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Atmospheric forcing drives recruitment variation in the Dungeness crab (*Cancer magister*), revisited

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ABSTRACT

For 12 yr (1997–2001, 2006–2012) daily abundance of *Cancer magister* megalopae was measured in Coos Bay, Oregon. Before 2007 from 2000 to 80 000 megalopae were caught annually. In 2007, catch jumped and has since varied from 164 000 to 2.3 million. The step change in catch size appears related to a shift to negative Pacific Decadal Oscillation (PDO) values. Late season catches, which cannot be due to local spawning, are negatively correlated to the PDO, suggesting that these megalopae derive from north of the California Current. During periods of lower and higher catches, annual returns of megalopae were significantly negatively correlated to the day of the year of the spring transition and positively correlated to the amount of upwelling during the settlement season. The size of the Oregon commercial catch lagged 4 yr to allow for growth of recruits into the fishery is set by the number of returning megalopae; the relationship is parabolic. At lower returns, the population is recruitment limited, but at higher returns, density-dependent effects predominate and set the commercial catch. Lagged commercial catches in Washington and Northern and Central California were also related to the number of megalopae returning to Coos Bay, suggesting that the forces causing variation in larval success are coast wide. If high return rates are due to a PDO regime shift, then for years to decades the commercial catch may be set by density-dependent effects following settlement and the huge numbers of returning megalopae may impact benthic community structure.

Key words: *Cancer magister*, density-dependent, Dungeness crabs, megalopae, Pacific Decadal Oscillation, recruitment limited, recruitment, spring transition, upwelling

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INTRODUCTION

In an earlier paper, Shanks and Roegner (2007) demonstrated an inverse relationship between the day of the year of the spring transition and the number of returning Dungeness crab (*Cancer magister*) megalopae (more megalopae returned when the spring transition was early). They also demonstrated a direct linear relationship between the number of returning megalopae and the size of the subsequent commercial catch within much of the California Current (CC). In a subsequent paper, Shanks *et al.* (2010) presented data suggesting that the number of returning megalopae also varies with the Pacific Decadal Oscillation (PDO); more megalopae tend to return during negative phase PDO years. Here, using data from an expanded 12-yr time series (three additional years of data), the effect of atmospheric forcing on the annual variation in the number of returning megalopae was further explored by investigating a third factor, the amount of upwelling during the period megalopae return to the shore, which affects larval success. Secondly, the relationship between the number of returning megalopae in a year and the subsequent commercial catch in Washington, Oregon and California was updated. This new relationship includes data from 2 yr of extremely large returns of megalopae and the commercial catch they generated. The very large numbers of returning megalopae has caused the previous linear relationship to evolve into a parabolic one in which density-dependent effects on recruit survival play a large role in setting the size of the commercial catch. Megalopae continue to settle late into the summer, past the time when locally hatched larvae should still be in the plankton. I present data suggesting that these larvae were from north of the California Current and have been transported southward by currents.

METHODS

A detailed description of the sampling methods used from 1997 to 2001 can be found in Shanks and Roegner (2007). Very similar sampling methods have been used since the time series was restarted in 2006 through to the present. Megalopae were caught using a light trap placed in the Charleston small boat harbor in Coos Bay, Oregon (43°20′41″ N, 124°19′15″W). The trap was fished from roughly the beginning of April through September (the local settlement season for *Cancer magister*) and megalopae were removed from the trap daily. The total number of megalopae captured in each settlement season was used as an index of the abundance of megalopae returning to the coast or annual larval success.

When a daily sample of megalopae was <2000, either the entire sample was counted or it was split using standard methods and then counted (Omori and Ikeda, 1984). Starting in 2007, the daily and annual abundance of megalopae increased dramatically, with daily catches during pulses on the order of tens of thousands of megalopae (5–10 L of megalopae). We could not count these huge samples efficiently. To estimate the number of megalopae, we carefully drained off the water, weighed the entire sample, and then divided by the weight of 100 megalopae.

To test the hypothesis that population size is limited by the number of returning megalopae, we correlated the index of settling megalopae to the size of the Oregon, Washington and California commercial catch landed 4 yr later in Oregon and California and 5 yr later in Washington, the time needed for megalopae to grow into the fishery (Shanks and Roegner, 2007). The Oregon Department of Fish and Wildlife, California Department of Fish and Game, and the Washington Department of Fish and Wildlife provided commercial catch data for each state. During the annual fishing season, essentially all legalized male crabs are caught (Hackett *et al.*, 2003), hence the size of the commercial catch is an excellent measure of the 4- or 5-yr-old year class. The day of the year of the spring transition was calculated using the methods described in Shanks and Roegner (2007). Data on the PDO index and the upwelling index for 45°N were obtained from internet sources (http://jisao.washington.edu/pdo/PDO.latest, and http://www.pfeg.noaa.gov/pfel, respectively).

RESULTS

We have sampled the number of returning megalopae for 12 yr; 1997–2000 and 2006 to the present. During this period the total number of megalopae caught during the settlement season has varied by a factor of over 1000. The lowest annual catch, 1987, was in 1997, an El Niño year, and the largest was in 2009 when 2 390 000 megalopae were caught (Fig. 1). Between 1997 and 2006, the largest annual catch of megalopae was about 80 000, but in 2007 the annual catch abruptly jumped to 1.7 million and remained near or above a million for the next 4 yr (Fig. 1). In Shanks *et al.* (2010), we reported a significant relationship between the summed monthly PDO values for winter and spring and the total number of returning megalopae and attempted to use this relationship to account for the 2007 shift to much annual catches. This relationship continues to hold (Fig. 2); the number of returning megalopae tends to be higher in negative PDO years; however, there is quite a bit of scatter in this relationship as well as data points that do not fit this simple interpretation (e.g., years with negative PDO, but lower catches).

The pattern of daily catch in 2010 was unique; initially the catch was quite high with hundreds of thousands of megalopae caught in each of the first two pulses, but then catch dropped off dramatically and remained low throughout the remainder of the summer (Fig. 1). 2011 was a negative PDO year (summed PDO-3) and, given previous results, catch was expected to have been very high, but catch was an order of magnitude less than expected (Fig. 1). Observations from these 2 yr suggested that other factors might be affecting returns.

In 2010, the spring transition was relatively early (15 March) but within a week of the spring transition, upwelling stopped and was replaced by downwelling with some quite strong events (Fig. 3). Upwelling did not return until mid-April, but even after this date upwelling continued to be interrupted by strong downwelling events. In 2011, downwelling was strong through March, as evidenced by large positive sea level anomalies (Fig. 3). The spring transition occurred during the first week in April but, as in 2010, repeated downwelling events interrupted subsequent upwelling. The summed daily upwelling index for March through September (the local settlement season for Dungeness crab megalopae) was negative or small in both years, indicating that upwelling was weak in both years. Upwelling conditions in 2009, a year with very large returns of megalopae, were quite different (Fig. 3); the spring transition occurred around the end of March, this initial upwelling event generated a sea level anomaly that was about twice as large as in 2010 and 2011, and downwelling events punctuated the upwelling season, but they were much weaker and shorter than in 2010 and 2011. The net effect was that in 2009, during the settlement period, the summed upwelling index was strongly positive, indicating that upwelling was strong through the season.

These observations suggested that the number of returning megalopae was affected by both the day of

Figure 1. Daily catch of *Cancer magister* megalopae in a light trap fished in Coos Bay, Oregon. The annual return of megalopae has been followed for 12 yr with total catch over the settlement season varying over three orders of magnitude from a low of 1987 in 1997 to a high of 2 390 000 in 2009.

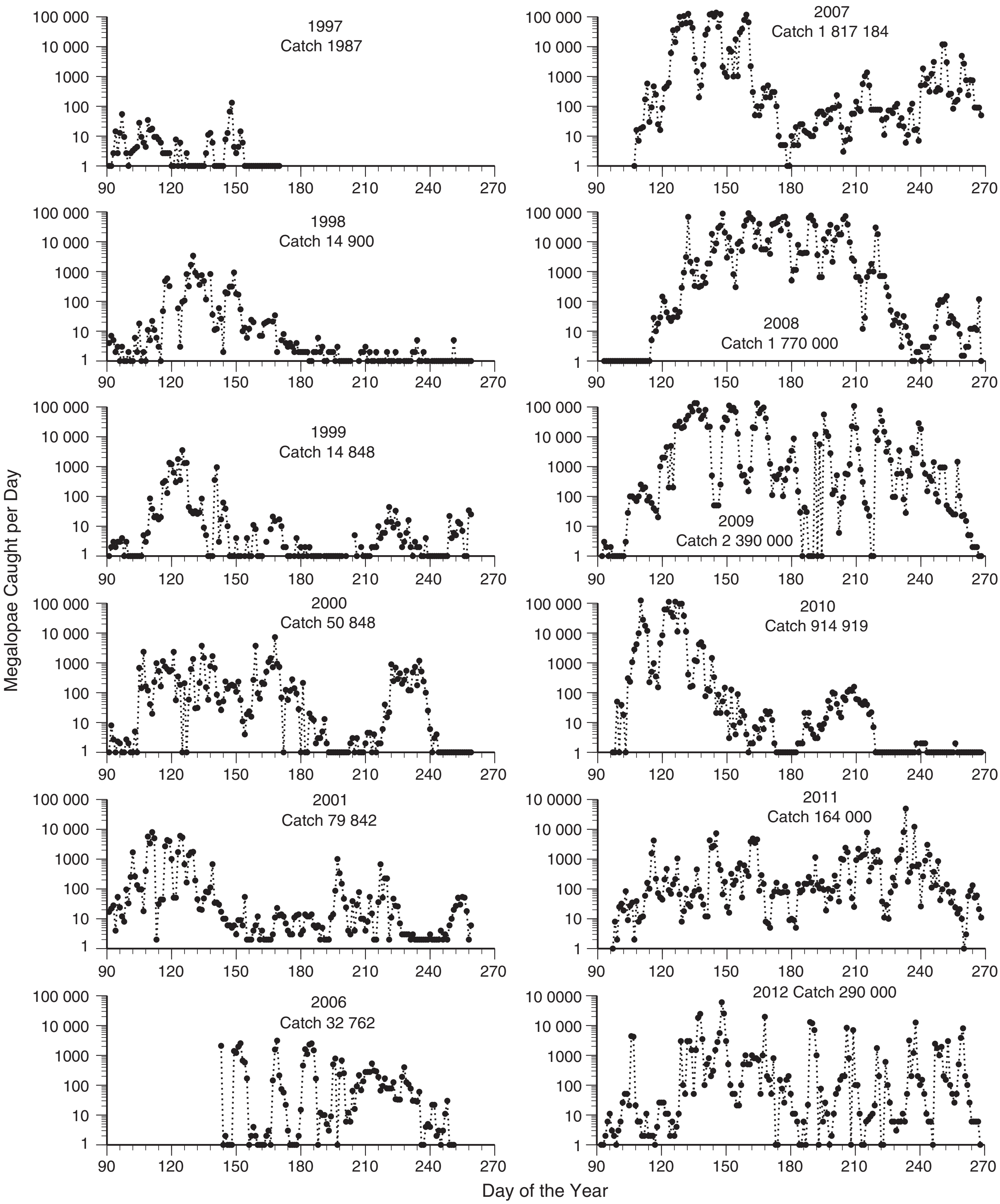
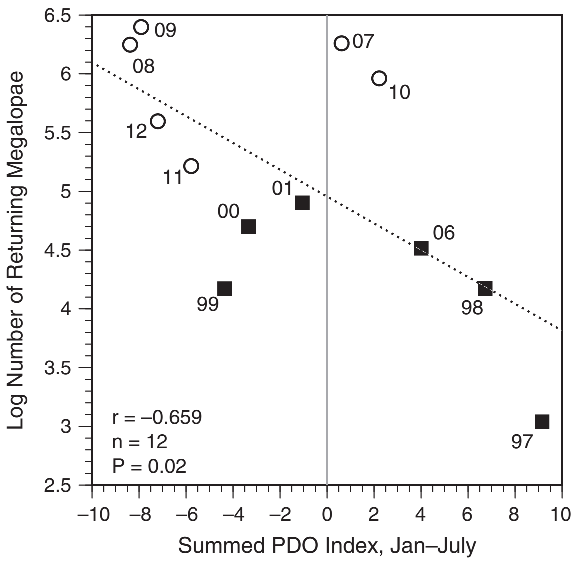


Figure 2. Relationship between the summed PDO index for January through July and the log number of megalopae caught per season. Data from 1997–2006 (solid squares) and 2007–2011 (open circles) settlement years plotted separately. Numbers beside data points are the sample years. The dashed line and statistics are the result of a regression run between the two factors using all the data.



the year of the spring transition and the amount of upwelling during the period when megalopae return to the coast. These relationships were tested by plotting day of the year of the spring transition and amount of upwelling during the settlement season against the number of megalopae caught each year, but the data were separated into years before (1997–2001 and 2006) and after the shift to large catches (2007–2011) (Fig. 4), years with catches <100 000 versus years with >100 000 caught. The two plots have two sets of roughly parallel lines with all correlations significant; both before and after the shift to high catches, catch varied inversely with the day of the year of the spring transition and directly with the amount of upwelling in spring.

One of the curious features of the pattern of returning megalopae is how long the settlement season lasts; we catch megalopae from early spring through the entire summer and some years into the fall (Fig. 1). Peak larval release along the coast from California through Washington occurs between January and February (Strathmann, 1987). If the megalopae we catch in the light trap are from this portion of the coast then, with up to a 5-month larval period (Strathmann, 1987), we should no longer catch megalopae after July, but we continue to catch megalopae for at least two additional months. In British Columbia hatching occurs from December through June and peak hatch off Queen Charlotte Island is in late April (Strathmann, 1987). Southward currents may transport larvae hatched in Canadian waters to Oregon within a 4- or 5-month pelagic development. During years with negative PDOs the flow to the south is stronger and this strengthened southward flow may carry larvae from coastal British Columbia south into the California Current. If this is true then we should see a significant negative correlation between the PDO and the number of megalopae caught in August and September. This is exactly what we found (Fig. 5).

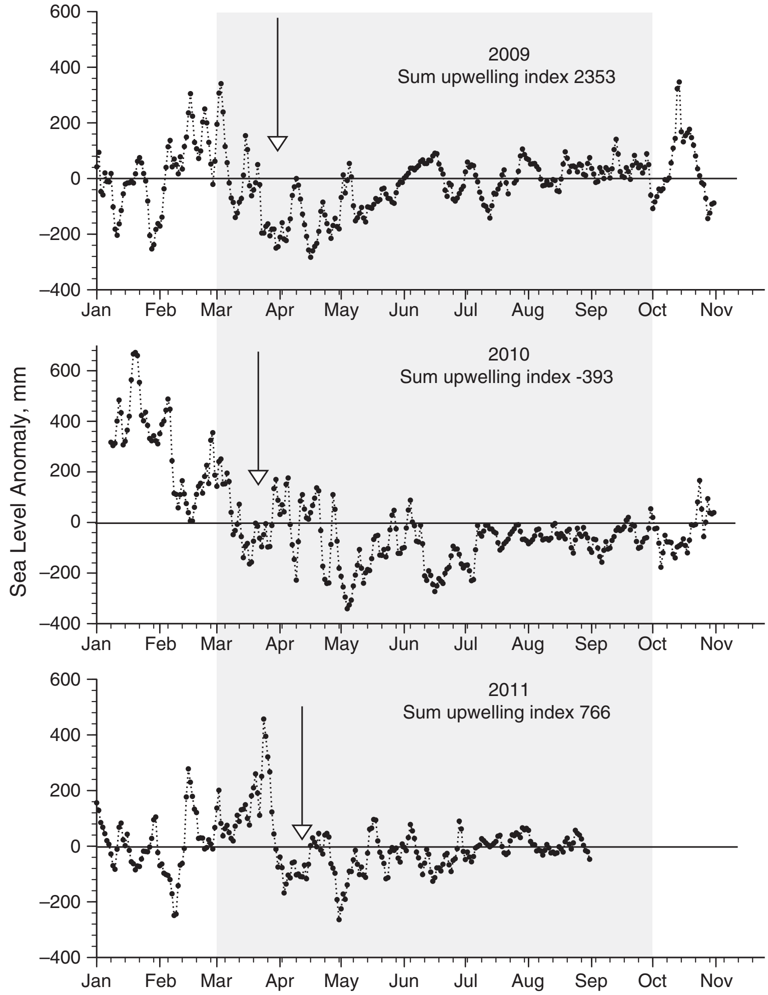
In the initial 6 yr of the time series (1997–2000 and 2006), the relationship between the log of the number of megalopae caught and the log of the size of the commercial catch was linear; during this period the adult population was recruitment-limited (Shanks and Roegner, 2007; Shanks *et al.*, 2010). With the huge increase in the number of returning megalopae that began in 2007 this linear relationship would likely not continue to hold; density-dependent mortality following settlement would cause the relationship to become parabolic rather than linear. Figure 6 is a log plot of megalopae returns and commercial catch in all of Oregon (lagged 4 yr) through the 2011/2012 fishing season. The relationship is parabolic and is described by a significant second order polynomial.

In addition, I compared the log of the number of returning megalopae to Coos Bay with the lagged commercial catch along the open coast of Washington, northern California (e.g., Oregon border to Sonoma County), and central California (south from Sonoma County). The commercial catch in Washington was lagged 5 yr to account for the slower growth of crabs there, whereas the commercial catch was lagged 4 yr for California. As in Oregon, the commercial catch in northern California was related to megalopae catch by a significant second order polynomial, but in central California the relationship was a significant linear correlation (Fig. 6). The commercial catch in Washington was also related to the Coos Bay catch of megalopae by a second order polynomial, but here the *P* value was larger, 0.101 (Fig. 6).

DISCUSSION

The number of returning megalopae varies significantly with the phase of the PDO; higher catches tend to occur during negative PDO years than during positive years. How might the PDO cause variation in larval success? In the CC, Dungeness crabs release larvae in the winter near the coast (Reilly, 1983). Hence, the initial stages of larval development take place in the

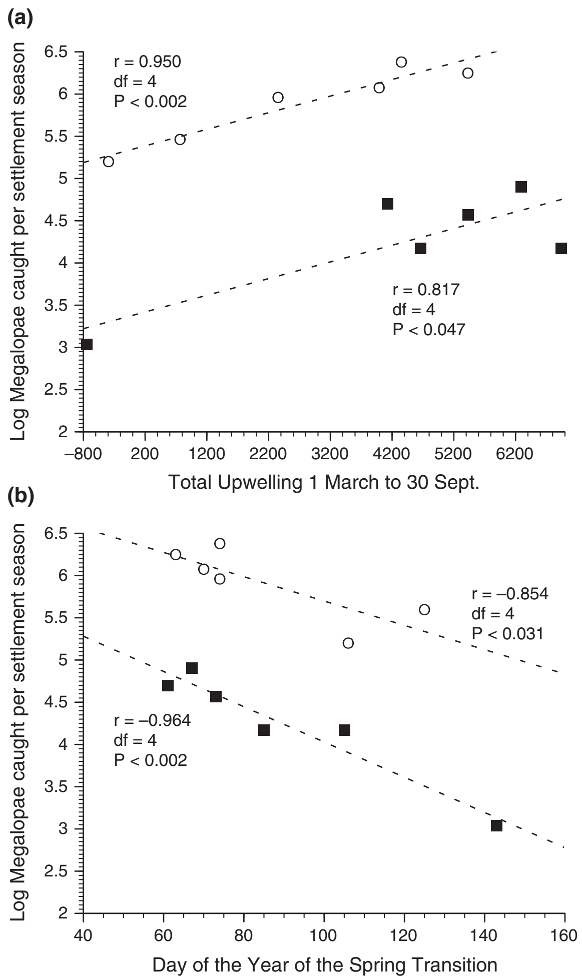
Figure 3. Daily sea level anomaly during the years 2009–2011; negative anomalies indicate upwelling, and positive anomalies downwelling. The shaded box represents the annual settlement period for *Cancer magister* megalopae. The upwelling index for 45°N was summed over this period. Arrows indicate the approximate date of the spring transition.



northward flowing Davidson Current. Given the speed of the Davidson Current (9–22 km/day) (Reid and Schwartzlose, 1962) and the length of the larval period [80–130 days; Strathmann, 1987), larvae could be carried easily to Vancouver Island and perhaps further north. As the larvae develop, they are found progressively further from shore and eventually are found off the continental shelf and in the southward flowing CC (Reilly, 1983). During their pelagic larval development, the larvae are transported first northward and then southward. In years with a positive PDO, the southward flowing CC is weaker, with less southward flow (Minobe and Mantua, 1999); larvae transported northward by the Davidson Current may not experience enough southward flow to settle in Oregon and northern California. It is possible that the larvae are transported far enough north that they are entrained by currents at the southern edge of the Gulf of Alaska (GOA) and carried northward. In contrast, when the PDO is negative, the southward flow is stronger and larvae may be carried further south before they settle, which may lead to high larval returns in Oregon.

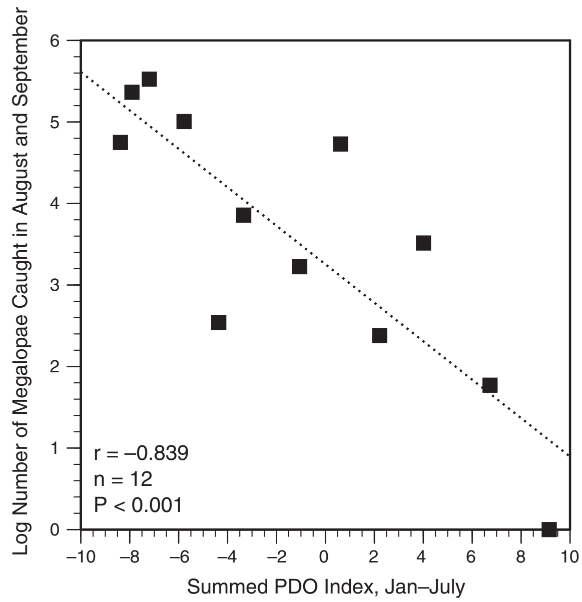
There is, in fact, evidence that *C. magister* larvae are transported from the CC into the GOA. In the CC, larval release takes place in the winter, whereas in the GOA this occurs in late spring to early summer (Strathmann, 1987). In May and June in the GOA, *C. magister* larvae that spawn there should be early stage zoea, but Park *et al.* (2007) found late stage zoea (zoea stage 4 and 5) and megalopae present in Alaskan coastal and offshore waters. These larvae were developmentally too far advanced to have been produced locally; they must have been transported to the area and, given their stage of development and the

Figure 4. Data from low (solid squares) and high (open circles) settlement years plotted separately. (a) The summed daily upwelling index from 1 March through 30 September (settlement season of *Cancer magister* megalopae) plotted against the log of the total number of megalopae caught each settlement season. (b) Day of the year of the spring transition plotted against the log of the total catch of megalopae. Dashed lines are calculated regressions with statistical results for high and low return years plotted above and below their respective lines.



hydrodynamics, their most likely source is the CC. Clearly these expatriates would at least genetically connect populations in the CC and GOA, but it is not clear whether enough larvae from the CC are exported this far north to influence fluctuations in adult crab populations in the GOA. In addition, Peterson and collaborators (Peterson and Keister, 2003; Peterson and Schwing, 2003; Hooff and Peterson, 2006) have found increased abundance of northern copepod species, species typical of GOA waters, in the CC off Oregon during negative PDO years. Their interpretation is

Figure 5. Summed PDO from January through July plotted against the log number of megalopae caught in August and September. Megalopae caught at this time were likely not hatched in the California Current but may be transported from British Columbia southward. Dotted line represents the significant negative correlation between these two variables.

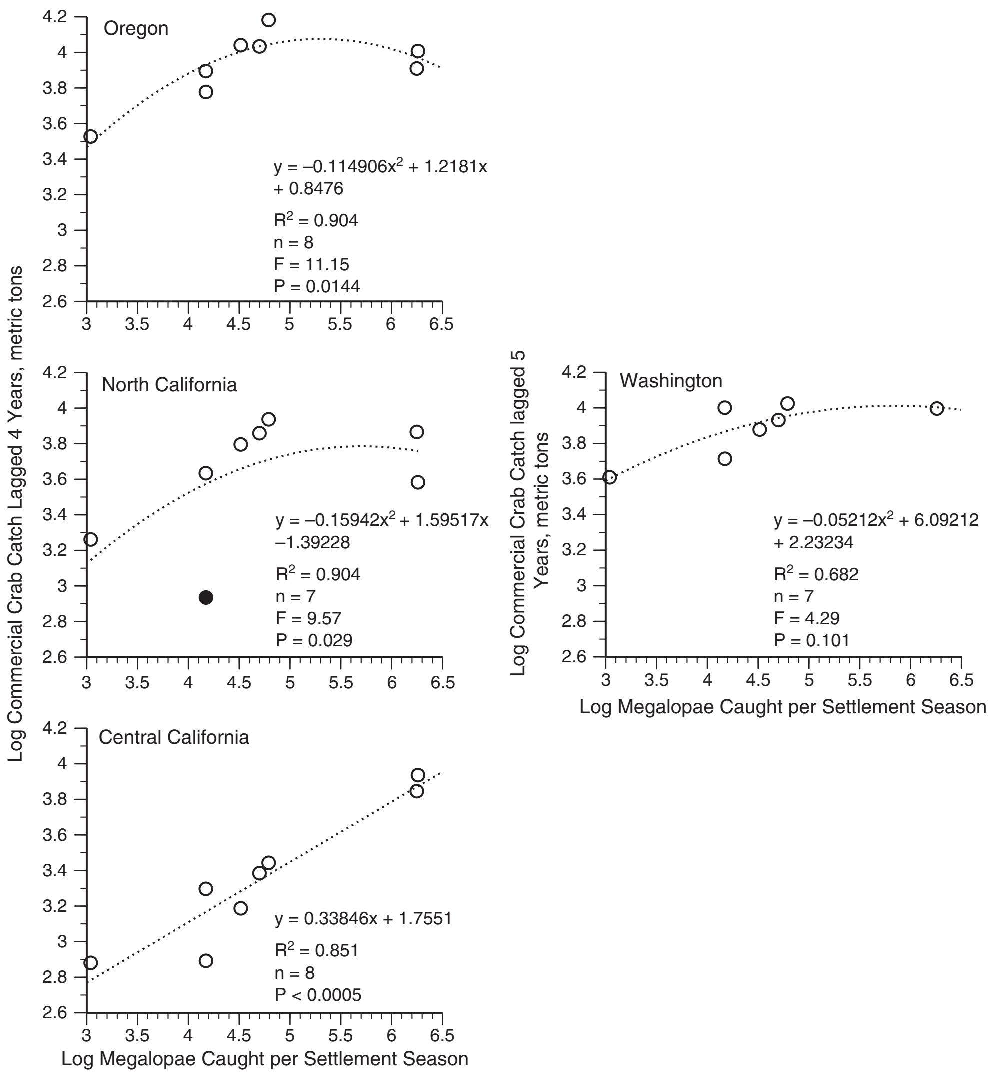


that the copepods are transported southward by the enhanced flow of the CC during the negative PDO years.

Megalopae catch in the light trap in Coos Bay in August and September could not have been produced in the CC, but might be due to larvae transported southward from British Columbia. There is a significant negative correlation between the PDO and the number of megalopae caught late in the season, lending support to this interpretation; when flow is stronger to the south during negative PDOs, more megalopae are caught late in the season. This evidence – the presence of Dungeness crab larvae from the CC in the GOA, GOA copepod species in the northern CC, and higher catches of megalopae during negative PDO years – suggests that this interpretation of the effect of the PDO on larval success in Dungeness crabs may be correct.

The catches in 1999–2001 were during the lower annual return period, but the summed PDO index values in these years were negative. Bond *et al.* (2003) compared the conditions during these years to typical conditions during warm and cool PDO years. They concluded that, although the PDO index was negative during 1999–2001, the distribution of sea level atmospheric pressure over the CC was atypical for a

Figure 6. Log of the total number of *Cancer magister* megalopae caught per settlement season plotted against the log of the Washington, Oregon, and Northern and Central California commercial crab catch. Commercial crab catch was lagged 4 yr for Oregon and California and 5 yr for Washington to account for the amount of time it takes settlers to grow into a commercial-sized crab. The dotted line and statistics are the results of regression analyses. The regression for the Northern California data was calculated without the outlier data point (filled circle). When the data point was included in the analysis the regression was not significant.



negative PDO; winds at 45° north were strongly from the west rather than from the north as in a typical negative PDO year. It is not clear how this might affect the dispersal of *C. magister* larvae but, assuming the effect was different from that of a typical negative PDO, I recalculated the correlation between the PDO index and the number of megalopae returning; without these three data points the correlation is markedly stronger (with all data $r = -0.659$, $n = 12$, $P < 0.02$, with 1999–2001 data removed $r = -0.897$, $n = 9$, $P = 0.001$).

The day of the year of the spring transition and the amount of upwelling in the spring both affect the larval success of *C. magister*; an early spring transition and steady upwelling during the spring both lead to higher returns of megalopae. I suspect that both of these factors are working in the same way to affect larval returns. By the time *C. magister* larvae have developed to late zoea or megalopae, they tend to be found well offshore (Reilly, 1983); however, the pattern of their daily catch in the Coos Bay light trap suggests that they are transported across the shelf by the internal tides (Roegner *et al.*, 2007). Shoreward transport by the internal tides does not occur beyond the shelf, so the first step in the shoreward migration of the megalopae is likely transport from ocean waters onto the shelf. The correlations between annual catch of megalopae and the day of the year of the spring transition and upwelling in spring both suggest that the likely transport mechanism is upwelling. Hobbs and Botsford (1992) and Shanks and Roegner (unpublished data) describe vertical migratory behavior in *C. magister* megalopae with the migration occurring between the neuston and depths >70 m. Shoreward transport onto the shelf by upwelling currents could occur at the lower end of this migration if the megalopae migrate deep enough to be entrained by the upwelling currents; the lower end of the vertical migration would have to be to depths of about 150–300 m, the depth from which upwelling waters tend to be drawn.

In most years, the spring transition marks the seasonal switch from winter downwelling winds to spring/summer upwelling winds, but in some years shortly after the spring transition the winds revert to a downwelling-favorable condition; this is what happened in 2010. The initial burst of upwelling that triggered the spring transition I hypothesize transported megalopae onto the shelf and this led to the two large pulses of settlement seen at the beginning of the 2010 settlement season, then downwelling returned and, if the hypothesis is correct, far fewer megalopae were transported onto the shelf, leading to low light trap catches for the remainder of the year (Fig. 1). For strong returns of megalopae, upwelling must continue through the summer; if and when upwelling stops for the season, megalopae present in the ocean off the shelf may be trapped there and lost as larval wastage.

Earlier papers (Botsford and Wickham, 1975; Johnson *et al.*, 1986; Hobbs *et al.*, 1992) found significant correlations between upwelling favorable winds or the upwelling index and the abundance of Dungeness crab larvae in spring or the lagged commercial catch. These studies suggest that upwelling winds or currents somehow affect the relative success of larval Dungeness crabs. Roegner *et al.* (2007) describe the daily catch of megalopae to the light trap as highly pulsed, with the pulses significantly cross-correlated to the spring/neap tidal cycle and they did not find significant cross-correlations with wind stress. This current study suggests that upwelling currents do affect larval success, but not by the transport of larvae across the shelf; rather the best fit to the observations appears to be that upwelling transports megalopae from the open sea onto the shelf where other mechanisms (likely the internal tides) transport the megalopae to shore.

In the CC, Dungeness crabs release their larvae in the winter during downwelling, the larval period is long (several months), and settlement takes place during the upwelling season. This combination of life history traits is shared by many CC shelf/slope fishes and benthic crustaceans (Shanks and Eckert, 2005). Hence, the combination of factors that influence the relative larval success of *C. magister*, the PDO, the day of the year of the spring transition, and the amount of upwelling in spring, may similarly affect many other CC species that occupy shelf waters. Indeed, measures of recruitment in pink shrimp (Hannah, 1993) and a variety of ground fish (Hollowed, 1990) are also inversely correlated to the day of the year of the spring transition.

In earlier studies (Shanks and Roegner, 2007; Shanks *et al.*, 2010) the number of returning megalopae ranged from around 2000 to just over 80 000 and we found a linear relationship between the log of the number of megalopae returning each year and the subsequent size of the log-transformed commercial catch 4 yr later. In this study, I extend this relationship to include larval returns of >2.3 million animals per year. Over this extended range of larval returns (2000 to 2.3 million) the relationship is parabolic and statistically significant. If this relationship holds into the future, then between about 1000 and 100 000 returning megalopae the relationship between larval success and commercial catch is roughly linear; at this level of larval return, the population is recruitment limited (Caley *et al.*, 1996). The relationship suggests that the maximum commercial catch would occur at around 175 000 returning megalopae. Above this number of returning megalopae the commercial catch will decrease with increasing numbers of returning megalopae; density-dependent effects on new recruits will set the adult population size. If the PDO has shifted to a cold phase and the extraordinary high returns of megalopae are due to this shift, then for years to decades the size of the commercial catch will ultimately be set by density-dependent effects on new-recruits. During warm phase PDOs, the data suggest that the commercial catch will be set directly by the relative success of the larval phase; the population will be recruitment limited.

With a 5-yr lag between the return of megalopae to Coos Bay and the commercial catch in Washington, I found a nearly significant parabolic relationship similar to what I found in Oregon (Fig. 6). The year longer lag between settling megalopae and commercial-sized crabs in Washington may be due to colder water slowing the growth of the crabs or perhaps a larger percentage of the returning megalopae in Washington are from British Columbia and arrive late in the summer, which would set their development back by a whole summer relative to megalopae settling in the spring off Oregon and California. The relationship between the commercial catch in Northern California and the number of returning megalopae in Coos Bay was quite similar to the relationship observed in Oregon (Fig. 6) but the relationship between the number of returning megalopae and the commercial catch in Central California, while significant, was linear not parabolic. A possible explanation for this difference is that the number of megalopae returning to Central California is lower than in Oregon; the annual pattern of returning megalopae is likely similar, hence the significant relationship, but the magnitude of the settlement in Central California may be lower. Light trap catches of megalopae in Bodega Bay, California, are indeed lower than in Coos Bay (L. Bennett, unpublished data). This suggests that settlement off Central California is recruitment-limited and that settlement has yet to achieve levels high enough to trigger a more dominant effect of density-dependent forces. The fact that the annual return of megalopae to one site, Coos Bay, is correlated to the commercial landings along much of the West Coast suggests that whatever causes annual variation in the success of Dungeness crab larvae must be coast-wide and this is exactly what the correlations reported here suggest. The annual larval success appears to be driven by the PDO, the DOY of the spring transition, and the amount of upwelling in spring and summer; all of these are coast-wide phenomena and all are driven by regional atmospheric forcers.

Shanks *et al.* (2010) reported average densities of Dungeness crab young-of-the-year (YOY) of 175/m^2 (range 93–439/m^2) at the end of summer in 2007 off the Oregon coast; the huge larval return of 2007 led to dense populations of new recruits and the returns in 2008–2010 undoubtedly did the same. In contrast, the highest densities that McConnaughey *et al.* (1992) observed off Washington between 1983 and 1988 were on the order of 6/m^{2,} one to almost two orders of magnitude lower than what was observed off Oregon in 2007. The extremely high densities observed in 2007 should lead to extreme competition for resources; indeed, the average size of the individuals was less than reported in previous studies (Shanks *et al.*, 2010). If the ocean is now in a cold phase PDO and the extraordinary high returns of megalopae are due to this shift in ocean conditions, then the nearshore benthos will experience persistent high densities of Dungeness crabs and, after the major settlement pulses in the spring and early summer, extremely high densities of new recruits. YOY Dungeness crabs prey on juvenile bivalves and polychaetes (Iribarne *et al.*, 1995). In the laboratory, YOY crabs can consume about five juvenile *Macoma balthica* per day. There is an ontogenic shift in diet, first towards crustaceans and then towards fish (Stevens *et al.*, 1982). Predation by Dungeness crabs, particularly during years of high larval returns, may affect benthic community structure. For example, during years of high larval returns, survival of juvenile bivalves may be poor, which may affect the age structure of the bivalve populations. This may be particularly important if, due to ocean conditions (e.g., the PDO), high crab settlement occurs for a number of years. Given that older crabs can feed on juvenile fish, recruitment of some types of fishes may also be reduced.

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