Final Report

The Potential for Mitten Crab Colonization of Estuaries on the West Coast of North America

Prepared for

Pacific States Marine Fisheries Commission

and
Alaska Department of Fish and Game

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April 2005

Executive Summary

Mitten crabs (*Eriocheir spp.)* are invasive species that pose a risk to the aquatic environments of the Pacific Northwest and the economic and social activities that depend upon intact aquatic systems. The recent establishment of a large population in the San Francisco Bay and the potential for introductions from California, Asia and Europe pose a significant invasion potential for estuaries and rivers from California to Alaska.

The Lacey Act lists mitten crabs as injurious species and California, Oregon, Washington and Alaska have recognized mitten crabs as invasive species. Mitten crabs exhibit many traits associated with invasive species. They are abundant and widely distributed in their native and introduced range, with a high reproductive capacity and a short generation time. Their invasiveness is facilitated by an adult stage that rears in brackish to freshwater and a larval stage that occurs in estuarine and near ocean habitat. The larvae are easily dispersed in ballast water and the adults have a broad diet, wide environmental tolerances and a broad range of habitat.

Mitten crab life history, habitat requirements and environmental tolerances suggest that estuaries with limited salinity intrusion and short flushing rates have a reduced risk of population establishment. Large, stable estuaries, such as the Puget Sound, may support large populations. Large estuaries provide adequate temperature and salinity regimes for optimal larval survival and flushing times of sufficient duration for development within the estuary. One estuary, Coos Bay, has a flushing time similar to estuaries with mitten crabs but below the threshold required for larval development within the Bay. Small or river-dominated estuaries, such as the Columbia River, have salinities below the threshold for larval development or have flushing times less than the duration of larval development.

The northern extent of a potential mitten crab population is likely to be limited by low water temperatures. Most estuary systems in Alaska have sufficient estuarine and freshwater habitat, but limited periods where water temperatures are above the mortality threshold for the larval stages and are at a low risk for the establishment of populations.

Few estuaries in the PNW are likely to develop large mitten crab populations and experience a significant impact on native species and habitat. If ongoing research demonstrates that mitten

crabs exhibit vertical migration behavior (which facilitates larval return to adult habitat), populations could develop in some of the smaller estuaries with moderate salinity intrusions and flushing times.

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Introduction

Mitten crabs, *Eriocheir spp.*, are catadromous species that could potentially invade estuary-river coupled systems from California to Alaska and impact their ecological functions and economic and human uses. Mitten crabs exhibit many of the traits associated with invasive species. They are abundant and widely distributed in their native and introduced range, have a high reproductive capacity and a short generation time (Ehrlich, 1986). The larval stage is easily dispersed through ballast water and the adult stage has the ability to utilize a broad range of habitats, a broad diet and wide environmental tolerances. The recent establishment of a large population of *E. sinensis* in the San Francisco Bay and the potential for unintentional and intentional introductions from California, Asia, and Europe pose a significant invasion risk to other west coast estuaries.

Policymakers recognize the invasion potential of mitten crabs and regulate their intentional introduction. The Federal Lacey Act recognizes mitten crabs as injurious and bans their importation and interstate transport (USFWS 1989). California (Section 671, Title 14), Oregon (OAR 635-056-0050,OAR 635-056-000), and Washington (WAC 220-12-090) recognize the mitten crabs invasion potential and ban its importation and sale. The interception of shipments of mitten crabs destined for illegal markets demonstrates that live mitten crabs are being transported across the United States (Cohen and Carlton, 1997).

Mitten crabs have a large indigenous range. *E. sinensis* is native to the Yellow Sea region in a latitude range of 24 to 42 ^{o} North, from Hong Kong, China to the Yalu River in South Korea (Hymanson et al. 1999, Panning, 1939). In Europe, the latitude range is ten degrees greater, from 36 to 55^{o} North. This latitude range in North America covers a region from Monterey Bay, California to Northern British Columbia. The current latitudinal range of mitten crabs is a function of environmental conditions, available habitat, and interaction with other species. Estuaries and rivers in the Pacific Northwest (PNW) and Alaska face an invasion potential if they meet the habitat and environmental requirements of the mitten crab.

Invasion History

The mitten crab invasion of the San Francisco Bay and Sacramento-San Joaquin River Delta (Bay-Delta) system and Europe illustrates the potential impact and invasion potential for the PNW. In California, the population size and range increased greatly from 1992 to 2000. Mitten crabs now occupy hundreds of miles of rivers, streams, canals, and wetlands where they interfere with recreational and commercial fishing, fish salvage operations, and damage stream and canal banks and levees (Rudnick et al., 2003, CMCWG, 2003).

The Chinese mitten crab was first reported in southern San Francisco Bay by shrimp trawlers in 1992 (Hieb, 1997). In 1996, several dozen mitten crabs were caught at the U.S. Bureau of Reclamation (USBR) Tracy Fish Collection Facility (TFCF). The number of crabs increased to tens of thousands in 1997 and to over 775,000 crabs in 1998, which disrupted TFCF salvage operations (Siegfried, 1999). In 1998, the combined daily crab count for the State and Federal water diversion projects in Tracy, California facilities peaked at 51,292 crabs per day in late September. Currently, mitten crabs are found up to 50 kilometers (km) upstream from the San Francisco Bay (Rudnick et al., 2003). Mitten crabs may eventually populate all waterways connected to the Bay-Delta and colonize most estuary-river systems in California (CMCWG, 2003).

The San Francisco Bay population is the only confirmed population of mitten crabs along the West Coast of North America. A single Japanese mitten crab (*Eriocheir japonica*) was collected in the Columbia River in 1997. Sightings have been reported in the Coos and Yaquina bays in Oregon but these sightings have not been confirmed. Limited surveys have been conducted for mitten crabs along the Oregon coast but no surveys have been conducted in California (outside of the San Francisco Bay) and Washington.

The Chinese mitten crab was first reported in a tributary to the Weser River in Germany in 1912 (Peters, 1933). It spread throughout Europe in two main invasive events, one in Northern Europe (ca 1910-1950) and another in Southern France (ca. 1950-1960) (Herborg, 2003). In the 1920s, 1930s, and 1940s the mitten crab population rapidly expanded and crabs were caught in Germany, Denmark, southeastern Sweden, southern Finland, Poland, the former Czechoslovakia, the Netherlands, Belgium and northern France (Peters and Panning, 1933; Peters, 1938; Panning, 1939; Wolff and Sandee, 1971; Ingle, 1986; Vincent, 1996 as cited in Herborg, 2003). The

Northern European river systems are extensive, interconnected by canals and with estuaries closely spaced along the coast. The population in southern France is considered to be the result of a separate invasion event, due to the distance (205 km) of the invaded estuary from other populations in Europe (Herborg, 2003). Populations were established in England and Portugal during the 1980's and in Spain during the 1990's (Clark, 1984; Cabral and Costa, 1999; Ferrero Rodriquez, 2001 as cited in Cohen and Weinstein, 2001). Mitten crabs have been caught in the Mediterranean, Baltic and North Sea, yet no established populations have been documented in these regions.

The spread to new estuary-river systems in Europe was mirrored by a rapid colonization of inland waters (Figure 1). By the mid 1930s (~20 year after initial discovery), the mitten crab had migrated inland 700 km in the Elbe River watershed to Prague in the Czech Republic, 512 km along the Rhine River and 464 km in the Oder River to Breslau (Herborg, 2003).

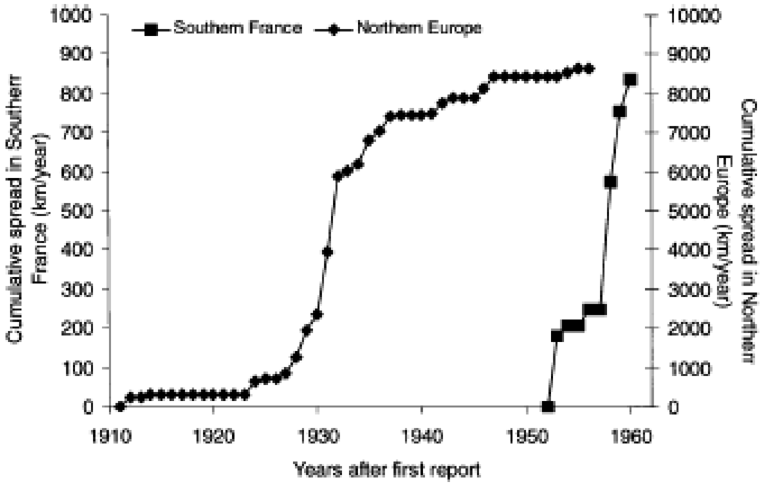

Figure 1. Spread of mitten crabs in Europe (from Herborg, 2003).

Impacts

The mitten crab invasion of Europe and the Bay-Delta has resulted in significant impacts on commercial and recreational activities and native species and habitat. Mitten crabs interfere with recreational and commercial fishing, water pumping and power plant stations, and flood control levees and banks. Costs to mitigate the impacts of mitten crabs can run into the millions of dollars. In 1998, peak fish mortality attributed to the crabs at the TFCF was 98-99% (Siegfried, 1998), with an estimated economic impact of over $1 million (White et al., 2000). In Germany, commercial fisheries suffered significant financial losses due to damaged catches and gear (Panning, 1939). Recreational fishing in the Bay-Delta is affected primarily through mitten crabs “stealing” bait from hooks (Rudnick & Resh, 2002). The water circulation in pumping facilities and power plants is impacted by crabs and shells clogging screens, pipes and valves. In 1997, natural gas power plants in the Delta had intermittent problems with crabs clogging water intakes (Hieb, 1998). In China and Korea, mitten crabs are reported to damage rice crops by feeding on young rice shoots (Ng, 1988).

The impact on native species and habitat has received less attention but its feeding habits and competition with other benthic scavenger species has been documented. Mitten crabs are opportunistic scavengers that primarily eat aquatic vegetation and invertebrates but will consume fish, eggs and other items if they are presented (Thiel, 1938 as cited in Panning, 1939; Tan et al., 1984, Rudnick, 2003). In tributaries to the Bay-Delta, mitten crabs consume 30-100% of their diet as invertebrates and at some locations primarily the native clam species of the genus *Pisidae* (Rogers, 2002). In the Elbe River, Germany, mitten crabs prey on native gastropods and bivalves, and possibly caused the local extinction of freshwater clams (*Sphaerium* spp). at several sites (Gollasch, 1999).

Mitten crabs alter habitat by their burrowing behavior. Burrows occur primarily in intertidal areas and occasionally in non-tidal river and stream banks. Potential impacts include increased sediment load, loss of saltmarsh habitat, bank erosion, and levee failure. The extensive burrows created by mitten crabs have been associated with river bank slumping in Germany and increased erosion and bank collapse in San Francisquito Creek, California (Panning, 1939; Johnson, 2001).

Mitten crab colonization of coastal streams in areas where salmon spawn creates an opportunity for predation on salmon eggs and fry and disturbance of salmon redds. Mitten crabs occupy salmon spawning habitat in California (Johnson, 2001 as cited in CMCWG, 2003). It is unknown if mitten crabs will actively predate on salmon eggs but laboratory research demonstrates that mitten crabs will manipulate redd material and consume buried salmon eggs (Culver pers comm. 2003). They may also feed on the demersal eggs of sturgeon.

Mitten crabs are secondary hosts for the Asian lung fluke (*Paragonimus westermani*), which can infect humans and animals (Yang et al., 2000). A recent study examined approximately eight hundred mitten crabs from locations throughout the Bay-Delta and detected no Asian lung fluke infections (Dugan et al., 2002). The same study confirmed that the primary host for the Asian lung fluke, the snail *Melanoides tuberculata*, and two likely but unconfirmed snail species occur in Bay-Delta habitats currently occupied by mitten crabs (Dugan et al., 2002).

Life History

The mitten crab's life history consists of two phases, larval (zoea and megalopae) and adult. The larvae occur primarily in lower estuary and near-ocean habitats. The adults occupy brackish and freshwater habitat with a migration to higher salinity estuarine waters for reproduction. Mitten crabs complete their life cycle over a one to five year period and normally die after one mating season.

The metamorphosis into a juvenile crab typically occurs in brackish and fresh water in the spring and summer (Rudnick et al., 2003), though it can be delayed until fall (Panning, 1939). The early juvenile crab resides in tidally influenced low salinity areas through the winter (Panning, 1939). The following Spring, juvenile mitten crabs migrate upstream to brackish and fresh water rearing areas. Mitten crabs remain in these upstream rearing areas for one to four years until they reach reproductive maturity (Jin et al., 2001, Panning, 1939). From an initial four to ten millimeters (mm) carapace width, the crabs grow to an adult size that can reach 95 mm but is typically in the 40 to 70 mm size range (Rudnick et al., 2003).

The highest densities of mitten crabs usually occur within estuaries and near river mouths but high densities have been reported as far as 90 km upstream of the mouth of the Thames River (Attrill and Thomas, 1996) and 450 km upstream of the mouth of the Elbe River (Panning, 1939). Mitten crab populations can become very large. In 1939, more than 21 million juvenile crabs were caught in the Elbe, Ems, Havel, Saale and Weser Rivers in Germany (Gollasch, 1999). The reported maximum migratory distance traveled by mitten crabs is 1000 km in China (Panning, 1939). Migration is primarily in-channel but the adult crabs are capable of limited overland travel.

Adult mitten crabs occupy a wide range of habitats in estuaries and freshwater from tidal mud flats and rocky shores, wetlands, lakes and ponds to fast flowing streams and rivers. They utilize a variety of refugia including weed beds, rocks, and other benthic structures (Veldhuizen and Hieb, 1998; Rudnick et al., 2000). In tidal areas and stream, river and levee banks they burrow extensively in mud and gravel substrate. Burrow densities can approach 40 per m^2. Individual burrows have been examined that reach depths of one meter over a five-meter length (Rudnick et al., 2003).

Mitten crabs are primarily nocturnal with movement and feeding concentrated in the early evening and predawn hours (Jin et al., 2001). Mitten crabs can remain active in temperatures down to 7^oC. Optimal temperatures for the development of juvenile mitten crabs range from 20^o to 30^oC, though growth can occur in a temperature range of 10^o to 35^oC (Jin et al., 2001). Food availability and water temperature are the most significant factors affecting growth and molting frequency. Under optimal conditions, a crab's body weight can double with each molt during the first year. In Germany, crabs molt six to eight, four to five and two to three times in their first, second and third years respectively and once annually in subsequent years (Panning, 1939). Newly settled crabs are herbivorous and within a few months switch to omnivorous feeding habits. Insect larvae, snails, and small freshwater shrimp are the primary food source (Rogers, 2002).

The mitten crab’s large size, protective shell, nocturnal habits, and ability to create and utilize refugia provide a high degree of protection from predators, although white sturgeon, striped bass, black bass, catfish, bullfrogs, loons, and egrets have been reported to prey upon the crabs in the San Francisco Estuary (Veldhuizen and Hieb, 1998a). A fish predation study found a negative correlation with mitten crab survival when stocked with *Peltobagrus fulvidraco*, *Channa argus* and *Cyprinus carpio,* though no crab remains were found in a gut content analysis (Jin et al., 2000). Humans are the dominant predator of crabs in China (Hymanson et al., 1999), primarily due to the harvest of ovigerous females and eggs for consumption. Predation is not considered as a primary factor that controls population size, except for the harvest in China.

Mitten crabs are tolerant of temperature and water stress. Crabs can survive up to 38 days in a wet meadow (Nepszy and Leach, 1973) and at least 10 days in a burrow in a desiccating field (Veldhuizen and Stanich, 1999). Adult crabs can live through the winter under ice at 4^oC

(Hymanson et al., 1999) and can tolerate 0^{o}C for up to seven days (Vincent, 1996). Water temperatures in systems with adult mitten crabs range from 0^{o}C in the winter to 25^{o}C in the summer (Jin et al., 2002).

Mature mitten crabs begin to migrate downstream, *en mass*, to spawn in high salinity estuarine waters in late summer to early winter (Panning, 1939; Kaestner, 1970; Anger, 1991; Rudnick et al., 2003). In the Bay-Delta system, ovigerous females are found from October through June (Veldhuizen and Hieb, 1998; Rudnick et al., 2000; Rudnick et al., 2003) in salinities from almost zero to 30 ppt, with a mean salinity at the collection point of 18 ppt (Rudnick et al., 2003). Researchers have suggested that salinities near 25 ppt are required for proper egg development and adherence to the pleopods (Vincent, 1996). Field studies have not been conducted on the movement of ovigerous females in the estuary and the salinities at sites where mating occurs.

Laboratory experiments have demonstrated that egg development can occur in salinities of seventeen ppt (Tullis pers comm. 2004). Females produce 250,000 to 1,000,000 eggs (Panning, 1939; Cohen and Carlton, 1995). The number of eggs produced is ten times higher than other freshwater, estuarine or terrestrial crab species from the Grapsidae family (Anger, 1995). The females maintain the eggs for one to two months before releasing the larvae. Egg development is probably temperature dependant. Both sexes normally die within several months after reproduction though some crabs produce a second batch of eggs (Hanson unpublished data 2004).

The planktonic larvae develop through a prezoea, five zoea and one megalopae stage, over a one to four month period (Anger, 1991; Kim and Hwang, 1995). Observations suggest that larvae are present in estuaries from winter through summer (Anger, 1991; Rudnick et al., 2002; Panning, 1939) with inter-annual and range variations likely due to differences in water temperatures. The prezoea is a brief (a few hours) stage followed by the zoea (4 to 15 days per stage), and the megalopae stage (20 to 30 days). Development time is variable and depends upon temperature, salinity and nutrition (Table 1).

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

The megalopae is the first larval stage that re-occupies brackish to freshwater habitat. It is sighted near river mouths in China in May or June and in the Elbe River, Germany, between July and October (Panning, 1939). In cold years, the megalopae appear later and are half the size of those in warm years (Panning, 1939; Gollasch, 1999). Mortality during the megalopae stage is low with a high rate of mortality during the metamorphosis to a juvenile crab (Hanson unpublished data 2004). The megalopae is primarily benthic and probably relies on environmental cues to migrate back to adult habitat. Water chemistry, adult odor and flow have been suggested as factors that influence the return of megalopae in other crab species (Anger, 2001).

Larval development and survival is temperature and salinity dependant, with survival in a range of salinities from 15 to 32 ppt and temperatures from 12 to 25^{o}C (Table 1). Optimal survival occurs in temperatures from 18 to 25^{o}C and salinities of 20 to 25 ppt (Anger, 1991; Kim and Hwang, 1995; Huang et al., 2001). The salinity optima of each zoea stage increases through development until the megalopae, which has the ability to survive in a wide range of salinities. Stages IV and V are stenohaline with maximum survival at salinities of 30 ppt, complete mortality at 15 ppt, and minimal survival at 20 ppt (Anger, 1991). The metamorphosis from megalopae to juvenile crab is optimal between 15 and 25 ppt, but can occur in salinities from five to 30 ppt (Anger, 1991). Additionally, Anger (1991) tested temperatures of 9 and 12^{o}C, with complete mortality at 9^{o}C and moderate survival at 12^{o}C. The northern extent of mitten crab populations is probably temperature limited but data on survival rates in intermediate temperatures do not exist. The cumulative survival rate for all zoeal stages suggests that mitten crab larvae can tolerate temperatures between 9 and 12^{o}C but that optimal survival rates are at higher temperatures (Figure 2).

Table 1. Larval development times (Anger, 1991).

Larval development in days					
12 °C					
	Salinity levels (ppt)				
Stage	10	15	20	25	32
zoeal 1	x	15	12	11	12
zoeal 2	x	21	14	10	9
zoeal 3	x	x	13	10	10
zoeal 4	x	x	15	10	12
zoeal 5	x	x	13	17	16
megalopa	x	x	42	32	32
total	x	x	109	90	59
15 °C					
	Salinity levels (ppt)				
Stage	10	15	20	25	32
zoeal 1	9	9	8	8	8
zoeal 2	x	10	8	6	6
zoeal 3	x	9	8	7	6
zoeal 4	x	9	10	6	8
zoeal 5	x	x	10	12	11
megalopa	26	24	21	24	27
total			65	63	66
18 °C					
	Salinity levels (ppt)				
Stage	10	15	20	25	32
zoeal 1	7	8	5	5	6
zoeal 2	8	5	4	4	4
zoeal 3	8	6	5	4	4
zoeal 4	x	6	7	4	5
zoeal 5	x	9	8	8	7
megalopa	x	x	19	18	20
total		42	48	43	46
Data from Anger 1991. X indicates complete mortality					

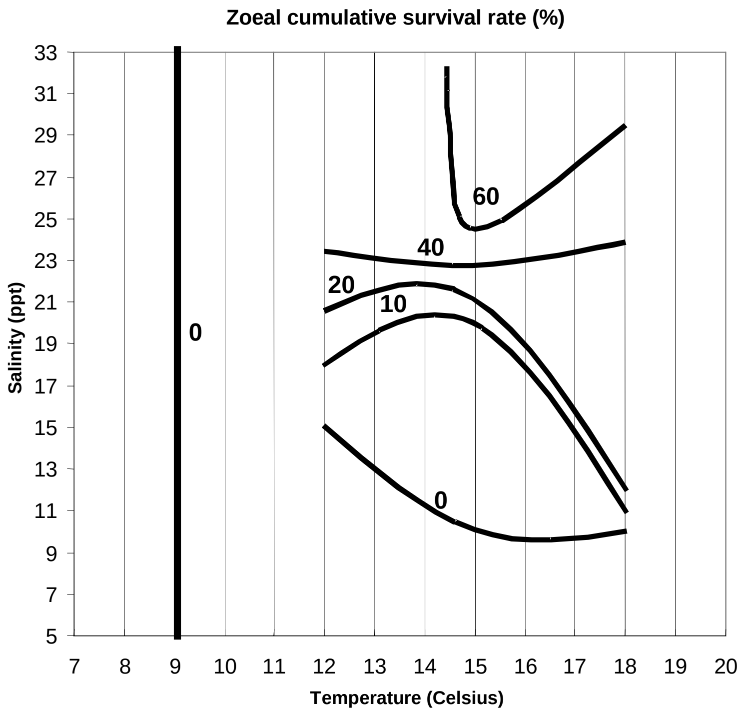

Figure 2. Larval cumulative survival (zoea I to megalopae) (isopleths indicate percent survival) (based on data from Anger, 1991).

The shift in salinity optima and the broad tolerances in the zoea I (Table 1) suggest an ontogenetic horizontal migration of larvae may occur, where larvae are transported from upper low salinity estuarine waters toward high-salinity, lower estuarine and near-ocean waters as the zoea develop. After the prezoea stage, the larvae migrate to the surface where currents propel the zoea toward the mouth of the estuary. The zoea is unable to counteract the net seaward currents because of a limited swimming ability. Estuary currents are on the order of 10 to 200 cm/s, while crab larvae swim at a rate of 0.14 to 2.46 cm/s (Anger, 2001). The zoea is unable to maintain a position in the upper estuary and the zoea may be washed into coastal ocean waters. The megalopae then returns to the adult habitat in onshore-directed near-bottom currents where they settle from spring to mid-summer and develop into benthic juvenile crabs (Anger, 1991; Rudnick et al., 2003).

The limited swimming ability, requirement for high salinities, and 25 to 60 days spent in the pelagic zone (as a zoea) suggests that mitten crab populations become established in estuaries with large high-salinity areas and low flushing rates, or where larvae flushed from the estuary would be retained near the estuary mouth. The megalopae is capable of moving landward in high salinity bottom currents but must remain near the estuary in order to return to adult habitat. Larvae that are flushed from estuaries and transported by currents away from the estuary mouth face a lower probability of return.

Population Patterns

In Europe, main mitten crab population centers occur in the Elbe, Weser, Ems, Rhine and Thames river systems, with mitten crabs found in the coastal areas of Germany, Belgium, France, Denmark and the Netherlands (Figure 5) (Panning, 1939; Hoestland, 1948; Ingle, 1986; Gollasch, 1999). Asian watersheds that support significant populations are the Liao, Yangtze, Oujiang and Hai Rivers (Figure 6) (Jin and Li, 1998). Small populations of crabs are found in most small coastal streams and rivers in China (Zhao, 1999). No populations are established in estuary-river systems that open into the Mediterranean (Petit and Mizoule, 1974) or Baltic Sea (Haahtela, 1963). Low salinity probably limits the ability of mitten crabs to colonize the Baltic Sea region (Figure 3). Mitten crabs have been collected as far north as Oslo, Norway (59.5 ^{o} N) but no established populations occur in Norway, Sweden or Finland (Christiansen, 1977, 1988). In Finland, between 1933 and 1963, 65 crabs were caught with the majority in the 1930s (Haahtela, 1963). In Lake Malaren, Sweden, which connects to the Baltic through a series of locks, approximately 30 crabs are caught per year, probably due to large volumes of discharged ballast water (Josefsson and Andersson, 2001).

Figure 3. Map of Baltic Sea salinity (OSPAR 2002).

Mitten crabs experience large populations fluctuations. Since the 1930s, Germany has seen five periods of abundant crab densities (1930-39, 1953-1960, 1969-75, 1979-1983 and 1993-present) (Gollasch, 1999) (Figure 4). Similar fluctuations occur in Asia. Some researchers suggest that population decreases are related to pollution, impacts on prey species, and larval mortality due to periodic cold spring temperatures and variable water flows (Gollasch, 1999; Atrill and Thomas, 1996). In China, mitten crab populations have fluctuated historically with drought or flood. In the Yangtze River, the population has declined since the 1960s, potentially due to habitat loss, pollution and excessive harvest (Hymanson et al., 1999). In the Thames River, a severe drought from 1989 to 1992 coincided with a large increase in the Chinese mitten crab population (Atrill and Thomas, 1996). High recruitment of young crabs during low-flow periods is suggested as an explanation for this population increase. The population in the Elbe River is currently increasing with 850 kg (75,000 individuals) caught in the river Elbe in two hours in 1998 (Gollasch, 1999).

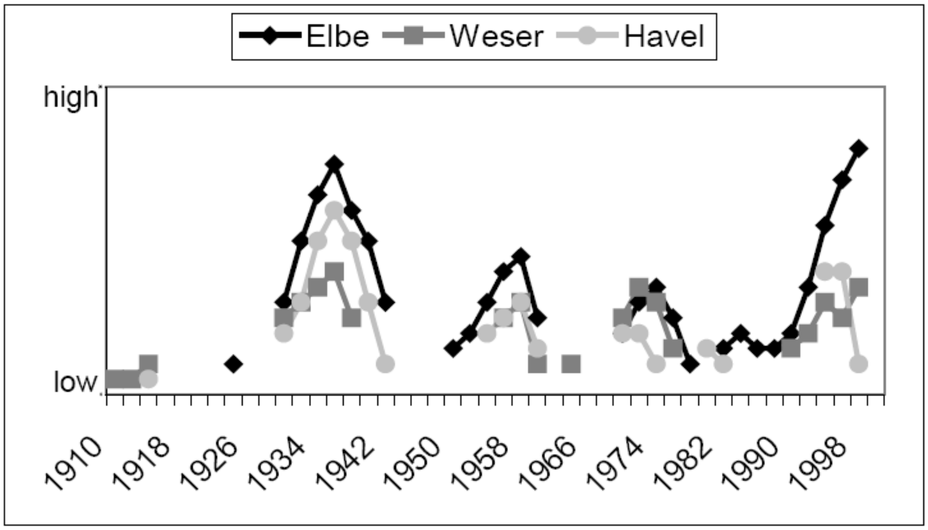

Figure 4. Relative abundance of mitten crabs in three German estuaries (Gollasch, 1999).

Loss of freshwater and estuarine habitat probably limits the current populations in Asia. Six to seven thousand years ago, The Yangtze estuary was large and had a salinity intrusion of approximately 230 km. During the last 2000 years, the deposition of sand and silt has reduced the length and area of the estuary at the rate of one km every 40 years and recently at a rate of one km per 23 years. The mouth has narrowed from 180 to 90 km and the salinity intrusion has decreased to 125 km (Chen et al., 1982, 1983 as cited in Schubel et al., 1986). Increased demand on freshwater resources has decreased flows in many rivers in China and altered hydrographic regimes. The Yellow (Huang Ho) River, the second longest river in China, which empties into the Bohai Sea, experiences low flows and has begun to stop flowing to the estuary year round. In 1997, the lower Yellow River was dewatered for 226 days. Many other estuaries and rivers in China have experienced severe hydrological alterations, which has impacted negatively on mitten crab distribution and abundance.

Invasion Potential

Introductions of mitten crabs to estuaries along the West Coast are probably ongoing, primarily through ballast water. Ships regularly discharge ballast water in estuarine areas where temperature and salinity levels are suitable for the development of mitten crab larvae and adults. West Coast ports receive a significant amount of international and inter-coastal shipping and ballast water discharge. Tankers arriving to Port Valdez in the Prince William Sound release the third largest volume of ballast water of any U.S. port (Hines and Ruiz, 2000) with tankers from U.S. ports accounting for 96% of the total segregated ballast water.

The large volume of discharged ballast water is coupled with voyage durations less than the average period of each mitten crab larval stage. Water that is discharged into Prince William Sound spends an average of seven days in ballast tanks (Hines and Ruiz, 2000). The length of the zoea stages is from four to 12 days and the megalopae stage averages 20 days. Studies have demonstrated the crab larvae can be transported in ballast water and survive the voyage (Hamer et al., 1998). While current ballast water management regulations require the reporting of ballast water exchange for transoceanic vessels and mandatory exchange for coastal vessels, not all ships comply and an exchange does not completely flush ballast water tanks.

West Coast estuaries exhibit similar climatic, habitat and environmental conditions as San Francisco Bay and European estuaries. Many aquatic invasive species on the West Coast occur over a large latitudinal range. The introduced species assemblages of many West Coast estuaries exhibit a substantial overlap with San Francisco Bay (Hines and Ruiz, 2000; Sytsma et al., 2004). As the uptake and release of ballast occurs inside estuaries, introductions can occur in areas with similar conditions as the source port. Introduction into the proper salinity and temperature conditions would permit for the development into an adult crab. The high environmental tolerances and broad habitat and food sources utilized by the adult crab suggests that introduced crabs would probably survive to reach sexual maturity. Colonization of new sites along the West Coast will probably be dictated by the environmental requirements and habitat utilized during reproduction and larval development. Estuaries that provide the proper conditions for the larval period are at a high risk for the establishment of mitten crab populations.

Figure 5. Map of European systems (OSPAR 2000).

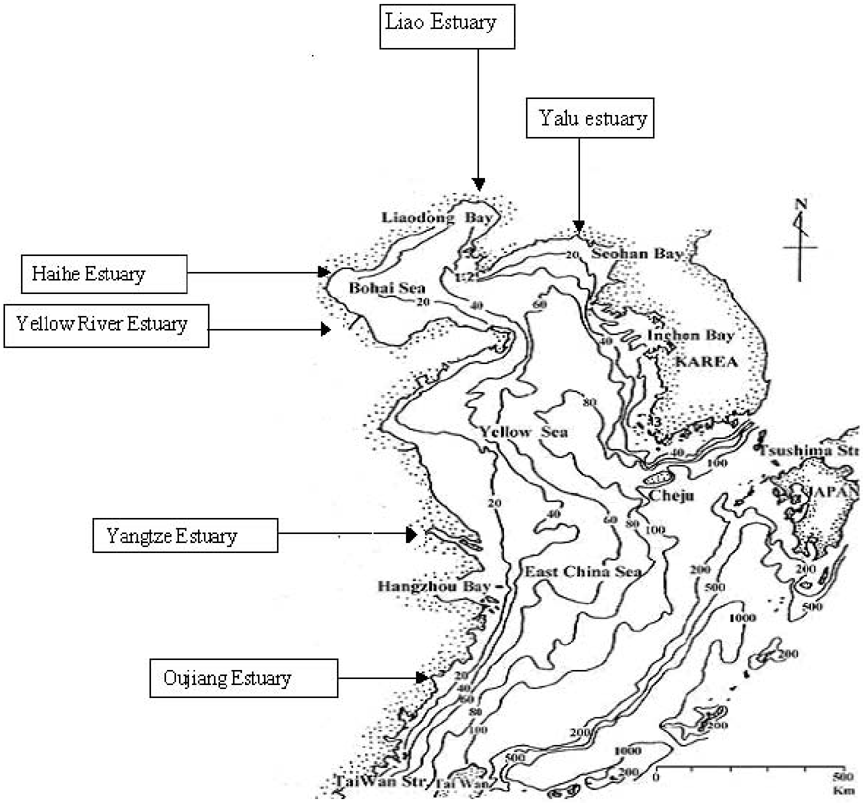

Figure 6. Map of Asian estuaries and seas (Lei and Lu, 2003).

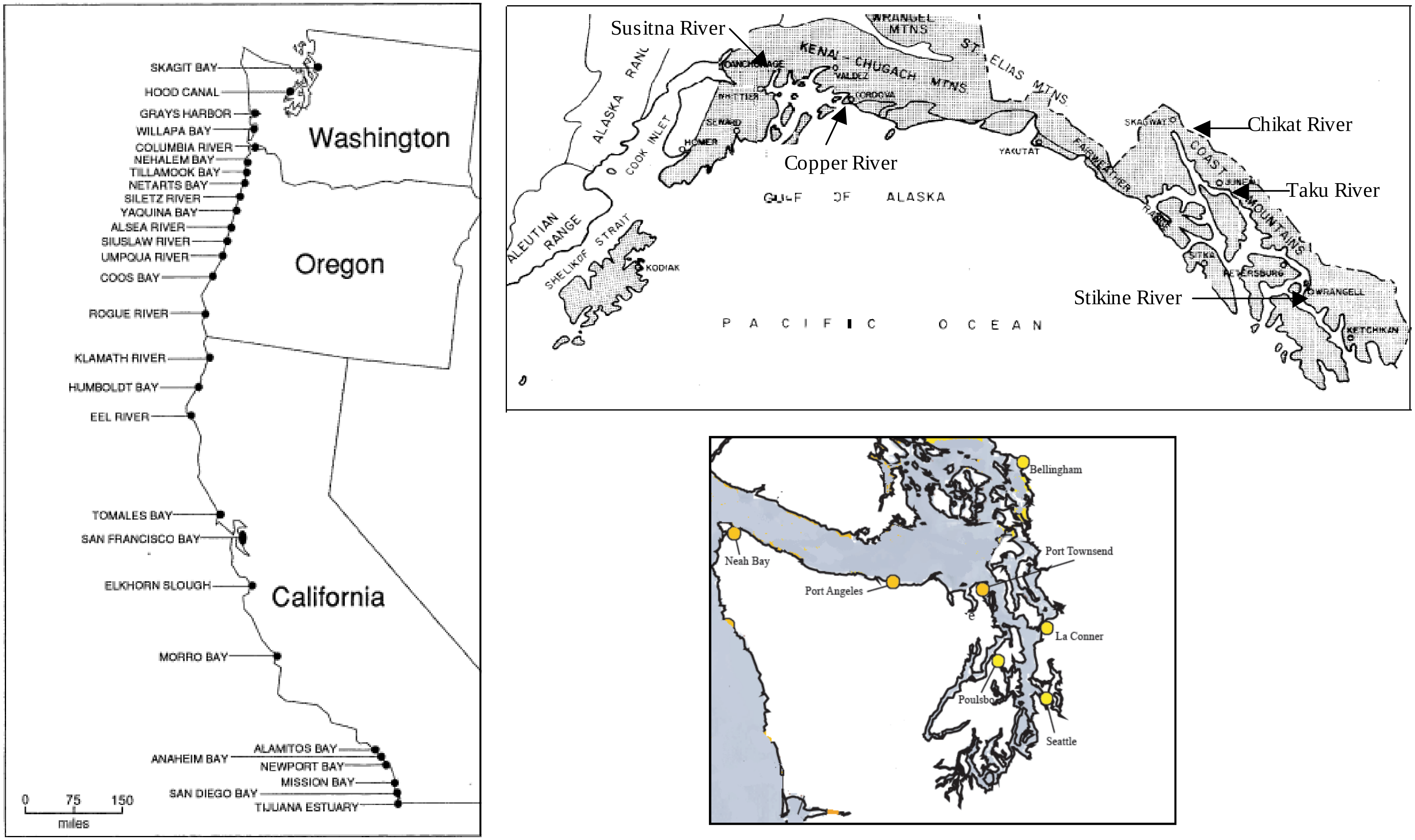

Figure 7. Map of West Coast estuaries.

Risk Analysis

The evaluation of invasion potential is based on the premise that mitten crab populations will be established in estuary-river systems that match ecological conditions that define the native and introduced range. This approach is an established method used to predict expansions and distributions of invasive species. Numerous studies have demonstrated that a species ecological niche represents a long-term stable constraint on distributional potential (Kolar and Lodge, 2001). This approach is combined with an analysis of the mitten crab's habitat requirements and environmental tolerances in the larval stage because it is this life history stage that requires the most specific environmental conditions and habitat characteristics. Salinity, temperature and hydrological processes largely determine the survival and retention of mitten crab larvae. Factors that define these variables and other characteristics of systems with large mitten crab populations were examined and compared to characteristics of PNW estuary-river systems to evaluate potential for establishment.

Temperature and dispersion are primary factors that determine the development time, mortality and recruitment potential for the larval stage. A temperature driven regression model of development time, based on Angers's data (1991), was utilized to predict development times in specific PNW and Alaskan estuaries (Figure 7). This model was used to develop estuarine specific developmental times that were compared to the thermal regimes and flushing times in specific estuaries. The thermal regime determines when larval development could occur, if a sufficient period of temperatures above the lethal limit exists and provides for an analysis of the potential geographic range (Hines et al., 2004). The flushing time is the average time water spends in the estuary. The estuarine specific zoeal development time was compared to the flushing time to determine whether larvae could be successfully retained within the estuary or would be subjected to dispersion in near ocean waters.

Habitat comparison

Approach

Data for variables that define the available estuarine and freshwater habitat of systems with established mitten crab populations was collected, analyzed and compared to PNW and Alaskan estuaries. Limited information exists on the habitat use of adult mitten crabs. The characteristics that are known are broad scale. For example, the adult crab is not limited to wetlands, tidal areas or lowland streams. All brackish and freshwater areas are potential habitat.

Detailed information does exist on the salinity and temperature requirements and development times of the larval stage. The interaction between salinity, estuarine circulation and temperature that would explicitly define larval habitat in an estuary is complex and can only be resolved on an individual estuary basis. Broad scale variables that define the freshwater and estuarine habitat and the interaction between estuarine circulation and salinity were utilized in this analysis. While these variables are broad scale, they are useful measures that have been utilized by other researchers to define environmental processes, estuary classifications and self-recruitment to estuarine populations (Sponaugle et al., 2002). Variables that were used include:

- Watershed area: the land area that drains to the estuary. An indicator of the freshwater habitat available for colonization.
- Estuary area: the total surface area of the estuary, defined variously by authors. In general, the area between the river mouth and the last extent of land before the ocean. This indicates the area available for reproduction, larval and early juvenile development.
- Tidal influence: the distance upstream from the mouth of the estuary that water level is affected by the tides. The tidal length is a secondary indicator of habitat available for reproduction, larval and early juvenile development.
- Salinity intrusion: the distance into an estuary that salinity penetrates. Salinity intrusion is correlated with the area of a salinity mixing zone in an estuary and indicates the area that is available for larval development
- Flushing time: the time it takes to replace the freshwater volume of an estuary at the rate of net flow through the estuary. The flushing rate defines the rate at which water masses are exchanged between the river, estuary and ocean. The likelihood of self-recruitment in estuarine populations is inversely related to the rate at which larvae disperse. Flushing time is a measure of dispersal forces in an estuary.

Analysis

The comparison between systems with mitten crab populations and PNW and Alaskan estuary-river systems consists of two parts: a measure of the habitat (watershed and estuary area) in systems with significant populations and a measure of the salinity (salinity intrusion and residence time) available for larval development within an estuary.

The habitat data indicates that the Columbia River, Puget and Prince William Sound and the Taku, Chikat, and Stikine River estuaries are within the range of systems with significant mitten crab populations (Table 2). The salinity data indicates that Coos Bay, Puget and Prince William Sound, and Taku, Chikat, and Stikine River estuaries can support larval development.

Table 2. Habitat characteristics of invaded estuaries and West coast estuaries.

	Rhine	Schedlt	Gironde	Elbe	Ems	Thames	Humber	Weser	Tagus	Bay-Delta	Yangtze	Hai he	oujiang	liao	Yalu
Watershed area (in 1000 km^2)	224[a]	22[a]	85[a]	146[a]	13[a]	15[a]	27[z]	44[h]	82[j]	120[l]	1808[n]	264[n]	18[r]	57[n]	62[n]
Estuary area (km^2)	324[a]	269[a]	442[a]	327[a]	500[f]	215[a]	200[z]	500[h]	325[k]	1170[l]	1328[o]	z	z	z	z
Tidal intrusion (km)	110[b]	150[c]	160[d]	120[b]	100[f]	100[g]	124[b]	120[i]	z	135[l]	220[p]	z	326[s]	z	z
Maximum Salinity intrusion (km)	x	100[c]	75[d]	70[e]	75[f]	70[g]	90[b]	67[i]	z	100[l]	85[q]	z	z	z	z
Mean Flushing Time (days)	x	65[a]	60[a]	23[a]	43[a]	45[a]	60[b]	45[b]	25[k]	80[b]	z	z	z	z	z

a.Frankignoulle and Middleburg 2002, b. Uncles 2002, c. Soetaert and Herman 1995.d. Castel 1995, e. Postman 1982, f. Jonge 2003, g. Thames Estuary Partnership 2001, h. Turner et al 1991, i Grabemann 1997, j. Camuuffo, D. et al. 2003, k. Thiel et al.2003, l NOAA 1998, n. Zhang 1995, o. Hua 2003, p. Dingman 2003, q. Li and Zhang 1998, r. Feng and Zhang 1983, s. Lu et al 2002, t. Schubel et al. 1986. x. data not usable z. no data available

	Watershed Area (1000km2)	Estuary Area (km2)	Tidal Intrusion (km)	Maximum Salinity Intrusion (km)	Mean Flushing time (days)
Established populations	**12.7 to 18000**	**200 to 1390**	**100 to 135**	**67 to 100**	**23 to 80**
Rogue River	**13.2[a]**	2.6[a]	6[d]	1[d]	x[z]
Coos Bay	2.7[a]	33.7[a]	54[d]	30[a]	**35[h]**
Umpqua River	1.6[a]	25.9[a]	45[d]	27[d]	x[z]
Siuslaw River	11.8[a]	10.4[a]	40[d]	27[d]	x[z]
Alsea River	1.2[a]	5.2[a]	26[d]	22[d]	9[i]
Yaquina Bay	0.6[a]	12.9[a]	41[d]	32[d]	7[j]
Siletz River	0.9[a]	5.2[a]	38[d]	21[d]	x[z]
Netarts Bay	0.04[a]	5.2[a]	8[d]	8[d]	2[j]
Tillamook Bay	1.4[a]	31.1[a]	21[k]	21[g]	10[k]
Nehalem Bay	2.2[a]	5.2[a]	25[d]	23[d]	x[z]
Columbia River	**670[a]**	**735.6[a]**	**234[e]**	43[e]	3[e]
Willapa Bay	1.9[a]	**238.3[a]**	45[a]	40[a]	x[l]
Grays Harbor	6.3[a]	150.2[a]	50[f]	45[a]	x[m]
Puget Sound	**237[a]**	**2632[b]**	**>300[a]**	**>300[a]**	**152[n]**
Taku Estuary	**13[c]**	17[c]	~	~	~
Chikat Estuary	**13[c]**	18[c]	~	~	~
Stikine Estuary	**19[c]**	88[c]	~	~	~
Prince William Sound	x	x	~	~	~

bold indicates within range, ~ indicates estimated within range, x indicates estimated below range.

a. NOAA 1985, b.Friebertshauser and Duxbury 1972, c.Charstensen, R. 2004, d. Percy et al 1974, e. Hamilton 1984, f. Uncles et al 2002, g. Komor 1997, h. Arnerson 1976, I Matson 1972, j. Zimmermann 1972, k. Colbert and McManus 2003, l. Hickey et al 2002, m. Duxbury 1979, n. Friebertshauser and Duxbury 1972, z. insufficient data

Discussion

The average system with a mitten crab population has an estuary area of 488 km^2 with a salinity intrusion of 86 km and a flushing time of 43 days. The total area of Oregon and Washington estuaries, excluding Puget Sound and the Columbia River, would fit inside the average estuary with a significant mitten crab population. A large, stable estuary is necessary to permit the development of zoea within the estuary and maintain population levels (Werner and Quinlan, 2002). A flushing time of 43 days is greater than the zoea development time at temperatures equal to or greater than 14^{o}C.

Data on the abundance of mitten crabs in the Elbe and Weser River supports the use of flushing time and salinity intrusion to predict which systems can support mitten crab populations. In the Weser River, periods of high abundance coincide with years of below average springtime flows (Figure 8). Decreased flows result in longer salinity intrusions and increased flushing times which provide a larger area for larval development, increased larval retention near the adult habitat and consequently larger populations. The flushing time of the Elbe River has been reported to range from 15 to 30 days and the Weser from two to 50 days depending on flow (Uncle, 2002). River flow varies inter- and intra-annually with periods of larval development potentially occurring during periods of high flows and short flushing times. Variability in flushing times may have a significant influence on mitten crab population fluctuations.

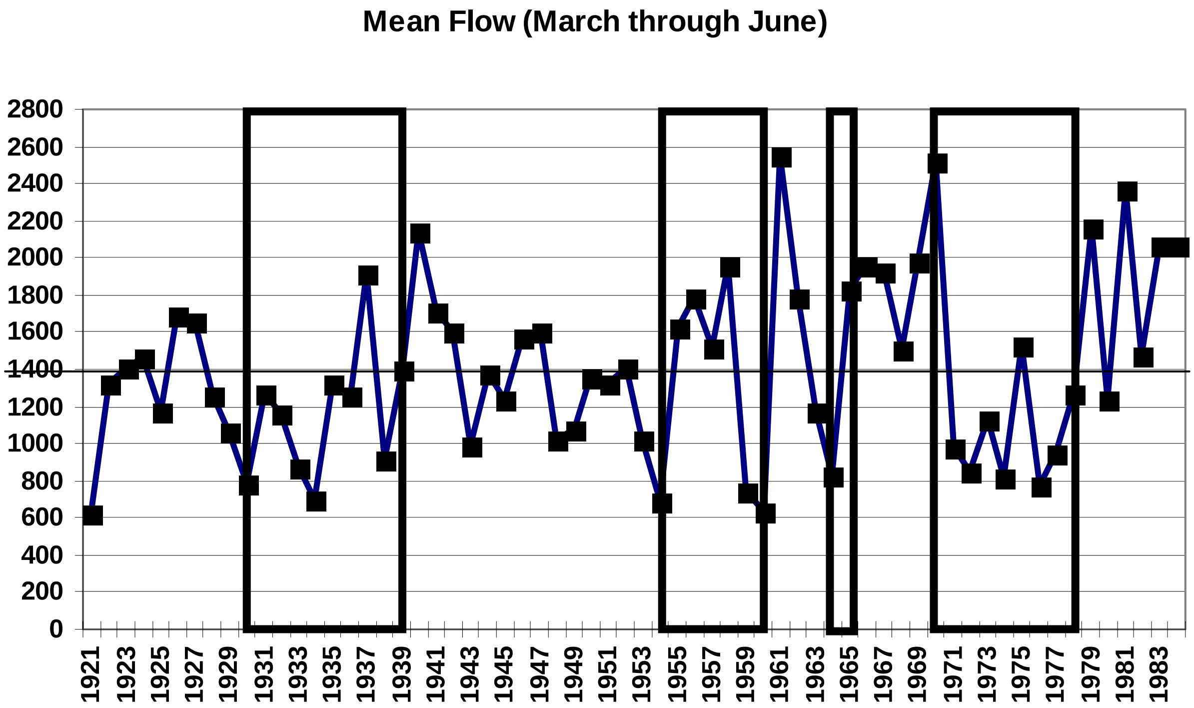

Figure 8. Weser River flow and mitten crab abundance (indicated in shaded boxes)(data from IHP 2004).

Salinity intrusion is also affected by the seasonality of flow. In the Yantze Estuary, seawater does not penetrate the river mouth during the flood season (July to October) but in the low flow season (Nov to May) it normally extends 40 to 60 km in the South Channel and 100 km in the North Channel (Schubel, 1982). European Rivers experience high flows in the winter that decrease in late spring and summer (Figure 18). These low flow periods coincide with the mitten crabs larval period.

The lack of a large mitten crab population in the Seine River, a major river within the European range of mitten crab populations supports the use of flushing time and salinity intrusion as a measure of habitat suitability. Between 1943 and 1996, only 50 crabs were caught in the Seine River and estuary (Vincent, 1996). Its watershed and estuary area are within the range expected to support mitten crab populations, but its flushing time (10 days), limited salinity intrusion (46 km) and distance from other mitten crab populations may limit larval recruitment (Gilles and Fitch, 2000)

The tidal intrusion is a less valuable characteristic to define mitten crab habitat. Dams, tide gates and other structures that limit the natural inland intrusion of tidal influence have altered the length of the tidal intrusion in many estuaries and ocean waters. For several European and Asian estuaries, tide gates define the tidal intrusion and estuary length. The Haihe estuary channel (106 km long) was a tidal influenced mixing zone and is now a freshwater storage reservoir through the use of a floodgate (Bai and Xu, 2003). The salinity intrusion is less affected by these structures but has probably increased in some estuaries due to dredging activities and water withdrawals that have limited the amount of freshwater that enters the estuary and deepened the estuary mouth.

A main characteristic of estuaries with mitten crab populations is a connection to the ocean through secondary seas and large shallow marine areas that are protected from ocean circulation patterns. These areas, the Wadden, Bohai and Yellow Seas, act as secondary estuaries with extensive salinity mixing zones and extended retention times. Larvae flushed out of estuaries into these seas are likely to remain near the estuary mouth. The potential utilization of near-shore areas and transfer between estuaries complicates the analysis of factors based on individual estuary-river systems.

The North Sea is a shallow shelf sea with an area of 750,000 km^2 (Jonge, 2000) that contains many shallow areas with slow cyclonic circulation patterns. The English Channel is about 30 meters (m) deep in the Strait of Dover and gradually deepens to about 100 m. In the area between the Netherlands and Great Britain, from the English Channel north to the Frisian Front, average depths are between 20 and 30 m. The Wadden Sea, into which the Ems, Weser and Elbe River flow, is a shallow inshore area with a surface area of roughly 13,000 km^2 that extends from the Netherlands to Denmark (Jonge, 2003). Barrier islands shelter most parts of the Wadden Sea (OSPAR, 2000). These shallow seas and barrier islands reduce circulation and prevent mixing with deep, cold ocean water.

The slow exchange of water between the North Sea and the Atlantic Ocean, and the shallow nature of the near shore areas limit the potential dispersion of crab zoea and provide higher and more stable thermal regimes. The flushing time for the entire North Sea is estimated to be about one year. Transit times from Cap de la Hague to the Strait of Dover are two to four months and six to eight months to the western German Bight. Flushing times of the coastal areas range from

73 days in the German Bight (108 km^3) and along the Dutch Coast (1323 km^3) to 446 days near the Thames (1138 km^3). Distances between estuaries in this area, especially along the Dutch coast and Wadden Sea are short and it is likely that larvae flushed from the estuaries remain within migration distances of their natal or adjacent estuaries.

Near-shore waters off of estuaries with mitten crab populations in Asia also exhibit slow exchanges, shallow depths, and gyre-like circulation (Li and Qin, 2003; Dingman, 2003). The Bohai Sea is a semi-enclosed coastal shallow sea off of the Yellow Sea with a surface area of 77,000 km^2. Its average depth is 18 m with a mean salinity of 30 to 32 ppt. The Bohai Sea has a limited exchange of water with the ocean as it takes three to four years for a 50% water exchange and 16 years for a complete exchange. The Bohai Sea circulation pattern is one big counterclockwise gyre, with a similar clockwise gyre in the Laidong Bay into which the Hiahe River empties (Guan, 1994). The South China Sea is also cyclonic in winter, spring and autumn (Figure 9) with a mean residence time of about 1.4 years (Liu and Chen, 2002).

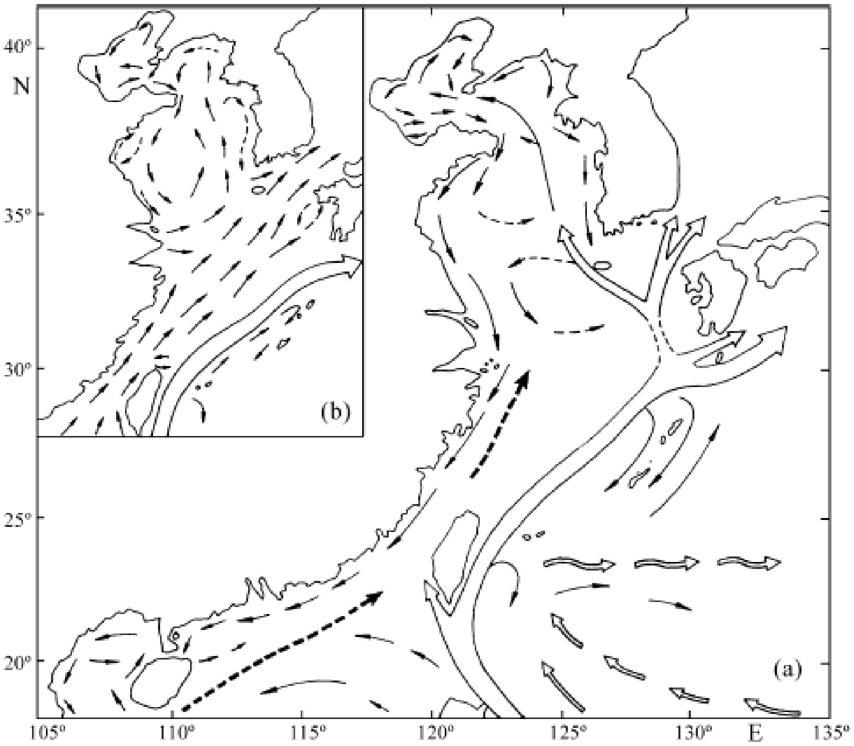

Figure 9. Circulation of the North China Sea, Yellow Sea and Bohai Sea (Guan, 1994).

The West Coast has few areas that serve as secondary retention zones. The continental shelf along the PNW is narrow; the 200 m depth contour is from eight to 32 km offshore (Hickey and

Banas, 2003). The circulation along the West Coast consists of a boundary current and is dominated by a wind-driven coastal upwelling. The alongshore currents are interrupted by river plumes, primarily the Columbia River plume that extends 300 to 400 km seaward. The strong currents and near-shore physiography would disperse larvae flushed into the ocean and prevent return to natal or nearby estuaries.

The Pacific Coast physiography also exhibits a more abrupt transition to the sea with few large estuaries and long distance between major estuaries (Emmet et al., 2000). Humbolt Bay is 336 km from San Francisco Bay and 251 km from Coos Bay. Coos Bay is 321 km from the Columbia River. Minimal shallow habitat exists between the estuaries that could help retain larvae alongshore, prevent offshore dispersal and permit larval exchange between estuaries. European estuaries are much closer to each other and discharge into the same shallow nearshore region. The Elbe and Weser estuaries are 60 km apart and border the Wadden Sea. As cited previously, the mitten crab population in southern France is considered to be separate from the spread in Northern Europe and the result of a separate invasion event, due to the distance (205 km) from other populations in Europe (Herborg, 2002).

Alaskan estuaries contain freshwater and estuarine habitat that is suitable for mitten crab populations. Their flushing times and salinity intrusions were estimated to be within range, due to immediate connections to major tidal inlets that have large areas of high salinity and long flushing rates. The hydrology of these near-shore regions would be suitable for the retention of mitten crab larvae in high salinity waters near estuary mouths. Temperature would probably limit the potential for mitten crabs to colonize these systems. Systems that contain mitten crabs have low wintertime temperatures but a significant warm spring and summer period.

As noted previously, mitten crabs feed at temperatures down to 7^{o}C and can molt at 10^{o}C. Some studies have suggested that cold wintertime temperatures have severely impacted populations. The mitten crab is known to survive short periods of low temperatures but it is unknown if it could over-winter in areas with significant periods of near freezing. The lack of established populations in Sweden and Norway suggests that mitten crabs either have a limited tolerance of long cold periods or require a longer period of high temperatures.

Many Alaskan rivers flow from high mountain snow-fields and empty into glaciated coastal inlets keep Alaskan rivers in a narrow temperature range. Temperatures in rivers that flow into the Taku, Stikine, and the Prince William Sound have an extended period of temperatures below 5°C and are normally below 10°C in the summer (Figure 10). The temperature in these systems typically rises to 7°C in May with approximately 30 days above 9°C. In contrast, the mean annual temperatures of large rivers in Europe (France, Denmark, Germany, Ireland and the U.K) range from 11 to 14°C (OSPAR 2000).

Significant mitten crab populations along the West Coast will be limited to a few estuaries. The potential northern range of mitten crab populations is constrained by temperature. Within range, the establishment of mitten crabs will be limited by the circulation and salinity patterns of specific estuaries. Most PNW estuaries have minimal salinity intrusions and flushing times that would limit the retention of larvae. The Puget Sound is the one estuary in the PNW that contains the necessary temperatures, salinity and circulation for the successful development and retention of larvae and habitat to sustain large populations.

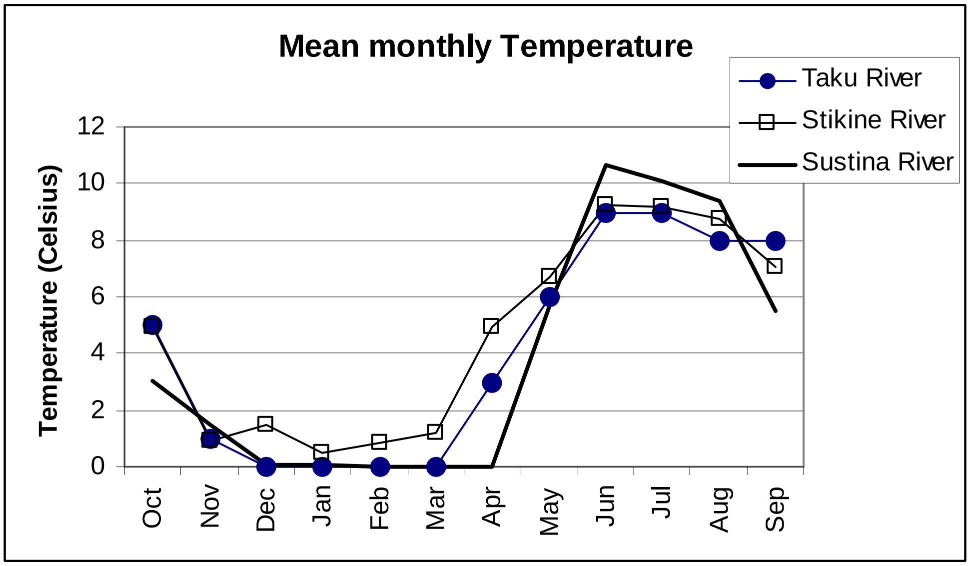

Figure 10. Temperatures of Alaskan Rivers (data from USGS 2004)

Larval Development in PNW and Alaskan Estuaries

Approach

Laboratory rearing times were used by Anger (1991) to develop stage-specific models of development. These stage-specific models were combined to develop a temperature-based regression model of development time for the larval (zoea and megalopae) period (Figure 11). This model was then applied to average daily temperatures for specific PNW estuaries (Figure 13). The equation for larval development is

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

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

Analysis proceeded on the premise that all temperatures above 9^{o}C permitted development. Mean daily water temperature was calculated using data from NOAA buoys and tide gage stations (Figure 12). Temperature data was collected within one meter of the surface and was recorded for a 10 to 20 year period. These data were used to calculate a daily increment (1/D) in development based upon a daily temperature (X). The (1/D) values were summed until the fractions equaled one and indicated the completion of a larval period.

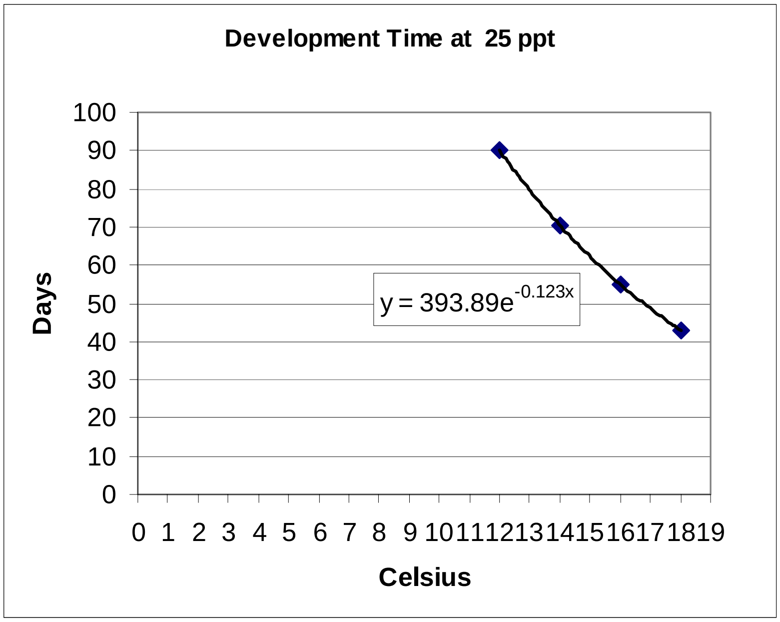

Figure 11. Model of temperature dependant larval development time (developed using data from Anger 1991).

Ovigerous females are found in San Francisco Bay from October to May, which corresponds to periods in other estuaries and provided the start date (October 1) for the period tested for larval development. An end date of August 31 was chosen because it provides a minimal period for juvenile crabs to accumulate enough resources to survive a winter period of limited food availability and low temperatures and is the last date when megalopae are sighted in estuaries. The start date was delayed in some estuaries due to extended periods of temperatures below 9^{o}C. The start date was incremented until the final date that would permit larval development by August 31. The larval development periods were averaged to provide a mean development time for each estuary. The number of days between the first and last start date were summed to provide an estimate of the period available for larval development and when larvae would be in the estuary.

Analysis

In San Francisco Bay, periods of larval development can begin as early as October 1 and run continuously through July 20 (Figure 12). The only other estuary that would permit for development to begin in October is Coos Bay. All other estuaries have an extended period of temperatures below 9^{o}C that would preclude larval development and delay the start of larval development until spring. For all estuaries, larval production would probably be greatest during spring, as temperatures become more consistent and favorable (McConaugha, 1988). Increased temperatures result in decreased larval development times and result in reduced mortality due to predation and lower larval dispersion.

Development and Temperature	**San Francisco Bay**	**Coos Bay**	**Columbia River**	**Willapa Bay**	**Puget Sound**	**Ketchikan**	**Juneau**	**Prince William Sound**
Average larval development (days)	22	65	38	46	64	56	59	51
Average larval and post larval development (days)	68	99	55	66	98	82	88	75
Start of larval period (Oct 1st to Sept 1st)	Oct 1st	Oct 1st	Apr 1st	Mar 12th	Apr 12th	May 20th	May 23rd	May 23rd
Last start date of larval period	July 20th	Jun 6th	July 29th	July 15th	Jun 13th	Jun 15th	Jun 7th	Jun 24th
Total developmental periods (daily increments)	293	249	120	126	63	27	16	33
Average number of days >12 degrees Celsius	259	102	160	154	93	73	64	75
Average number of days >11 degrees Celsius	294	200	175	108	140	89	78	90
Average number of days >10 degrees Celsius	320	294	192	207	193	110	98	106
Average number of days >9 degrees Celsius	330	330	210	246	262	136	128	124

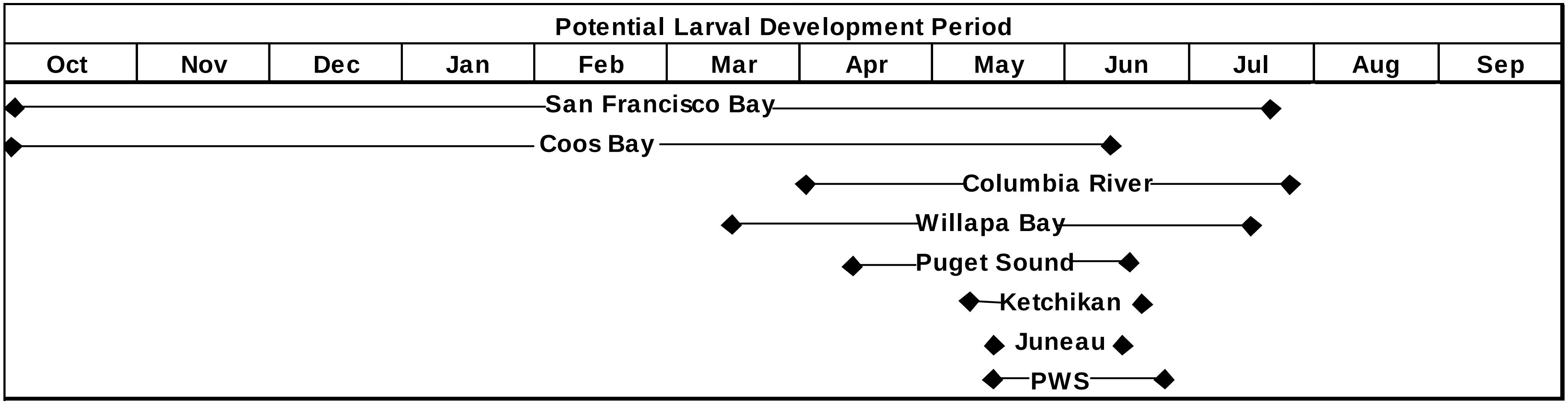

Figure 12. Development times and periods for PNW and Alaskan Estuaries

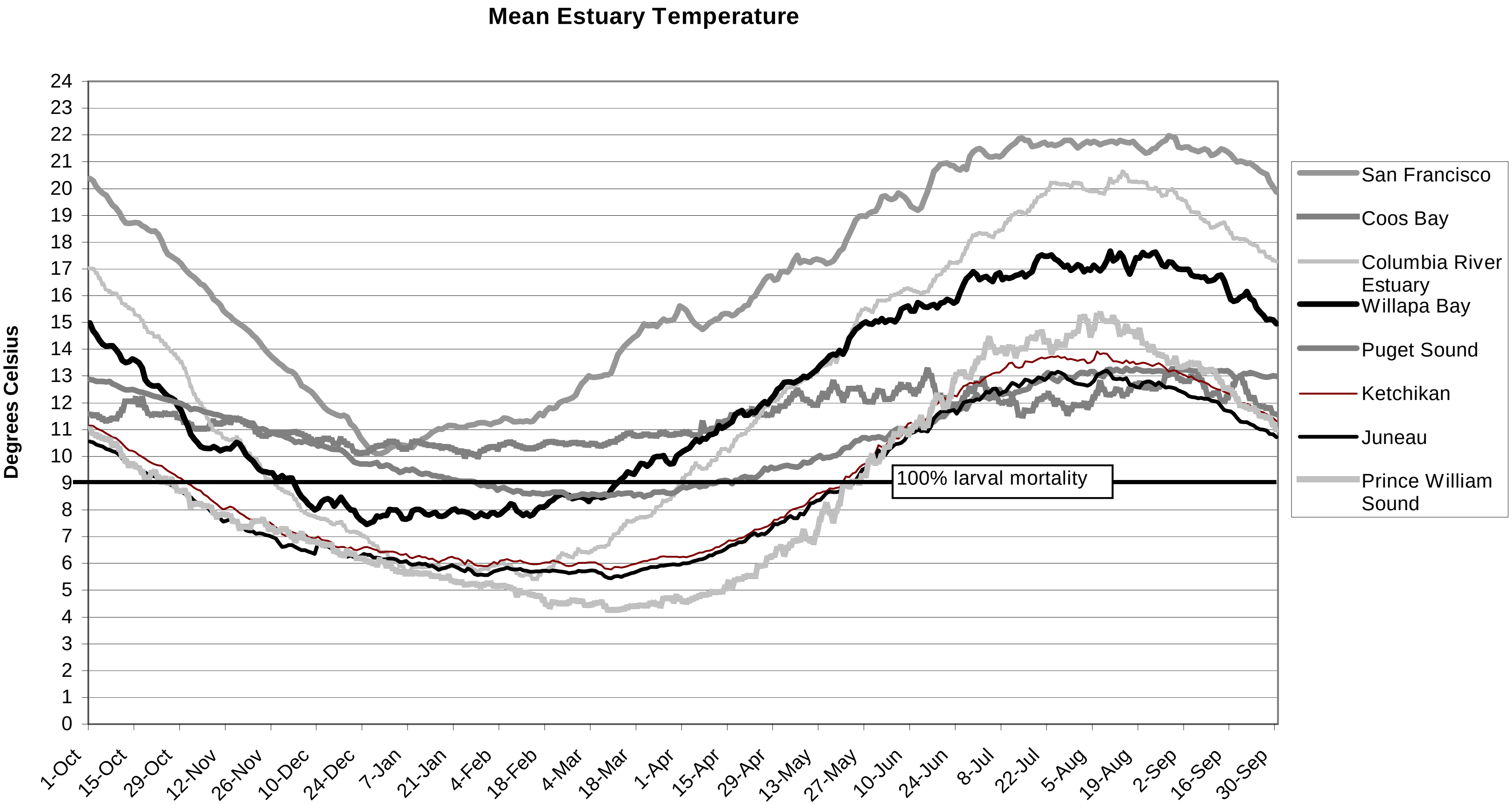

Figure 13. Pacific Coast Estuary Temperatures (data from CO-OPS 2004)

A measure of larval development is the number of potential periods of larval development incremented on a daily basis (Figure 12). In San Francisco Bay, the period begins on October 1 and runs until July 20 for a total of 293 periods. In contrast, Willapa Bay has 126, Puget Sound 63, and the Alaskan estuaries average 25. For Alaskan waters, the average window for larval development begins on May 22 and ends on June 15.

The number of days above a specific temperature compared to the development time at that temperature is a measure of the system's thermal suitability. At 9, 10, 11 and 12^{o}C the development time is 125, 104, 93 and 80 days respectively. In systems where the number of days above a temperature is less than the larval development time at that temperature, it is unlikely that the mitten crab larvae would be successful. Estuaries from San Francisco Bay to Puget Sound have temperature regimes sufficient for larval development but the Alaskan estuaries are at or below the minimal threshold (Figure 14).

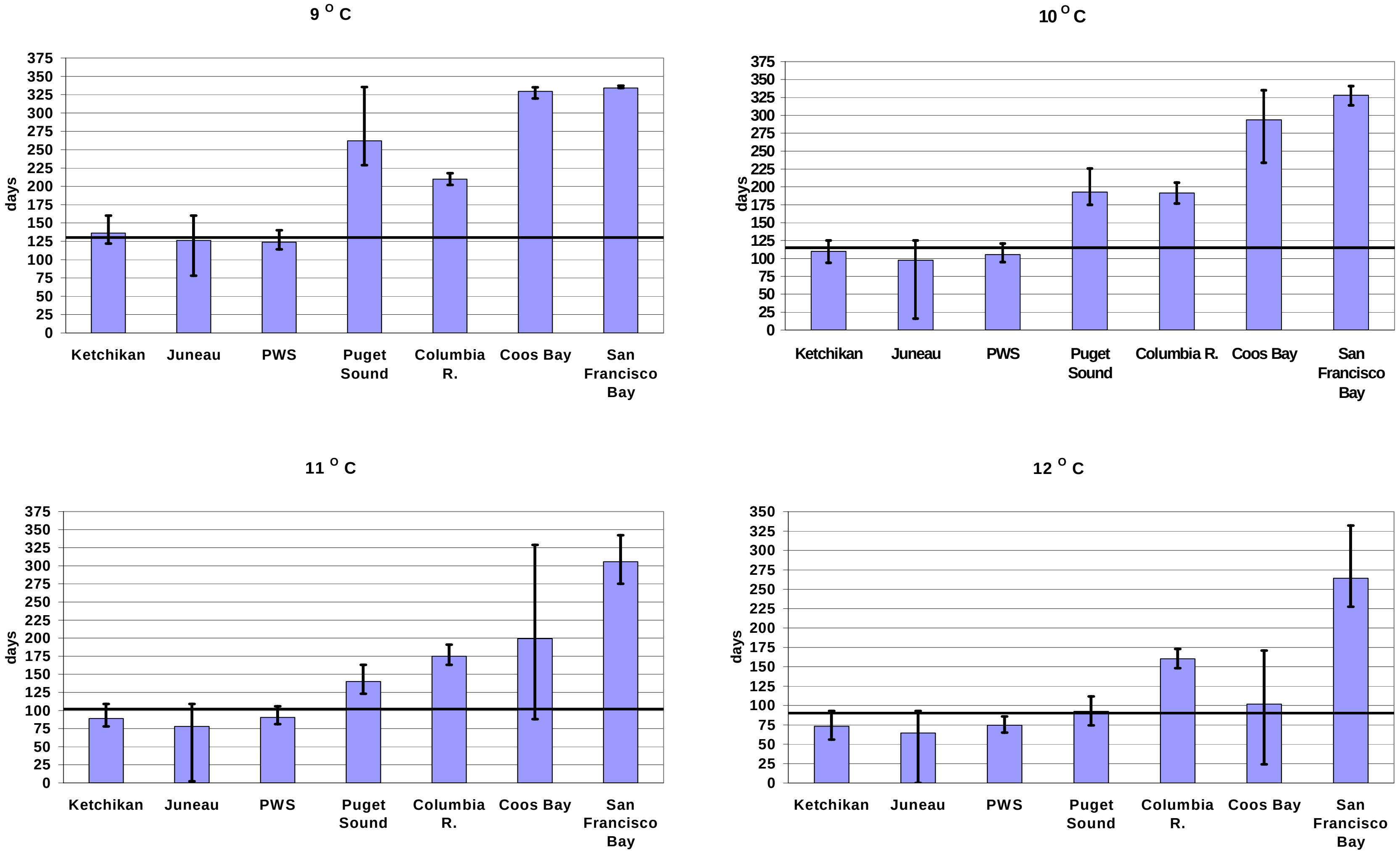

Figure 14. Estuary thermal suitability

Discussion

The analysis utilized 9°C, the temperature at which complete mortality occurred, as the minimum temperature for larval development. The survival rate at temperatures between 9 and 12°C is unknown so a conservative approach was used. It is likely that lethal temperatures occur above 9°C. Evidence for a higher temperature can be seen in Figure 15, which represents zoea I survival rates in temperature and salinity combinations and clearly shows a trend towards higher survival rates in higher temperatures and minimal survival rates in low temperatures.

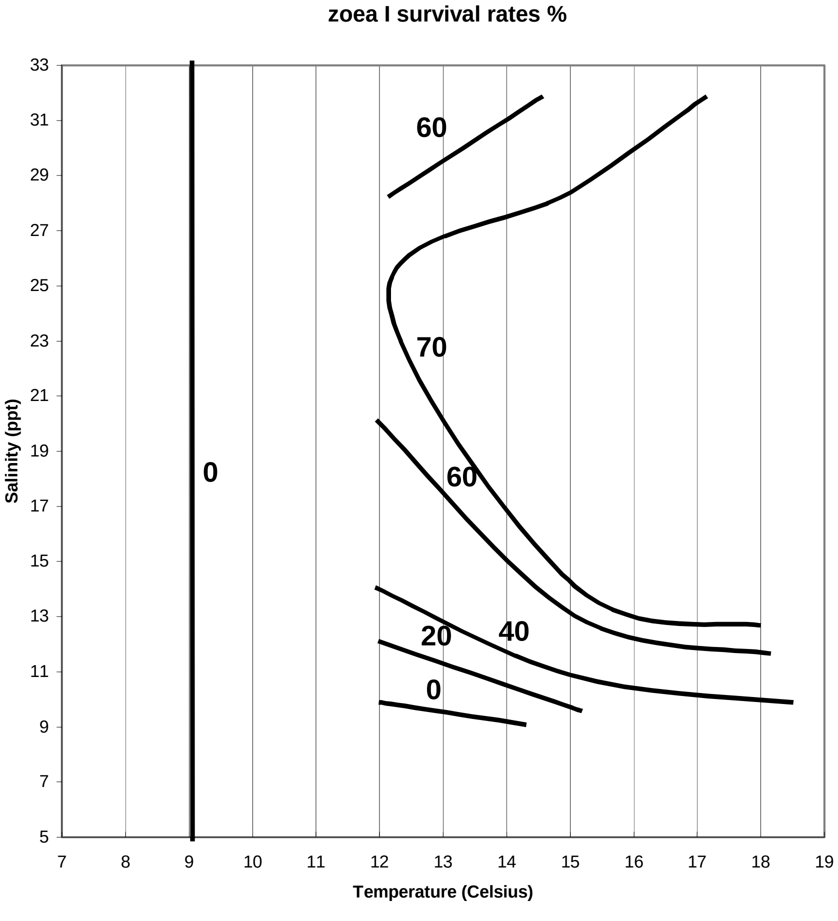

Figure 15. Zoea I survival (percentages indicated in isopleths) (data from Anger, 1991).

The lethality of low temperatures on zoea may be a greater factor if the lethal level is higher than 9°C. The table provides the number of days within the potential larval development period (Oct 1 to Aug 31) when temperatures are above a certain degree. For Alaskan estuaries there is an average of 129 and 105 days above 9^{o}C and 10^{o}C respectively. The available period of 25 days was based on 9^{o}C. A cutoff at 10^{o}C reduces the period to May 30 to June 15, a period of 16 days. The cutoff point of August 31 in Alaskan waters provides only 50 to 60 days for juvenile development before temperatures drop below the growth limit of 10^{o}C.

Most estuaries do not have thermal regimes that would permit larval development. North of Puget Sound, average temperatures are at or below the threshold necessary to maintain populations. In years with below average temperatures, the potential development period would not be sufficient for larval development. Larval development is only a portion of the reproductive cycle that requires moderate to high temperatures. It is unknown what effect low temperatures would have on reproduction, egg development and juvenile growth.

A similar approach was used to examine the potential green crab, *Carcinus maenas*, invasion of Alaskan waters (Hines et al., 2004). The study focused on the larval stage based on the hypothesis that limits for a self-sustaining population in Alaska would be determined by temperature tolerances for reproduction and larval development. *C. maenas* is an invasive species of estuarine, nearshore and bay habitat. Mitten and green crabs have threshold temperatures of 7-10^{o}C that limit adult feeding and growth (Ropes, 1968; Berrill, 1982). The study found a temperature range for larval survival similar to mitten crabs, with 10^{o}C as the threshold for development into a juvenile crab (Hines et al., 2004). Minimal survival occurred at 10^{o}C, peaked at 15 to 17.7^{o}C, and then declined at higher temperatures (Hines et al., 2004). Using a similar species-specific regression model created by Dawirs (1985) for larval development and data from some of the same NOAA buoys, they compared development times to the number of days above 10^{o}C. For many sites, the number of days above 10^{o}C was greater than the 60 days required for larval development and deemed at risk for invasion (Hines et al., 2004).

The predictions for green crab invasion in Alaska contrast with results for mitten crabs, primarily due to a difference in development time. Green crab larvae develop into juvenile crabs in about 60 days at 10^{o}C and 30 days at 22^{o}C. Mitten crab larvae require 115 days at 10^{o}C and 27 days at 22^{o}C. In Alaskan waters, larval development of the green crab can occur in 45 days versus the 69 days for mitten crabs.

The different larval thermal tolerances of mitten crabs and green crabs suggest that green crab larvae would have a higher survival rate in Alaskan waters. Mitten crab zoea have a higher temperature optima of 18 to 25^{o}C versus the 15 to 17.5^{o}C for green crabs (Anger, 1991; Kim and Hwang, 1995; Huang et al., 2001). Green crab zoea are more tolerant of low temperatures than the mitten crab zoea with development to zoea II or higher in 5^{o}C. Mitten crabs experience complete mortality in zoea I at temperatures of 9^{o}C. These differences suggest that the mitten crab is adapted to a warmer climate than the green crab and would fair poorly in Alaskan waters.

The temperature regime of estuary and near ocean waters in regions with mitten crabs exhibit a much higher range than most PNW estuaries. While areas in the Bohai Sea and the North Sea experience low wintertime temperatures, they have an extended spring and summer period of temperatures above 15^{o}C that peak at 20^{o}C (Figure 16). These temperatures are favorable to larval development and greater than temperatures along the Pacific Coast. Of the tested estuaries, only the Columbia River and Willapa Bay peaked at 20 degrees and had an extended period of temperatures above 15 degrees.

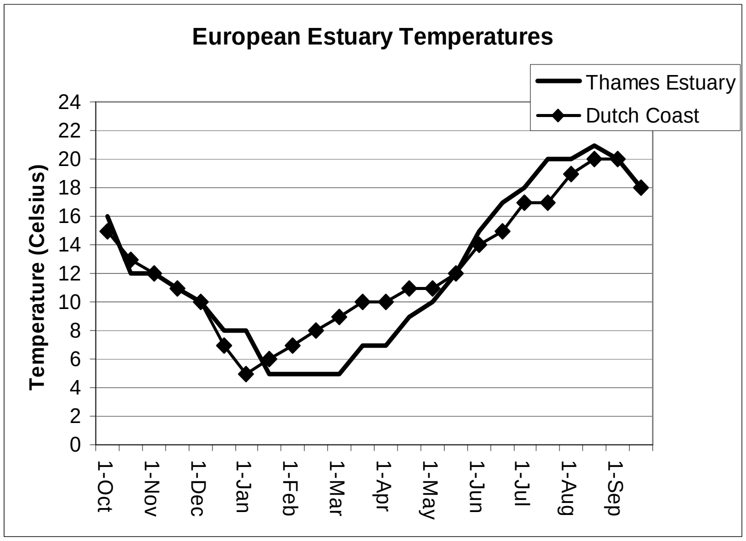

Figure 16. Temperatures of two European Estuaries (NMWMP 2005).

Mitten crab populations exist in estuaries with extended periods of temperatures above 15^{o}C. Pacific Coast estuaries south of Alaska have temperature regimes sufficient for larval development. The period when Pacific Coast estuaries have temperature regimes that would permit larval development is April to June, when the larvae would take from 45 to 90 days to develop. This period coincides with increased freshwater flows through estuaries due to snow pack melt and runoff (Figure 17). Increased flows decrease the salinity levels and the flushing time of the estuary. The overlap between the potential larval development period and increased flows would probably result in lower survival rates and increased levels of larval export into near ocean waters.

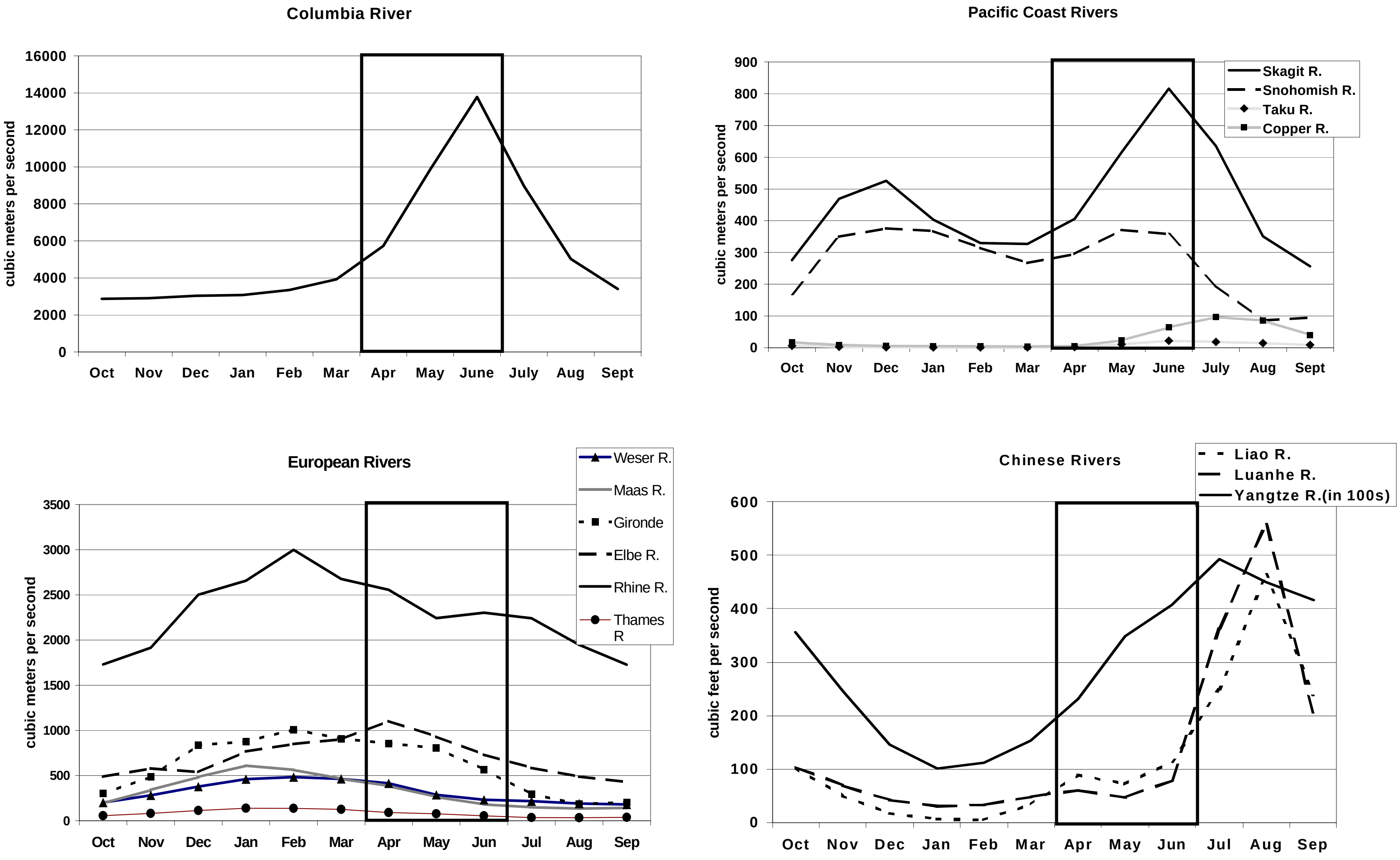

Figure 17. River Flows (data from USGS 2004 and IHP2004).

Estuary retention of larvae

Approach

The larval development time was split into periods for zoeal and megalopal development. A zoea development model was utilized to calculate the mean number of days that mitten crabs would spend as a zoea in each estuary. This value was compared to the flushing rates to evaluate the relative rate of retention within each estuary.

Analysis

The estuaries with flushing times greater than the calculated zoeal development time are the Puget and Prince William Sound and the tidal inlets near Ketchikan and Juneau (Table 3). Data from the San Francisco Bay also show that flushing time is greater than the calculated zoea period. The other estuaries have flushing times that are a fraction of the zoea development time.

Estuary	**Mean zoea period (days)**	**Flushing Time (days)**
San Francisco (South Bay)	39	160
San Francisco (North Bay)	45	60
Coos Bay	65	35
Columbia River	38	5
Willapa Bay	46	10
Puget Sound	64	152
Ketchikan (Tongass narrows)	56	long
Juneau (Gatineau channel)	59	long
Prince William Sound AK	51	long

Table 3. Zoea development and Flushing Time

Discussion

The development period determines the duration of the zoea stages. If the flushing time is less than the development period, zoea will be transported into coastal waters, and result in decreased numbers of megalopae that return to adult habitat (Roegner, 2000). Most estuaries would subject mitten crab zoea to an extended period of drift in the ocean. As the length of the drift period increases, the likelihood of return by the megalopae diminishes.

Zoea are pre-competent, subject to passive dispersal without the ability to actively maintain their position. Megalopae are competent and can actively maintain their position or move toward settlement sites but their limited swimming ability requires them to remain within a certain distance. For larvae to return to the adult habitat a balance must occur between the period moving away as pre-competent and returning as competent larvae. More time as pre-competent larvae increases the risk of transport beyond a colonization distance of the adult habitat (Jackson and Strathmann, 1981).

Due to the distances between estuaries along the West Coast, limited larval exchange would occur between estuaries. Mitten crab populations would be closed and self-recruiting. The greatest variable affecting self-recruitment is the duration of the planktonic larvae period (PLD) and flushing (residence) time. Self-recruitment is inversely related to the rate at which larvae flux away from the parent population. The interrelationship between the flushing time and the PLD determines whether self-recruitment can occur in mitten crab populations. The probability of larval return to the brackish settlement sites decrease in systems where water residence times are short (Sponaugle et al., 2002). Gaines and Bertness (1992) explained reduced barnacle settlement in Narragansett estuary in years of low water residence times due to higher freshwater flow rates, with high correspondence between settlement rates and flushing times ($R^2 = 0.77$, $P < 0.001$). Flushing times also explained most of the variation between sites in the Narragansett Bay and coastal sites. Longer flushing times permitted higher levels of recruitment in the bay than coastal sites (Gaines and Bertness, 1992). The dynamics of herring in the North Sea as well as hake and barnacles in the North Pacific all correlate with changes in transport processes and suggest that variable dispersal is a widespread source of recruitment variation (Paris and Cowen, 2004).

Siegel et al. (2003) developed a model of marine larval dispersion based on data for 32 species with a planktonic larval stage. The model demonstrated a high correlation between larval displacement and planktonic larval duration (r^2 value of 0.802). The model was compared to a Langrangian particle-tracking model based on quasi-realistic velocity fields for a turbulent coastal flow. The equation is:

$$D = 1.33(\mathrm{PLD})^{1.30}$$

where D = the mean absolute dispersal distance in kilometers, and PLD is planktonic larval duration (Siegel et al., 2003).

Mitten crab larvae that spend 10, 30, and 50 days outside an estuary would be displaced an average of 26, 110, and 210 km respectively. The difference between the zoeal development time and the flushing times for many of the PNW estuaries is greater than 30 days, which would imply an average dispersal of over 100 km from the estuary mouth. This is less than the distance suggested by an estimate of the alongshore flow rates along the Oregon coast which can run at 9 to 26 km day (Huyer et al. as cited in Johnson and Gonor, 1982). These distances probably exceed the ability of megalopae to return to adult habitat within an estuary.

The method of larval displacement simplifies variation in flow and ignores geographic, climatic and local conditions such as headlands that create local retention zones, river plumes that increase and concentrate dispersion, fronts, upwelling effects and wind driven surface currents. These conditions can lengthen or shorten the dispersal distance and create local retention zones. It is unknown if these local conditions dictate or simply create variability in larval dispersal. On average, larvae that spend a significant amount of time outside of an estuary are likely to be transported beyond the ability of the megalopae to return to the estuary.

Flushing times are flow dependant; during periods with high flow rates, flushing time will be greatly reduced. The rivers and streams in the indigenous range of the mitten crab experience high flows in the summer and low flows in the spring when larvae are likely to be present in the estuary. This increases the likelihood of estuarine retention in the native range. The PNW experiences high flows during the period when mitten crab larvae are likely to be in estuaries. This increases the likelihood that mitten crabs will be flushed from PNW estuaries (Figure 15). The relative abundance of mitten crabs in the Weser demonstrates a clear correspondence to years and periods when the flow during the larval period (May through June) is below average (Figure 8).

This method suggests that on average mitten crabs would be able to complete their larval development within Puget Sound and the tidal inlets in Alaska. In estuaries such as Coos Bay and Willapa Bay the larvae would probably spend an extended period in near-ocean waters where they would quickly be moved off and along-shore. This is even greater in the Columbia River where the larvae would spend almost all of the larval period in the ocean with a very low probability of return.

Vertical Migration

Many crab species have larvae that develop in the open ocean and then return to near shore and estuarine habitats as megalopae or juvenile crabs. Most of these species have an adult form that can complete its lifecycle in coastal embayments, shorelines and high salinity estuarine waters. The mitten crab is one of a few crab species that occurs in freshwater with a larval form that utilizes high salinity waters for development. In order to remain near the adult habitat, the zoea must maintain a horizontal position in an estuary through vertical migration. A migration into net landward currents during flood tide transports larvae up the estuary. During ebb tide, the larvae will migrate down in the water column to avoid the surface net seaward currents. The capability to perform vertical migrations may develop in later zoea stages so that early zoeal stages drift passively toward higher salinity zones in the lower estuary and near ocean and then later larval stages exhibit a vertical migration that prevents further seaward movement. It is unknown if mitten crab zoea exhibit this behavior.

It has been suggested that the mitten crab reinvades estuaries at later larval stages or as a megalopae (Panning, 1939; Anger, 1991). Salinity tolerances of the zoea indicate that the zoea move seaward through development and then return as a megalopae. Early larval stages are tolerant of lower salinities (10 and 15 ppt) that are lethal to later larval stages. Tolerance to lower salinities is finally exhibited in the megalopae stage. Anger (1991) tested the cumulative development and survival of larvae in salinity and temperature combinations, not the survival of individual stages. It is unknown whether zoea that develop to later larval stages in high salinities are able to tolerate and complete development if exposed to lower salinities.

The accepted model of mitten crab larval development is one where the larvae undergo an ontogenetic progression in their maintenance of a horizontal position through vertical migration into and out of salinity, tidal and wind driven currents. Early larval stages are expected to occur at the surface of the water column where they are transported to lower estuarine (high salinity) areas. Later zoea and megalopae stages must exhibit some form of vertical migration that allows them to move in opposition to the average seaward current in order to return to brackish and freshwater.

Studies have documented three types of vertical migration that mediate horizontal transport of larvae: ontogenetic, diel, and tidal. Strong evidence exists in support of ontogenetic (Sandifer, 1975) and tidal (Cronin and Forward, 1979; Dittel and Epifanio, 1982) vertical migrations. The mud crab, *Rithropanopeus harissii*, undergoes a tidally driven vertical migration that allows the zoea to remain in upper estuarine areas and avoid export to near ocean waters (Cronin & Forward, 1982). Blue crabs, *Callinectes sapidus*, exhibit a vertical migration cycle that increases the export to near ocean waters and a return in the megalopal stage or as a juvenile crab (McConaugha, 1988). Various patterns of vertical migration are exhibited by other crab species.

An examination of the vertical migration capabilities and the onset of behavioral patterns that would allow a return to brackish water are essential to determine the risk of invasion to PNW and Alaskan estuaries. Vertical migration in the mitten crab zoea would reduce export from the estuary and dispersion into coastal waters. If zoea actively migrate in the later zoeal stages, the retention time necessary to maintain populations in an estuary would be much less than calculated in the previous analysis.

Approach

Larvae from ovigerous females were collected and cultured in dishes at densities of one larvae per 5 ml, at 18 ±1°C and a salinity of 25 ppt. The primary experimental apparatus consisted of a clear Plexiglass 2m tall tank, with ports for the introduction of larvae and the measurement of salinity and temperature. Larvae were introduced to the tanks, allowed to acclimate and their movements recorded on an hourly basis. Experiments ran for 48 hours. The movements of the larvae were recorded with a video camera in near infrared light and the videos analyzed at a later date for larval position. Experiments were performed on zoea I, III and V. Two experiments were conducted that tested the response to diurnal and tidal cycles and to salinity layers.

Analysis

Approximately fifty percent of the experiments have been completed. The remainder of the experiments will be completed by April 2005. Funding was obtained through a grant from the U.S Fish and Wildlife Service to complete the vertical migration experiments. Initial data suggests that all zoeal stages remain in the upper portion of the water column and exhibit a diurnal cycle. The mean depth of the larvae throughout the course of the experiment varies from

0.2 to 1.0 meter. Stage one zoea exhibited a salinity avoidance behavior, with the mean depth of larvae below the 25 to 15 ppt halocline.

Discussion

The initial analysis suggests that the larvae do not exhibit vertical migration behavior in response to tidal cycles. A vertical migration based on the tidal cycle is the primary means by which crab zoea can avoid being flushed out of an estuary. The strong response to light and mean vertical position of the larvae throughout the experiment suggests that they would be continually subjected to net seaward surface currents.

Only the megalopae stage exhibited a mean depth near the bottom of the tank. This depth would be most suitable for return to the adult habitat and upper estuary areas and suggests that this is the developmental stage where this process occurs . Not enough data exist as to a potential diurnal or tidal rhythm in movement for the megalopal stage, though data show they will occasionally swim to the waters surface.

Conclusion

The examination of the key factors necessary for larval development of mitten crabs, habitat suitability and environmental condition suggests that the majority of PNW and Alaskan estuaries are not at risk of establishment of significant mitten crab populations. Puget Sound and Coos Bay are the only estuaries that have the proper combination of temperature, salinity and retention time for mitten crab establishment. Because of the much larger dimensions of Puget Sound, it may be expected to support larger populations than Coos Bay. Alaskan waters were deemed at a low risk due to insufficient temperatures to support larval development. The potential for a period of increased temperatures due to global warming or natural warming trends may place Alaskan waters at a higher risk.

The ongoing vertical migration experiments will result in a prediction of the rate at which larvae are flushed out of an estuary and at what developmental point they begin to return to brackish waters. These data will be used to provide a minimum retention time necessary for the larvae to develop in an estuary and distance traveled in near ocean waters prior to return.

Mitten crabs pose a significant threat to the aquatic resources of the PNW. This study was conducted to provide resource managers with a greater ability to predict what areas are at risk for an invasion. The approach and data generated from this research can be utilized to predict the range and risk of invasion beyond the PNW for this and other species.

Research Recommendations

Development in Low Temperatures

Experiments on larval survival at temperatures between nine and 12^{o}C would provide a more refined analysis of survival in Alaskan and near ocean waters. The current model allows for survival at temperatures above 9^{o} C. Mortality at 10^{o}C would greatly restrict the potential northern range of mitten crabs and reduce the period available for larval development. Most estuaries exhibit higher temperatures than near ocean waters. Larvae flushed from estuaries, such as the Columbia River, would experience lower oceanic temperatures that would reduce survival.

Megalopae Recruitment and Settlement

The ability of megalopae to return to brackish and freshwater areas needs to be investigated. It is unknown what cues the megalopal stage to return to upper estuary areas and at what rate they can travel. These factors can determine if megalopae flushed into near ocean areas can home in on the estuary mouth and the distance from the estuary mouth that larva must not exceed to ensure return to adult habitat.

Juvenile Development

Larval release and development is timed to ensure optimal conditions for metamorphosis and juvenile crab survival. It is likely that there is a minimum period of juvenile growth and development necessary for survival in low wintertime temperatures. Estimates of growth rates at specific temperatures exist but limited knowledge exists on wintertime survival. Experiments on post-settlement mortality after limited periods of juvenile growth would provide input on the period necessary for juvenile growth prior to temperatures that limit feeding and growth.

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