesized physical factors that influence each life stage. Chinese mitten crabs follow a type III survivorship curve; the larvae have a relatively high mortality rate, but survivorship increases for individuals who survive the larval period (Deevey, 1947).

Environmental parameters influence many aspects of mitten crab life history, including migration, growth, and reproduction (Rudnick et al., 2005b). Chinese mitten crabs are catadromous, juvenile mitten crabs remain in freshwater for 2 to 5 years, and at sexual maturity migrate to brackish water to spawn. Females can produce up to one million eggs that are laid within 24 hours of mating in brackish water. The eggs are cemented under the female to small setae on the pleopods that branch off the ventral surface of the abdomen. Time of hatching, larval survivorship, and development are strongly influenced by temperature and salinity (Panning, 1939a; Anger, 1991). The zoea is the free-swimming pelagic larva. Mitten crab zoeae typically have five stages (zoeae I – V), and then metamorphose into post-larval megalopae. Both life stages require brackish water. The megalopae have been reported to use tidal currents to migrate into fresh water and then metamorphose into benthic juveniles, which will journey upstream (Panning, 1939b). The life history model for the California population suggests a lifespan of 3 – 5 years based on sizes of downstream migrating crabs (Rudnick et al., 2005b).

Environmental Factors Affecting Zoeae Survivorship and Development

Environmental parameters that may affect zoeal survival and development under field conditions include temperature, salinity, freshwater discharge, and predation. Complete development of zoeae to juvenile crabs has been reported to occur at temperatures $\geq 12^{\circ}\text{C}$, when salinity is 20 – 25‰ (Anger, 1991). Additionally, increasing the water temperature (12°C – 18°C) causes the rate of development to increase exponentially and enhance both survival and salinity tolerance. Zoeae exposed to $\leq 9^{\circ}\text{C}$ do not survive beyond the first zoea stage (Anger, 1991). During the mitten crab's reproductive season, the temperature range of North San Francisco Bay shoals is between 10°C in the winter and 20°C in the summer (Herrgesell et al., 1983). However, during extreme years the temperatures can range from 8°C in the winter to 25°C in the summer. Early in the mitten crabs' reproductive season, zoeae in the San Francisco Bay/Delta System are likely to experience temperatures outside of their tolerance range. Based upon Anger's (1991) temperature and salinity tolerance experiments, this exposure to low temperature and salinity may prolong time of hatching, duration of larval stages, and decrease survivorship. Determining thermal tolerance between 9°C – 12°C is important in understanding a temperature threshold for zoeae survivorship that may dictate larval recruitment dynamics.

Similarly, temperature has been shown to be one of the most important factors influencing development, growth, and metabolism in subtropical decapod larvae (Dawirs, 1985; Dawirs et al., 1986; Anger, 1991; Nagaraj, 1993). Power functions have been used to express the effects of temperature on development of the green crab, *Carcinus maenas*. A predictive model was developed by combining power functions from laboratory data with long-term water temperatures in the field to estimate larval abundance of *C. maenas* (Dawirs,

1985). Such models provide a useful tool to examine larval dynamics in a pelagic ecosystem.

Mitten crab zoeae are euryhaline and are capable of surviving a wide range of salinities (Anger, 1991). Under laboratory conditions, first stage zoeae had the shortest stage duration at salinities between 15 – 25‰. Complete mortality occurred at salinities below 10‰ when temperatures were $\leq 12^{\circ}\text{C}$, and zoeae stage duration increased when exposed to low (10‰) or high (32‰) salinity (Anger, 1991). Optimum salinity for later zoeae stages (II – V) shifted toward seawater (32‰), and megalopae shifted back toward brackish water (15 – 25‰). Survival increased with temperature at all salinities tested (10 ‰ – 32‰). These laboratory experiments suggest there is a positive relationship between temperature and salinity that affects zoeae development and survival.

Salinity in the northern part of the San Francisco Bay system is variable, depending on the amount of freshwater outflow coming from the Sacramento and San Joaquin Rivers. For example, the salinity range is typically between 10 and 30 ‰ in San Pablo Bay, which is within the tolerance range of mitten crab zoeae, but during high outflow period's salinity can decrease to ~ 2 ‰. Despite periods of increased flow, mitten crab zoeae are likely retained in San Pablo Bay because of the enclosed shape of the bay and swimming behavior of the zoeae. Field studies of brachyuran larvae revealed light, salinity, and current speed affected vertical migration patterns, allowing retention of larvae in the estuary (Cronin, 1982).

High freshwater discharge may cause planktivores to migrate to central San Francisco Bay where the salinity is higher, thus decreasing predation on mitten crab larvae. Mid-water trawls conducted by the California Department of Fish and Game (CDFG) provide spatial and temporal distributions of planktivores that are

likely to prey on mitten crab larvae. Examination of planktivore distribution may suggest whether predation affects mitten crab zoeae year-class strength.

Ten fish species make up 98.9% of the CDFG planktivore catch (Hieb and Flemming, 1996) (Appendix B, Table 1). Of these fish, Northern anchovy, *Engraulis mordax*, are the most common, accounting for 73.2% of the total catch (Jones and Stokes, 2004). Northern anchovy are indiscriminate filter feeders, feeding during the daytime on any prey of suitable size, rather than species-specific feeding (Koslow, 1981). Crustaceans of all developmental stages from egg to adult appear to be the dominant food source for adult northern anchovy, while copepods are the predominant food source of larvae (Loukashkin, 1970; Hunter and Kimbrell, 1980).

Research Objectives

Implementing a theoretically based management plan has not previously been possible because of gaps in our understanding of the San Francisco Bay mitten crab population dynamics. Year-class strength of each new cohort may strongly influence the year-class strength of future adult mitten crabs. Ovigerous females have been collected in the San Francisco Bay Estuary from October to June, the highest percentage caught at the end of fall and in early winter. Larval duration through metamorphosis to a juvenile crab can last from 80 – 130 days at 12°C, but duration decreases to 35 – 55 days at 18°C (Anger, 1991), suggesting zoeae are likely to be present from December through July (Rudnick et al., 2003). Zoeae abundance can be determined by examining zooplankton samples but few zooplankton samples have been examined specifically to find mitten crab larvae in San Francisco Bay (Rudnick et al., 2005b). Determining *E. sinensis* zoeae density from zooplankton tows can be problematic because several species of crab zoeae

are present at one time. Invasions of *E. sinensis*, and the green crab, *Carcinus maenas*, have rendered previous means to identify crab larvae unusable.

Therefore, the development of a dichotomous key was necessary to determine the abundance of brachyuran zoeae in the San Francisco Bay.

Understanding mitten crab recruitment dynamics may answer many questions pertaining to dramatic fluctuations in annual abundance of migrating mitten crabs. This research focuses on environmental parameters influencing recruitment dynamics of *E. sinensis* and the predictability of development in the field. My objectives were to: 1) create a dichotomous key to identify species of brachyuran crab zoeae in the San Francisco Bay Estuary; 2) investigate patterns of zoeae density and environmental parameters (i.e., salinity, temperature, outflow, and planktivore community composition); 3) predict the rate of zoeae development in the field using daily temperature averages; and 4) perform laboratory experiments investigating thermal tolerance between 9°C and 12°C.

Within the scope of these goals, the following hypotheses were tested: 1) zoeae densities will be low during periods when temperature is $\leq 12^{\circ}\text{C}$; 2) only stage one zoeae will be present when the temperatures are $\leq 12^{\circ}\text{C}$; 3) zoeae densities will be low during periods of low outflow and high planktivore abundance; and 4) zoeal density will correlate with adult abundance.

MATERIALS AND METHODS

Study System

The San Francisco Bay/Delta (N 37°45', W 122°26') consists of south San Francisco Bay, central San Francisco Bay, San Pablo Bay, Suisun Bay, and the Sacramento-San Joaquin Delta. The San Francisco Bay Estuary drains ~40% of California's surface area, and is the largest estuary on the west coast of North America (Nichols et al., 1986). Freshwater outflow from the Sacramento-San Joaquin Delta creates highly variable salinities in the dredged channels and shoals of Suisun Bay located east of San Pablo Bay (Herrgesell et al., 1983). The increased salinity and shallow mudflats of San Pablo Bay create an advantageous spawning ground for the Chinese mitten crab. San Pablo Bay is large (272 km²) with depths ranging from <1 – 5 m in shallow open water and 2 – >15 m in channels (Hymanson et al., 1994).

Zoeae Identification

A dichotomous key with emphasis on *E. sinensis* was developed to identify zoeae to species and to determine developmental stage. Zooplankton samples were obtained from the CDFG *Neomysis* and Clarke-Bumpus zooplankton tows from 1993 – 2005. Samples examined were from five sites between San Pablo Bay and upstream Suisun Bay. The zoeae were separated into species using published literature and specimens reared in our laboratory. The key includes zoeae from adult crab species that have been identified from the CDFG mid-water and otter trawls. Using characters that remain consistent throughout all zoal stages, the key was devised to identify 12 species in the families Grapsidae,

Xanthidae, Majidae, Cancridae, and Pinnotheridae. Zoeae of each species known to be present in the San Francisco Bay had been previously described (Appendix B, Table 2).

Zoeae in the plankton tows were sorted using traits such as length of the telson, presence or absence of lateral carapace spines and midlateral spines on the abdomen, and the number of spines on each furca. Additional zoeae reared in our laboratory served as type specimens used for identification. Gravid *Cancer antennarius* and *Cancer gracilis* were collected from Bodega Bay and San Pablo Bay, respectively, and brought to our laboratory. Eggs from both species hatched successfully in 12°C seawater. *Eriocheir sinensis* were bred by Dr. R. Tullis, California State University, East Bay. Gravid females were brought to California State University, Fresno, and zoeae were hatched in the laboratory in 12°C, 20‰ saltwater. Stage I zoeae of *C. antennarius*, and stages I, II, and III of *C. gracilis* and *E. sinensis* were preserved in 70% EtOH. Species descriptions and morphological characters observed on the specimens were used to assemble a dichotomous key. Couplets used characters that remain consistent through all zoeal stages. Descriptions provided are for stage I zoeae, unless otherwise stated. Drawings were made freehand to provide a visual description of morphological differences between species.

Zoeae Abundance

Zoeae abundance in North San Francisco Bay/Delta was evaluated using zooplankton samples from CDFG *Neomysis* and Clarke-Bumpus zooplankton tows, which monitor *Neomysis sp.* and zooplankton densities throughout the San Francisco Bay Delta system. Monthly zooplankton tows were examined from San Pablo Bay stations D41 (Z1) and 325 (Z2) (Appendix A, Fig. 2). Analysis was

restricted to 1998 – 2004, during the Chinese mitten crab reproductive season (December – July), and all months in 2003 and 2004. Investigating the years that *E. sinensis* was present in San Francisco Bay prior to 1998 was not possible due to lack of CDFG sampling in San Pablo Bay during the early 1990s and/or the condition of archived samples.

Neomysis/zooplankton tows followed CDFG protocol. Clarke-Bumpus nets are made of 154 mesh nylon cloth (No. 10 mesh), with a mouth diameter of 10 cm. The total net length is 73 cm, which tapers to 45 mm at the cod end. Organisms are collected by a stainless steel bottle with a screened opening. The nets are towed from bottom to surface in a stepwise oblique tow lasting 10 minutes (Orsi, 1999).

Neomysis and Clarke-Bumpus samples were preserved in 10% formalin and stained with Rose Bengal stain by CDFG. The samples were examined in the laboratory at California State University, Fresno using a Leica MZ7.5 dissecting microscope and Leica KL 750 light source. Zoeae from each sample were identified to species, counted, and placed into separate vials. Zoéal stage was determined by counting the number of setae present on each maxilliped. The total number of mitten crab zoeae from each sample was divided by the tow volume (m^3) to produce zoeae density/ m^3 .

Rate of Development

Anger (1991) expressed zoeae stage development as an exponential function of temperature (T, in °C) at different salinities (Appendix B, Table 3). The salinity in San Pablo Bay is >20‰ for the majority of the time that mitten crab zoeae are present. To determine the shortest developmental duration, the 20‰ exponential regression equations were used. Two rates of development

curves were plotted to show stage duration in days at 20‰: 1) zoeal stages and 2) complete development to a megalopae (Appendix A, Fig. 3; Fig. 4). The exponential regression equations were also used to create a zoeae development model, which estimated stage duration in the field. Hypothetical stage duration on the basis of varying field temperatures was calculated by adding the reciprocal values of the estimated duration of subsequent daily mean temperatures. When the sum of the reciprocal values reached 1, zoeae completed a particular stage. The duration of all 5 subsequent zoeal stages were found for zoeae that hatched on a predetermined date. This process was repeated for each year to estimate the number of days required for zoeae to metamorphose to megalopae. Zooplankton samples for each month were examined for zoeae stages that were predicted to be present. The hatch dates were selected by performing a *t*-test to test for significant differences in zoeae density at different temperatures.

Environmental Parameters

Temperature and salinity data were obtained from a USGS continuous monitoring gauge in San Pablo Bay, at Point San Pablo (PSP) (Appendix A, Fig. 2). PSP has an upper, middle, and lower sensor; the upper sensor (between 3.5 and 9 m) was used because those readings are most relevant to the pelagic larval stages. USGS continuous monitoring gauges recorded measurements every 15 minutes; daily temperature and salinity averages were used to allow daily growth rates to be calculated.

Monthly outflow data were obtained from the Interagency Ecological Program (IEP) Dayflow Program website (<http://iep.water.ca.gov/dayflow/index.html>). The IEP measures freshwater outflow from the Delta in cubic feet per second at Chipps Island (O) (Appendix A, Fig. 2).

Annual abundances of adult mitten crabs and planktivores were plotted on separate x-axes; when offset by 4 years the peaks and troughs of adult mitten crab abundance were inversely related to planktivore abundance (Rudnick, unpublished data). The observation that predation on mitten crab larvae may cause low adult abundance 4 years later was tested by examining the monthly abundances of planktivores and zoeae in San Pablo Bay.

Planktivore and adult mitten crab abundance data used for this study were collected by CDFG mid-water and otter trawls from 1995 through 2004. CDFG mid-water trawls are conducted monthly throughout the San Francisco Bay/Delta using a trawl mesh graduated in 9 sections ranging in size from 20.3 cm at the mouth to 1.3 cm at the cod end, and the mouth measuring 3.7 m². Volume of water filtered was calculated by the product of the net mouth area and the distance traveled, measured by a flowmeter on the side of the boat (Orsi, 1999).

Thermal Tolerance

During this study, thermal tolerance tests were performed to evaluate the survival threshold between 11.7°C. Gravid crabs collected by CDFG mid-water and otter trawls in December, 2004; December, 2005; and January, 2006, from south San Francisco Bay were brought to California State University, Fresno and slowly acclimated to 20‰ saltwater at a constant 12°C. Once the eggs hatched, actively swimming zoeae were transferred with wide-bore pipettes to glass bowls containing 500 ml millipore filtered 20‰ saltwater mixed from Instant Ocean salt mix. Each bowl contained 100 zoeae. The bowls were placed in environmental control chambers at 10°C, 11.7°C, and a control of 15°C with a 12/12 LD cycle. Variation in the number of zoeae produced by each female produced different numbers of treatments. There were six replicate treatments for the control at

15°C, four replicates at 11.7°C, and four replicates at 10°C. Each day the water was changed to fresh filtered 20‰ seawater and the zoeae were fed freshly hatched *Artemia* nauplii. Developmental stage and larval mortality were recorded daily.

Statistical Analysis

The Chinese mitten crab reproductive season was based on the year-class of a new cohort that begins in December and ends in June the following year. Zoeae density was found by dividing the total number of zoeae found in a sample by the tow volume (m^3), and zoeae catch per unit effort (CPUE) was found by multiplying the density by 100. Planktivore and adult mitten crab abundance were also measured in CPUE, which was calculated by dividing abundance data by the tow volume and multiplying the product by 100. Pearson's correlation and regression among time series of physical and biological variables were used to develop a conceptual model of the mechanisms driving mitten crab recruitment dynamics during 1998 – 2004. Differences in zoeae density between 9°C and 12°C in the field, and mean values of zoeae survival during thermal tolerance experiments in the laboratory were analyzed with a *t*-test. All statistical tests were conducted in SPSS 13.0 or SYSTAT 11.0.

RESULTS

A dichotomous key of brachyuran crab zoea for San Francisco Bay was generated to provide a tool to determine the abundance of Chinese mitten crab zoeae (Appendix C). Each couplet used descriptions of first stage zoeae, unless otherwise stated. The key only included zoeae of species that were identified from CDFG sampling. Any species not caught in CDFG trawls or any future invasive crabs were not included in this key.

The dichotomous key was used to identify mitten crab zoeae from CDFG *Neomysis* and Clarke-Bumpus zooplankton tows. Zoeae density was variable among months and years (Appendix A, Fig. 5; Fig. 6). Zoeae were found in San Pablo Bay as early as December (mean = 1.912/m³), typically peaking in April (mean = 12.235/m³), then declining until June (mean = 1.570/m³). No mitten crab zoeae were observed in July. Annual zoeal supply was generated by summing each monthly density and was highest in 1999 (39.090/m³), 2002 (47.100/m³), and 2003 (56.452/m³).

Influences of Physical Factors on Zoeae

At the beginning of the mitten crab zoeae recruitment period (December – February) in San Pablo Bay, temperature and salinity were variable and typically not suitable for survival. The earliest date during a calendar year that water temperatures reached 11.7°C was February 7, 2003, and latest date that water temperatures reached 11.7°C was March 10, 2000. Salinity was above 10‰ throughout 2001, 2002, and 2004, but during 2000 was below 10‰ until March 28 (Appendix B, Table 4). All zoeae that were found in December and January were stage I; the only stage II zoeae found in February were during 2003. In March,

only stage I (84.7%), stage II (12.6%), and stage III (2.7%) zoeae were present in the samples, and no stage IV or V were found. Nearly half of the total zoeae seen in April were later stages: stage II (22.3%); stage III (19.7%); and stage IV (3.5%). Stage V zoeae first appeared in April, and in May comprised 3.8% of the total zoeae (Appendix A, Fig. 7).

A thermal threshold was hypothesized between 9 and 12°C, above which zoeae mortality is not affected by temperature. Analysis of zoeae densities found a significant difference between means above and below 11.7°C using a *t*-test ($p < 0.04$), which suggests that 11.7°C may be a thermal tolerance threshold (Appendix A, Fig. 8). To confirm 11.7°C is a threshold, and to ensure the difference between means is not due to seasonal effects, a predictive model was used to estimate the earliest date of hatching for zoeae. The date an average of 11.7°C was reached in San Pablo Bay was used as the hatch date. During 1998 – 2004, the daily average temperature of 11.7°C occurred in San Pablo Bay on different days of the month, and in some years different months (Appendix B, Table 4). Developmental duration of zoeae I – V varied each year depending on daily average temperatures, ranging in length from 47 to 65 days (Appendix A, Fig. 9). Only stage I zoeae were found in samples that were collected when temperatures were <11.7°C and salinities were <10‰. Zoeal stages were found during the predicted months during all years, except 2000. During 2000, stages I – IV were predicted to be found in the April 14th sample, however only stages I and II were found. The salinity was very low this year, and did not reach 10‰ until March 28th, 18 days after 11.7°C occurred. After moving the hatch date to March 28th, the predicted zoeae stages reflected the April sample.

During this study, thermal tolerance experiments were performed in the laboratory to test for thermal thresholds between 9 and 12°C. At 10°C and 20‰,

complete mortality occurred within the 15 days, and all zoeae were in the first zoeal stage (Appendix A, Fig. 10). Zoeae in the 11.7°C treatment showed increased survivorship, and 33.9% molted to stage II after 15 days (Appendix A, Fig. 11). The zoeae in the 15°C treatment demonstrated the highest survivorship, with 68.3% molting to stage II, and 49.6% molting to stage III (Appendix A, Fig. 12). Stage duration for the 15°C treatment was 8 days for stage I, and 7 days for stage II. Survivorship means at the end of stage I were significantly different using a *t*-test at 11.7°C than 15°C ($p = 0.0004$). Duration of stage I was 7 days longer for zoeae at 11.7°C than those at 15°C.

Influence of Biological Parameters

Mitten crab zoeae density was hypothesized to directly correlate with adult abundance. Linear regression between the two variables ($N = 55$) detected a significant relationship between the adult CPUE and zoeae density, as did Pearson's correlation ($p < 0.01$; $r = 0.465$) (Appendix A, Fig. 13).

Freshwater outflow into the San Francisco Bay Delta significantly correlates with salinity ($p < 0.0001$). Periods of high outflow caused a decrease in salinity in San Pablo Bay (Appendix A, Fig. 14). Planktivore abundance in San Pablo Bay is significantly correlated with outflow ($p < 0.01$; $r = -0.375$) (Appendix A, Fig. 11).

Monthly zoeae abundances were plotted with planktivore CPUE to determine how planktivores may be impacting zoeae (Appendix A, Fig. 15). Independent variation exists in both zoeae and planktivore CPUE. Northern anchovy CPUE is lowest early in the larval life history, and during this time other factors would influence larval density, such as temperature and salinity. High planktivore CPUE and low zoeae densities occur in May and June. However,

neither linear regression nor Pearson's correlation detected a significant relationship between planktivore CPUE and zoeae density ($p = 0.173$; $r = 0.194$) (Appendix B, Fig. 13).

In summary, a dichotomous key was generated to identify species of brachyuran crab zoeae in the San Francisco Bay Estuary. This proved to be a useful tool in the identification of mitten crab zoeae. The rate of zoeae development was predicted using an exponential regression model. The model combined with zoeae of varying stages found in the zooplankton samples were used to estimate the earliest date of hatching each year. Patterns of zoeae density were investigated in relation to several environmental parameters. Zoeae densities were low and only stage one zoeae were present when temperatures were $\leq 12^{\circ}\text{C}$, therefore hypotheses 1 and 2 were supported. Zoeae densities declined during low outflow and high planktivore abundance. However, there was no correlation between these two variables and zoeae density, thus hypothesis 3 was not supported. Lastly, zoeae density and adult abundance were correlated, therefore hypothesis 4 was supported.

DISCUSSION

In order to develop a sound understanding of the life history for the north San Francisco Bay population of *Eriocheir sinensis*, it is essential to understand the species ecology and life history in San Francisco Bay. Marine invertebrates with complex life histories develop through several different stages, each of which must be examined to explain the population dynamics of the species. In this study, I examined the relationship between Chinese mitten crab larval dynamics and environmental factors in the field and lab. Identifying environmental components that affect larval recruitment may allow for predictions of benthic juvenile year-class strength.

Conceptual Model for Zoeae Recruitment

Patterns of zoeae development, peak densities, and annual abundance suggest that physical and biotic factors strongly influence development and survivorship of mitten crab zoeae. The timing of adult migration in relation to temperature and salinity thresholds directly affects the supply of zoeae into the system. Decreasing freshwater outflow causes salinity to increase in San Pablo Bay throughout the season, allowing planktivores to migrate into the system, and thus increase predation pressure. Physical factors and planktivores create boundaries for zoeae recruitment, between which zoeae development and survivorship are less affected. The more time that exists between these boundaries will allow larger year-classes to be recruited (Appendix A, Fig. 16).

Chinese Mitten Crab Zoeae Recruitment Dynamics in
North San Francisco Bay

A 7-year data set of mitten crab abundance from San Pablo Bay was generated and analyzed relative to long-term data sets for temperature, salinity, outflow, and planktivore abundance during the period when the crabs were in the larval stages. Zooplankton samples collected from San Pablo Bay were examined for *E. sinensis* zoeae every month of the reproductive season (December – July), 1998 – 2004, and all months during 2003 and 2004. Zoeae densities were variable between months and years and correlated with adult abundances ($p < 0.01$) and temperature ($p < 0.05$). Temperature and salinity thresholds were found to exist at 11.7°C and 10‰, respectively, which suggests that environmental factors are influencing development and survivorship of *E. sinensis* zoeae in the San Francisco Bay Estuary.

Temperature and salinity are known to affect development and survivorship of brachyuran larvae (Dawirs, 1985; Dawirs et al., 1986; Anger, 1991; Nagaraj, 1993; Giménez and Anger, 2003). This study suggests the influence of temperature and salinity on recruitment dynamics of Chinese mitten crab zoeae at the beginning of each season strongly affected year-class strength of each new cohort. The majority of gravid female Chinese mitten crabs are found in San Francisco Bay between November and March (Rudnick et al., 2005b). During the beginning of the recruitment period (December – February) temperature and salinity are frequently below the tolerance of mitten crab zoeae (Appendix B, Table 4). As temperature increases, the duration of each zoeal stage decreases. At 20‰, zoeae are theoretically competent to complete the zoeae stage in 66.5 and 22.0 days, at 12°C and 20°C, respectively. Mitten crab zoeae can complete development at 12°C, but do not survive past zoeal stage I at 9°C (Anger, 1991). Determining a thermal threshold for *E. sinensis* zoeae between 9 and 12°C was an

important step in understanding the mechanisms involved early in recruitment of new cohorts. Our laboratory experiments tested the rate of development and survival at 10, 11.7, and 15°C at a constant 20 ‰. At 10°C mitten crab zoeae survive for 15 days, but complete mortality occurred before development to stage II (Appendix A, Fig. 10). Zoeae maintained at 11.7°C had stage I duration of 15 days and 23.9% survivorship to stage II (Appendix A, Fig. 11). Zoeae at 15°C demonstrated the best performance, with 68.3% survivorship to stage II (Appendix A, Fig. 12).

Mitten crab zoeae are euryhaline, demonstrating tolerance to a wide range of salinities. Laboratory reared first stage zoeae had the shortest stage duration and highest survival at salinities between 15 – 25‰, and complete mortality occurred during stage I when combining salinities ≤ 10 ‰ with temperatures ≤ 12 °C (Anger, 1991). During our study, salinities in the field were above tolerance throughout 2001, 2002, and 2004. Salinities were above 10 ‰ within less than one week of the daily temperature average reaching 11.7°C in 1998, 1999, and 2003. During 2000, salinity dropped to ~ 3 ‰ March 14th, and did not reach 10‰ until March 28th.

The relationships between physical factors in the San Francisco Bay/Delta and temporal distribution of developmental stages were examined using a predictive model. The model used exponential regression equations (Anger, 1991), and estimated when subsequent zoeal stages should occur depending on daily temperature averages.

Only stage I zoeae were found in San Francisco Bay Delta samples when temperatures were < 11.7 °C during 1998 – 2005. A significant relationship ($p < 0.04$) was found between zoeae densities of all stages in San Pablo Bay above and below 11.7°C, suggesting that 11.7°C is the minimum temperature required for

successful zoeal development from stage I into II (Appendix A, Fig. 8). The date an average of 11.7°C occurred in San Pablo Bay was used as the hatch date.

During the years examined (1998 – 2004), daily temperature averages of 11.7°C occurred in San Pablo Bay on different dates. Therefore, when development rates were examined each year, zoeae stages II – V were expected to occur on different dates. Model predictions were supported in zooplankton samples of all 7 years, except 2000. During this year, the thermal threshold of 11.7°C occurred March 10th during a period of low salinity (~3‰). The salinity increased to 10‰ on March 28th. After moving the hatch date to March 28th, predicted zoeae stages were found when expected. This suggests that there is both a thermal and salinity threshold.

Seasonal fluctuations of temperature and salinity in Elkhorn Slough, CA, and nearshore coastal waters are believed to be responsible for different hatching patterns of several brachyuran species (Hsueh, 1991). Temperature and salinity have also been shown to influence annual distribution, hatching, and abundance of copepods, cladocerans, rotifers, and tintinnids throughout San Francisco Bay (Ambler et al., 1985).

The timing of adult mitten crab migration in relation to temperature and salinity thresholds will determine the strength of the larval supply. Spikes in adult mitten crab abundance have occurred twice since their invasion of San Francisco Bay (Appendix A, Fig. 17); however, temperature and/or salinity were below threshold for 1 – 2 months after adult abundance peaked both years. The first spike of adult mitten crab abundance was in 1999, peaking in February with 244 CPUE. Temperatures were below 11.7°C until March 4th, the salinity was <10‰ until March 11th, and the zoeae density did not peak until May (17.5/m³). In December 2002 the largest adult CPUE recorded in San Pablo Bay to date

(261 CPUE), produced only $9.90/\text{m}^3$ zoeae in December. Temperatures were $<11.7^\circ\text{C}$ until February 20th, and zoeae density peaked at $29.2/\text{m}^3$ in March when the adult abundance had declined to 89 CPUE. During 1999 and 2002, the larval supply may not have reached its potential because of temporal separation between peak adult abundance and tolerable environmental thresholds. The zoeae that are produced by the early migrating adult mitten crabs would have high mortality. The high mortality of early zoeae may cause a shift towards later migration in the San Francisco Bay Estuary mitten crabs.

In 2003, adult mitten crab abundance peaked in February (81 CPUE), and temperature and salinity were above the hypothesized zoeae threshold within the first week of February. When the adult abundance declined to 23 CPUE in April, zoeae density spiked at $40.64/\text{m}^3$. Over half (53%) of the zoeae found in the April 2003 sample were stages II and III, suggesting high survival for zoeae that hatched at the end of March when temperatures were $\sim 14^\circ\text{C}$ and salinities were $\sim 21\text{‰}$. This year was the largest zoeae year-class found of the 7 years examined, despite only having 1/3 of the adult abundance seen in previous years. This suggests that adult mitten crabs that arrive when the environment is tolerable demonstrate increased reproductive fitness.

The life history model for the San Francisco Bay population hypothesizes the life span of the San Francisco Bay Chinese mitten crabs to be 3 – 5 years (Rudnick et al., 2005b). An inverse relationship between planktivores and adult crabs 4 years later (Rudnick, unpublished data) led to the hypothesis that predation on zoeae may affect adult mitten crab populations. Gravid mitten crabs and stage I zoeae have been found as late as June, but mitten crab zoeae were not found in July samples during any of the 7 years examined. Northern anchovy are indiscriminate filter feeders. Stomach content analyses have found crustaceans of

all developmental stages from egg to adult to be the dominant food (Loukashkin, 1970; Hunter and Kimbrell, 1980).

High freshwater outflow into the San Francisco Bay Delta positively correlates with decreasing salinity (Appendix A, Fig. 14), and decreasing outflow significantly correlates with increasing planktivore CPUE ($p < 0.01$; $r = -0.375$) (Appendix A, Fig. 13). Outflow data from the IEP were consistent from 1990 – 2005 and used when examining the effects of salinity on planktivores.

Planktivores start to migrate into San Pablo Bay in April (Appendix A, Fig. 18). Northern anchovies are the most common planktivore and tolerate salinities between 22 – 32‰. Ambler et al. (1985) suggested when northern anchovies are most abundant in San Pablo Bay the copepod *Acartia californiensis* may experience more intense predation than its congeneric, *A. clausi*, which is found in the South Bay. Although there was not a significant correlation between mitten crab zoeae and planktivores, planktivores may be a factor affecting zoeae recruitment because of the crab's "r-selected" nature. Predation by indiscriminant filter feeders late in the larval life history could have strong impacts on year-class strength. It is possible that the inverse patterns between planktivores and adult abundances 4 years later are due to predation on mitten crab megalopae, which was not examined during this study. Very few mitten crab megalopae and juvenile crabs have been collected in the San Francisco Bay Estuary, and employing more effective trapping techniques, such as light traps, in the San Francisco Bay Estuary could produce valuable data.

Conclusion

In this study we have identified several factors that play significant roles in driving recruitment dynamics of the Chinese mitten crab, *Eriocheir sinensis*. The

mitten crab's native temperate and subtropical climate of China is not typical of the San Francisco Bay/Delta system, thus larval growth and development are affected differently throughout this region. Colder temperatures and occasionally low salinities are found in the San Francisco Bay/Delta System, and these factors combined with the timing of migrating adults caused poor survivorship of mitten crab larvae.

Zoeae development was successfully predicted using temperature-dependent functions. Thresholds were shown to exist, after which zoeae densities increase and development to zoeae stages II – V occurs. Zoeae recruitment is framed by thresholds and the immigration of planktivores into San Pablo Bay. The time between temperature and salinity rising above 11.7°C and 10 ‰, respectively, and when planktivores enter San Pablo Bay create a window during which mitten crab zoeae mortality is less affected.

Identifying the mechanisms driving adult population fluctuations was an underlying goal of this study. However, a relationship between year-class strength of zoeae and later adult populations was not identified. This relationship could only be examined for 3 to 4 years because of the length of time between zoeae data being available and the cohorts return as adults. Different sizes of migrating adults suggest that crabs of different cohorts become sexually mature, which may decouple the relationship between cohorts of zoeae and reproducing adults. Implementing a theoretically based management plan has not been possible because of gaps in our understanding of the San Francisco Bay mitten crab population dynamics. This study has addressed several issues pertaining to larval dynamics, but many questions remain unanswered. For example, do the zoeae densities in south San Francisco Bay follow similar patterns? Where do the megalopae migrate to in north San Francisco Bay? How is megalopae year-class

strength affected by physical factors and predation? The complex life history of the Chinese mitten crab leaves several areas to be explored. Thorough knowledge about the dynamics of each life stage may provide effective predictors for adult abundance, as well as better management and control.

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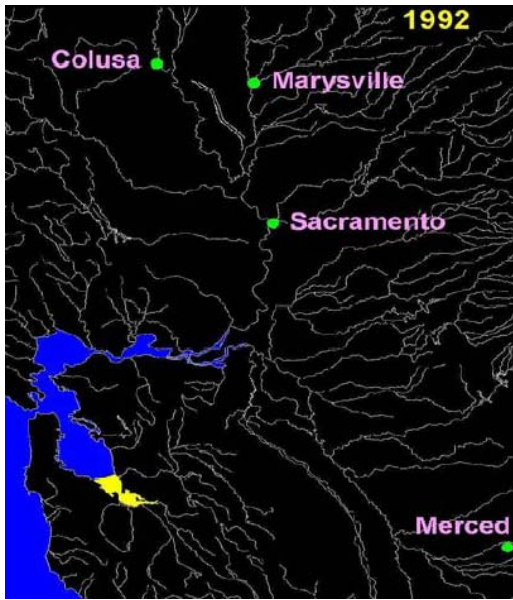
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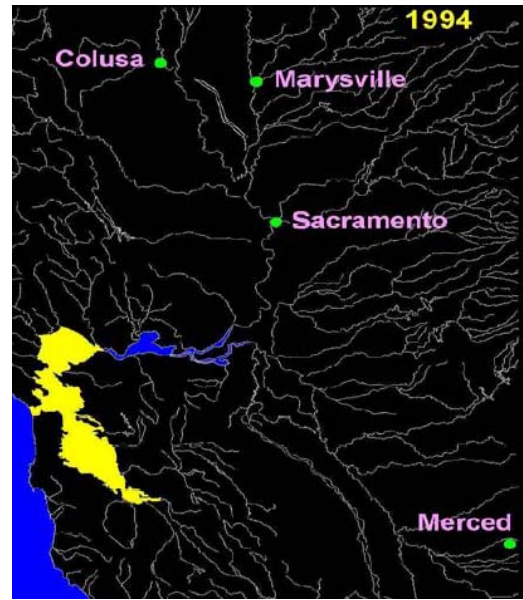
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APPENDICES

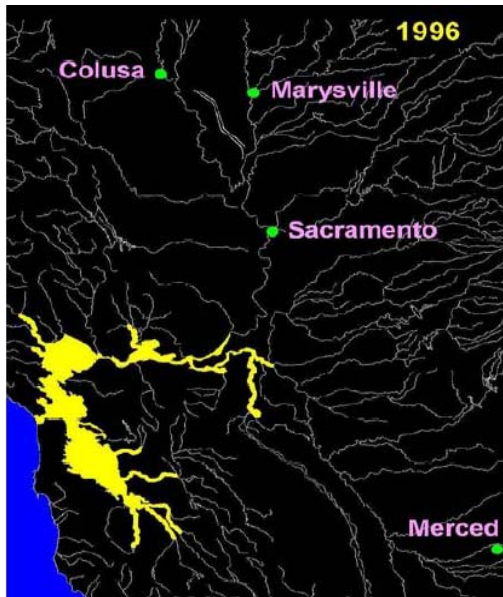
APPENDIX A
FIGURES



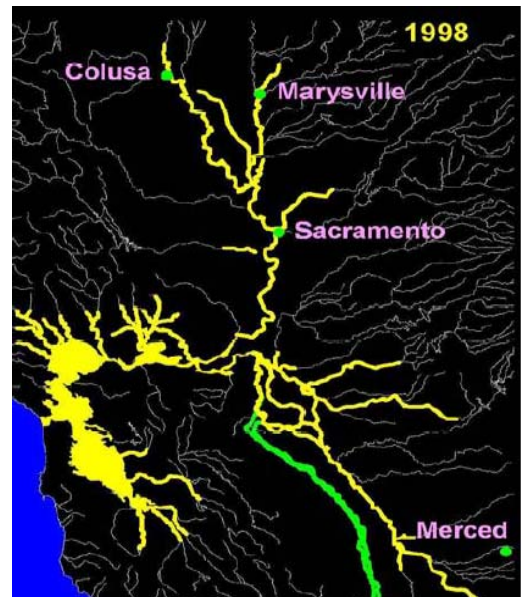
a.



b.



c.



d.

Figure 1. The range expansion of the Chinese mitten crab in San Francisco Bay-Delta 1992-1998.

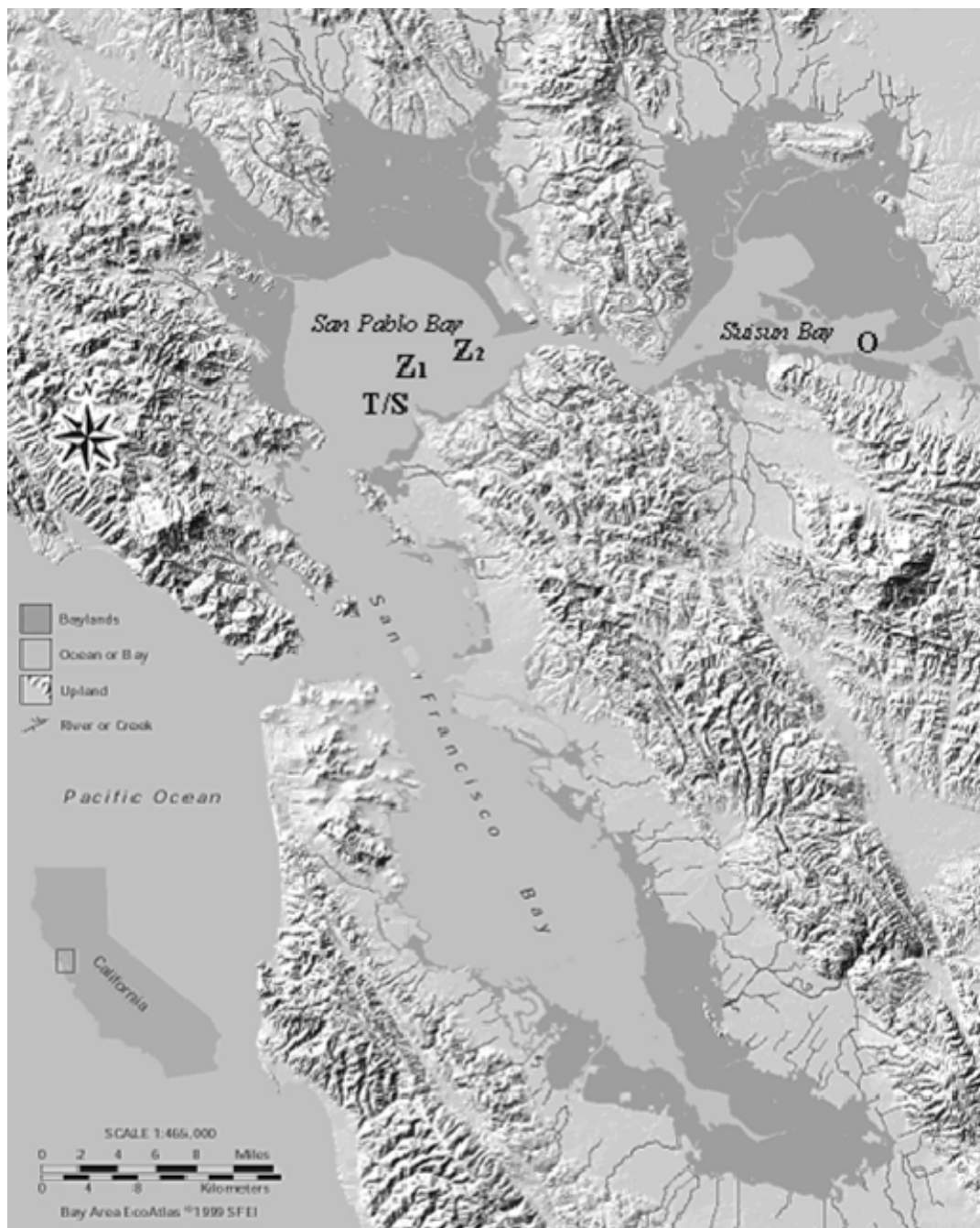


Figure 2. CDFG *Neomysis* and Clarke-Bumpus zooplankton sampling locations in San Pablo Bay, station D41 (Z_1) and station 325 (Z_2). USGS continuous monitoring gauge, PSP (T/S) provided temperature ($^{\circ}\text{C}$) and salinity (‰) data. Outflow (CFS) was measured by IEP at Chipps Island (O).

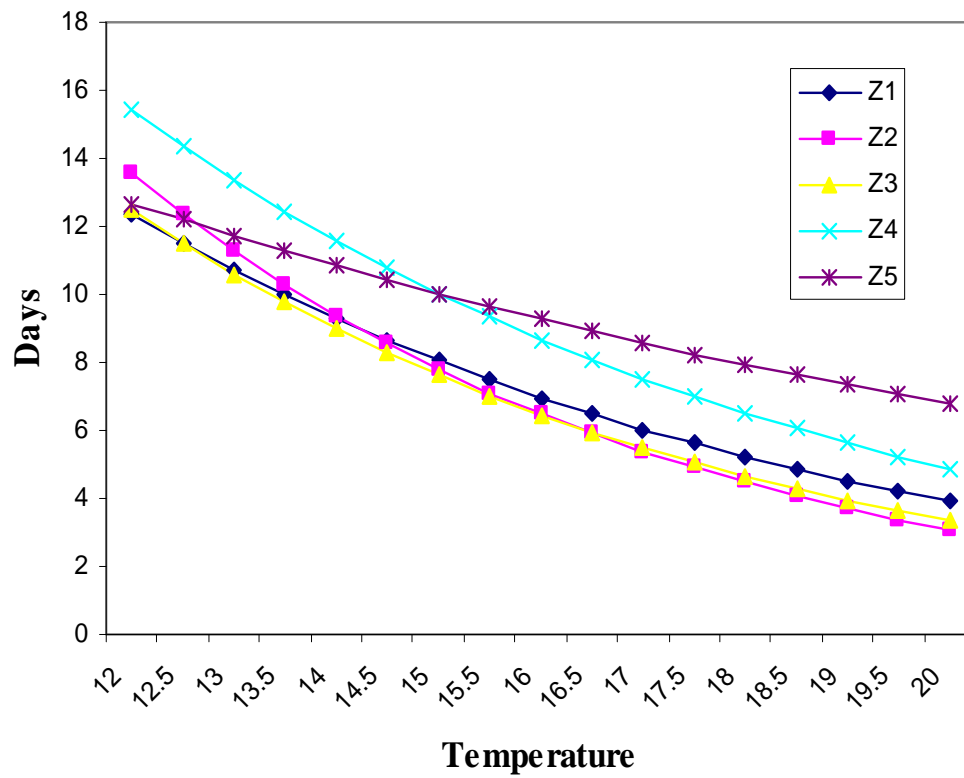


Figure 3. Zoeae stage (I – V) development in days expressed using an exponential function of temperature (T , in $^{\circ}\text{C}$) at 20‰ (Anger, 1991).

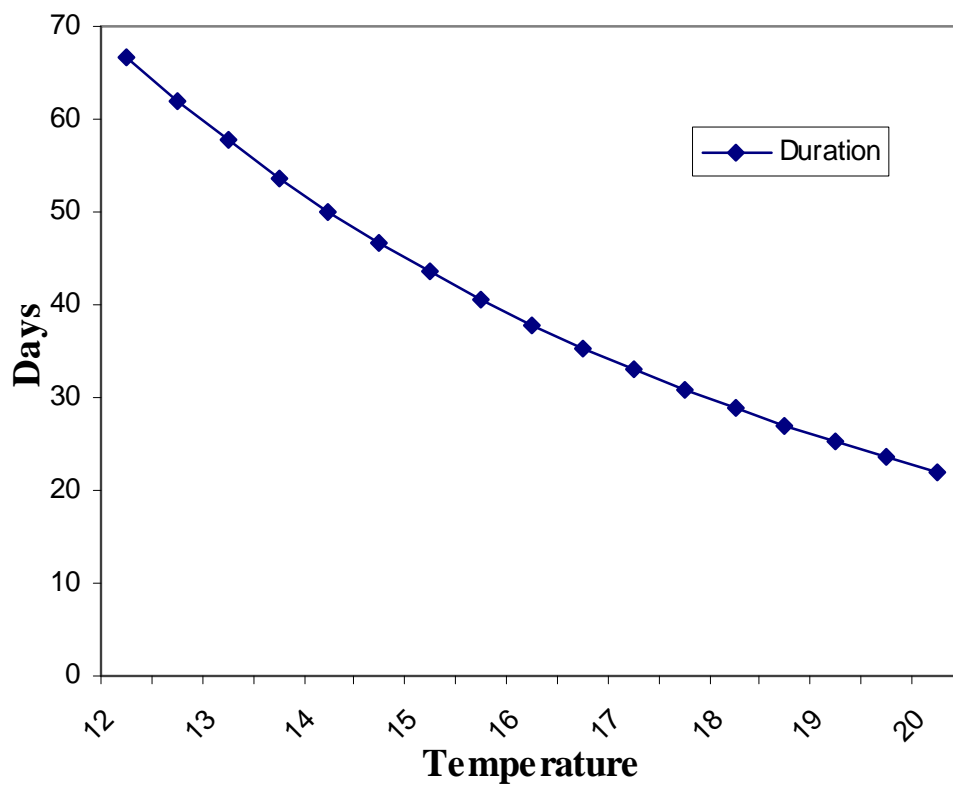


Figure 4. Complete zoeae development in days to a megalopae expressed as an exponential function of temperature (T, in °C) at 20‰ (Anger, 1991).

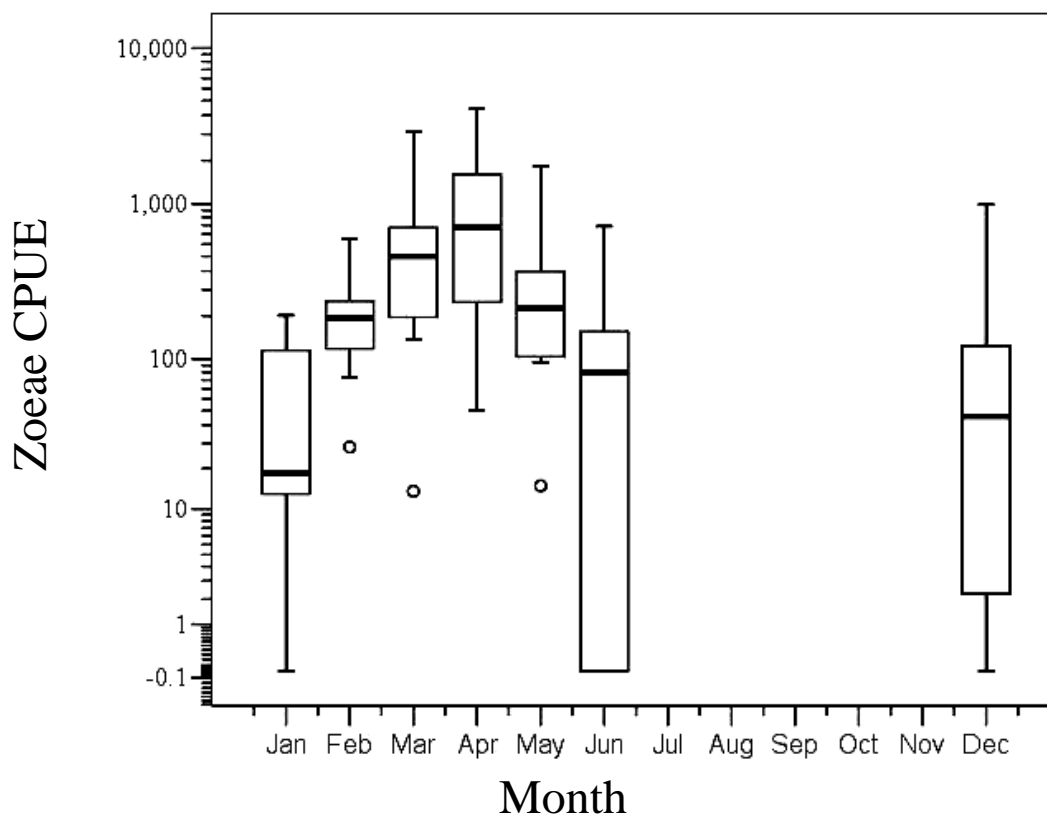


Figure 5. *Eriocheir sinensis* zoeae abundance by month in San Pablo Bay, 1998 – 2004.

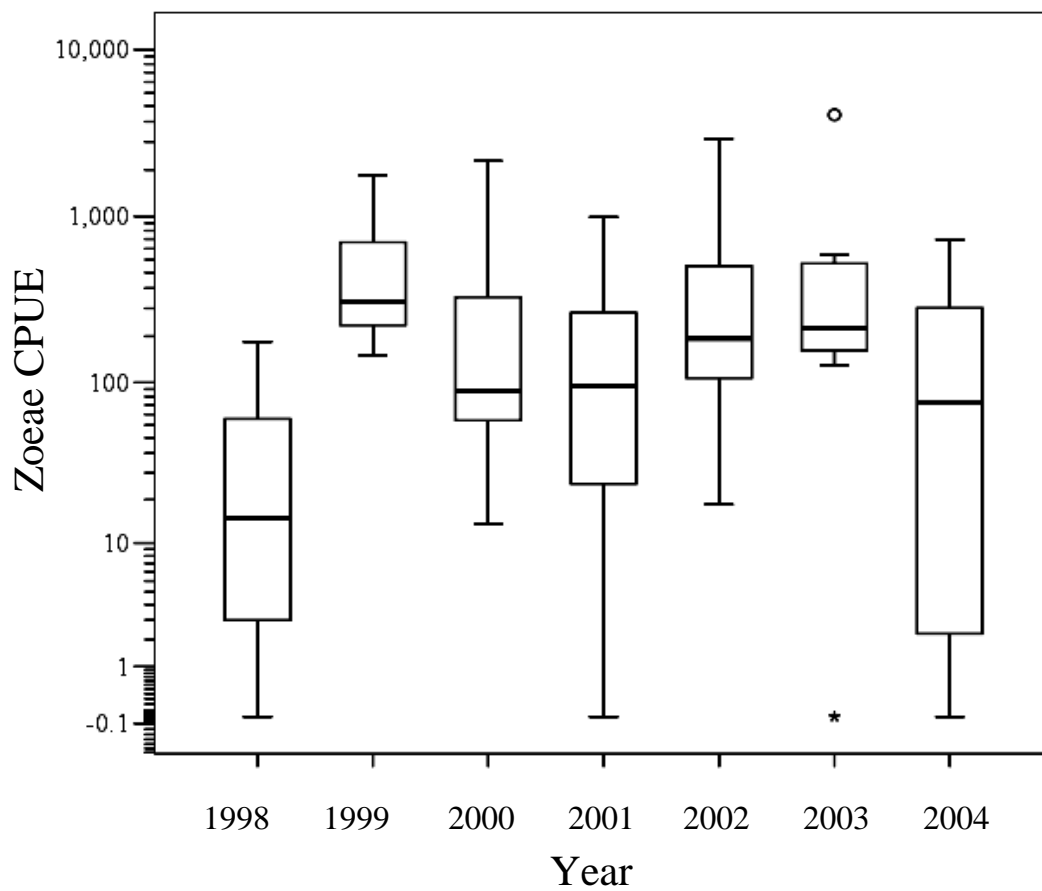


Figure 6. *Eriocheir sinensis* zoeae abundance by year in San Pablo Bay, 1998 – 2004.

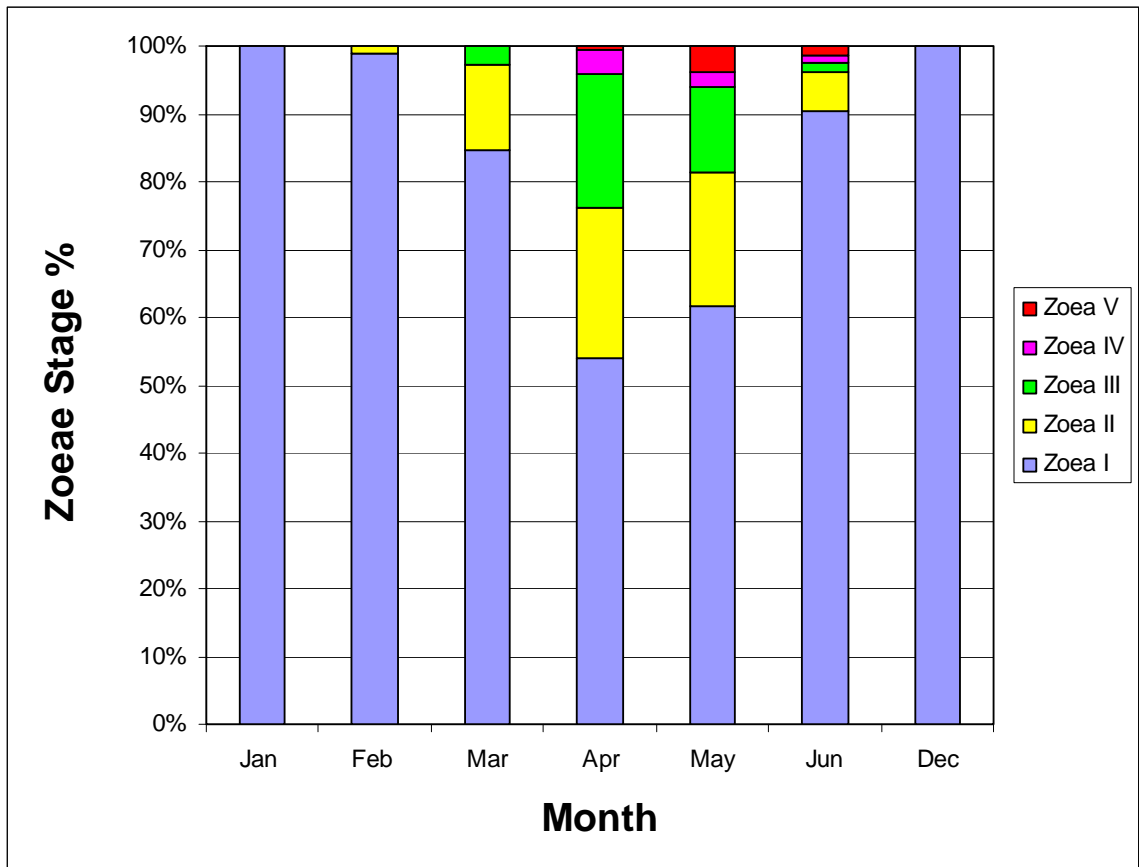


Figure 7. *Eriocheir sinensis* zoeae stages (cumulative %) identified December – June, from CDFG zooplankton samples from San Pablo Bay, 1998 – 2004.

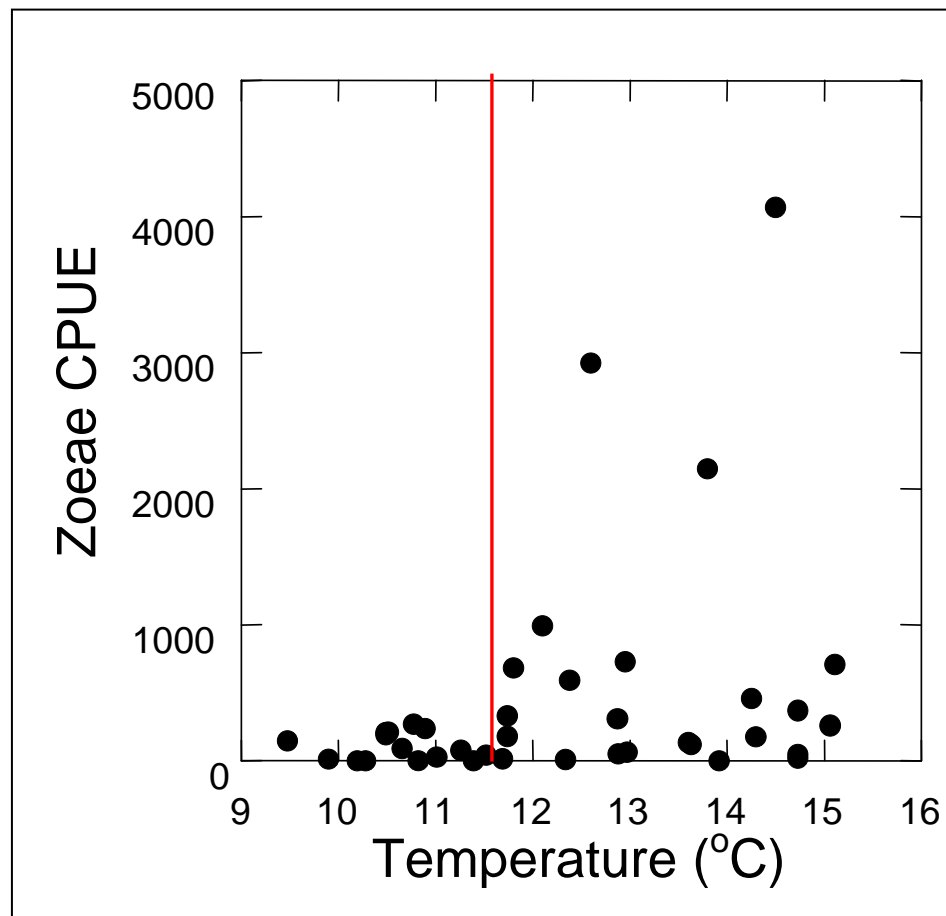


Figure 8. *Eriocheir sinensis* monthly zoeae densities (Dec. – Apr.) vs. temperature recorded from the USGS continuous monitoring gauge at PSP. Analysis of zoeae densities found a significant difference between means above and below 11.7°C using a *t*-test ($P < 0.04$), which suggests that 11.7°C may be a thermal tolerance threshold.

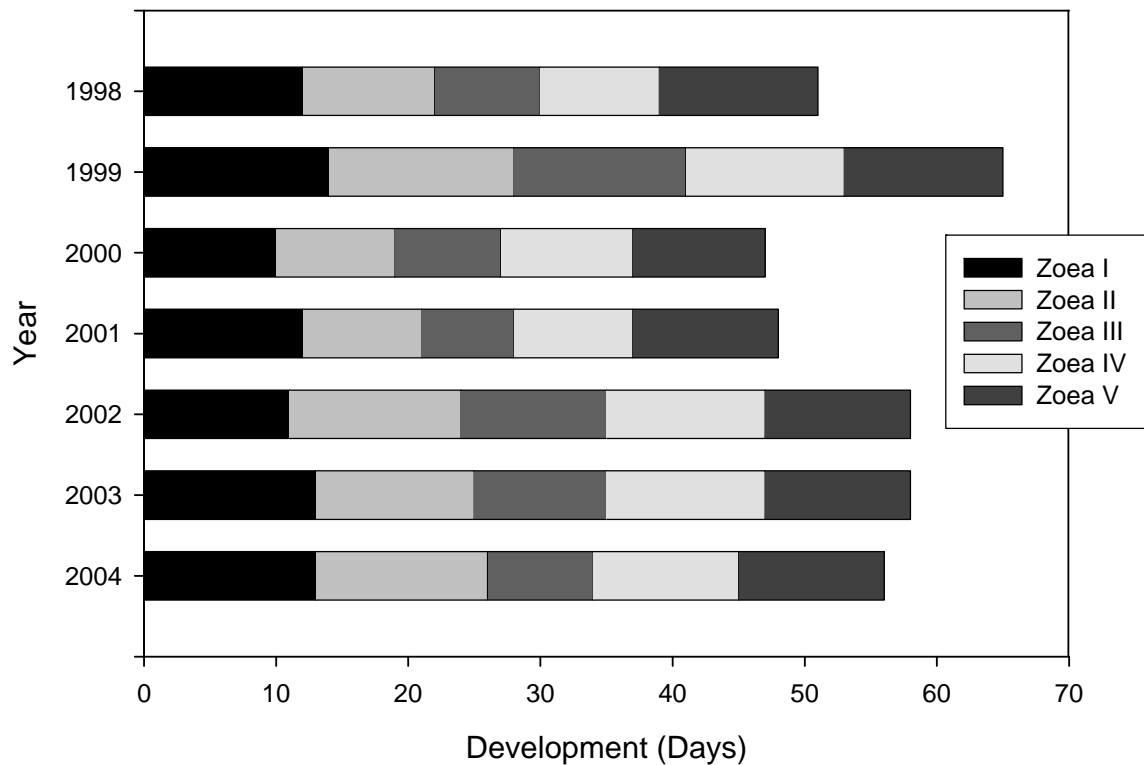


Figure 9. Developmental duration of *Eriocheir sinensis* zoeae I – V, 1998 – 2004. Stage duration was calculated using exponential regression equations and daily average water temperatures from San Pablo Bay.

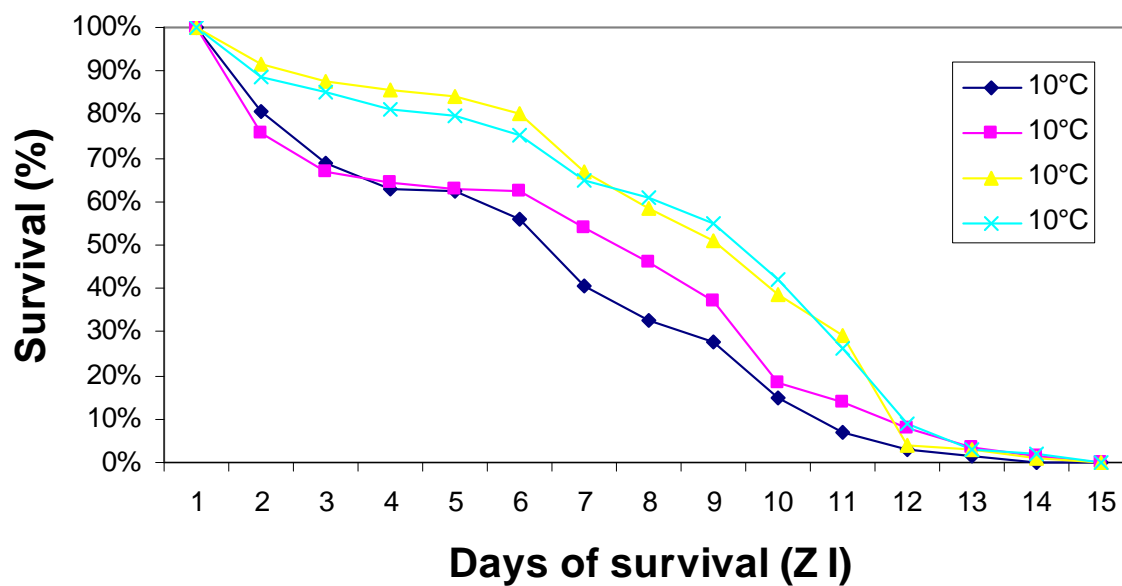


Figure 10. Survival (cumulative %; initial n = 50) of *Eriocheir sinensis* zoeae in relation to temperature (°C) at 20‰; complete mortality occurred at 10°C during zoeal stage I.

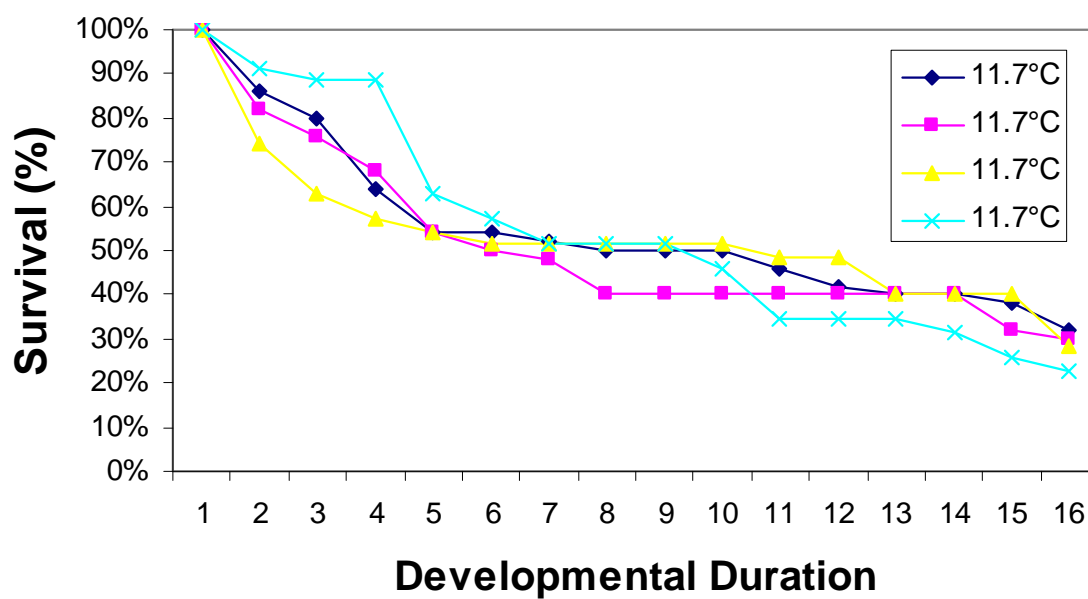


Figure 11. Survival (cumulative %; initial n = 50) of *Eriocheir sinensis* zoeae in relation to temperature ($^{\circ}\text{C}$) at 20‰; 33.9% survivorship at 11.7 $^{\circ}\text{C}$ after zoeal stage I. Duration of stage I was 15 days.

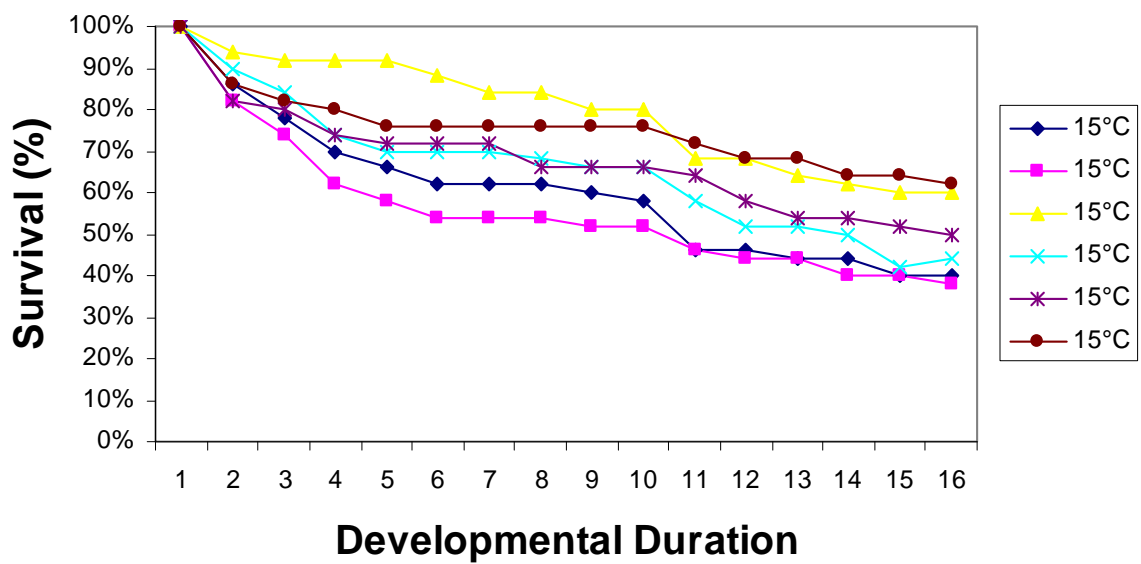


Figure 12. Survival (cumulative %; initial n = 50) of *Eriocheir sinensis* zoeae in relation to temperature ($^{\circ}\text{C}$) at 20‰; 68.3% survivorship at 15°C after zoeal stage I and 49.6% after stage II. Duration of stage I was 8 days, and stage II was 7 days.

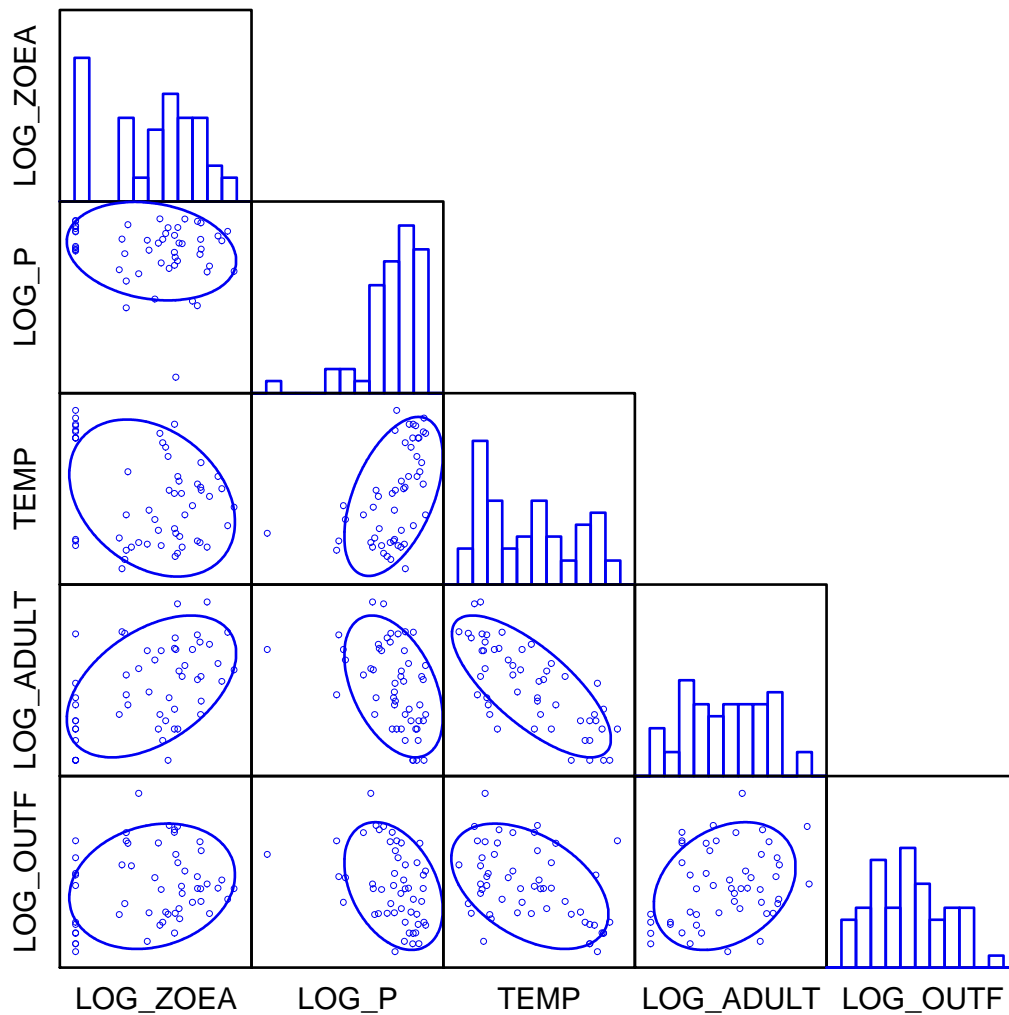


Figure 13. Multiple correlations between physical and biological variables in San Pablo Bay from December – June, 1998 – 2004. Pearson Correlation detected significant relationships between zoeae density and adult CPUE ($p < 0.01$; $r = 0.465$), and zoeae density and temperature ($p < 0.05$; $r = 0.304$); there was not a significant relationship detected between zoeae density and planktivore CPUE ($p = 0.173$; $r = 0.194$), or zoeae density and freshwater outflow ($p = 0.183$; $r = 0.182$). A significant relationship exists between planktivores and freshwater outflow ($p < 0.01$; $r = -0.375$).

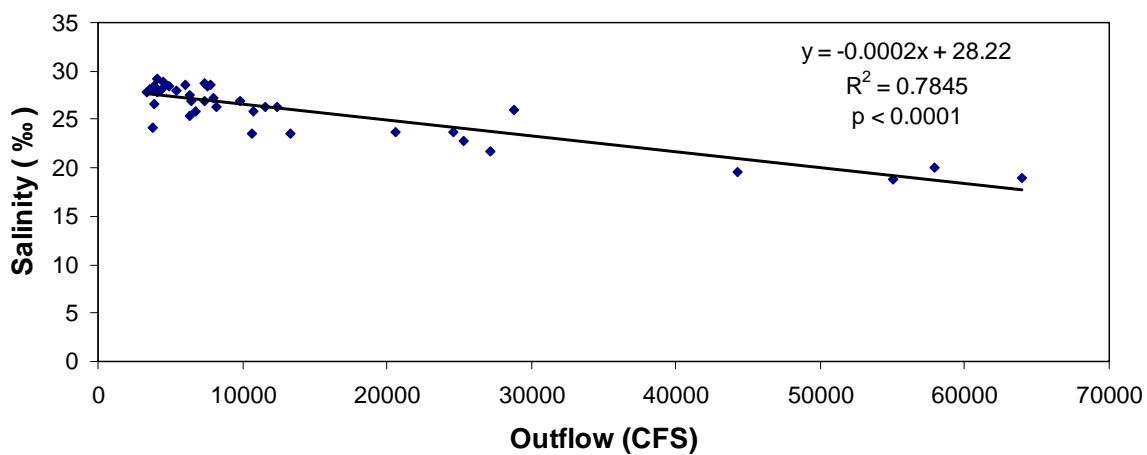


Figure 14. Regression between monthly average salinity (‰) and outflow measured at the confluence of the Sacramento-San Joaquin Rivers. A significant relationship was detected with regression ($p < 0.0001$; $r^2 = 0.7845$).

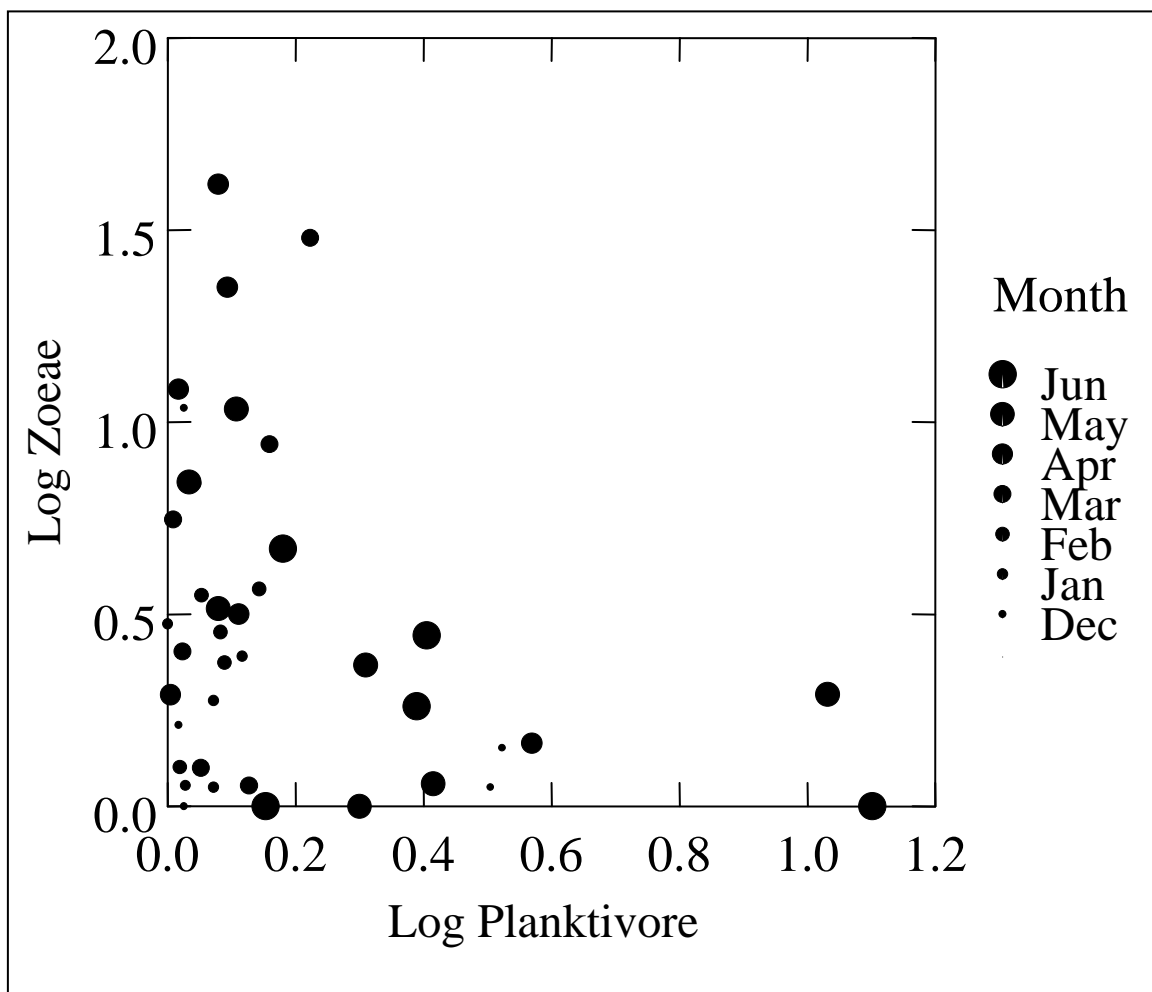


Figure 15. Correlation between *Eriocheir sinensis* zoeae density (log) and planktivores (log) in San Pablo Bay (November – June), 1998 – 2004. No significant correlation was found ($r = 0.051$).

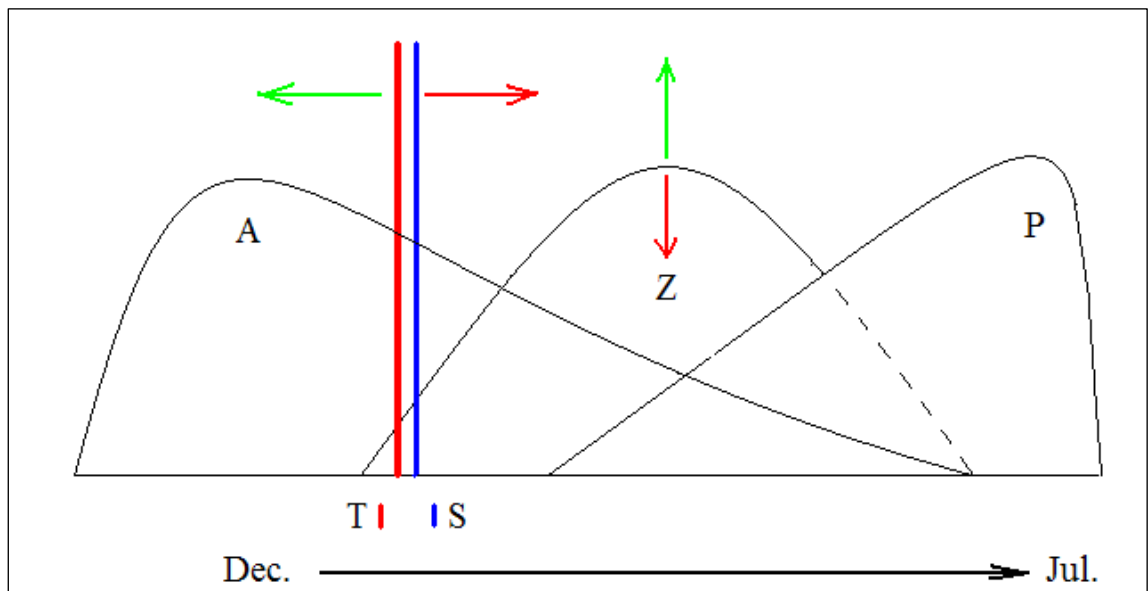


Figure 16. Model for zoeae recruitment. The number of adults that will contribute to the supply of larvae each year will depend on the number of adult crabs present when temperature (T) and salinity (S) thresholds occur. When temperature (T) and salinity (S) occur early in the season (green arrow, left) more adults (A) will contribute to the larval supply, and the zoeae density (Z) will increase (green arrow, up). When temperature and salinity occur late in the season (red arrow, right) fewer adults will contribute to the larval supply, and the zoeae density will decrease (red arrow, down). Planktivores (P) that arrive later in the recruitment period will create predation pressure for the zoeae that remain in the system, and thus bringing an end to the recruitment period.

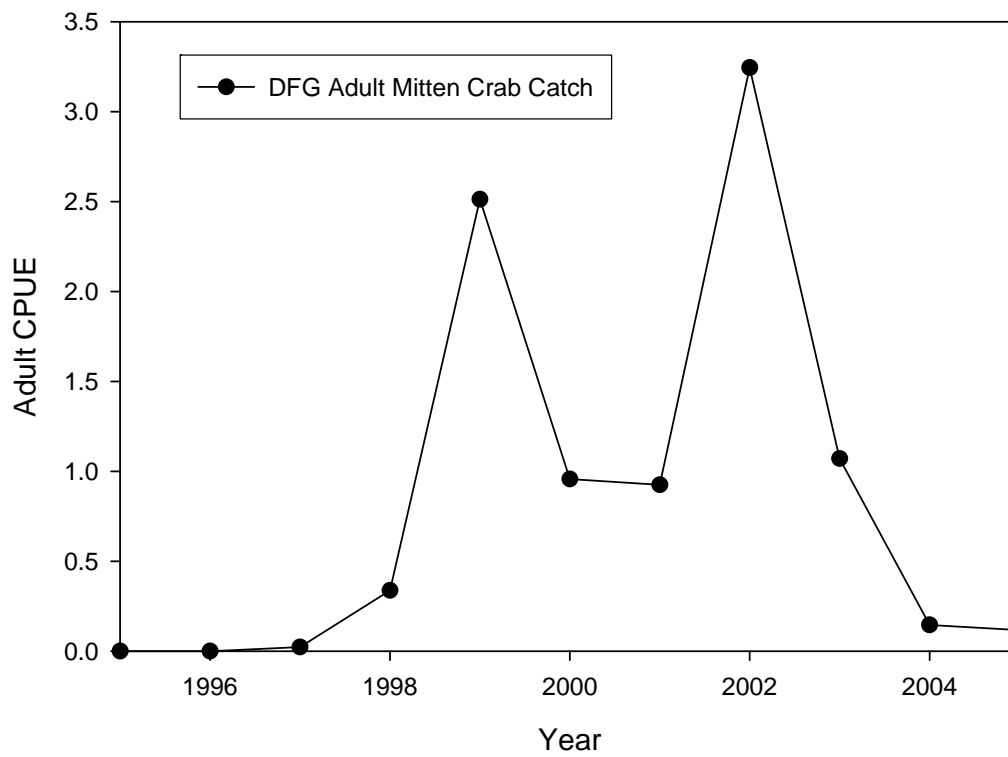


Figure 17. *Eriocheir sinensis* adult CPUE in San Francisco Bay, 1996 – 2005. Populations have the potential to rapidly achieve large abundances which has created an ecological concern. Population explosions have occurred in San Francisco Bay in 1999 and 2002.

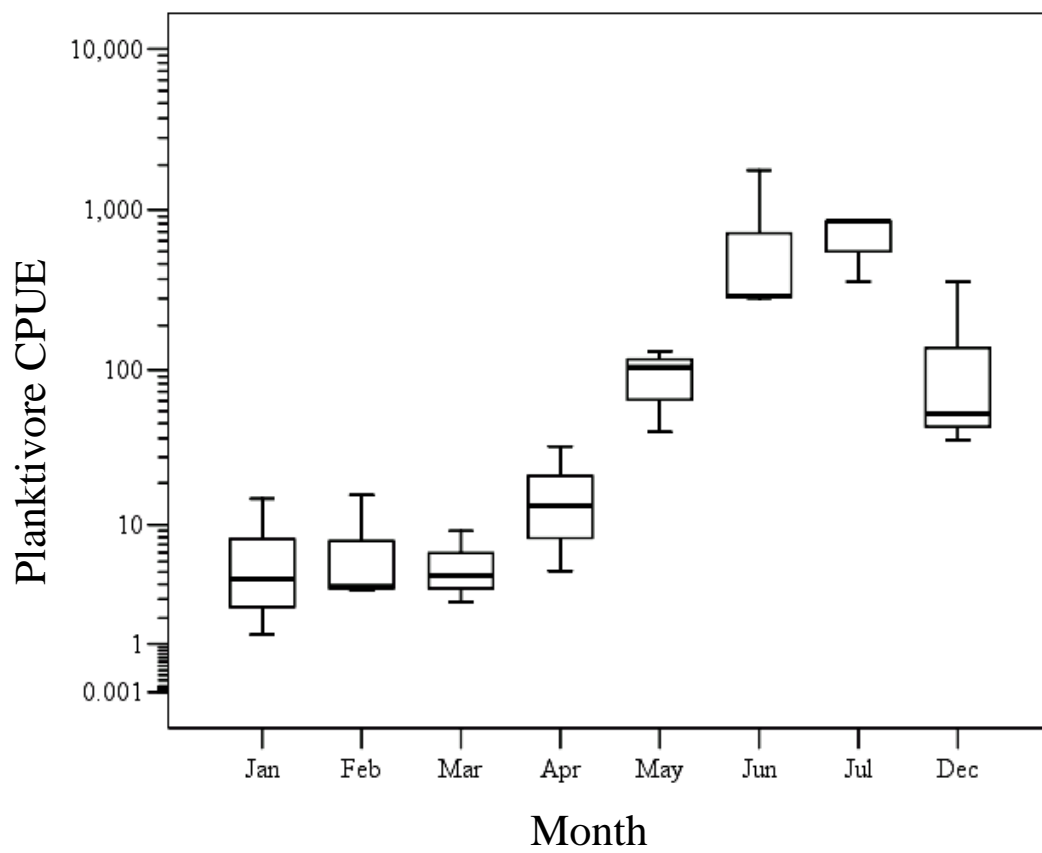


Figure 18. Planktivore CPUE during the mitten crab reproductive season (December – July), in San Pablo Bay, 1998-2004.

APPENDIX B
TABLES

Table 1. CDFG fish species surveyed monthly in San Pablo Bay. The ten most abundant planktivorous fish in decreasing total catch, and categories of estuarine use.

Common Name	Scientific Name	Estuarine Use
northern anchovy	<i>Engraulis mordax</i>	Opportunist
longfin smelt	<i>Spirinchus thaleichthys</i>	Anadromous
jacksmelt	<i>Atherinopsis californiensis</i>	Obligate Nursery
topsmelt	<i>Atherinops affinis</i>	Resident
chinook salmon	<i>Oncorhynchus tshawytscha</i>	Anadromous
threadfin shad	<i>Dorosoma petenense</i>	Opportunist
delta smelt	<i>Hypomesus transpacificus</i>	Resident
Pacific sardine	<i>Sardinops sagax</i>	Opportunist
Pacific pompano	<i>Paprilus simillimus</i>	Opportunist
California grunion	<i>Leuresthes tenuis</i>	Opportunist

Table 2. Species included in the dichotomous key to brachyuran zoeae of San Francisco Bay Estuary.

Name of Species	Reference for Larval Description
<i>Cancer antennarius</i>	Roesijadi, 1976
<i>Cancer gracilis</i>	Ally, 1975
<i>Cancer magister</i>	Poole, 1966
<i>Cancer productus</i>	Trask, 1970
<i>Carcinus maenas</i>	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
<i>Pachygrapsus crassipes</i>	Schlotterbeck, 1976
Pinnotheridae	Hart, 1935
<i>Pyromaia tuberculata</i>	Fransozo and Negreiros-Fransozo, 1997
<i>Rhithropanopeus harrisi</i>	Connolly, 1925

Table 3. *Eriocheir sinensis* zoeae developmental duration (D, in days) expressed as an exponential function of temperature (T in °C). D: developmental duration (days); a: constant; b: regression coefficient; r: correlation coefficient; T: water temperature (°C).

20‰: $D = a * e^{(b * T)}$			
	a	b	r
Zoea I	69.7	-0.144	-0.992
Zoea II	125.0	-0.144	-0.999
Zoea III	90.5	-0.165	-0.999
Zoea IV	86.9	-0.144	-0.999
Zoea V	32.3	-0.078	-0.928

Table 4. Dates when water conditions reached temperature and salinity thresholds for zoeae survival in San Pablo Bay.

Date	Temperature	Date	Salinity
3/1/1998	11.7°C	3/7/1998	10‰
3/4/1999	11.7°C	3/11/1999	10‰
3/10/2000	11.7°C	3/28/2000	10‰
2/28/2001	11.8°C	2001	10+‰
2/20/2002	11.7°C	2002	20+‰
2/7/2003	11.7°C	2/8/2003	10‰
2/17/2004	11.9°C	2004	10+‰

APPENDIX C

A KEY TO BRACHYURAN ZOEAE OF THE SAN FRANCISCO
BAY ESTUARY

1A. Telson above the furca is two times the length of the fifth abdominal segment (Appendix C, Fig. 1a) or fifth abdominal segment flared (Appendix C, Fig. 1b).

Carapace may be with or without lateral spines. If lateral spines are present, form a tripod with rostral spine (Hart, 1935).....
 Pinnotheridae (Appendix C, Fig. 1c, d).

1B. Telson length above the furca is equal to or lesser than the length of the fifth abdominal segment (Appendix C, Fig. 7a).....2

2A. Length of the antenna is equal to the length of the rostral spine (Appendix C, Fig. 2a, 3a).....3

2B. Length of the antenna is shorter than the length of the rostral spine (Appendix C, Fig. 8b), or the rostral spine is absent (Appendix C, Fig. 9a).....4

3A. Dorsal and rostral spines are equal in length (Appendix C, Fig. 2a, b).

Carapace with dorsal, rostral, and lateral spines present and smooth. Antennule conical, with two long aesthetes and three setae. In the first zoeal stage: first maxilliped endopodite is five segmented with one, two, one, two and five setae; exopodite with four plumose natatory setae at the tip. Second maxilliped endopodite is three segmented with one, two and three setae; exopodite with four natatory setae. Abdomen composed of five segments plus a telson, segments two and three with small lateral spines. Abdominal segments three, four and five with posterior lateral extensions. Telson bifurcated with two very small lateral spines and one dorsal spine on each fork, and three barbed spines on posterior margin of each furca (Knudsen, 1959) (Appendix C, Fig. 2c).....
*Lophopanopeus bellus*.

3B. Rostral spine two times the length of the dorsal spine (Appendix C, Fig. 3a).

Length of antenna is equal to rostral spine. Carapace with dorsal, rostral, and lateral spines present. First and second maxilliped exopodites with four

plumose setae. Abdomen composed of five segments plus a telson. Second abdominal segment with small lateral spines. Abdominal segment four with shorter posterior lateral extensions, and segment five with long posterior lateral extensions. Telson bifurcated, each fork with one dorsal spine, telson lateral spines absent, and three spines on posterior margin (Connolly, 1925) (Appendix C, Fig. 3b).....*Rhithropanopeus harrisi*.
 4A. Telson lateral spines absent (Appendix C, Fig. 5a).....5
 4B. Telson lateral spines present (Appendix C, Fig. 11a).....8
 5A. Abdominal segment 4 with lateral spines present (Appendix C, Fig. 5a).....6
 5B. Abdominal segment 4 without small lateral spines (Appendix C, Fig. 6a).....7
 6A. Telson with a large knob on midventral surface (Appendix C, Fig. 4a), no exospines, and three barbed spines on posterior margin of each fork.

Carapace lateral spines are absent during zoea stage I, stages II-V with carapace lateral spines present. Dorsal and rostral spines are equal in length. Antennule conical and smooth with two long aesthetes and one long seta. Antenna is uniramous with exopodite absent. In first zoeal stage: first maxilliped with four pairs of setae on the protopodite; endopodite five segmented with one, two, one, two and five setae; exopodite with four natatory setae on tip. Second maxilliped protopodite with four setae; endopodite three segmented, second segment with one seta, one barbed spine, and two plumose setae, and third segment with two short bare setae; exopodite with four natatory setae on the tip. Abdomen composed of five segments plus a telson. Abdominal segments two, three and four have small lateral spines. Segments three, four and five with posterior lateral extensions (Schlotterbeck, 1976) (Appendix C, Fig. 4b).....*Pachygrapsus crassipes*.
 6B. Midventral surface of telson without knob.

Carapace with dorsal, ventral, and lateral spines present (Appendix C, Fig. 5b, c). Carapace dorsal spine is longer than rostral spine; all spines covered with small spinules. Antennule conical and narrow, with three esthetes and two setae at the tip. In the first zoeal stage: first maxilliped with six setae on protopodite; endopodite five segmented with one, one, two, two and five setae; exopodite with four natatory setae. Second maxilliped with three slightly plumose setae on protopodite; endopodite three segmented with zero, one and five slightly plumose setae; exopodite with four natatory setae. Abdominal segments two, three and four with small lateral spines (Appendix C, Fig. 5a). Abdominal segment five with posterior lateral extensions, which overlap the telson. The telson is bifurcated with no exospines, and three barbed spines on posterior margin. Zoea V abdominal segments two, three, four, and five with posterior lateral extensions (Montu et al., 1996).....*Eriocheir sinensis*.

7A. Second abdominal segment with lateral spines and smaller pair on the third abdominal segment (Appendix C, Fig. 6a).

Carapace with dorsal, rostral, and lateral spines present (Appendix C, Fig. 6b, c). Antennule conical with two aesthetes and one seta at the tip. In the first zoeal stage: first maxilliped with nine setae on protopodite; endopodite five segmented with two, two, one, two and five setae; exopodite with four natatory setae. Second maxilliped with four setae on protopodite; endopodite with zero, one and six setae; exopodite with four natatory setae. Abdomen composed of five segments plus a telson. Telson bifurcated, no lateral spines, and each furca with three barbed spines on posterior margin (Hart, 1935).....*Hemigrapsus nudus*.

7B. Third abdominal segment without lateral spines (Appendix C, Fig. 7a).

Carapace with dorsal, rostral, and lateral spines present (Appendix C, Fig. 6b, c). Antennule conical with two aesthetes and one seta at the tip. In the

- first zoeal stage: first maxilliped with nine setae on protopodite; endopodite five segmented with two, two, one, two and five setae; exopodite with four natatory setae. Second maxilliped with four setae on protopodite; endopodite with zero, one and six setae; exopodite with four natatory setae. Abdomen composed of five segments plus a telson. Telson bifurcated, no lateral spines, and each furca with three barbed spines on posterior margin (Hart, 1935).....
-*Hemigrapsus oregonensis* (Appendix C, Fig. 7b, c).
- 8A. Carapace lateral spines absent (Appendix C, Fig. 8a).....9
- 8B. Carapace lateral spines present (Appendix C, Fig. 10b).....10
- 9A. Carapace with dorsal and rostral spines only (Appendix C, Fig. 8a, b).

Antennule with two aesthetes and two setae at the tip. In the first zoeal stage: first maxilliped protopodite with 8 or 9 medial setae; endopodite five segmented with two, two, one, two and five setae; exopodite with four natatory setae on tip. Second maxilliped propodite with four medial setae; endopodite three segmented with one, one and five setae; exopodite with four natatory setae on tip. Abdomen composed of five segments plus a telson, second segment with small lateral spines. Telson bifurcated, each furca with one large and one small dorsal spine, one thin lateral spine, and three barbed spines on posterior margin (Rice and Ingle, 1975) (Appendix C, Fig. 8c).....*Carcinus maenas*.

9B. Carapace with only the dorsal spine present and long antennae (Appendix C, Fig. 9a, b).

Antennule roughly conical, with three aesthetes and one seta at the tip. In the first zoeal stage: first maxilliped with eight plumose setae on the inner margin of the protopodite; endopodite composed of five segments with three, two, one, two and five plumose setae; exopodite composed of two segments with four natatory setae at the tip. Second maxilliped protopodite with four plumose setae

on the inner margin; endopodite is three segmented with zero, one and four plumose setae; exopodite two segmented, with four natatory setae on the tip. Abdomen composed of five segments, second segment with small lateral spines. Telson bifurcated, each furca with one dorsal spine, and three barbed spines on posterior margin (Fransozo and Negreiros-Fransozo, 1997) (Appendix C, Fig. 9c).....*Pyromaia tuberculata*.

10A. Telson lateral spines approximately $\frac{1}{2}$ length of furca (Appendix C, Fig. 10a).....11

10B. Telson lateral spines approximately $\frac{1}{5}$ length of furca (Appendix C, Fig. 11a).....12

11A. Telson lateral spines approximately at a right angle to the outer margin of the furca, lateral spines are $\frac{1}{2}$ length of furca, telson dorsal spines present, and each furca with three barbed spines on posterior margin.

Carapace with dorsal, rostral, and lateral spines present. The dorsal and rostral spines are equal in length. Antennule with two aesthetes and one seta on the tip. In the first zoeal stage: first maxilliped endopodite composed of five segments with three, two, one, two and five setae; exopodite with four natatory setae on tip. Second maxilliped endopodite composed of three segments with one, one and five setae; exopodite with four natatory setae on the tip. Abdomen composed of five segments, second abdominal segment with one pair of small lateral spines. All abdominal segments with posterior lateral extensions (Poole, 1966).....*Cancer magister*.

11B. Telson lateral spines form a 45 degree angle with furca, telson dorsal spines present, and each furca with three barbed spines on posterior margin (Appendix C, Fig. 10a).

Carapace with dorsal, rostral, and lateral spines present. Dorsal and rostral spines are approximately equal in length. Antennule with three setae on the tip. In the first zoeal stage: first maxilliped endopodite composed of five segments with three, two, one, two and five setae; exopodite with four natatory setae on the tip. Second maxilliped endopodite composed of three segments with one, one and five setae; exopodite with four natatory setae on the tip. Abdomen composed of five segments, second abdominal segment with small lateral spines, and all segments with posterior lateral extensions (Trask, 1970).....
*Cancer productus* (Appendix C, Fig. 10b, c).

12. *Cancer antennarius* and *Cancer gracilis* are very similar in appearance and can be identified by size at each larval stage.

12A. Length from tip of the telson to tip of the rostrum at each zoea stage is as follows: Zoea I) 1.8 mm; Zoea II) 2.0 mm; Zoea III) 2.3 mm; Zoea IV) 3.1; Zoea V) 4.4 mm.

Carapace with dorsal, rostral, and lateral spines present. Dorsal and rostral spines are equal in length. Antennule with two long and two short setae. In the first zoeal stage: first maxilliped endopodite composed of five segments with two, two, one, two and five setae; exopodite with four natatory setae on the tip. Second maxilliped endopodite composed of three segments with one, one and five setae; exopodite with four natatory setae on tip. Abdomen composed of five segments, second abdominal segment with small lateral spines, and segments three, four and five with posterior lateral extensions. Telson with lateral and dorsal spines, each is approximately 1/5 length of the furca, and three barbed spines on posterior margin of furca (Roesijadi, 1976) (Appendix C, Fig. 11a).....
*Cancer antennarius* (Appendix C, Fig. 11b, c).

12B. Length from tip of the telson to tip of the rostrum at each zoea stage is as follows: Zoea I) 1.1 mm; Zoea II) 1.5 mm; Zoea III) 1.9 mm; Zoea IV) 2.5 mm; Zoea V) 3.3 mm.

Carapace with dorsal, rostral, and lateral spines present. Dorsal and rostral spines are equal in length. Antennule with two long unequal aesthetes, and three shorter unequal setae. In the first zoeal stage: first maxilliped endopodite composed of five segments with two, two, one, two and five setae; exopodite with four natatory setae on tip. Second maxilliped endopodite composed of three segments with one, one, and five setae; exopodite with four natatory setae on the tip. Abdomen composed of five segments, second abdominal segment with small lateral spines, and segments three, four and five with posterior lateral extensions. Telson with lateral and dorsal spines, each is approximately $1/5$ length of the furca, and three barbed spines on posterior margin of furca (Ally, 1975) (Appendix C, Fig. 11a).....*Cancer gracilis* (Appendix C, Fig. 11b, c).

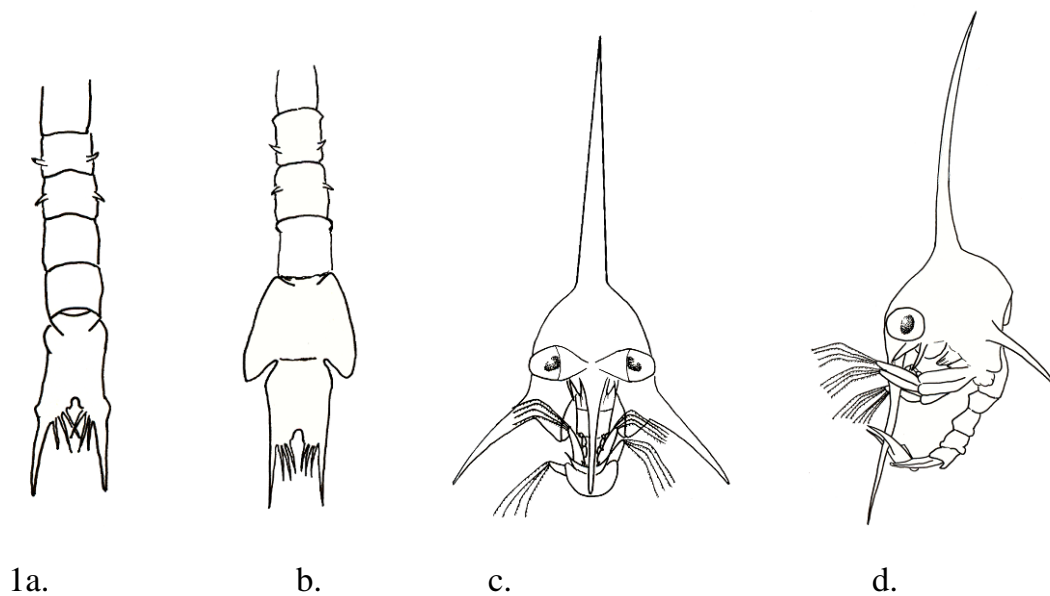


Figure 1. Pinnotheridae, zoeal stage I, a. abdomen dorsal view; b. abdomen dorsal view; c. anterior view of whole body; d. lateral view of whole body.

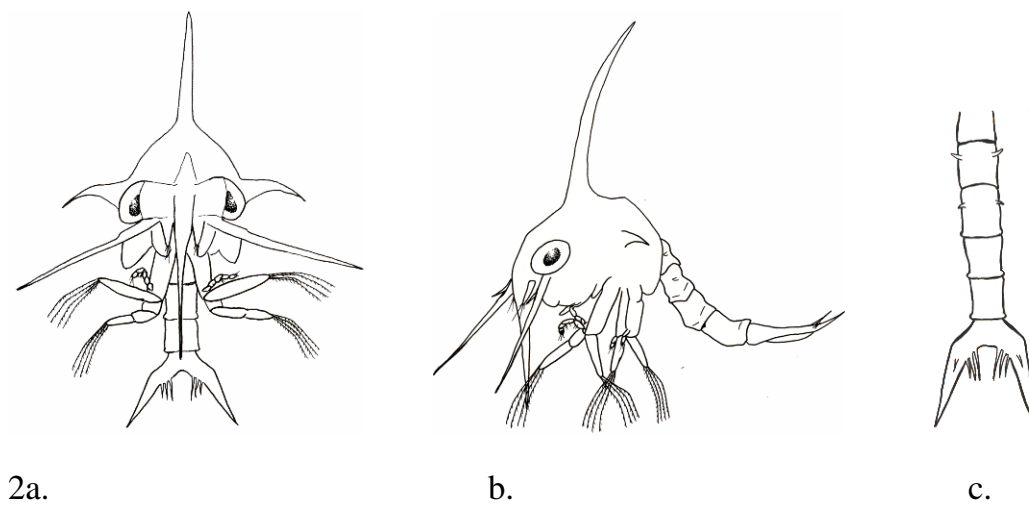


Figure 2. *Lophopanopeus bellus* Rathbun, zoeal stage I, a. anterior view of whole body; b. lateral view of whole body; c. abdomen dorsal view.

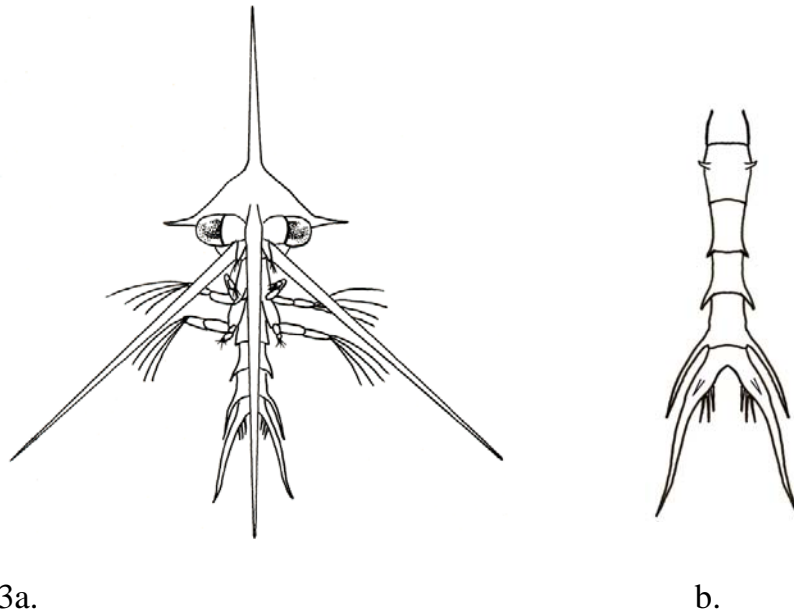


Figure 3. *Rithropanopeus harrisi* Gould, zoeal stage I, a. anterior view of whole body; b. abdomen dorsal view.

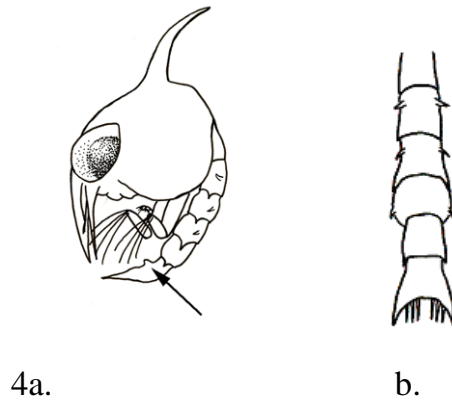


Figure 4. *Pachygrapsus crassipes* Randall, zoeal stage I, a. lateral view of whole body; b. abdomen dorsal view.

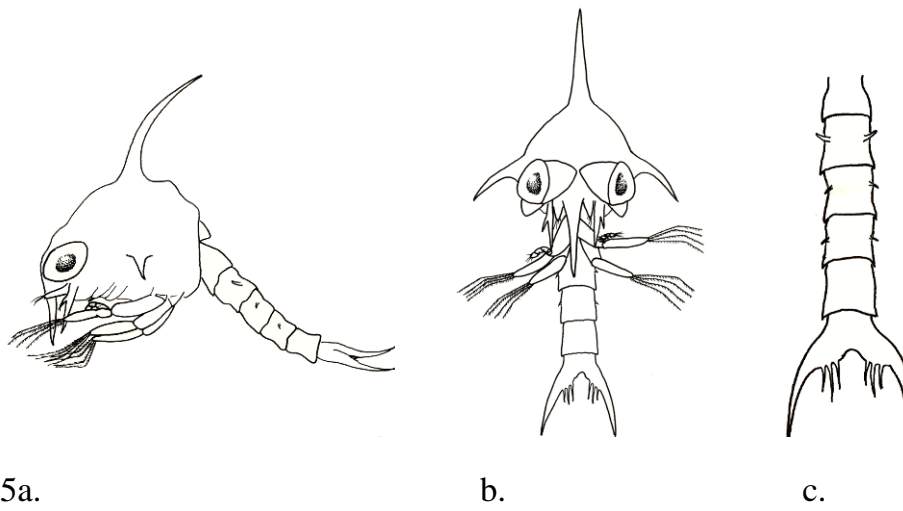


Figure 5. *Eriocheir sinensis* Milne-Edwards, zoeal stage I, a. lateral view of whole body; b. anterior view of whole body; c. abdomen dorsal view.

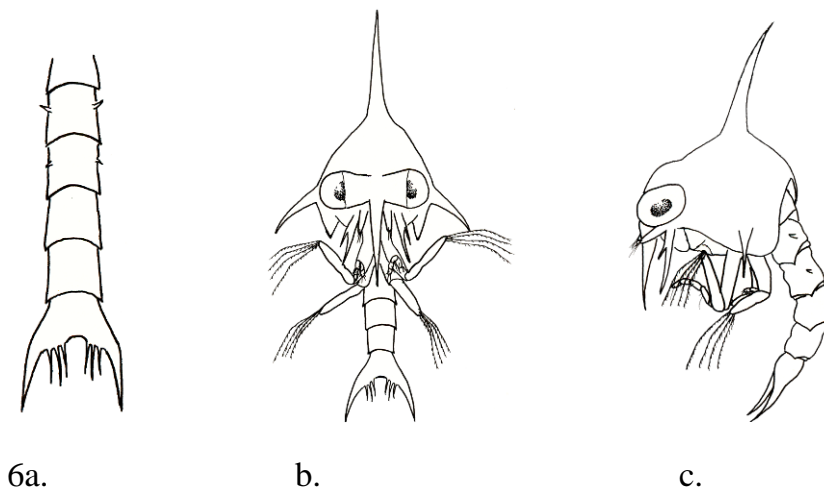


Figure 6. *Hemigrapsus nudus* Dana, zoeal stage I, a. abdomen dorsal view; b. anterior view of whole body; c. lateral view of whole body.

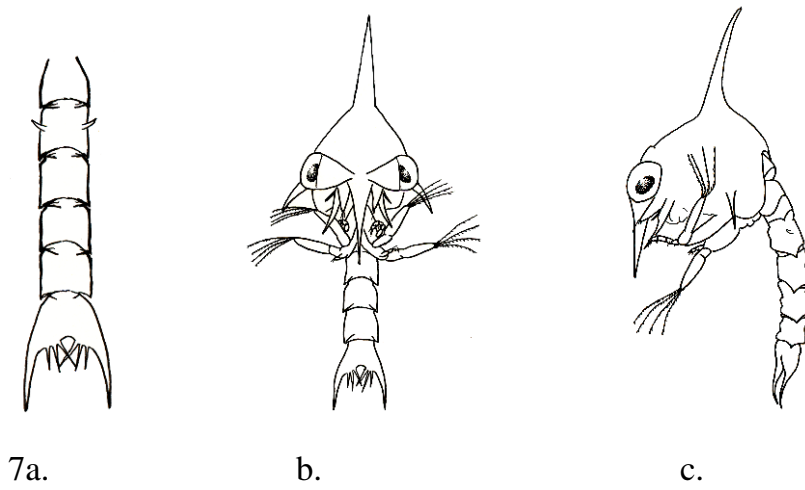


Figure 7. *Hemigrapsus oregonensis* Dana, zoeal stage I, a. abdomen dorsal view; b. anterior view of whole body; c. lateral view of whole body.

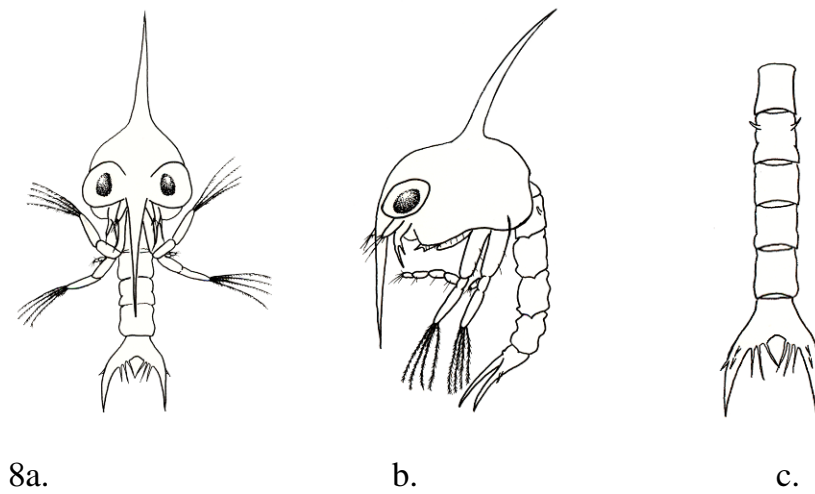


Figure 8. *Carcinus maenas* Linnaeus, zoeal stage I, a. anterior view of whole body; b. lateral view of whole body; c. abdomen dorsal view.

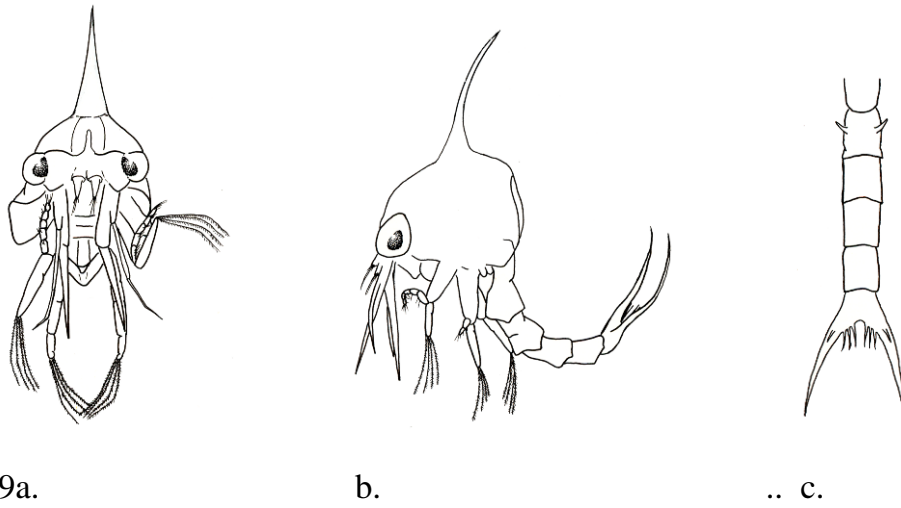


Figure 9. *Pyromaia tuberculata* Lockington, zoeal stage I, a. anterior view of whole body; b. lateral view of whole body; c. abdomen dorsal view.

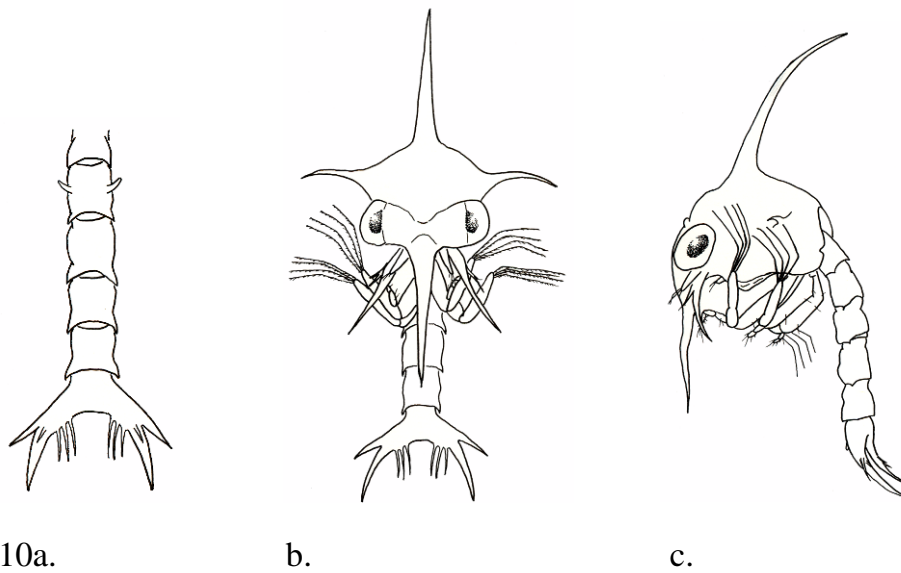


Figure 10. *Cancer productus* Randall 1839, zoeal stage I, a. abdomen dorsal view; b. anterior view of whole body; c. lateral view of whole body.

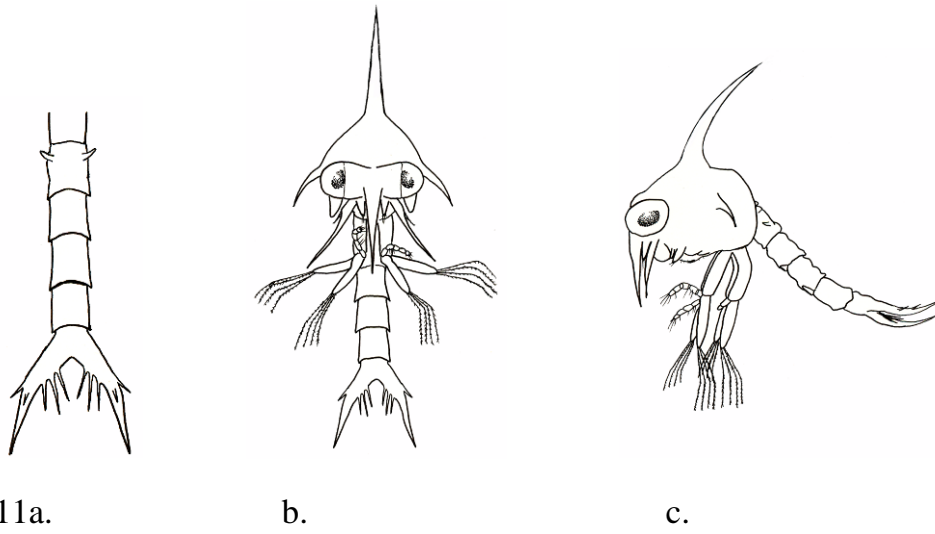


Figure 11. *Cancer antennarius* Stimpson, and *Cancer gracilis* Dana, zoeal stage I, a. abdomen dorsal view; b. anterior view of whole body; c. lateral view of whole body.