



A decade of modeled dispersal of Dungeness crab *Cancer magister* larvae in the California Current

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ABSTRACT: Marine populations are often typified by large annual variations in the number of larvae that return to the adult population. The Dungeness crab *Cancer (Metacarcinus) magister* is an important economic and ecological species along the western seaboard of the continental USA. Research suggests larval returns of Dungeness crabs vary annually by a factor of 1000, strongly influencing the population dynamics of the species. To understand how hydrographic conditions affect population dynamics, a light trap in Coos Bay, Oregon, was monitored daily during the recruitment season (April to September) from 1997 to 2001 and from 2006 to the present. Using an individual-based biophysical model, we tested the hypothesis that more Dungeness crab larvae recruit during negative-phase Pacific Decadal Oscillation (PDO). The model uses the Regional Oceanic Modeling System to simulate circulation in the California Current and an offline Lagrangian particle-tracking algorithm (Larval TRANSPORT Lagrangian Model, LTRANS) to model larval dispersal. We validated our model by comparing the model data to the light trap data. Our findings support the hypothesis that more megalopae (pelagic postlarvae) recruit during the negative phase of the PDO. In addition, megalopae appear to spend longer in the water column during positive-phase PDO as a result of faster development rates likely due to warmer seawater temperature. Lastly, our model suggests that the population experiences more self-recruitment than previously thought, albeit not to an extent to suggest there are multiple metapopulations.

KEY WORDS: Larval dispersal · Dungeness crab · Modeling · Vertical migration · Connectivity

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1. INTRODUCTION

The Dungeness crab *Cancer (Metacarcinus) magister* is an economically and ecologically important shelf/slope species along the west coast of the USA. The species ranges from Alaska (USA) to Baja California (Mexico); however, the population within the California Current has received the most attention from researchers because it is the most economically important fishery in the region (Rasmussen 2013). The California Current population exhibits large annual

fluctuations in size, which are hypothesized to be driven by the effect of ocean conditions (reviewed by Rasmussen 2013) and ultimately larval success (Methot 1989, Rasmussen 2013, Shanks 2013).

The California Current is one of the most well-studied currents in the world's oceans (Hickey 1979). It begins where cold, nutrient-rich waters of the West Wind Drift collide with North America approximately at the latitude of Vancouver Island, Canada (Hickey 1979). The collision causes water to flow northward as the Alaska Current, and southward as the Califor-

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nia Current. The amount of water that enters the California Current varies with the phase of the Pacific Decadal Oscillation (PDO), with more water entering the current during a negative PDO (Minobe & Mantua 1999, King et al. 2001). 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). Just seaward of the continental shelf break is the California Undercurrent, a deeper jet-like poleward current. During winter months, winds are from the south, and an inshore countercurrent (the Davidson Current) flows poleward over the continental shelf. Over a short time period (~7 d) in the spring, the winds switch from being predominately southerly to northerly (Huyer et al. 1979, Strub & James 1988); this wind change is known as the physical spring transition (Huyer et al. 1979). This pulls the California Current back onto the continental shelf causing southward flow along the shelf and favorable upwelling conditions. Following the spring transition, wind events are predominately from the north, causing the surface waters (Ekman Layer) to be advected offshore and replaced with cold, nutrient-rich waters, which are advected onto the shelf from depth (Checkley & Barth 2009).

Shanks & Eckert (2005) tested the hypothesis that the seasonal shift in currents influences dispersal by compiling an extensive data set on the life history traits of marine fishes and benthic crustaceans in the California Current. They found 3 groups of organisms with coherent sets of life history traits associated with where the benthic adult stage of the species resided. The groups were (1) adult habitat at depths <30 m (shallow subtidal and intertidal species), (2) adult habitat at depths >30 m (shelf/slope species), and adult population centered in the Southern California Bight. The shelf/slope cluster contains many important recreational and commercial species, including Dungeness crabs. In general, shelf/slope species (1) have relatively long pelagic larval durations (PLDs), (2) release their larvae during winter and spring months, and (3) have larvae that experience seasonally dependent northward and southward flow over the continental shelf due to the timing of their larval release and the length of their PLDs. The highly conserved dispersal patterns of many species within each cluster suggest that the shared life history traits may have evolved to aid in the closure of the larval pelagic phase.

Previous studies (Shanks & Roegner 2007, Shanks et al. 2010, Shanks 2013) have demonstrated that annual catch of Dungeness crab larvae in southern Oregon is significantly correlated with the PDO.

Light trap catches of megalopae (pelagic postlarvae) in Coos Bay, Oregon, increased by multiple orders of magnitude during negative-phase PDO years (Shanks & Roegner 2007, Shanks et al. 2010, Shanks 2013). They also observed a correlation between the phase of the PDO and number of megalopae caught at the end of the recruitment season, with more megalopae caught during negative-phase PDO years when flow from the north is stronger. The authors hypothesized that these patterns are attributable to more water being shifted into the California Current from the West Wind Drift during the negative PDO phase, thus enhancing southward advection of larvae. Ultimately, they posited that the 'member/vagrant' hypothesis proposed by Sinclair (1988) best explains the dispersal dynamics of Dungeness crabs.

The member/vagrant hypothesis suggests that populations persist in locations where enough planktonic larvae return to the adult population to sustain the population. Those that return are classified as members, whereas those that do not return are classified as vagrants (Sinclair 1988). Larvae must return to a location suitable for settlement, development, and reproduction (Sinclair 1988). If there are too many vagrants, the population will not persist, thus population size is, at least in part, a function of the physical oceanographic processes influencing the movement of larvae. Which individuals in the population become members and which become vagrants is established by the larval dispersal distance (Olson 1985, Cowen & Sponaugle 2009, Shanks 2009). Dispersal distances are highly variable among species, with some larvae having short dispersal distances and others traveling >1000 km (Kinlan et al. 2005, Levin 2006, Cowen et al. 2007, Shanks 2009). Under the member/vagrant hypothesis, species with large dispersal distances have more and/or larger larval retention areas, ultimately creating a more demographically open system (Sinclair 1988).

A growing body of literature suggests that the interannual variability in the number of members and vagrants in a population is influenced by large-scale climactic processes (e.g. El Niño, North Atlantic Oscillation, and PDO; Hollowed et al. 2001, Brander & Mohn 2004, Le Port et al. 2014). Despite the evidence suggesting that decadal-scale processes influence populations, studies to understand how these large-scale processes influence population dynamics are challenging to implement due to the large temporal and spatial scales at which they operate (Dickey 1990). As a result, biophysical models are an important tool for studying the effects of large-scale processes on dispersal dynamics (North et al. 2009)

because they allow researchers to expand upon what is possible with most *in situ* methods. However, models need data to validate their results. As models have become more powerful, researchers are employing novel techniques to validate the model outputs, including correlating modeled and measured settlement (Domingues et al. 2012, Drake et al. 2015), associating modeled and measured fisheries recruitment data (Kough et al. 2013), using genetic parentage data to link populations (Bode et al. 2019), and associating data with elemental fingerprints (Nolasco et al. 2018).

Here, we used a biophysical model to study the dispersal dynamics of Dungeness crabs throughout the California Current during different phases of the PDO to understand how large-scale climactic forcing events influence connectivity of the species. We simulated the transport of larvae using regional ocean models coupled with an offline particle-tracking algorithm. To validate the model, we used light trap data from earlier studies (Shanks & Roegner 2007, Shanks et al. 2010, Shanks 2013).

2. METHODS

The individual-based model (IBM) used in this study is described using the Overview, Design Concepts and Details (ODD) protocol devised by Grimm et al. (2006) and further updated by Grimm et al. (2010).

2.1. Purpose

We used an IBM of larval dispersal of Dungeness crab larvae to evaluate hypotheses presented by Shanks & Roegner (2007), Shanks et al. (2010), and Shanks (2013) to explain variability in the number of recruits. This model allowed us to assess how (1) connectivity patterns and (2) dispersal processes of Dungeness crab in the California Current differ with the phase of the PDO. To evaluate model skill, results were compared to daily measures of megalopae abundance in a light trap fished in Coos Bay, Oregon. The IBM was run using the Larval TRANSPORT (LTRANS) Lagrangian model (North et al. 2006, 2008). LTRANS models the movement of particles in the ocean from stored hydrodynamic model output, adding random vertical displacements to represent sub-grid scale processes. Model outputs were analyzed using MATLAB version 2014b.

2.2. State variables and scales

The IBM tracks the movement of particles, which represent *Cancer magister* larvae through their corresponding oceanographic habitat. For each time step in the model, a particle was defined by its age (days since hatch or release), location (latitude, longitude, and depth), developmental stage (zoeae stages I–V and megalopa), and the number of larvae represented by each individual particle, i.e. ‘super individuals.’ Super individuals were used to scale the number of larvae released into the model domain each year (Scheffer et al. 1995). Using super individuals allows the modeler to have each particle represent many individuals. This enables the model to be more computationally efficient while allowing larval production and mortality to be included (see super individual discussion in Section 2.5.1 for how they were scaled).

Environmental data were simulated using the Regional Ocean Modeling System (ROMS), a hydrostatic free surface terrain following system that is ideal for coastal and regional modeling applications (Shchepetkin & McWilliams 2005). The spatial domain of the model was adapted from Veneziani et al. (2009) and updated to include newly available forcing reconstructions. It ranges from 134 to 115.5° W and from 48° N (Washington State near La Push) to 30° N (Baja California, Mexico) and has a horizontal resolution of ~1/30° (Fig. 1). This ROMS implementation provides greater resolution near the surface and bottom of the water column, which are areas of special importance to larval movement. The model employs 42 vertical layers providing a vertical resolution ranging from ~0.3 to 8 m in the surface and bottom mixed layers (shelf/slope versus open ocean) and roughly 1 to 300 m in the interior layers (shelf/slope versus open ocean regions). Atmospheric forcing was provided by the Coupled Ocean Atmosphere Mesoscale Prediction System (<https://doi.org/10.5670/oceanog.2002.39>). More information on the model configuration, its performance, and application to larval transport studies can be found in Drake et al. (2011, 2013, 2015). Model output consisted of daily-averaged fields from 1999 to 2013. 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) were used for analysis. The model was analyzed to ensure net southward flow in the California Current was greater during negative- than positive-phase PDOs. Data to determine PDO phase were obtained from NOAA (<https://www.ncdc.noaa.gov/teleconnections/pdo/>) and gen-

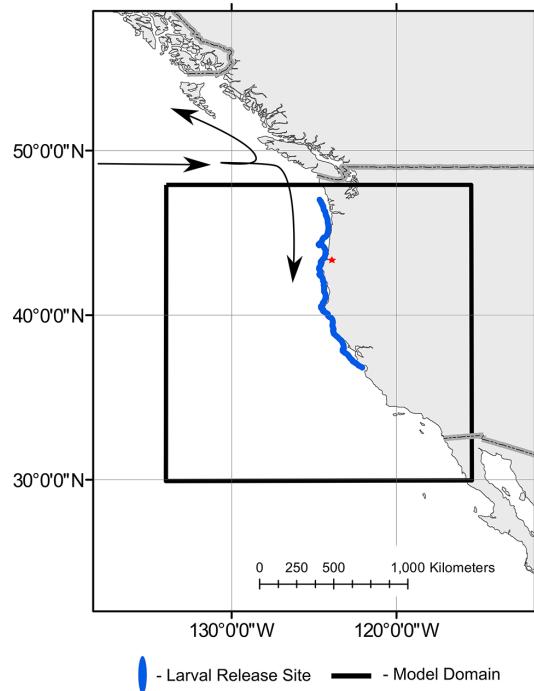


Fig. 1. Regional Ocean Modeling System model domain (black box), Dungeness crab larval release sites (blue line), prevailing current directions (black arrows), and light trap monitoring location at Coos Bay, Oregon (red star)

erated using a sum of the index values from January through July (Shanks et al. 2010). These and additional validations of the physical model specific to this study are presented in Supplement 1 at www.int-res.com/articles/suppl/m686p127_supp.pdf.

2.3. Process overview, scheduling, and initialization

Larvae were released daily from 1 December through 31 March of the following model year. Releases occurred every 3 km of coastline from nearly the southern extent of the range of Dungeness crabs, 37° N, to 47° N. Although the range of Dungeness crabs extends north of 47° N, our model domain only extended to 48° N, and thus, particles were only released as far north as 47° N to provide a 1° spatial buffer at the northern extent of the model domain. Release depths ranged from 20 to 100 m in 10 m increments based on the depths at which ovigerous females are routinely found (Rasmussen 2013). After being released, particle location, developmental stage, the number of larvae being represented by the particle, and whether or not the individual had settled was determined every 150 s.

2.4. Design concepts

2.4.1. Stochasticity

While ROMS explicitly simulates turbulent flow, the scale of this motion is necessarily larger than the grid spacing, which is multiple orders of magnitude larger than local turbulence experienced by a larva (North et al. 2006). Therefore, LTRANS includes a random displacement sub-model in order to impart horizontal and vertical sub-grid scale turbulence to each individual (Visser 1997). The random displacement is based on the vertical diffusivity from the circulation model evaluated at the location of the particle. The diffusivity incorporates a random process with a mean of 0 and standard deviation of 1 and ultimately satisfies the criterion that the time step of the displacement is much less than 1 over the second derivative of the vertical diffusivity.

2.4.2. Observations

We recorded the location of each individual particle and its status (developmental stage, the number of larvae represented by the individual, and whether or not the individual had settled) for every 30 min of simulation time from 1 December to 30 September of the following model year.

2.5. Submodels

2.5.1. Production and mortality module

Prior to scaling, each particle represented 1×10^6 individuals. Each of these particles was then multiplied by a scaling factor to make the super individuals represent the number of larvae released that year (see Supplement 2 for an in-depth explanation of how the scaling factors were calculated). For the 1999–2000 model year (i.e. the year with the lowest total number of larvae released), a super individual represented 3.5×10^5 , and for 2005–2006 (i.e. year with the highest total number of larvae released) a super individual represented 1×10^6 individuals.

Using super individuals allowed the inclusion of larval mortality in the model. A constant larval mortality rate of 0.025 d^{-1} , regardless of larval stage, was used. This mortality rate was estimated from simulations of larval mortality based on production and settlement (see Supplement 2 for more details). The effect of mortality on the number of individuals rep-

resented by each super individual for each day was calculated as:

$$N_t = N_0 e^{-0.025t} \quad (1)$$

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.

2.5.2. Development module

Larval development was modeled as a factor of temperature and time using data from Moloney et al. (1994). For simplicity, salinity was excluded from this module since its affect was minimal relative to the effect of temperature (Moloney et al. 1994). 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) (Sulkin & McKeen 1996).

2.5.3. Behavior module

Vertical location in the water column was changed depending on the development stage of simulated larvae. Zoeae were modeled to exhibit a standard diel vertical migration (Queiroga & Blanton 2005). In our model, we defined a standard diel vertical migration as larvae occupying the neuston at night and depth during day. Megalopae were modeled to exhibit a twilight migration while off the continental shelf and remain in the neuston while on the continental shelf (Jamieson & Phillips 1988). We defined a twilight vertical migration as larvae occupying the neuston for 30 min on either side of sunrise and sunset, swimming randomly at night and being at depth during the day. During the day, zoeae and megalopae resided near the bottom. These behaviors were chosen based on more extensive simulation modeling and validation (Rasmussen 2015) and *in situ* observations (Rothlisberg & Pearcy 1976, Reilly 1983). These vertical migratory behaviors were validated in this model and results are provided in Supplement 3.

The timing of the vertical migration was based on the time of sunrise and sunset for Trinidad, California (i.e. approximately in the middle of the latitudinal range in which we released particles). When particles were at depth, they were normally distributed around the depth they occupied. When they were at

the surface or near the bottom, they had a 1-sided normal distribution away from the surface or bottom. In both instances, a standard deviation of 6 m was used to define the distribution. For each larval stage, swimming speeds were altered to represent values from laboratory or *in situ* studies; zoeae I-II vertically migrated at 1 cm s⁻¹, zoeae III-V vertically migrated at 1.5 cm s⁻¹, and megalopae vertically migrated at 10 cm s⁻¹ (Rasmussen & Shanks 2014).

2.5.4. Settlement module

Once a particle had become a megalopa, we determined if it was in a suitable settlement habitat at each time step. Suitable habitat was defined as depths <50 m (McConaughey et al. 1992, Eggleston & Armstrong 1995, Rasmussen 2013). No time limit was incorporated into the settlement module since megalopae held in captivity have been successfully kept alive and unsettled for ~300 d (Gaumer 1971). Larvae continued to be tracked after their initial settlement and were allowed to settle multiple times. The reason for this choice is that megalopae are often observed swarming in the same location for days at a time, indicating that while some individuals of that swarm may settle in a given location, other individuals in the swarm continue to disperse. Thus, since computational limitations restricted the number of particles we could effectively track, the combination of continual tracking and super individuals allowed us to capture these swarming dynamics.

2.6. Model validation

From approximately 1 April to 30 September of the years 2000–2001 and 2006–2013 we monitored the daily catch of Dungeness crab megalopae to a light trap operated in Coos Bay, Oregon. Each day, all of the megalopae caught in the light trap were enumerated using a dissecting microscope. If the total number of individuals was >2000, the number of individuals was determined by weighing the sample (Shanks & Roegner 2007, Shanks et al. 2010). We compared the light trap time series to a time series of modeled settlers. The modeled time series was defined as the number of megalopae that settled within 10 km of Coos Bay on each day. Time series were statistically associated with each other by calculating the Pearson correlation coefficients between the time series. Periodograms of both the light trap and model time series were also calculated and com-

pared to each other visually. Periodograms allow researchers to search for regular events in a time series, in our case testing if the number of returning megalopae was cyclic. A peak at 7 d, for example, suggests there is a 7 d cycle in the time series. As the daily return of megalopae is influenced by a multitude of abiotic and biotic variables, a shared cycle between the model and the light trap would suggest that the model is capturing, at minimum, the largest drivers of returning megalopae. Peaks observed in only 1 of the time series obviously indicates dissimilarities. This could be a result of missing processes in the model, loss of spectra because of the light trap being operated in the estuary, or many other reasons. Regardless, if the peaks are not consistently observed in every year, it is likely the pattern is not one that affects dispersal consistently across years.

2.7. Analysis

Patterns of larval connectivity were examined using connectivity matrices (Cowen & Sponaugle 2009). Larval release locations were aggregated into 0.1° latitudinal bins. For each release location, the numbers of settlers (see Section 2.5.4) for every 0.1° of latitude along the coast were summed and associated with the release location. To assess connectivity differences in association with the phase of the PDO, we averaged the annual settlement values for all years associated with a specific phase of the PDO. Finally, to examine differences with PDO phase, we subtracted the average number of settlers from the negative PDO connectivity matrix from the average number of settlers from the positive PDO connectivity matrix. No formal statistical analyses were conducted due to known issues with running statistics on simulations (White et al. 2014).

To better understand how dispersal patterns differed with the phase of the PDO, we calculated the average number of days that a simulated larva took to molt to a megalopa. We also examined how the length of the PLD (larval release to settlement) differed with PDO. Both of these analyses were conducted by summing the number of settlers in each year into categories (days from hatch or length of PLD), averaging years with the same PDO phase (i.e. positive or negative). To determine the dispersal distance of simulated larvae, for each settlement event we measured the linear distance from release to settlement. These data were then summed for each year, and then years with the same PDO phase were averaged. All of these analyses were calculated

using the first settlement event of each particle being tracked. As above, no formal statistical analyses were conducted due to the fact that the data are simulations.

3. RESULTS

3.1. Model validation

A total of 10 larval dispersal years were modeled and associated with the corresponding light trap data (Fig. 2). The light trap and model time series for the 2006 settlement season were the most strongly correlated ($r = 0.96$) and the time series for 2007 settlement season were the least correlated ($r = 0.49$; Fig. 2). Correlations were not significant in 2007 and 2008 but were ($p < 0.001$) in all other years (Fig. 2). Distinct periodicities in both the light trap and the modeled time series were obvious. Although the trends were similar, the number of returning larvae to the light trap and in our model were not that closely associated, suggesting the model represented trends in larval dynamics but missed things that influenced magnitude. Based on the periodogram analyses, both the modeled and light trap time series had spectral peaks at ~4–5 d (Fig. 3). The modeled time series often had secondary peaks at additional longer time periods, which were not often observed in the light trap data.

3.2. Hypothesis testing

Consistent with earlier hypotheses (Shanks & Roegner 2007, Shanks et al. 2010, Shanks 2013), southward advection of larvae was increased during negative-phase PDO years, and the converse, more northward advection of larvae during positive-phase PDO years, also occurred. These patterns are apparent throughout the connectivity matrix and are somewhat hidden at the northern extent because of model boundary effects. In total, 71% of settling larvae were advected south during negative PDO years and 61% during positive PDO years.

In general, over the course of their larval development, most larvae were advected to the south regardless of PDO phase. Larvae were advected a slightly greater distance to the south during negative PDO years and a greater distance to the north during positive PDO years (Table 1). However, on average, particles were advected <100 km from their larval release site. No larvae were lost to the southern boundary of the model. There was little

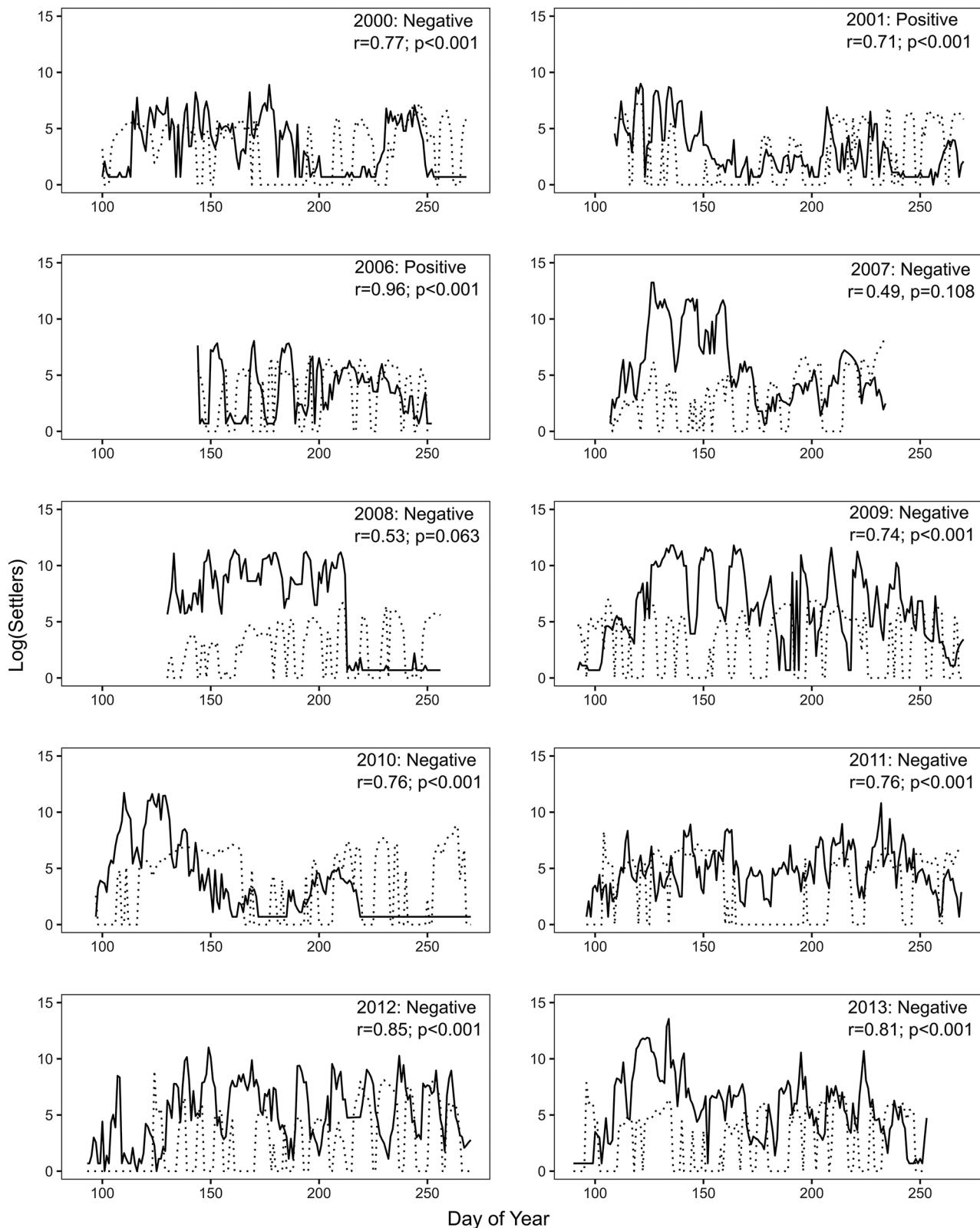


Fig. 2. Daily settlement of Dungeness crab megalopae to a light trap monitored in Coos Bay, Oregon (solid line) and the number of settlement events in the model occurring within 10 km of Coos Bay (dashed line). Pearson's correlation is the correlation between the modeled settlement time series and the light trap data. Positive (negative): positive-phase (negative-phase) Pacific Decadal Oscillation

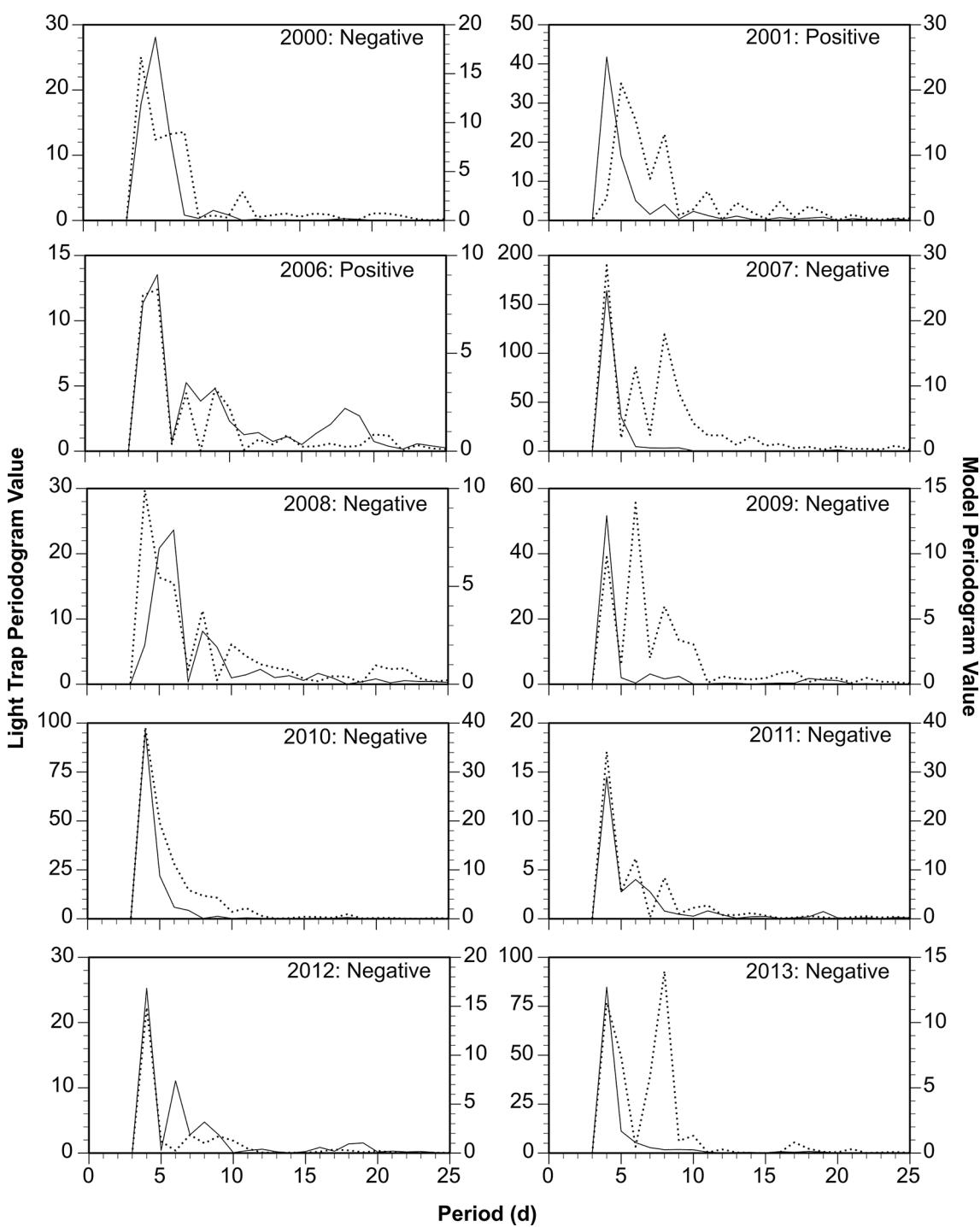


Fig. 3. Power spectral density for the light trap catch of Dungeness crab megalopae (solid line) and model output (dashed line). Positive (negative): positive-phase (negative-phase) Pacific Decadal Oscillation

difference in the percentage of particles lost offshore between PDO phases (Table 1). More larvae were lost out of the northern boundary during positive PDO years than negative PDO years; however, in both instances, the number lost from this bound-

ary was relatively low. This is likely due to not releasing larvae near the northern extent of the model domain.

Connectivity matrices demonstrated that a large amount of interannual variability in the alongshore

Table 1. Average dispersal metrics for positive- and negative-phase Pacific Decadal Oscillation (PDO). All averages are presented as mean \pm SD

	Positive	Negative
Number of model years	2	8
Number of larvae released per year ^a	$3.4 \times 10^{11} \pm 1.9 \times 10^{11}$	$3.7 \times 10^{11} \pm 8.6 \times 10^{10}$
Average number of settlers ^b	$1.6 \times 10^{12} \pm 2.2 \times 10^{11}$	$2.3 \times 10^{13} \pm 1.4 \times 10^{12}$
Average time from hatch to molting to megalopa (d)	115 \pm 9	150 \pm 19
Average pelagic larval duration (d)	175 \pm 11	180 \pm 17
Average temperature experience during development (°C)	8.75 \pm 0.89	7.25 \pm 0.55
Average dispersal distance (km) ^c	-72 \pm 10	-40 \pm 14
Percentage of number released lost from domain to north (%)	1.5	0.05
Percentage of number released lost offshore (%)	53.1	55.8
Percentage of total settlers settling south of release site (%)	62.1	71.3
Percentage of total settlers settling north of release site (%)	37.9	28.7

^aAverage number of larvae released each year is based on the scaled number of super individuals
^bNumber of settlers is greater than larvae released because particles were continually tracked after their initial settlement event and allowed to settle more than one time
^cNegative dispersal distances denote southward transport

settlement patterns (Fig. 4), with years such as 2008 having small settlement events and years such as 2010 experiencing large settlement events. Further, the location of settlement hot spots varied annually as well. Despite this, most connectivity occurred near the 1:1 line. Combining connectivity matrices by their PDO phase, we observed more settlement events during negative than positive PDO years (Fig. 5). During negative PDO years, there were more settlement events at the latitudes in the middle of our model domain ($\sim 38\text{--}44^\circ\text{N}$). Regardless of PDO phase, there was evidence of self-recruitment (settlement at larval release sites) in the population.

The length of time from larval release to molting into a megalopa was 115 ± 9 d during positive PDO years and 150 ± 19 d during negative PDO years (Fig. 6, Table 1). These differences were likely associated with the temperature experienced by the larvae during development (Table 1). Regardless of PDO phase, the average PLD (time from larval release to settlement) was essentially the same: 175 ± 11 d during positive PDO years and 180 ± 17 d during negative PDO years (Fig. 6, Table 1). In other words, a larva remained as a megalopa 35 d longer on average during positive PDO years.

4. DISCUSSION

Our simulations are consistent with the findings of Shanks et al. (2010) and Shanks (2013); we found more settlement during negative- than positive-phase PDO years, although it is worth noting that we

only had 2 modeled years that were positive PDO phases. Further, the increased southward flow in the California Current during the negative PDO also likely explains why settlement was greater at the northern extent of the model range during negative than positive PDO years. On average, fewer larvae were lost through the northern boundary and were excluded from analyses during negative than during positive PDO years. This suggests that during negative PDO years, larval retention at the northern end of the California Current is enhanced (less loss to the Alaska Current), which is corroborated by the greater catch of smaller megalopae later in the recruitment season (Siegel et al. 2003, Shanks et al. 2010). These small megalopae appear to originate from Puget Sound, and genetic studies were unable to reject a hypothesis that late-season megalopae may originate in Puget Sound (Lee & O'Malley 2020). 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 apparently originating from the California Current have been reported in the Alaska Current system (Park et al. 2007). This, combined with the greater number of larvae advected to the south of their release site during negative PDO years, is consistent with prior observation and hypothesis (Shanks & Roegner 2007, Shanks et al. 2010, Shanks 2013) that there has been more settlement, larger light trap catches, during negative PDO years because the increased southward flow during negative PDO years enhances the retention of larvae in the California Current.

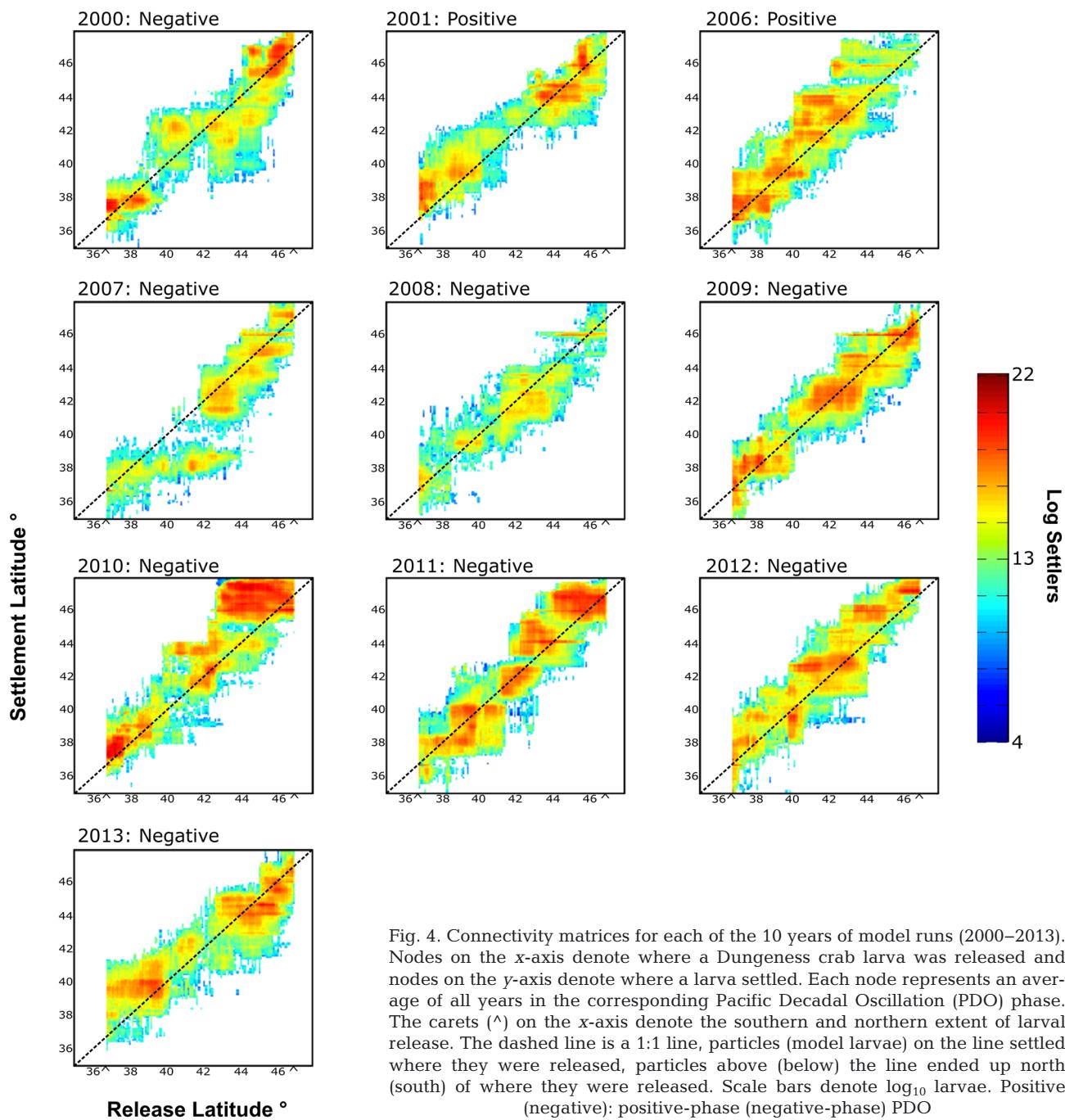


Fig. 4. Connectivity matrices for each of the 10 years of model runs (2000–2013). Nodes on the x-axis denote where a Dungeness crab larva was released and nodes on the y-axis denote where a larva settled. Each node represents an average of all years in the corresponding Pacific Decadal Oscillation (PDO) phase. The carets (^) on the x-axis denote the southern and northern extent of larval release. The dashed line is a 1:1 line, particles (model larvae) on the line settled where they were released, particles above (below) the line ended up north (south) of where they were released. Scale bars denote \log_{10} larvae. Positive (negative): positive-phase (negative-phase) PDO

Although modeled larvae developed into a megalopa faster during positive than negative PDO years, the average PLD varied little. The difference in the length of time from hatch to molting into a megalopa is driven by the differences in temperature experienced by the larvae. The average temperature experienced by a larva during a positive PDO was 1.5°C higher than that of a larva experienced during a negative PDO. Moloney et al. (1994) developed a model of the relationship between temperature and larval de-

velopment rate. They found that development was faster in warmer water. Using this same model, we found that the phase of the PDO strongly influences this development rate. However, a surprising discovery is that average PLD did not differ greatly with the phase of the PDO. Since megalopae start to return after the day of the year of the spring transition (Shanks & Roegner 2007), it is possible that larvae develop faster because of warmer temperatures during positive PDO years, but are unable to recruit because set-

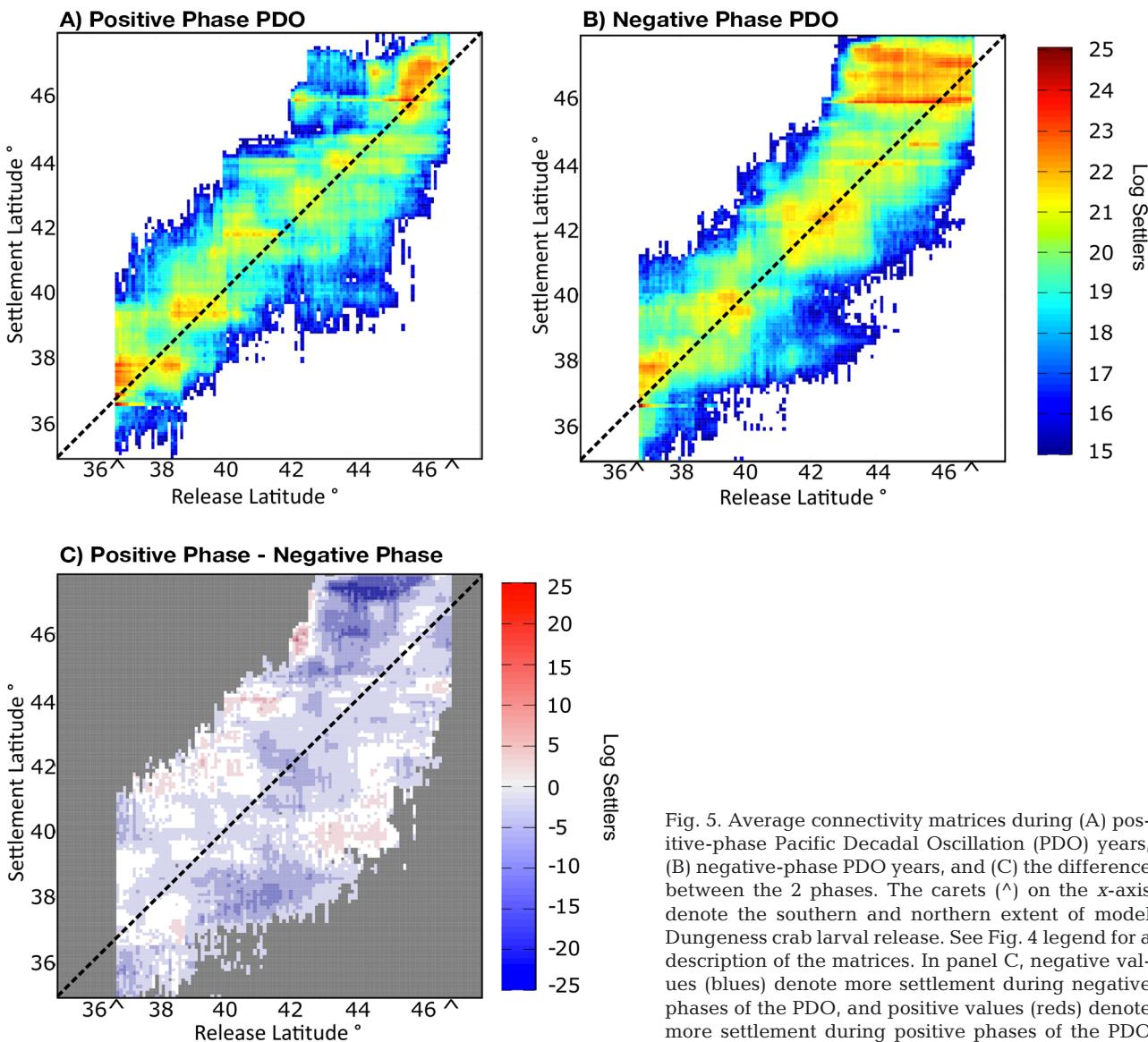


Fig. 5. Average connectivity matrices during (A) positive-phase Pacific Decadal Oscillation (PDO) years, (B) negative-phase PDO years, and (C) the difference between the 2 phases. The carets (^) on the x-axis denote the southern and northern extent of model Dungeness crab larval release. See Fig. 4 legend for a description of the matrices. In panel C, negative values (blues) denote more settlement during negative phases of the PDO, and positive values (reds) denote more settlement during positive phases of the PDO

lement only occurs following the spring transition. Regardless, remaining a megalopa in the water column for a longer period of time likely negatively influences recruitment success of the species since megalopae are a common food of many marine organisms in the California Current (Rasmussen 2013).

The current paradigm suggests that particles with a longer PLD are likely transported greater distances and larval retention and recruitment near their natal origin is infrequent (Siegel et al. 2003, Shanks 2009). Many of the species living on the continental shelf in the California Current have long PLDs and thus have been hypothesized to have long transport distances (Siegel et al. 2003). Our model demonstrates that despite a long PLD, there is a higher level of larval retention than would have been predicted by theory.

This finding is consistent with the member/vagrant hypothesis of Sinclair (1988) that the PLD of a species is adapted to the oceanographic region that encompasses the population in such a way as to enhance membership in the population.

Our findings also support the hypothesis of Shanks & Eckert (2005) that the timing of larval release (winter) and 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-phase PDO years, the maximum dispersal distance of larvae occurred at a PLD of ~90 d. Dispersal distance declined and approached 0 with both shorter and longer PLDs. This result may indicate that larvae transported larger distances recruit

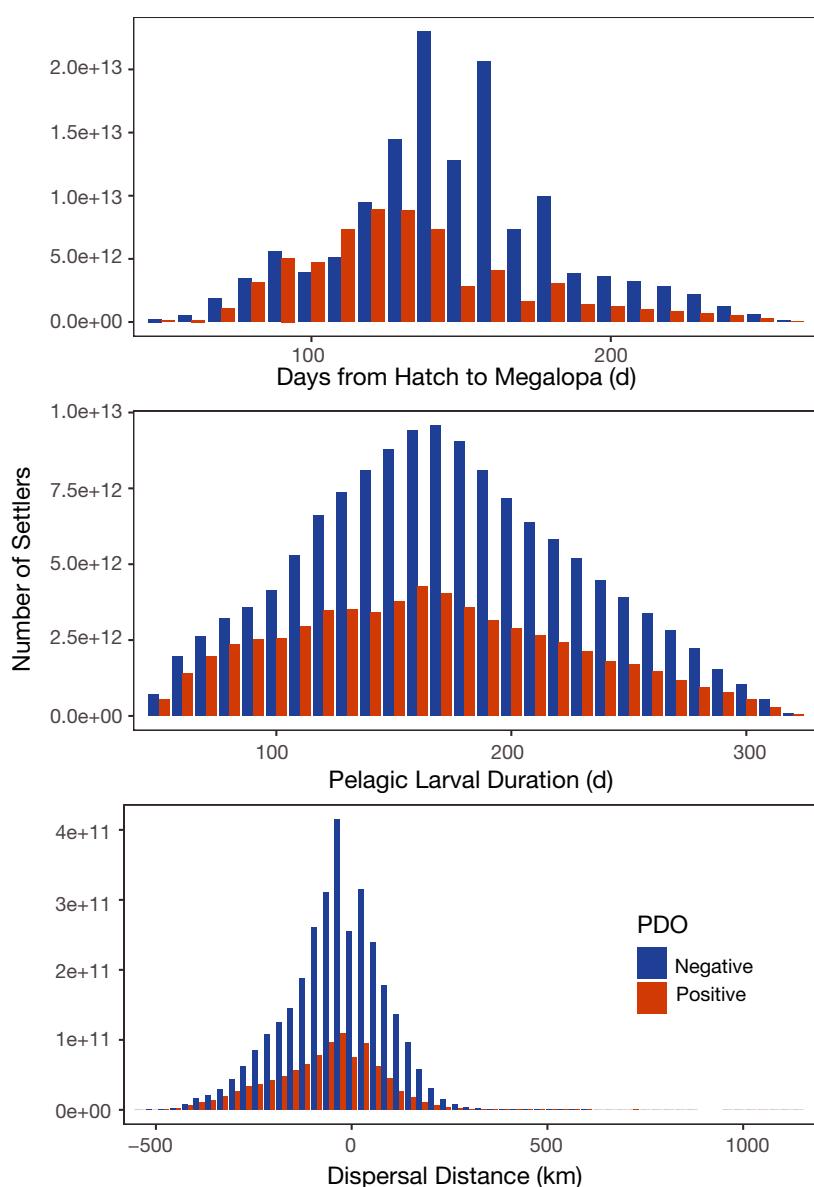


Fig. 6. (A) Number of Dungeness crab settlers from time of release to molting into a megalopa, (B) pelagic larval duration (i.e. time from hatching to larval settlement), and (C) dispersal distance for positive-phase (red) and negative-phase (blue) Pacific Decadal Oscillation (PDO) years. Negative (positive) dispersal distances denote southward (northward) transport. Average values are presented in Table 1

earlier. Moreover, as the recruitment season progresses, the probability of self-recruitment actually increases. Shanks & Eckert (2005) demonstrated that the life history characteristics of many shelf/slope species (a group to which Dungeness crabs belong) 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 Dungeness crab larvae.

The recruitment of larval pink shrimp *Pandalus jordanii* and rockfish (*Sebastodes spp.*) is correlated with many of the same variables (e.g. the spring transition and upwelling) as is the recruitment of Dungeness crabs (Hannah 1999, 2011). Both shrimp and rockfish release larvae with a long PLD during winter months and exhibit vertical migration behavior (Hannah 1999, 2011, Love et al. 2002); thus it is likely larvae of both of these species groups also experience an advective regime similar to that of Dungeness crabs. The similarities with other species may suggest that although some aspects of adult life histories of these species are very different, the physical oceanographic processes influencing larval dispersal are similar and may have acted as a selective force to enhance recruitment of larvae to the adult population ('membership'; per Sinclair 1988).

A population genetics study of adult Dungeness crabs along the west coast in 2012 found that genetic differences increased with increasing geographic distance between sampling sites (Jackson et al. 2018), indicating the presence of isolation by distance (Wright 1943). This finding suggests that in at least some generations, Dungeness crabs maintain a pattern of gene flow that follows geographically limited dispersal. In this manner, gene flow occurs within spatially restricted 'neighborhoods,' which are linked together as described by the 1-dimensional stepping-stone model (Kimura & Weiss 1964). However, neighborhoods appear to be continuous as opposed to discrete, thereby lacking well-defined boundaries (Jackson et al. 2018).

Further, genetic relatedness among individuals was greater in several areas in which we observed the strongest rates of self-recruitment. However, this weak genetic structure was not apparent 2 yr later (2014). A subsequent genetic analysis of megalopae caught in light traps in 2017 and 2018 further corroborated evidence of strong gene flow in the region, but suggested that selective pressures and ocean conditions influence the genetic composition of larval recruits both intra- and inter-annually (Lee

& O'Malley 2020). Viewed in combination, genetic studies and our modeling data suggest that while self-recruitment occurs, the population is demographically open and the amount of self-recruitment varies annually.

Our oceanographic model provides deeper insight into how large climactic cycles affect the dispersal of Dungeness crab larvae in the California Current. This understanding of how dispersal is influenced by decadal shifts in circulation will be of use to managers attempting to understand population connectivity, both now and as populations undergo climate-mediated shifts in distribution. In the future, attempts should be made to examine the connectivity among Dungeness crab populations throughout the Alaska and California Currents. These 2 ecosystems have different hydrography, which likely dramatically affects the transport of larvae. Our model suggests that vagrants from the crab populations residing in either current regime end up in the population of the other current regime. Quantifying the role and importance of these vagrants could provide interesting insight into the connectivity between highly different hydrographic regimes.

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