THE INFLUENCE OF BEHAVIOR AND HYDRODYNAMICS ON THE DISPERSAL OF DUNGENESS CRAB, *CANCER MAGISTER,* LARVAE

by

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A DISSERTATION

Presented to the Department of Biology
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DISSERTATION ABSTRACT

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The Dungeness crab fishery is the most economically important on the West Coast; however, it has experienced dramatic fluctuations in annual catch. Previous research has shown the annual catch of megalopae is correlated with the commercial catch. The catch of megalopae is correlated with the phase of the Pacific Decadal Oscillation (PDO), the day of the year of the spring transition and the amount of upwelling following the spring transition. Further, the daily catch of megalopae is correlated with the internal tide.

We developed individual based models of Dungeness crab dispersal, which we validated with results from a light trap. We demonstrated that the retention of larvae in the California Current is enhanced during negative phase PDOs. Further, we suggest that larvae migrate to or almost to the bottom each day. Specifically, megalopae exhibit a twilight vertical migration off of the continental shelf and remain in the neuston on the continental shelf. This concentrates megalopae at the continental shelf break.

We also observed megalopae *in situ* and demonstrated that they swim in the neuston with the surface current at speeds of ~ 10 cm s^{-1}. Using these results and data from a mooring, we demonstrated that this behavior would increase the distance internal waves would transport larvae. We analyzed mooring data and suggest that catch of megalopae is greater when the thermocline is deep and weak and there is less horizontal shear. We hypothesize this allows internal waves to remain coherent longer on the continental shelf. We show that the spring transition coincides with a shallowing of the thermocline, which would ultimately lead to the development of internal waves of depression rather than elevation. We hypothesize that the change in surface flow, based on whether the wave is one of elevation or depression, explains why most megalopae are caught following the spring transition.

In general, these findings help us better understand the dispersal of Dungeness crabs. We suggest the dispersal patterns support Michael Sinclair's member vagrant hypothesis. Further, we suggest these findings apply to many of the continental shelf species in the California Current.

This dissertation includes both published and unpublished co-authored materials.

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TABLE OF CONTENTS

Chapter Page

Chapter Page

LIST OF FIGURES

Figure Page

Figure Page

Figure Page

LIST OF TABLES

CHAPTER I

INTRODUCTION: THE BIOLOGY, ECOLOGY, AND FISHERY FOR THE DUNGENESS CRAB, *CANCER MAGISTER*

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1.1. 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 cancrid 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 cancrid 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 1.1; 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 1.1). 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.

1.2. 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 1.1; Hickey, 1979; Mann and Lazier, 2006). The location of the bifurcation shifts to the south (~47 °N) in the winter and northwards to ~50 °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

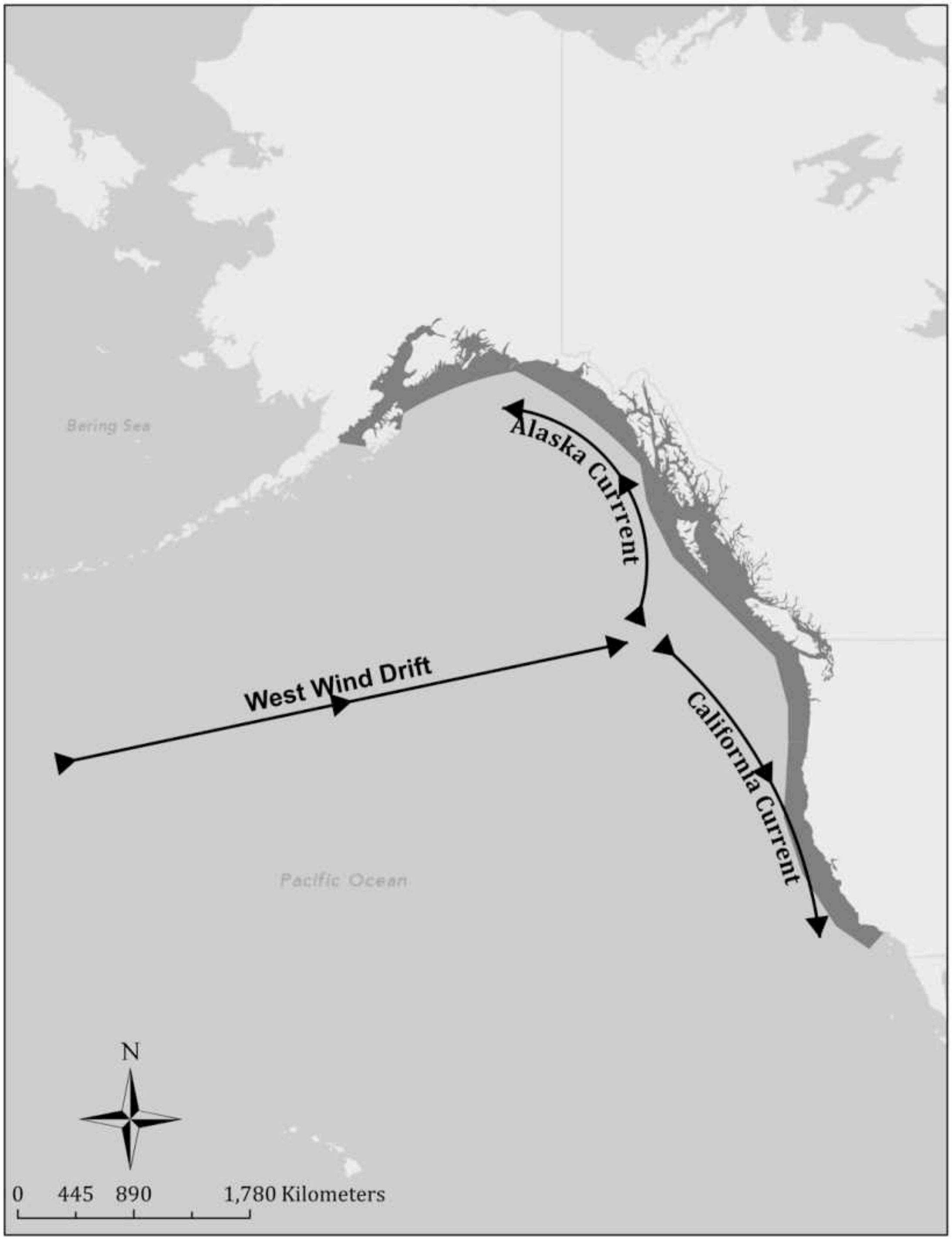

Figure 1.1. Distribution of *Cancer magister* (dark gray shading) throughout California and Alaska Currents. Arrows denote the general direction of currents. Base map provided by ESRI (2011).

Table 1.1. Peak reproductive timing throughout the range of *Cancer magister*.

Location	Molting/ mating	Egg Deposition	Hatching	Larval Duration (Range of time)	Settlement
California	March-June	September-November	December-February	115 (105-125)	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

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).

1.2.1. California Current

1.2.1.1. Oceanography

The California Current is the eastern boundary of the North Pacific Sub- tropical

Gyre and is characteristically broad (~500 km wide) and slow- moving (5–10 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 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 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 favorable, while during the fall and winter, winds are downwelling favorable.

1.2.1.2. Habitat

In the California Current, unconsolidated sediments (sand, mud and sand/ mud mixtures) are 4.5 times more abundant than hard substrates (Romsos, 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.

1.2.2. Alaska Current

1.2.2.1. Oceanography

Where the West Wind drift collides with Vancouver Island, the ocean is characterized by 'confused' (non-directional) currents with numerous eddies (10–25 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 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 favorable with mean velocities of ~30 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.

1.2.2.2. 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).

1.3. BIOLOGY AND ECOLOGY

1.3.1. Reproduction

1.3.1.1. Mating

In brachyurans, mating occurs between recently molted (soft) females and males that have already molted and since re-hardened (Figure 1.2; 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 (~3 years old) (Butler, 1961; Cleaver, 1949; Hankin et al., 1989; Scheding et al., 1999). When females are close to molting, 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 molting for up to 2 weeks in a 'premating embrace'. The data conflict about what happens when the female is ready to molt: either (1) the female is released by the male and molts outside the embrace of the male (Cleaver, 1949) or (2) the female molts while being embraced by the male (Butler, 1960; Cleaver, 1949; Snow and Nielson, 1966). After the female molts, 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; Orensanz and Gallucci, 1988). Females who did not undergo an annual molt 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. Rasmuson, unpublished work).

1.3.1.2. 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 1.2; 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 1.1; 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 molt or extrude eggs annually and (2) smaller females (carapace width <141 mm) molt, 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 1.1). Whereas the earlier hatching times of smaller females provide a

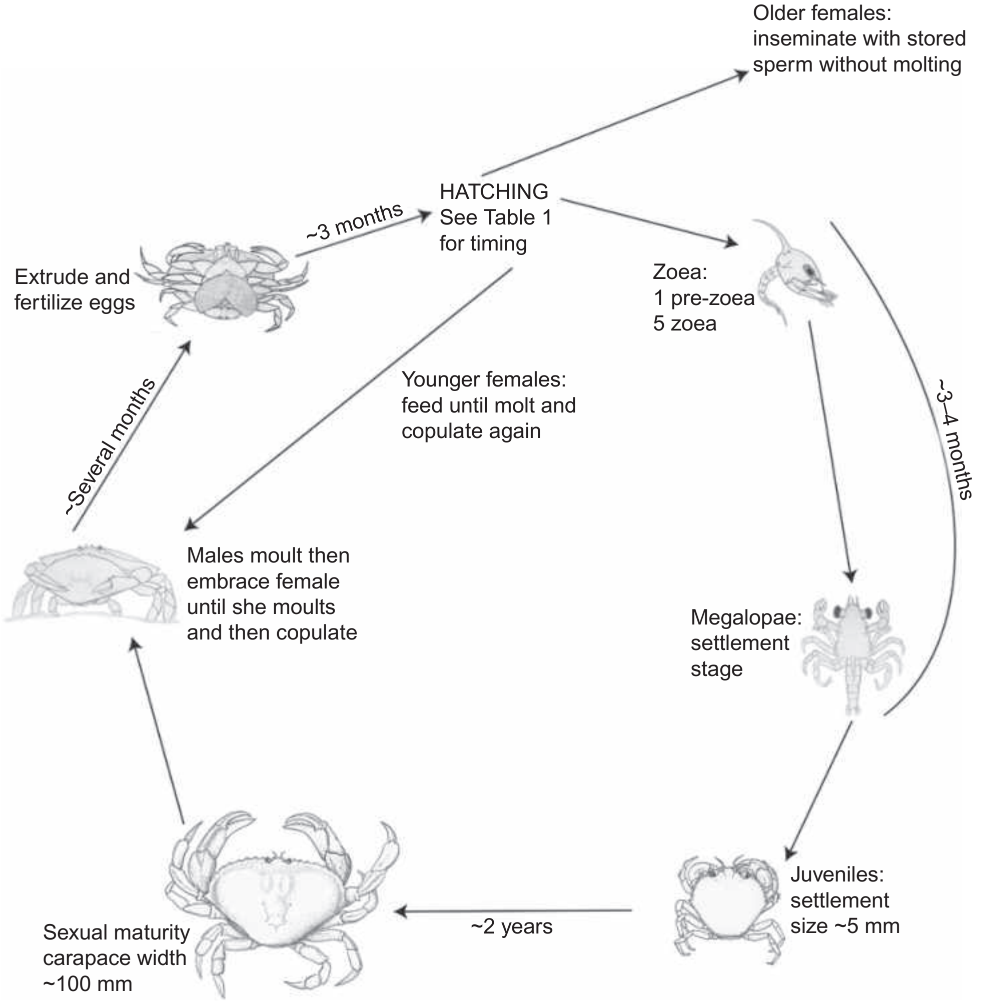

Figure 1.2. Life cycle of *Cancer magister*. Timing is relative and varies throughout the range of the species (see Table 1.2 for timings).

sufficient time period between hatching and molting 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. Rasmuson, 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.

1.3.2. Larval Biology

1.3.2.1. Hatching

Hatching occurs when prezoeae 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 1.1; 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 prezoeae released into the water column did not survive, but more recent studies have demonstrated that prezoeae survive and develop into stage-I zoeae (Buchanan and Milleman, 1969; MacKay, 1942; Poole, 1966). In the laboratory, the transition from prezoeae to stage-I zoea takes only a few seconds, and thus prezoeae are only in the water column for seconds to minutes. *C. magister* then progress through five zoeal stages and one megalopal stage in the water column (Figure 1.2; Poole, 1966). All five zoeal stages of *C. magister* have large compound eyes, four spines (one dorsal, one rostral and two lateral) and swim by flexing their maxillipeds. Zoeal 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 intermolt 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 zoeae. The development of zoeae 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 zoeae reared in 10 °C water, but the duration of each stage drastically decreased as water temperature increased (Table 1.2). 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 zoeae reared at Puget Sound water temperatures were in the water column 44% longer than larvae raised at open ocean temperatures.

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

Table 1.2. Effect of temperature on the day of molting (mean day), length of the stage (days) and percentage of larvae surviving.

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

Adapted from Sulkin and McKeen (1989)

simulations of water temperatures and salinities in the California Current. Modeled larval duration ranged from 74 to 163 days depending on latitude, which is slightly different than the measured durations (Table 1.1). 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 over- all 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.

1.3.2.2. 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 zoeae on a diet solely of diatoms were unsuccessful (Hartman and Letterman, 1978). Zoeae that were fed mussel larvae (*Mytilus edulis*) did not survive but did well when fed barnacle larvae (*Balanus glandula*) (Gaumer, 1971; Reed, 1969). Zoeae 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^{-1}, then survival of zoeae 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 stage zoeae 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 zoeae (Garcia et al., 2011). Results indicated that fewer zoeae 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).

1.3.2.3. Predation

No literature reports selective feeding by pelagic invertebrates or fishes on the zoeae of *C. magister*. In the field, I have dissected English sole (*Parophrys vetulus*) and found their stomachs completely full of zoeae-I larvae (L.K. Rasmuson, 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).

1.3.2.4. Larval Behavior and Swimming

The zoeae 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, zoeae swim into currents (positive rheotaxis), and megalopae have slightly stronger rheotaxis than zoeae (Gaumer, 1971). Ninety-five percent of megalopae observed in situ displayed strong positive rheotaxis (L.K. Rasmuson, 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 zoeae (I–III) are capable of swimming at speeds ranging from 0.58 to 0.95 cm s^{-1} (Gaumer, 1971; Jacoby, 1982), while later-stage zoeae (IV and V) are capable of swimming at a speed of 1.5 cm s^{-1}. In situ swimming speeds of the megalopae average 12 cm s^{-1} with a range of 5–20 cm s^{-1} (L.K. Rasmuson, in preparation), but swimming speeds of megalopae determined in the laboratory are more variable and range from 4.2 to 44 cm s^{-1} (Fernandez et al., 1994b; Jacoby, 1982).

1.3.2.5. Vertical Migration

Zoeae 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 intermolt 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* zoeae and megalopae may undergo a crepuscular (occupying the surface only at dusk/dawn) rather than diel migration (Park and Shirley, 2005).

1.3.2.6. 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 zoeae 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 north- wards 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 zoeae molt 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.

1.3.2.7. 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 1.3 & 4).

Table 1.3. Influence of physical factors on the biology of *Cancer magister*.

Year	**Findings**
Peterson 1973	Time lags 0.5 - 1.5 yrs between upwelling index and catch (does not correlate with recruitment). Suggest the correlations due to food availability.
Botsford & Wickham 1975	Time lag 9 - 12 years does not correlate with recruitment; suggest correlation due to food availability.
Love & Westphal 1981	Correlation to sunspot number; other researchers suggest this article may have been written in jest.
Wild 1983	Low catch years correlated with warmer winter water temperatures (and weaker southward transport) four years earlier.
Johnson et al. 1986	Correlation between catch and southward wind four years earlier.
McConnaughey 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 northward transport.
McConnaughey et al. 1994	Suggest that larvae may be retained in the nearshore environment rather than being transported offshore.
Botsford & Lawrence 2002	Commercial catch correlated with overall cooler conditions in the California Current.
Shanks et al. 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, 2013	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 one year.

Table 1.4. Influence of biological factors on the biology of *Cancer magister*.

Year	**Findings**
Botsford & Wickham 1978	Suggested that fluctuations may be caused cannibalism. Botsford 1984 stated if it was the cause the cycles would likely have been more stable.
Wickham 1979	Suggested predation by *C. errans* may impact reproductive output but the affect is not big enough to cause fluctuations.
McKelvey et al. 1980	Density dependent egg/larval survival influenced by production.
Botsford 1982	No correlation between catch and Chinook and Coho Salmon catch four years earlier.
Botsford 1983	No correlation between catch by humans and fluctuations in population
Shanks 2013	Suggested that when recruitment it high, cannibalism and competition among juvenile crabs impacts the population.

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 zoeae 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 south- ward 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 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, McConnaughey 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 zoeae 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 (McConnaughey 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 zoeae 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, 2013). 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, 2013).

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 molting of one megalopa will induce other megalopae to molt (Fernandez et al., 1994a).

1.3.3. 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.

1.3.3.1. 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).

1.3.3.2. 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; Waldron, 1958). The average daily movement was

1.1–3.2 km day^{-1}. 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 were *C. magister* usually inhabit. Thus, many individuals that forage in the intertidal must retreat to depth in order to digest their food.

1.3.3.3. 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 corroborates 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 molted 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^{-1} 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.

1.3.3.4. 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 molting (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.

1.3.3.5. 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.

1.3.3.6. 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).

1.3.3.7. 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 molting their shell (Jaffe et al., 1987; Ruppert, 1994). Unlike adults, juvenile *C. magister* molt 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, molting occurs annually during a relatively short time period of 6–8 weeks (Hankin et al., 1989; Mohr and Hankin, 1989). Prior to molting, crab shells are often heavily fouled with barnacles and other sessile organisms, whereas crabs are free of fouling after molting (Cumbrow, 1978). Just prior to molting, a suture line forms where the shell will open and the crab will back out of the old exoskeleton. Molting occurs from March to June in California, April to September in the San Juan Islands, and June to July in Alaska (Table 1.1; Jaffe et al., 1987; Knudsen, 1964; Park and Shirley, 2008; Wild, 1983b). Approximately, 90% of female crabs with a carapace width of ~135 mm molt annually, while almost no female crabs with a carapace width of >155 mm molt annually (Hankin et al., 1989).

Adult crabs gain between 8.1- and 19.7-mm carapace width following each molt (Hankin et al., 1989). After molting, it takes approximately 2 months for the exoskeleton to completely refill with tissue. Miller and Hankin (2004) provide descriptions of individual molt stages for determining molt stage of crabs in the laboratory; Washington Department of Fish and Wildlife also conducts routine field surveys in Puget Sound and collects extensive molt 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).

1.3.4. Mortality (All Stages)

1.3.4.1. Natural Mortality

Estimates of intra-annual mortalities of larvae are predicted to be consistent and the average daily survival rate is 0.066 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).

1.3.4.2. Diseases

In the laboratory, zoeae 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 micro-sporidia *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.

1.3.4.3. 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 mg l^{-1} and killed 50% of zoeae at a concentration of 0.01 mg l^{-1} (Buchanan, 1970). When adult crabs consumed cockles that had been exposed to the insecticide Sevin at 10 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 mg l^{-1} of the insecticide Sevin (Buchanan, 1970). Fifty percent of adults exposed to Sevin at a concentration of 0.26 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 mg 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).

1.3.4.4. 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).

1.3.4.5. 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 behaviors of adult *C. magister* in hypoxic conditions and determined that crabs cease feeding below 3.2 kPa O_2 (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 behaviors (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., 2014). Their results demonstrated that crabs migrated into the shallow nearshore environment rather than northwards out of hypoxic waters.

1.3.4.6. 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^{-1} day^{-1} (Wickham, 1980). Throughout the range of *C. magister*, 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.

1.3.4.7. 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* (McConnaughey 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 behaviors to cope with climate change.

1.4. FISHERY

1.4.1. 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 in 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 molting. 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 program 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 1.3; Demory, 1990). Early on, these oscillations were decadal in cycle, but since 1980s, the decadal pattern to the oscillation is no longer present (Figure 1.3; Shanks and Roegner, 2007). It

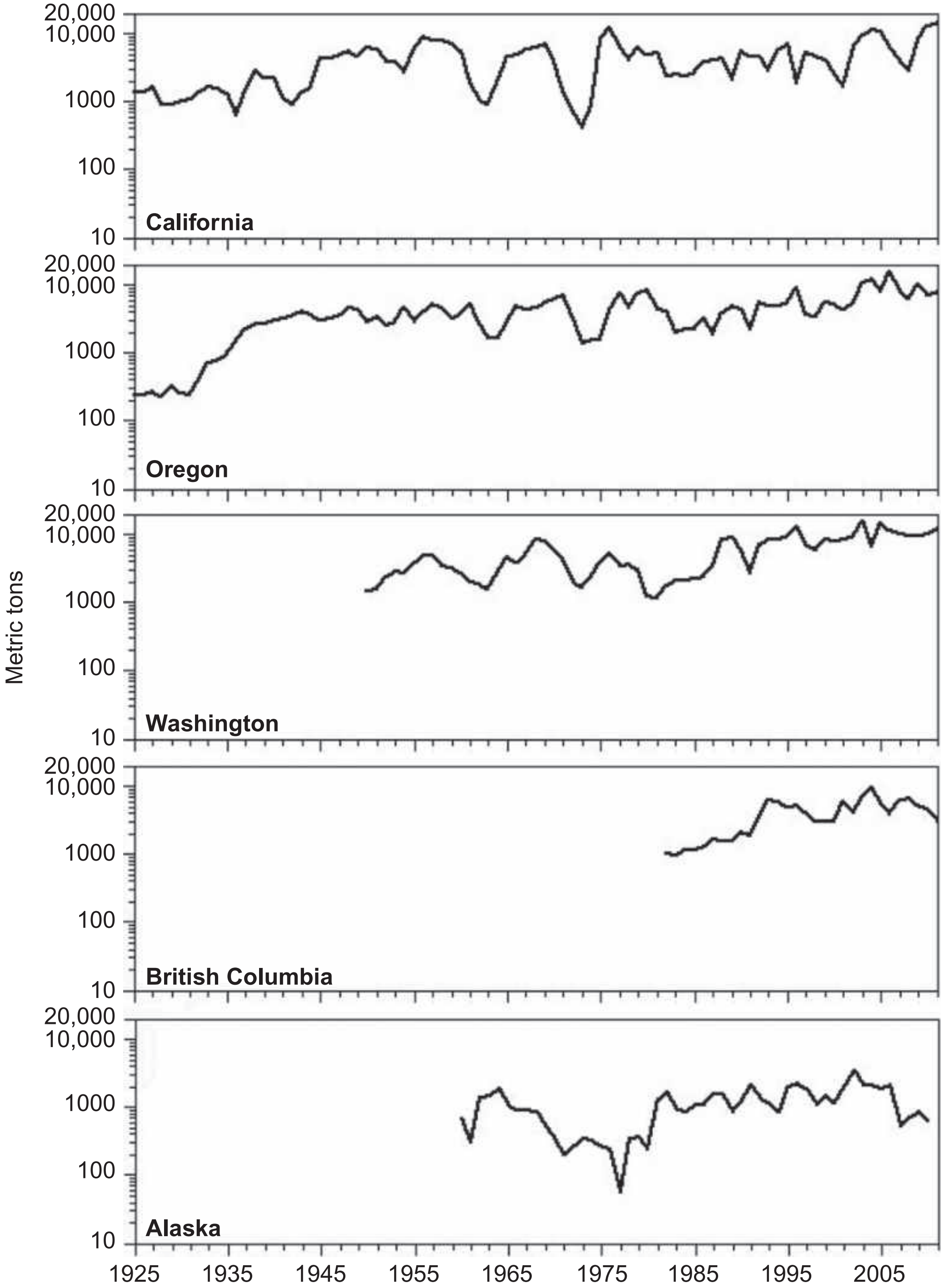

Figure 1.3. Commercial catch of *Cancer magister* in California, Oregon, Washington, British Columbia and Alaska. Catch data were not available back to 1925 in al regions. Note the decadal patterns (significant autocorrelation) in catch from the 1950s to 1980s in commercial catch in California, Oregon and Washington (Shanks and Roegner 2007). This decadal oscillation has not occurred since the 1980s (no further autocorrelation).

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 1.4; 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.

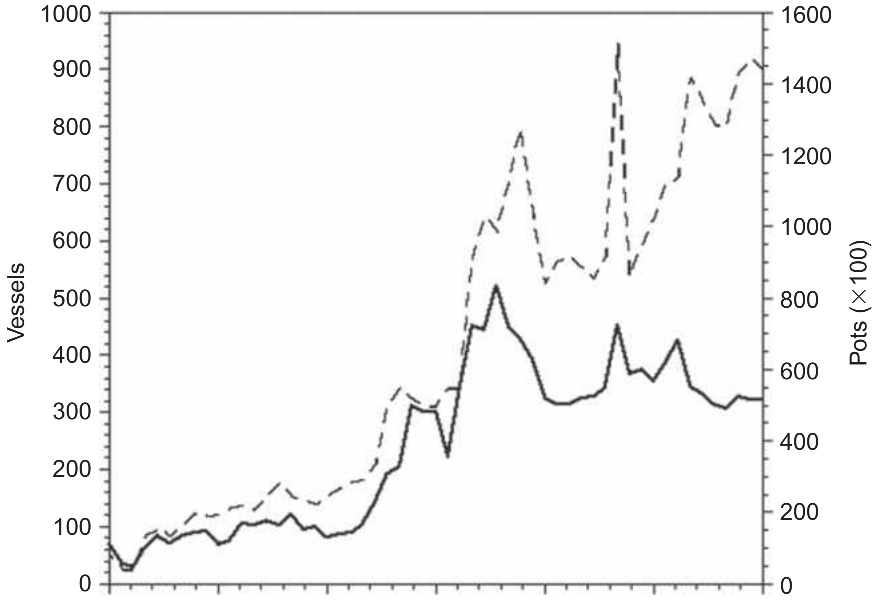

Figure 1.4. Number of boats (solid line) and pots (dashed line) participating each year in the commercial *Cancer magister* fishery in Oregon. Note the dramatic increase in the effort (both pots and vessels) that occurred in the mid 1970's. This timing coincides with the federal plan to enhance U.S. fisheries following the establishment of the Exclusive Economic Zone (Gelchu and Pauly, 2007). Data on effort were spotty and thus are not presented here.

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 1.3). 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 1.5–1.7). 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. 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 (Dewees et al., 2004). A survey of fishermen in

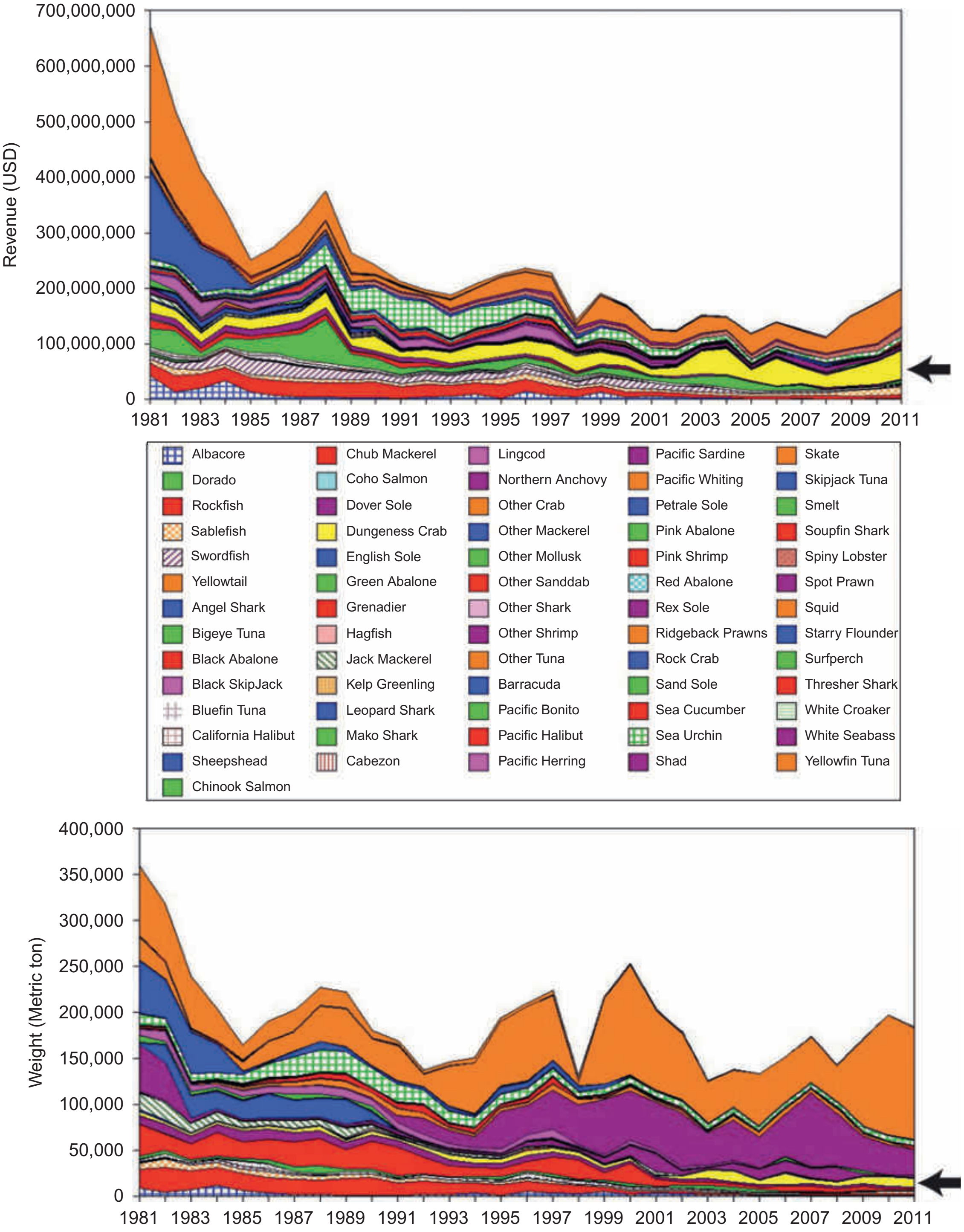

Figure 1.5. Annual revenue (top panel) inflated to 2012 USD value and annual catch (bottom panel) for commercial fisheries in California from 1981 through 2011. (Pacific Fisheries Information Network (PacFIN) retrieval dated December, 2012, Pacific States Marine Fisheries Commission, Portland, Oregon (www.psmfc.org).) Arrows on the right side of the figure point to the area that represents *Cancer magister*.

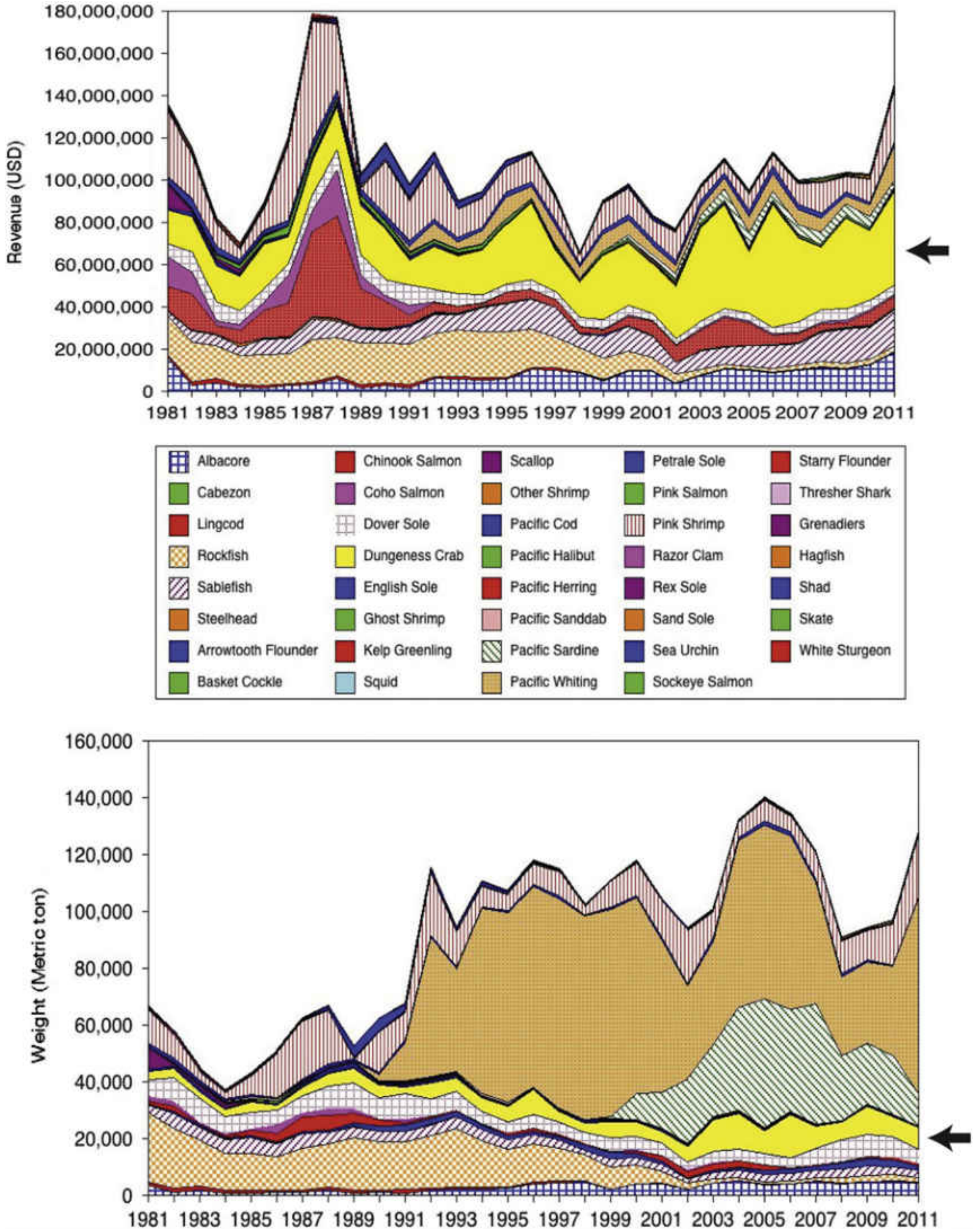

Figure 1.6. Annual revenue (top panel) inflated to 2012 USD value and annual catch (bottom panel) for commercial fisheries in Oregon from 1981 through 2011. (Pacific Fisheries Information Network (PacFIN) retrieval dated December, 2012, Pacific States Marine Fisheries Commission, Portland, Oregon (www.psmfc.org).) Arrows on the right side of the figure point to the area that represents *Cancer magister*.

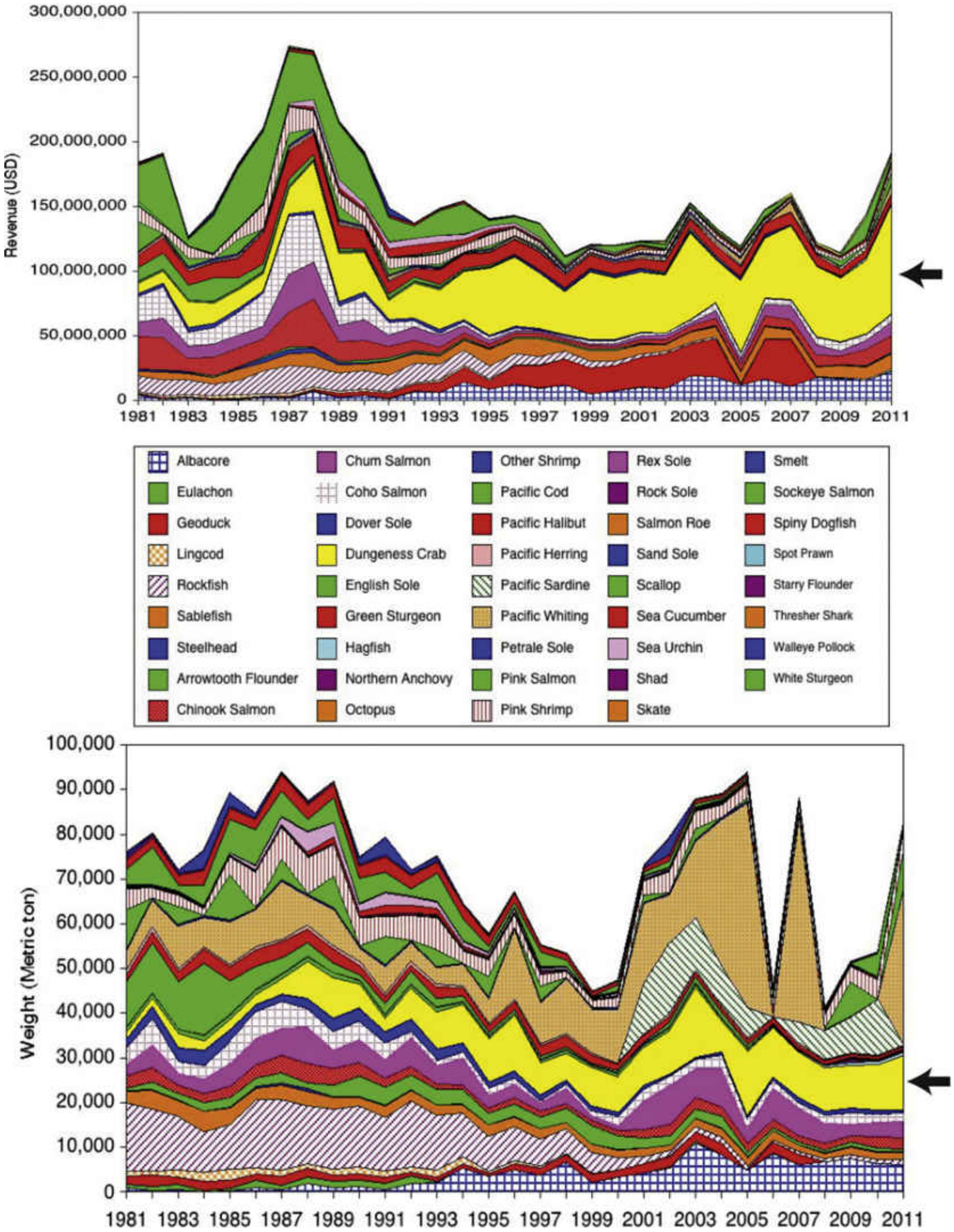

Figure 1.7. Annual revenue (top panel) inflated to 2012 USD value and annual catch (bottom panel) for commercial fisheries in Washington from 1981 through 2011. (Pacific Fisheries Information Network (PacFIN) retrieval dated December, 2012, Pacific States Marine Fisheries Commission, Portland, Oregon (www.psmfc.org). Arrows on the right side of the figure point to the area that represents *Cancer magister*.

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 (Dewees et al., 2004).

1.4.2. 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 1.5 & 6). 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 1.5 & 6). Commercial fisheries throughout the range of *C. magister* are only allowed to harvest male crabs, though this is a recent change in British Columbia where it used to be legal to retain females (Table 1.6). For recreational fisheries, all states except California restrict catch to only male crabs (Table 1.5. The size of individuals that can be retained in commercial and sport fisheries varies throughout the crabs range from 145 to 165 mm (Table 1.5 & 6). 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 molting and, due to the variability in the timing of molting, the dates of closure change with latitude with openings occurring later further north (Tables 1.1 and 1.4). 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).

Table 1.5. Sport fishery retention size, season and unique regulations to each region throughout the range of *Cancer magister*.

	Legal Size (mm)	Season	Notes
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)

Table 1.6. Commercial fishery retention size, season and unique regulations to each region throughout the range of *Cancer magister*.

	Legal Size (mm)	Season	Notes
California	160	December 1-June 30 (Varies North to South)	
Oregon	160	Bay fishery open weekdays January-Labor 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.	

1.4.3. Direct and Indirect Impacts of the Fishery

1.4.3.1. 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–\$91 pot^{-1}) and compared to the cost of removing derelict gear ($93–$193 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).

1.4.3.2. 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).

1.4.3.3. 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.

1.4.3.4. 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.

1.4.4. 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.

1.4.4.1. 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 (Stefferud, 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 molting 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. McConnaughey 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 ~12%. In recent years, catch of megalopae has increased to the point that their early linear model would have predicted a commercial catch of ~700,000,000 lbs (10 times greater than historic maximum). Commercial catch correlated with these high megalopae returns has leveled off with (and declined; Figure 1.8; Shanks, 2013). 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 ~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 1.8).

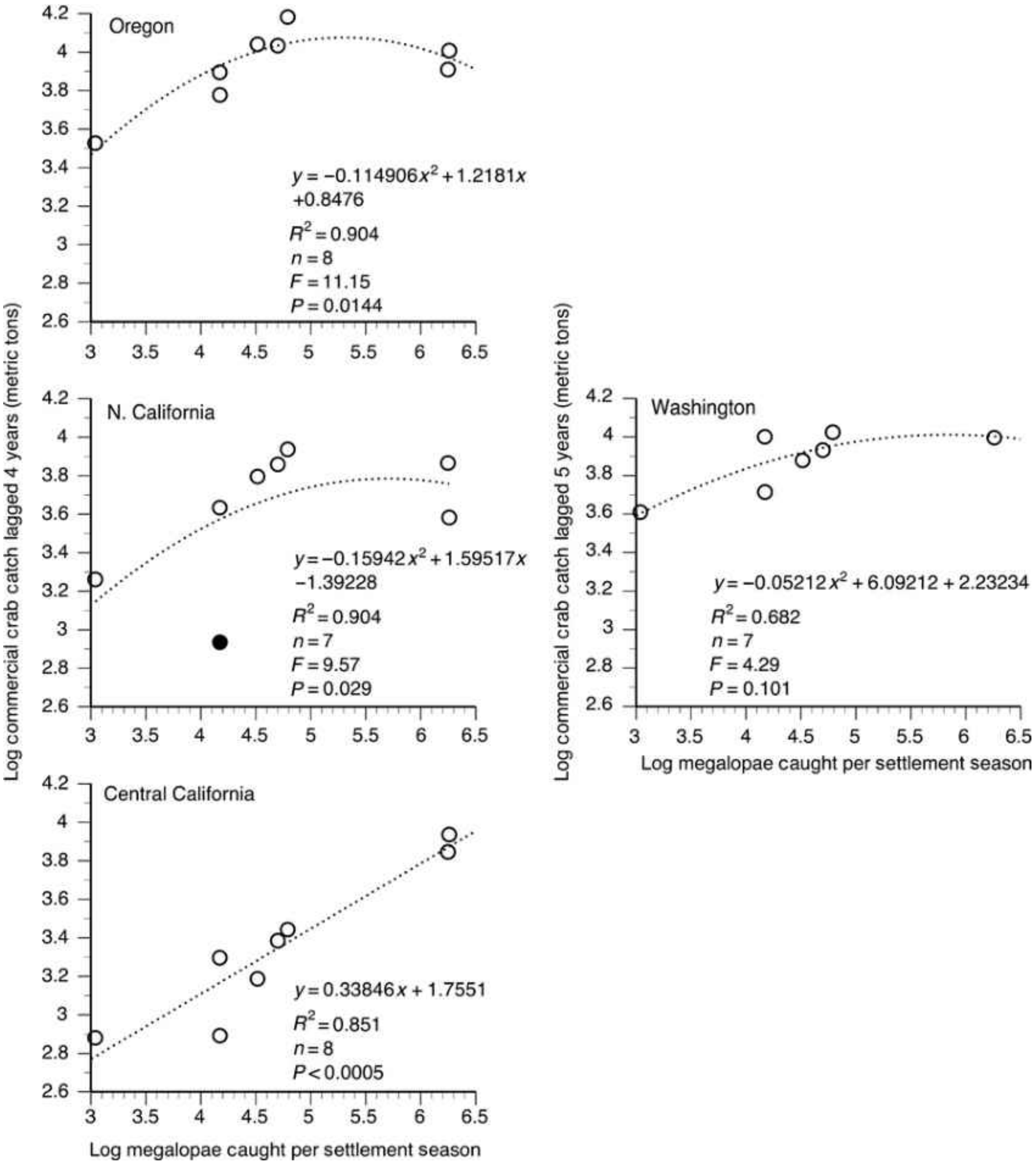

Figure 1.8. Log catch of *Cancer magister* megalopae caught annually versus commercial catch in Central California (south of Sonoma County), Northern California (Sonoma County north), Oregon and Washington (adapted from Shanks, 2013). Commercial catch is lagged 4 years after settlement season except 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.

1.4.4.2. 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 1.3). 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 commercial catch. Using a data set collected over 12 years, Shanks (2013) 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 1.3 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 1.3). 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, 2013; Shanks and Roegner, 2007; Shanks et al., 2010) provide the best explanation for the fluctuations of the population (see above for a 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.

1.5. 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.

1.6. ORGANIZATION OF THIS DISSERTATOIN

In this dissertation I use a variety of techniques to better understand the correlations between physical oceanography processes and the recruitment of Dungeness crab megalopae.

Chapter II " The influence of decadal scale climactic events on the transport of larvae" is co-authored with Alan Shanks. We present results from an individual based biophysical model and suggest that the Dungeness crab population supports the member vagrant hypothesis. Specifically, during negative PDO's membership of larvae in the California Current population is enhanced by the increased southward flow. Additionally, we demonstrate that a large number of individuals return approximately back to their release location. The results suggest that the population has evolved to promote membership of larvae within the California Current. Additionally, since these species occupy the continental shelf and many species on the shelf exhibit similar life history characteristics it is likely that these results are applicable to additional species. As this model was encompassed the large mesoscale processes influencing dispersal the remaining chapters aim to better understand some of the smaller scale processes that influence dispersal.

Chapter III "The influence of spatial and temporal variation of diel vertical migration on larval dispersal and concentration: Results from a highly validated individual based model" is co-authored with Alan Shanks. We present results from an individual based biophysical model and suggest that megalopae exhibit a twilight vertical migration. Further, during daytime the megalopae migrate to or almost to the bottom. Model results are validated using time series techniques and daily catch of Dungeness crab megalopae in a light trap. Additionally, we test a variable behavior where megalopae exhibit a twilight vertical migration to 1 meter of the bottom offshore from the continental shelf break and remain in the neuston on the continental shelf. The results suggest megalopae are concentrated at the shelf break where we hypothesize they remain until they are transported across the continental shelf by internal waves. The remaining chapters attempt to better understand the characteristics of transporting internal waves.

Chapter IV "*In situ* observations of Dungeness crab megalopae used to estimate transport distances by internal waves" is published in *Marine Ecology Progress Series* and is co-authored with Alan Shanks. In this chapter we conduct *in situ* observations of Dungeness crab megalopae and demonstrate that they 1) swim with the surface current and 2) swim at speeds of ~10 cm s^{-1}. We subsequently deployed a thermistor mooring in 30 m of water to collect observations of internal waves. Using data from the observed internal waves and the results from our observations of megalopae we calculated potential transport distances for each internal wave. We calculated transport distance for both passive particles and particles that swam with the wave at speeds ranging from 0.1-10 cm s^{-1}. We demonstrate that the behavior exhibited by Dungeness crab megalopae would dramatically increase the potential transport distance of megalopae. We conclude by discussing why, although our results suggest all internal waves should transport larvae, only certain waves cause transport. In the final chapter, we assess the variability in potential transport by internal waves on a daily, seasonal and decadal time scale.

Chapter V "Daily, seasonal and decadal variations in transport by the internal tide" is under review in the journal *Journal of Marine Research* and is co-authored with Alan Shanks. In this chapter we analyze 12 years of daily catch of megalopae and demonstrate that despite a dramatic change in the total annual catch of megalopae (correlated with phase of the PDO), cross-shelf transport still is correlated with the daily maximum tidal range. We hypothesize this is indicative of transport by internal waves generated by the internal tide. Subsequently, we use data from a mooring deployed as part of the GLOBEC project and generalized additive models to examine the effect of factors well known to influence the internal tide on the daily catch of megalopae. We demonstrate that more megalopae are caught when the thermocline is located at a depth of 21-35 m. Additionally, more megalopae are caught with a weaker thermocline and less horizontal shear. We hypothesize these three variables allow internal waves to remain more coherent as they transit across the continental shelf. Finally, we examine thermocline depth during winter and summer months and show that the thermocline is deeper during the winter than during the summer. We hypothesize this change in thermocline depth correlates with a change of internal wave shape, which ultimately is why megalopae return to the near shore during the summer.

CHAPTER II

THE INFLUENCE OF DECADAL SCALE CLIMACTIC EVENTS ON THE TRANSPORT OF LARVAE

This chapter is in preparation for the journal *PLoS One.* The chapter is co-authored with Alan Shanks. Alan Shanks maintained the light trap and provided the samples used to validate the model. I developed and implemented all of the models as well as did all of the initial writing.

2.1. INTRODUCTION

Many marine species have a biphasic life cycle that begins with a planktonic larva [1, 2]. A number of hypotheses have been proposed to explain the variability of larval success [3, 4]. One hypothesis, the member/vagrant hypothesis, suggests that populations persist in locations where planktonic larvae return to the adult population; those that return are considered members whereas those that do not return are considered vagrants [5]. Further, the hypothesis suggests the size of the population is a function of the physical oceanographic processes influencing the movement of larvae. The member/vagrant hypothesis states that regardless of the distance the larva is transported, the larva must return to a location where it is able to settle, develop and reproduce [5]. Ultimately, if there are to many vagrants from the population then the population will not persist in its current location.

Research has suggested that the large fluctuations observed in some adult populations is driven by the relative success of the planktonic phase of the species [6, 7].

Larval advection distances are highly variable between species; with some larvae having short transport distances and others traveling >1000 km [8-10]. Additionally, for species with fewer and/or smaller populations there are fewer larval retention areas and for species with more and/or larger populations there are more or larger larval retention areas, ultimately creating a more demographically open system [5]. Knowing the number of populations and retention areas (essentially whether populations are open or closed) is important for effective fisheries management and the development of marine reserves [11-13]. For populations with a large number of populations and thus retention areas, it is important to be able to quantify 1) the amount of connectivity between populations and 2) the directionality of the connectivity between populations [14, 15].

In recent years, studies have suggested that population connectivity can be dramatically influenced by large climactic variations e.g., El Nino and North Atlantic Oscillation [16-18]. However, studying the effects of these climactic variations on larval transport is difficult due to their large scale, both temporally and spatially [19-21]. In this paper we examine, using biophysical models, the effect of the Pacific Decadal Oscillation (PDO) on the transport of Dungeness crab, *Cancer magister*, larvae in the California Current for 10 years.

Larval transport has been studied extensively in the California Current Ecosystem [22, 23]. Shanks and Eckert [24] compiled an extensive data set on the life history traits of marine fishes and benthic crustaceans in the California Current. They found coherent sets of traits associated with species that as adults inhabit the shelf/slope, depths < 30 m, and the Southern California Bight. They suggested that the combination of life history traits might have evolved to aid in the closure of the larval pelagic phase. In general, they demonstrated that shelf/slop species 1) have relatively long pelagic larval durations (PLD), 2) release pelagic larvae during winter and spring months, and 3) due to the timing of their larval release, experience both northward and southward flow over the continental shelf. Despite the range of species covered in the paper, the dispersal patterns were highly conserved depending on the location where adults lived. Thus, although this paper focuses on *Cancer magister*, the findings are likely applicable to many important shelf/slope species in the California Current such as rockfish (*Sebastes sp.*), pink shrimp (*Pandalus jordanii*), etc.

The fishery for the Dungeness crab is the most economically important on the West Coast of the continental United States [25]. Economists have suggested that if the fishery were to collapse, the majority of the West Coast fishing industry would collapse as well [26]. These is because most vessels on the West Coast participate in multiple fisheries and are reliant on the income from the Dungeness crab fishery to maintain their vessels. The fishery has historically experienced dramatic catch fluctuations, which researchers hypothesize are influenced by larval success [25, 27]. Recently, Shanks et al. [28-30] have demonstrated that annual catch of Dungeness crab larvae is strongly influenced by the PDO. The PDO manifests as anomalously warm or cold water in the Northeast Pacific Ocean [20]. Additionally, it alters circulation along the West Coast by varying the amount of water entering the California Current from the West Wind Drift (Fig. 2.1). Specifically more water is shifted into the California Current during negative PDOs, increasing southward transport. Shanks et al. demonstrated that the catch of megalopae increased by multiple orders of megalopae during negative PDOs. They have also found a correlation between the PDO and amount of megalopae caught at the end of the recruitment season, with more megalopae caught during negative PDO years.

Shanks et al. also demonstrated that the annual catch of larvae is greater when the day of the year of the spring transition is earlier [28-30]. The day of the year of the spring transition is considered to be the day that circulation on the continental shelf shift from winter to summer patterns [31, 32] (Fig. 2.1). Finally, they also have a positive correlation between the total annual catch of megalopae and the amount of upwelling following the day of the year of the spring transition. From these correlations Shanks et al. present the following hypotheses to explain the correlations between these physical process and the catch of megalopae. They hypothesize the increased southward flow during negative PDOs ultimately acts to retain more larvae within the California Current. Further, they hypothesize more megalopae are caught following an early spring transition because it lengthens the time period where megalopae can return to the nearshore. Finally, the catch of megalopae is correlated with upwelling because megalopae are advected onto the shelf with the deep upwelled waters.

Studying larval transport is inherently difficult, especially for species that migrate long distances [10]. In recent years, biophysical modeling has become an increasingly important tool for examining the transport of larvae [33]. Biophysical models allow researchers to study larval dispersal relatively cheaply. As models have become more powerful, researchers are employing novel techniques to validate the model outputs [34, 35]. Though, to our knowledge there have been no modeling studies that have examined the influence of decadal scale climatic variations on larval transport.

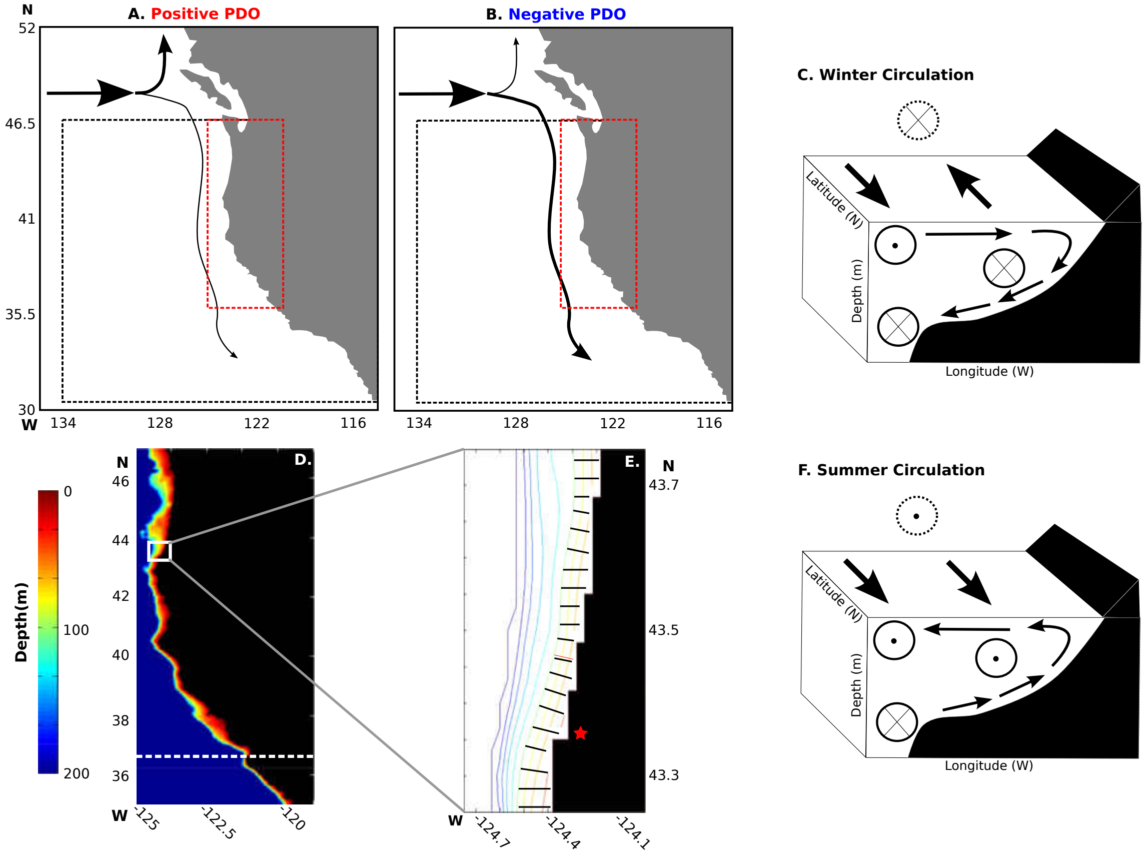

Figure 2.1. Maps of California Current circulation (A-C,F) and model parameterizations (A,B,D,E). During positive PDO's more water is shifted into the Alaska Current from the West Wind Drift and more is shifted into the California Current during negative PDO's (A-B). During the winter flow along the continental shelf is northward and winds are from the south (C). Off of the continental shelf at the surface flow is southward and at depth northward. During the spring transition, winds switch to coming from the north and on the continental shelf and in the surface waters off the continental shelf flow is southward (F). At depth on the continental slope flow is northward. Circles with dots (⦿) denotes flow out of the page and circles with an 'x' in it (⊗) denotes flow into the page (C,F). Solid circles denote direction of water flow and dashed circles denote wind direction (C,F). The black dashed line (A-B) is the spatial extent of the ROMs model. The red dashed line (A-B) is the region particles were released and succeeded this area is more closely represented in panel D. Particles were released every 3 km north of the white dashed line (D). The region south of the white dashed line is the southern extent of where larvae succeeded. For every 3 km of coastline, particles were released along a cross-shelf transect (black lines) from 20-100 m water depth (E). The light trap was operated in Coos Bay Oregon (red star).

We combined data generated using the Regional Ocean Modeling System (ROMS) with the Larval TRANSport Lagrangian Model (LTRANS) to simulate the transport of larvae. Our models (both physical and biological) simulated the effect of the PDO well and suggests that during negative PDO years larvae do not migrate as far from their release site as during positive PDO years and that fewer larvae are lost into the Alaska current. In this study we used data from 10-years of daily catch of Dungeness crab larvae to validate our biophysical model of larval transport. This data set allowed us to compare different types of vertical migratory behaviors and assess the skill of our model. We show that there is a potentially a surprising amount of larval successes at the location of larvae were released (herein we refer to this as self-recruitment) in the population and that potentially the amount of self-recruitment increases as PLD increases.

2.2. MATERIALS AND METHODS

2.2.1. Hydrodynamic Model

2.2.1.1. Parameterization

The physical model was developed using the Regional Ocean Modeling System (ROMS); a hydrostatic free surface terrain following system that is ideal for coastal and regional modeling applications [36]. The model provides greater resolution near the surface and bottom of the water column, which are of special importance when studying larval movement. The models spatial domain was adapted from Veneziani et al. [37] and updated to include new forcing. The model was configured to capture most of the circulation characteristics of the California Current. It ranges from 134 to 115.5 °W and from 48 (Washington State) to 30 °N (Baja California) and has a horizontal resolution of ~1/30° (Fig. 2.1). The model employs 42 vertical layers providing a vertical resolution in the thinner surface and bottom layers ranging from ~0.3 - 8 m (shelf/slope versus open ocean) and in the thicker middle layers 7 - 300 m (shelf/slope versus open ocean regions). Outputs were generated daily from 1999-2013.

2.2.1.2. Validation

Maximum and minimum values of U, V and W current velocities and temperature were obtained for each modeled day for the entire model domain and on the continental shelf. Data were assessed visually to ensure that 1) there were no single time point values that were significantly higher or lower than the values at adjacent time points and 2) that both maximum and minimum values reasonably reflected values from observational studies for the California Current system [38].

The goal of this manuscript was to examine the effect of the PDO phase on the larval transport of *Cancer magister.* The PDO is defined as the leading empirical orthogonal function (EOF) of sea surface temperature in the North East Pacific [20]. It manifests as anomalously warm or cold sea surface temperatures in the North Pacific Ocean during winter months (December-February). We generated a wintertime sea surface temperature anomaly and calculated the leading EOF for data from 34-47 °N. The modeled EOF was correlated with reported PDO Index values [39].

2.2.2. Individual Based Model

2.2.2.1. Lagrangian Particle Tracking

The individual based model was run using the Larval TRANSport Lagrangian Model (LTRANS) [40, 41]. LTRANS uses stored hydrodynamic outputs from ROMS and allows the user to tailor the model to their specific application. Further, it has a scheme to model random vertical displacement at a scale that is smaller than ROMs models are capable of modeling. Based on results from initial sensitivity analyses, we parameterized the model with an internal time step of 150 s. The model was run from Oct 1 through September 30 of the following year since this is the time period when larvae are known to be released and return to the near shore. Outputs were generated each day. Larvae were tracked for a total of 10 larval transport years 1999-2000, 2000-2001, 2005-2006, 2006-2007, 2007-2008, 2008-2009, 2009-2010, 2010-2011, 2011-2012, 2012-2013 based on the availability of light trap data for validation (see section 2.2.2.6. for more details about methods for comparing light trap and model output data).

In the event that particles collided with one of the oceanic boundaries of the ROMs model, the particle was first reflected back into the model domain the distance it would have been transported out of the model. In the event that the particle collided with the boundary at the next time step the particle was removed from the model and both the location and time it left the model domain were recorded. In all events where particles collided with the shoreward boundary, they were reflected back into the model domain.

Coastal habitat maps from 35 °N to 47 °N were assessed to determine the extent of suitable (soft sediment) habitat for adult *Cancer magister* [25]. Despite small pockets of unsuitable habitat at a latitude of ~40 °N, the entire range from 35 – 47 °N was suitable for adult *C. magister.* Sensitivity analyses suggested 3 km was the minimum resolution necessary to provide sufficient alongshore resolution, thus, particles (i.e., larvae) were released every 3 km of coastline from 37-47 °N (Fig. 2.1). The southern release site was chosen because 37 °N is essentially the southern range of *C. magister.* Although *C. magister's* range extends well north of 47 °N, our model domain only extended to 48 °N (Fig. 2.1) and thus, particles were only released as far north as 47 °N to provide 1 ° buffer at the northern extent. At each release site, larvae were released at water depths ranging from 20-100 m in 10 m increments (Fig. 2.1). These are the depths at which ovigerous females are routinely found [42]. Larvae were released each day from December 1 –March 30 of each model year since this is the time period larvae are released in the California Current [25]. In total 470,448 simulated larvae were tracked each model year.

2.2.2.2. Development Module

Using data from Moloney et al. [43] larval development was modeled as a factor of temperature and time. Moloney et al. [43] included salinity as a factor for development rate in their model, however, the influence of salinity was minimal compared to temperature, and thus was excluded from this module for simplicity and to reduce computation time. Further, Moloney et al. [43] modeled the rate of development from larval release to megalopa and did not differentiate development rate between the different zoeal stages. Sulkin and McKeen [44] reported development rates at different temperatures for each zoeal stage. Dividing the stage duration by the total time from release to megalopae demonstrated that development was approximately equal between stages. Thus, we assumed that development rate was similar across larval stages, e.g., at the same temperature, a stage-I zoea would develop into a stage-II zoea at the same rate as a stage-V zoea would molt into a megalopa.

2.2.2.3. Behavior Module

Using the output from the development module, we generated a module that controlled the vertical migratory behavior of each larval stage. The timing of the vertical migration was based on the time of sunrise and sunset. Sunrise and sunset times were extracted for Trinidad, California [45]. A single site was used to maintain computational efficiency. Trinidad, California was selected because it is approximately in the middle of the latitudinal range in which we released particles. Zoeae were modeled to exhibit a standard diel vertical migration (occupy the neuston at night and depth during day). Evidence suggests megalopae make a similar vertical migration when off of the continental shelf, but remain in the neuston on the continental shelf and thus we modeled megalopae to alter their behavior in response to their location [46, 47]. Based on results from recent modeling work and observations, when megalopae were off the continental shelf they were modeled to exhibit a twilight vertical migration [46, 48-50]. More specifically, they would occupy the neuston for 30 min on either side of sunrise and sunset, descend to a depth of 50 m at night (below the Ekman layer) and be at depth during the day; the depth varied between simulations (Table 2.1). For species exhibiting a twilight vertical migration, evidence suggests that at night they either disperse randomly or sink [51]. We chose to have megalopae occupy a 50 m depth based on results from another modeling project and for computational efficiency [46]. In the model, when megalopae were on the continental shelf they were modeled as remaining in the neuston. For both zoeae and megalopae, particles were normally distributed around the depth they were simulated to occupy except when they were at the surface, where they had a 1-sided normal distribution from the surface downward. In both instances a standard deviation of 6 was used to define the distribution. For each larval stage, swimming speeds were altered to represent values from laboratory or *in situ* studies (Table 2.1).

Table 2.1. Depth and swimming speed parameters for the shallow and deep simulations. Swimming speeds denote the speed that larvae moved vertically in the water column and values are from laboratory and *in situ* studies [52, 53]. Depths denote the depth larvae occupied during the day. Zoeae exhibited a standard vertical migration; occupying surface waters at night and depth (denoted in the table) during the day. Megalopae exhibited a twilight vertical migration; occupying surface waters at twilight, 50 m water depth at night and depth (denoted in the table) during the day. Shallow depths are based on observational findings [54]. Deep simulations depths are based on additional observations and modeling studies [46, 47]. Off shelf is defined as seaward of the 200 m isobaths and on shelf is defined as shoreward of the 200 m isobaths. mab- meters above bottom

Stage	**Swimming Speed (cm s $^{-1)}$**	**Shallow Migration Simulation Depth**	**Deep Migration Simulation Depth**
Zoeae I	1	20 m	1 mab
Zoeae II	1	20 m	1 mab
Zoeae III	1.5	20 m	1 mab
Zoeae IV	1.5	80 m	1 mab
Zoeae V	1.5	80 m	1 mab
Megalopae (Off shelf)	10	300 m	1 mab
Megalopae (On Shelf)	NA	0 m	0 m

2.2.2.4. Simulations

The depth *Cancer magister* larvae occupy during the day is not well known and thus we simulated two different migration depth scenarios (Table 2.1). Since the goal of this study was to examine variations in larval transport in relationship to the phase of the PDO we simulated each behavior using the ROMs outputs from 2000-2001 (positive PDO) and 2009-2010 (negative PDO). These two years were selected since they had the most complete light trap time series data and thus could be most closely validated. For the shallow migration depth simulations, depths were chosen based on migration depths suggested in the literature [54]. Sensitivity analyses suggested that only major variations in depths significantly altered transport trajectories. Since these major variations were either 1) unrealistic or 2) captured by the deep migration simulation, we restricted the simulations to these two different behaviors. Statistical analyses (see Section 2.2.2.6) suggested the deep migration was more coherent with the light trap data and thus for the remaining 8-years we modeled the vertical migration of larvae using the deep simulation behavior.

2.2.2.5. Super Individuals: Production and Mortality

Ideally we would have liked to change the number of particles released each year to match the predicted number of larvae released each year, however, computationally this was impossible. Thus, we used super individuals in order to allow us to scale the number of larvae released into the model domain each year [55]. Initially each particle was considered to represent 10^6 individuals. Then we multiplied each of these particles by a scaling factor in order to adjust the super individual to represent the number of larvae released that year (see Appendix A for an explanation of how the scaling factors were calculated). Thus for the 1999-2000 model year (year with the lowest total amount of larval release) a super individual represented 3.5×10^5 and for 2005-2006 (year with the highest total amount of larval release) a super individual represented 1×10^6 individuals (see Appendix A for more information).

Using super individuals allowed us to include larval mortality in our model. We used a constant larval mortality rate of 0.025 regardless of stage. A mortality rate of 0.025 was based on examining larval morality rates based on production (see Appendix A for an explanation). The number of individuals represented by each super individual for each day was calculated as:

$$N_t = N_0 e^{-0.025t} \tag{2.1}$$

where N_t is the number of individuals represented by the super individual, N_0 is the scaled number of particles initially released and t is number of days the particle had been tracked since it was released.

2.2.2.6. Validation and Analysis

From ~ April 1- September 30 of the years 2000-2001 and 2006-2013 we monitored the daily catch of *Cancer magister* megalopae to a light trap operated in Coos Bay, Oregon (Fig. 2.1). Each day the number of megalopae was enumerated using a dissecting microscope unless the total number of individuals was >2000, in which case the number of individuals was determined by weight of the sample [29, 30].

To compare the model results with the light trap data we had to define a measure of transport success. We defined transport success as a particle that 1) was a megalopa and 2) was located on the continental shelf. We continued to track successful particles after they were successful. We compared the light trap data and modeled number of successes each day using standard time series techniques [56]. All data were assessed visually to ensure they were stationary and long-term trends were removed using the "detrend" function in MATLAB. Research suggests that daily variation in catch of *Cancer magister* megalopae is influenced by the internal tide [57]. However, our ROMs model did not include tides and thus we could only examine the effects of mesoscale processes on larval transport. Therefore, data were smoothed using 10-day running mean to remove large daily variations that are likely related to transport by the internal tides [58]. After smoothing, data were $\log_{10}$ transformed. The light trap and model time series were compared by calculating the maximum magnitude squared coherence, cross-Fourier analysis and comparing spectral densities [56].

2.3. RESULTS

2.3.1. Hydrodynamic Model

The observed and modeled PDO indices were positively associated with one another (R=0.92; Fig. 2.2). During negative PDO years, alongshore currents were, in general, more southward than during positive PDO years (see Appendix B for graphs and analyses). The modeled day of the year of the spring transition was strongly associated with the observed day of the year of the spring transition (R=0.95, Appendix B). Finally, mooring and model data were highly associated for alongshore velocities and temperature data (see Appendix B for graphs and analyses). Observed and modeled data of cross-shelf flow did not agree as well. We hypothesize that the poor association is due to the grid cell size we used which prevents the model from capturing some of the influences that shelf bathymetry has on flow. Additionally, it is possible that although the observed cross-shelf flow data was filtered to remove the tide, there was still some tidal noise in the data causing the two to be poorly associated. However, the focus of this study was primarily alongshore transport of larvae and thus the strong correlations between modeled and observed alongshore flow suggests the model simulated the dynamics necessary for this study. Finally, based on visual inspection, the hydrodynamic model used in this study accurately depicted mesoscale circulation patterns of the California Current.

2.3.2. Individual Based Model

We examined transport success and settlement distance of particles to better understand the role of California Current circulation patterns on the transport of *Cancer magister* larvae. Transport success (defined more thoroughly in Section 2.2.2.6) was defined as a particle that 1) was a megalopa and 2) was on the continental shelf.

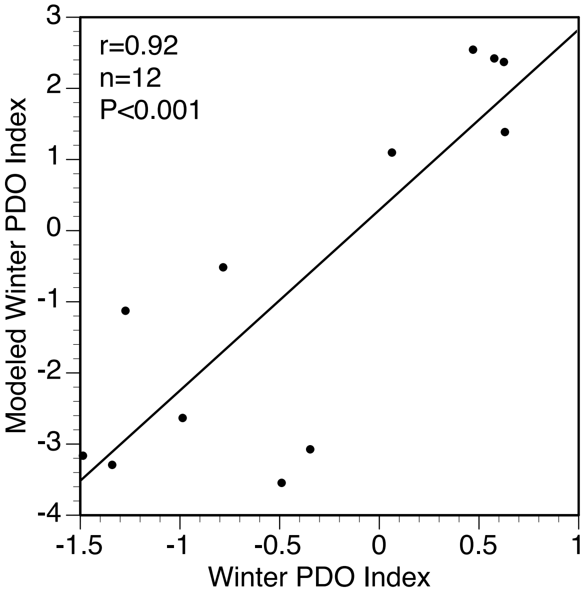

Figure 2.2. Measured versus modeled PDO index. Values differ numerically from one another since the index is calculated from a long-term anomaly and the mean value used to calculate the anomaly differed between the datasets.

Settlement distance was calculated as the linear distance (km) from the location the particle was released to the location of transport success.

2.3.2.1. Depth Comparison Simulations

The modeled time series for the deep migration simulation more closely matched the light trap time series than the shallow migration simulation (Fig. 2.3). Overall, the deep migration simulations resulted in more transport successes than the shallow migration simulations (see Appendix C for connectivity matrices). Most transport successes during for the shallow migration simulations occurred at the northern and southern extent of the model range and fewer transport successes occurred in the middle of the model domain. There were especially few transport successes near ~ 43 °N, an area with a large and well established population of *Cancer magister* [25]. This further corroborates that the deep migration simulation more closely depicts the realized dispersal of *C. magister* larvae. Thus, for the remaining simulations, particles were modeled to exhibit the deep migration depth behavior.

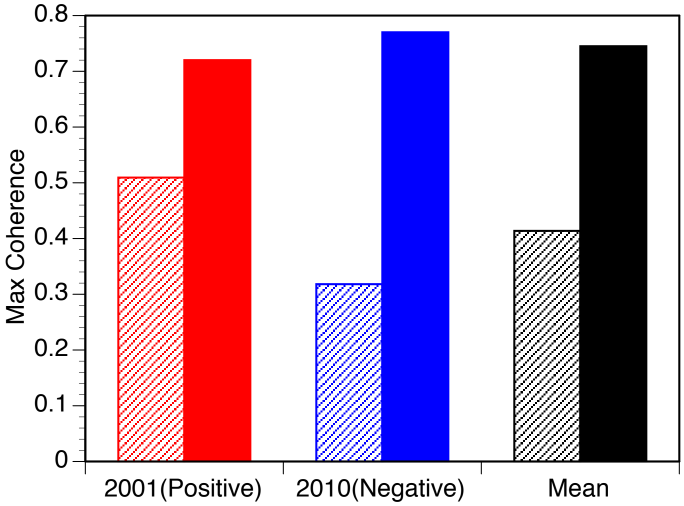

Figure 2.3. Maximum magnitude squared coherence between the light trap and the shallow migration simulation (dashed bars) and deep migration simulation (solid bars) during 2001- a positive PDO year (red bars), 2010- negative PDO year (blue bars) and an average of the two PDO phases (black bars).

2.3.2.2. Deep Migration Simulation

While analyzing the results from the deep migration simulations we examined the effects of many variables on both transport successes and settlement distance (Table 2.2). Throughout this results section we will only discuss those variables that had discernable effects. However, knowing which variables had no discernable effect on transport success or settlement distance is almost as informative as knowing those that had a discernable effect. This is because it allows one to know which variables to include and exclude when generating conceptual hypotheses regarding the transport of larvae. All results presented here are standardized to remove effects from the larger number of negative PDO years that were modeled (7 versus 3 yrs).

Table 2.2. The effect of different variables on average transport success and settlement distance. Transport success is defined as a particle that is 1) a megalopae and 2) on the continental shelf. Settlement distance is linear distance (km) from release site to location of transport success. NP- no pattern observed. Fig. 2.5-8 denotes the figure where the patterns are depicted.

Effect Variable	**Response Variable Effect** Transport Successes	 Settlement Distance
PDO Phase	Fig. 2.5	Fig. 2.7
Year	NP	NP
Day of the Year of the Spring Transition	NP	NP
Release Date	NP	NP
Release Depth	NP	NP
Release Latitude	Fig. 2.8	Fig. 2.8
Release Shelf Width	Fig. 2.8	NP
Success Date	NP	NP
Success Latitude	Fig. 2.8	Fig. 2.8
Success Shelf Width	Fig. 2.8	NP
Development Rate	Fig. 2.6	NP
Pelagic Larval Duration (PLD)	Fig. 2.6	Fig. 2.6
Distance	Fig. 2.7	NA

The light trap and model time series for the 2006 settlement season were the most coherent and the time series' for 2007 settlement season were the least coherent (Fig. 2.4). On average the positive PDO model years were more coherent (0.86) than the negative PDO years (0.82), however, the difference was minimal. The modeled and light trap time series' both had spectral peaks at ~4-5 d (Fig. 2.4). The modeled time series' often had secondary peaks at additional greater time periods, which were not often observed in the light trap data. For all of the modeled years (except 2009), the two time series were significantly cross-correlated at all time lags from -10 to 10 d. In 2009 all lags from -10 to 10 d were significant except the lag at -4 d.

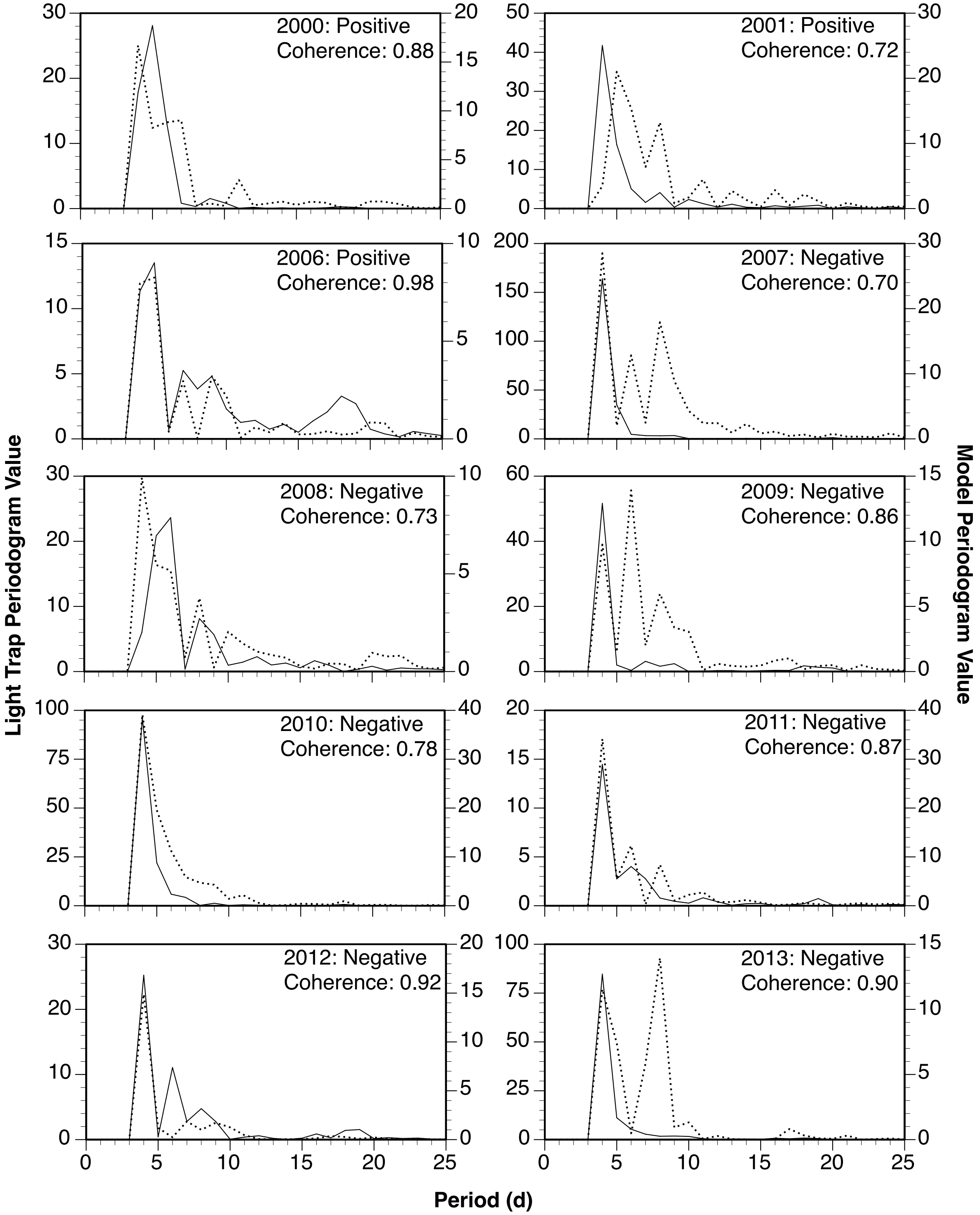

Figure 2.4. Power spectral density for the smoothed light trap (solid line) and smoothed model output (dashed line) for each of 10 model runs. The coherence is the maximum magnitude squared coherence between the two time series (can roughly be interpreted as an R^2 value). For all of the modeled years (except 2009), the two time series were significantly cross-correlated at all lags from -10 – 10 d. In 2009 all lags from -10 – 10 d were significant except the lag at -4 d.

There were more successes during negative than positive PDO years (Fig. 2.5). During negative PDO years, there were more successes at the latitudes in the middle of our model domain (~ 38 – 44 °N). Regardless of PDO phase, there was evidence of self-recruitment (larval success at larval release site) in the population; however, during positive phase PDO years there was a greater difference between the release and success latitudes. Northward advection of larvae was greater during positive PDO years than negative and the converse, more southward advection of larvae during negative PDO years, also occurred.

On average, there were more transport successes at slower development rates (time from hatching to molting into a megalopa) during negative PDO years than during positive PDO years (Fig. 2.6A). Development rate was approximately the same for temperatures ranging from 4-10 °C and then slowed at higher temperatures. Data from the positive and negative years closely mirrored each other until 18 °C at which point they diverged. During negative PDO years it took a larvae ~150 d to molt into a megalopa and during positive PDO years ~115 d. Although development rates differed, with larvae becoming megalopae much earlier during positive PDO years, the average PLD (time from hatching to settlement) was essentially equal, regardless of PDO phase, 175 vs. 180 d (positive versus negative) (Fig. 2.6B). In other words the megalopae stage was longer during positive PDO years. Transport successes increased as PLD increased from 50 d to ~ 150 d and then leveled off. Transport successes declined slightly from ~180 d to 250 d suggesting a minimal effect of larval mortality.

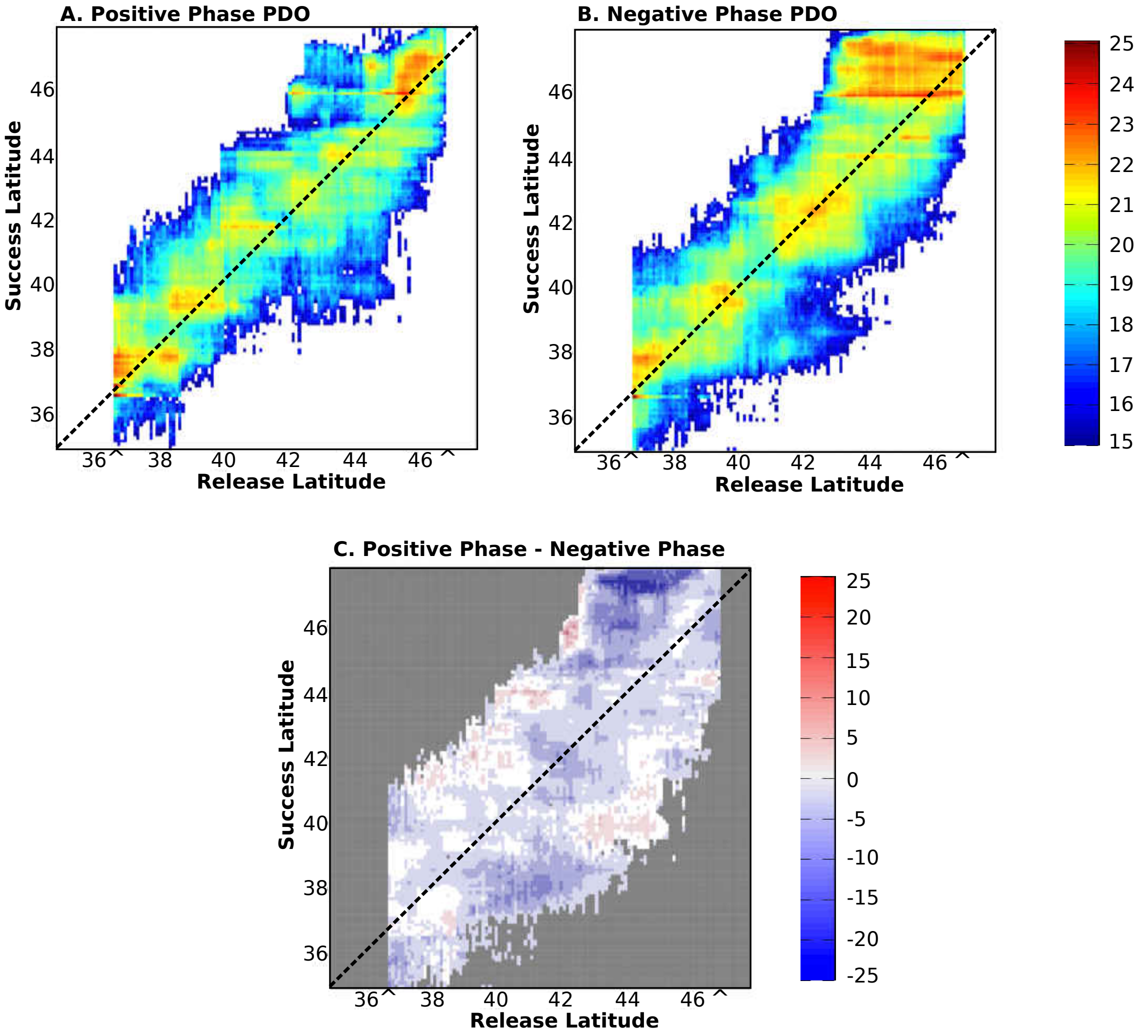

Figure 2.5. Average connectivity matrices during positive PDO years (A), negative PDO years (B) and the difference between the two (C). The carrots on the x-axis denote the southern and northern extent of larval release. The dashed line is a 1:1 line, successes on the line denote self-recruitment, above the line ended up north of where they were released and below ended up south of where they were released. Scale bars denote $\log_{10}$ larvae.

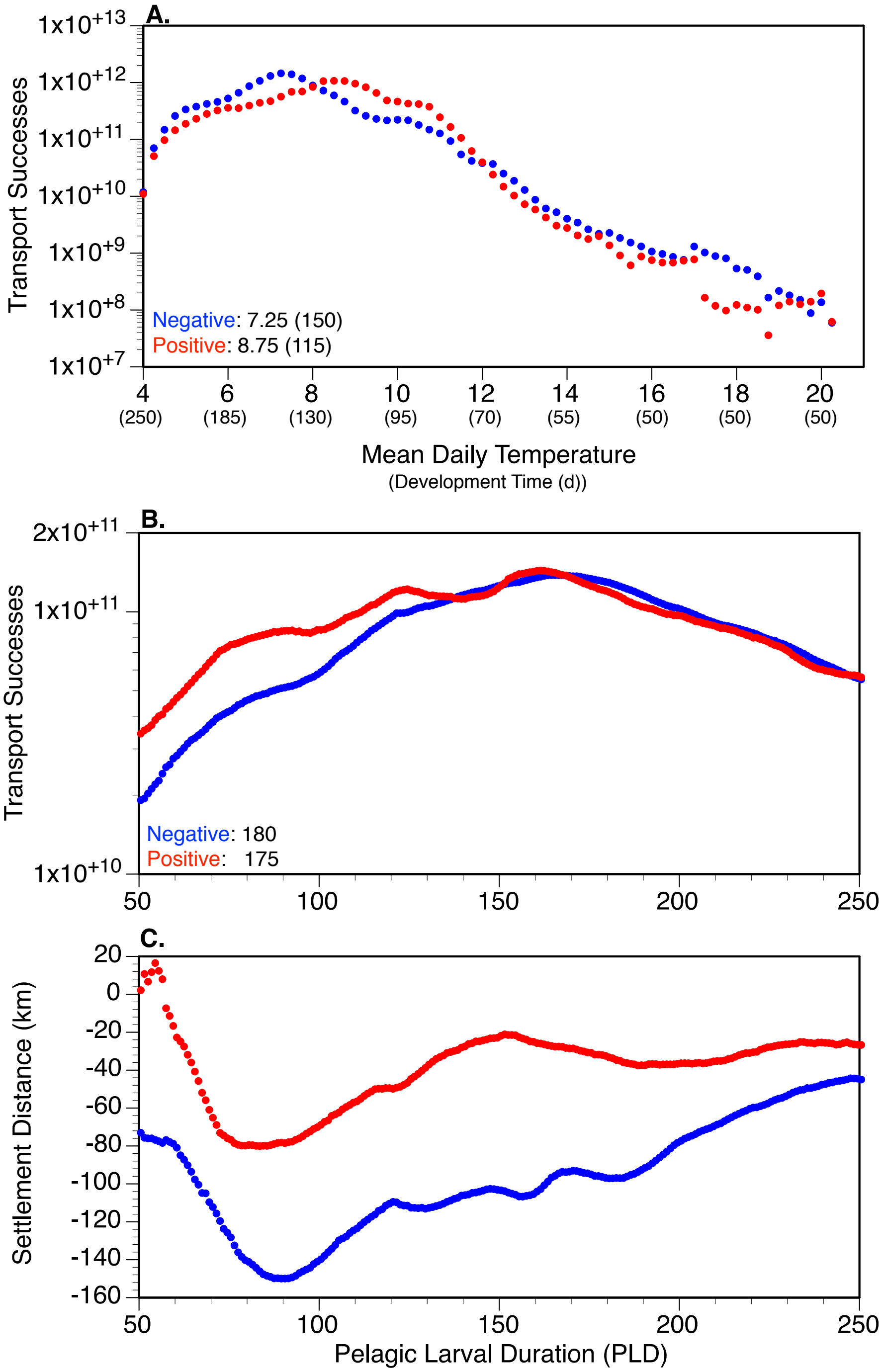

Figure 2.6. Average transport successes by average daily temperature experienced by the particle (time from release to megalopae) (A) and pelagic larval duration (B) as well as average settlement distance by pelagic larval duration (C) for positive (red) and negative (blue) PDO years. Values in panel A denote the average development rate (time from release to megalopae) for positive and negative PDO's. Values in panel B denote the average PLD during positive and negative PDOs. Transport success is defined as a particle that is 1) a megalopae and 2) on the continental shelf. Settlement distance is linear distance (km) from release site to location of transport success.

The connectivity matrices suggest there is some level of self-recruitment in the population, which is corroborated by the fact the most transport successes occurred at settlement distances, linear distance from release site to transport success site, of ~ 10 km (Fig. 2.5 & 2.7A). The maximum southward settlement distance (~600 km) occurred during a negative PDO year and the maximum northward settlement distance (~1200 km) occurred during a positive PDO year. For both the positive and negative PDO years, the number of transport successes was dome shaped, with the number of successes as settlement distance approached zero. In general, there were a greater number of instances where particles were advected northward during positive than negative PDO's (Fig. 2.7B). Average settlement distance was also heavily influenced by the PLD of the particles (Fig. 2.6C). For both negative and positive PDO's, the mean settlement distance became more negative over a range of PLDs from ~50-90 d and then rose slightly until 250 d. Based on PLD, average settlement distance was only northward at a PLD ~ 50 d.

During positive PDO's, there was little variation in transport success for particles by release latitude (Fig. 2.8A). Particles released between ~37-39.5 °N were advected short distances northwards (Fig. 2.8A). North of 39.5 °N particles, on average, were advected southwards (Fig. 2.8C). For negative PDO's, maximum transport success occurred for particles released around 39 °N but was relatively high from ~37 - 42 °N. In general, during negative PDO years, transport successes occurred when particles were advected to the south (Fig. 2.8C). Advection distance from release latitude was southward from ~36.5 - 39.65°N and relatively minimal north of this. The width of the continental shelf where particles were released had a slight positive correlation with

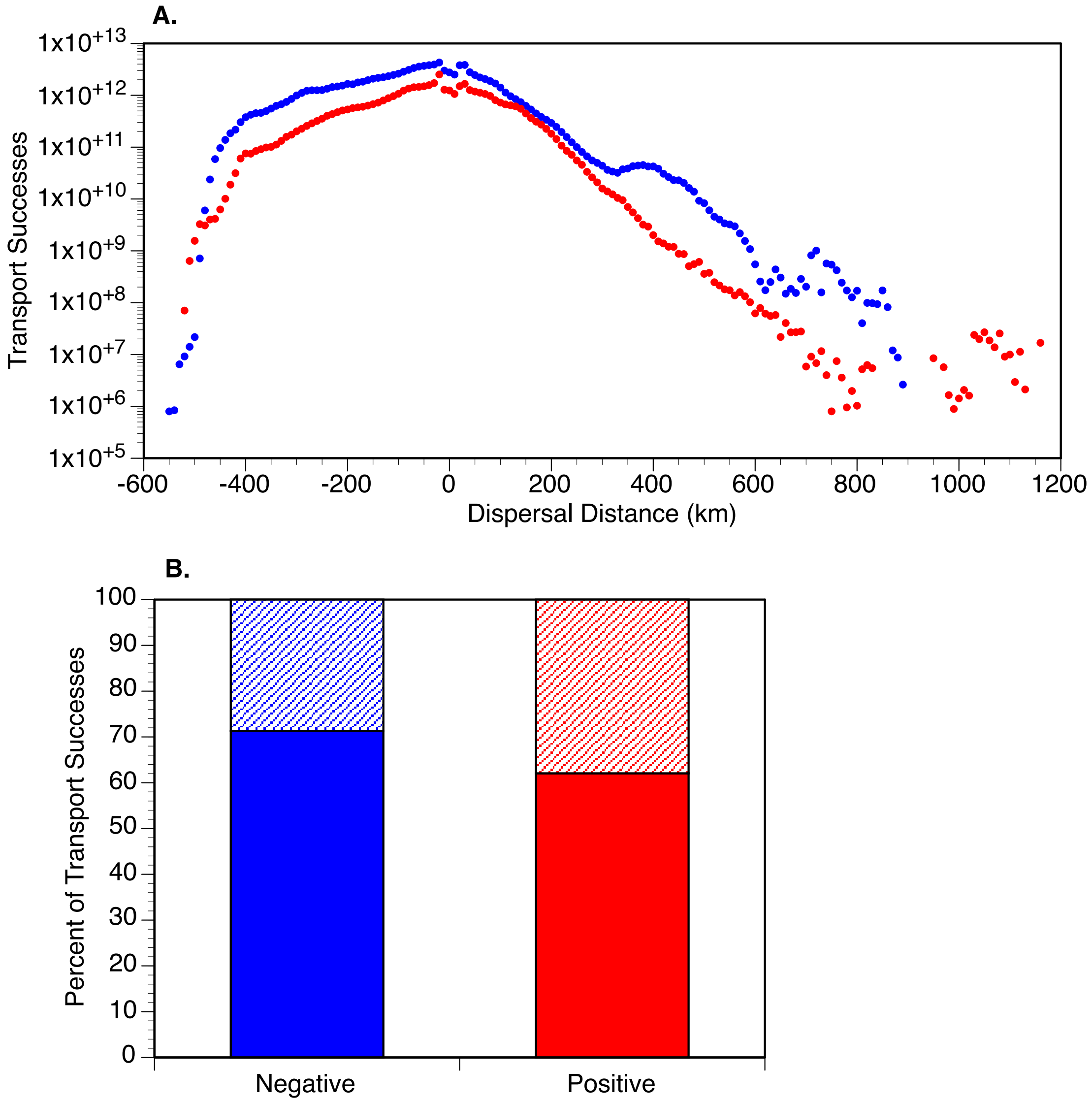

Figure 2.7. Average successes by settlement distances (A) and percent of transport successes by advection direction (B) for positive (red) and negative (blue) PDOs. Dashed boxes (B) denote situations where particles were advected to the north solid boxes denote situations where particles were advected to the south. Transport success is defined as a particle that is 1) a megalopae and 2) on the continental shelf. Settlement distance is linear distance (km) from release site to location of transport success.

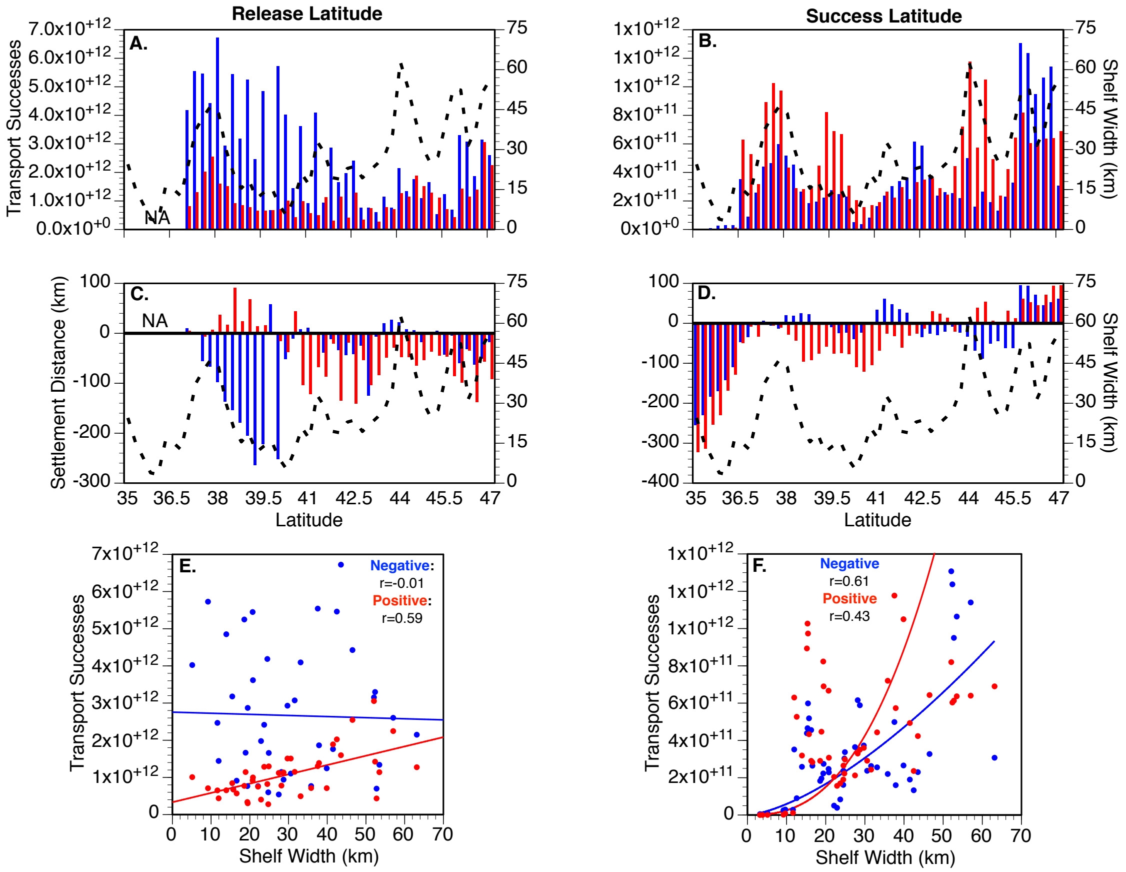

Figure 2.8. Number of transport successes (A,B,E,F) and settlement distance (C,D) by release latitude (A,C), success latitude (B,D) and release (E) and success (F) shelf width during positive (red) and negative (blue) PDO years. Negative distances (C,D) denote southward advection. Shelf width was calculated as the distance from the shoreline to a water depth of 200 m with a perpendicular line. The black dashed line (A-D) denotes the shelf width at each latitude. Transport success is defined as a particle that is 1) a megalopae and 2) on the continental shelf. Settlement distance is linear distance (km) from release site to location of transport success.

transport successes for the positive PDO years and no correlation for negative PDO years (Fig. 2.8E).

During positive PDO's, transport successes, particle that is a megalopae and on the continental shelf, peaked at success latitudes of ~ 44 °N but there were additional peaks at 37 and 39 °N as well (Fig. 2.8B). Transport successes peaked at the northern end of the model domain during negative PDO's and there were additional peaks at 37 and 42.5 °N (Fig. 2.8B). There were few transport successes at latitudes further south than

36.5 °N for both positive and negative PDO's (Fig. 2.8B). In general transport successes at latitudes ranging from ~ 35 - 37 °N had negative (southward) and relative large settlement distances (Fig. 2.8D). For positive PDO's, north of 37 °N, average settlement distance was relatively low. For negative PDO's, settlement distance was small from ~37 - 45.5 °N at which point particles were advected primarily from the south at relatively large distances. Transport success increased dramatically with shelf width, with a steep curve during positive than negative PDO years (Fig. 2.8F).

2.4. DISCUSSION

Our simulations suggest that Dungeness crab larvae vertically migrate to or almost to the bottom each day. These findings are supported by previous observational work and other modeling work we have been doing [46, 47]. The spectral density peaks for our deep vertical migration simulations associated well with the light trap data at ~ 5 d, though, on certain occasions additional peaks were observed in the modeled spectra that were not observed in the light trap data. We hypothesize these additional peaks are related to how we defined successes (particles was a megalopae and on the continental shelf) and the lack of tides in our physical model.

Migrating to depth each day causes larvae to enter the benthic boundary layer, which has been shown to effectively decrease the overall transport distance of larvae [59, 60]. Further, when particles are near the shelf break, a deep vertical migration would cause particles to be in the northward flowing California Undercurrent while in the lower portion of the water column and while in the upper portion of the water column in the southward flowing California Current [38]. Experiencing northward and southward flow each day should decrease the amount of alongshore advection, possibly increasing self-recruitment (larval success at larval release site). These findings are consistent with the hypothesis presented by Shanks and Eckert [24] that the timing of larval release and the length of the PLD of shelf/slope species in the California Current, by allowing the transport phase to be affected by the back and forth movement of the currents, acts to reduce net alongshore advection ultimately enhancing membership in the population.

A large number of particles appeared to be self-recruiting during both positive and negative PDO's (Fig. 2.5). During positive PDO years there were more transport successes at greater distances from the 1:1 line, suggesting less self-recruitment at these times. Chhak and DiLorenzo [61], demonstrated that there is more horizontal advection of particles during positive PDO's, which likely explains the greater distance of particles from the 1:1 line. Further, during positive PDO years, on average, settlement distance and linear distance from release site to transport success site were greater than during negative years. In addition, positive PDO years had a larger settlement distance on average than negative PDO years, there was a greater number of southward advection events during the negative PDO years.

Our simulations found similar pattern as Shanks et al. [28, 29], with more successes during negative than positive PDO's. They hypothesized this is because the enhanced southward flow during negative PDOs enhances the retention of larvae in the California Current. Our model supports the hypothesis that enhanced southward flow during periods of negative PDOs helps to maintain particles within the California Current system. This also likely explains why success was greater at the northern extent of the model range during negative than positive PDOs. On average during negative PDOs, 2806 particles passed through the northern boundary, and were excluded from analyses (i.e., lost from the system), whereas during positive PDOs on average 7056 particles were excluded from analysis. Thus, it appears that during negative PDO years, there is more retention of larvae in the California Current (less loss to the Alaska Current) which is corroborated by the greater catch of megalopae later in the recruitment season [29]. Further, it suggests that during positive PDO years there may be a greater influx of larvae from the California Current population into the Alaska Current population. Larvae from the California Current have been reported in the Alaska Current system [62].

In our models we were somewhat surprised that there was no effect of the day of the year of the spring transition, the date of birth of the particles and depth at which particles were released. Shanks et al. [28-30] demonstrated that the day of the year of the spring transition strongly influences the amount of Dungeness crab larvae that recruit each year. However, in recent work we have suggested that this correlation may be explained by the deepening of the thermocline, which subsequently increases the probability that particles are transported by the internal tide [46]. Since our model did not include any tidal forcing and ROMs is a hydrostatic model, our model did not resolve the internal tide; these limitations of the model may explain the lack of correlation. Although many studies have reported significant effects of release date and depth, we found no effect in our model [63-65]. We hypothesize that the migration of particle to or near the bottom each day decreases any potential effect release date and depth would have on transport successes or settlement distance. This hypothesis is corroborated by the fact that release date and depth had significant trends for the simulation of particles that vertically migrated to moderate depths. Our finding that there is no pattern to release date or depth is not surprising. If releasing larvae at a specific date or depth enhanced membership in the population, one would assume that over many generations release would coalesce on the date or depth that was more successful. However, it is likely that the circulation patterns across the depth and time range we released larvae were similar so there was no selective pressure.

Although particles developed faster during positive than negative PDO years, (115 versus 150 d) the average PLD of particles varied little (175 versus 180 d). This suggests that although during positive PDO years a zoea may molt into a megalopa at a younger age, it remains in the water column as a megalopa for a longer period of time during positive PDO years. The current paradigm suggests that particles with a longer PLD are likely transported greater distances and thus are less likely to self-recruit (larval success at larval release site) [66, 67]. Many of the species living on the continental shelf in the California Current have long PLD's and thus have been hypothesized to have long transport distances [68]. In our work we show that despite a long PLD, there is a higher level of self-recruitment than would have been predicted by theory. However, this finding is supported by Sinclair's hypothesis in that he suggests that a species' PLD is associated with the oceanographic region that encompasses the population, again, ultimately to enhance membership in the population [5]. Our work also supports the hypothesis of Shanks and Eckert [24], that that long PLD of shelf/slope species allows the larvae to capture the seasonal change in flow on the continental shelf from northward to southward, ultimately reducing their net alongshore advection. For both positive and negative PDO's, the maximum settlement distance occurred at a PLD of ~ 90 d and settlement distance approached zero with both shorter and longer PLD's. We hypothesize that this may indicate that larvae migrating larger distances recruit earlier and, further, as the recruitment season progresses the probability of self-recruitment actually increases. Near the shelf break eddies are often form that subsequently move offshore and away from the shelf break [69, 70]. Thus, larvae entrained in these eddies would be advected away from the continental shelf break ultimately not recruiting back to he population [71, 72]. Visual examination of our model demonstrated that eddies generated near the shelf break could entrain particles and subsequently advect them off the shelf causing them to ultimately not recruit. In the California Current a number of studies have demonstrated that larval rockfish (*Sebastes sp.*) are entrained by eddies [70, 73]. In our model, we found that during positive PDO years there were more successes for particles released where the average shelf width was wider but there was no effect during negative PDO years. We hypothesize a wider shelf enhances self-recruitment of particles by preventing them from being advected far from the continental shelf break and effectively not recruiting back to the population. The greater diffusion of particles during positive PDO years increases the probability of particles being lost and thus a wider shelf near the release location decreases the chance of particles being lost [61].

Researchers have wondered why the Dungeness crab population stops south of San Francisco Bay (~37.5 °N) [25]. Our model suggests that the population(s) south of San Francisco Bay is/are sink population(s) and is/are reliant on larvae from northern populations. Further, our model suggests most larvae return to these sink population(s) during negative PDO years. We hypothesize more larvae end up in the southern populations during negative PDOs because of 1) enhanced southward advection and 2) enhanced retention on the continental shelf. This southern limit of the specie's range coincides with the beginning of a stretch of very narrow shelf (< 5 km) and our model has demonstrated that shelf widths < 20 km result in significantly less transport successes. We hypothesize variations in cross-shelf transport processes greatly decreases the number of immigrants to populations associated with narrow shelves and that the circulation pattern would not cause particles to be retained and subsequently self-recruit to these populations. Two brief simulations with particles released south of 37 °N and exhibiting the deep migration behavior, demonstrated that particles were quickly advected away from shore and did not recruit to any region of the model domain.

Our findings support the member vagrant/hypothesis in the sense that the *Cancer magister* population in the California Current release larvae into oceanographic conditions that ultimately result in the closure of the planktonic phase returning larvae back to their natal population [5]. Additionally, during a negative phase PDO there are either fewer vagrants from the California Current population that end up in the Alaska Current population or some (more) vagrants from the Alaska Current end up in the California Current population. We hypothesize it is the latter, since there is a change in the carapace size of megalopae late in the season which associates with reported smaller carapace widths from the Puget Sound [25]. Our model suggests the population south of San Francisco is a sink population and reliant on larvae from other locations and the relatively few larvae that settle here likely indicates this southern range is influenced by local oceanography and bathymetry [74].

Shanks and Eckert [24] demonstrated that the life history characteristics of many shelf/slope species (a group which *Cancer magister* is a part of) in the California Current are very similar (species with long PLDs and larvae released during the winter). Thus, it is likely that our findings are applicable to many of these species as they would ultimately experience similar advection patterns as *Cancer magister*. One species that is likely similar to *Cancer magister* is the Pink Shrimp, *Pandalus jordanii*, a species whose larvae has been hypothesized to exhibit a vertical migration to or almost to the bottom [75, 76]. The recruitment of larval Pink Shrimp is correlated with many of the same variables that the recruitment of Dungeness crabs is correlated with [76, 77]. Additionally, rockfish (*Sebastes spp.*) that inhabit the shelf/slope waters and spawn larvae with a long PLD during and spawn during the winter it is likely their larvae experience the similar advective regime. Thus, this suggests that although the some aspects adult life histories of these species are very different, the physical oceanographic processes influencing the larvae are similar and may have acted as a selective force to enhance membership of larvae in the adult population.

Based on the findings from this manuscript and the results of additional studies we suggest that the word ‘dispersal’ does not adequately capture the role the larval phase plays in the movement of larvae [78, 79]. We believe the word ‘dispersal’ suggests larvae are being advected randomly from point A to a point B, however, this work (as supported by the member/vagrant hypothesis) suggest that rather, larvae move away from their release site but ultimately interact with the local oceanography to return back to the adult population [5]. Thus, ‘migration’ (as proposed by previous studies) more closely relates to what we hypothesize occurs during the larval phase in the sense that it is non-random [80, 81]. We further suggest that the migration is an onto-retentive migration. We use ‘onto’ since this migration occurs over the course of the larval development. Further, we use ‘retentive’ because the local oceanography has acted as a selective force to drive species to spawn in specific locations at specific times to promote membership;

essentially retention within the population. Thus, ‘onto-retentive’ refers to the retention of larvae over the course of its development within and the advective regime that will results in closure within the adult’s population.

Overall our model results were well validated by the light trap data and captured the migration of Dungeness crab larvae throughout the California Current. Our work demonstrates that although some larvae are advected long distances there is a high amount of self recruitment in the population; recruitment to the larval release [25]. Our results were consistent with the hypothesis that increased southward flow of the California Current enhanced shelf retention during negative PDO years acts to maintain crabs in the California Current and increase overall success. These findings likely have implications for other species that inhabit the continental shelf in the California Current. In the future, attempts should be made to examine the connectivity of the Dungeness crab population throughout the Alaska and California Currents as these two areas have different oceanographic regimes, which likely dramatically affect the transport of larvae. Our model suggests that vagrants from either population end up in the other population and quantifying the role of these vagrants on the populations could provide interesting insight into the connectivity between highly different oceanographic regimes. As better datasets of larval recruitment and dispersal become available, modeling studies should act to incorporate these data in order to validate the findings, as well; more studies of larval dispersal should incorporate modeling studies as they allow researchers to better study dispersal processes that are not possible with traditional methods.

2.5. BRIDGE TO CHAPTER III

In chapter II I modeled the dispersal of Dungeness crab larvae and showed that larvae likely migrate to or almost to the bottom each day. Additionally, my work supports previous hypotheses suggesting that the population is influenced by the phase of PDO, which ultimately results in an increase in the number of megalopae that return back to the population. These finings suggest more larvae are retained in the California Current during a negative PDO by the increased southward advection that occurs. In chapter III I develop a higher resolution model of upwelling circulation to examine the effect of upwelling circulation on the shoreward advection of megalopae.

CHAPTER III

THE INFLUENCE OF SPATIAL AND TEMPORAL VARIATION IN DIEL VERTICAL MIGRATION ON LARVAL DISPERSAL AND CONCENTRATION: RESULTS FROM A HIGHLY VALIDATED INDIVIDUAL BASED MODEL

This chapter is in preparation for the journal *Progress in Oceanography.* The chapter is co-authored with Alan Shanks. Alan Shanks maintained the light trap and provided the samples used to validate the model. I developed and implemented all of the models as well as did all of the initial writing.

3.1. INTRODUCTION

Migrations such as those exhibited by birds and large mammals have fascinated scientists for years (Richardson 1978, Hobson 1999). The higher viscosity of water relative to air creates a three dimensional environment allowing many species to migrate vertically in the water column (Sclafani et al. 1993). Vertical migrations are exhibited by species as small as cyanobacteria (Kromkamp & Walsby 1990) to those as large as basking sharks (Sims et al. 2005). On a temporal scale of days to months, is an ontogenetic vertical migration, where a species changes its location in the water column as it develops (eg. Hays 1995). On a daily or subdaily time scale are diel vertical migrations (Ringelberg 2009), the most common migration in the ocean (Ringelberg 2009). Work suggests light acts as the exogenous cue animals alter their depth in response to; however, there are multiple hypotheses regarding how light specifically acts as a cue (Cohen & Forward 2009). One type of diel migration is a nocturnal diel migration: organisms occupy depth during the day and surface water during the night (Fig 3.1; Ringelberg 2009). For this paper we will refer to a nocturnal diel migration as a standard migration since this is the type of migration most commonly observed. Work in lakes suggests this is in response to visual predation pressure: species that live in lakes with predators migrate and those in lakes without predators do not (Zaret & Suffern 1976), however, additional hypotheses such as foraging and mating have been proposed as causes of the migration (Ringelberg 2009). Another form of diel migration is a twilight diel migration: species occupy depth during the day, surface waters during twilight and at night are either randomly distributed in the water column of occupy a specific depth (Fig 3.1; Ringelberg 2009). It has been suggested the lack of light at night causes animals to swim randomly or to sink, a process described as midnight or nocturnal sinking (Cohen & Forward 2009). Regardless if species exhibit a standard diel or twilight diel migration, changing their position in the water column can cause the animal to be exposed to dramatically different flow patterns since flow often changes with depth (Cronin & Forward 1986).

Many marine organisms begin their life as small pelagic larvae and many of these larvae vertically migrate (McEdward 1995). The transport of larvae is dramatically influenced by three factors: hydrodynamics, behavior and time (Shanks 1995, Metaxas 2001, Queiroga & Blanton 2004). Vertical migratory behaviors not only alter the hydrodynamics transporting the larva but can alter the larva's development rate by exposing individuals to different water temperatures or food concentrations (McLaren 1963). Although some larvae exhibit horizontal swimming behaviors, vertical swimming

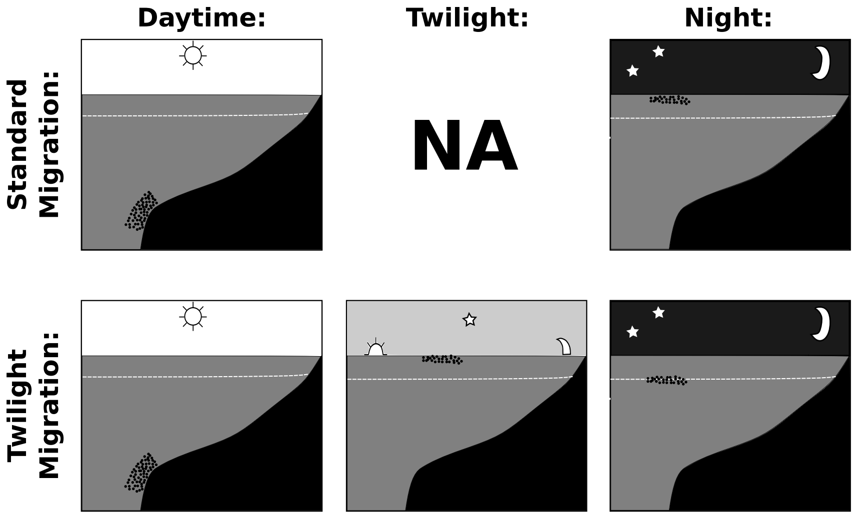

Fig. 3.1. Idealized representation of standard and twilight vertical migrations. The location of particles during the day (near bottom) for both types of migrations is purely artistic; the depth is likely variable between species and stages. For a twilight migration, evidence is unclear what species do at night. Some work suggests they migrate to a specific depth while other work suggests they disperse randomly in the water column.

behaviors are likely the most common (Metaxas 2001, Leis & McCormick 2002). Work from numerous observational and modeling studies has demonstrated that vertical migrations can profoundly influence the transport trajectory of larvae (Cronin & Forward 1986, Marta-Almeida et al. 2006, Criales et al. 2007, Drake et al. 2013). The trajectory of larvae is influenced by hydrodynamic processes ranging from as small as turbulence to as large as geostrophic currents (Shanks 1995, Queiroga & Blanton 2004).

The California Current is one of the best-studied currents in the world's oceans (Hickey 1979). Upwelling drives high rates of primary production in the California Current, which ultimately leads to large commercial fisheries (Mann & Lazier 2006). The California Current begins where the West Wind drift collides with North America, approximately Vancouver Island (Hickey 1979). The collision causes water to flow northward as the Alaska Current and southward as the California Current. The Pacific Decadal Oscillation (PDO) alters the amount of water that enters the California Current with more water entering the Current during a negative PDO (Minobe & Mantua 1999). The California Current is an eastern boundary current and is therefore broad (~500 km wide) and slow (0.1-0.25 m s^{-1}) (Hickey 1979). Underneath the California Current just seaward of the continental shelf break is the California Undercurrent, a jet like poleward current. During winter months, winds are from the south and an inshore countercurrent (the Davidson Current) flows poleward along the continental shelf. In the spring during a short (~7 d time period) the winds switch from being predominately southerly to northerly (Huyer et al. 1979, Strub & James 1988). This pulls the California Current back onto the continental shelf causing southward flow along the shelf. During this time period, conditions are considered upwelling favorable. During wind events from the north, the surface water (Ekman Layer) are advected offshore and replaced with cold nutrient rich waters, which are advected onto the shelf from depth (Mann & Lazier 2006).

The dispersal of marine invertebrate and fish larvae has been studied extensively in upwelling ecosystems (eg. Pedrotti & Fenaux 1992, Aiken et al. 2007, Peliz et al. 2007). In particular, some of the most influential works on larval dispersal have been conducted in the California Current (Bakun et al. 1979, Parrish et al. 1981, Roughgarden et al. 1988). In particular, the paper by Roughgarden et al. (1988) suggested larvae are transported ashore by the upwelling front during relaxation conditions. This immensely influenced the study of larval dispersal and following this, a large number of studies have attempted to associate recruitment with upwelling and downwelling dynamics (Morgan 2014). Recent work has demonstrated that the larvae of many marine species remain nearshore and are not transported by the upwelling front (Shanks & Brink 2005, Morgan et al. 2009, Shanks & Shearman 2009). Not surprisingly, behavior plays an important role in the maintenance of larvae in the nearshore environment (Morgan 2014). Much of the work discussed above focused on the recruitment of intertidal species. Shanks and Eckert (2005) compiled data from a number of species of fishes and benthic crustaceans in the California Current and demonstrated that species could be divided into three general groups: 1) shelf/slope species, 2) nearshore (e.g., adult depth < 30 m) fishes and 3) other nearshore species found primarily in the waters of the Southern California Bight. They hypothesized the groups differed in the length of PLD, spawning season, fecundity etc. because the factors interacted with the local seasonal oceanography to influence dispersal. Although there is evidence that nearshore species differ dramatically from shelf/slope species, and most commercially important species occupy the shelf/slope group, relatively little in known about the dispersal of the shelf/slope group.

In the California Current one species in the shelf/slope group, which has been relatively well studied, is the Dungeness crab, *Cancer magister* (Rasmuson 2013). In the California Current, larvae are released close to shore during the winter and subsequently migrate across and off of the continental shelf during the course of their pelagic larval development. Following the spring transition, larvae move onto and across the continental shelf settling in the nearshore environment. Throughout the dispersal phase, evidence suggests zoeae (early larvae) vertically migrate, though the depths they occupy is not known (Lough 1975, Reilly 1983). For the megalopae (post larval stage) some evidence suggests they exhibit a standard vertical migration (Reilly 1983, Hobbs & Botsford 1992), while other work suggests they exhibit a twilight migration (Jamieson & Phillips 1988, Shenker 1988, Park & Shirley 2005). Additionally, some work suggests megalopae always vertical migrate (eg. Hobbs & Botsford 1992) while other research suggests they only vertically migrate when they are off of the continental shelf and remain in the neuston when over the continental shelf (eg. Reilly 1983). Regardless of stage, it is not known 1) how deep larvae migrate and 2) if they exhibit a standard diel migration or twilight diel migration

Variations in the size of *C. magister* populations has been attributed to variation in recruitment success (Rasmuson 2013). To better understand the factors that drive recruitment success, Shanks and colleagues (2007, 2010, 2013) have been using a light trap to collect daily samples of megalopae and correlate these catches with hydrodynamic indices. Doing so they have demonstrated that the total annual catch of megalopae each year is correlated with the phase of the PDO: more megalopae are caught during a negative phase PDO. They hypothesize more megalopae are caught during negative phase PDO's because more water is shunted into the California Current from the West Wind Drift enhancing southward advection of larvae. Additionally, more megalopae are caught when the day of the year of the spring transition is earlier and there is more upwelling following the spring transition. They hypothesize these correlations suggest megalopae are transported onto the shelf with the deep waters that are advected onto the shelf during upwelling. Thus, an earlier spring transition increases the amount of time that conditions would be upwelling favorable, ultimately, increasing the number of megalopae advected onto the continental shelf.

We examined the relative influence of vertical migration and upwelling circulation on the transport of *Cancer magister* megalopae. Since megalopae are located far from shore, traditional methods of sampling are costly. Thus, we developed a physical model of upwelling circulation and coupled it with a suite of larval behaviors in order to better understand the dispersal of *C. magister*. We used the daily measures of recruitment to a light trap in order to validate the results of our modeling study.

3.2. MATERIALS AND METHODS

3.2.1. Hydrodynamic Model

A 2-dimensional model of upwelling circulation was generated using the regional ocean modeling system (ROMS) (Shchepetkin & Mcwilliams 2005). ROMS is a terrain following s-coordinate model; which allows for greater vertical resolution near the surface and bottom of the water column. The model domain in this study ranged from the coastline out 300 km. The vertical resolution was from the surface to the bottom or 1000 m; which ever came first (Fig. 3.2). The bathymetric profile was extracted from the NOAA coastal relief model to mimic the across shelf bathymetry just north of the entrance to Coos Bay (http://www.ngdc.noaa.gov/mgg/coastal/crm.html). The model grid was established with a constant horizontal resolution of 65 m and 42 vertical terrain following s-levels. Vertical resolution ranged from 0.25 m in the nearshore to 12.5 m in the offshore environment. Cross-shelf boundaries were modeled as walls, with flow being reflected, while alongshore boundaries were modeled as periodic boundaries, with flow from the northern boundary feeding into the southern boundary.

In order to provide a simplified depiction upwelling circulation, the model was only forced with alongshore wind stress. Two idealized models were generated using an absolute wind stress value of 0.05 N m^{-2} (Table 3.1). Along the Oregon Coast, summer time winds are predominately upwelling favorable (causing surface waters to be advected offshore) with intermittent periods of weak winds from the south (causing dense waters near shore to sink and warmer offshore waters to be advected shoreward). Thus, the first idealized model oscillated between upwelling and relaxation events to provide a simplified model of upwelling periods followed by relaxation events. The upwelling season off Oregon beings with the spring transition which is a ~7 day switch from downwelling favorable (surface waters advected towards the shore) to upwelling favorable conditions. Following the spring transition is when Dungeness crab megalopae begin to be caught in the light trap. Thus, the second idealized model was used to represent the spring transition, the annual switch from downwelling to upwelling favorable conditions, followed by oscillations between relaxation and upwelling events.

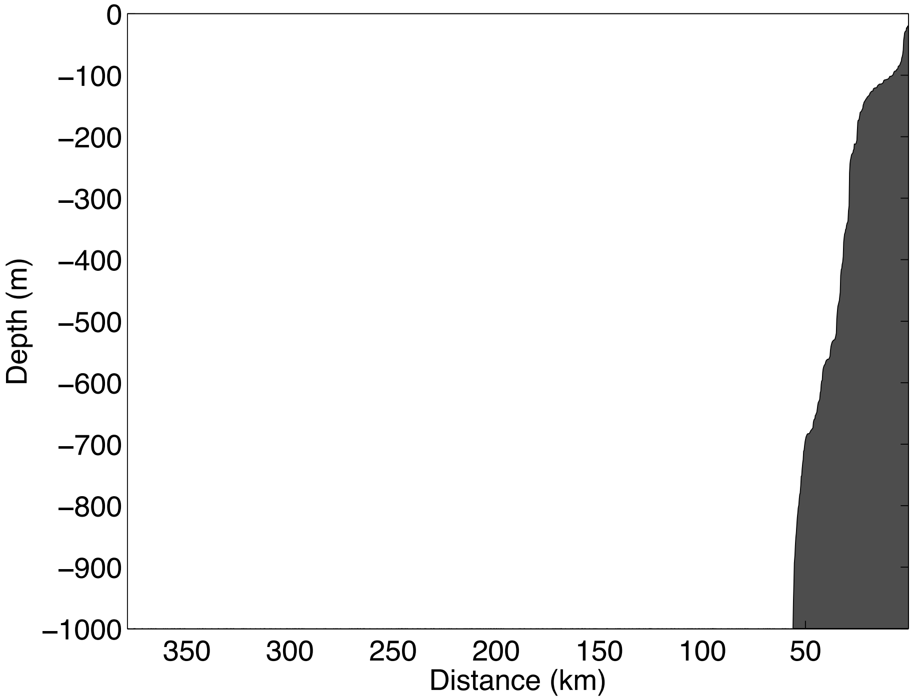

Fig. 3.2. Horizontal (km) and vertical (m) extent of the model domain to mimic cross-shelf bathymetry just north of Coos Bay. Bathymetry data were obtained from the NOAA coastal relief model. The same domain was used for both the idealized and semi-realistic hydrodynamic models (see text for explanation). The model domain extended well beyond the area of interest (particles were released from the shelf break out 25 km) in order to remove wall effects at the offshore boundary. The image is not to scale.

Table 3.1. Forcing parameters for idealized upwelling and spring transition circulation models. The model was only forced with alongshore wind stress. Wind stress was 0.05 N m^{-2} and negative for upwelling favorable (winds from the north) and positive for downwelling favorable (winds from the south) conditions. No forcing was applied during relaxation conditions.

Model Type	Total Model Days	Number Upwelling Days	Number Relaxation Days	Number Downwelling Days
Upwelling	42	22	20	NA
Spring Transition	42	20	12	10

Eleven semi-realistic models were forced with alongshore wind stress values extracted from the European Center for Medium-Range Weather Forecasting (ECMWF) (http://apps.ecmwf.int/datasets/data/interim_full_daily/). Daily alongshore wind stress values were extracted for 1998-2001 and 2006-2012 with a cross-shelf resolution of ¼ ° longitude (Table 3.2). Models were run for 15 days prior to that years spring transition through the end of August. Model outputs were assessed visually to ensure that flow from the boundary walls was not reflected in accurately and no spurious circulation occurred near the shelf break due to the change in bathymetry. Additional, particles were released randomly throughout the model domain to ensure that particles were not concentrated in regions where hydrodynamics should not have caused concentration passive particles.

3.2.2. Individual Based Model

Particle tracking was conducted using the Larval TRANsport Lagrangian Model v2b (LTRANS) (North et al. 2011). The focus of our work was to examine the combined effects of upwelling circulation and swimming behaviors of *Cancer magister* megalopae. Therefore only vertical migratory behaviors were included in the model. Models were run

Table 3.2. Forcing parameters for eleven years of semi-realistic models (models were forced only with “realisitic” alongshore windstress). Models were run from 15 days prior to the spring transition through the end of August with ¼ degree longitude resolution wind stress values obtained from the ECMWF reanalysis (http://apps.ecmwf.int/datasets/data/interim_full_daily/). Upwelling favorable winds were winds from the north (negative) and downwelling favorable winds were winds from the south (positive).

Year	**Total Model Days**	**Upwelling Favorable**		**Downwelling Favorable**	
		Num. Days	**% of Run**	**Num. Days**	**% of Run**
1998	152	138	91	14	9
1999	170	142	83	28	17
2000	196	143	73	53	27
2001	191	152	80	39	20
2006	181	131	72	50	28
2007	185	130	70	55	30
2008	185	150	81	35	19
2009	184	149	81	35	19
2010	153	124	81	29	19
2011	133	119	90	14	10
2012	131	105	80	26	20

using an internal time step of 120 s. Sensitivity analyses suggest this internal time step was short enough so the trajectory of particles changed as particles changed depth but long enough to allow for efficient computations. LTRANS was coupled with the outputs from the two idealized physical models and the eleven semi-realisitic models.

3.2.2.1. Behavior

Three different suites of megalopae behaviors were coupled with the physical models: passive particles, standard diel migration, and a twilight diel migration. Regardless of which behavior was being exhibited particles were normally distributed around the depth they occupied, except at the surface where the distribution was one sided. Passive particles were released at the surface (0), 50, 100, 200 and 300 m below the surface. For the standard vertical migration, megalopae migrated to the neuston at sunset and to depth at sunrise (Fig. 3.1). For twilight migration megalopae migrated to depth during the day and occupy the neuston for one half hour before and after sunset and sunrise. At night (following sunset and prior to sunrise) megalopae would migrate below the Ekman layer, in our model a depth of 50 m (Fig. 3.1). For the twilight migration, we did not have megalopae swim randomly in order to simplify the analyses. For both the standard and twilight migrations, during the day particles migrated to depths of 50, 100, 200, and 300 m as well as 1 meter above the bottom (mab). For all behaviors with active swimming, megalopae vertically migrated at a speed of 10 cm s^{-1} (Rasmuson & Shanks 2014).

3.2.2.2. Simulations

Sensitivity analyses demonstrated that a total of ~20,000 particles were needed to accurately resolve variation in recruitment success and distribution using the methods suggested by North et al. (2009). For each model run 22452 evenly spaced particles were released from the shelf break (depth = 200 m) and out 50 km. The physical model was run for two days to allow for circulation patterns to fully establish before particles were released into the model domain.

Some researchers have suggested that *Cancer magister* megalopae only vertically migrate when they are off the continental shelf and remain in the neuston when over the continental shelf (Reilly 1983). To assess the potential impact of only migrating off the continental shelf, we coupled each of the 11 years of semi-realistically forced physical models with a behavior to model those proposed in the literature. Off the shelf megalopae exhibited a twilight migration occupying 1 mab during the day and the neuston for one half hour before and after sunset and sunrise. At night particles were normally distributed around the 50 m water depth. On the shelf, particles remained in the neuston regardless of time. For this behavior we defined the shelf break as the location of the 200 m water depth. All other parameters were identical to those used for the other semi-realistically forced models.

3.2.2.3. Validation and Analysis

From 1998-2001 and 2006-2012 we monitored daily recruitment to Coos Bay, Oregon using a light trap (Shanks 2013). Samples were preserved in buffered formalin and enumerated using a dissecting microscope. When the number of megalopae was > 2000 animals the number was determined by sample weight (Shanks et al. 2010).

In order to compare the light trap data with the model data we needed to generate a daily measure of success from the model. Success was defined as the number of particles that were advected onto the continental shelf (depth < 200 m) in a 24 hr period. In events where particles were advected off of the continental shelf the success was considered 0. This was done because once on the continental shelf additional processes (likely internal tides) drive cross-shelf transport (Shanks 2002). Daily output from each model run (year X behavior) time series was compared to daily recruitment to the light in order to 1) validate the models and 2) assess the skill of each model. Calculating the magnitude-squared coherence between the two signals allowed us to compare the time series. Each time series was plotted to ensure data were stationary and if necessary seasonal trends were removed using the "detrend" function in Matlab (Emery & Thomson 1997). The data from the light trap was lagged relative to the modeled data since recruitment in the nearshore would occur after shoreward advection. For each comparison we considered only the largest value of the magnitude-squared coherence. Additional analyses suggest year had a minimal effect (see below) and thus the coherence value was averaged across years.

The effects of different variables on daily success for the idealized and semi-realistic models were determined by using an analysis of variance (ANOVA). Daily success was Log_{10} transformed and effects were normalized to sum to 1. For the idealized models, effects were calculated using a 3-factor ANOVA with surface flow direction, model type and behavior as the categorical variables and daily success as the dependent variable. For the semi-realistic models, effects were calculated using a 3-factor ANOVA with surface flow direction, year and behavior as the categorical variables and daily success as the dependent variable.

We also calculated a standardized transport distance for twilight migrating particles for each depth the occupied. First, we calculated the difference between the number of particles on the shelf between successive time steps. Positive values were denoted as 1, negative values as -1 and no change as 0. These values could then be averaged for each behavior, depth and time combination for comparability.

3.3. RESULTS

3.3.1. Hydrodynamic Model

Since no heating was included in the model, measures of temperature and density were static and thus current velocity was the only variable we could validate. However, there are no current velocity measurements available for our model domain that we could used to validate our model. Further the highly idealized nature of the model would likely have cause the measured and observed flows to differ. The upwelling and downwelling circulation patterns in our model matched well with those reported in observational studies (Huyer 1983) and modeling studies (Allen et al. 1995). Briefly, during upwelling conditions the isopycnals in the model tilted towards the surface and during downwelling pointed towards the bottom. Flow (to depths of ~ 15 m) in surface waters responded quickly to changes in wind direction ($t \approx 0.5 – 1$ d). Bottom flows were slower to respond ($t \approx 2 – 3$ d) to changes in wind direction. During weak downwelling, upper waters were advected shoreward at velocities of ~0.025 m s^{-1} and deep waters were weakly advected offshore (Fig. 3.3A). During weak upwelling the surface water to a depth of ~15 m, was advected offshore at velocities of ~0.025 m s^{-1} (Fig. 3.3B). Additionally during weak upwelling, at depth there was a very weak (almost 0) shoreward advection of water. Following multiple days of sustained unidirectional wind stress, downwelling and upwelling conditions strengthened (Fig. 3.3 C&D). For both upwelling and downwelling, the surface flow thickened to encompass the upper ~25 m of water and velocities increased and often exceeding 0.05 m s^{-1}. During strong upwelling conditions waters within ~15 m of the bottom were advected at speeds often exceeding 0.05 m s^{-1}, similar to those near the surface. In general both surface and bottom water velocities were greater during downwelling conditions than during upwelling conditions.

For the semi-realistic circulations on average 80% of the days were forced with upwelling favorable winds and 20% were forced with downwelling favorable winds. 1998 had the most upwelling favorable days (91%) where as 2007 had the least (70%) (Table 3.2).

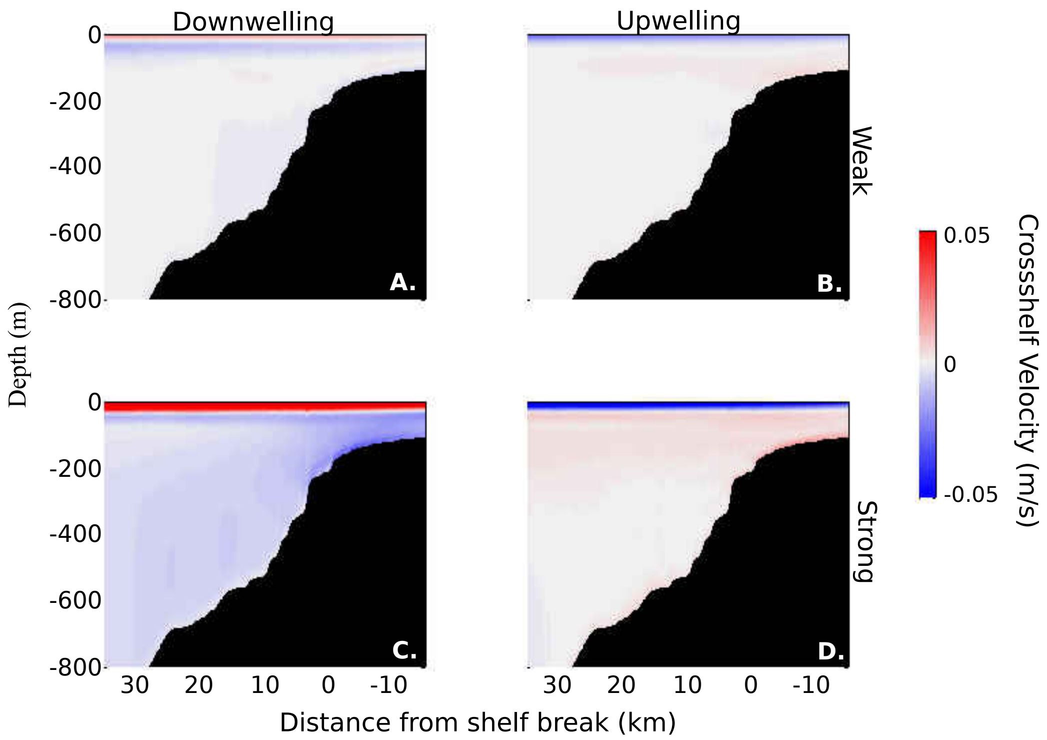

Fig. 3.3. Cross-shelf velocities during both weak (A&B) and strong (C&D) upwelling (B&D) and downwelling (A&C) conditions. Negative (blue) values denote offshore flow and positive (red) values denote onshore flow. Only the region of interest to our experiments is depicted. The images are not to scale.

Hydrodynamic models are notoriously bad at modeling the flow at the very surface of the ocean, often causing surface flows to be too fast (Reed et al. 1994). Since many of our behaviors had particles (e.g., model organisms) occupying the neuston we assessed the variability in the flow at the ocean's surface between wind stress and cross-shelf velocity. Combining the eleven semi-realistic models we compared the magnitude of the wind forcing and the surface flow to determine how much velocity was imparted to the surface waters by the alongshore wind stress. On average, surface water velocities were ~5% of the speed of the alongshore wind stress Thus, our surface flows were slightly faster than the 3% reported in the literature (Reed et al. 1994) but in general were not much higher, suggesting our surface flows were somewhat realistic. Therefore, the modeled advection of particles in the neuston is likely somewhat representative of real conditions.

3.3.2. Individual Based Models

Frequently studies of upwelling and downwelling dynamics refer to conditions as either upwelling favorable or downwelling favorable. The favorable is included because upwelling circulation is often inferred from wind stress data and flow is not measured. In numerical models it is possible to quantify water flow direction. Thus, throughout this manuscript when we refer to upwelling and downwelling these are based on flow direction of surface waters at the shelf break. During upwelling surface waters are advected offshore and during downwelling surface waters are advected shoreward.

3.3.2.1. Idealized Simulations

Behavior had the largest effect on daily success (68 %) and an interaction of behavior and forcing type (upwelling or spring transition) had a 29 % effect (Table 3.3). Other variables had a minimal effect on success. For the idealized spring transition passive particles located at the surface (0 m) and 50 m were only advected onto the shelf during downwelling (Fig. 3.4). Passive particles located at 100, 200 and 300 m water depth were advected onto the shelf during upwelling and relaxation but not during downwelling conditions. Particles exhibiting a standard vertical migration were predominantly advected onto the shelf during downwelling conditions. Particles exhibiting a twilight vertical migration were advected onto the shelf at a slower rate than the standard migrating particles but were advected onto the shelf during all conditions (upwelling, downwelling and relaxation).

Table 3.3. Effect of behavior, surface flow direction and forcing on the daily success of particles in the idealized hydrodynamic models. Effects are reported as percent of the magnitude of the effect.

Variable	df	MS	Effect (%)
Behavior	14	14.2	63
Surface Flow	1	0.21	<1
Forcing	1	3.2	1
Behavior X Forcing	14	6.46	29
Behavior X Surface Flow	14	0.18	<1
Surface Flow X Forcing	1	5.2	2
Behavior X Surface Flow X Forcing	14	1	4
Residuals	1200	0.2	

For the idealized upwelling test case, passive particles that remained at the surface were never advected onto the continental shelf (Fig. 3.5). Passive particles located at 50, 100, 200 and 300 m were advected onto the shelf during upwelling and relaxation conditions. Except for two small pulses, particles exhibiting a standard migration to 1 mab were not advected onto the continental shelf. Similar to the spring transition test cast, particles exhibiting a twilight vertical migration were advected onto the shelf during both upwelling and relaxation events.

3.3.2.2. Semi-Realistic Simulations

Behavior explained 46 % of the variation in success and an interaction of flow direction and behavior accounted for 30 % of the variation (Table 3.4). All other variables had minor effects on the daily success of particles. As stated in the methods, since year had a minimal effect, the results of the semi-realistic model validation were averaged across years (Table 3.4). Particles exhibiting a standard vertical

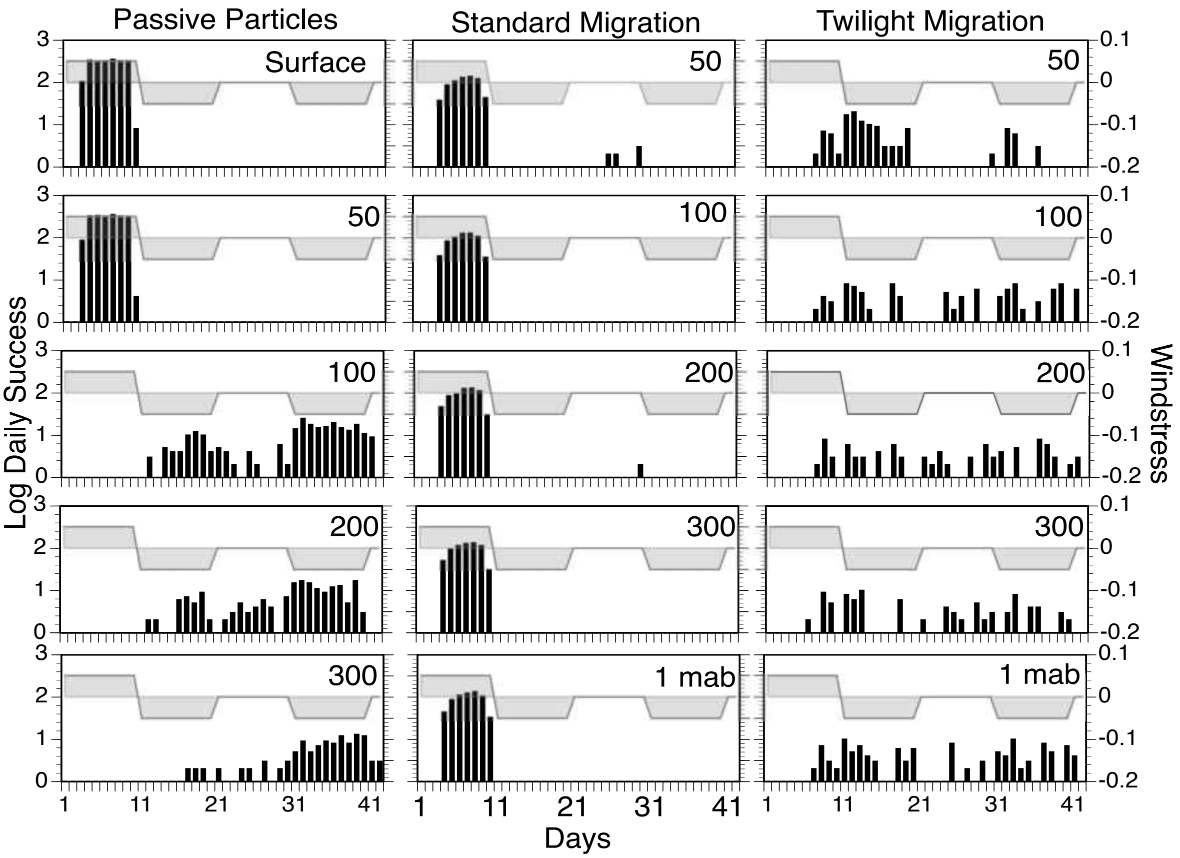

Fig. 3.4. Log daily success, particles advected onto the continental shelf, (black bars) and wind stress direction and velocity (shaded gray bars) for each of the 15 behavior X depth combinations during the idealized spring transition model. Negative wind stresses are upwelling favorable, positive wind stresses are downwelling favorable and no wind stress is relaxation conditions.

migration and passive particles located at 0 m had the least coherent signal with the light trap (Fig. 3.6). Passive particles at 50 m and twilight migrating particles at 50 and 100 m were slightly more coherent with the light trap than standard vertical migration particles. Time series of passive particles at 100, 200 and 300 m and twilight migrating particles art 200, 300 m and 1 mab were the most coherent with the light trap data.

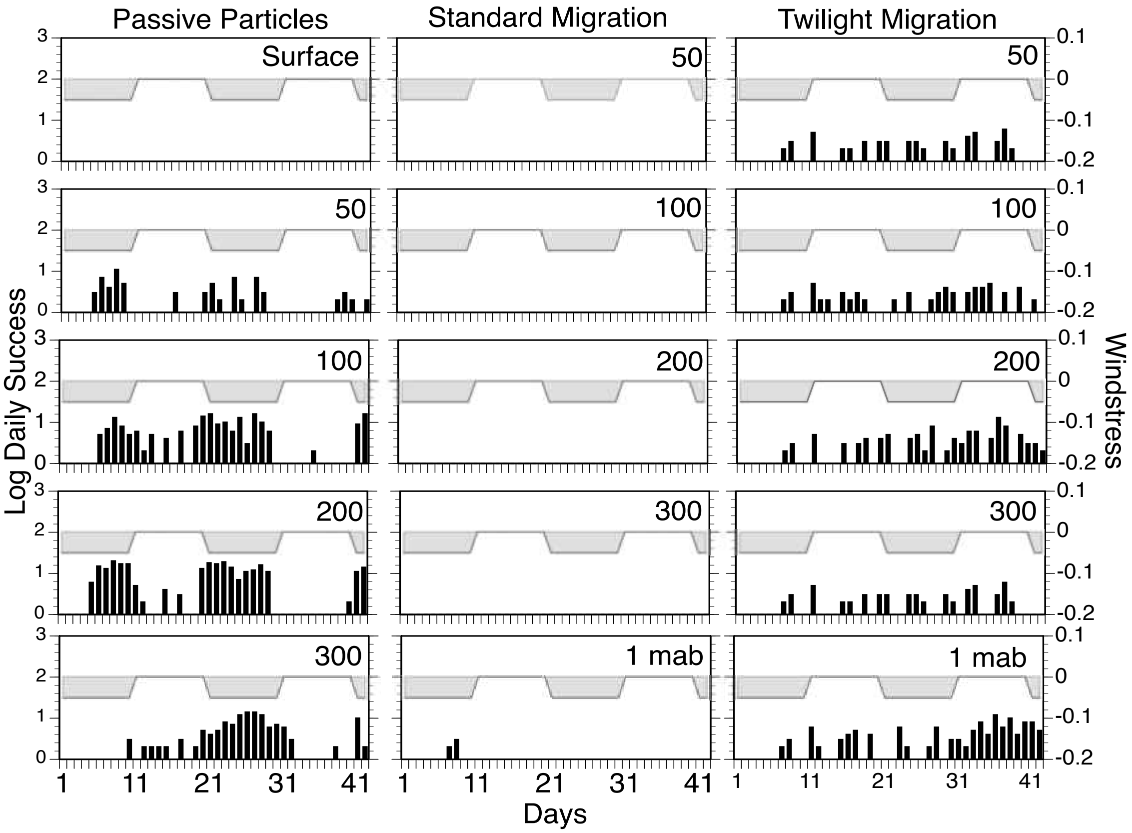

Fig. 3.5. Log daily success, particles advected onto the continental shelf, (black bars) and wind stress direction and velocity (shaded gray bars) for each of the 15 behavior X depth combinations during the idealized upwelling/relaxation model. Negative wind stresses are upwelling favorable and no wind stress is relaxation conditions.

Table 3.4. Effect of behavior, surface flow direction and year on the daily success of particles in the semi-realistic hydrodynamic models. Effects are reported as percent of the magnitude of the effect.

Variable	df	MS	Effect (%)
Behavior	14	199.82	46
Surface Flow	1	342.28	5
Year	10	20.07	3
Behavior X Year	140	2.9	7
Behavior X Surface Flow	14	132.9	30
Wind X Year	10	28.75	5
Behavior X Surface Flow X Year	140	1.78	4
Residuals	27809	0.47	

On average the daily number of passive particles transported onto the self, successful particles, during downwelling conditions decreased with as the depth occupied by the particle increased (Fig. 3.7). During upwelling conditions success increased as the depth particles occupied increased (Fig. 3.7). For standard migrating particles, success was higher during downwelling conditions than upwelling conditions. For twilight migrating particles to depths of 50 and 100, there was little difference between success during upwelling and downwelling conditions. For particles exhibiting a twilight migration to a depth of 200 or 300 m, success was slightly higher during downwelling conditions. For particles exhibiting a twilight migrating to 1 mab, success was greater during upwelling conditions. The most particles were transported onto the shelf when particles made a twilight migration to 1 mab during upwelling conditions.

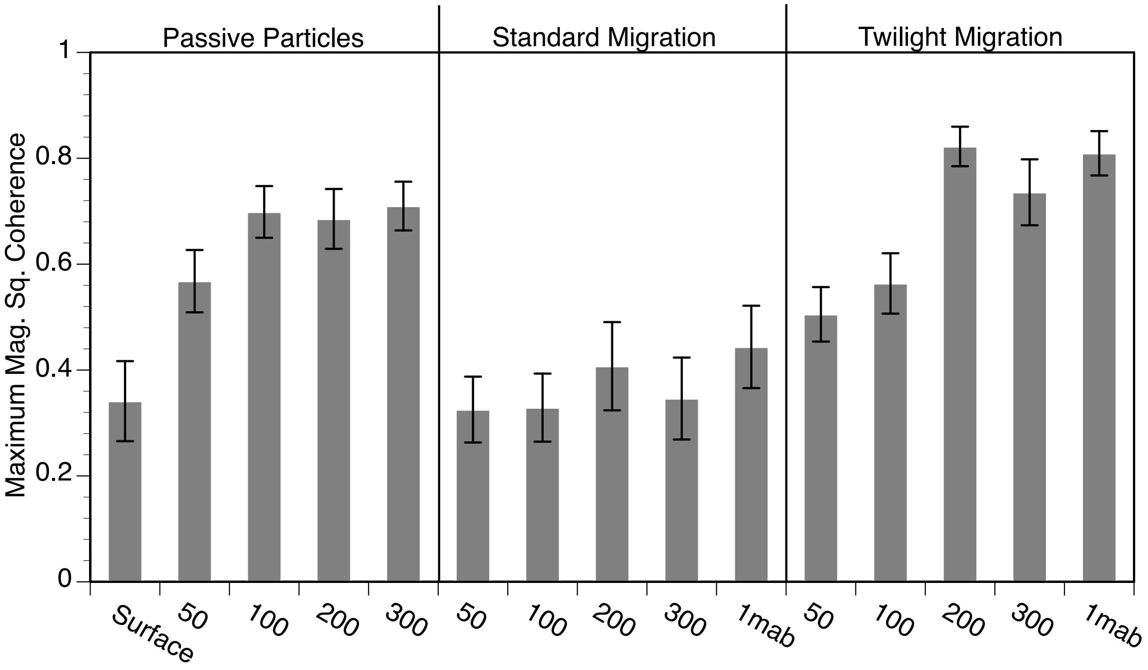

Fig. 3.6. Maximum magnitude squared coherence between the light trap time series and modeled daily success time series for each of the 15 behavior X depth combinations. Bars denote an average of the 11 years of semi-realistic models due to the minimal effect of year (Table 3.2). Error bars are standard error.

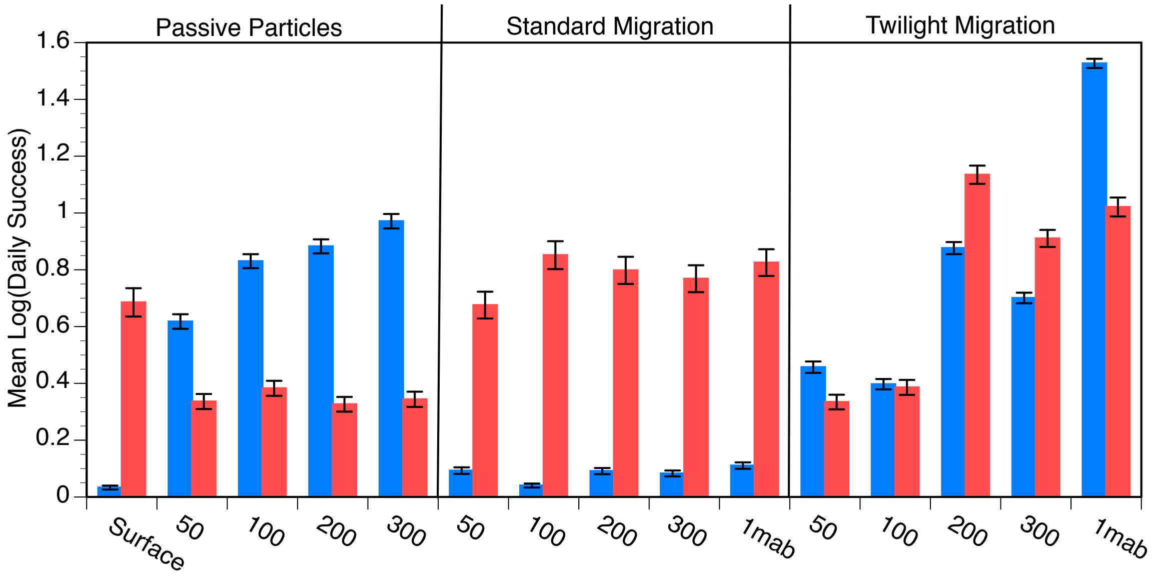

Fig. 3.7. Average daily success, particles advected onto the continental shelf, (± S.E.) for each behavior X depth combination during upwelling (blue bars) and downwelling (red bars) conditions. Since year had a minimal effect on daily success, results from each of the 11 semi-realistic models were averaged (Table 3.2).

Transport distance was highly variable between model type and surface flow direction (Fig. 3.8). On average, during upwelling conditions passive particles at the surface and standard migrating particles were not advected onto the shelf but outliers were advected as far as ~6 km shoreward. During downwelling conditions, passive particles at the surface and standard migrating particles were advected ~0.5 and as far as 10 km onto the shelf. Passive particles at 50, 100, 200 and 300 m were on average advected 0.5 km onto the shelf during both upwelling and downwelling conditions. Passive particles at 50, 100, 200 and 300 m were advected as far as 6.5 km during both upwelling and downwelling conditions. For the twilight migrations, particles at 50 and 100 m had the most variability in transport distance during upwelling conditions. For all other flow and depth conditions particles making a twilight migration had the least variability in their transport distance with an average transport distance (during both upwelling and downwelling) of 0.5 km. Maximum transport distances for twilight migrating particles were ~ 1.25 km.

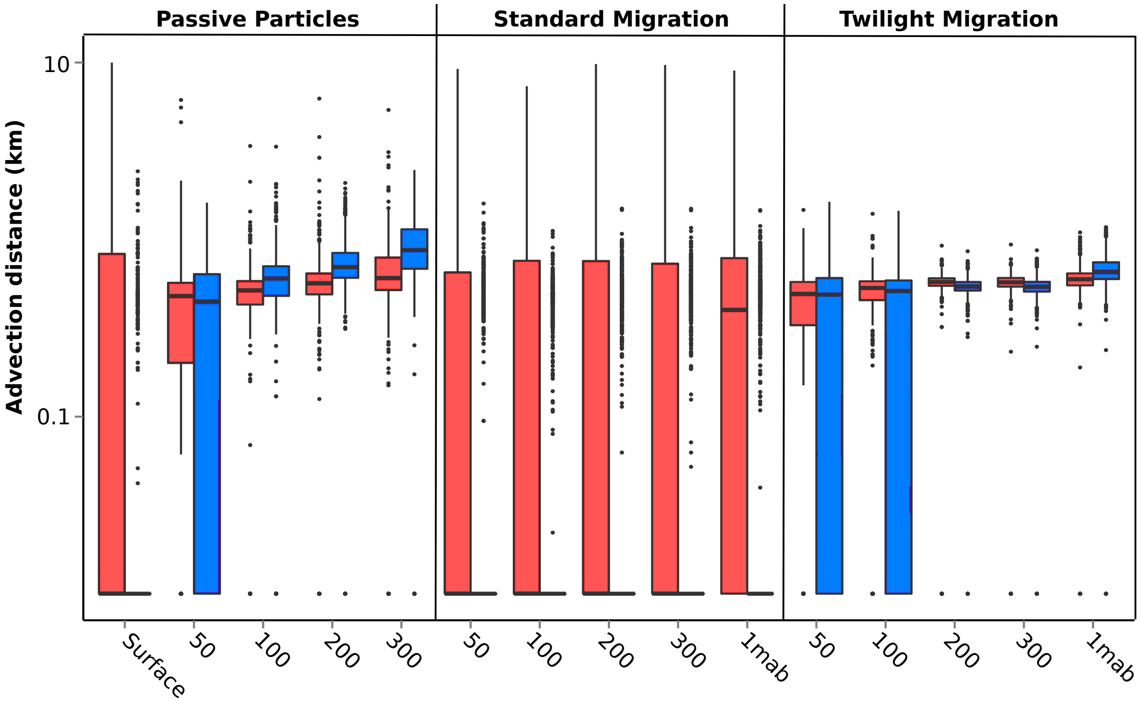

Fig. 3.8. Shoreward transport distance of successful particles for each behavior X depth combination during upwelling (blue bars) and downwelling (red bars) conditions. Since year had a minimal effect on daily success, results from each of the 11 semi-realistic models were averaged (Table 3.2).

For the 11 semi-realistic test cases, passive particles at the surface were advected onto the shelf on ~10 % of the modeled days and this predominately occurred during downwelling (Fig. 3.9). Success for passive particles remained at ~10% of modeled days regardless of depth but average success during upwelling increased to ~40% of modeled days with passive particles at 300 m. particles making a Standard vertical migration were advected onto the shelf ~ 15 % of the modeled days regardless of depth. This advection occurred predominately during downwelling conditions. For particles making a twilight migration, the percent of days with shoreward transport increased from ~30% of the model days, for particles migrating to 50 m, to 85 % of model days for particles migrating to 1 mab. Regardless of behavior or depth, differences in success were predominately driven by variation in success or lack of success during upwelling conditions.

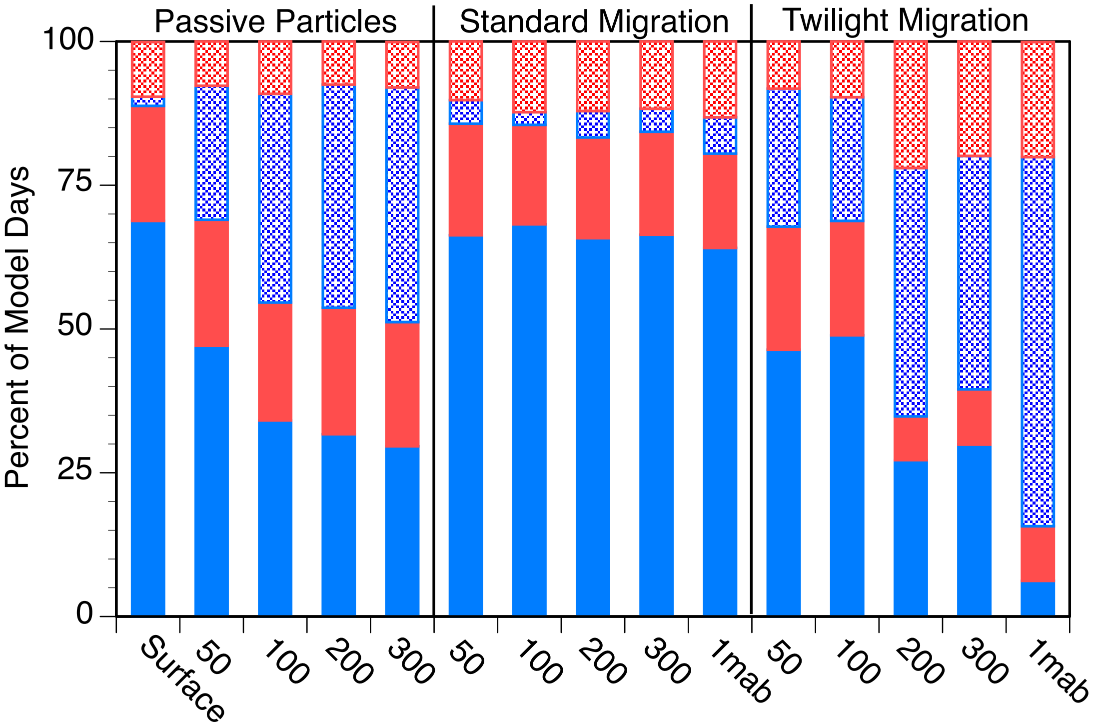

Fig. 3.9. Percentage of days with either no shoreward advection (solid pattern) or shoreward advection (hatched pattern) during upwelling (blue) or downwelling (red) conditions for each behavior X depth combination. Since year had a minimal effect on daily success, results from each of the 11 semi-realistic models were averaged (Table 3.2).

In order to better understand the difference between standard and twilight vertical migrations, we examined the advection direction for each depth the particles occupied. Regardless of behavior, when particles were in surface waters they are advected shoreward during downwelling and offshore during upwelling (Fig. 3.10). For particles exhibiting a twilight migration at night, when they were at a depth of 50 m, they were advected offshore during downwelling and shoreward during upwelling. For particles making a standard vertical migration when at depth, regardless of depth, they were in general advected offshore during downwelling conditions and onshore during upwelling, predominately when occupying the surface. Particles making a twilight migration to a daytime depth of 50 or 100 m were advected offshore during downwelling conditions and weakly shoreward during upwelling when at depth. Twilight migrating particles migrating to daytime of depths of 200, 300 m or 1 mab were strongly advected shoreward during upwelling and during downwelling there was little change in the direction these particles were advected.

3.3.2.3. Variable Behavior Simulation

Based on the above data, we hypothesize that megalopae make a twilight vertical migration to 1 mab. Some literature suggests Dungeness megalopae cease vertically migrating when in the waters over the continental shelf so we tested a combined behavior where megalopae resided in neustonic when over the shelf and exhibited a twilight vertical migration to 1 mab off the shelf. Regardless of year, larvae were advected towards the shelfbreak from offshore (Fig. 3.11). If particles were advected onto the shelf, residence in the neuston caused offshore advection. This created a concentration of particles at the shelf break that was maintained regardless of upwelling and downwelling. The nature of this simulation is such that particles were repeatedly advected onto and off of the shelf at a relatively quick rate. Thus, a time series of the particle successes was highly autocorrelated and therefore the results were not validated with the light trap.

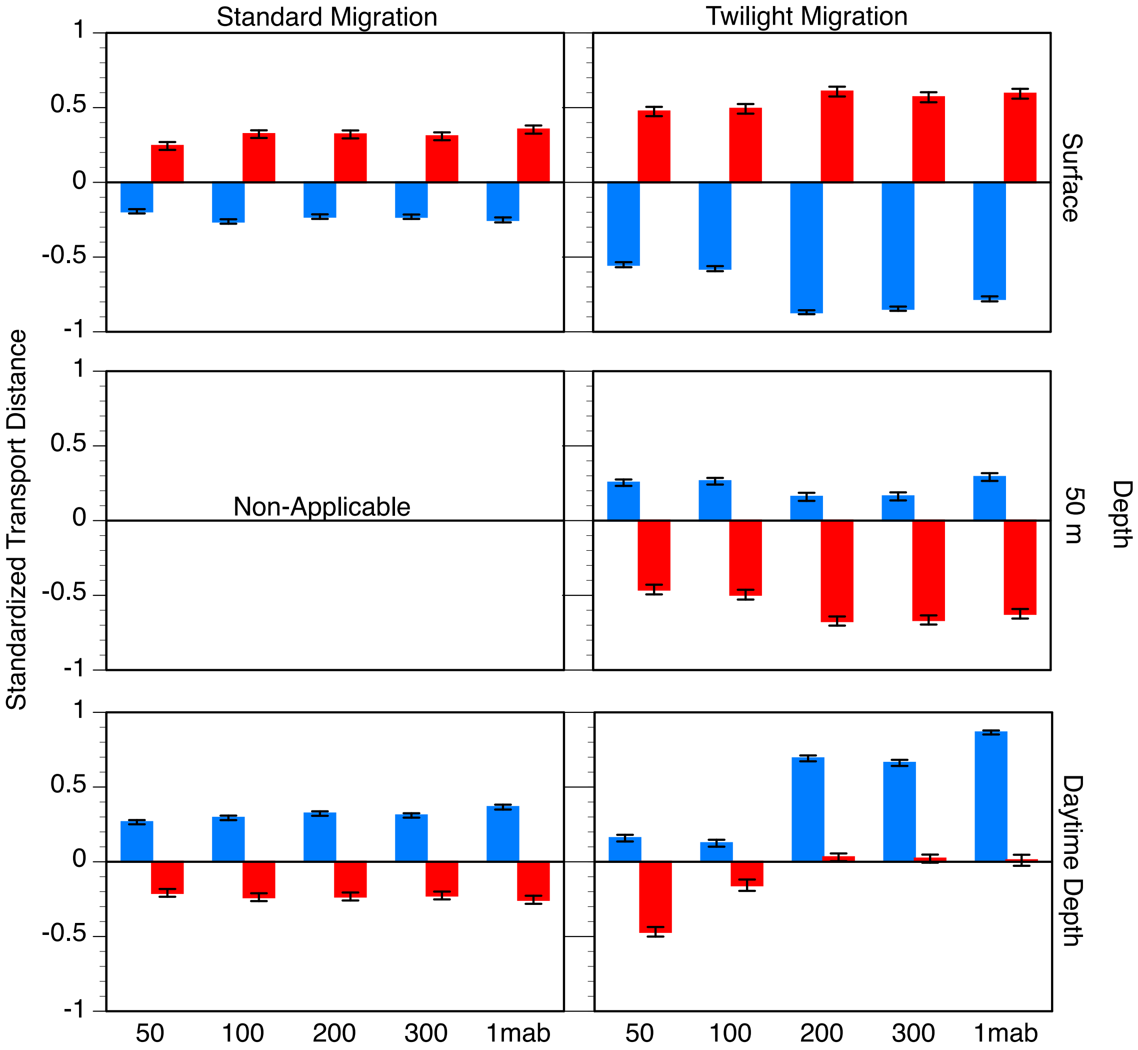

Fig. 3.10. Standardized transport direction for each of the standard and twilight migration X depth combinations during upwelling (blue) and downwelling (red) conditions for each daily depth level occupied by the particles. Daytime depth is the depth denoted on the x-axis. Negative values denote offshore transport and positive values denote shoreward transport. Data appear slightly discordant with other figures due to the advection direction being calculated at a higher temporal frequency (hourly) than for other figures (daily). Error bars denote standard error. Results from each of the 11 semi-realistic models were averaged since year had a minimal effect on daily success (Table 3.2).

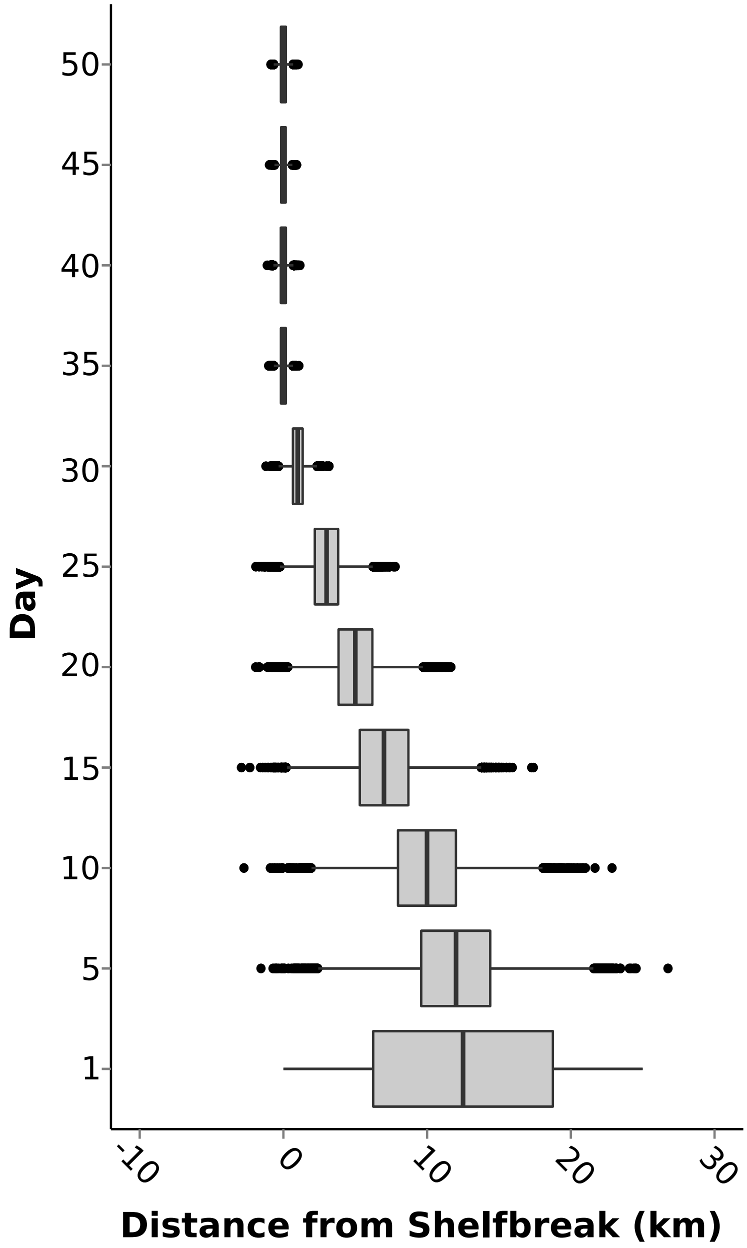

Fig. 3.11. Distance of particles from the shelf break for the variable behavior simulation. Negative values denote shoreward of the shelf break and positive values denote offshore of the shelf break. Results from each of the 11 semi-realistic models were averaged since year had a minimal effect on daily success (Table 3.2).

3.4. DISCUSSION

A statistical comparison of observed (light trap data) and modeled time series' demonstrated that passive particles at depths of 100-300 m and particles exhibiting twilight vertical migration to 200 – 300 m or 1 mab were the most highly associated (Fig. 3.6). It is well established that Dungeness megalopae are active swimmers (Rasmuson & Shanks 2014). Additionally observational studies, suggest that *Cancer magister* megalopae exhibit a twilight vertical (Jamieson & Phillips 1988, Shenker 1988, Park & Shirley 2005). Therefore, it is more likely megalopae exhibit a twilight vertical migration rather than act as passive particles. Our previous work has demonstrated that more megalopae are caught when there is more upwelling following the spring transition (Shanks 2013). In this study, for particles exhibiting a twilight migration to 200-300 m during the day there was no difference between average success during upwelling and downwelling. For particles exhibiting a twilight vertical migration to 1 mab there were more successes during upwelling than downwelling conditions (Fig. 3.7). Thus, we hypothesize megalopae exhibit a twilight migration to 1 mab.

How realistic is it that megalopae migrate close to or onto the bottom? In Glacier Bay, Alaska researchers attempted to catch *Cancer magister* megalopae using plankton nets and only captured them on when they accidentally hit the bottom (J. Fisher Pers. Comm.). Further the late stage larvae of another crustacean in the California Current, pink shrimp (*Pandalus jordani*), are predominately found near the bottom (Rothlisberg & Pearcy 1976). Thus, it seems very likely that *C. magister* megalopae migrate to or close to the bottom each day. Since the boundary layer near the benthos is not often sampled by biological oceanographers, it is possible that a number of species migrate to or near the bottom.

In our work, if megalopae exhibit a twilight vertical migration to 1 mab we find that they are slowly advected onto the shelf regardless of upwelling or downwelling. The following explanation explains what happens on average during each flow regime. When particles are at depth during upwelling, they are advected shoreward (Fig. 3.12). At twilight, when the particles migrate to the neuston, they are advected quickly offshore and at night, while below the Ekman layer, they are advected slowly shoreward. Overall, during upwelling, megalopae are predominately advected shoreward. When particles are at depth during downwelling, there is little change in their location. This is due to two factors: 1) during summer months conditions are predominately upwelling favorable with few downwelling events and 2) the downwelling events that do occur are brief causing flow near the bottom to be relatively weak resulting in little or no advection of larvae (Fig. 3.3A). However, these summer time downwelling events, though brief, are often due to strong winds, which surface waters respond to quickly (Allen & Newberger 1996). Therefore, during twilight, when particles are in the neuston, they are advected shoreward quickly. At night, when the particles are below the Ekman layer, they are slowly advected offshore. Overall, during downwelling conditions there is a net shoreward advection driven by the strong surface advection, however, the advection distance is not as great as during upwelling conditions due to the brief period megalopae occupy the neuston. Thus, regardless of upwelling or downwelling, the model suggests there is a slow onshore advection of megalopae if their behavior is a twilight migration to 1 mab during the day.

The above explanation makes sense unless we consider two things. First, Dungeness crab larvae migrate across and off the continental shelf during the winter. For four years, Roegner et al. (2007) operated a light trap daily in Coos Bay and did not catch any megalopae during the winter months. If our above explanation were true, there would be a slow shoreward advection of larvae regardless of conditions, resulting in megalopae being caught prior to the spring transition. Secondly, if the above explanation were correct we expect a small relatively constant catch of megalopae in the light trap each day. However, following the spring transition, daily catch of megalopae in the light trap is highly pulsed (changing by multiple orders of magnitude in a single day).

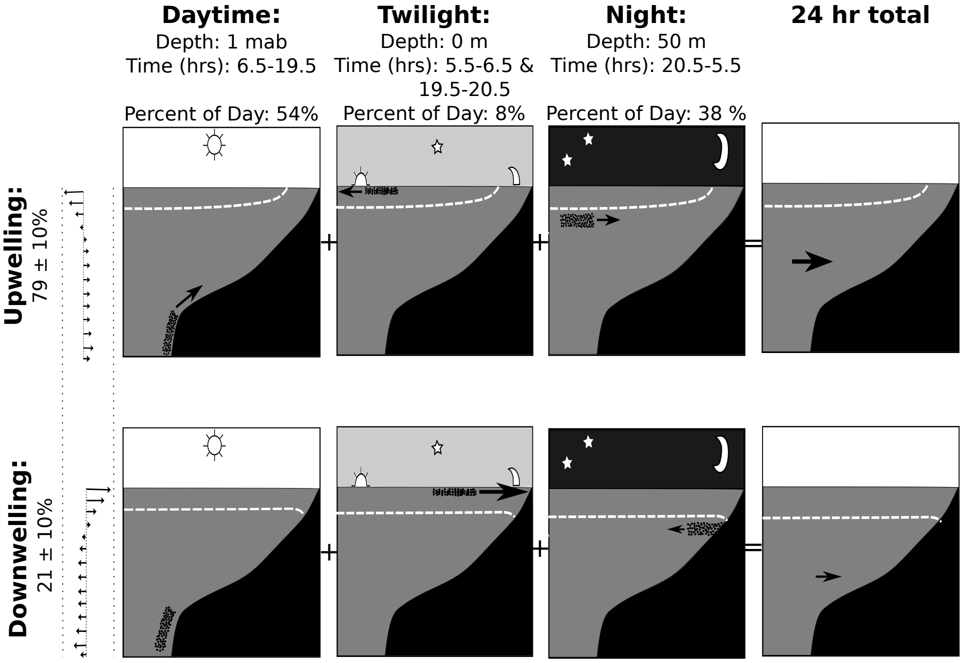

Fig. 3.12. Two-layer model of advection of particles exhibiting a twilight migration to 1 mab during upwelling and downwelling conditions. Black dots denote particle locations and black arrows denote direction of particle advection. No arrow indicates little or no advection. The cumulative effect for each depth occupied during the day for upwelling and downwelling is onshore advection of particles. Percentages below 'upwelling' and 'downwelling' denote the average number of days where forcing was in favorable for the condition listed above. The arrows next to these percentages denote the average flow direction at each depth for each type of circulation.

Some researchers have suggested that megalopae alter their behavior in response to the continental shelf. They propose that offshore of the continental shelf, megalopae vertically migrate while on the continental shelf they remain in the neuston (Reilly 1983). By having megalopae exhibit this behavior in our model, we observed that megalopae were advected towards the shelf break and subsequently concentrated at the shelf break

(Fig. 3.11). We hypothesize that remaining in the neuston on the shoreward side of the shelf break predominately results in offshore advection whereas twilight vertical migration to 1 mab offshore of the break results in shoreward advection as proposed above (Fig. 3.13). Overall, this creates a concentration of megalopae near the shelf break. Central to this hypothesis is that megalopae are able to determine the location of the shelf break and alter their behavior in response. At the shelf break a front (the shelf break front) is often formed (Le Fevre 1986). Recently, Powell and Ohman (2015b, a) operated a glider in the Southern California Bight and observed that offshore of the shelf break front there was evidence of vertically migrating organisms and shoreward of the front there was little migration. These results suggest that the shelf break front may influence the vertical migration of species. Lacking from this explanation is if megalopae are concentrated at the shelf break then how do they get ashore?

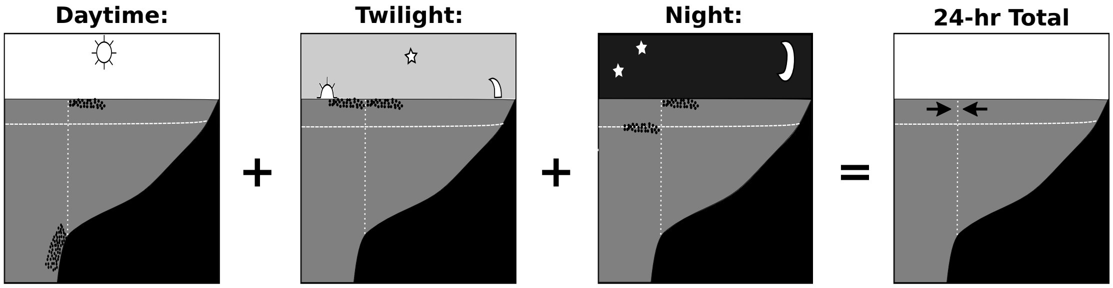

Fig. 3.13. Two-layer model of advection of particles during upwelling and downwelling conditions of particles exhibiting variable behavior. The model assumes particles exhibit a twilight migration to 1 mab offshore of the shelf break (vertical dashed white line) and remain in the neuston onshore of the shelf break. This leads to shoreward advection offshore of the shelf break and offshore advection shoreward of the shelf break. Ultimately this causes particles to concentrate at the shelf break.

Roegner et al. (2007) analyzed 4 years of a daily time series of catch of Dungeness crab megalopae and suggested that megalopae were advected across the continental shelf by internal waves generated by the internal tide. Internal waves are generated at the shelf break by the ebbing tide and have been shown to be effective at transporting larvae long distances (Shanks 2002). Recently we have shown that the spring transition alters the depth of the thermocline, which alters the types of waves formed by the internal tide (Rasmuson and Shanks, in review). Prior to the spring transition, waves of elevation are predominately formed and following the spring transition waves of depression are more likely to be formed. The circulation around these waves is such that for an animal in the neuston (e.g. Dungeness megalopae) transport would likely only occur during waves of depression because flow is offshore above a wave of elevation and shoreward above a wave of depression. Thus, if a species were to swim in the direction of flow (a behavior exhibited by *Cancer magister* megalopae), they would swim offshore and through a wave of elevation and shoreward and with a wave of depression (Rasmuson & Shanks 2014). Therefore, if megalopae exhibited the variable behavior around the continental shelf they would be concentrated at the break during winter but not transported by the internal tides. Following the spring transition, when more internal waves of depression are formed, the megalopae concentrated at the continental shelf could be transported across the continental shelf by the internal tides.

In his member/vagrant hypothesis, Sinclair (1988) suggests successful populations require the closure of the pelagic portion of their lifecycle. Individuals that are capable of closing the pelagic portion of their lifecycle are members in the population they return to whereas others are vagrants. In the case of Dungeness crab megalopae closure of the pelagic portion of their lifecycle, means migrating from the continental shelf break (or further) to the nearshore environment to settle. There are relatively few hydrodynamic processes off of the continental shelf that would concentrate larvae in such a way that they would ultimately be advected shoreward. Therefore, the concentration of the population at the shelf break front followed by subsequent shoreward transport of megalopae is ultimately a more stable strategy than larvae being off of the continental shelf. This strategy is more stable because the hydrodynamic processes (e.g. internal tides) that would results in cross-shelf advection from the continental shelf break to the nearshore are coherent in time and space.

In addition to being more stable for the cross shelf transport processes, the concentration of megalopae at the shelf break front would likely act to promote membership of megalopae in the California Current population. While megalopae are offshore of the shelf break, they would likely experience southward flow in the surface waters of the California Current and northward flow at depth in the California Undercurrent. Prior to the spring transition, shoreward of the shelf break they would experience northward flow in the Davidson Current. Ultimately, alternating between northward and southward flows would likely decrease the magnitude of the alongshore transport of larvae promoting membership in the California Current population.

In the marine environment, quantifying the vertical migration of marine larvae is difficult due to the large vertical and horizontal scales often involved (Pearre 1979). There is only one study we know of that has examined the twilight migrations of a marine larva (Ziegler et al. 2010) and none that have the vertical resolution to address migration to or near the bottom in shelf or offshore waters. Although so few studies have assessed the vertical migration of marine larvae, the hypotheses presented in many larval dispersal studies is reliant on the effects of vertical migratory behaviors (reviewed in Queiroga &

Blanton 2004). Specifically in upwelling ecosystems, vertical migrations have long been proposed to play a role in advection of larvae (Morgan 2014). Even in this study, we initially hypothesized that the correlation between catch of Dungeness crab megalopae and upwelling indicated shoreward transport in deep upwelled waters. This hypothesis was based on the assumption that megalopae exhibited a standard vertical migration rather than a twilight vertical migration. To our knowledge this is the first study directly examining the implications of a twilight vertical migration in an upwelling regime. A long-standing question in marine ecosystems has been to link the highly advective nature of an upwelling regime with the large abundance of organisms (Bakun et al. 1979, Roughgarden et al. 1988). Recent studies have demonstrated that species from the intertidal assemblage (as proposed by Shanks & Eckert 2005) remain close to the shore despite upwelling and downwelling (Shanks & Brink 2005, Morgan et al. 2009, Shanks & Shearman 2009), however, few studies have considered the dispersal of the shelf/slope assemblage and how these populations are maintained (Hannah 2011). Assuming a sunrise at 0600 and sunset at 2000, a twilight vertical migration results in a decrease from 42% of the day to 8 % of the day spent in the highly advective surface waters. As we have shown, this would have profound effects on the advection of larvae and may ultimately lead to less overall advection.

Many of studies use data from plankton tows to provide some idea of the temporal and spatial extent of the larvae's vertical migration (DiBacco et al. 2001, Marta-Almeida et al. 2006, Carr et al. 2008). Although observations collected with neuston specific nets (e.g. Manta nets) often suggest that at some point during the day larvae occupy the uppermost region of the water column, most models, however, do not have particles migrate all the way to the surface. Models that have animals occupy the uppermost extent of the water column parameterize the migration as depth bins, which may encompass both the highly advective surface regime and the less advective waters below them. Thus, it is important for modeling studies to have larvae occupy the uppermost waters if the data suggest animals exhibit this behavior.

The hypothesis we present here is purely that, a hypothesis. In next steps a more complex 3-D model of upwelling that includes tides and other forcing variables should be used to allow for greater understanding of interannual variation in recruitment dynamics. This is especially important as recent work suggests upwelling may be more complex than traditionally proposed in two layer models (McCabe et al. 2014). Ideally, an extensive sampling project should be conducted to better quantify the actual vertical migration of Cancer magister larvae and both if and why megalopae stop migrating once on the continental shelf.

3.5. CONCLUSION

By combining our unique 11-year time series of catch of Dungeness crab megalopae with an individual based biophysical model we were able to assess the influence of behavior and hydrodynamics on the dispersal of megalopae. Our work is the first modeling study to examine the influence of a twilight vertical migration on the transport of larvae. We propose that Cancer magister megalopae when off the continental shelf exhibit a twilight vertical migration to 1 mab and on the shelf they occupy the neuston. Ultimately this leads to a concentration of megalopae near the shelf break where they can be advected across the continental shelf by internal waves of depression generated following the spring transition. A twilight vertical migration has the potential to greatly influence dispersal of larvae especially in upwelling regimes and studies should more specifically quantify the spatial and temporal extent of vertical migrations.

3.6. BRIDGE TO CHAPTER IV

In chapter III I modeled the vertical migration of megalopae and showed that a twilight migration to 1 mab best explained our observed results. Based on results from the literature and an additional simulation I suggest megalopae exhibit a twilight migration to 1 mab while off of the continental shelf and remain in the neuston on the continental shelf. Ultimately, I hypothesize this causes megalopae to be concentrated at the shelf break where they are subsequently transported by internal waves. In Chapter IV I test whether megalopae exhibit the behaviors that would increase transport by internal waves and use the results to calculate potential transport distances for internal waves observed in a thermistor mooring.

CHAPTER IV

IN SITU OBSERVATIONS OF DUNGENESS CRAB MEGALOPAE USED TO ESTIMATE TRANSPORT DISTANCES BY INTERNAL WAVES

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4.1. INTRODUCTION

Larvae of many intertidal and shallow subtidal organisms develop offshore but must migrate back to the nearshore environment to settle (Shanks 1995a). Two migration mechanisms are often proposed in the literature: swimming ashore and migration enhanced by physical oceanographic processes (Shanks 1995a). For larvae to swim ashore they must swim in the right direction and be strong swimmers. Multiple physical oceanographic processes are proposed to enhance migration such as internal waves, land/sea breezes, shoreward propagating upwelling fronts and geostrophic flow (Shanks 1995a, Queiroga & Blanton 2004). The effectiveness of these physical mechanisms are further enhanced by organisms that swim in the right direction (whether vertically or horizontally). Thus, larval behavior may play a critical role in cross shelf dispersal (Queiroga et al. 2007). However, behaviors proposed to enhance migration are often based on findings from laboratory studies or assumptions based on larval morphology (Metaxas 2001).

Field observations of larval behavior have focused, due to their large size, on crustacean postlarvae, ascidian tadpoles and coral reef fish larvae (Bingham & Young 1991, Shanks 1995b). Leis & Carson-Ewart (1997) examined in situ swimming speeds of 54 coral reef fish larvae and found a mean swimming speed of 20.6 cm s^{-1}, a speed well above all but the fastest currents; these larvae were able to actively move through the water and, in the field, orient toward reefs. Coral reef fish larvae orient their swimming to a combination of scent, reef sounds and sun (Elliott et al. 1995, Tolimieri et al. 2000, Leis & Carson-Ewart 2003). In situ, decapod larvae oriented their swimming towards reef sounds and light or parallel with surface currents (Shanks 1995b, Jeffs et al. 2003, Radford et al. 2007). Off Rhode Island, American lobster larvae primarily swam northeast towards the shore (Cobb et al. 1989). In situ swimming speed of decapods has only been determined for late stage lobster larvae (ranging from 15 to 46 cm s^{-1} depending on species) and not for brachyuran crabs (Phillips & Olsen 1975, Cobb et al. 1989).

One physical oceanographic mechanism proposed to transport larvae is internal waves. Transport by internal waves occurs when surface current speed above the wave is greater than the wave's propagation speed (Shanks 1995b, Lamb 1997). Lamb's (1997) model states that if the surface current speed is greater than the wave phase speed, particles are transported continuously by the wave until the characteristics of the wave changes. If the surface current is slower than the wave phase speed, particles are transported a finite and short distance. The distance internal waves transport particles can be determined by (1) combining physical observations of internal waves with Lamb's (1997) model to calculate transport distance or (2) measuring transport distance in situ by interpolating distance from measured plankton concentration in front of and within internal waves. Studies that combine Lamb's (1997) model with physical observations report transport distances on the order of meters with rare events of 1–2 km (McManus et al. 2005, Shroyer et al. 2010). Transport distances calculated from concentrations of plankton in net tows suggest larger transport distances ranging from 3.5–23 km (A. L. Shanks unpubl. data). Thus, there is a discord between transport distances calculated from Lamb's (1997) model and in situ observations. From the perspective of a larva crossing the continental shelf, the differences would be significant. A possible explanation for the discord is that calculations using Lamb's (1997) model have not historically included larval behavior and previous work suggests synergistic effects of larval behavior with internal waves should greatly increase transport distances (Shanks 1995b, Lamb 1997). Specifically if larvae are strong swimmers and swim in the direction of wave propagation, the distance they are trans- ported by internal waves should increase dramatically (Shanks 1995b, Lamb 1997). In the field, megalopae of *Pachygrapsus crassipes* and *Lophopanopeus bellus bellus* have been observed in the surface convergence of internal waves and swimming in the direction of wave propagation, suggesting this phenomenon of increased transport distance does indeed occur (Shanks 1995b). Thus, it is likely behavior plays an important role in the transport of organisms by internal waves.

Due to their commercial importance, many studies have examined the larval dispersal and transport of the Dungeness crab (*Cancer magister,* Dana, 1852). Their abundance is strongly affected by recruitment processes (reviewed in Rasmuson 2013). Zoeae of *C. magister* are released in the nearshore environment during winter and are found at greater distances from shore as they develop (reviewed in Rasmuson 2013). By the time they molt into megalopae, they are far from the shore but must migrate to the nearshore environment to settle. Two laboratory studies report swimming speeds of *C. magister* megalopae ranging from 4.2 cm s^{-1} (Jacoby 1982) to 44.7 cm s^{-1} (Fernandez et al. 1994). Thus, megalopae are strong swimmers and may make the shoreward migration by swimming east; however, no studies have determined if *C. magister* megalopae orient their swimming. Conversely, correlations of daily abundance of megalopae and daily maximum tidal range suggest megalopae are transported across the continental shelf by internal waves (Johnson & Shanks 2002, Roegner et al. 2007). Thus, it is likely one of the commonly proposed migration mechanisms (swimming ashore or transport by internal waves) is the pathway by which *C. magister* return to the nearshore environment.

Therefore, due to its extensive research history and evidence that the fishery is driven by recruitment, we used in situ observations of *C. magister* orientation and swimming speed to test whether megalopae exhibit behaviors suggestive of cross shelf migration by swimming or transport by internal waves. We hypothesized that (1) megalopae would swim with surface currents rather than swim east. We further hypothesized that (2) the behaviors of *C. magister* megalopae would enhance transport by internal waves. We tested these hypotheses by combining our in situ observation data with mooring observations of internal waves to calculating potential transport distances by internal waves.

4.2. MATERIALS AND METHODS

4.2.1. *In Situ* Observations

Cancer magister megalopae were caught in a light trap in Coos Bay, Oregon (Fig. 4.1; for details, see Shanks & Roegner 2007), and their swimming behavior was observed on the day of capture. Individuals were transported in a bucket of seawater equipped with an aerator to Sunset Bay, Oregon (Fig. 4.1), where they were released and their behavior was observed. Release sites within Sunset Bay were chosen haphazardly, and offshore distance of the releases was dictated by safety concerns. The depth of each experimental site was not determined, because observation sites were reached by kayak, and strong currents prevented depth measurements using the anchor rope.

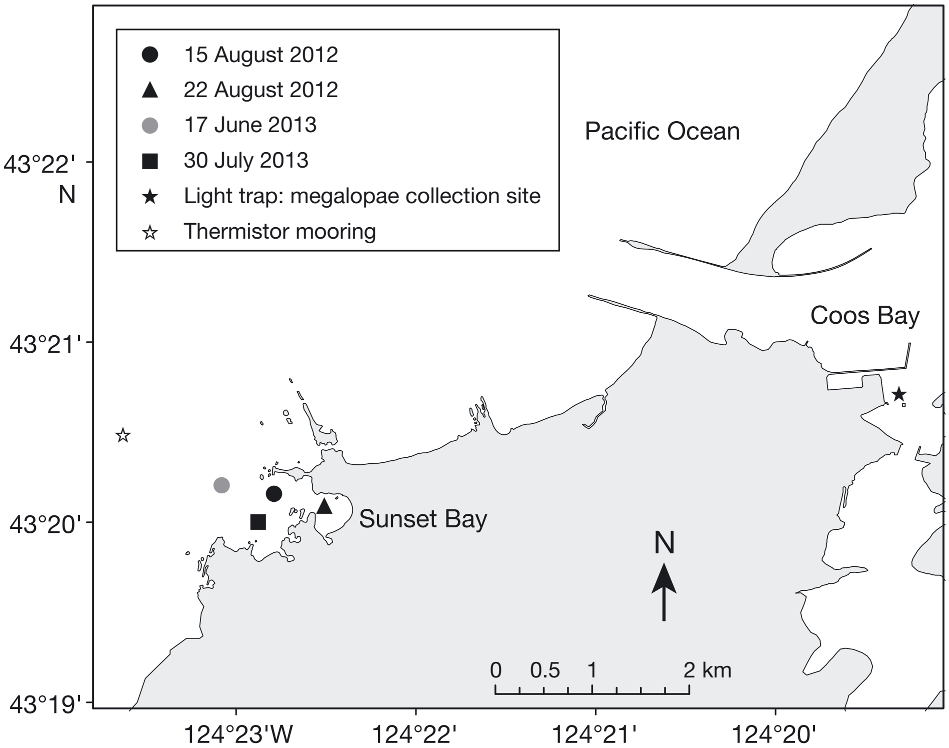


Fig. 4.1. Collection site for megalopae of *Cancer magister* in Coos Bay, Oregon, USA, observation sites on 4 different dates in Sunset Bay, and site of thermistor mooring just outside of Sunset Bay.

On 15 and 22 August 2012 and 17 June 2013, using protocols similar to Shanks (1995b), megalopae were observed in order to determine if they oriented the direction of their swimming. A snorkeler observed megalopae during daylight in the upper 1 m of the water column. An individual megalopa was placed in a 225 ml jar and handed to a snorkeler. After swimming ~5 m from the kayak (alternating direction haphazardly), the snorkeler opened the jar ~1 m below the surface. Each megalopa was observed until it vanished, and its bearing was recorded. The snorkeler haphazardly oriented the location of his body relative to the sun, wave direction, surface current and shore to minimize the effects of the snorkeler's presence. Using a compass, the snorkeler recorded the bearing of the sun and swell direction. To determine surface current direction, a 2 m weighted line with strips of plastic every 0.25 m was hung from a float at the surface of the water column. The direction of the floating strips was recorded as a bearing for the direction of the surface current. Current direction was determined in the upper 2 m of the water column since megalopae swam near the surface.

On 22 August 2012, 17 June and 30 July 2013, megalopae were released at ~1 m depth and followed to determine their horizontal swimming speeds using protocols similar to Leis & Carson-Ewart (1997). Each megalopa (n = 10 per date) was followed by the snorkeler for 30 s at a distance of ~1 m. Megalopae were only followed for 30 s to prevent the snorkeler from getting too far from the kayak. The snorkeler held a General Oceanics Flow Meter with a low-flow propeller (Leis & Carson-Ewart 1997). Recording time and flow meter revolutions allowed us to determine the speed of the megalopa. Surface water speeds were determined on 17 June and 30 July 2013. A plastic jar was filled with water, leaving a small air bubble, and the snorkeler followed the jar for 1 min using the same flow meter (Hamilton & Russel 1981). The jar floated with ~5 cm^2 of surface area exposed to the air right at the air-water interface, thus wind effects were minimal. On these dates, the speed of the water flow was subtracted from the measured swimming speed of megalopae that swam with the current and added to that of megalopae that swam against the current.

Swimming orientation data were analyzed using circular statistics (Batschelet 1981). A Rayleigh test was used to determine whether data were significantly different from random. In cases where the distributions were non-random, a V-test was used to determine if mean swimming direction was similar to the bearing of the sun, wave direction, surface current and shore. Swimming speeds were square-root transformed to ensure that the data met the assumptions of normality and homogeneity of variances. Swimming speeds from 17 June and 30 July 2013 (corrected for water speed) were compared to each other using a Student's t-test, while those from 22 August 2012, 17 June 2013 and 30 July 2013 (no correction for water speed was applied) were compared using ANOVA.

4.2.2. Comparison to Physical Data

From 19 August to 13 September 2012, we deployed a thermistor chain in 30 m of water (Fig. 4.1) to observe internal waves. The thermistor chain was deployed as close to the observation locations as possible but in deep enough water to prevent loss due to boat traffic and/or wave action. Four Seabird SBE-56 thermistors were deployed at 5, 10, 15 and 19 m from the surface and recorded data every 0.5 s. Depths were chosen to provide sufficient resolution around the thermocline using the available thermistors. We used these data to describe the internal waves in the study area and calculate the probability of transport by internal waves.

McManus et al. (2005) calculated transport distance using Lamb's (1997) equation as:

$$\Delta x = 2L\left(\frac{b^2}{1-b^2}\right)^{1/2} \arctan\left[\left(\frac{b^2}{1-b^2}\right)^{1/2}\right] \tag{4.1}$$

where Δx is the transport distance of the particle, L is the soliton half-width, and b^2 is defined as:

$$b^2 = \frac{U_{\max}}{V - U_d} \tag{4.2}$$

U_{max} is the maximum particle velocity at a specific interface, V is the linear propagation speed of the wave, and U_d is the swimming speed of the organism. However, thermistor moorings do not record current velocities, and thus McManus et al. (2005) used the following soliton solution from Holloway (1987) to convert thermistor data into velocity data:

$$\eta = \eta_0 \sec h^2\left(\frac{x-ct}{L}\right) \tag{4.3}$$

$$c = c_0\left[1 + \frac{\eta_0}{2}\left(\frac{h_1 - h_2}{h_1 h_2}\right)\right] \tag{4.4}$$

$$c_0 = \left[g\frac{(\rho_2 - \rho_1)}{\rho_2}\frac{h_1 h_2}{h_1 + h_2}\right]^{1/2} \tag{4.5}$$

$$L^2 = \frac{4}{3}\frac{h_1^2 h_2^2}{(h_1 - h_2)\eta_0} \tag{4.6}$$

where η is the deviation of the thermocline from ambient, η_0 is the amplitude of the soliton, x is the horizontal position of the particle, c is nonlinear phase speed, c_0 is the linear phase speed, g is the acceleration due to gravity, and h denotes the thickness and density of respective layers (h_1 and denote upper layers). Combining Lamb's (1997) equation and Holloway's (1987) solution, McManus et al. (2005) proposed (assuming $U_d = 0$):

$$b^2 = \frac{U_{\max}}{c} \tag{4.7}$$

where $U_{\max}$ is calculated at the surface and depth as:

$$Surface U_{\max} = c_0 \eta_0 h_1^{-1} \tag{4.8}$$

$$Depth U_{\max} = -c_0 \eta_0 h_2^{-1} \tag{4.9}$$

This allowed McManus et al. (2005) to calculate transport distance from a single thermistor chain despite not having velocity data.

An assumption of McManus et al. (2005) was that $U_d = 0$; however, the focus of our study was on the contribution of swimming speed of an organism and therefore we used

$$b^2 = \frac{U_{\max}}{c - U_d} \tag{4.10}$$

to calculate transport distance. We calculated $U_{\max}$ (using Eq. 4.8) only for the surface of the water column, because megalopae swam at the surface in all of our observations.

Using these equations, we calculated transport probability for passive and actively swimming organisms exhibiting the behaviors we observed in *C. magister* megalopae. To find internal waves in the mooring data, data were interpolated onto a 0.2 m grid and plots of daily average temperature generated to determine the depth of the thermocline. On all days the average thermocline depth was 12 m. The temperature record from the 10 m thermistor (the thermistor closest to the thermocline) was assessed visually for the presence of internal waves of elevation and depression (Fig. 4.2). For each wave observed variables needed for the above equations were recorded. Transport calculations require estimates of density above and below the thermocline. Density was calculated from the 10 and 15 m thermistors using the equation of state of seawater with zero pressure and an assumed salinity of 33. Routine CTD casts conducted in this area show that salinity remains relatively constant at 33 (M. Jarvis pers. comm.).

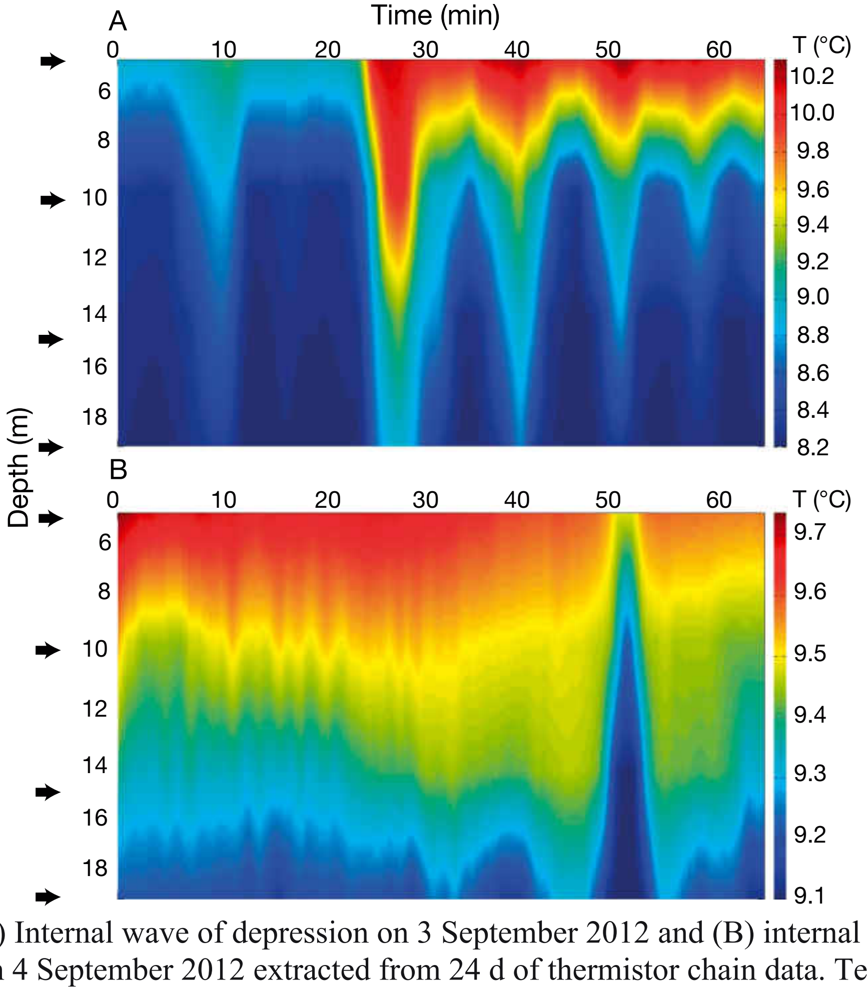


Fig. 4.2. (A) Internal wave of depression on 3 September 2012 and (B) internal wave of elevation on 4 September 2012 extracted from 24 d of thermistor chain data. Temperature (T) scales differ between panels. Arrows: depths of the thermistors.

Using the recorded data, transport distance was calculated for swimming speeds ranging from 0 to 10.0 cm s^{-1} in 0.1 cm s^{-1} increments. We assumed that larvae swam with the surface current, as did the *C. magister* megalopae. In the above equations in situations where U_d= V, the particle is transported an infinite distance by the wave until the characteristics of the wave or the organism's behavior change.

Our focus was to determine transport of megalopae across the continental shelf, which is ~25 km wide near our study site in Coos Bay. Since internal waves are generated at the continental shelf break by the internal tide, we considered waves to be transporting if the transport distance was ~25 km (i.e. the maximum transport distance near Coos Bay). We use the terms 'transport' and 'transporting' to denote distances <25 km and 'shelf-transport' and 'shelf-transporting' to denote distances >25 km.

We assumed that organisms were capable of reducing their swimming speed to match wave propagation speed. Based on the nature of the transport model, this means that a 'shelf-transporting' wave that occurred for larvae with swimming speeds ranging from 0 to 0.2 cm s^{-1} was presumed to be 'shelf- transporting' for organisms with swimming speeds ranging 0 to 10.0 cm s^{-1}. Had we not made these assumptions, megalopae swimming at faster speeds would not have been transported by the waves that transported slower swimming megalopae. In marinas with turbulent eddies, *C. magister* megalopae alter their swimming speed relative to local currents, so it is probable that megalopae do indeed reduce their speed (L. K. Rasmuson pers. obs.). The above calculations only apply to non-linear internal waves; therefore, internal bores were excluded in this analysis.

4.3. RESULTS

4.3.1. *In Situ* Observations

In all trials, megalopae swam up from 1 m depth to the very surface of the water, close enough to dimple the surface of the water. After release, megalopae extended their legs and spun in a circle. In most cases, megalopae did not begin swimming horizontally until their anterior end pointed in the direction of the surface current. When swimming horizontally, they tucked their legs against their carapace and swam with the surface current. In some rare instances, megalopae swam towards the observer and either clung to the observer (these individuals were excluded from analysis) or swam past the observer (included in analyses).

On all dates, the swimming direction of megalopae was significantly clustered (Fig. 4.3). Megalopae did not swim east or with the swell on any day (Table 4.1, Fig. 4.3). On 2 of the 3 sample days, megalopae did not swim towards the sun, while on the third day, swimming was slightly similar to the sun's bearing (Table 4.1, Fig. 4.3). Mean swimming direction on all dates was, however, statistically similar to the direction of the surface current (Table 4.1, Fig. 4.3). On one occasion, 8 megalopae were released when no surface current was detected. During this trial, megalopae appeared to swim randomly ($n = 8$, $Z = 0.90$, $p > 0.05$); however, the small sample size limits the power of the statistical test.

Mean swimming speed (prior to removal of background speed) was 11.1 cm s^{-1} (range: 5.6–23.8 cm s^{-1}) and did not differ among sampling dates ($F_{2,27} = 0.0724$, $p > 0.05$; Table 4.2). Because megalopae swam with surface currents, we removed the contribution of the surface current to their swimming speed. After correcting for current

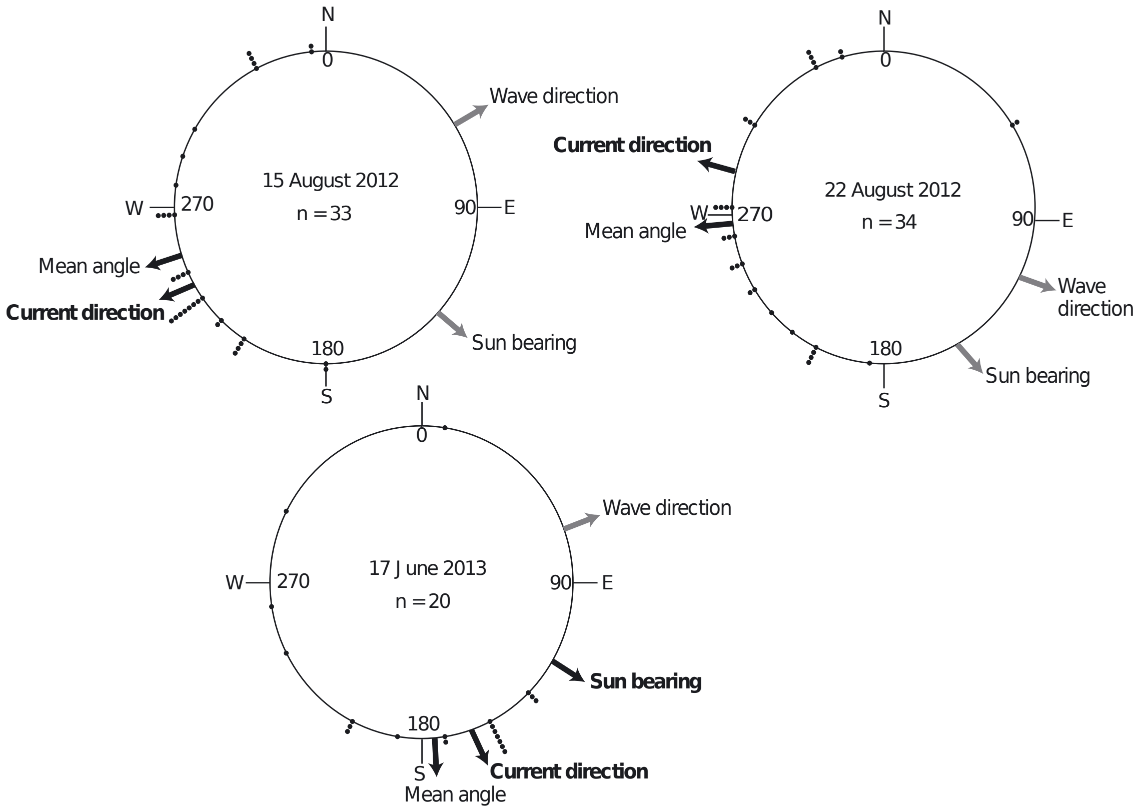


Fig. 4.3. Swimming direction of individual *Cancer magister* megalopae (dots) on each sampling day relative to different abiotic factors (arrows). **Bold** labels: bearings of abiotic factors that were statistically similar (V-test, $p \leq 0.05$) to the mean swimming direction; gray arrows: insignificant factors (see also Table 4.1).

Table 4.1. Oriented swimming of *Cancer magister* megalopae. Data were first analyzed to determine if they were significantly clustered. Mean swimming direction was compared to the bearing of abiotic factors to determine if they were statistically similar (see also Fig. 4.3). $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

Date	Rayleigh's Z	Mean (±SE) swimming angle (°)	Abiotic factor bearing	V-test u-values
15 Aug 2012	16.61***	253 ± 43	Swell: 60°	-5.68
			Sun: 135°	-2.82
			Current direction: 240°	5.68***
22 Aug 2012	14.93***	268 ± 47	Swell: 150°	-4.64
			Sun: 120°	-2.57
			Current direction: 280°	5.35***
17 Jun 2013	5.08***	176 ± 63	Swell: 60°	-1.44
			Sun: 120°	1.79*
			Current direction: 160°	3.10***

speed, the average swimming speed of megalopae on 17 June and 30 July 2013 was 9.8 cm s^{-1} (range: 5.0–23.1 cm s^{-1}) and did not differ between sampling dates ($t_9 = 0.618$, $p > 0.05$; Table 4.2).

Table 4.2. Swimming speed (cm s^{-1}; including and excluding water speed) of *Cancer magister* megalopae. n = 10 on each date. NA: data not available since water speed is unknown.

Sample date	Including water speed		Swimming speed only	
	Mean ± SE	Range	Mean ± SE	Range
22 Aug 2012	11.5 ± 1.8	5.9-21.9	NA	NA
17 Jun 2013	11.4 ± 0.6	7.6-13.5	9.0 ± 0.6	6.1-12.1
30 Jul 2013	10.4 ± 2.1	5.6-23.8	10.8 ± 2.1	5.0-23.1
Mean	11.1 ± 0.9		9.8 ± 1.0	

4.3.2. Transport Distances

Over 24 d, we observed 69 internal waves, 54 waves of depression and 15 waves of elevation. Waves of depression would frequently occur in rank ordered packets with the largest amplitude wave leading. Leading waves had ‘idealized’ soliton shapes whereas subsequent waves in packets did not conform as well. Waves of elevation were always solitary and conformed well to the presumed shape of ‘idealized’ solitons. A total of 24 internal bores were observed (18 of depression and 6 of elevation), though they were not included in the analysis.

None of the waves would have been ‘shelf-transporting’ (distances > 25 km) for non-swimming organisms (Table 4.3, Fig. 4.4). As swimming speeds of organisms increased (assuming they swam in the direction of wave propagation), the number of transporting waves increased dramatically and at swimming speeds of 0–10 cm s^{-1} all waves would have been transporting (Table 4.3, Fig. 4.4). Additionally, mean transport distance increased very slightly and maximum transport distance increased as well (Table 4.3, Fig. 4.4).

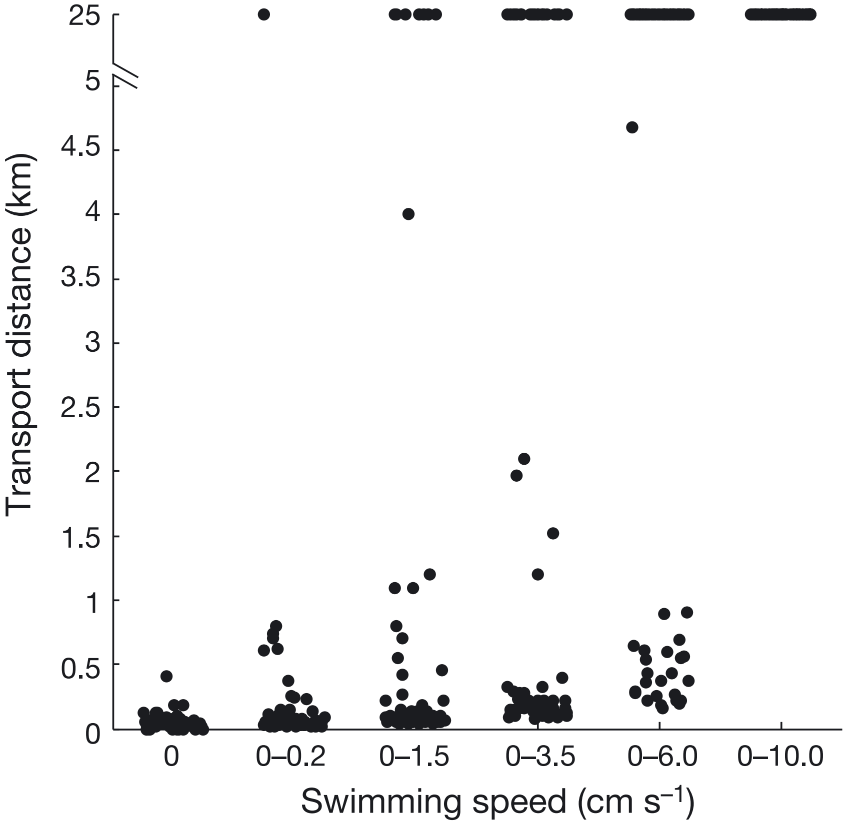


Fig. 4.4. Influence of larval swimming speed, assuming the larvae swam in the direction of wave propagation, on calculated transport distance of internal waves (n = 69). x-axis labels denote the range of speeds in each bin, and data points are scattered in the x-direction for ease of reading. Data at y = 25 km represent particles that remained in the wave and were transported until the characteristics of the wave or behavior of the organism changed.

Table. 4.3. Mean and maximum transport distance for transporting internal waves (distances <25 km) and the number of waves considered 'shelf-transporting' (distances ≥25 km) out of 69 observed internal waves for larvae with different swimming speeds. 'Shelf-transporting' waves were excluded from calculations of mean and maximum values for transporting waves except at swimming speeds of 0 to 10 cm s^{-1}, because at this speed all waves were 'shelf-transporting'. See section 4.2.2. for an explanation of why shelf transport distance is ≥25 km.

Swimming Speed (cm s^{-1})	Transport distance (km) Mean	Maximum	No. of 'shelf-transporting' waves
0 (passive)	0.05	0.41	0
0-0.2	0.11	0.80	1
0-1.5	0.24	4.00	7
0-3.5	0.30	2.10	21
0-6	0.60	4.68	44
0-10	≥ 25.00	≥ 25.00	69

4.4. DISCUSSION

Our work demonstrated that the megalopae of *C. magister* actively oriented the direction of their swimming and were capable of swimming at speeds of ~10 cm s^{-1}. Including these behaviors in calculations of potential transport distance suggests that in the presence of an internal wave, the behaviors and swimming of *C. magister* megalopae would greatly increase transport distance.

Since the megalopae used in this study had already migrated across the continental shelf to reach Coos Bay, their swimming behaviors may have been altered. However, in offshore waters, the megalopae of *Cancer magister* have been observed swimming with surface currents (L. K. Rasmuson pers. obs.), suggesting that the behaviors we observed in Sunset Bay occur offshore as well. Repeating the present study in offshore waters with megalopae collected offshore would determine whether the swimming behaviors we observed here are representative of the natural migration process of *C. magister* megalopae. Larvae of some lobsters and coral reef fish are reported to swim ashore (Leis 2002, Jeffs et al. 2005). In the Northeast Pacific, organisms trying to swim ashore would need to swim approximately towards the east. Near Coos Bay, the continental shelf is ~25 km wide, so organisms swimming at 9.8 cm s^{-1} would require ~3 d to swim across the shelf. This time period is short enough relative to the megalopa stage duration that it is possible megalopae could swim ashore. However, megalopae did not swim east on any of the sample dates (Fig. 4.3). Thus, the swimming direction of the *C. magister* megalopae would not have resulted in their swimming ashore.

Other studies suggest that crab megalopae and coral reef fish larvae use reef sounds as a cue for navigating to settlement sites (Leis et al. 2002, Jeffs et al. 2003). *C.*

magister primarily settles on soft sediments on the continental shelf (depth varies greatly) so it seems unlikely that intertidal sounds would act as a navigation cue. Sounds or chemical cues generated by either conspecifics or organisms living in soft sediments could act as a cue for navigation. However, this seems unlikely since both conspecifics and organisms living in soft sediments are common across the shelf and thus would not provide a directional cue. However, since this study was conducted over soft sediment bottoms where *C. magister* settle (L. K. Rasmuson unpubl. data) and was not designed to test orientation to bottom habitat features, we could not test this hypothesis.

In a previous study in the enclosed inland waters of Puget Sound, congeneric species (*Cancer oregonensis* and *Cancer gracilis*) swam in the direction of the sun's bearing (Shanks 1995b). *C. magister* swam in the direction of the surface current on all 3 observation days, and on 1 of these 3 days (17 June 2013), this happened to be also similar to the direction of the sun. However, even on that day, swimming direction was more similar to the direction of the surface current ($p < 0.001$) than the direction of the sun's bearing ($p < 0.05$). Studies on *C. magister* (other congeners not as well studied) have clearly demonstrated biological differences between enclosed inland and open ocean populations (reviewed in Rasmuson 2013). For example, *C. magister* larvae from Puget Sound are smaller than open ocean larvae and adults in Puget Sound more frequently utilize intertidal habitats (reviewed in Rasmuson 2013). In a different species, *Pachygrapsus crassipes*, a recent comparative study of vertical migration from enclosed estuarine and open ocean populations suggests that estuarine populations vertically migrate while oceanic populations do not (Miller & Morgan 2013). Thus, it is possible that the observed differences between congeneric species arose from biological differences between populations that inhabit enclosed inland waters and those in the open ocean. Regardless of whether the differences (sun versus surface current orientation) were due to the study being conducted in enclosed inland waters or due to species differences, megalopae of other Cancridae genera did not swim towards the east and thus likely do not swim ashore.

The behavior we observed for *C. magister* was identical to that reported for *P. crassipes* and *Lophopanopeus bellus bellus* megalopae (Shanks 1995b); megalopae swam at the ocean's surface and oriented their swimming with the direction of the surface current. In the current study, megalopae did not appear to orient their swimming when no surface current was observed, suggesting that megalopae orient their swimming direction relative to surface currents; though more data are needed.

The average in situ swimming speed we measured (9.8 cm s^{-1} after correction for current speed) is intermediate between previously reported swimming speeds: 4.2 (Jacoby 1982) or 8.5 cm s^{-1} (Fernandez et al. 1994) in still water and 44.7 cm s^{-1} in a flume with a strong current (Fernandez et al. 1994). The slowest current speed tested by Fernandez et al. (1994) was 14 cm s^{-1}, whereas the current speeds we observed were ~1.5 cm s^{-1}. The results from these 2 studies suggest that the megalopae of *C. magister* alter their swimming speed and may do so relative to local current speed.

Daily abundance at the coast of *C. magister* megalopae varies with a fortnightly periodicity that is out of phase with the spring neap tidal cycle and is highly pulsed (Johnson & Shanks 2002, Roegner et al. 2007). Fortnightly periodicity in recruitment is considered indicative of cross-shelf transport by internal waves (Shanks 1986, 2006, Pineda 1991). This recruitment pattern is not considered indicative of selective tidal stream transport, because the level of recruitment would be directly proportional to the size of the tidal prism, and thus recruitment would be in phase with and proportional to the spring neap cycle (Shanks 2002). Furthermore, concentrated patches of *C. magister* megalopae have been observed in surface convergences, some of which were internal waves (Shenker 1988, L. K. Rasmuson & A. L. Shanks pers. obs.).

Transport by internal waves occurs when the speed of the surface current over the internal wave is greater than the propagation speed of the wave. Reported horizontal current velocities over internal waves are highly variable (centimeters to meters per second; Jackson 2004). An organism swimming in the direction of the surface current would increase their speed relative to the propagation speed of the wave and thus increase the possibility of being trans- ported by a wave. Megalopae of *L. bellus bellus* were observed swimming in the convergence over an internal wave and in the direction the internal wave was propagating (Shanks 1995b). Given the behavior of *C. magister* megalopae, e.g. swimming in the direction of the surface current, it is likely that if megalopae were exposed to flow over an internal wave they would swim with the wave (Shanks 1995b).

Over 24 d, none of the observed internal waves would have caused 'shelf-transport' (distances > 25 km) for passive particles (Fig. 4.4). Calculations suggest, however, that for organisms that swim in the direction of wave propagation, many of the internal waves would cause 'shelf-transport'. At swimming speeds of 10 cm s^{-1}, all 69 waves would have been 'shelf-transporting', so that 'shelf-transport' would have occurred daily. Thus, the behaviors exhibited by *C. magister* may dramatically increase the possibility of being transported shoreward by internal waves. We did observe 24 internal bores in our temperature record, and some of these may have caused 'shelf-transport' for passive particles, but lack of suitable models prevented us from calculating transport potential (Pineda 1991, Helfrich & Pineda 2003).

Previous studies have demonstrated that only some waves transport megalopae (Shanks 1983, 1988, Shanks & Wright 1987). However, our data suggest that *C. magister* megalopae would have been transported by all of the waves we observed. This is inconsistent with work showing that recruitment of *C. magister* megalopae is pulsed (values can change by more than 3 orders of magnitude fortnightly; Shanks 2013). Our mooring was deployed where the water column depth was only 30 m. The waves we observed likely had been slowed by friction on the bottom in shallow water and thus were travelling at speeds that larvae could more easily match. Thus it is possible that the greater variability of internal wave speeds and amplitude in deeper waters would decrease the number of waves that could potentially transport megalopae significant distances. For this hypothesis to be tested, daily recruitment of megalopae should be associated with high frequency measurements of internal waves at different sites across the continental shelf to determine the characteristics of a transporting internal wave.

Our study indicates that *C. magister* megalopae swim in the direction of a surface current and swim at speeds of ~10 cm s^{-1}. Transport by internal waves occurs if the speed of the surface current over the wave is greater than the speed of the wave. As an increasing number of studies examine larval behavior in situ it is essential to understand how these findings influence how larvae migrate back to settle. We have demonstrated that larval behavior greatly increases transport by internal waves, and since internal tides, and thus waves, are ubiquitous around the world, future work will likely demonstrate that larvae of many species are transported by internal waves.

4.5. BRIDGE TO CHAPTER V

In chapter IV we conducted *in situ* observations of Dungeness crab megalopae and demonstrated that megalopae swim with the surface current and swim at speeds of ~10 cm s^{-1}. We deployed a thermistor mooring where we observed 69 internal waves. We used the data from these observed internal waves and calculated potential transport distance for passive particles and particles that exhibited the behavior we observed for Dungeness crab megalopae. We demonstrate that the behavior exhibited by Dungeness megalopae dramatically increases the potential distance internal waves could transport larvae. The results also suggest that all internal waves would transport larvae, which is not supported by other studies. Thus in chapter V we use time series analyses to better understand variability in possible transport by the internal tide.

CHAPTER V

DAILY, SEASONAL AND DECADAL VARIATIONS IN TRANSPORT BY THE INTERNAL TIDE

This chapter is under review in the journal *Journal of Marine Research* and is co-authored by Alan Shanks. Alan Shanks maintained the light trap and provided the samples used to validate the model. I conducted all of the analyses and did all of the initial writing.

5.1. INTRODUCTION

Understanding the mechanism(s) employed by larvae to migrate across the continental shelf in order to settle in a suitable habitat continues to be an important question in marine ecology (Shanks, 1995a). The migration is influenced by many factors such as the type of larva released (Chia et al., 1984) and both where and when the larva is released (Morgan, 1995; Sinclair, 1988). In many situations, evidence suggests migration is a synergistic effect of larval behavior and hydrodynamics (Metaxas, 2001). Larval swimming is often posited as the behavior that influences the migration of larvae (Metaxas, 2001). Numerous hydrodynamic processes have been proposed to transport larvae (Queiroga and Blanton 2004; Shanks, 1995a). One such mechanism is transport by the internal tide (either by bores or waves).

The word "tide" in marine ecology is often used to refer to the barotropic tide, i.e., flow which is approximately along isopycnals (Laurent et al., 2012). The barotropic tide causes the high and low tides observed in the nearshore. The barotropic tide interacts with ocean stratification and bathymetry to generate the baroclinic or internal tide. Baroclinic flow can occur across isopycnals (Laurent et al., 2012). The baroclinic tide creates the features commonly referred to as tide rips (Jackson, 2004). Since the barotropic tide generates the internal tide, both exhibit a fortnightly periodicity, however, complex interactions between the barotropic tide and both ocean stratification and topographic features often cause the barotropic and baroclinic tides to be out of phase with one another.

In the coastal ocean the most common way the barotropic tide generates the baroclinic tide is a process known as lee wave generation (Laurent et al., 2012). As the barotropic tide ebbs off the continental shelf, the pycnocline is depressed generating a lee wave over the continental slope. When the barotropic tide reverses the lee wave can be reflected offshore or move onto and across the continental shelf. The lee wave (internal tide) can move across the continental shelf as different types of waves and/or bores (Vlasenko et al., 2005). The internal tide can manifest as both linear and nonlinear waves but only nonlinear waves are capable of transporting mass (Jackson, 2004).

Solitons (nonlinear solitary waves) move across the continental shelf as packets of rank ordered waves (Jackson, 2004). Waves can manifest as either waves of elevation, the pycnocline within the wave is shallower than the average pycnocline depth, or waves of depression, the pycnocline within the wave is deeper than the average pycnocline depth (Fig. 5.1A & B). As waves move across the continental shelf they can interact with either the surface of the water or the seafloor causing them to flip vertically in the water column (Fig. 5.1C). For example, consider a wave of depression propagating across the continental shelf. As the shelf shallows the wave begins to interact with the bottom causing it to flip and become a wave of elevation (Fig. 5.1C). Regardless if the wave is a wave of elevation or depression, the flow around a wave can generate a convergence, which concentrates oils producing a surface slick and, under the right conditions, flotsam and larvae (Osborne and Burch 1980). Shanks (1988)collected neuston samples in front of and within the surface slicks of internal waves and demonstrated that megalopae and a variety of meroplankters were concentrated and transported within the slicks and surface convergence. This work was further corroborated in different parts of the world (Criales et al., 2007; Kingsford and Choat, 1986; Shanks and Wright, 1987; Weidberg et al., 2014). Lamb (1997) modeled the transport of larvae by solitary waves demonstrating that larvae can be transported substantial distances and that the presence of larval behavior greatly increases the transport distance. *In situ* observations indicate some larvae swim rapidly in the direction of surface currents, which, if they did this in the flow over an internal wave, would dramatically increase the distance an internal wave would transport them (Rasmuson and Shanks, 2014; Shanks, 1995b).

In addition to solitary waves, the internal tide can manifest as internal bores (internal hydraulic jumps) (Simpson, 1999). Similar to solitons, internal bores can manifest as either bores of elevation or depression. Internal bores associated with the internal tide are generated on the continental slope or shelf. On the continental slope, if the quotient of bathymetric slope and internal wave slope is > 1 (super critical) then the lee wave will manifest as an internal bore. As waves move across the continental shelf, water column depth decreases, which can increase shear forces in the wave (Jackson et al., 2012). If the Richardson number decreases to < 0.25, shear forces cause the wave to break. This can occur if the current speed above the wave is greater than the phase speed

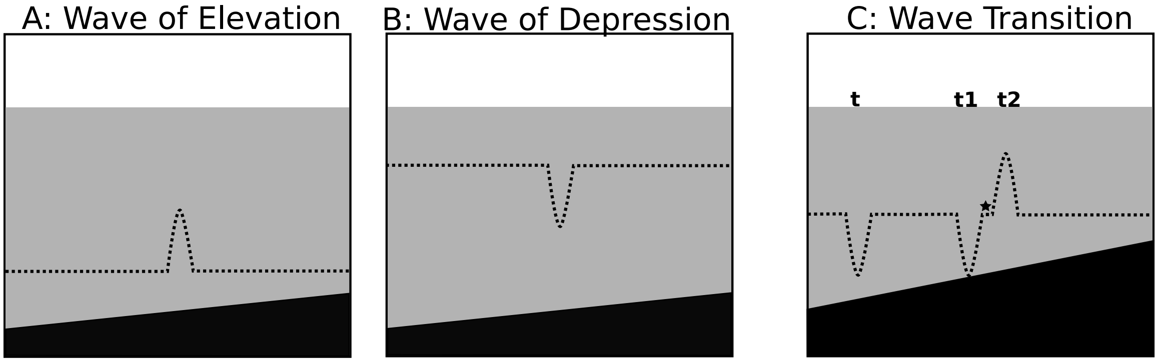


Fig. 5.1. Two layer model of internal wave shape and transition. When the pycnocline is deep relative to water column depth, waves often manifest as waves of elevation (A). When the pycnocline is shallow relative to water column depth, waves often manifest as waves of depression (B). As waves move across the shelf if they interact with either the surface or bottom they can flip (C). For example, at time **t** the wave is a wave of depression and is not interacting with the bottom. As it moves across the shelf it interacts with the bottom at time **t1** causing it to change (denoted by the star) into a wave of elevation at time **t2**. This process is not restricted to waves of depression. E.g. waves of elevation can also transition to a wave of depression if they begin to interact with the surface.

of the wave (Simpson, 1999). Internal bores can manifest as a single bore (often with trailing solitary waves) or as a packet of solibores (multiple solitary bores). Pineda (1994) hypothesized that larvae located at depth can be transported within an internal bore. It should be noted that in the literature bores and solitons are discussed separately, however, observations often show internal bores being trailed by a packet of solitons (Winant, 1974).

Despite the important role the internal tide plays in transporting larvae, there have been relatively few studies that have attempted to define the characteristics of transporting waves/bores (Criales et al., 2007; Pineda, 1999; Shanks, 1995b). However, evidence suggests only certain waves are capable of transporting larvae (Shanks, 1983; Shanks and Wright 1987; Shanks, 1988). For example, Shanks and Wright (1987) demonstrated that surface drifters were only transported by some waves (others passed by the drifters). Further evidence that only certain waves transport larvae is evident in many studies, which have correlated measures of recruitment with hydrodynamic indices in order to determine transport mechanisms (Mace and Morgan, 2006; Pineda and Lopez, 2002; Shanks, 2009). Recruitment in these studies often exhibits a fortnightly periodicity, which varies by multiple orders of magnitude between days. Internal waves are always present since they are generated by the barotropic tide, yet studies report recruitment events only occurring at certain times of the month suggesting that at these time conditions are right for the production of transporting internal waves.

In addition to the large between day variations in recruitment rate, many species exhibit dramatic intra-annual variation in recruitment as well (Clark et al., 1999; Zheng & Kruse, 2006). In recent years large multiyear cycles and oscillations have been reported in many of the worlds oceans (Hurrell, 1995; Mantua and Hare, 2002) and these oscillations have been shown to profoundly influence the total number of annual recruits to certain populations (Brander and Mohn, 2004; Clark et al., 1999; Mantua et al., 1997). Although these oscillations have profound impacts on the number of recruits, we do not know of any time series that have been maintained for enough years with the necessary temporal resolution to understand the influence of climactic variability on transport by internal waves.

The California Current is the predominant ocean current along the continental shelf off the West Coast of the United States and is characterized as a monsoonal upwelling system (reviewed in Hickey, 1979). On a decadal time scale the Pacific Decadal Oscillation (PDO) manifests as a warm or cold sea surface temperature anomaly in the North Pacific (Mantua and Hare, 2002). It impacts flow in the California Current by shunting more water from the West Wind Drift into the California Current during cold phase PDO's (Minobe and Mantua, 1999). On an annual scale, during winter months winds are from the south generating a poleward inshore current (Davidson Current) and conditions are downwelling favorable (Strub et al., 1987). During the spring the winds shift to coming from the north; an event known as the spring transition (Huyer et al., 1979). These wind from the north during spring and summer winds are often upwelling favorable. In addition to a change in wind direction, following the spring transition the Davidson Current disappears and the California Current flows southward on the continental shelf (Hickey, 1979).

The internal tide on the Oregon coast (within the California Current) has been studied extensively (Jackson, 2004). The characteristics of the internal tide off of Oregon is strongly seasonal due to weak winter and strong summer stratification (Erofeeva, 2003). Further, the thermocline depth is often deeper during winter months, leading to more waves of elevation and shallower during the summer, leading to more waves of depression (Moum et al., 2007b). Although the ocean is more stratified during summer months than winter months, upwelling influences stratification by decreasing stratification during upwelling conditions and the ocean becoming more stratified during relaxation conditions (Hayes and Halpern, 1976; Kurapov et al., 2010). Work in the nearshore environment has demonstrated that internal waves generated by the internal tide are observed in the nearshore environment suggesting they are capable of moving across the continental shelf (Apel et al., 1975; Klymak, 2003; Lucas et al., 2011). Despite the large amount of work done on the physical characteristics of the internal tide off Oregon, there have been no *in situ* studies on the transport of larvae.

The dispersal of Dungeness crab, *Cancer magister*, larvae has been studied extensively (reviewed in Rasmuson, 2013). In the California Current, larvae are released in the nearshore during winter months and migrate across and off the continental shelf. Following the spring transition, megalopae begin recruiting back to the nearshore. Using a daily catch time series of Dungeness crab megalopae, Roegner et al. (2007) demonstrated that catch of megalopae was significantly cross-correlated with the daily maximum tidal range. The cross-correlation, however, was out of phase with the spring neap cycle, which is considered indicative of transport by the baroclinic rather than barotropic tide. This is not considered indicative of transport by the barotropic tide because catch would be 1) in phase with the spring neap cycle and 2) proportional to the magnitude of the tide.

In the years since Roegner et al. (2007) was published, Shanks (2013) has continued to monitor daily catch of megalopae and has shown that total annual catch has increased by two orders of magnitude since 2007. He demonstrated that these patterns correlate with the phase of the PDO and attributes the increase in the catch of megalopae to a greater retention of larvae in the California Current during negative phase PDOs. Further, annual catch is greater when the day of the spring transition is earlier and there are more upwelling favorable conditions following the spring transition. No work has assessed whether the cross-correlation between the daily maximum tidal amplitude and daily catch has persisted despite the phase change of the PDO.

We tested whether the daily catch of *Cancer magister* megalopae in the years following the initial study were still significantly cross-correlated with the daily maximum amplitude tide. We reanalyzed the data of Roegner et al. (2007) so that variation was attributable to differences between years rather than statistical technique. Secondly, we used data from a mooring deployed off of Coos Bay from 2000-2004 and generalized additive models (GAMs) to associate catch of megalopae with different hydrodynamic factors known to influence the internal tide.

5.2. MATERIALS AND METHODS

5.2.1. Megalopae Settlement

For 12 years (1998-2001 & 2006-2013), daily samples of *Cancer magister* megalopae were captured using a light trap in the Charleston, Oregon Marina (43° 20’ 40.75” N, 124° 19’ 15.02” W) (Roegner et al., 2007; Shanks and Roegner, 2007). From 1998-2001 samples were collected for the entire calendar year, while from 2006-2013 samples were collected during the peak return season (~April 1 – September 30). Samples were preserved in buffered formalin and enumerated using a dissecting microscope. When the number of megalopae in a daily sample exceeded 2000 individuals, the number of megalopae was determined by mass (Shanks et al., 2010). These samples were used to create 12 time series of the daily abundance of megalopae. These time series were analyzed first using standard time series techniques and then the time series from 2000 and 2001 were analyzed using GAMs.

5.2.2. Standard Time Series Analysis

5.2.2.1. Physical Data

For each year the light trap was operated, we generated five time series of physical variables (lunar phase, daily maximum amplitude tidal range, sea surface temperature, and alongshore and cross-shelf wind stress). Daily lunar phase was obtained from the US Navy (http://aa.usno.navy.mil/data/docs/MoonPhase.php). Daily lunar phase is defined as the percent of the moon that is illuminated each day. Daily maximum tidal range and means of surface temperature were obtained from the NOAA station located on the US Coast Guard pier in the Charleston Marina (http://www.ndbc.noaa.gov/station_page.php?station=chao3). The sea surface temperature record in Coos Bay was the only continuous sea surface temperature record available. Daily maximum tidal range was calculated as the difference between the two high tides each day and the subsequent lows. We then took the maxima of these two values as the daily maximum. Hourly wind speed and direction was obtained from the NOAA Cape Arago weather station (NDBC-CARO3) and converted into daily means of alongshore and cross-shelf wind stress (http://www.ndbc.noaa.gov/station_page.php?station=caro3). The station was shutdown in 2012 and thus wind stress was not calculated for 2013. The wind stress should be thought of as a pseudo wind stress because constant values for the coefficient of drag (0.002) and air density (1.18 kg m^{-3}) were used (Cushman-Roisin and Beckers, 2011). The coast near Coos Bay is oriented approximately north south and thus wind stress components were not rotated on their principal axes.

5.2.2.2. Statistical Analysis

Temporal associations between biological and physical variables were examined using standard time series techniques (Emery and Thomson, 1997). Prior to analysis, biological data were $\log_{10}$ transformed. Both physical and biological data were plotted to ensure they were stationary. If data were not stationary they were made stationary using the “detrend” function in Matlab. A periodogram of each individual biological and physical time series was generated to look for peaks in the data. The physical and biological data were compared to each other using cross-correlations and cross-Fourier analysis. Since organisms respond to their environment, physical variables were held stationary and biological variables were lagged. Since lunar and tidal cycles are periodic and an animal could "predict" events positive lags were examined for these two variables. Since wind stress and sea surface temperature could not be "predicted" by animals only negative lags are considered.

In the initial analysis, both the biological and temperature data had a strong fortnightly periodicity and therefore a strong cross-correlation with daily maximum amplitude tidal range. To determine if variables other than the daily maximum amplitude tidal range had a significant cross-correlation with daily catch of megalopae, the fortnightly periodicity was filtered out of the biological and temperature record by removing first 16 d and then a 4 d running mean. Following filtering, new cross-correlations and cross-Fourier analyses were conducted for all physical variables except for daily maximum tidal range. As above, physical variables were held stationary and biological variables were lagged.

5.2.3. GAM Time Series Analysis

5.2.3.1. Physical Data

From April 2000- September 2004 the GLOBEC project had a mooring deployed in 100 m of water off Coos Bay (43° 09' 24.0" N, 124° 34' 06.0" W). Data from this mooring were used to associate factors known to influence the baroclinic tide with daily catch of megalopae. Temperature and salinity were recorded every 30 min using Seabird SBE 37's at 21, 35, and 95 meters above the bottom (mab). Temperature was recorded every 30 min using Vemco thermistors at 28, 50 and 80 mab. There were three current meters on the mooring: InterOcean S-4 current meter at 22 mab, Aanderaa RCM (model 4 or 5 depending on deployment time) at 65 mab and a Teledyne RD Instruments Workhorse Sentinel at 94 mab. Data from the current meters were recorded every 30 min in 2 m bins from 10 – 90 m.

We calculated of horizontal shear and stratification from the mooring since these variables are well known to influence the internal tide (Jackson 2004). Horizontal shear was calculated as

$$Shear = \left| \frac{(U_{10} + U_{12})}{2} - \frac{(U_{88} + U_{90})}{2} \right| \tag{5.1}$$

Where U_x is cross-shelf velocity and x denotes the depth bin the velocity was recorded. Additionally, the Brunt-Väisälä frequency, a measure of stratification, was calculated using

$$N^2 = -\frac{g}{\rho_0} * \frac{\partial \rho}{\partial z} \tag{5.2}$$

where g is the acceleration due to gravity, ρ is water density and z is depth. Density (ρ) was calculated using the Equation of State

$$\rho = \rho(T, S, p) \tag{5.3}$$

using the GSW toolbox in Matlab (McDougall & Barker 2011). Where T is temperature, S is salinity and p is pressure. Salinity measurements were interpolated linearly for each SBE 37 to the closest Vemco thermistor. The Brunt-väisälä frequency was then calculated for each pair of depths (21→28, 28→35, 35→50 etc.)

$$\bar{N} = \left(\sum_{21\to 28}^{80\to 95} N \right) * \left(\frac{1}{4} \right) \tag{5.4}$$

and then converted into a depth-averaged measure of stratification. Mooring data were band-pass filtered with a 4th order Butterworth filter with cutoffs of 6 and 30 hr to remove the barotropic tide and decimated to a single value per day.

Ideally we would have liked to include a measurement of thermocline depth from the mooring, however, the lack of temperature data above 21 m made it impossible to exactly calculate the depth of the thermocline. Therefore, we used data from the 14 km resolution sea surface temperature (SST14A) NOAA Comprehensive Large Array-Data Stewardship System (CLASS) satellite to obtain a value of Sea Surface Temperature (SST) (http://www.class.ngdc.noaa.gov/saa/products/search?sub_id=0&datatype_family=SST14NA&submit.x=24&submit.y=6). A grid cell that encompassed the mooring was obtained for each 48 hr period. Due to the nature of time series analyses, we need a measure of SST for each day. Therefore we used a linear interpolation to convert SST data into a daily value. Using temperature data from the satellite and each thermistor (21, 35, 50, 80 and 95 m), we interpolated the data onto a 2 m vertical grid. Using this gridded data we calculated the rate of change in temperature over depth. The region with the greatest rate of change was subsequently classified as the region of the thermocline. Using these same data, thermocline strength was calculated as the rate of change of temperature over depth. Thermocline strength was used as an index for the amount of mixing: strong thermocline corresponds with little mixing.

Measures of daily of maximum amplitude tidal range as well as cross and alongshore wind stress were included in the model. Data were the same as those used for the standard time series (See section 5.2.2.1.).

5.2.3.2. Statistical Analysis

Standard time series techniques only allow the researcher to determine if there is a temporal correlation between two variables and do not quantify the effect of the explanatory variable on the response variable. We used GAMs to examine the temporal variations and effect of specific physical variables on the daily catch of megalopae. GAMs are a nonparametric extension of generalized linear models (GLM) which allow researchers to model complex relationships between variables (Guisan et al., 2002). GAM construction followed the equation

$$RV = g^{-1}\left(\beta_o + \sum_k S_k\left(x_k\right)\right) \tag{5.5}$$

where RV is the response variable that is modeled for one (denoted x) of k explanatory variables. g represents the link function, β_0 is the intercept and S_k denotes the smoothing function assigned to each explanatory variable. Due to the pulsed nature of catch, the data had a large number of zeros and were modeled using a negative binomial distribution. Models were run using the mgcv package in R (Hastie and Tibshirani 1990; Wood, 2006). Possible collinearity between explanatory variables were examined using a Spearman ranked correlation coefficient. No explanatory variables were significantly (>0.5) correlated with one another.

Our goal was to examine the influence of explanatory variables on the daily catch of megalopae at different temporal lags. Only data collected during the season when megalopae returns were included in the models (i.e., April 19 – Sept 30, 2000 & 2001). Eight data sets were generated by manual lagging (one day increments) the biological data relative to the physical data. Thus, we had a dataset for 0 d lag, 1 d lag, 2 d lag etc. to 7 d. As above, the biological data was lagged relative to the physical data. Each time lag was compared to the other time lags using the Aikake Information Criterion (AIC). We assumed that models with lower AIC values represent models with a better fit. AIC is influenced by the sample size (n), thus in order to compare the different time lags we had to maintain an equal n between time lags. Therefore, when generating new time lags the leading value of the physical data set was removed for each dataset and a new value of the physical variable added to the end of the dataset to ensure that n=330 for all time lags.

For each lag, initially a model containing all explanatory variables was analyzed. A complete model consisted of six smoothed continuous variables: horizontal shear, Brunt-Väisälä frequency, daily maximum amplitude tide, thermocline strength, cross-shelf (U) and alongshore (V) wind stress and two categorical factors: month and thermocline depth. No interactions were included in the model for simplicity. Non-significant variables were subsequently dropped until all variables were significant. During the two years where the mooring was deployed and we monitored megalopae catch, thermocline depth only exceeded 35 m on one day and therefore thermocline depth was defined as 0-21 m or >21 m. Month was included in the model structure as a way of addressing potential seasonal effects such as a decrease in daily catch over the course of the catch season. For each model structure, the model was run with and without a correction for autocorrelations (Zuur et al., 2007; Zuur, 2009). In the event a model with an autocorrelation had a lower AIC this model would have been chosen as the better model, however, this did not occur.

5.2.4. Seasonal Thermocline Variation

In order to quantify changes in the depth of the thermocline preceding and following the spring transition, daily thermocline depth was determined from the 4 years

(2000-2004) of GLOBEC mooring (and satellite SST) data (see section 5.2.3.1. for methods). Thermocline depth data were divided into two groups: summer and winter. Summer was classified as the day of the spring transition until the day of the fall transition and winter was defined as the day of the fall transition to the day of the spring transition. Dates of the spring and fall transition were obtained from (http://damp.coas.oregonstate.edu/windstress/).

5.3. RESULTS

5.3.1. Megalopae Settlement

Total catch of *Cancer magister* during 1998-2001 and 2006 was much lower than from 2007-2013, which Shanks (2013) attributes to a phase shift in the PDO (Fig. 5.2). In general, settlement began in April and persisted through the summer with average daily catch declining from late August through September (Fig. 5.2). However, this pattern did not hold for all years, such as 2008 and 2010 when catch effectively ceased at the end of July (Fig. 5.2). Catch was strongly pulsed, changing by as much as three orders of magnitude between days. The power spectral density of *C. magister* catch each year had significant peaks at ~17-19 d, except 1999 where the largest peak occurred at 11 d (Fig. 5.3). Secondary peaks at ~10 d were observed in some but not all of the power spectral density plots (Fig. 5.3).

5.3.2. Standard Time Series Analysis

Plots of some of the physical data (lunar phase, sea surface temperature, and alongshore and cross-shelf windstress) used as correlates for the standard time series are presented in Appendix D. Daily maximum tidal range is presented as a secondary axis with daily catch of megalopae (Fig. 5.2). Catch of *Cancer magister* was significantly

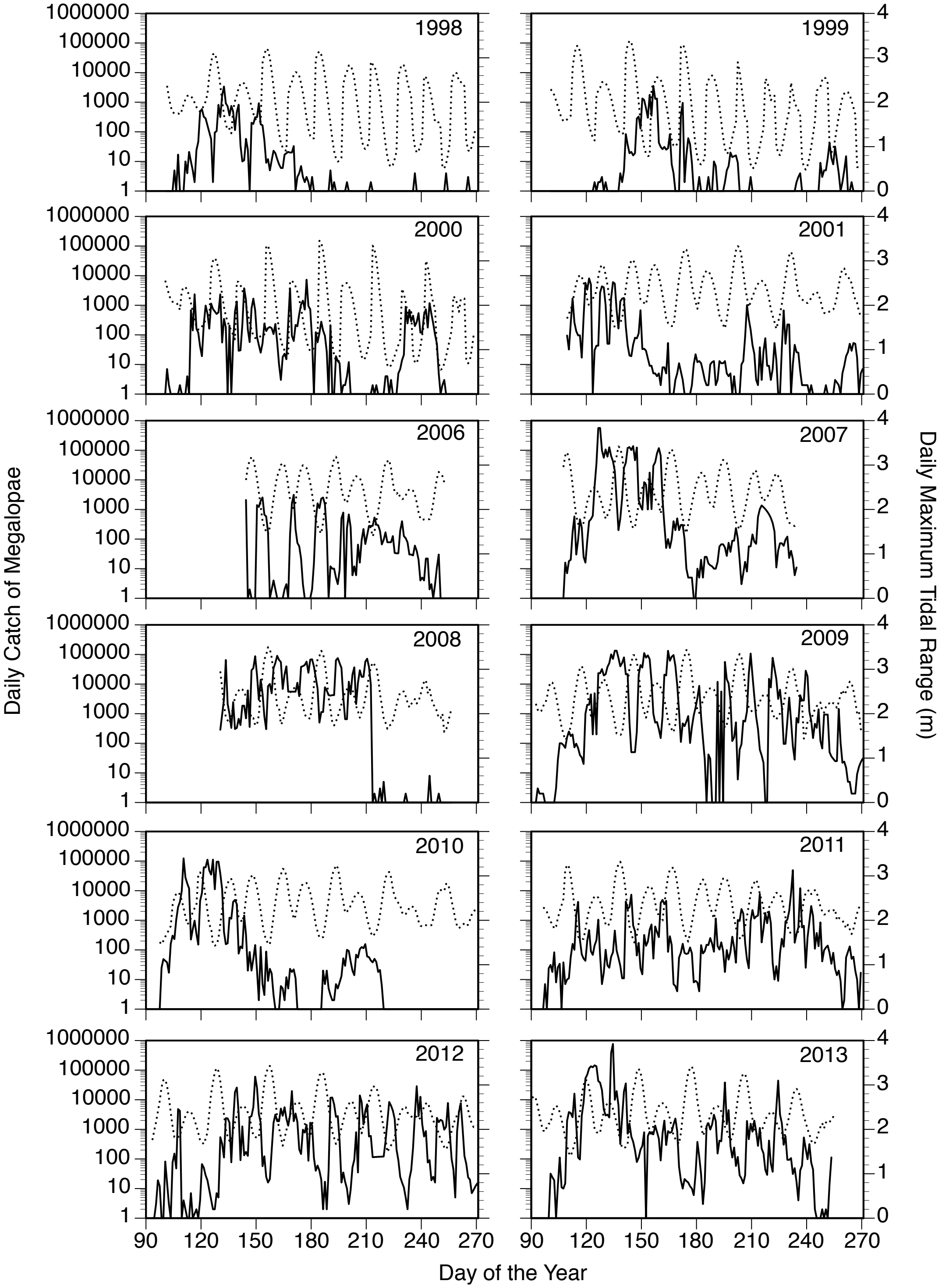


Fig. 5.2. Daily catch of *Cancer magister* megalopae (solid line) to a light trap in Charleston, Oregon for 12 years plotted with the daily maximum amplitude tidal range (dotted line). Catch during the first five years (1998-2006) was significantly lower than during the following seven years (2007-2013). In all years, catch was pulsed changing by multiple orders of magnitude in a single night; considered indicative of cross-shelf transport by internal tides.

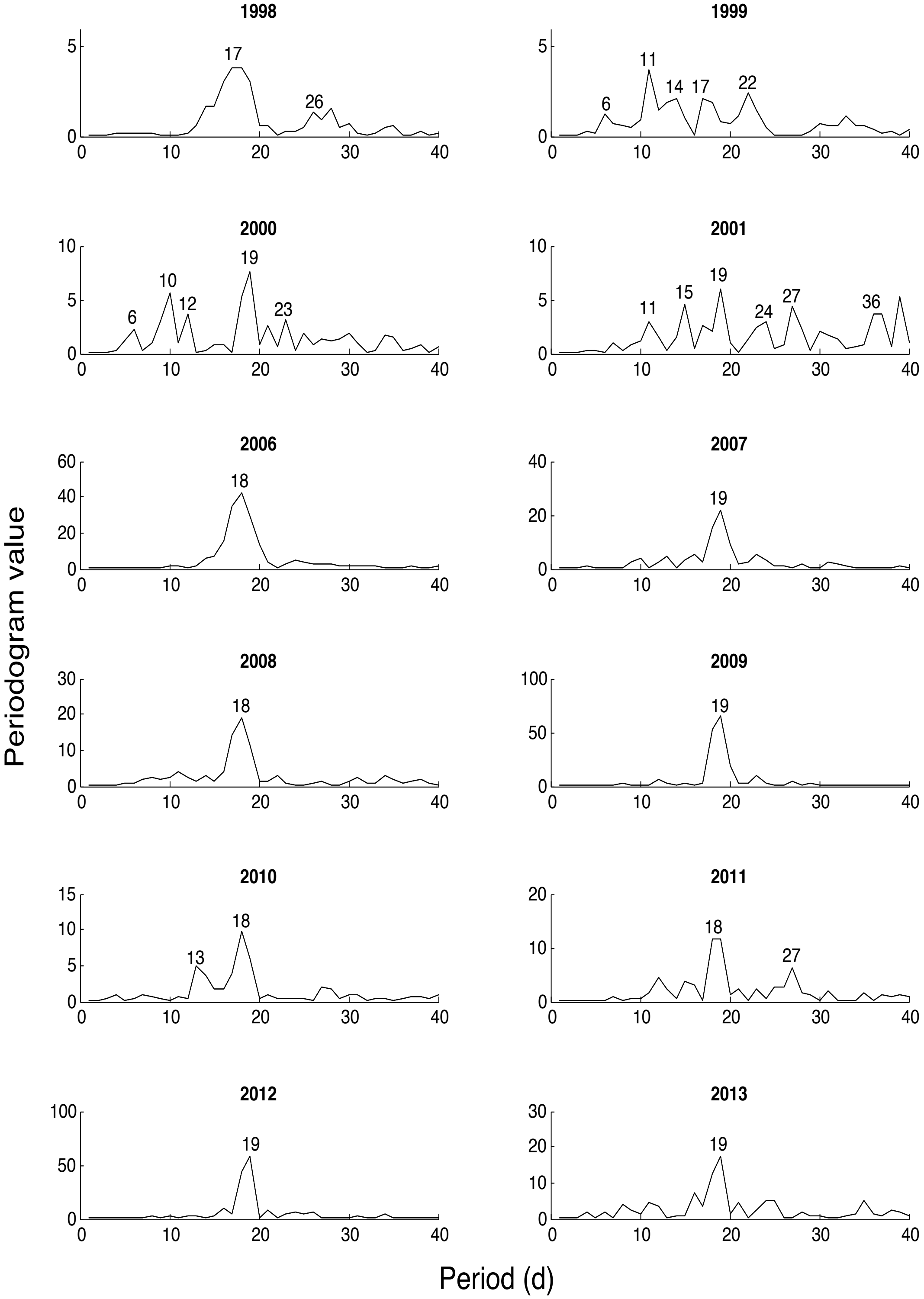


Fig. 5.3. Power spectral density of $\log_{10}$ daily catch of *Cancer magister* megalopae. Seasonal trends have been removed to ensure data are stationary. Numbers over peaks denote period of significant peaks.

cross-correlated with the daily maximum tidal range each year (Table 5.1). The most consistent cross-correlations were at lags of -7, -1, 0, 6 and 7 d (Table 5.1). The most significant cross-correlations were often out of phase with the spring neap cycle (Table 5.1). Catch was cross-correlated with the lunar cycle, alongshore wind stress, cross-shelf wind stress and bay SST in certain years but no consistent trends occurred across all years (Tables 5.1 & 5.2). After filtering out the fortnightly periodicity in the catch there were no consistent cross-correlations between lunar cycle, alongshore wind stress, cross-shelf wind stress or bay SST with catch (Table D1). Cross-Fourier Analysis of catch and daily maximum tidal range had significant peaks at ~19 d for each year (Fig. 5.4). The squared coherence of these peaks (can be thought of similar to an R^2 value) ranged from 0.266-0.761 with a mean of 0.519 (Fig. 5.4). Some years had secondary peaks around 7 d with an average squared coherence of 0.233.

5.3.3. GAM Time Series Analysis

Plots of raw physical data for the GAM time series are presented in the electronic supplement (Fig. D5). The inclusion of month as a factor was not significant for any model structure. The GAMs at lags of 0 and 7 d had the lowest AIC values; AIC values increased towards a time lag of 4 (Table 5.3). For each time lag, catch was higher when thermocline depth was > 21 m (Table 5.3, Fig. 5.5). Thermocline strength was the only continuous smoother that was significant for every time lag (Table 5.3). As thermocline strength increased daily catch decreased (Fig. 5.6). Horizontal shear was the second most common continuous variable in model structures (only insignificant in lags of 4 and 6 d) (Table 5.3). Catch declined as horizontal shear increased (Fig. 5.7).

Alongshore wind stress was significant for model structures with lags of 0, 4, and 5 d (Table 5.3). For lags of 4 and 5 d catch roughly increased as winds changed from coming from the south to coming from the north and further increased as velocity increased (Fig. 5.8). For a lag of 0 d, catch decreased as alongshore wind stress increased with more catch during greater velocity winds from the north (Fig. 5.8). Cross-shelf wind stress was significant for the model structure with a lag of 0 d (Table 5.3). There was a negligible effect for winds blowing to the west from -10 - 0 cm s^{-1} and a positive effect for winds towards the east blowing 0-10 cm s^{-1} (Fig. 5.9).

5.3.4. Seasonal Thermocline Variation

The thermocline depth was more variable during winter months (fall transition-spring transition) than during summer months (spring transition-fall transition) (Fig. 5.10). Thermocline depth during summer months was shallower on average than during winter months.

5.4. DISCUSSION

5.4.1. Daily Variation

Our findings corroborate the conclusions of Roegner et al. (2007); from 1998-2001 catch of *Cancer magister* megalopae was cross-correlated with the daily maximum amplitude tide and thus megalopae likely were transported across the continental shelf by the internal tide. Why does a significant cross-correlation between the daily maximum tidal range and the number of recruiting megalopae indicate transport by the baroclinic (internal) tide rather than the barotropic tide? For organisms being transported by barotropic tidal currents, the catch of megalopae would be directly proportional to the magnitude of the tide. However, the catch of *C. magister* often increased by multiple

Table 5.1. Cross-correlations between $\log_{10}$ transformed daily catch of *Cancer magister* megalopae and daily maximum tidal range and lunar cycle. Seasonal trends were removed from the biological and physical data to ensure data were stationary. Biological data was lagged relative to physical data. Correlation coefficients are only reported for significant cross correlations. Bold numbers denote the most significant positive and negative correlation for each year.

Daily Maximum Tidal Range

	-7	**-6**	**-5**	**-4**	**-3**	**-2**	**-1**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**
1998	0.29	**0.33**	0.27				-0.17	-0.25	**-0.27**	-0.21				0.16	0.22
1999	**-0.17**						0.20	**0.21**							
2000			-0.17				**0.17**	0.17						-0.19	**-0.26**
2001						-0.19	**-0.21**	-0.17				0.26	**0.32**	0.31	0.26
2006	0.35	0.26	0.13		-0.22	-0.37	-0.46	**-0.49**	-0.41	-0.26			0.33	0.46	**0.52**
2007	0.30			-0.21	-0.33	**-0.39**	-0.35	-0.23			0.32	0.46	**0.49**	0.42	0.28
2008	**0.55**	0.54	0.42	0.24			-0.30	-0.38	**-0.38**	-0.31				0.22	0.31
2009	**0.46**	0.37	0.21		-0.19	-0.36	-0.45	**-0.48**	-0.43	-0.30			0.27	0.38	0.42
2010	0.25			-0.26	-0.35	**-0.41**	-0.39	-0.32	-0.20			0.24	**0.30**	0.28	0.21
2011	**0.33**	0.22			-0.21	-0.31	-0.35	-0.34	-0.25			0.22	-0.32	**-0.38**	-.34
2012	0.44	0.38	0.24			-0.34	-0.48	**-0.53**	-0.49	-0.36	-0.16		0.30	0.47	**0.55**
2013	**0.37**	0.30	0.18		-0.16	-0.31	-0.41	**-0.44**	-0.40	-0.29			0.16	0.29	0.36

Lunar Cycle

	-7	**-6**	**-5**	**-4**	**-3**	**-2**	**-1**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**
1998															
1999															
2000	-0.40	-0.45	-0.48	**-0.48**	-0.47	-0.44	-0.39	-0.33	-0.25	-0.16				0.23	**0.31**
2001															
2006															
2007	0.20	**0.21**	0.20	0.19	0.17									-0.18	**-0.20**
2008	**-0.21**	-0.20										0.19	**0.21**	0.21	0.20
2009															
2010															
2011															
2012															
2013															

Table 5.2. Cross-correlations between $\log_{10}$ transformed daily catch of *Cancer magister* megalopae and Coos Bay sea surface temperature (Bay SST), alongshore and cross-shelf wind stress. Seasonal trends were removed from the biological and physical data to ensure data were stationary. Biological data was lagged relative to physical data. Correlation coefficients are only reported for significant cross correlations. Bold numbers denote the most significant positive and negative correlation for each year. ND denotes "No Data" because the weather station was taken offline.

Alongshore Wind

	-5	**-4**	**-3**	**-2**	**-1**	**0**
1998						
1999						
2000						
2001						
2006	**0.13**	0.11				
2007						
2008						
2009						
2010						
2011				**-0.17**		
2012						
2013	ND	ND	ND	ND	ND	ND

Cross-Shelf Wind

	-5	**-4**	**-3**	**-2**	**-1**	**0**
1998						
1999						
2000						
2001						
2006						
2007						
2008						
2009						
2010						
2011	**-0.16**	-0.14	-0.13	-0.13		
2012						
2013	ND	ND	ND	ND	ND	ND

Bay SST

	-5	**-4**	**-3**	**-2**	**-1**	**0**
1998						
1999	-0.20	-0.24	-0.22	-0.18	-0.23	**-0.26**
2000		-0.17	**0.18**		-0.23	**-0.24**
2001					-0.16	**-0.19**
2006					0.13	**0.16**
2007						
2008						
2009						
2010						
2011						
2012						
2013						**-0.26**

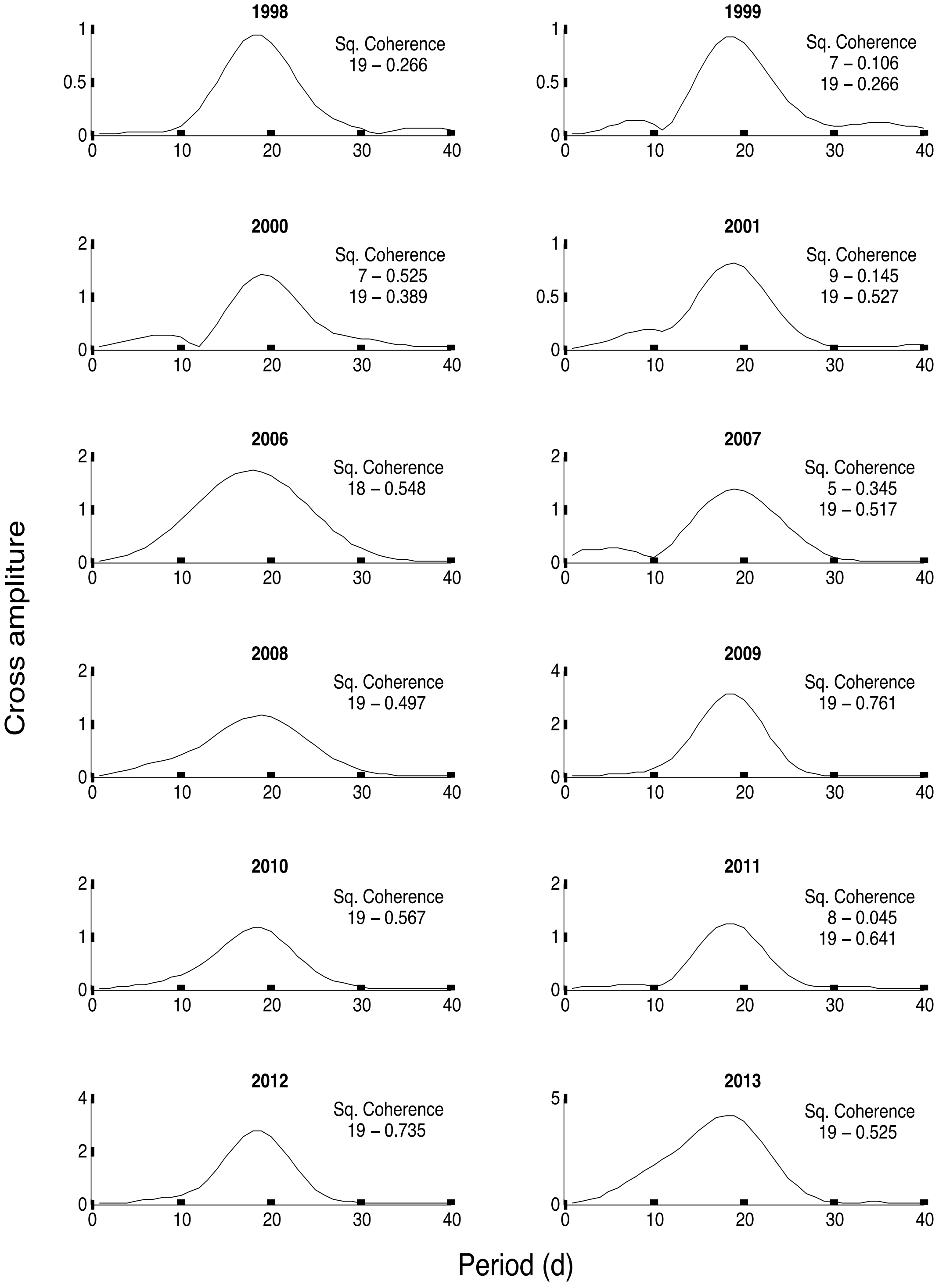


Fig. 5.4. Cross-spectral density between maximum daily tidal range and $\log_{10}$ daily catch of *Cancer magister* megalopae. Seasonal trends in catch have been removed to ensure data are stationary. Catch was lagged relative to daily maximum tidal range. Values in each plot denote the squared coherence (similar to an R^2 value) for the significant peaks.

Table 5.3. Generalized additive model structures describing daily catch of megalopae at eight time lags. Data were modeled using a negative binomial distribution due to the large number of days when no megalopae were caught. Parametric coefficients are for thermocline depth and month (not included in table due to non-significance), which are modeled as categorical variables. Horizontal shear, thermocline strength, Brunt-Väisälä frequency, daily maximum tidal range, alongshore and cross-shelf windstress were modeled as smoothed continuous variables. Brunt-Väisälä frequency and daily maximum tidal range are not included in table due to non-significance. The effective degrees of freedom (edf) estimates linearity of the model. % Dev: percent deviations; AIC: Aikake's information criterion; Rank denotes best model fit assuming a lower AIC indicates a better model fit.

Parameter	Estimate	SE	Z	p	Parameter	edf	F	p	Theta	R^2	% Dev	AIC	Rank
Lag 0									0.233	0.05	24.9	3158	1
Thermo(0-21)	4.59	0.14	32.75	<0.001	V	2.32	12.89	0.005					
Thermo(>21)	5.89	0.30	19.76	<0.001	U	1.00	13.38	<0.001					
					Shear	1.00	11.04	<0.001					
					Strength	4.82	25.69	<0.001					
Lag 1									0.218	0.01	19.1	3184	3
Thermo(0-21)	4.77	0.14	33.54	<0.001	Shear	1.00	20.03	<0.001					
Thermo(>21)	6.09	0.30	20.13	<0.001	Strength	3.46	17.97	<0.001					
Lag 2									0.202	0.02	14.7	3205	6
Thermo(0-21)	4.95	0.14	34.83	<0.001	Shear	1.00	17.39	<0.001					
Thermo(>21)	6.51	0.29	22.77	<0.001	Strength	1.00	13.00	<0.001					
Lag 3									0.211	-0.15	16.6	3229	8
Thermo(0-21)	4.86	0.14	34.59	<0.001	Shear	4.94	29.47	<0.001					
Thermo(>21)	6.46	0.30	21.77	<0.001	Strength	1.74	9.66	0.01					
Lag 4									0.205	-0.18	14.9	3211	7
Thermo(0-21)	4.87	0.14	33.79	<0.001	V	5.30	20.76	0.001					
Thermo(>21)	6.46	0.32	20.15	<0.001	Strength	2.31	20.57	<0.001					
Lag 5									0.215	-0.26	18.9	3194	5
Thermo(0-21)	4.77	0.14	33.7	<0.001	V	6.17	18.80	0.008					
Thermo(>21)	6.14	0.33	18.67	<0.001	Shear	5.46	16.48	0.02					
					Strength	4.52	28.54	<0.001					
Lag 6									0.207	0.08	16.3	3193	4
Thermo(0-21)	4.88	0.14	34.46	<0.001	Strength	4.74	26.10	<0.001					
Thermo(>21)	6.34	0.33	19.49	<0.001									
Lag 7									0.213	0.01	19.0	3183	2
Thermo(0-21)	4.77	0.13	34.50	<0.001	Shear	1.00	8.50	0.003					
Thermo(>21)	6.41	0.32	19.95	<0.001	Strength	4.11	29.63	<0.001					

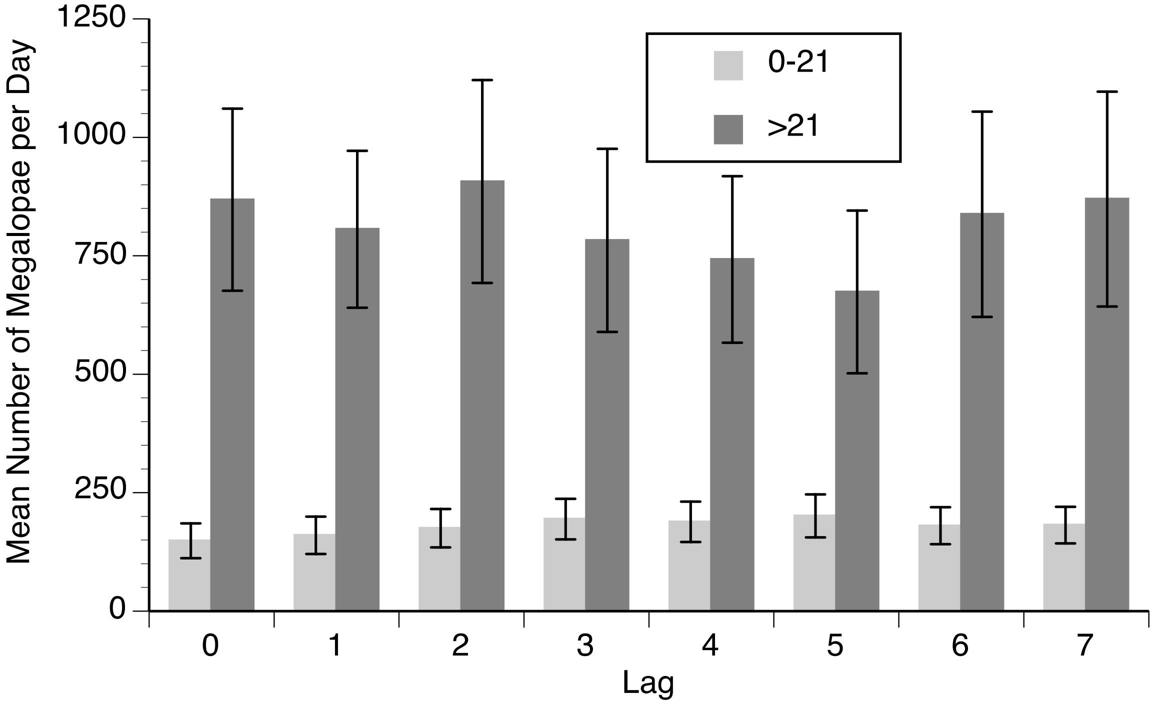


Fig. 5.5. Average daily megalopae catch for 2000 and 2001 by thermocline depth and time lag. During 2000 and 2001 on only one occasion was the thermocline depth >35 m and thus values categorized as >21 m denote a thermocline depth range from 21-35 m for 329 of 330 d. See text for an explanation of how thermocline depth was calculated. Error bars denote a 95% confidence interval.

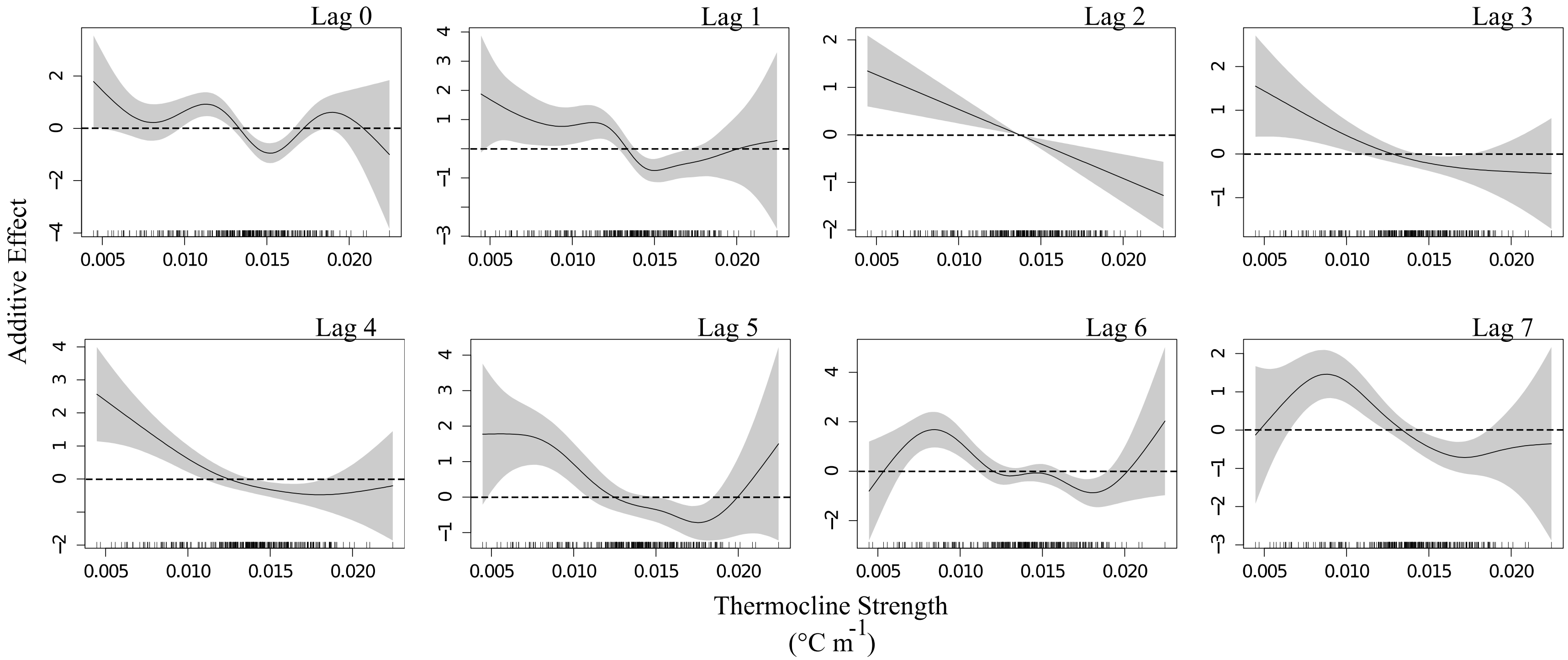


Fig. 5.6. Additive effect of thermocline strength on daily catch of *Cancer magister* megalopae at eight time lags. The black line within each shaded gray areas (95% CI) is the smoothed response for each lag. The horizontal dashed line denotes where y=0. This can be roughly interpreted as the mean of the response variable for the explanatory variable at each lag. Responses above this line indicate a positive influence on the mean and values below this line indicate a negative effect on the mean. Ticks on the horizontal axis locations of data points.

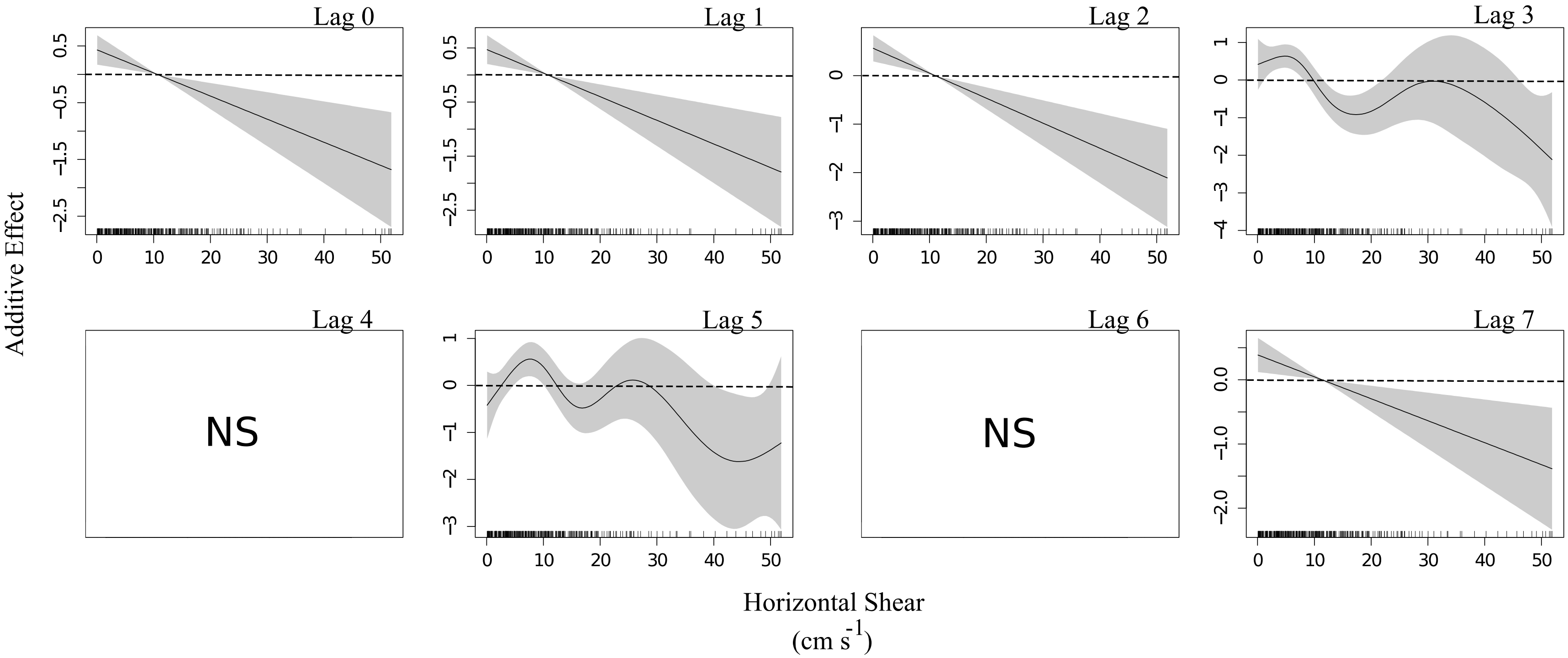


Fig. 5.7. Additive effect of horizontal shear on daily catch of *Cancer magister* megalopae at eight time lags. NS denotes time lags where horizontal shear was a non-significant response variable. See Fig. 5.6 for an explanation of how to interpret the plots.

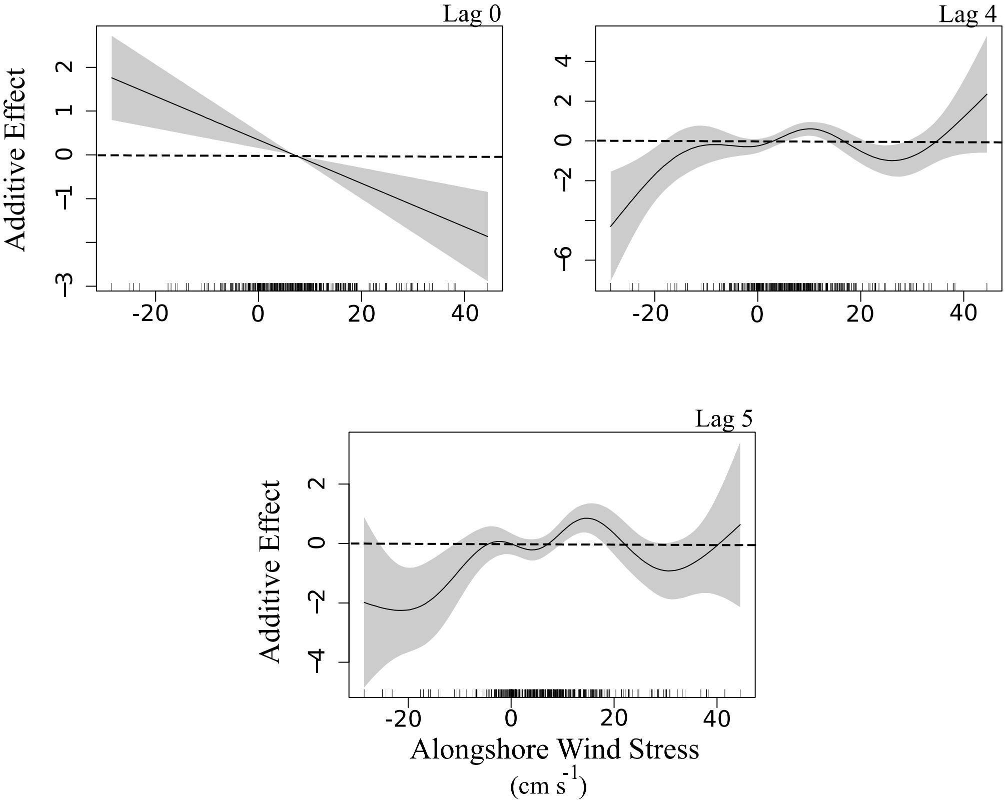


Fig. 5.8. Additive effect of alongshore wind stress on daily catch of *Cancer magister* megalopae at time lags of 0, 4 and 5 d. All other time lags were non-significant. See Fig. 5.6 for an explanation of how to interpret the plots.

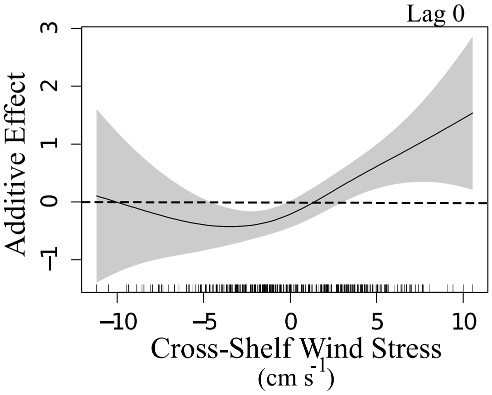


Fig. 5.9. Additive effect of cross-shelf wind stress on daily catch of *Cancer magister* megalopae at a time lag of 0 d. All other time lags were non-significant. See figure 5.6 for an explanation of how to interpret the plots.

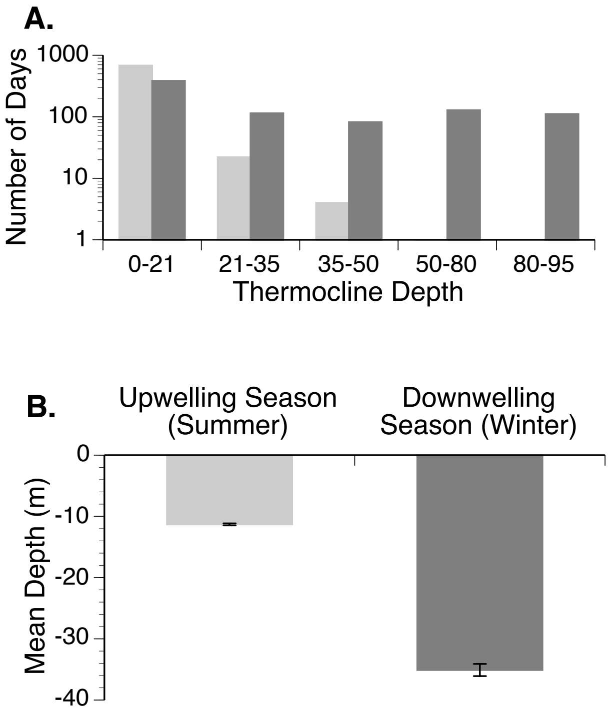


Fig. 5.10. Seasonal variation in the number of days (log scale) the thermocline was in each depth bin (A) and the average thermocline depth (± SE) during the upwelling and downwelling seasons (B) for 2000-2004.

orders of magnitude in a single night; clearly catch was not proportional to the magnitude of the tide. In addition, catch was not in phase with the spring neap cycle. The highly pulsed nature of catch suggest megalopae arrive at the coast in a relatively small temporal window; suggesting discrete transport events (Fig. 5.2). Further, the most significant lags in cross-correlation between the daily maximum tidal range and *C. magister* catch are frequently out of phase with the spring neap cycle (Fig. 5.4). Although both studies found significant correlations between daily maximum amplitude tide and catch of megalopae, which time lags were significantly cross-correlated differed between the studies (Roegner et al., 2007). For example, for the 1998 catch year, Roegner et al. (2007) reported significant cross-correlations between daily maximum tidal range and catch at lags ranging from -1 to -4 d whereas we found significant lags at -1, -6, -5 and -7 d. It is likely these differences are due to differences in the techniques used to remove seasonal trends from the data or computer software used to process data.

Using GAMs allowed us to more closely examine the associations between variables that influence the internal tide and catch of *Cancer magister* megalopae at different time lags. The lags of 0 and 7 d had the lowest AIC values and thus were presumed to be the best fit models. Since we filtered out the barotropic tide from the mooring data, this suggests catch was in phase with the baroclinic rather than the barotropic tide. Further, the daily maximum tidal range (proxy for barotropic tide) was not significant in any of the model structures further suggesting catch was more likely associated with the internal tide. Although model structure varied between the different time lags, thermocline depth, thermocline strength and horizontal shear were the most consistently significant variables (Figs 5.5-7, Table 5.3). We propose the following explanation for why these three variables were the most commonly significant variables. Catch was greater when the thermocline was >21 (21-35 m on all but one day in our data). This thermocline depth would allow larger amplitude waves to move across the continental shelf a greater distance before they interact with either the surface of the water column or the bottom. Similar to surface waves, the motion of water around internal waves and bores is approximately orbital (Osborne and Burch, 1980; Simpson, 1999). Thus, there is an orbital of motion surrounding the wave/bore and if the orbital above or below the wave interacts with the surface of the water column or the seafloor, the circulation and characteristics of the wave are altered. Thus, a deeper thermocline would allow larger amplitude waves to move across the shelf for a greater distance before they interact with either the surface or bottom.

We hypothesize catch was greater when the thermocline was weaker because 1) the strength of the thermocline decreases as upwelling increases and 2) a weaker thermocline indicates more vertical mixing (Huyer, 1983). First, we have recently developed a highly validated individual based biophysical model, which suggests megalopae exhibit behaviors concentrating them near the continental shelf break (Rasmuson and Shanks, In Preparation). However, during strong upwelling events the average location of this concentration is shifted slightly shoreward. Therefore, the pool of megalopae "available" for internal waves to transport across the shelf would be increased. Second, when the thermocline is located at depths >21 m it is on average weaker than when it is at 0-21 m (Fig. 5.11). We hypothesize that vertical mixing weakens the thermocline but also deepens it. As stated above, we hypothesize more megalopae are caught when the thermocline is deeper because it allows for larger waves to form which would occur when vertical mixing deepens it.

As horizontal shear increased, catch of *C. magister* decreased. We hypothesize this is because increased horizontal shear decreases the water column stability (Cushman-Roisin and Beckers, 2011). Increased catch with a weaker thermocline and a decrease in catch with increasing with horizontal shear (thus stronger thermocline) appear to contradict each other. We do not believe these two things contradict each other but suggest an "optima" for water column conditions for cross-shelf transport. Essentially a weaker thermocline is indicative of upwelling conditions, which leads to a larger pool of megalopae that can be transported, and a deepening of the thermocline, which allows for

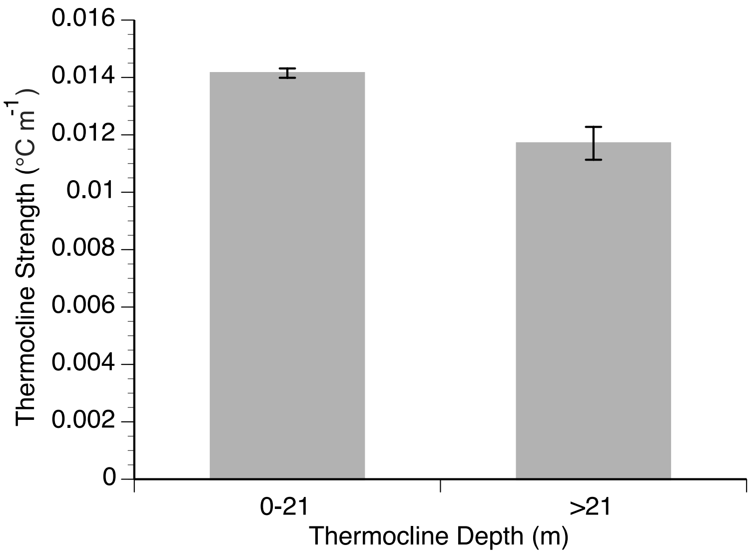


Fig. 5.11. Average thermocline strength for each thermocline depth from 2000 and 2001. During 2000 and 2001 on only one occasion was the thermocline depth >35 m and thus values categorized as >21 m most frequently denote a thermocline depth range from 21-35 m. See text for an explanation of how thermocline strength was calculated. Error bars denote a 95% confidence interval.

larger waves to form, however, if the thermocline is too weak there is not a coherent interface for the waves to travel along.

Our interpretation of the three variables from the GAM time series is that they play a significant role in allowing nonlinear internal waves/bores to be coherent for a greater distance across the continental shelf leading to more megalopae being transported to shore. If we assume that megalopae are equally distributed across the continental shelf, a wave traveling a longer distance would ultimately concentrate more larvae leading to larger pulses in catch. However, megalopae are notoriously patchy (Natunewicz and Epifanio, 2001) and thus these dynamics are more complex. It is also possible that waves generated at the shelf break could remain coherent all the way across the continental shelf thus transporting megalopae from the shelf break to the nearshore. To fully assess these hypotheses a series of moorings and settlement devices established across the continental shelf need to be operated to associate catch of megalopae with the internal tide.

How likely is it that nonlinear internal waves remain coherent from the shelf break to the nearshore environment? For this to occur two things must happen 1) the wave must be “stable” at the shelf break and 2) must be capable of moving across the continental shelf. Measurements of internal waves at the shelf break demonstrate the presence of well formed internal waves/bores (Martini et al., 2011). Thus, it is likely at least some of the waves are “stable” at the shelf break and could transport megalopae from the shelf break. Second, only 250 km north of Coos Bay, Moum et al. (2007b) tracked a packet of nonlinear internal waves across the continental shelf for ~32 km and demonstrated that the energy within the wave packet remained relatively constant and the waves persisted as waves of depression. After 32 km (~3 km from shore), at a water depth of 50 m, the waves dissipated and lost their coherency. This (and other studies) demonstrate that waves do remain coherent across the majority of the continental shelf (Apel and Gonzalez, 1983; Stanton and Ostrovsky, 1998).

There has been discussion in the literature about transport by internal tides and whether transport is caused by linear internal waves, nonlinear waves or internal bores despite the fact that both likely occur at the same time and place (Franks, 1997; Queiroga and Blanton, 2004; Shanks, 1995a). Our understanding of the nature of internal waves has changed considerably since the first papers suggested internal waves may transport organisms (Shanks, 1983; Zeldis and Jillett, 1982); one major change has been the understanding that internal waves can manifest as either linear or non-linear waves. Based on the available data of the time, early researchers suggested transporting waves were linear (Shanks, 1983; Zeldis and Jillett, 1982). Subsequent work has demonstrated that linear internal waves are incapable of transporting mass whereas nonlinear waves are capable of transporting mass (Jackson, 2004). The early studies were unable to collect observations of the structure of the transporting wave and thus it is probable the waves were actually nonlinear. Because early influential papers referred to internal waves as linear, a number of reviews have stated that internal waves are incapable of causing transport because they are linear (Epifanio and Garvine, 2001; Queiroga and Blanton, 2004). However, these reviews often ignore the potential for transport by nonlinear waves. Thus, the debate over whether or not internal waves can cause transport stems from a historical misunderstanding of the nature of internal waves. An additional debate has questioned whether transport is driven by internal waves or internal bores (Pineda, 1991; Shanks, 1983). However, in their review Le Fevre and Bourget (1992) demonstrate that both internal waves and bores are capable of transporting larvae but point out waves would transport larvae at the surface and bores at depth. Therefore, the vertical location of the larva in the water column dictates which feature is more likely to transport larvae and both types of features are theoretically capable of transport. Evidence suggests *Cancer magister* remain in the neuston on the continental shelf and thus for our study would be more likely to interact with the surface manifestation of a nonlinear internal wave rather that an internal bore (Reilly, 1983). Despite the debate that has occurred in the literature, considerable evidence suggests the internal tide (both waves and bores) are critical processes for transporting larvae.

5.4.2. Seasonal and Decadal Variation

Our findings suggest that from 2007-2013 (after PDO phase change) *Cancer magister* megalopae were transported across the continental shelf by the internal tide (Shanks, 2013). This suggests that despite huge inter-annual variation in catch (annual catch varied by a factor of 1000), the internal tide remains the predominant cross-shelf transport mechanism for *C. magister* megalopae despite decadal changes in circulation patterns. Our lack of mooring data during negative PDO conditions prevents us from examining whether the PDO influenced the shelf hydrodynamics ultimately altering the internal tide and possibly driving the annual variation in total catch.

Previously, Shanks (2013) proposed that more megalopae are caught when the day of the year of the spring transition causes the upwelling season to begin earlier. Further, he hypothesized the positive correlation between the amount of upwelling following the spring transition and the catch of megalopae may have indicated the megalopae were transported onto the continental shelf with the deep upwelling waters. Recently, using our individual based model we have suggested that megalopae remain near the continental shelf break throughout their development. Thus, the correlation with catch and the day of the year of the spring transition does not appear to be indicative of onshore transport by deep upwelled waters.

Moum et al. (2007a) examined the Oregon shelf during winter and summer months and demonstrated that the thermocline is deeper during winter months and thus most internal waves that are generated during winter will be waves of elevation and the converse was true for summer months (shallower thermocline and waves of depression). Using the data from the GLOBEC mooring we see that the day of the year of the spring transition coincides with a shallowing of the thermocline, which would lead to the generation of waves of depression rather than waves of elevation (Fig. 5.10). We hypothesize that the correlation between the day of the year of the spring transition and the number of recruiting megalopae is indicative of a shift from conditions favorable to the generation of waves of elevation to waves of depression. An earlier day of the year of the spring transition leads to a greater annual catch of megalopae because there is a longer period for waves of depression to be generated and transport megalopae across the continental shelf.

We propose the following explanation for why waves of depression would be more likely to transport Dungeness crab megalopae (Fig. 5.12). First we assume (based on previous studies), megalopae 1) swim with the surface current and 2) are capable of swimming at speeds of ~10 cm s^{-1} (Rasmuson and Shanks, 2014). Lamb's (1997) model suggests this behavior should increase transport distance and calculations based on a local mooring corroborate this hypothesis (Rasmuson and Shanks, 2014). In this work we calculated hypothetical transport distances for both waves of depression and elevation and reported that regardless of shape megalopae would be transported if they swim quickly with the current (Rasmuson and Shanks, 2014). While mathematically it is correct that both types of wave could transport megalopae, we now hypothesize the behavior of *C. magister* megalopae would not interact with a wave of elevation in such a way to cause transport. Assuming megalopae swim with the surface current regardless of their location, in the presence of a wave of elevation megalopae would swim in the opposite direction of wave propagation (Fig. 5.12). This would lead to megalopae swimming over and possibly out of the convergences generated by the wave. However, megalopae near a wave of depression would swim in the direction of the waves propagation (Fig. 5.12). Shanks (1995) suggests that when the speed of the surface current over the wave is at least as fast as the speed of wave propagation the wave will cause transport. Therefore, by swimming in the direction of wave propagation megalopae greatly increase the possibility of transport. If this is the case then why is catch so pulsed? First, although during initial formation the waves would manifest as a wave of depression, if they were large enough they would interact with the bottom as the waves move across the shelf causing them, eventually, to flip and become waves of elevation. Secondly, many hydrodynamic processes can destabilize the water column, which may cause fewer waves to develop. Ultimately meaning there are certain times when waves more conducive to transport are formed.

5.5. CONCLUSION

To our knowledge this work provides the first evidence that internal waves transport larvae despite major climactic variation. Overall our data are consistent with previous findings that *Cancer magister* megalopae are transported across the continental shelf by the internal tide (Roegner et al., 2007; Shanks, 2013); despite a major in total annual catch. Additionally, we provide the first evidence that seasonal variability in thermocline depth (and thus internal waves) likely determines when megalopae start returning. Finally, comparing mooring data to catch, we suggest catch is higher when the thermocline is deeper (relative to summer time depths) because it allows larger internal waves of depression to form. Additionally, we hypothesize that more megalopae are caught when horizontal shear is low because internal waves would remain more stable

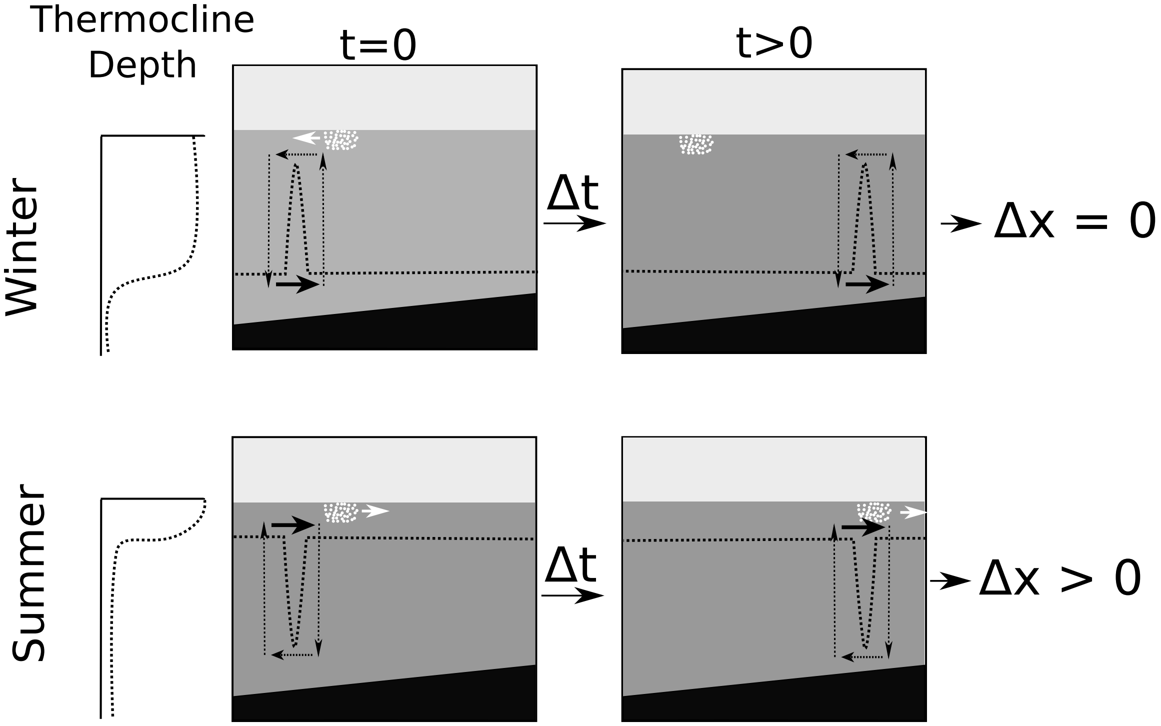


Fig. 5.12. Two-layer model of cross-shelf transport by solitons of elevation and depression. The model assumes Dungeness crab megalopae are on the continental shelf, remain in the neuston and swim in the direction of the surface current. Black arrows denote circulation around the internal wave (dashed: weak flow and solid: strong flow) and white arrows denote the swimming direction of megalopae. During winter months the thermocline is deeper causing most solitons to be waves of elevation. The circulation above the wave is weak and offshore causing megalopae to swim in the opposite direction of wave propagation. Thus, there is likely no net transport of megalopae by the internal wave. During summer months (following the spring transition) the thermocline is shallower causing most waves to be waves of depression. The flow above the wave is onshore causing megalopae to swim in the direction of wave propagation ultimately leading to a net transport of megalopae.

over the continental shelf and thus be less likely to break. Finally, we hypothesize a weaker thermocline is indicative of 1) upwelling conditions and 2) more vertical mixing. We suggest that more megalopae are caught when the thermocline is weaker because upwelling increases the larval pool that could be transported by internal waves and vertical mixing deepens the thermocline allowing for larger internal waves to form. In this system, as well as others, long term moorings sampling at high frequency need to be correlated with daily catch and *in situ* observations to more fully understand the role of the internal tide in transporting larvae. Studies like this should focus on multiple species groups to more fully assess which larvae are transported by internal waves and which by internal bores.

CHAPTER VI

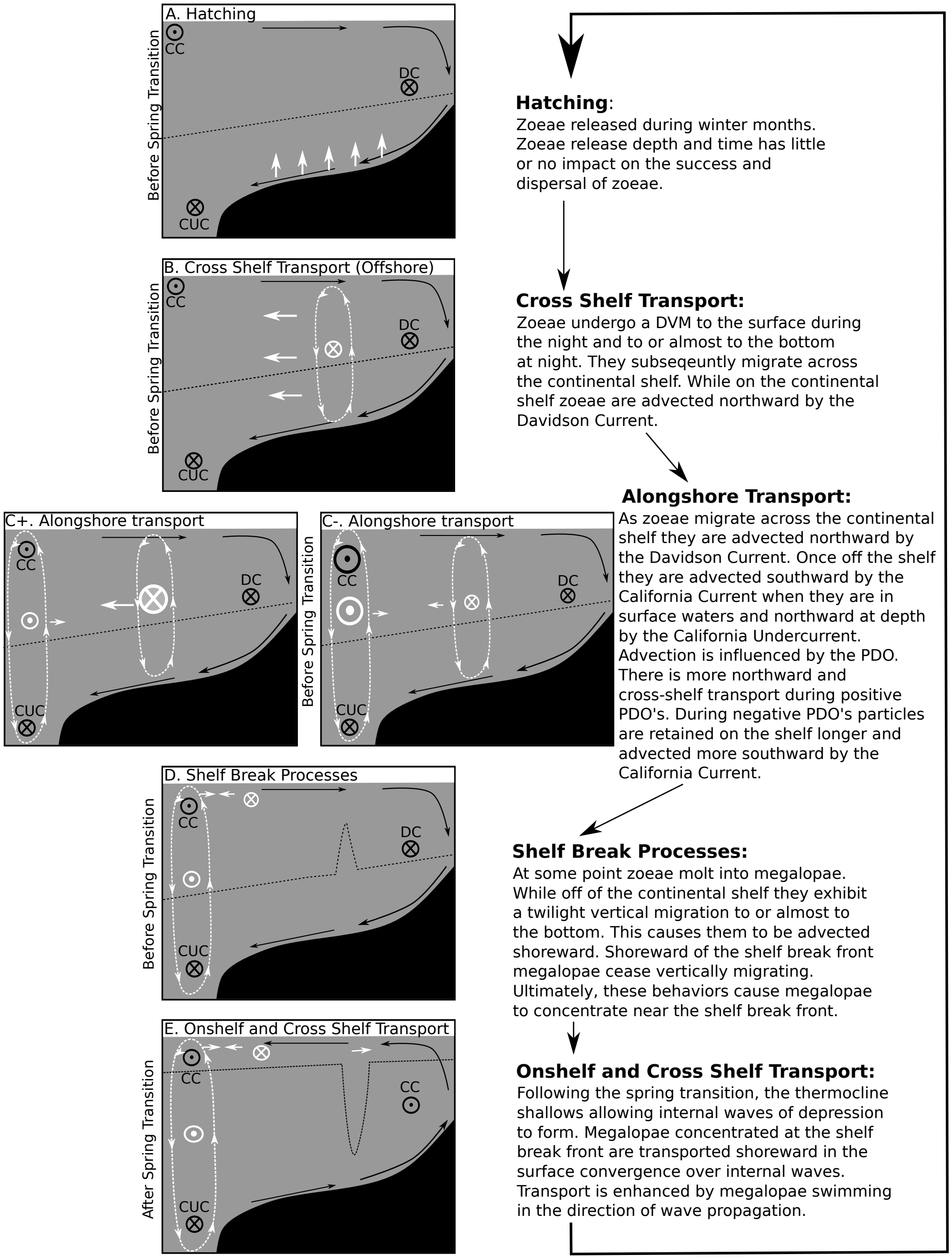
GENERAL CONCLUSIONS

The Dungeness crab, *Cancer magister*, fishery is the most economically important fishery along the West Coast of the United States and is considered highly sustainable (Rasmuson 2013). Although the fishery is sustainable, total annual catch has fluctuated dramatically between years, ranging from a low of 224,000 kg to a high of 15,112,000 kg. Understanding the cause of these fluctuations has been the focus of many research projects; the majority suggesting the fluctuations are influenced by the larval phase (Methot 1989). Recently, Shanks et al. (2007, 2010, 2013) have collected daily samples of Dungeness crab megalopae with a light trap and have demonstrated that the total annual catch of megalopae is positively correlated with the total annual catch of Dungeness crabs 4 years later (the time it takes for crabs to enter the fishery).

In addition to demonstrating that annual catch of megalopae is correlated with commercial catch, Shanks et al. have shown that catch of megalopae is correlated with oceanographic events (2007, 2010, 2013). First, they have shown that the total annual catch of megalopae is correlated with the phase of the Pacific Decadal Oscillation (PDO), with more megalopae caught during negative phase PDOs. The PDO alters the amount of water that is shifted into either the Alaska or California Currents from the West Wind Drift; with more water entering the California Current during negative PDOs (Mantua & Hare 2002). Shanks et al. hypothesize that the retention of megalopae within the California Current is enhanced by the increased southward flow of the California Current during negative PDOs, which ultimately leads to a higher annual catch of megalopae.

Second, the total annual catch is negatively correlated with the day of the year of the spring transition; the day when alongshore winds switch from being predominately downwelling favorable to being predominately upwelling favorable (Huyer et al. 1979). Additionally, they have demonstrated that the catch of megalopae is positively correlated with the amount of upwelling that occurs during the recruitment season (Huyer 1983). They hypothesize that more megalopae are caught following an early spring transition because it increases the amount of time that megalopae can return to the near shore. They further hypothesize that catch of megalopae is associated with the amount of upwelling because megalopae are advected onto the continental shelf with the deep upwelled waters.

In addition to examining the correlation between oceanographic processes and annual catch of megalopae, Roegner et al. (2007) examined the influence of oceanographic processes on the daily catch of megalopae. They demonstrated that catch is correlated with the tide, but is out of phase with the spring neap cycle. They hypothesize this correlation suggests megalopae are transported across the continental shelf by internal waves. In this thesis my goal was to further examine the associations between oceanographic processes and catch of megalopae using a combination of individual based biophysical models, *in situ* observations of larvae and statistical models. Using these techniques we helped develop a better understanding of the processes that influence the larval phase of Dungeness Crabs (Fig 6.1).



Hatching:
Zoeae released during winter months. Zoeae release depth and time has little or no impact on the success and dispersal of zoeae.

Cross Shelf Transport:
Zoeae undergo a DVM to the surface during the night and to or almost to the bottom at night. They subseqeuntly migrate across the continental shelf. While on the continental shelf zoeae are advected northward by the Davidson Current.

Alongshore Transport:
As zoeae migrate across the continental shelf they are advected northward by the Davidson Current. Once off the shelf they are advected southward by the California Current when they are in surface waters and northward at depth by the California Undercurrent. Advection is influenced by the PDO. There is more northward and cross-shelf transport during positive PDO's. During negative PDO's particles are retained on the shelf longer and advected more southward by the California Current.

Shelf Break Processes:
At some point zoeae molt into megalopae. While off of the continental shelf they exhibit a twilight vertical migration to or almost to the bottom. This causes them to be advected shoreward. Shoreward of the shelf break front megalopae cease vertically migrating. Ultimately, these behaviors cause megalopae to concentrate near the shelf break front.

Onshelf and Cross Shelf Transport:
Following the spring transition, the thermocline shallows allowing internal waves of depression to form. Megalopae concentrated at the shelf break front are transported shoreward in the surface convergence over internal waves. Transport is enhanced by megalopae swimming in the direction of wave propagation.

Figure 6.1. Two layer model of the different steps that occur during the dispersal of Dungeness crab larvae. White arrows and circles denote the movement of larvae and black arrows and circles denote the movement of the water. Circles with dots (⦿) denotes flow out of the page and circles with an ‘x’ in it (⊗) denotes flow into the page. The size of circles and arrows are roughly scaled to represent the magnitude of the velocity. DVM- Diel Vertical Migration, PDO- Pacific Decadal Oscillation, CC- California Current, CUC- California Under Current, DC- Davidson Current

In chapter II we developed an individual based biophysical model of the dispersal of Dungeness crab larvae. We showed that the timing of larval hatching had little effect on the dispersal of larval trajectory (Fig. 6.1A). We further demonstrated that larvae exhibit a vertical migration to or almost to the bottom each day, which significantly affects their dispersal trajectory (Fig. 6.1B). The findings from the model support the hypothesis that more megalopae are caught during negative PDO years because retention of larvae within the California Current is enhanced (Fig. 6.1C).

In chapter III we developed a two dimensional individual based biophysical model of upwelling circulation along the Oregon coast. We suggest that megalopae exhibit a twilight vertical migration, occupying the surface at twilight, a depth below the Ekman layer at night and migrate to or almost to the bottom each day off of the continental shelf and remain in the neuston while on the continental shelf (Fig. 6.1D). This causes megalopae to be concentrated at the shelf break. We hypothesize they are advected shoreward by internal waves generated by the internal tide.

In chapter IV we conducted *in situ* observations of megalopae and demonstrated that they swim at speeds of ~ 10 cm s^{-1} and swim in the direction of the surface current. Using these results and data from a thermistor mooring, we calculated the potential transport distance of nonlinear waves with and without larval behavior demonstrating that the distance a wave would transport larvae increased dramatically for larvae that swam relatively quickly and with the surface current.

In chapter V we analyzed 12 years of daily catch of megalopae and showed that despite the phase change of the PDO, megalopae still appear to be transported across the continental shelf by the internal tide. We then used generalized additive models and data from a mooring to better define the oceanographic conditions that associate with transporting internal waves. We demonstrated that transport is associated with a deeper weaker thermocline and less horizontal shear. We hypothesize these conditions act to stabilize the water column allowing waves to remain coherent as they cross the continental shelf. Additionally, we demonstrated that the spring transition correlates with a shallowing of the thermocline. This would associate with a switch from conditions that are conducive to the formation of internal waves of elevation (before the spring transition) to internal waves of depression (after the spring transition). We further hypothesize that waves of depression are more likely to transport Dungeness crab larvae since the flow at the surface above the wave is shoreward for a wave of depression and offshore for a wave of elevation.

The findings from this thesis help us better understand the processes that influence the dispersal of Dungeness crab larvae, which ultimately have direct implications for the fishery. Overall, we hypothesize that the results of this thesis support Michael Sinclair's member vagrant hypothesis (Sinclair 1988). Briefly, his hypothesis states that populations persist where oceanographic processes promote membership (return of larvae to the adult population) of larvae and that larvae that do not return are vagrants and are lost to the population. Our work suggests that the dispersal of Dungeness crab larvae occurs during a time period, which decreases the net alongshore transport of larvae enhancing membership within the population a pattern hypothesized by Shanks and Eckert (2005). Further, Shanks and Eckert (2005) demonstrated that many of the species that live on the continental shelf have very similar life history characteristics: spawning during winter months and having larvae with a long pelagic larval duration (PLD). Dungeness crabs are part of this group and thus it is very likely the results of this work have implications for many of the other species that inhabit the continental shelf within the California Current.

APPENDIX A

LARVAL PRODUCTION AND MORTALITY CALCULATIONS FOR CHAPTER II

A.1. LARVAL PRODUCTION

The Dungeness crab fishery is managed using a 3-S management structure; a technique that regulates the size of crabs harvested, sex of crabs harvested and the season when crabs are harvested [1]. The 3-S management structure results in the annual extraction of nearly all 4-yr old male crabs. This allows us to relatively accurately predict 1) the number of females in the population and 2) the number of larvae that are released annually. Our model uses the following assumptions from McKelvey et al. [2]. First, that the sex ratio between males and females is 50:50. Second, that female crabs begin reproducing at age 2 and are capable of reproducing until they are 8-yr old. Third, we assume that 78% of the population survives each year. Fourth, all females mate successfully. Finally, we assume that on average a 4-yr old crab weighs 2 lbs (0.9 kg).

In order to calculate annual larval production, we first compiled total annual catch (in lbs) in California, Oregon and Washington from 1981-2014 [3]. Since our hydrodynamic model was run from 2000-2001 and 2006-2013, we needed catch data for 2015-2017 to calculate larval production for the final years our model was run. Since these fishery years have not occurred, we fit the catch data from 1981-2014 with a first order autoregressive integrated moving average (ARIMA). Using this model, we conducted 100,000 simulations to predict commercial catch from 2015-2017. We calculated a mean of the 100,000 simulations for each year from 2015-2017. We used these data in order to calculate larval production similar to the methods used by Shanks & Roegner [4].

We calculated the number of 4-yr old females using:

$$F_{yr} = 2^{-1} C_{yr} \tag{A.1}$$

where F_{yr} is the number of 4 year old females and C_{yr} is the total commercial catch in a given year. Then we calculate the number of 2 and 3 year old females using:

$$F_{yr+k} = (2^{-1} C_{yr+k} + 0.12k(2^{-1} C_{yr+k}), \text{ for k=1, 2} \tag{A.2}$$

Where k is scaling factor to adjust for the catch years following C_{yr} and $0.12k$ adjusts C_{yr} to account for the larger population size due to fewer years of annual mortality. We calculate the number of 5-8 yr old female crabs using:

$$F_{yr-k} = (2^{-1} C_{yr-k}) 0.78^{k}, \text{ for k=1, 2, 3, 4} \tag{A.3}$$

Where again k is a scaling factor used to adjust for catch years preceding C_{yr} and 0.78^{k} decreases the population size based on a fixed mortality rate (0.78) and the number of years since the commercial catch, *k*. Thus, using equations A.1-3, the total number of female crabs (age 2-8) in any given year can be expressed as:

$$F_{yr} = \left(\sum_{k=1}^{2} F_{yr+k} \right) + F_{yr} + \left(\sum_{k=1}^{4} F_{yr-k} \right) \tag{A.4}$$

Where F_{yr} is the total number of female crabs that produced larvae in a given year. If we assume each female releases approximately $2*10^{9}$ larvae [5] then the total number of larvae produced is calculated as:

$$L_{yr} = F_{yr}(2*10^{9}) \tag{A.5}$$

Where L_{yr} is the annual total number of larvae released into the California Current each year and F_{yr} is the total number of females calculated in equation A.5. From these calculations it is evident that the total amount of larvae released into the California Current is not equal between years, ranging from a low of ~$2*10^{13}$ in 1984 to a high of $7.7*10^{13}$ in 2005 (Fig. A1).

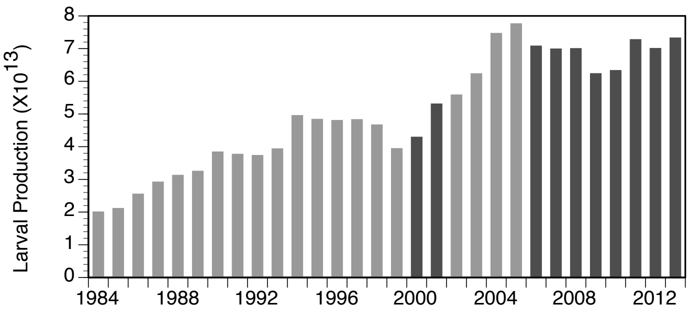


Figure A.1. Number of larvae produced each year from 1984-2013. Darker gray bars denote years we modeled larval dispersal.

For our model, ideally we would have liked to alter the number of particles released each year to match the number of larvae produced that year. However, the large number of larvae released each year made this computationally prohibitive. Thus, we scaled the annual larval production on a scale of 0 -1 using:

$$SL_{yr} = \frac{\left(L_{yr} - \min(L_{yr})\right)}{\left(\max(L_{yr}) - \min(L_{yr})\right)} \tag{A.6}$$

Where SL_{yr} is the scaling factor for each year, $min(L_{yr})$ is the minimum value of larval production from 1984-2013 and $max(L_{yr})$ is the maximum value of larval production over this period. This generated a scaling value that we could multiple the initial super individuals to better include potential impacts of larval production in our model (Fig. A2). Super individuals are a technique where each particle in the Lagrangian model represents a greater number of individuals (in our case 10^6) which allows researchers to include mortality in the model while maintaining a computationally efficient model [6].

Although the values are scaled from 0 -1, none of the years that we modeled (2000-2001 & 2006-2013) were scaled to a zero.

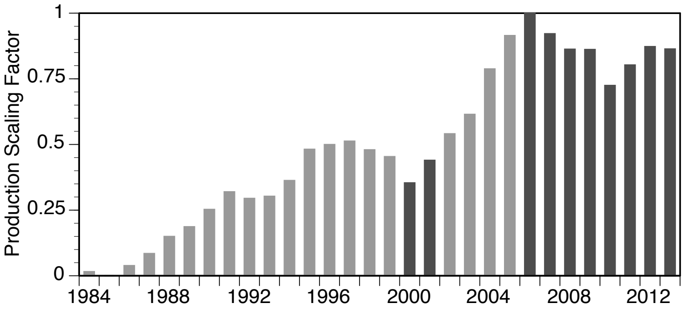


Figure A.2. Scaling factor for larval production from 1984-2013. Darker gray bars denote years we modeled larval dispersal.

A.2. LARVAL MORTALITY

In addition to altering the number of larvae produced for each model year, we wanted to include a measure of mortality rate in our model as this has been shown to profoundly impact model results [7]. Mortality rates of marine larvae are notoriously difficult to measure [8], especially for widely dispersing species like Dungeness crabs. Using the number of larvae produced each year (L_{yr}) we were able to calculate the number of settlers using:

$$Nt_{yr} = N0_{yr} e^{-M*t} \tag{A.7}$$

where Nt_{yr} is the total number of settlers in a given year, t is the amount of time from larval release to settlement, M is mortality rate and $N0_{yr}$ is the number of larvae released each year which can be assumed to be:

$$L_{yr} = N0_{yr} \tag{A.8}$$

To calculate the number of settlers, we assumed t was equal to the day of the year of the spring transition (St_{yr}) since this is the first day that large numbers of Dungeness megalopae are often caught [9]. Essentially this assumes that the pelagic larval duration is from January 1 until the day of the year of the spring transition, likely a large underestimation of since megalopae are caught in the light trap for upwards of 100 days following the spring transition. Thus, by substituting equation A.8 into A.7 and St_{yr} for t we can calculate larval settlement over a range of mortality rates as:

$$Nt_{yr} = L_{yr}e^{-M*St_{yr}}, for\ m = 0.01, 0.02, \ldots, 0.25 \tag{A.9}$$

To assess which mortality rate best reflects the population, we calculated the number of settlers in a year (Nt_{yr}) using equation A.2 and a k value (scaling factor for catch data) of 4. We then could determine a range of mortality rates for both the maximum and minimum number of settlers.

Total number of settlers dropped quickly as mortality rate increased (Fig. A.3). From 1984-2013 the maximum number of settlers would have been ~10^{13} individuals, which would have occurred over a range of mortality rates from 0.02-0.05. The minimum number of settlers would have been ~10^{12} individuals which would have occurred over a range of mortality rates from 0.04-0.08.

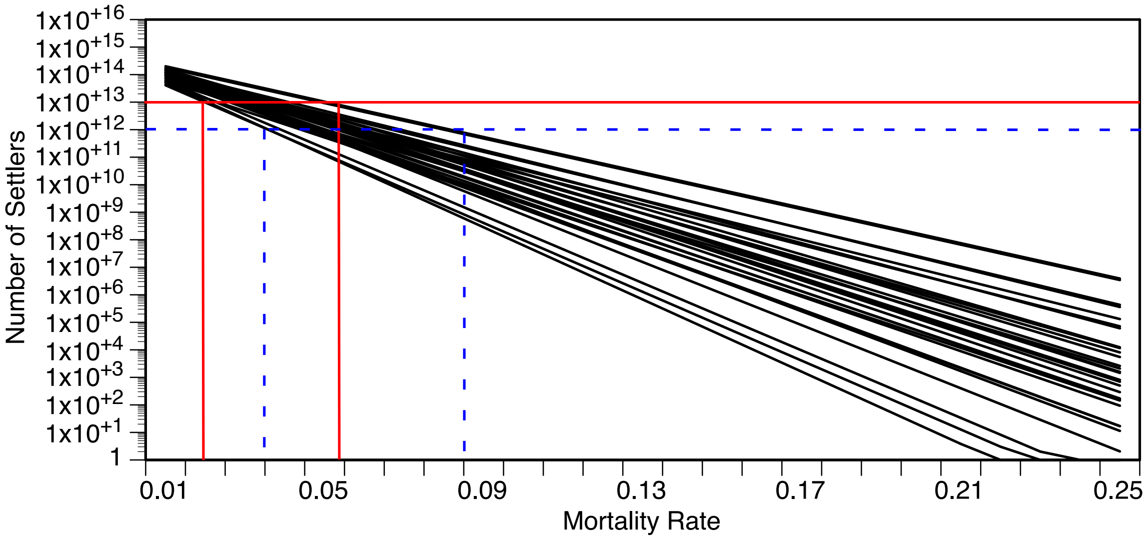


Figure A.3. Total number of settlers versus mortality rate based on annual larval production values from 1984-2013. The horizontal lines denote the calculated maximum (red solid line) and minimum (blue dashed line) settlement rates. Vertical lines denote the mortality rate range for the calculated maximum (red solid line) and minimum (blue dashed line) settlement rates. Vertical line color corresponds with horizontal line color.

Larval production values calculated from commercial catch, suggest that the average mortality rate for Dungeness crab larvae falls between 0.02-0.08. In order to further define an average mortality rate, we used data from Shanks et al. [10] where they reported an average density of newly settled Dungeness crabs of 175 crabs m^{-2}. First, we assumed that crab settlement density was equal across the continental shelf. Using bathymetry data we calculated the shelf area (*SA*) in ranges from 0-50, 0-75, 0-100 and 0-200 m [11]. Then we could calculate the total density of juvenile crabs that settled on the continental shelf

$$\sum Dens = SA * 175 \tag{A.10}$$

The above assumptions likely overestimate the total number of settlers. However, sensitivity analyses showed that a reduction of shelf area by as much as 75% had no effect on mortality rate. We can manipulate equation A.9 to solve for mortality rate:

$$M_{yr} = \ln\left(\frac{L_{yr}}{Nt_{yr}}\right) ST_{yr}^{-1} \tag{A.11}$$

and if we assume:

$$\sum Dens = Nt_{yr} \tag{A.12}$$

we can then calculate the mortality rate for each of the 30-years of catch data as:

$$M_{yr} = \ln\left(\frac{L_{yr}}{\sum Dens}\right) ST_{yr}^{-1} \tag{A.13}$$

We see that mortality rates between 0.02-0.03 are the rates that result in the settlement density most similar to that reported in Shanks et al. (2010) (Fig. A.4). Further, on average, mortality rate ranges from 0.023-0.028 depending on amount of shelf area used to calculate settlement. Thus, we used a mortality rate of 0.025 for our model. We conducted sensitivity analyses for rates as high as 0.08 and found little difference in the model results. These values are lower than those historically proposed for *Cancer magister* but are very similar to those determined from more recent in depth observational and modeling studies [12-14].

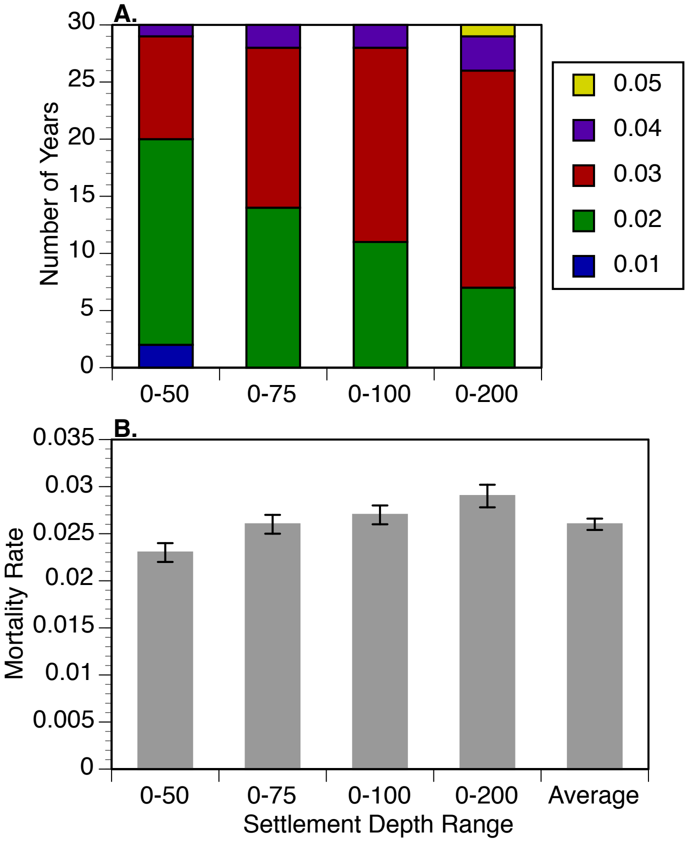


Figure A.4. Number of years where each mortality rate was closest to observed settlement data with (A) and average mortality rate (B) versus settlement depth range. Colors in (A) denote mortality rates (0.01 – 0.05). Bars (B) are averages calculated based on the number of years from plot A. Bars denote ± 1 SE.

APPENDIX B

ADDITIONAL VALIDATIONS OF THE PHYSICAL MODEL USED IN CHAPTER II

Shanks [1] hypothesizes more megalopae are caught during a negative phase PDO because more water is transferred into the California Current from the West Wind Drift during negative phase PDO's. For each PDO phase, we generated a wintertime average of alongshore flow off of the continental shelf in order to compare variations in alongshore flow. On average flow was more southward during negative PDO years than positive PDO years (Fig. B.1).

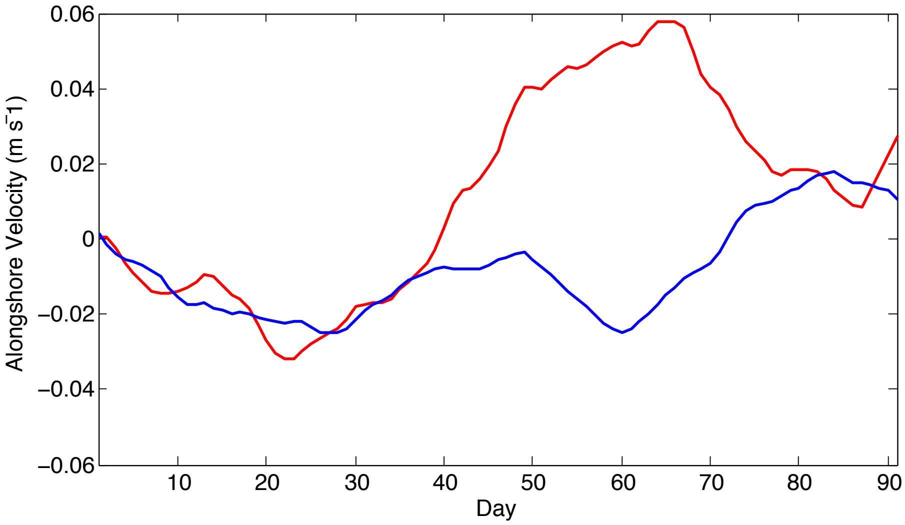


Figure B.1. Average alongshore flow off of the continental shelf during winter months during positive (red) and negative (blue) PDO phases. Negative values denote southward flow and positive values denote northward flow.

Shanks et al. [1-3] also hypothesized that more Dungeness crab megalopae are collected when the day of the spring transition is earlier in the year. We calculated the modeled the day of the spring transition for each model year, as the day the flow along the continental shelf changed from being predominately from the south to predominately from the north. The date of the observed spring transition was correlated with the modeled day [4]. Overall the model did a good job of representing the day of the spring transition (Fig. B.2).

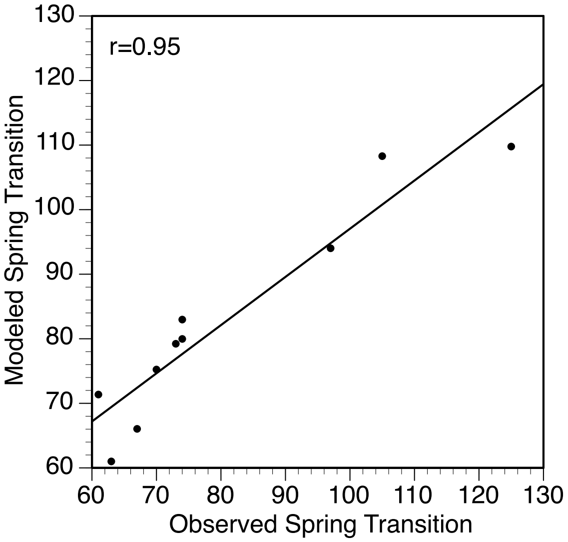


Figure B.2. Observed versus modeled day of the year of the spring transition.

We also compared observed velocity and temperature data from the GLOBEC mooring (see Section 5.2.3.1 for details) near the surface, middle and bottom of the water column. Globec data were filtered with a 25hr running mean to remove tidal residuals. Additionally, we obtained the depth averaged leading EOF for both the observed and modeled velocity and temperature data. Alongshore flow was well represented in the model data (Fig. B.2). Cross-shelf flow was well represented near the surface of the water column but at middle and bottom water depths. Temperature was well correlated at the surface and bottom of the water columns but not as well in the middle of the water column. As the focus of this study was on the movement of larvae, the strong correlation between the observed and modeled alongshore velocity suggests the alongshore currents are well represented by the model.

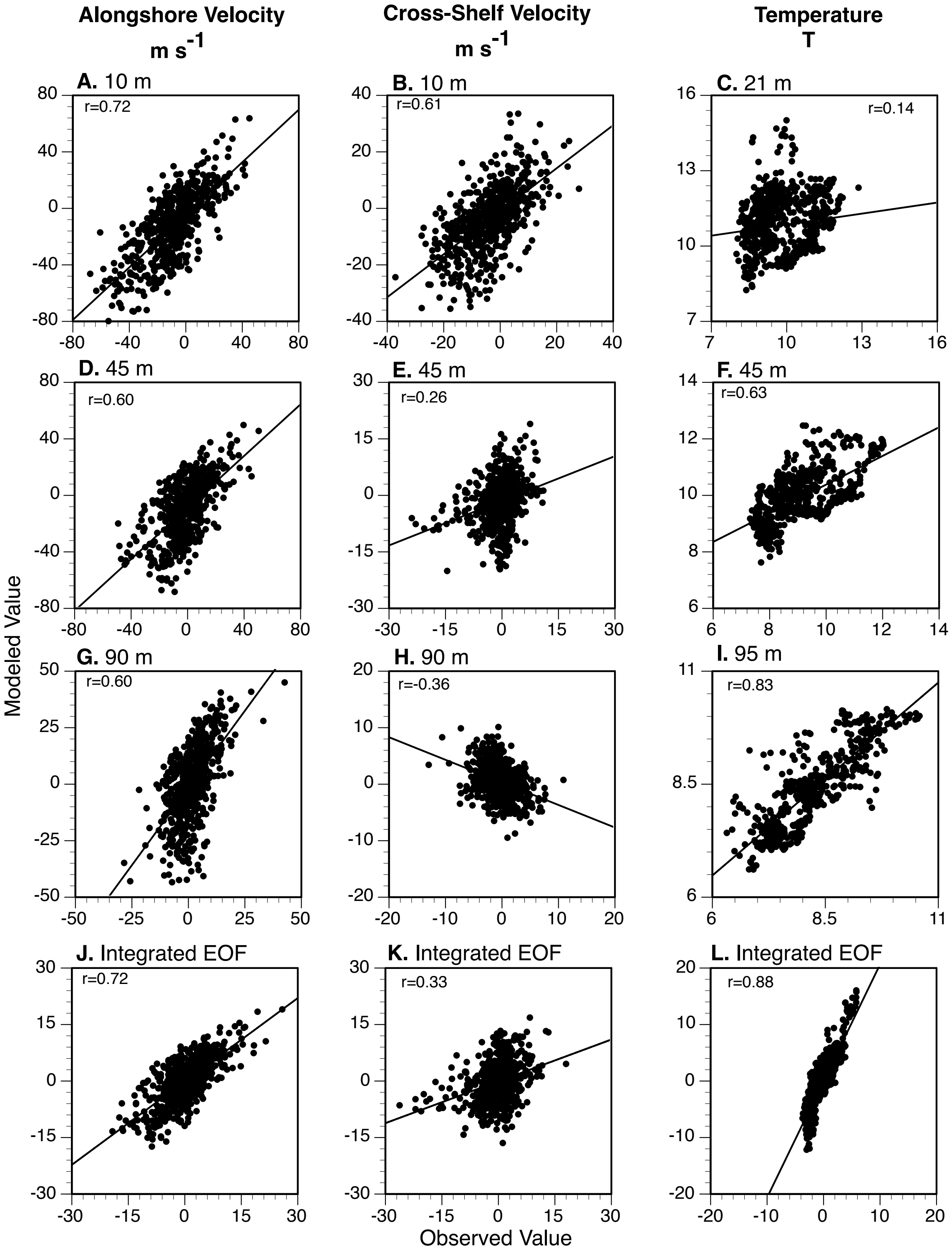


Figure B.3. Observed versus modeled alongshore flow (A,D,G,J), cross-shelf flow (B,E,H,K) and temperature (C,F,I,L). Values are determined near the surface (A-C), mid water column depth (D-F), near the bottom (G-F) and as a depth integrate EOF (J-L).

APPENDIX C

CONNECTIVITY MATRICES FOR CHAPTER II SIMULATIONS

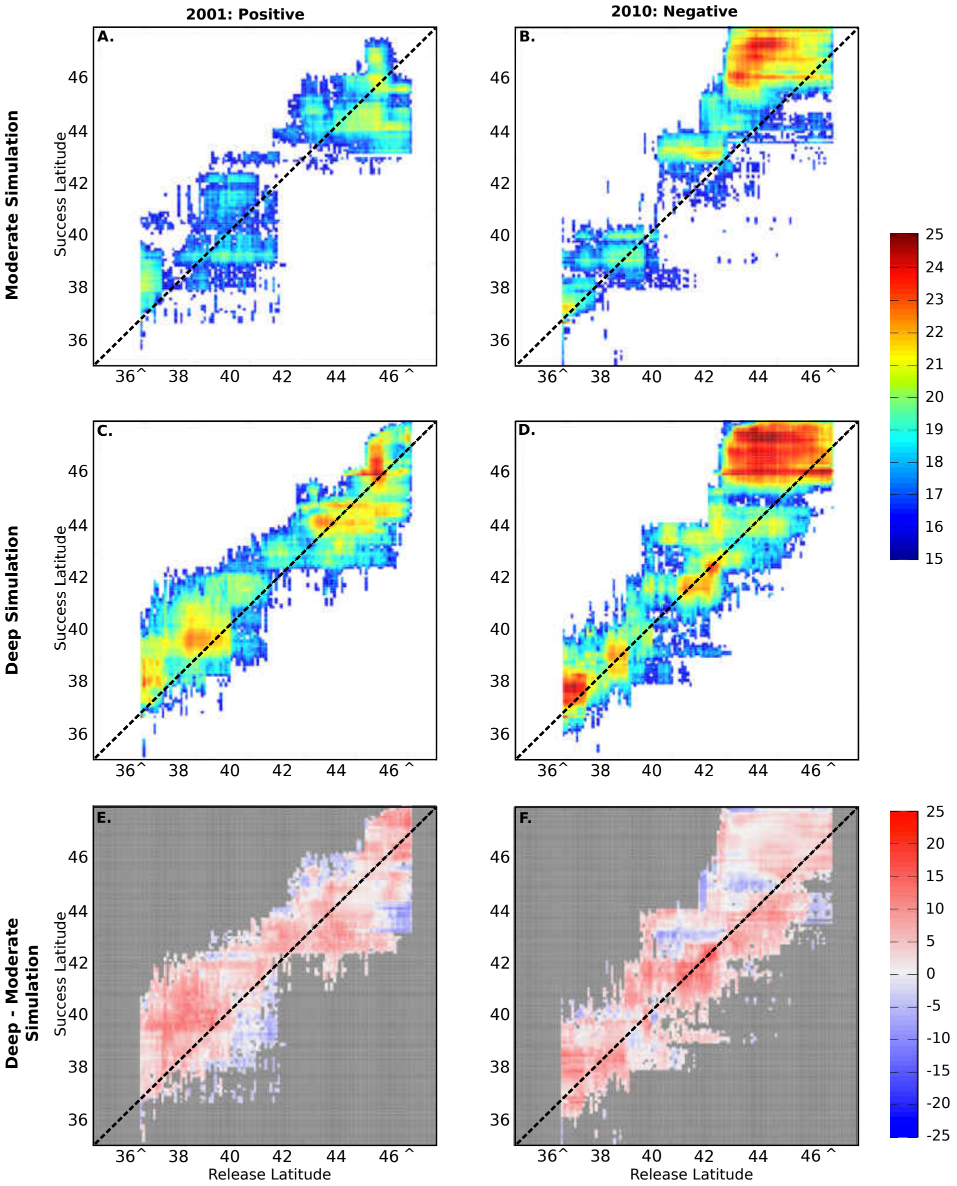


Figure C.1. Connectivity matrices during positive (A,C,E) and negative (B,D,F) years for particles exhibiting the moderate simulation (A,B), deep simulation (C,D) and the difference between the two simulations (E,F). The carrots on the x-axis denote the southern and northern extent of larval release. The dashed line is a 1:1 line, particles on the line recruit to where they were released, above the line ended up north of where they were released and below ended up south of where they were released. Scale bars denote $\log_{10}$ larvae.

APPENDIX D

CORRELATION TABLES AND FIGURES FROM CHAPTER V

Table D1. Cross-correlations between daily catch of *Cancer magister* megalopae and physical variables after the fortnightly periodicity in the catch time series was removed. Catch was $\log_{10}$ transformed. Seasonal trends were removed from the biological and physical data to ensure data were stationary. Biological data were lagged relative to physical data. Bold numbers denote the most significant positive and negative correlation for each year. ND denotes "No Data" because the weather station was taken offline by NOAA.

Lunar Cycle

	-7	-6	-5	-4	-3	-2	-1	0	1	2	3	4	5	6	7
1998															
1999															
2000															
2001															
2006															
2007															
2008															
2009															
2010															
2011															
2012															
2013															

V-Wind

	-5	-4	-3	-2	-1	0
1998						
1999						
2000						
2001			**0.20**			
2006						
2007						
2008						
2009						
2010						
2011				**-0.17**	-0.16	
2012						
2013	ND	ND	ND	ND	ND	ND

U-Wind

	-5	-4	-3	-2	-1	0
1998						
1999						
2000						
2001						
2006						
2007						
2008						
2009						
2010						
2011						
2012						
2013	ND	ND	ND	ND	ND	ND

Bay SST

	-5	-4	-3	-2	-1	0
1998						
1999						
2000						
2001						
2006						
2007						
2008						
2009						
2010						
2011						
2012						
2013						

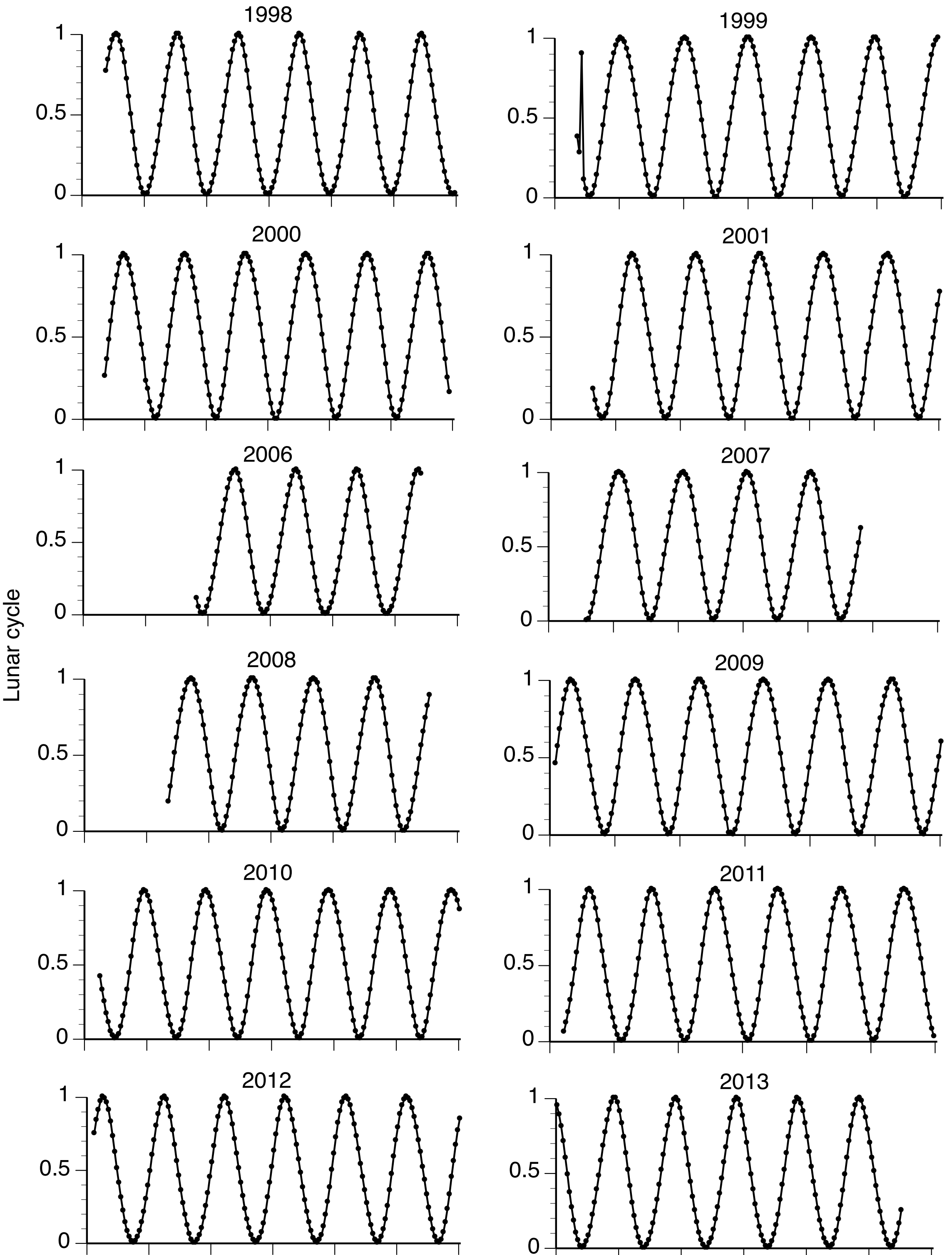


Fig. D1. Daily lunar phase for each year and day catch was monitored.

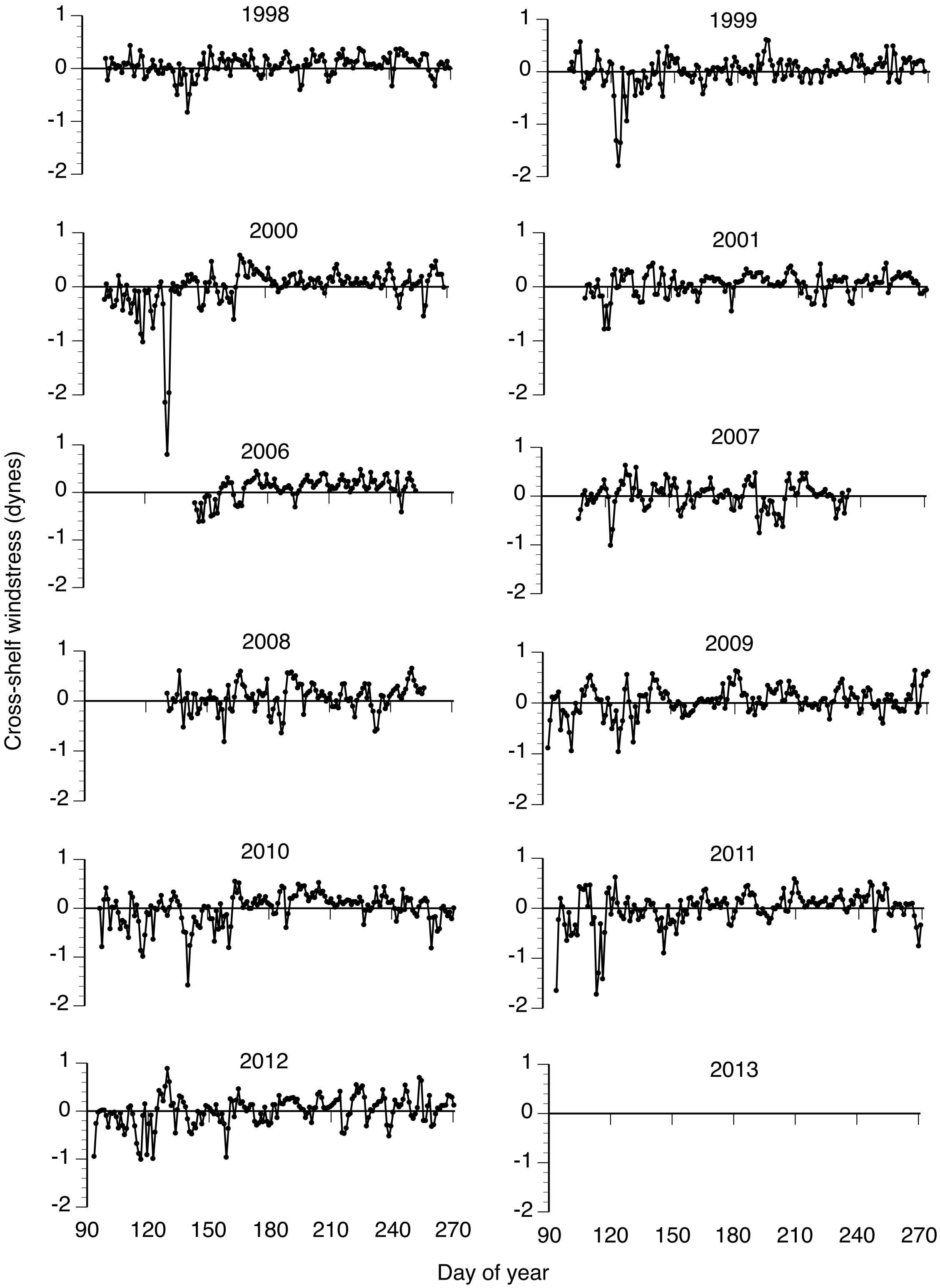


Fig. D2. Daily mean cross-shelf wind stress for each year and day catch was monitored. No data are shown for 2013 because the weather station was taken offline.

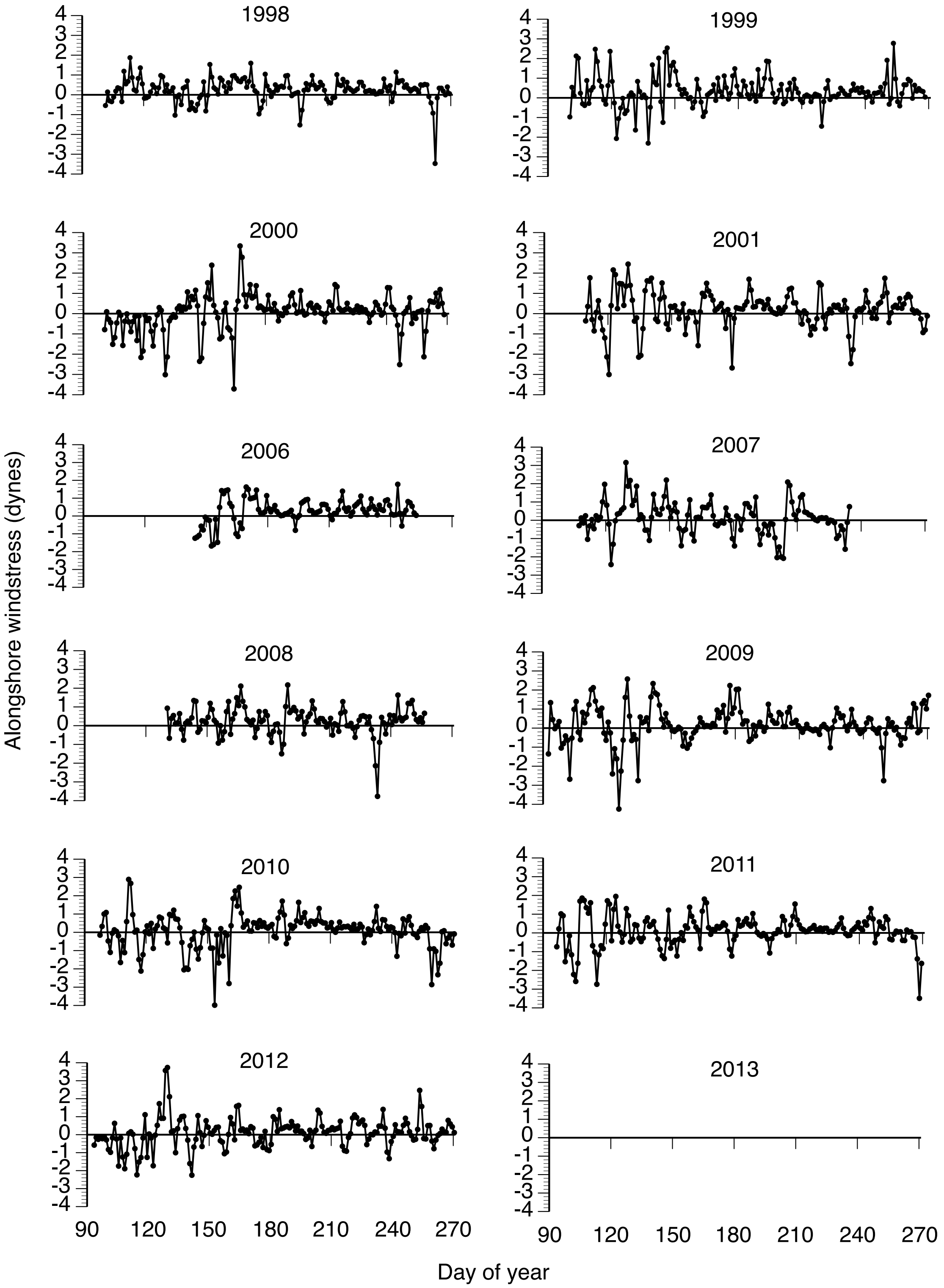


Fig. D3. Daily mean alongshore wind stress for each year and day catch was monitored. No data are shown for 2013 because the weather station was taken offline.

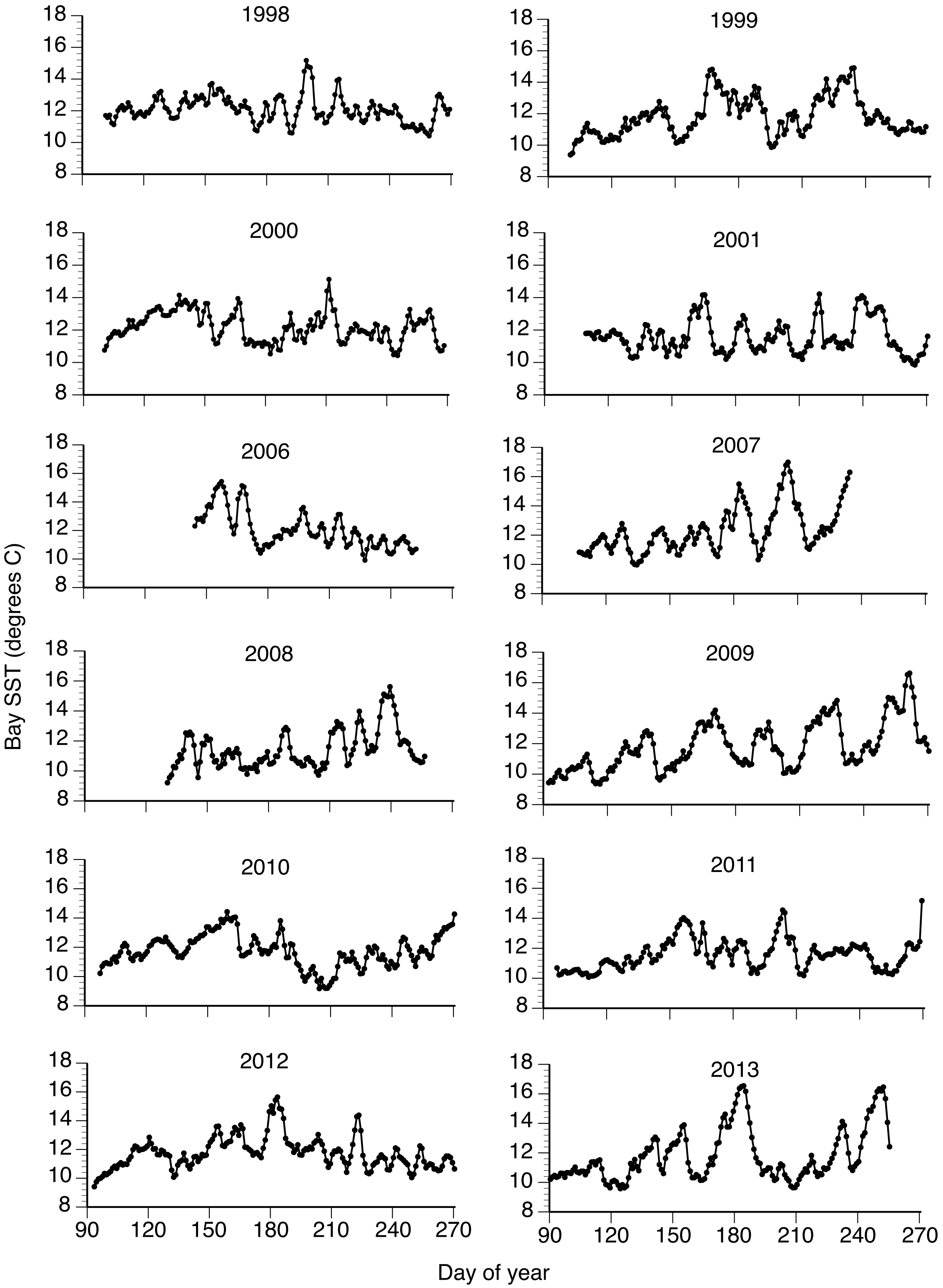


Fig. D4. Daily mean sea surface temperature in Coos Bay for each year and day catch was monitored.

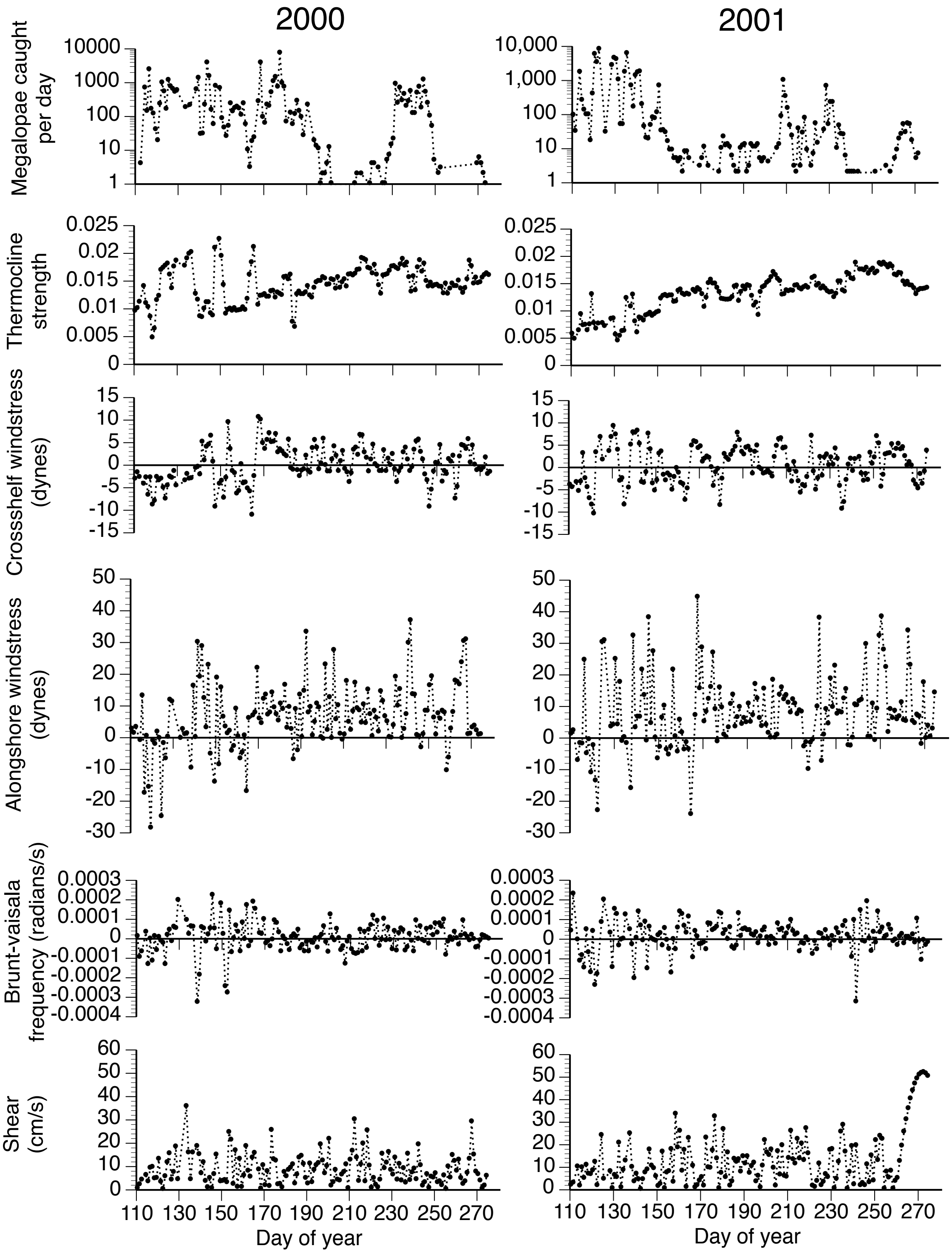


Fig. D5. Daily mean values for physical and biological variables used for the generalized additive model time series analysis.

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Chapter II

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