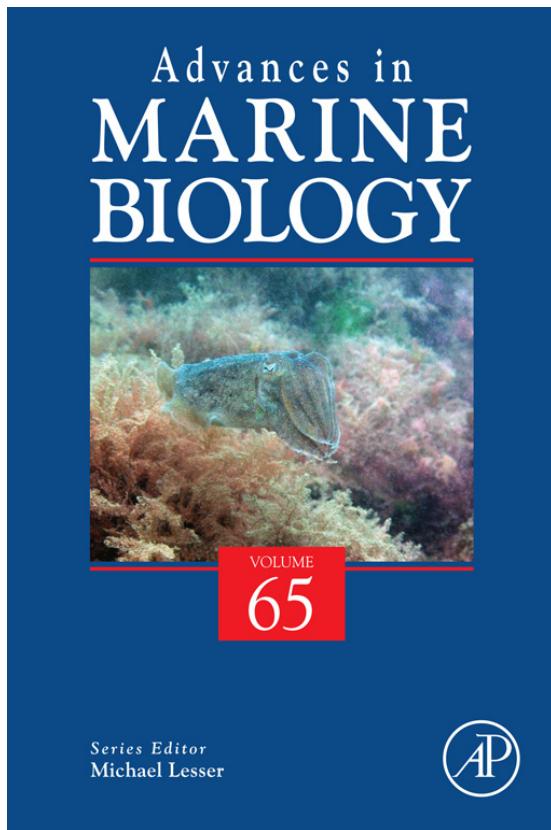


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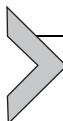
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## CHAPTER THREE

# The Biology, Ecology and Fishery of the Dungeness crab, *Cancer magister*

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## Abstract

The Dungeness crab, *Cancer magister*, is a commercially important crustacean that ranges from the Pribilof Islands, Alaska, to Santa Barbara, California. Mating occurs between recently moulted females and post-moult males. After approximately 90 days, females release planktonic larvae into the water column. Stage-I zoea are found in the nearshore environment and subsequent zoeal stages are found at greater distances. After approximately 80 days, zoea moult into megalopa, which move first from the open ocean onto the continental shelf and then across the shelf to settle in the nearshore environment or estuaries. Crabs reach sexual maturity at 2–3 years of age. The fishery for *C. magister* is managed using a 3-S management strategy which regulates catch based on size, sex and season. As more fisheries seek sustainability certifications, the

Dungeness crab fishery presents an excellent test case of how to sustainably manage a crustacean fishery.

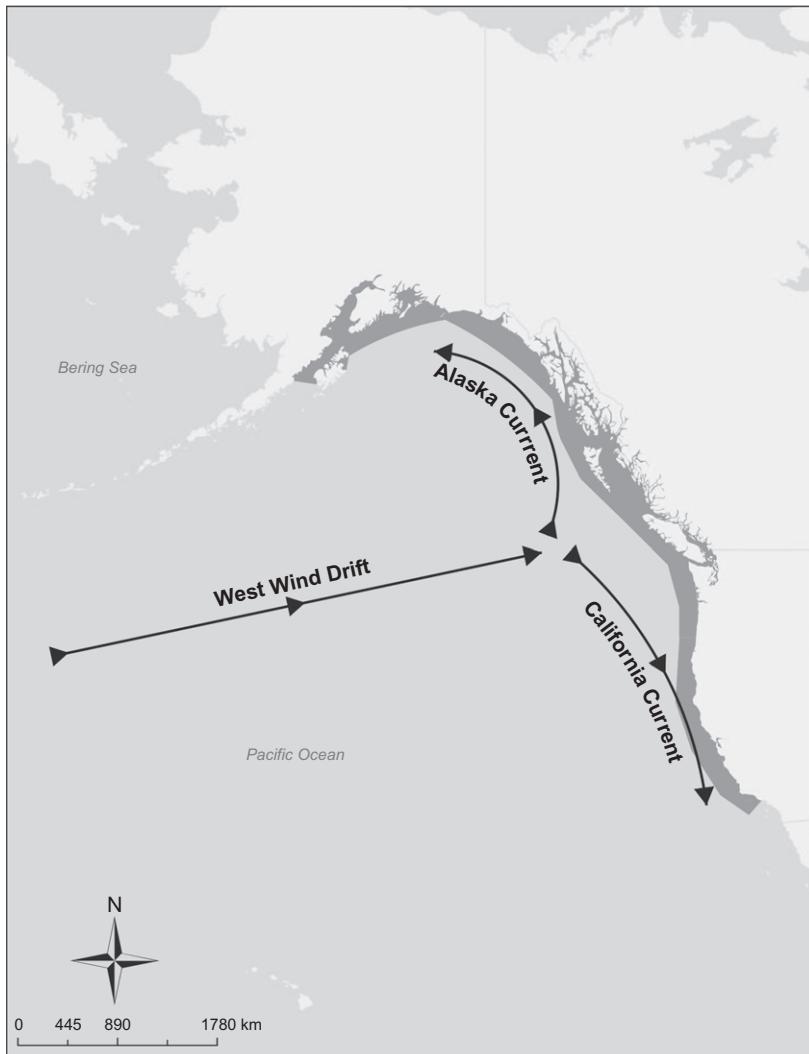
**Keywords:** Dungeness crab, *Cancer magister*, *Metacarcinus magister*, Crab fishery, Decapod, Crustacean, Invertebrate fishery



## 1. INTRODUCTION

The Dungeness crab was originally described in 1852 by James Dana ([Dana, 1852](#); [Jensen and Armstrong, 1987](#)). Recent publications ([Wicksten, 2009](#)) have referred to the Dungeness crab as *Metacarcinus magister*, based on morphological studies by [Schweitzer and Feldmann \(2000\)](#), who elevated the older subgenus name *Metacarcinus*, established in 1862, to full genus level. However, molecular work by [Harrison and Crespi \(1999\)](#) does not support the monophyly of the genus *Metacarcinus* nor of some other cannid genera used by [Schweitzer and Feldmann \(2000\)](#). Thus, I follow [Kuris et al. \(2007\)](#) in retaining the name *Cancer magister*. Both [Kuris et al. \(2007\)](#) and [Wicksten \(2009\)](#) provide excellent dichotomous keys to the adult cannid crabs of the California and Alaska Currents. As with all brachyurans, males have a narrow pointed abdomen, while females have a broader, rounded abdomen.

This chapter updates historic reviews and synthesizes the literature on the biology, ecology and fishery of *C. magister* throughout its range ([Fisher and Velasquez, 2008](#); [Melteff, 1985](#); [Pauley et al., 1986](#); [Wild, 1983c](#)). Since *C. magister* ranges from the Pribolof Islands, Alaska, to Santa Barbara, California, the organism inhabits both open oceans (California and Alaska Currents) and inland fjords (Puget Sound through the inside passage) ([Figure 3.1](#); [Jensen and Armstrong, 1987](#)). Due to the multitude of environments that *C. magister* lives in, the biology of the organism changes over the species range ([Table 3.1](#)). For example, off California and Oregon, larvae are released during the winter, while in Alaska, larvae are released during the summer ([Jaffe et al., 1987](#)). Therefore, throughout this review, I state where research was conducted, so readers can view the studies in the broad context of the entire population. Historic reviews have focused on the population in the California Current and relatively little coverage of the Alaska Current has been given. Many of these reviews have primarily focused on the fishery and only briefly touched on the biology and ecology of *C. magister*. Thus, in this review, I first provide a brief introduction to the habitats *C. magister* occupies, followed by an extensive review of the biology and ecology of the species. I conclude by reviewing the management of the fishery, the impacts of the fishery (both direct and indirect) and recent breakthroughs in catch prediction.



**Figure 3.1** Distribution of *C. magister* (dark grey shading) throughout California and Alaska Currents. Arrows denote the general direction of currents. *Base map provided by ESRI (2011).*



## 2. HABITAT AND OCEANOGRAPHY

The Alaska and California Currents originate where the West Wind Drift collides with Vancouver Island and divides into currents that move north as the Alaska Current and south as the California Current (Figure 3.1; Hickey,

**Table 3.1** Peak reproductive timing throughout the range of *C. magister*

Location	Moultng/ mating	Egg deposition	Hatching	Larval duration (range of time)	Settlement
California	March– June	September– November	December– February	115 (105–125) <small>Text</small>	April–May
Oregon– Washington	March– June	October– December	January– March	130 (89–143)	April– August
Puget Sound	April– September	October– December	February– May	150	June– August
British Columbia	No data	September– February	December– June	No data	July–Later
Alaska	June–July	September– November	April– August	154 (146–162)	September– October

See text for citations

1979; Mann and Lazier, 2006). The location of the bifurcation shifts to the south ( $\sim 47^{\circ}\text{N}$ ) in the winter and northwards to  $\sim 50^{\circ}\text{N}$  in the summer. Both the California and Alaska Currents are subject to large inter- and intra-annual variations that affect the hydrodynamics of the ecosystem (Huyer et al., 1979; Mantua and Hare, 2002). A large multiyear cycle known as the Pacific Decadal Oscillation (PDO) is driven by changes in the amount of water transferred into the California and Alaska Currents from the West Wind Drift (Minobe and Mantua, 1999). During a cool (negative) phase PDO—characterized by colder than average water temperatures in the Northeast Pacific ocean—more cold water is shifted into the California Current and southward flow is enhanced. During a warm (positive) phase, the converse is true and more water is shifted into the Alaska Current and southward flow in the California Current is decreased. PDO phase affects all trophic levels throughout the California and Alaska Current ecosystems (Hooff and Peterson, 2006; Keister et al., 2011; Mantua et al., 1997).

## 2.1. California Current

### 2.1.1 Oceanography

The California Current is the eastern boundary of the North Pacific Subtropical Gyre and is characteristically broad ( $\sim 500\text{ km}$  wide) and slow-moving ( $5\text{--}10\text{ cm s}^{-1}$ ) (Bakun, 1996; Strub and James, 1988). Below the California Current on the continental slope is a poleward counter current known as the California Undercurrent (Hickey, 1979). The undercurrent

flows at depths of 200–300 m with a mean velocity of  $10 \text{ cm s}^{-1}$  (Collins et al., 2000; Pierce et al., 2000; Reed and Halpern, 1976). On an intra-annual level, changes in atmospheric pressure systems cause seasonal changes in winds and currents (Lynn and Simpson, 1987). During the winter, winds blow towards the north, creating an oceanic surface current (known as the Davidson Current or Inshore Counter Current) that flows north at a mean velocity of  $15 \text{ cm s}^{-1}$  (Austin and Barth, 2002; Huyer et al., 1989; Strub and James, 1988). While the Davidson Current is flowing northwards, the California Current is still flowing southward off the continental shelf. Our understanding of how far off the shelf northwards flow occurs is minimal; northwards flow is reported as far as 300 km from shore in some areas and in others to be restricted to the continental shelf (Hickey, 1979). Over the course of about 1 week in the spring, during an event known as the spring transition, winds start blowing towards the south and the California Current begins flowing south over the continental shelf (Huyer, 1977). The California Current ecosystem is a monsoonal upwelling system driven by the change in the location of the North Pacific High (Huyer, 1983). Following the spring transition, during the spring and summer, winds are characteristically upwelling favourable, while during the fall and winter, winds are downwelling favourable.

### **2.1.2 Habitat**

In the California Current, unconsolidated sediments (sand, mud and sand/mud mixtures) are 4.5 times more abundant than hard substrates (Ramosos, 2004). On the continental shelf, soft sediments (the habitat of *C. magister*) account for ~53% of the bottom, the majority of which is sandy. Although *C. magister* often preferentially settle in estuaries, there are relatively few estuaries and inlets in the California Current system, and thus, the majority of *C. magister* reside in the open ocean.

## **2.2. Alaska Current**

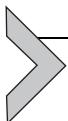
### **2.2.1 Oceanography**

Where the West Wind drift collides with Vancouver Island, the ocean is characterized by ‘confused’ (non-directional) currents with numerous eddies ( $10\text{--}25 \text{ cm s}^{-1}$ ) and meanders (Thomson, 1981). Along Vancouver Island, a summertime nearshore current flows northwest along the continental shelf. The Alaska Current flows northwards off the shelf at an average velocity of  $25 \text{ cm s}^{-1}$  (Thomson, 1981). The same change in atmospheric pressure that influences the California Current causes the Alaska Current

to accelerate northwards during the winter. The interaction between fresh-water runoff from the numerous rivers in Alaska and British Columbia and winds causes the circulation of the Alaska Current to be variable (Stabeno et al., 2004). The Alaska Current is characteristically downwelling favourable with mean velocities of  $\sim 30 \text{ cm s}^{-1}$  (Favorite, 1967). The current flows northwards into the Gulf of Alaska where it turns eastward as the strong Alaska Stream. The Alaska Stream then flows along the Aleutian Peninsula until it collides with the Oyashio Current and flows southward. Extending from Puget Sound (Washington) northwards through the Gulf of Alaska is a network of inland waters with complex circulation driven by tidal currents and freshwater input. The complex circulation patterns likely have significant effects on the biology of *C. magister* especially as the larvae disperse.

## 2.2.2 Habitat

I was unable to find any literature on the subtidal habitats of the Alaska Current. A recent publication by the National Marine Fisheries Service's Alaska Fisheries Science Center has discussed future plans to fill this gap in knowledge (Sigler et al., 2012).

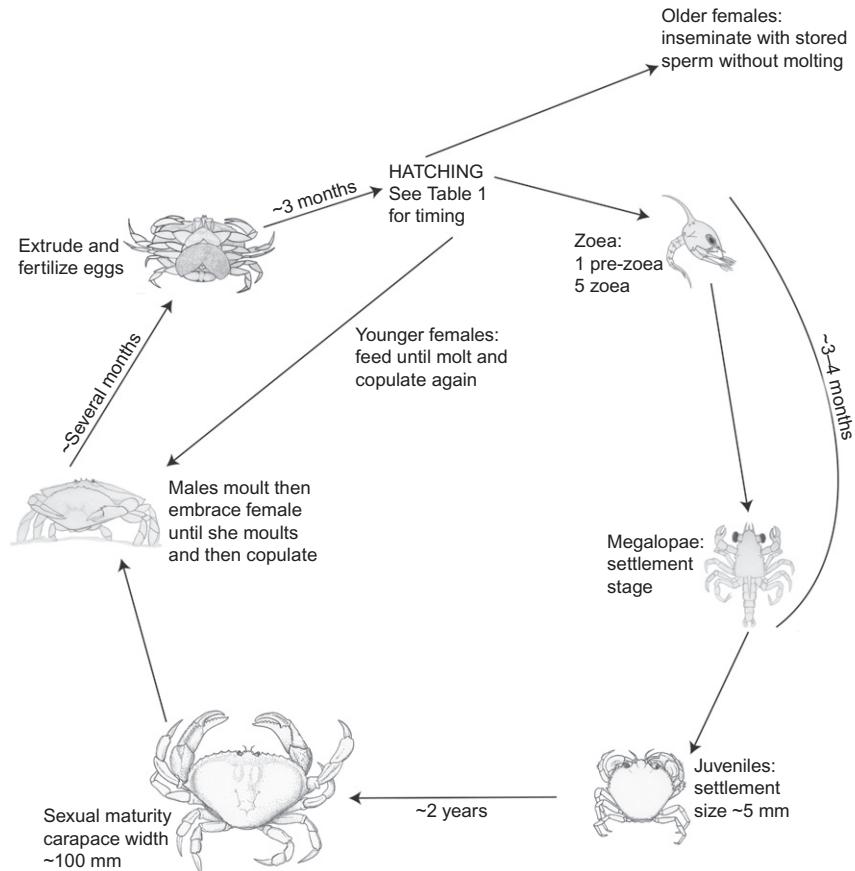


## 3. BIOLOGY AND ECOLOGY

### 3.1. Reproduction

#### 3.1.1 Mating

In brachyurans, mating occurs between recently moulted (soft) females and males that have already moulted and since re-hardened (Figure 3.2; Hartnoll, 1969; Snow and Nielson, 1966). Dungeness crabs reach sexual maturity at a carapace width of 100 mm, which occurs at 2 years of age in Humboldt County, California; however, in Alaska, crab gonads are not fully developed at a carapace width of 100 mm, so eggs are not extruded until the following year ( $\sim 3$  years old) (Butler, 1961; Cleaver, 1949; Hankin et al., 1989; Scheding et al., 1999). When females are close to moulting, males become more active and move towards the nearshore (Barry, 1985; Cleaver, 1949; MacKay, 1942). Males will grasp and carry a female that is close to moulting for up to 2 weeks in a 'premating embrace'. The data conflict about what happens when the female is ready to moult: either (1) the female is released by the male and moult outside the embrace of the male (Cleaver, 1949) or (2) the female moult while being embraced by the male (Butler, 1960; Cleaver, 1949; Snow and Nielson, 1966). After the female



**Figure 3.2** Life cycle of *C. magister*. Timing is relative and varies throughout the range of the species (see Table 3.2 for timings).

moult, the male stands over the female who lies with her dorsal side on the substrate and they both extend their abdomens out and away from their bodies. Then using modified pleopods, the male deposits spermatophores into the female gonopores. Following copulation, some of the seminal fluid hardens into a sperm plug which prevents other males from mating with the female (Jensen et al., 1996). Since males mate multiple times each year and the sex ratio of males to females is 1:1, competition for females is high and thus the sperm plug reduces sperm competition (Oh and Hankin, 2004; Orensan and Gallucci, 1988). Females who did not undergo an annual moult were found to have retained sperm and researchers hypothesized that the sperm remain viable for up to 2.5 years (Hankin et al., 1989) and recent molecular analysis corroborates this hypothesis (Jensen and Bentzen, 2012).

Researchers have speculated that intensive fishing on male crabs reduces reproductive output of females (Smith and Jamieson, 1991b). To test this, two techniques have been suggested to determine whether or not females mated during the previous mating season. First, the process of embracing during mating injures the limbs of the crabs which cause scarring, and early work suggested that the presence of mating scars could be used to assess mating success (Cleaver, 1949). A recent in-depth examination of this technique determined that not all crabs are scarred during mating and that limbs are also scarred by other processes, making the technique ineffective (Ainsworth, 2006). The second technique is more promising. Sperm plugs are found to still be present in the female reproductive tract 180 days after copulation, and thus, dissecting females to look for sperm plugs provides a reliable indicator of whether or not females mated that year (Oh and Hankin, 2004).

Studies in Northern California and Oregon that used sperm plugs to indicate mating success determined that reproductive output is not limited and ~83% of females showed evidence of successful mating the previous year (Dunn and Shanks, 2012; Hankin et al., 1997). Mating success in Hood Canal, Washington, an enclosed glacial fjord, was comparable (~80% of females had mated) to values in the open ocean (L.K. Rasmussen, unpublished work).

### 3.1.2 Brooding

In Central and Northern California, the weight of ovarian tissue increases linearly until the eggs are extruded (Wild, 1983a). A few months following copulation, females extrude their eggs, thereby inseminating them, and attach them to the setae on the pleopods below the abdominal flap (Figure 3.2; Wild, 1983b). When the eggs are extruded, they are bright orange (Buchanan and Milleman, 1969). The timing of egg deposition varies greatly throughout *C. magister*'s range, with females becoming ovigerous from September–November in California, October–December in Oregon and Washington, September–February in British Columbia and September–November in Alaska (Table 3.1; Jaffe et al., 1987; Shirley et al., 1987). Laboratory studies in Alaska have demonstrated that female crabs do not extrude eggs annually (Swiney and Shirley, 2001). In a comprehensive follow-up to their 2001 work, Swiney et al. (2003) conducted a field study that corroborated their laboratory finding that females do not extrude their eggs annually. They suggest that there are two reproductive pathways based on the size of female crabs: (1) large (carapace width >141 mm) females store sperm but do not moult or extrude eggs annually and (2) smaller females (carapace width <141 mm) moult, mate and extrude eggs annually. Larger female

crabs extrude their eggs later in the season than smaller crabs and thus their eggs hatch later in the season. The most probable explanation is that the time period between hatching and mating is too short for the gonads of large females (carapace width >141 mm) to fully develop, forcing them to spawn every other year ([Table 3.1](#)). Whereas the earlier hatching times of smaller females provide a sufficient time period between hatching and moulting for their gonads to fully develop.

Females carry between 1.5 and 2.5 million eggs and there is no correlation between carapace width and fecundity ([Hankin et al., 1989](#); [Wickham, 1979b,c](#)). Due to the large number of eggs that are extruded, the abdominal flap is raised significantly from the cephalothorax limiting female movement (L.K. Rasmussen, personal observation). Females must bury themselves in sand 5 to 10 cm deep in order for eggs to remain attached to the setae ([Fisher and Wickham, 1976](#); [Wild, 1983b](#)). After egg extrusion, females in enclosed waters (Puget Sound and Alaska) migrate to shallow water and form dense aggregations ([Armstrong et al., 1988](#); [Scheding et al., 1999](#)). In Puget Sound, aggregations of brooding females were observed in 1 to 3 m depth of water within dense eelgrass bands, whereas in Alaska, dense aggregations of brooding females occur at a depth of ~16 m ([Armstrong et al., 1988](#); [Stone and O'Clair, 2002](#)). Anecdotes from the Washington coast during winter razor clam (*Siliqua patula*) openings describe numerous ovigerous females in the surf zone ([Northrup, 1975](#)). It is likely that females in the coastal ocean form aggregations, but the depth at which this occurs is unknown ([Diamond and Hankin, 1985](#)). A 12-year time series of brooding location collected in an enclosed fjord in Alaska, determined that females returned to a specific site characterized by unconsolidated, homogeneous, highly permeable sand ([Stone and O'Clair, 2002](#)).

[Wild \(1983b\)](#) found a negative linear correlation between water temperature and the length of time that egg masses were brooded. Brooding times ranged from 130 days at 9 °C to 65 days at 17 °C. Although rate of development decreased with a decrease in temperature, the researcher noted that as temperature rose from 13 to 17 °C, fewer eggs were produced and hatching success declined. [Mayer \(1973\)](#) suggested that at a salinity of 25, 12 °C may represent the maximum temperature at which eggs develop normally.

## 3.2. Larval biology

### 3.2.1 Hatching

Hatching occurs when prezoea are fully developed, at which time the egg masses are dark brown ([Buchanan and Milleman, 1969](#)). Timing of hatching

varies over the range of *C. magister* and occurs in late December–February in Central California, January–March in Northern California and Oregon, February–May in Puget Sound, December–June on the outer coast of British Columbia, April in the Queen Charlotte Islands and April–August in Alaska (Table 3.1; Fisher, 2006; Jaffe et al., 1987; Shirley et al., 1987; Swiney and Shirley, 2001). Many species of crabs synchronize the release of their larvae to specific tides and light levels; however, no study has yet examined the larval release patterns of *C. magister* (Morgan, 1995; Stevens, 2003, 2006). Plots of hatching date from laboratory studies suggest that there are no endogenous cues to larval release (Wild, 1983b). *In situ* studies should be conducted to ascertain whether or not larval release is synchronized.

The biology and dispersal of the larval stages of *C. magister* are well studied. The larvae are often released as prezoea, and initially, researchers thought prezoea released into the water column did not survive, but more recent studies have demonstrated that prezoea survive and develop into stage-I zoea (Buchanan and Milleman, 1969; MacKay, 1942; Poole, 1966). In the laboratory, the transition from prezoea to stage-I zoea takes only a few seconds, and thus prezoea are only in the water column for seconds to minutes. *C. magister* then progress through five zoal stages and one megalopal stage in the water column (Figure 3.2; Poole, 1966). All five zoal stages of *C. magister* have large compound eyes, four spines (one dorsal, one rostral and two lateral) and swim by flexing their maxillipeds. Zoal spine lengths increase as incubation temperature decreases (Shirley et al., 1987). The megalopa of *C. magister* has large compound eyes, two spines (one dorsal and one rostral) and swim with their pleopods. A set of intermoult stages have been developed for megalopae that allow researchers to determine the relative age of megalopae (Hatfield, 1983).

In a multiyear project, the Oregon Fish Commission worked to develop methods for culturing the larvae of *C. magister* (Gaumer, 1969, 1970, 1971; Reed, 1966, 1969). While rearing larvae, the Oregon Fish Commission tested the effects of multiple factors on the growth and development of zoea. The development of zoea is influenced by water temperature and to a lesser extent salinity. Normal development occurs over a temperature range of 10.0–13.9 °C and a salinity range of 25–30. The duration of each larval stage decreases as water temperature increases, though at temperatures >14 °C, mortality increases (Ebert et al., 1983). *C. magister* from Oregon were used for these studies, so the results likely apply to the open ocean population in the California Current and not to populations in inland waters and/or the Alaska Current.

It appears that although temperatures within the range of 14–22 °C do not affect the number of juveniles that metamorphose into adults ([Sulkin et al., 1996](#)), temperature may influence larval survival in the open ocean. [Sulkin and McKeen \(1989\)](#) used crabs from Puget Sound to examine the potential effects of elevated water temperatures on development. They tested higher water temperatures (10, 15 and 20 °C) and determined that survival was highest for zoea reared in 10 °C water, but the duration of each stage drastically decreased as water temperature increased ([Table 3.2](#)). [Sulkin and McKeen \(1996\)](#) examined historic temperature records and mimicked weekly temperatures from the open ocean (~10–12 °C) and Puget Sound (~7–12 °C) in the laboratory. They determined that zoea reared at Puget Sound water temperatures were in the water column 44% longer than larvae raised at open ocean temperatures.

**Table 3.2** Effect of temperature on the day of moulting (mean day), length of the stage (days) and percentage of larvae surviving

Stage	Temperature	Mean day	Length of stage	Percent of population surviving
Zoea I	10	13.2	13.2	87
	15	8.3	8.3	85
	20	7.5	7.6	72
Zoea II	10	24.5	11.3	83
	15	14.3	6.2	82
	20	13	5.5	62
Zoea III	10	37.1	12.7	79
	15	20.8	6.8	75
	20	18.8	6.1	57
Zoea IV	10	50.8	13.7	71
	15	28.2	7.3	66
	20	25.1	6.9	44
Zoea V	10	68.9	18.8	46
	15	38.5	10.4	27
	20	NA	NA	0

Adapted from [Sulkin and McKeen \(1989\)](#).

Moloney et al. (1994) combined results from multiple laboratory studies on the development rate and mortality of larvae at different temperatures and salinities to generate a numerical model of development that was combined with historically accurate simulations of water temperatures and salinities in the California Current. Modelled larval duration ranged from 74 to 163 days depending on latitude, which is slightly different than the measured durations (Table 3.1). Additionally, they argue that it is inaccurate to assume that mortality of larvae within the plankton is constant, and additional work is needed to determine what the mortality rate of larvae is while they are in the plankton. Their results demonstrate that the influence of water temperature and salinity can alter the rate of larval development by a factor of two. The extended length of development in colder water may increase the overall mortality of larvae and thus may explain inter-annual variation and north-south variation in the population. They note that their work only applies to open ocean populations in the California Current and that enclosed populations in areas such as Puget Sound are not represented.

### 3.2.2 Diet

Laboratory studies have found that unfed larvae and larvae fed only in the first 24 h after hatching can subsist on their yolk reserves for approximately 15 days before they die (Reed, 1969; Sulkin et al., 1998a). Attempts to rear zoea on a diet solely of diatoms were unsuccessful (Hartman and Letterman, 1978). Zoea that were fed mussel larvae (*Mytilus edulis*) did not survive but did well when fed barnacle larvae (*Balanus glandula*) (Gaumer, 1971; Reed, 1969). Zoea fed diets of brine shrimp (*Artemia* sp.) successfully metamorphosed, and when diatoms (*Skeletonema* sp.) were added to the diet, survival was >88%; however, if brine shrimp concentration exceeded 5 shrimp ml<sup>-1</sup>, then survival of zoea decreased (Gaumer, 1971; Hartman, 1977). The larvae of *C. magister* are capable of feeding in the dark, suggesting they are not ocular hunters (Sulkin et al., 1998a). A short period of feeding each 24-h period is sufficient in preventing mortality of larvae (Sulkin et al., 1998a). Early zoea of *C. magister* feed on protists that naturally occur in the water column (Sulkin et al., 1998b). Stable isotope work on wild megalopae suggests that they are omnivorous, which coincides with findings from the aforementioned laboratory studies (Kline, 2002). Larvae also commonly consume heterotrophic prey that ingest toxic algae, and thus, researchers examined the effect of the toxins on the survival of zoea (Garcia et al., 2011). Results indicated that fewer zoea survived that consumed toxic prey than those that did not, and not surprisingly individuals that had consumed

toxic prey and survived remained at each stage longer than those that did not. Following up, researchers have demonstrated that the consumption of toxic food sources decreases larval survival not because the food is toxic, but rather the food is nutritionally deficient (Burgess, 2011).

### 3.2.3 Predation

No literature reports selective feeding by pelagic invertebrates or fishes on the zoea of *C. magister*. In the field, I have dissected English sole (*Parophrys vetulus*) and found their stomachs completely full of stage-I *C. magister* larvae (L.K. Rasmussen, personal observation). The megalopae of *C. magister* are consumed by a variety of fish species such as coho salmon (*Oncorhynchus kisutch*), chinook salmon (*Oncorhynchus tshawytscha*) and hake (*Merluccius productus*) (Botsford et al., 1982; Emmett and Krutzikowsky, 2008; Methot, 1989).

### 3.2.4 Larval behaviour and swimming

The zoea of *C. magister* respond to light in laboratory studies, moving deeper in the water column as light intensity increases (Gaumer, 1971; Jacoby, 1982). In the laboratory, zoea swim into currents (positive rheotaxis), and megalopae have slightly stronger rheotaxis than zoea (Gaumer, 1971). Ninety-five percent of megalopae observed *in situ* displayed strong positive rheotaxis (L.K. Rasmussen, in preparation). As megalopae approach settlement, they are attracted to light (positive phototaxis) and cling to objects they encounter while swimming (thigmokinesis) (Hatfield, 1983; Reilly, 1983a).

Reported values of swimming speed for different larval stages vary between studies; however, all studies demonstrate that compared to many other planktonic organisms, *C. magister* are strong swimmers (Fernandez et al., 1994b; Gaumer, 1971; Jacoby, 1982). In general, early zoea (I–III) are capable of swimming at speeds ranging from 0.58 to 0.95 cm s<sup>-1</sup> (Gaumer, 1971; Jacoby, 1982), while later-stage zoea (IV and V) are capable of swimming at a speed of 1.5 cm s<sup>-1</sup>. *In situ* swimming speeds of the megalopae average 12 cm s<sup>-1</sup> with a range of 5–20 cm s<sup>-1</sup> (L.K. Rasmussen, in preparation), but swimming speeds of megalopae determined in the laboratory are more variable and range from 4.2 to 44 cm s<sup>-1</sup> (Fernandez et al., 1994b; Jacoby, 1982).

### 3.2.5 Vertical migration

Zoea and megalopae vertically migrate and occupy the neuston at night and/or early evening, returning to deeper waters during the day (Booth et al., 1986). The depth they occupy during the day has eluded researchers for

many years. In a comparative study of the Puget Sound (inland waters) and the open ocean off Vancouver Island (on the continental shelf), researchers determined that late intermoult stage megalopae were migrating to depths of ~160 m in Puget Sound and ~25 m in the open ocean during the day (Jamieson and Phillips, 1993). Off the continental shelf, megalopae migrate to depths >70 m, and upon returning to the continental shelf, may stop vertically migrating (A.L. Shanks and G.C. Roegner, unpublished data). Puget Sound megalopae are smaller and settle later than oceanic megalopae, and researchers speculate that differences in vertical migration depth between oceanic and inland megalopae may aide in the retention of larvae within Puget Sound which could be the cause of the overall small size of Puget Sound megalopae. (Hobbs and Botsford, 1992; Lough, 1976; Reilly, 1983a). In Alaska, *C. magister* zoea and megalopae may undergo a crepuscular (occupying the surface only at dusk/dawn) rather than diel migration (Park and Shirley, 2005).

### **3.2.6 Cross-shelf distribution**

The movement of *C. magister* larvae within enclosed waters (e.g. Puget Sound, British Columbia and Alaska Fjords) and the Alaska Current has not been studied enough to provide a description of the movement of larvae. Thus, this section pertains to the open ocean population in the California Current. Stage-I larvae are released within 8 km of shore and migrate off the continental shelf as they develop (Lough, 1976; Reilly, 1983a). Stages I and II zoea are commonly found on the continental shelf, while stages III–V are found off the continental shelf at distances >150 km (Reilly, 1983a). While over the continental shelf, larvae will be transported northwards by the Davidson Current, but as they migrate off the shelf, they may enter the California Current (depending on the distance of southward flow from shore) and be transported southward. The majority of stage V larvae are concentrated 50–100 km from shore (Reilly, 1983a). After migrating off the shelf, the zoea moult into megalopae. Although megalopae can be found at great distances offshore, they must settle in the nearshore habitat (Jamieson and Phillips, 1988). Thus, there are mechanisms that advect the megalopae of *C. magister* from seaward of the continental shelf to shelf waters and subsequently back to the nearshore environment.

### **3.2.7 Dispersal patterns**

The commercial catch of *C. magister* on the outer coast of California, Oregon and Washington has undergone many oscillations, and considerable

research has attempted to explain them ([Methot, 1989](#)). I will discuss later why these oscillations are not likely caused by intensive fishing pressure. Many researchers speculate that the effects of oceanographic conditions on dispersal and recruitment of larvae are the cause of these fluctuations. Thus, many studies have examined the influence of oceanography in the California Current by correlating commercial catch to physical factors ([Table 3.3](#)). Since it takes approximately 4 years for a Dungeness crab to recruit from a larva to the fishery, many researchers correlate commercial catch with physical indices that occurred 4 years prior to the fishery ([Hackett et al., 2003](#)). These numerous studies provide us with an idea of how the larvae of *C. magister* disperse in the ocean.

In his thesis, [Lough \(1975\)](#) enumerated plankton from samples off Newport Oregon over a 2-year period. He determined that initially, larvae are released into the Davidson Current and swept north until the spring transition occurs and at which point larvae are swept south with the California Current. However, as discussed earlier, we are unsure how far off the shelf larvae migrate and how far off the continental shelf the Davidson Current occurs, so it is possible that the cross-shelf migration of larvae moves them from the Davidson Current into the California Current before the spring transition occurs shifting the direction larvae are advected. Upwelling indices are correlated to commercial catch with a time lag of 0.5–1.5 years ([Peterson, 1973](#)). However, since it takes 4 years for *C. magister* to recruit to the fishery, this correlation does not demonstrate any effects of upwelling on the dispersal of larvae ([Botsford and Wickham, 1975](#); [Peterson, 1973](#)). Correlations between catch and sunspot number have also been attempted, though other articles suggest that this publication may have been in jest and catch patterns cannot be explained by sunspots ([Hankin, 1985](#); [Love and Westphal, 1981](#)). A study off California suggests that stage-I zoea are transported offshore by a combination of estuarine runoff and upwelling circulation, though there are relatively few estuaries in the California Current, and most upwelling occurs a few months after larvae are released, implying that these hypotheses are likely incorrect ([Reilly, 1983a](#)). Comparing catch to wind data, researchers found a correlation (with a 4-year lag) with southward wind stress ([Johnson et al., 1986](#)). Recalculating the wind stress reported in [Johnson et al. \(1986\)](#) and including data on the distribution (including vertical migration) of megalopae, megalopal abundance in the nearshore environment was shown to be correlated with onshore winds ([Hobbs et al., 1992](#)). Off British Columbia (just north of the California Current), for multiple years there were no recruitment events of *C. magister* even

**Table 3.3** Influence of physical and biological factors on the biology of *C. magister*

Year	Findings
<i>Physical factors</i>	
Peterson (1973)	Time lag 0.5–1.5 years between upwelling index and catch (does not correlate with recruitment). Suggest the correlations due to food availability
Botsford and Wickham (1975)	Time lag 9–12 years does not correlate with recruitment; suggest correlation due to food availability
Love and Westphal (1981)	Correlation to sunspot number; other researchers suggest this chapter may have been written in jest
Wild (1983b)	Low catch years correlated with warmer winter water temperatures (and weaker southward transport) 4 years earlier
Johnson et al. (1986)	Correlation between catch and southward wind 4 years earlier
McConaughey et al. (1992)	Increased megalopae in nearshore environment during years of increased shoreward transport
Hobbs et al. (1992)	Increased settlement of larvae during years with decreased northwards transport
McConaughey et al. (1994)	Suggest that larvae may be retained in the nearshore environment rather than being transported offshore
Botsford and Lawrence (2002)	Commercial catch correlated with overall cooler conditions in the California Current
Shanks and Roegner (2007)	Recruitment and commercial catch correlated with day of the year of the spring transition and amount of returning larvae
Shanks et al. (2010)	Recruitment and commercial catch negatively correlated with Pacific Decadal Oscillation index; population limited by recruitment at beginning until levels off and possibly cannibalism affects recruitment
Shanks (in press)	Recruitment and commercial catch correlated with amount of upwelling following spring transition. Catch did indeed level off when recruitment was approximately 1 million megalopae in 1 year
<i>Biological factors</i>	
Botsford and Wickham (1978)	Suggested that fluctuations may be caused cannibalism. Botsford (1984) stated if cannibalism was the cause the cycles would likely have been more stable

**Table 3.3** Influence of physical and biological factors on the biology of *C. magister*—cont'd

Year	Findings
Wickham (1979b)	Suggested predation by <i>C. errans</i> may impact reproductive output, but the effect is not big enough to cause fluctuations
McKelvey et al. (1980)	Density-dependent egg/larval survival influenced by production
Botsford et al. (1982)	No correlation between catch and Chinook and Coho Salmon catch 4 years earlier
Botsford et al. (1983)	No correlation between catch by humans and fluctuations in population
(Shanks, in press)	Suggested that when recruitment is high, cannibalism and competition among juvenile crabs impact the population

though many megalopae were found in the neuston on the continental shelf which caused researchers to suggest that the Vancouver Coastal Current flowing northwards in the opposite direction of the shelf break current acts as a barrier to the transport of megalopae across the continental shelf (Jamieson et al., 1989). Thus, megalopae only make it back to the nearshore environment when the Vancouver Coastal Current relaxes. Additionally, they examined surface drifter tracks and noted that the drifters were transported across the shelf by winds from the south and thus hypothesize that megalopae may be transported across the shelf by similar winds.

Over a 5-year period, McConaughey et al. (1992) used a modified beam trawl in estuaries and on the continental shelf to collect recently settled juveniles. They correlated recruit density to oceanic indices and concluded that westward Ekman transport may not be transporting zoea off the shelf. Additionally, they found a negative correlation between the number of settlers and the amount of northward alongshore transport. They demonstrated that in years when larvae are transported further north by the Davidson Current, recruitment in the California Current is limited. Further they hypothesize that since larvae are initially transported northwards, it is possible that they could be transported into the Alaska Current and thus do not move southward when the Davidson Current disappears (spring transition). Thus, the geographic closeness of the Washington coast to the Alaska Current may mean that the populations in Washington are dependent on recruitment from populations that are further south. In follow-up work, they found a positive correlation with recruitment and the amount of

onshore winds ([McConaughey et al., 1994, 1995](#)). They use the findings from these three studies to suggest that larvae of *C. magister* do not undergo an ontogenetic migration off the continental shelf but rather are retained in the nearshore. The hypothesis that larvae are retained in the nearshore is based on sampling of settled juveniles; however, extensive plankton sampling efforts by other researchers ([Jamieson and Phillips, 1993](#); [Jamieson et al., 1989](#); [Reilly, 1983a](#)) have not corroborated that larvae are retained in the nearshore.

Researchers in Alaska reported finding late-stage zoea and megalopae in their plankton samples at the time when hatching occurs in Alaska ([Park et al., 2007](#)). Based on the stage of these larvae, it was clear that they had been released much earlier, and thus likely hatched in the California Current. Therefore, the most likely explanation for the presence of these late-stage larvae is that they were transported north by the Davidson Current into the Alaska Current. These data demonstrate that there is connectivity (at least in some years) between the populations in the California and Alaska Currents.

Using the annual return of megalopae to the shore as measured by the number of megalopae caught in a shore-based light trap in Coos Bay, Oregon, [Shanks and Roegner \(2007\)](#) correlated oceanographic indices to the number of returning megalopae (as measured by the light trap) and commercial catch 4 years later. They determined that larval recruitment explained ~90% of the variability in the adult population from the Washington/Oregon border to San Francisco, California. Furthermore, they found a strong positive correlation between the date of the year of the spring transition and number of recruits, which suggests that the shift in currents caused by the spring transition (from the Davidson to California) strongly influences the recruitment of *C. magister* larvae. Shanks and colleagues published follow-up work (2010) examining 4 additional years of recruitment and reported a negative correlation between recruitment and the PDO index. They suggest that enhanced southward transport in the California Current during negative PDO index years may be the cause of the increased recruitment. Additionally, there appears to be a positive correlation between recruitment and the amount of upwelling that occurs following the spring transition ([Shanks, in press](#)). By combining the three physical factors that affect larval return (date of spring transition, PDO index phase and amount of upwelling), one can observe a strong three-factor linear relationship. By splitting recruitment seasons into high (>100,000) and low (<100,000) settlement years, two parallel relationships are observed. When recruitment is correlated to the date of the spring transition, there is a negative relationship

and when recruitment is correlated to the amount of upwelling following the spring transition, there is a positive relationship. Shanks proposes the following conceptual model to explain these three correlations. First, he hypothesizes that a negative PDO index increases southward transport of larvae, which increases the possibility of the larvae settling in Oregon rather than further north. He hypothesizes that larvae are transported onto the shelf with the water that is brought onto the shelf by wind-driven upwelling which would mean that an earlier spring transition would result in a longer period of time that larvae can be advected onto the continental shelf. However, the amount of upwelling following the spring transition is not consistent, and thus, during years with increased upwelling, more megalopae are advected onto the continental shelf.

For both correlations, more larvae tended to recruit during negative phase PDO index years. Recently, Shanks has determined that there is a negative relationship between the number of megalopae recruiting in August and September and the PDO index from January through July, suggesting that the enhanced southward transport during negative PDO index years may transport larvae from as far north as British Columbia to Oregon (Shanks, *in press*).

After being transported onto the continental shelf, most likely by upwelling, larvae must migrate back to the nearshore environment to settle in the adult habitat. Historically, researchers hypothesized that megalopae may be transported across the shelf by clinging to the pleustonic (living in the surface of the water column) hydroid *Vellela vellela*, although subsequent research has disproved this hypothesis (Reilly, 1983a; Wickham, 1979c). Alternatively, the megalopae of *C. magister* have been observed to be concentrated in surface convergences on the continental shelf (L.K. Rasmuson unpublished data; Shenker, 1988). Johnson and Shanks (2002) created a daily time series of *C. magister* recruitment to an Oregon estuary and report pulsed recruitment events suggestive of cross-shelf transport by internal tides. Building on Johnson and Shanks (2002), Roegner et al. (2007) correlated daily larval settlement with multiple environmental factors and found that megalopal abundance was strongly correlated with the spring-neap tidal cycle, but settlement did not peak on the day of the spring tide, but rather occurred a few days after the spring tide. The lag in recruitment relative to the spring tide is characteristic of cross-shelf transport by internal waves (Shanks, 2006). Therefore, the researchers' findings corroborate earlier work and they suggest that internal waves were the mechanism of cross-shelf transport for *C. magister* megalopae.

Movement of larvae in enclosed fjords system is not well studied, but most work demonstrates that recruitment is highly variable. In Alaska, using light traps similar to those used by Shanks on the Oregon Coast, [Herter and Eckert \(2008\)](#) found that variations in settlement in the complex fjord systems of Alaska were correlated with tidal and lunar cycles. The large variations in settlement between fjords may be explained by small-scale variations in hydrodynamics. Extending the dataset of [Herter and Eckert \(2008\)](#), [Smith and Eckert \(2011\)](#) found highly variable recruitment at both regional ( $>300$  km) and small scales (2–6 km) in different fjords in Southeast Alaska. They suggest that the variability in recruitment both spatially and temporally can be explained by the complex circulation patterns present in the study area. In the enclosed waters of Puget Sound, [Dinnel et al. \(1993\)](#) tracked juvenile cohorts and reported that enclosed basins appear to rely on self-recruitment, and recruitment from other sources such as the ocean is limited. Additional research is needed to understand the movements and/or retention of larvae in enclosed basins.

In the California Current, most megalopae settle on the continental shelf; however, some migrate into estuaries to settle ([Miller and Shanks, 2004](#)). Estuaries have numerous fronts which concentrate larvae and may act as a conduit for the transport larvae into the estuaries from the continental shelf ([Eggleston et al., 1998](#)). For tidally generated fronts to transport megalopae into an estuary, megalopae must be concentrated in the tidal prism (the volume of water advected into or out of the estuary by the tide; [Roegner et al., 2003](#)). Once megalopae are ready to metamorphose into juveniles, it appears that most megalopae metamorphose under the cover of darkness, and the moulting of one megalopa will induce other megalopae to moult ([Fernandez et al., 1994a](#)).

### 3.3. Adult and juvenile biology

Although most *C. magister* settle on the continental shelf (within 10–15 km of shore), most available information is on the settlement and biology of juvenile crabs inside estuaries ([Carrasco et al., 1985; Methot, 1989](#)). Thus, throughout this section, unless stated otherwise, studies on the biology of juvenile crabs occurred in estuarine systems.

#### 3.3.1 Habitat

Many studies suggest that shell habitat (more specifically oyster beds) is important for the survival of juvenile crabs. However, shell habitats similar to oyster beds are not common in most Pacific Northwest estuaries or on the continental shelf and the majority of settlement likely occurs in open habitats

([Dumbauld, 1993](#)). The large number of studies examining the role of shell habitat is due to attempts by the Army Corp of Engineers to mitigate the effects of dredging shipping channels in estuaries ([Iribarne et al., 1995](#)). In areas without significant shell deposits, gravel/rocky habitats covered with macroalgae and eelgrass (*Zostera marina*) beds have the highest concentrations of juveniles ([McMillan et al., 1995](#)).

Adult Dungeness crabs live in coastal regions including the continental shelf, small estuaries and extensive inland waters (e.g. Puget Sound and Southeast Alaska) at water depths ranging from the intertidal to approximately 230 m ([Jensen, 1995](#)). In Puget Sound, based on observations from a submersible, most non-ovigerous females were distributed at depths from 20 to 80 m, while males were distributed at depths from 10 to 20 m ([Armstrong et al., 1988](#)). In an Alaskan fjord, the use of acoustic tags demonstrated that both males and females reside at depths >40 m during the winter and moved into shallow nearshore waters, <8 m, during the spring when larvae are released ([Stone and O'Clair, 2001](#)). Adults are primarily found in sandy-mud bottoms ([Cleaver, 1949](#)), where they bury into the sediment and possibly bury on a circadian rhythm, most commonly emerging from the substrate during nocturnal high tides ([McGaw, 2005](#); [Stevens et al., 1982](#)).

### **3.3.2 Movement**

Tracking juvenile cohorts in an estuary demonstrated that many 1-year-old crabs migrated out of the estuary onto the continental shelf, and by 2 years of age, all juvenile crabs had migrated onto the continental shelf ([Collier, 1983](#); [Stevens and Armstrong, 1984](#)). Tagging studies of adult males and females in the open ocean off Northern California and Oregon have found that distances travelled over nine months ranged from ~0.2 km to as great as ~100 km, but the majority of adults move less than 20 km ([Cleaver, 1949](#); [Diamond and Hankin, 1985](#); [Hildenbrand et al., 2011](#); [Snow and Wagner, 1965](#); [Stone and O'Clair, 2001, 2002](#); [Waldrone, 1958](#)). The average daily movement was 1.1–3.2 km day<sup>-1</sup>. Prior to spawning, many crabs move into the nearshore and/or estuaries ([Barry, 1985](#)). This does not imply that mating and larval release only occurs within estuaries, rather most larval release likely occurs on the continental shelf. Most female movement is across the continental shelf, but for males, most movement occurs in the alongshore direction ([Diamond and Hankin, 1985](#); [Hildenbrand et al., 2011](#)). In the inland waters of British Columbia, research suggests that males retreat to greater depth during winter than females, but overall, female crabs are more active over the course of a year ([Smith and Jamieson, 1991a](#)).

In estuaries, many populations move in and out of the intertidal each day to forage. Intertidal foraging is necessary to account for the extreme energy requirements of the large number of individuals present in estuaries (Holsman et al., 2003). Most migration into the intertidal environment occurs under the cover of darkness, so crabs can avoid visual predators (Holsman et al., 2006). If a preferred prey source of adults is present in the intertidal (and crabs are close enough to migrate), they will migrate into the intertidal to forage, even though their need to osmoregulate dramatically decreases the rate of digestion (Curtis et al., 2010; Stevens et al., 1982). Individuals must osmoregulate since salinities and oxygen level in the intertidal are lower from that of subtidal waters where *C. magister* usually inhabit. Thus, many individuals that forage in the intertidal must retreat to depth in order to digest their food.

### 3.3.3 Diet

Dungeness crabs are opportunistic feeders that are highly adapted to feeding in sandy habitats and do not appear to display strong preferences for specific prey items (Lawton and Elner, 1985). Juvenile *C. magister* are omnivorous and estuarine populations are able to capture more prey than continental shelf populations, which likely explains the increased growth rate of juveniles in estuaries (Jensen and Asplen, 1998; Tasto, 1983). Near San Francisco Bay, stomach contents of crab caught in an estuary had more bivalves in them and juveniles caught in the ocean had more fish (Tasto, 1983). However, in Washington, 1-year-old individuals mostly had crustaceans and mollusks in their stomachs, and 2-year-olds had high concentrations of crustaceans and fish (Stevens et al., 1982). The variety of food sources in these studies corroborate the opportunistic feeding of *C. magister*. This strong ontogenetic shift in feeding patterns of *C. magister*, as shown in Washington estuaries, may minimize competition and cannibalism between cohorts. However, there is no evidence of seasonal cycle in feeding (Stevens and Armstrong, 1984; Stevens et al., 1982).

Diets of adult *C. magister* have been closely examined, and overall, bivalves appear to be the most important food source (Butler, 1954; Gotshall, 1977; Stevens et al., 1982). However, the three studies just referenced found that different food items were most prevalent in the stomach contents: Butler (1954) clams, Gotshall (1977) fish and Stevens et al. (1982) Crangon shrimp. All of these studies, however, also found high concentrations of bivalves in the stomachs of crabs. *C. magister*, especially females, are well known to be highly cannibalistic on recently moulted

juveniles (Botsford and Hobbs, 1995; Eggleston and Armstrong, 1995; Fernandez, 1999; Stevens et al., 1982).

Adult crabs feed by probing the substrate with their claws (chelae) until a prey item is detected, at which point they contract their claws and remove the food. Adult *C. magister* have been observed excavating heart cockles (*Clinocardium nuttallii*; Butler, 1954). In the laboratory, bivalves buried in artificially oiled sediments were unable to bury as deep and thus were consumed more frequently by *C. magister* (Pearson, 1981). *C. magister* are also able to detect (at a distance) ground-up clams frozen in sea water using chemosensory abilities at concentrations of  $10^{-10}$  g l<sup>-1</sup> of clam extract (Pearson, 1979). In laboratory studies, crabs preferentially consumed smaller clams when given a choice (Juanes and Hartwick, 1990). Consumption of larger clams increased the probability of claws being damaged when cracking open clams, and crabs with damaged claws were unable to crack open clams.

### 3.3.4 Cannibalism

Cannibalism by young-of-the-year crabs on newly settled megalopae can be extremely high (Armstrong et al., 1988; Dumbauld, 1993; Eggleston and Armstrong, 1995). Juvenile crabs are highly cannibalistic and researchers hypothesize that moulting (from megalopae to juvenile and between juvenile instars) under the cover of darkness minimizes cannibalism. Cannibalism by the first settlement cohort strongly influences survival of later cohorts (Fernandez et al., 1993). In one study, as population density of young-of-the-year crabs increased, the total number of juveniles consumed by cannibalism increased, but the likelihood of juveniles being eaten decreased proportionally (Fernandez, 1999). Additionally, as the density of crabs increased, individuals emigrated away from areas of high density even when food abundance was artificially enhanced (Iribarne et al., 1994). This suggests that density-dependent cannibalism may strongly influence population dynamics.

### 3.3.5 Predation

Juvenile *C. magister* are common food items for a multitude of predators such as starry flounder (*Platichthys stellatus*), English sole (*Parophrys vetulus*) and the Staghorn sculpin (*Leptocottus armatus*), probably the most significant predator in estuaries (Armstrong et al., 1995, 2003). Juvenile *C. magister* are also consumed by adults of the introduced European Green crab (*Carcinus maenas*), although their habitats (vertical range in the intertidal) do not overlap, and thus, predation pressure is minimal (McDonald et al., 2001). Due to the large size of adult *C. magister*, they have relatively few predators. Well-known

predators of adult crabs are lingcod (*Ophiodon elongatus*), Cabezon (*Scorpaenichthys marmoratus*) and wolf eel (*Anarrhichthys ocellatus*; [Reilly, 1983c](#)). The primary habitat of these three fish species (rocky bottom) and *C. magister* (sandy bottom) often does not overlap. In Southeast Alaska, crabs make up ~15% of the diet of sea otters (*Enhydra lutris*) ([Garshelis et al., 1986](#)). Repeated test fisheries after the introduction of otters reported a 61% decline in the abundance of adult *C. magister* in areas where otters were prevalent. In recent years, where sea otter populations have recovered, the test fishery catch was not significantly different from zero for pots fished in <60 m depth of water ([Shirley et al., 1996](#)). Depths >60 m are likely a predator refuge for *C. magister* since most otters do not dive to depths >60 m to forage ([Bodkin et al., 2004](#)). In a nearby estuary where otters were not present, test fishery catch was significantly higher than catch where otters were present. These data suggest that otters strongly influence the location and depth at which adult *C. magister* reside.

### **3.3.6 Competition**

Although many studies report increased juvenile abundance in habitats created with shell hash, these studies only assessed juvenile abundance in the years directly following the creation of the habitat. Recent work has shown that after multiple years, the shell habitat is colonized by adult Hairy (Yellow) Shore Crabs (*Hemigrapsus oregonensis*) which have a strong negative effect on *C. magister* recruitment, reducing recruitment of *C. magister* to almost zero ([Visser et al., 2004](#)). *H. oregonensis* are capable of outcompeting juvenile *C. magister* for food and evicting them from refuges; however, they inhabit the high–low intertidal, so there is relatively little overlap of the two species habitats. *C. maenas* is also a stronger competitor than juvenile *C. magister* and outcompetes *C. magister* in nocturnal feeding trials. Additionally, *C. maenas* causes *C. magister* to emigrate away from ‘higher-quality’ habitat ([McDonald et al., 2001](#)). However, in Washington, where the studies were conducted, the habitat of *C. magister* and *C. maenas* does not currently overlap, so competition is minimal. In addition to interactions with other crab species, conspecific interactions have demonstrated that first and second juvenile instars are less aggressive towards other stages than later stages, with stages 3–6 being the most aggressive ([Jacoby, 1983](#)). Additionally, interactions between adult males and females often result in females submitting to males ([Jacoby, 1983](#)).

### **3.3.7 Growth and development**

The carapace width of newly settled juveniles is approximately 5 to 7 mm ([Butler, 1961](#)). *C. magister*, like other crustaceans, grow by moulting their

shell (Jaffe et al., 1987; Ruppert, 1994). Unlike adults, juvenile *C. magister* moult multiple times over the course of their first (~6 times) and second years (~4 times), which allows them to grow rapidly (Tasto, 1983). Within estuaries, the growth rate of juveniles is much faster than for juveniles that settle on the continental shelf; by the end of their first summer, estuarine crabs are ~40-mm carapace width, while oceanic juveniles are ~10-mm carapace width (Gunderson et al., 1990). However, by comparing reported carapace width to those observed in ROV videos during extraordinarily high recruitment years, Shanks et al. (2010) demonstrated that the carapace width of crabs was significantly smaller in years of high recruitment.

For adults, moulting occurs annually during a relatively short time period of 6–8 weeks (Hankin et al., 1989; Mohr and Hankin, 1989). Prior to moulting, crab shells are often heavily fouled with barnacles and other sessile organisms, whereas crabs are free of fouling after moulting (Cumbrow, 1978). Just prior to moulting, a suture line forms where the shell will open and the crab will back out of the old exoskeleton. Moulting occurs from March to June in California, April to September in the San Juan Islands, and June to July in Alaska (Table 3.1; Jaffe et al., 1987; Knudsen, 1964; Park and Shirley, 2008; Wild, 1983b). Approximately, 90% of female crabs with a carapace width of ~135 mm moult annually, while almost no female crabs with a carapace width of >155 mm moult annually (Hankin et al., 1989).

Adult crabs gain between 8.1- and 19.7-mm carapace width following each moult (Hankin et al., 1989). After moulting, it takes approximately 2 months for the exoskeleton to completely refill with tissue. Miller and Hankin (2004) provide descriptions of individual moult stages for determining moult stage of crabs in the laboratory; Washington Department of Fish and Wildlife also conducts routine field surveys in Puget Sound and collects extensive moult status using *in situ* tests based on shell hardness. Department of Fish and Oceans in British Columbia uses a durometer to measure shell hardness and defines soft shells as shells under 70 units (Canada. Dept. of Fish. and Oceans. Pacific Region., 2012).

### 3.4. Mortality (all stages)

#### 3.4.1 Natural mortality

Estimates of intra-annual mortalities of larvae are predicted to be consistent and the average daily survival rate is  $0.066 \text{ day}^{-1}$  (Hobbs et al., 1992). This calculation is based on daily survival of larvae from plankton tows collected in the upper portion of the water column. As larvae migrate to depth each day, it is likely that their sampling missed a large percentage of larvae and thus

underestimated daily survival. Annual mortality rates of adults have been estimated at 2.5% for sublegal males and 1.3% for females, though the results are controversial due to the statistical techniques used (Butler and Hankin, 1992; Smith and Jamieson, 1989a, 1991a, 1992). Models based on metabolic rates of adult crabs suggest that their lifespan ranges from 8 to 10 years (Gutermuth, 1989).

### 3.4.2 Diseases

In the laboratory, zoea are highly susceptible to infection (e.g. *Lagendium* sp.) and need to be reared with fungicides and antibiotics to prevent infections (Armstrong, 1976; Caldwell et al., 1978; Fisher and Nelson, 1977, 1978). Adult *C. magister* can have a multitude of diseases and parasites such as microsporidia in skeletal muscles, systemic ciliates and trematodes in the nervous and connective tissue (Morado and Sparks, 1988). Although most of these diseases have not been reported to have detrimental effects on the adult population, one *Chlamydia*-like bacteria may have caused mass mortalities in crab pots and holding tanks in Willapa Bay (Sparks et al., 1985). The microsporidia *Nadelspora canceri* infects crabs in the California Current (Childers et al., 1996), and populations in small estuaries along the coast were more heavily infected than offshore populations and populations in Puget Sound and Glacier Bay, Alaska, were not infected. Although infections do not appear to influence patterns of abundance in *C. magister*, they could potentially have an effect on populations in confined systems such as aquaculture or flow-through tanks for resale.

### 3.4.3 Pesticides

Pesticides can kill *C. magister*. For instance, the insecticide Sevin®, which is commonly used in oyster culture, prevented eggs from hatching at a concentration of  $1 \text{ mg l}^{-1}$  and killed 50% of zoea at a concentration of  $0.01 \text{ mg l}^{-1}$  (Buchanan, 1970). When adult crabs consumed cockles that had been exposed to the insecticide Sevin at  $10 \text{ mg l}^{-1}$ , all were irreversibly paralyzed and 77% of crabs were paralyzed when they consumed clams that had been maintained at a concentration of  $3.2 \text{ mg l}^{-1}$  of the insecticide Sevin (Buchanan, 1970). Fifty percent of adults exposed to Sevin at a concentration of  $0.26 \text{ mg l}^{-1}$  died within 24 h of exposure. The insecticide methoxychlor was tested at much lower concentrations than Sevin, and 50% of adults died after exposure for 96 h at a concentration of  $130 \mu\text{g l}^{-1}$ . In those that survived, the chemical was concentrated in their exoskeleton (Armstrong et al., 1976). Additionally, multiple different herbicides and

heavy metals (e.g. cadmium, copper and mercury) also have lethal effects on the larvae of *C. magister* (Caldwell et al., 1979; Martin et al., 1981).

### **3.4.4 Dredging**

Multiple studies have examined the effects of dredging the Gray's Harbor, WA shipping channel on *C. magister* and assessed potential ways to mitigate the effects of dredging (e.g. creating oyster shell habitat) (Armstrong et al., 1987). The effects of hopper, pipeline and clamshell dredges have all been examined; however, hopper dredges are the most commonly used, and therefore, I only report results from studies on this form of dredging. The average hopper dredge entrains between 0.046 and 0.587 juvenile crabs with each cubic yard of sediment. Of the crabs that were entrained, 86% with a carapace width of >50 mm died and 46% of crabs with a carapace width of <50 mm died. Adults captured in dredges that were not killed were able to dig out of sediments less than 20 cm deep (Chang and Levings, 1978).

### **3.4.5 Hypoxia**

Another threat to *C. magister* population is hypoxia. Recent die-offs of adult *C. magister* observed off the coast of Oregon have been attributed to low dissolved oxygen (hypoxia) events (Chan et al., 2008). Laboratory studies have examined feeding rates and behaviours of adult *C. magister* in hypoxic conditions and determined that crabs cease feeding below 3.2 kPa O<sub>2</sub> (Bernatis et al., 2007; McGaw, 2008). These researchers suggest that reduced feeding lowers the number of physiological processes that occur and minimizes oxygen consumption. Thus, consuming more food prior to entering the hypoxic regions likely increases the survival of crabs. In an estuary in British Columbia, using acoustic tags equipped with CTDs, researchers found that crabs actively avoided areas of lower salinity and have behaviours (not described) that aid them in avoiding and surviving hypoxic conditions (Bernatis et al., 2007; Curtis and McGaw, 2008). In a seasonally hypoxic fjord, researchers used acoustic tags to determine whether crabs would migrate into the shallow nearshore environment or north to avoid the hypoxic region of the fjord (Froehlich et al., in review). Their results demonstrated that crabs migrated into the shallow nearshore environment rather than northwards out of hypoxic waters.

### **3.4.6 Egg predation**

Within the egg masses of *C. magister*, there are often predatory nemertean worms, *Carcinonemertes errans*, which consume developing eggs (Wickham,

1978, 1979b). The worms can consume approximately 5 eggs worm<sup>-1</sup> day<sup>-1</sup> (Wickham, 1980). Throughout the range of *C. magsiter*, both juvenile and adult worms cover the surface of adult crabs (Wickham, 1979a). The majority of work on *C. errans* is based on adult crabs that were collected in the open ocean even though *C. magister* is well known to inhabit estuaries throughout its range. Recent work has demonstrated that the level of infection decreases as crabs move further up estuaries into lower salinity waters, suggesting that estuaries provide adults *C. magister* with a refuge from *C. errans* (Dunn, 2011). One would expect that the decrease in infestation would be due to decreases in salinity; however, mortality studies showed that *C. errans* were able to tolerate similar temperatures and salinities as adult *C. magister*, which suggests that some other factor causes infestation to decrease along an estuarine gradient.

### 3.4.7 Climate change

As the climate continues to change, researchers have hypothesized that increasing ocean temperatures will cause a northwards movement of predators and competitors of *C. magister* (McConaughey and Armstrong, 1995). Additionally, they suggest that *C. magister* will likely inhabit greater water depths and release their larvae earlier in the year. Early work on ocean acidification suggests that there will be minimal impacts on adult *C. magister* since the adults are able to recover their haemolymph pH after exposure to acidic waters (Pane and Barry, 2007; Ruttimann, 2006). Work on the effects of acidification on the development of *C. magister* larvae suggests that there will be few effects on development (R. Descoteaux, personal communication). Research seems to demonstrate that the wide range of habitats currently occupied by *C. magister* makes the organism relatively plastic, and thus the organism will be able to change habitats or behaviours to cope with climate change.



## 4. FISHERY

### 4.1. History

The *C. magister* fishery has been reviewed extensively in other articles and I will only provide a brief overview and emphasize recent management protocols (Demory, 1990; Didier, 2002; Melteff, 1985). The following history of the fishery is adapted from Dahlstrom and Wild (1983) and augmented to include more recent findings.

Tribes along the West Coast of North America consumed *C. magister* ([Dahlstrom and Wild, 1983](#)). The Yurok tribe in Northern California is reported to have speared crabs, while other tribes gathered them by hand, often focusing on young adults and juveniles in the nearshore environment ([Greengo, 1952; Losey et al., 2004](#)). The non-tribal fishery began in San Francisco Bay in the 1860s using hoop nets equipped with cedar, cork or copper floats. The first reported annual commercial catch occurred in the late 1840s, and in 1863, the California Department of Fish and Game recorded the first landing. In 1897, due to observed declines in the San Francisco Bay population, a moratorium was placed on retaining female crabs. The hope was that releasing female crabs would minimize the effect of the fishery on reproductive output. Subsequently, San Francisco fishermen requested seasonal closures and the first seasonal closure occurred in 1903. The fishery was closed from September 2–October 31 to avoid catching soft-shelled crabs. In California, the first size restriction was initiated in 1905; that is, crabs had to be a minimum size of 6" or 152 mm. Small sailing vessels that were capable of operating approximately 50 hoop nets a day dominated the early fleet. In the early 1900s, gasoline engines started to be more common, and vessels were able to operate as many as 100 hoop nets each day. The number of participants in the fishery dramatically increased in the 1930s when crab pots were introduced.

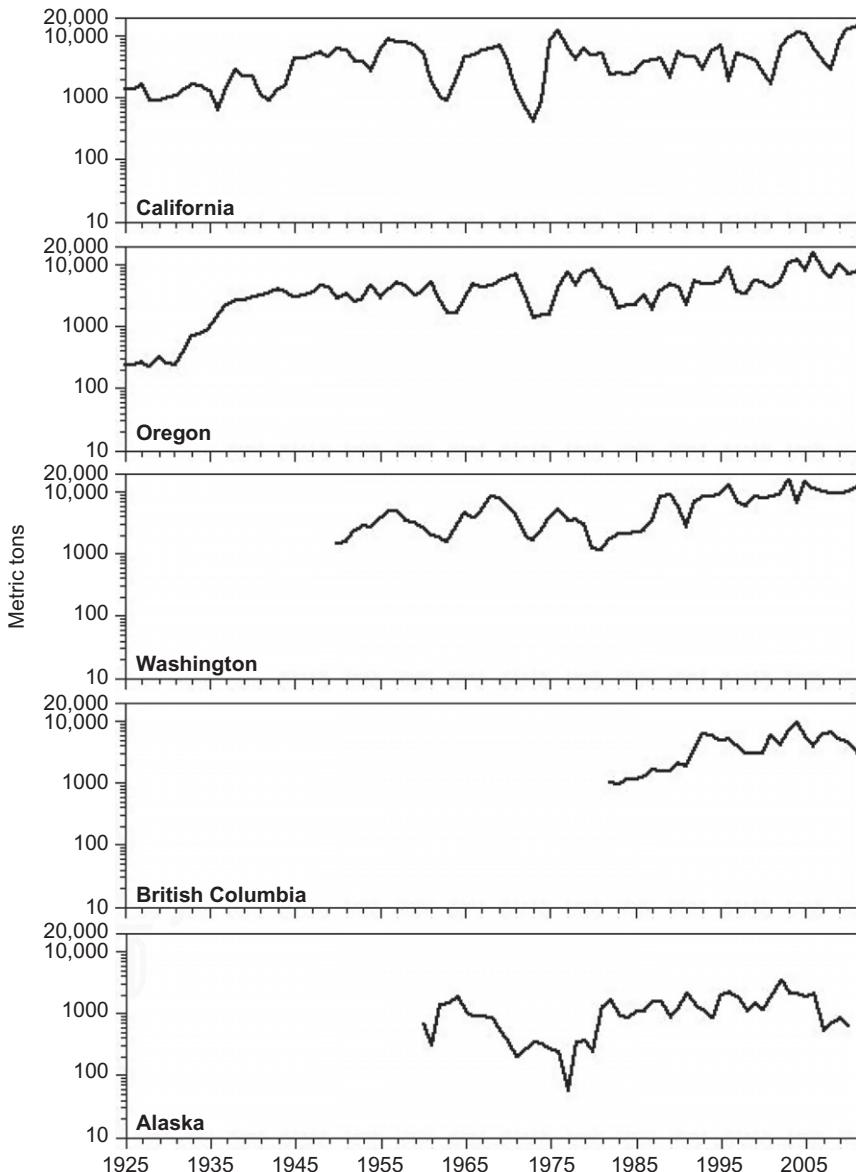
In Oregon, the first Dungeness crab landings occurred in 1889 ([Demory, 1990](#)). The first seasonal closures in Oregon occurred during the 1948–1949 season in order to minimize the retention of crabs in poor condition (low yield of meat), but the timing of the closure was different north and south of Cascade Head to account for latitudinal variation in the timing of moulting. Additionally, at this time, the first closure to the retention of female crabs occurred. From 1909 to 1933, commercial fishermen had daily and/or annual catch limits. When catch limits were repealed, annual landings increased dramatically ([Waldron, 1958](#)). In 1996, Oregon established a limited-entry programme to prevent a large number of boats from entering the fishery when catch levels are high. I was unable to find historical reviews of the fisheries in Washington, British Columbia and Alaska. It should be noted that in Washington, the 1994 federal court order known as the Rafeedie Decision stated that Washington Treaty tribes had the right to shellfish under their treaties and thus Dungeness crabs have been co-managed by the tribes and state since.

Landings in the California Current fishery (California, Oregon and Washington) continued to rise until 1948 at which point catch began to

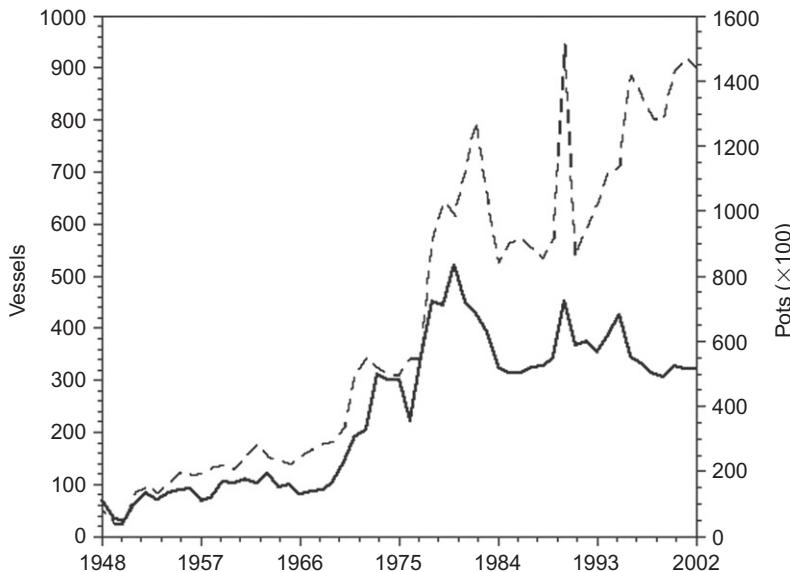
oscillate (Figure 3.3; Demory, 1990). Early on, these oscillations were decadal in cycle, but since 1980s, the decadal pattern to the oscillation is no longer present (Figure 3.3; Shanks and Roegner, 2007). It is well known that in the late 1970s, fleet size (and effort) increased dramatically with the creation of exclusive economic zones, which coincides with the end of the oscillations (Figure 3.4; Gelchu and Pauly, 2007; Shanks and Roegner, 2007). Further it has been estimated that historically as little as 40% of the legal males were extracted annually and following the fleet expansion in 1970s >90% of legal males have been/are extracted annually (Methot and Botsford, 1982). Based on models developed by Botsford et al. (1983), Shanks and Roegner (2007) suggests that during periods when effort was low some crabs escaped and contributed to the next year's fishery, but in years with increased effort, effectively all legal crabs were extracted. Thus, he hypothesizes that the early oscillations in catch may have been due to increases and decreases in effort based on the relative abundance of legal crabs.

In the Alaska Current, catch in British Columbia and Alaska has fluctuated but not on a decadal cycle like that of the California Current (Figure 3.3). In the Alaska Current, the fishery primarily occurs in inland waters where larval dispersal is influenced by complex hydrodynamics that likely lead to area of larval retention. I hypothesize that the effect of the complex hydrodynamics on larval dispersal has contributed to the fluctuations and crashes in certain fisheries; however, limited research has been conducted and future work should examine the dispersal of larvae in these complex hydrodynamic environments (Orensanz et al., 1998).

Despite the fluctuations, in 2011, *C. magister* accounted for only ~5%, 6% and 15% of the total biomass harvested in California, Oregon and Washington but accounted for 25%, 30% and 44% of the total revenue (Figures 3.5–3.7). These numbers demonstrate that although Dungeness crab does not account for the greatest biomass harvested it is the most economically important species harvested (second to squid in California) in the California Current. As the fishery has become more lucrative, the fishery is essentially a race fishery with most landings occurring within the first 2 months of the fishery opening, which floods the market with crab (Hackett et al., 2003). In other fisheries, extending catch over a longer time period has increased the profit margin of the fishery; however, an economic analysis of the California fishery surprisingly found that there would likely be little profit increase by extending the fishery (Hackett et al., 2003). The researchers determined that frozen-picked crabmeat is the most profitable and, since it is frozen when it is caught, does not increase the value.



**Figure 3.3** Commercial catch of *C. magister* in California, Oregon, Washington, British Columbia and Alaska. Catch data were not available back to 1925 in all regions. Note the decadal patterns (significant autocorrelation) in catch from 1950s to 1980s in commercial catch in California, Oregon and Washington ([Shanks and Roegner, 2007](#)). This decadal has not occurred since 1980s (no further autocorrelation).

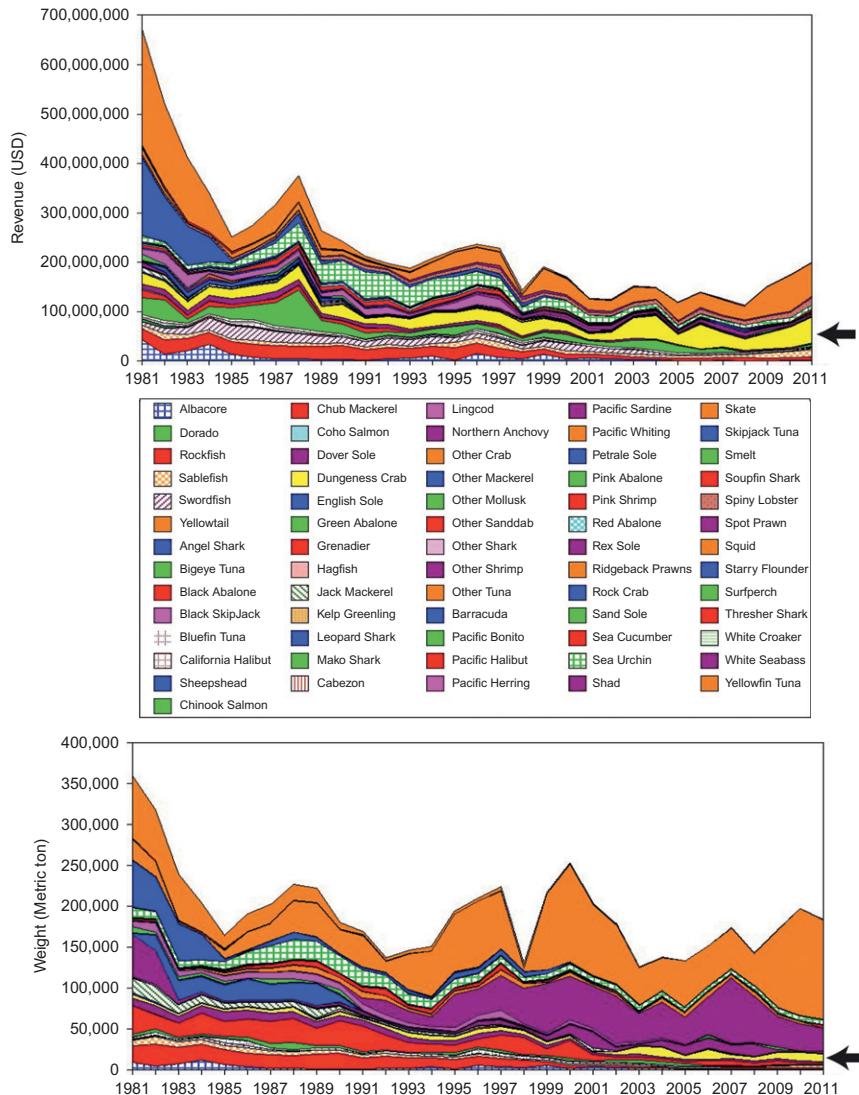


**Figure 3.4** Number of boats and pots participating each year in the commercial *C. magister* fishery in Oregon. Note the dramatic increase in the effort (both pots and vessels) that occurred in the mid 1970s. This timing coincides with the federal plan to enhance U.S. fisheries following the establishment of the Exclusive Economic Zone ([Gelchu and Pauly, 2007](#)). Data on effort were spotty and thus are not presented here.

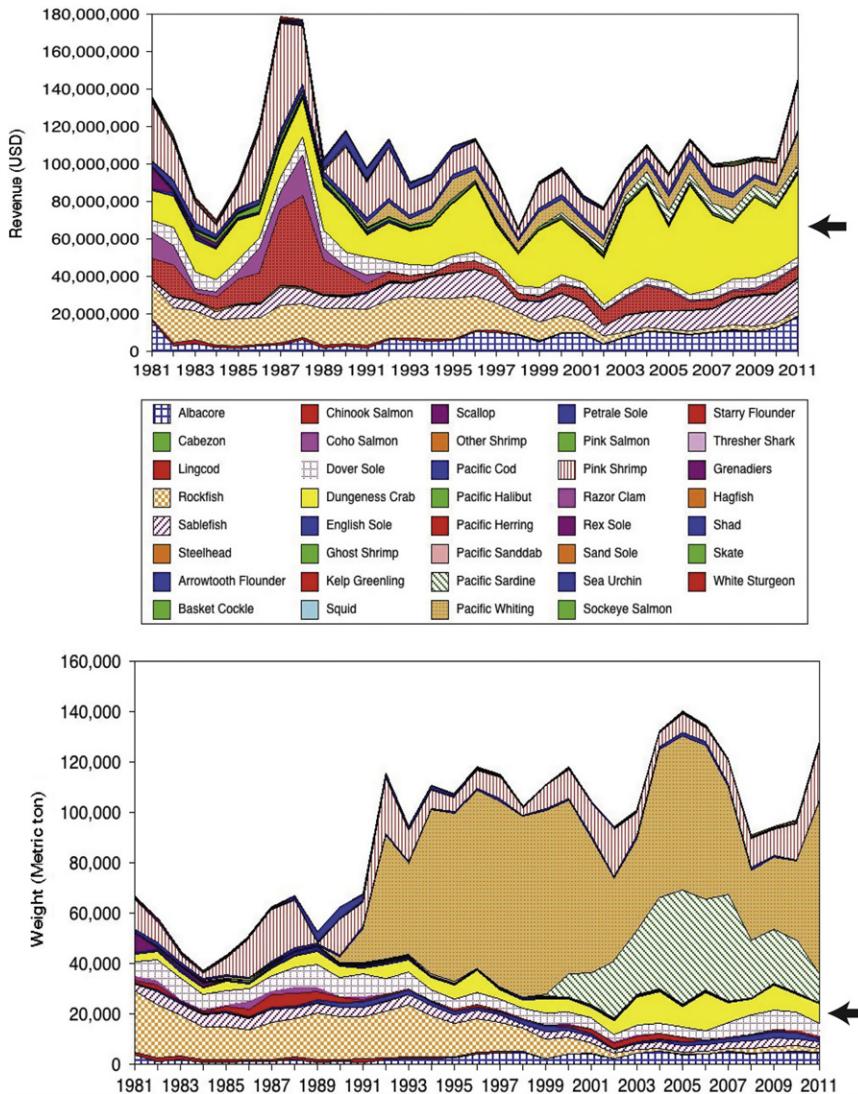
However, the race fishery increases the number of pots on the fishing ground and causes fishermen to take extra risks often leading to loss of life ([Deweese et al., 2004](#)). A survey of fishermen in California found that the only 2 (out of 12) accepted options for stretching out the season are either fixing a trap limit regardless of vessel size or restricting fishing to daylight hours, though the authors note that in other regions where similar restrictions have been implemented, the number of pots has not decreased ([Deweese et al., 2004](#)).

## 4.2. Management

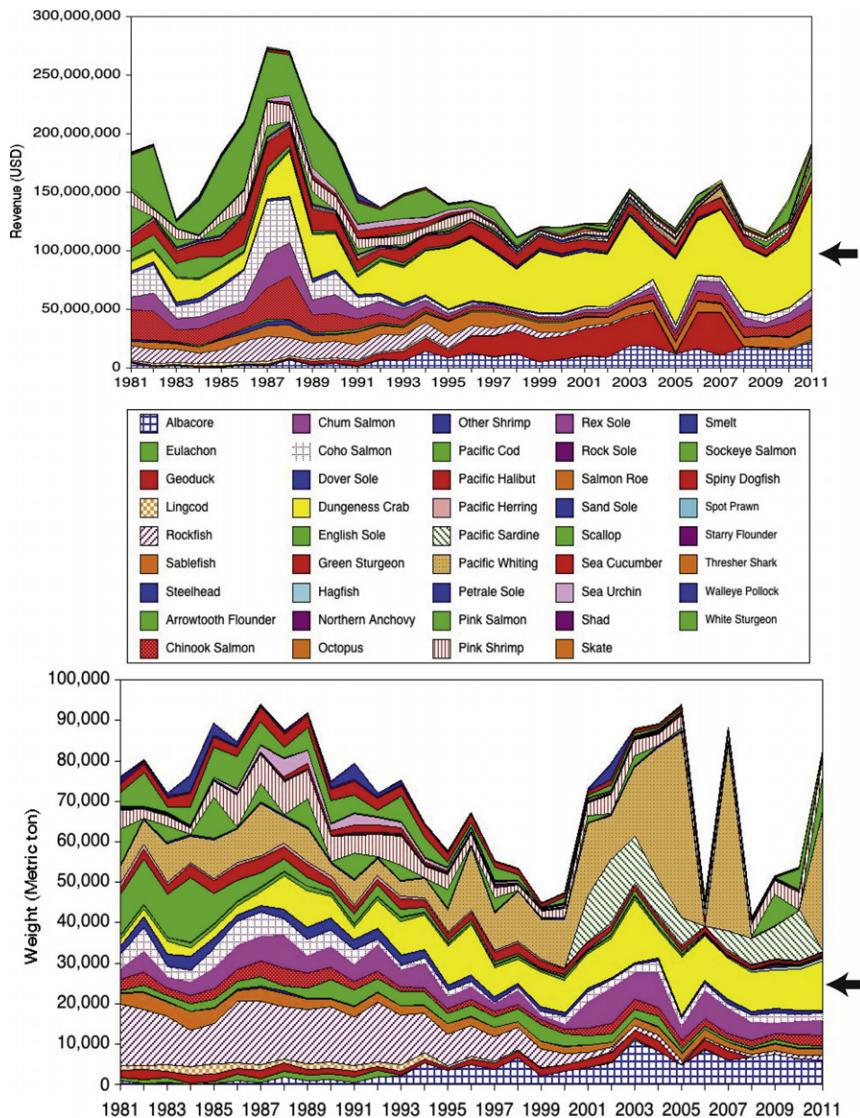
The fishery for *C. magister* is managed using the 3-S management technique. The 3-S management technique controls the sex of individuals that are harvested, the minimum size of the individuals that are harvested and the season when harvesting occurs ([Table 3.4](#)). [Didier \(2002\)](#) provides excellent comparative tables of the regulations for California, Oregon and Washington and I include only a small portion of these tables here ([Table 3.4](#)). Commercial fisheries throughout the range of *C. magister* are only allowed to



**Figure 3.5** Annual revenue (top panel) inflated to 2012 USD value and annual catch (bottom panel) for commercial fisheries in California from 1981 to 2011. (Pacific Fisheries Information Network (PacFIN) retrieval dated December 2012, Pacific States Marine Fisheries Commission, Portland, Oregon ([www.psmfc.org](http://www.psmfc.org)).) Arrows on the right side of the figure point to the area that represents *C. magister*.



**Figure 3.6** Annual revenue (top panel) inflated to 2012 USD value and annual catch (bottom panel) for commercial fisheries in Oregon from 1981 to 2011. (Pacific Fisheries Information Network (PacFIN) retrieval dated December 2012, Pacific States Marine Fisheries Commission, Portland, Oregon ([www.psmfc.org](http://www.psmfc.org)).) Arrows on the right side of the figure point to the area that represents *C. magister*.



**Figure 3.7** Annual revenue (top panel) inflated to 2012 USD value and annual catch (bottom panel) for commercial fisheries in Washington from 1981 to 2011. (Pacific Fisheries Information Network (PacFIN) retrieval dated December 2012, Pacific States Marine Fisheries Commission, Portland, Oregon ([www.psmfc.org](http://www.psmfc.org))). Arrows on the right side of the figure point to the area that represents *C. magister*.

**Table 3.4** Sport and commercial fishery retention size, season and unique regulations to each region throughout the range of *Cancer magister*

	<b>Legal size (mm)</b>	<b>Season</b>	<b>Notes</b>
<i>Sport fishery</i>			
California	145	November 5–July 30	Limit 10, females can be retained
Oregon	145	Bays Open Year Round, Ocean December 1–September 30	Limit 12
Washington: Coast	152	December 1–September 15 for pots, year round all other gear	Limit 5 southern coast, Limit 6 northern coast
Washington: Puget Sound	160	July 1–September 3 (Thursday–Monday)	Limit 5 (many small regional closures)
British Columbia	165	Year round	Limit 4–6 (many small regional closures)
Alaska	165	Year round	Limit 20 crabs (multiple regional regulations)
<i>Commercial fishery</i>			
California	160	December 1–June 30 (varies North to South)	
Oregon	160	Bay fishery open weekdays January–Labour Day Ocean Fishery Open December 1–August 15	Pot limits allocated by historic catch
Washington: Coast	160	December 1–September 15	Pot limits allocated by historic catch
Washington: Puget Sound	160	October 1–April 15	100 pots per permit
British Columbia	165	Due to the complex hydrodynamic regulations are variable	Number of pots variable based on region
Alaska	165	Due to the complex hydrodynamic regulations are variable	

harvest male crabs, though this is a recent change in British Columbia where it used to be legal to retain females (Table 3.4). For recreational fisheries, all states except California restrict catch to only male crabs. The size of individuals that can be retained in commercial and sport fisheries varies throughout the crabs range from 145 to 165 mm (Table 3.4). Most research suggests that crabs retained in the fishery are ~4 years of age (Botsford, 1984). However, models of growth rates based on water temperatures suggest that the range could be from 2 to 8 years for crabs to enter the fishery with longer time periods occurring where average water temperatures are lower (Gutermuth, 1989). The commercial season is set to eliminate fishing while crabs are moulting and, due to the variability in the timing of moulting, the dates of closure change with latitude with openings occurring later further north (Tables 3.1 and 3.4). In the California Current, the season is delayed if the percentage of meat/body weight is not above 25–30%. At the northern extent of the fishery, in Puget Sound, inland waters of British Columbia and Alaska, regulations are complex due to the convoluted coastline and stocks are managed as multiple subunits. While in the California Current the population is well connected, it is likely that the complex hydrodynamics of inland waters reduces connectivity between populations ultimately making them into separate stocks. The recreational season varies throughout the range of *C. magister* and also changes with gear type (e.g. hoop net vs. pot).

### 4.3. Direct and indirect impacts of the fishery

#### 4.3.1 Ghost fishing

Each year a large number of crab traps are lost; in Puget Sound, an estimated 12,193 pots are lost in the commercial and recreational fisheries combined, and in British Columbia, an estimated 11% of traps are lost each year (Antonelis et al., 2011). Due to their effective design, crab pots have a propensity to continue to capture crabs (ghost fish) after they are lost. In Puget Sound, 72 h after pots were returned to the water with their original catch, 79% of legal crabs, and 33% of sublegals remained in traps (High, 1976). Over the course of a year, it was estimated that as much as 7% of the annual catch is harvested by ghost fishing (Breen, 1985a,b). An examination of the economic value of crabs caught and killed by ghost traps ( $\$37\text{--}\$91 \text{ pot}^{-1}$ ) and compared to the cost of removing derelict gear ( $\$93\text{--}\$193 \text{ per pot}$ ) suggests that there is usually little economic incentive for removing derelict pots (Antonelis et al., 2011). It is becoming a requirement throughout the California Current for the lids of pots to be secured with cotton twine that will rot away when pots are lost. Thus, cord attached to the enclosure

that rots away in seawater should be reduced in diameter so that it will rot within 50 days and subsequently open the door to the pot. Additionally, having pots with doors that open on the top of the pot may not allow trapped crabs to escape even after the clasp breaks since the lids are often held closed by encrusting organisms. Crabs in pots (and more specifically small crabs) have an increased probability of being injured as soak time (the time the pot is in the water) increases (Barber and Cobb, 2007). However, preventing crabs from utilizing their pinchers did not decrease in pot mortality, suggesting that cannibalism within pots is not common (Shirley and Shirley, 1988).

#### **4.3.2 Handling mortality**

Sixteen percent of soft-shell crabs die after being handled only once, while only 4% of hard-shell crabs die from a single handling event (Tegelberg, 1970). By tagging individuals and returning them to pots in the water, Tegelberg (1971) determined that mortality of soft-shell crabs was 10% after 2 days and 25% after 7 days. If crabs were handled three times in 6 days, handling mortality increased to 41%. These findings of mortality on soft-shell crabs were corroborated in additional studies off the Washington coast (Barry, 1981).

#### **4.3.3 Trawl fishery**

The indiscriminate nature of many benthic trawl fisheries has led researchers to speculate that by-catch of *C. magister* is high in benthic trawl fisheries. A study in California near the Farallon Islands reported a mortality of 0.53 male crabs per hour of trawling and a mortality of 0.12 legal-sized male crabs per hour of trawling (Reilly, 1983b). All sluggish crabs caught in the trawl that were held in flowing seawater for 3–20 h fully recovered. However, these estimates are likely low as the study was conducted off San Francisco (a region with a relatively small population). This chapter references (without citation) a study off Washington that reported trawling induced mortalities of ~4.2% for both sexes. NOAA observer data from 2008 reported that ~387 metric tons of *C. magister* were discarded in both the limited entry bottom trawl fishery and California halibut (*Paralichthys californicus*) bottom trawl fisheries in California, Oregon and Washington (Bellman et al., 2010). In 2008, a total of 19,899 metric tons were landed by the crab fishery in California, Oregon and Washington and thus by catch from the trawl fisheries only accounted for ~2% of the total catch. A comparison between a mark-recapture study where crabs were caught with an otter trawl and a study where crabs were caught with crab pots

determined that recovery rates were equal between the two studies and it was argued that this demonstrates that trawl fisheries have a minimal effect on *C. magister* ([Anonymous, 1949](#)). However, no data to substantiate this claim are provided in the report.

#### **4.3.4 Impact to benthos**

To my knowledge, no work has examined the effect of *C. magister* traps on the benthos. In British Columbia, a study examined the impact of Spot Prawn (*Pandalus platyceros*) pots on benthic communities with a primary focus on damage to sea whips (*Halipteris willemoesi*) ([Troffe et al., 2005](#)). They found that in 600 hauls, 30 sea whips were brought to the surface and of these 50% were damaged. A project over 4 years compared areas fished with pots to soft-sediment areas not fished with pots and demonstrated that there was no difference in the benthic communities ([Coleman et al., 2013](#)). A study of traps deployed on reefs demonstrated that there were significant impacts on the benthos, especially when wind caused the traps to be moved across the reef ([Lewis et al., 2009](#)). Research seems to suggest that pots have a minimal effect on soft sediment communities; however, the ecological impact of traps on benthic communities is a topic that needs extensive research in the future.

### **4.4. Fishery prediction**

Due to the economic importance of *C. magister* and historic fluctuations in catch, many research projects have attempted to predict commercial catch the year prior to a fishery and predict the cause of large-scale population variations observed throughout the range of the species.

#### **4.4.1 Catch prediction**

By using crab pots modified to retain juvenile crabs, researchers are able to predict commercial catch one year in advance with 10–20% accuracy; however, to my knowledge, this has not been implemented by any state ([Steffrud, 1975](#)). In Puget Sound, standard crab pots with the escape rings closed are used to help predict fisheries ([Fisher and Velasquez, 2008](#)). Since soak times vary between pots, [Smith and Jamieson \(1989b\)](#) presented a statistical model that can be used to standardize catch between traps with different soak times. In a comparison of pots and SCUBA methods for predicting catch, pot surveys were more effective except in time periods when crabs were moulting and, hence, not actively moving ([Taggart et al., 2004](#)). [Gunderson and Ellis \(1986\)](#) developed a modified plumb staff beam trawl that is highly effective at sampling juvenile *C. magister*.

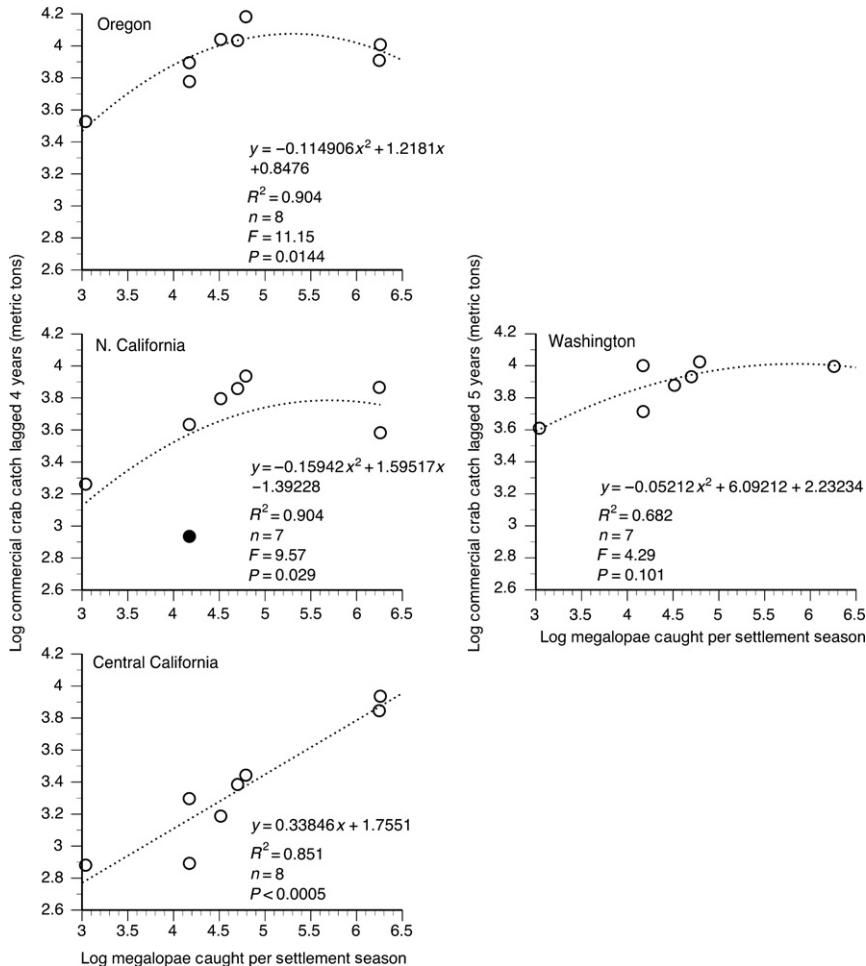
[McConaughey and Conquest \(1993\)](#) examined data collected during these trawl surveys and concluded that geometric means are a better estimator of abundance than arithmetic means. A comparison of towed camera sleds and trawls demonstrated that trawls routinely underestimated the abundance of adult crabs ([Spencer et al., 2005](#)). Although there appear to be methods that are successful for predicting fisheries, to my knowledge, none of these procedures have been implemented and thus their validity cannot be assessed.

Shanks and colleagues (2010, 2007) have been using light traps to capture the megalopae of *C. magister* (see earlier discussion in [Section 3.2](#)). Using the amount of megalopae caught annually, they have been able to predict commercial catch 4 years later (the time it takes megalopae to grow into commercial-sized crabs) with an accuracy of  $\sim 12\%$ . In recent years, catch of megalopae has increased to the point that their early linear model would have predicted a commercial catch of  $\sim 700,000,000$  lbs (10 times greater than historic maximum). Commercial catch correlated with these high megalopae returns has levelled off with (and declined; [Figure 3.8](#); [Shanks, in press](#)). In years when a large number of crabs recruit to the population, density-dependent effects increase, causing commercial catch to level off and decline. Below 100,000 returning megalopae, the population is recruitment limited, and above 175,000 returning megalopae, density-dependent effects cause the population to decrease. This predicts that the greatest commercial catch should occur when  $\sim 175,000$  megalopae recruit to the light trap. Although the predictive curve has changed to a second-order polynomial (for everywhere except Central California), the predictive power of the curve is still highly significant ([Figure 3.8](#)).

#### **4.4.2 Fluctuation predictions (California Current)**

Early on commercial catch of *C. magister* historically oscillated on nearly a decadal cycle; however, the cycles have recently become less regular or have disappeared altogether ([Figure 3.3](#)). As discussed earlier, it is likely that these oscillations ceased due to a dramatic increase in effort following the creation of exclusive economic zones. However, commercial catch does fluctuate (not decadally) and considerable research has attempted to explain these fluctuations.

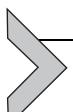
Although the species is fished extensively, the fluctuations are not induced by the fishery mortality or impacted mating success ([Botsford et al., 1983](#); [Hankin et al., 1997](#); [McKelvey et al., 1980](#)). [McKelvey et al. \(1980\)](#) generated numerous multistage recruitment models and argued that factors influencing the early egg and/or larval stages cause the variation in



**Figure 3.8** Log catch of *C. magister* megalopae caught annually versus commercial catch in Central California (south of Sonoma County), Northern California (Sonoma County north), Oregon and Washington (Shanks, *in press*). Commercial catch is lagged 4 years after settlement season except for Washington where it is lagged by 5 years. Dotted lines and statistics are the results of regressions. The filled circle in Northern California is an outlier that was excluded from analysis.

commercial catch. Using a data set collected over 12 years, Shanks (*in press*) demonstrated that relationship between larval success and adult population size varies with the amount of larval success. It is relatively widely accepted by researchers who suggest that larval success is influenced by hydrodynamics (summarized in Table 3.3 and reviewed earlier when discussing dispersal patterns).

Density-dependent factors alone have not been able to explain the variations in commercial catch (summarized in [Table 3.3](#)). Predation on larvae by salmonids and consumption of eggs by *C. errans* do not cause the observed fluctuations ([Botsford et al., 1982](#); [Hobbs et al., 1992](#)). Some researchers have suggested that cannibalism on recently settled juveniles may cause the cyclic patterns, though the hypothesis is controversial ([Botsford, 1981, 1984](#); [Botsford and Wickham, 1978](#); [Botsford et al., 1983](#); [McKelvey and Hankin, 1981](#)). Most research has attempted to explain the fluctuations by examining either physical or biological perturbations, though it is likely that a combination of the two causes the population fluctuations ([Higgins et al., 1997](#)). Shanks and colleagues ([Shanks, in press](#); [Shanks and Roegner, 2007](#); [Shanks et al., 2010](#)) provide the best explanation for the fluctuations of the population (see earlier for more in depth explanation). Overall, they have demonstrated that the number of larvae recruiting is positively correlated with adult population size, and during years with high larval success, density dependence affects survival of juveniles.



## 5. CONCLUSIONS

A large body of the literature has been generated over the years on the biology of *C. magister*, and this review provides an extensive review of the biology of *C. magister* and a brief overview of the commercial fishery. Potential impacts of future changes on the environment are only briefly covered, as this literature is still in the process of being published. Although much has been published on *C. magister*, the research has been surprisingly patchy, for example, most juvenile work occurring in the Grays Harbor and Willapa Bay estuaries. There is an apparent difference that is not well understood between the California Current population and the Alaska Current population with the population in the California Current being much more resilient to exploitation. Further, in years with extremely high recruitment, there are no studies on the density-dependent effects that are occurring. Thus, more studies should be conducted throughout the range of *C. magister* in order to allow researchers and managers to understand which characteristics apply to the entire population and which apply to only certain portions of the population.

## ACKNOWLEDGEMENTS

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