USING MEGALOPAE ABUNDANCE TO PREDICT FUTURE COMMERCIAL CATCHES OF DUNGENESS CRABS (*CANCER MAGISTER*) IN OREGON

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ABSTRACT

We explore the possibility of predicting the commercial catch of Dungeness crabs (*Cancer magister*) from the abundance of returning megalopae. In the first six years of a nine-year time series (1997–2001, 2006–2009), there is a strong relationship between megalopal abundance and Oregon commercial catch, and early spring transitions led to higher numbers of returning megalopae. During this period, we could make reasonable predictions of commercial catch. In the last three years (2007–2009), megalopal abundance ranged from 1.2 to 2.4 million animals. The previous relationship between megalopal abundance and commercial catch is unlikely to hold given these huge abundances; density-dependent factors should lead to an asymptotic relationship between the number of returning megalopae and commercial catch and, if this holds, commercial catch should be predictable. The high abundances of megalopae do not appear to be due to improved larval growth conditions, but significant correlations between megalopal abundances and hydrographic and climatic indices suggest that reduced northward and enhanced southward transport during the pelagic phase may have contributed to the huge returns.

INTRODUCTION

This research explores the possibility of predicting the commercial catch of Dungeness crabs (*Cancer magister*) from a measure of the number of megalopae returning to shore. The data presented were collected during two periods. Data in the first year (1997) was part of a Masters thesis (Johnson and Shanks 2002) and during the next four years (1998–2001) were collected as part of the Pacific Northwest Coastal Ecosystem Regional Study (PNCERS) (Roegner et al. 2007). There was a hiatus of four years due to a lack of funding and then, with support from the Oregon Dungeness Crab Commission, the time series was restarted in 2006 and has continued to the present.

Methods, data and the initial model relating the numbers of settlers to the commercial catch were presented in a previous paper (Shanks and Roegner 2007). Following a description of the Dungeness crab life history and fishery in the California Current, which is based upon the review by Wild and Tasto (1983), the results and conclusions from the Shanks and Roegner study will be presented. In this present paper, the last four years of data will be combined with this initial time series and reanalyzed.

The following presentation of Dungeness crab life history relates to the the California Current portion of the species range; the species range extends up into coastal Alaska and here the life history characteristics are different (Swiney and Shirley 2001). In the California Current system mating occurs in spring during a female's molt. Males can mate with multiple females. Females store sperm until egg extrusion in the fall. Egg development takes three to four months with hatching occurring sometime in winter (Strathmann 1987). There are five zoeae stages and a megalopal stage. The larval period is from three to four months (Strathmann 1987). Larvae hatch close to shore and, as they develop, they move further offshore. By the late zoeae stages, many if not most larvae are present in waters beyond the continental shelf (Wild and Tasto 1983). In Oregon, megalopae begin returning to shore in spring and returning megalopae are usually present until October or November (Roegner et al. 2007). The daily abundance of megalopae at the shore (as measured with light traps, see Methods) is highly pulsed; pulses are one to several orders of magnitude larger than abundances between pulses. Pulses tend to occur between spring and neap tides suggesting that shoreward transport of megalopae is due to the internal tides (Roegner et al. 2007). In Oregon waters, crabs reach sexual maturity in about 1.5 years and male crabs enter the fishery at about four years of age (Wild and Tasto 1983).

The following description of the history of the Dungeness crab fishery is taken from the review by Wild and Tasto (1983). The commercial fishery for Dungeness crab began in San Francisco Bay in 1848. Initially, the fishery was entirely within the Bay, but within several decades this fishing ground was over-fished and the fishery moved to waters between the Golden Gate and the Farallon Islands. There was a steady increase in landings through the 1880s at which time landings began to drop and crabs became scarce. To protect the fishery, the California State Board of Fish Commissioners lim-

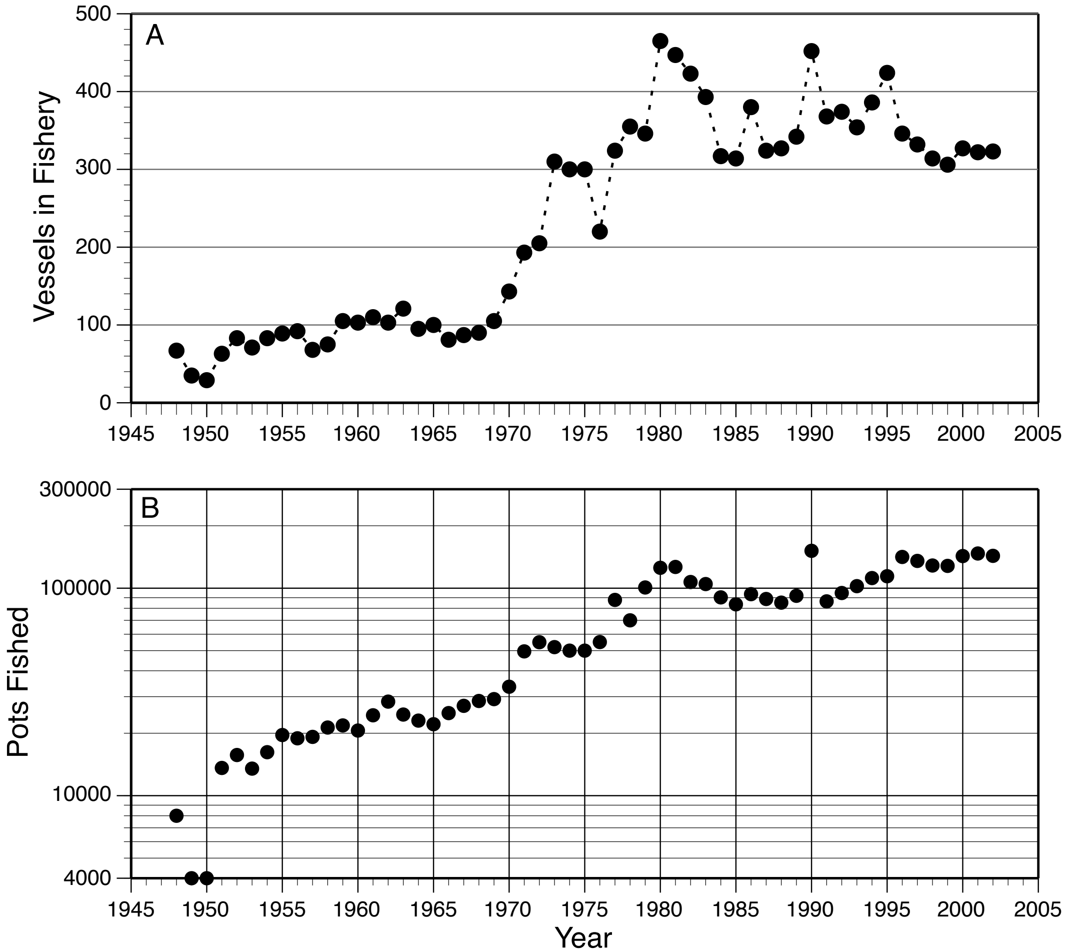

Figure 1. (A) Number of vessels participating in Oregon Dungeness crab fishery from 1947–2004 and (B) the number of crab pots fished over the same period (data are from the Oregon Department of Fish and Wildlife).

ited the catch to male crabs in 1897. The intense fishing pressure, however, continued to cause a decline in the population and additional restrictions were placed on the fishery. In 1903 the fishery was closed during September and October to prevent fishing when males are molting. In 1905 a size limit was placed on male crabs and in 1907 the size limit was increased to limit the take of female crabs (male crabs are significantly larger than female crabs). In addition, the larger size limit allows male crabs several opportunities to mate before they enter the fishery. These basic regulations, with minor changes, have been utilized in Dungeness crab fisheries throughout the California Current system. Starting in 1915, fish dealers were required to keep records of their transactions (landings). As the fishery expanded north into Oregon and Washington, similar record keeping was instigated in these states. These records provide an excellent time series of the commercial catch of Dungeness crabs in the California Current.

During the first half of the 20th century, the fishery expanded northward and the number of boats fishing crab increased. During the 1970s, following the initiation of the 200-mile economic exclusion zone, there was a rapid increase in the crab fishing fleet. For example, in Oregon (data from Oregon Dept. of Fish and Wildlife), the fishing fleet fluctuated around 100 boats during the 1960s. Between 1970 and 1975, the fleet increased to 300 boats and has remained between 300 and >400 boats since (fig. 1). During the 1960s, the fleet fished around 30 thousand crab pots, but > 100,000 pots have been fished since the growth of the fleet (fig. 1). Fishing pressure on Dungeness crabs is intense and has been since at least the 1970s. By the close of the fishing season, > 90% of the legal-sized crabs (four-year olds) have been caught and, as a consequence, annual catch is a good measure of the abundance of the four-year old cohort (Hackett et al. 2003). Despite the intense fishing pressure there is no indication that the crab population is suffering from overfishing. That is, while the size of the commercial catch has fluctuated over the years, there is no apparent downward trend in the size of the commercial catch (pers. obs.); the fishery appears to be

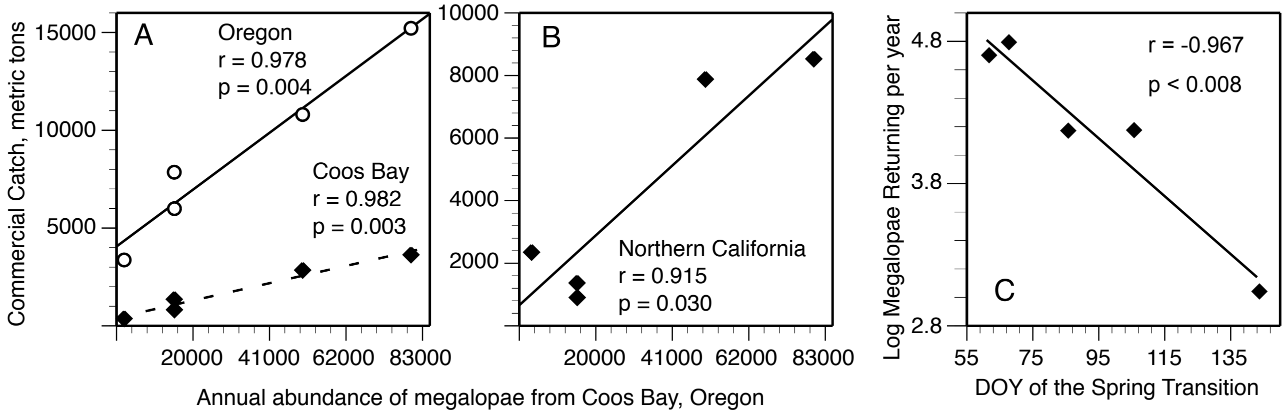

Figure 2. (A and B) The annual abundance of megalopae returning to Coos Bay, Oregon as measured as the sum of the daily catch of megalopae to a light trap plotted against the commercial catch landed in Coos Bay, all Oregon, and Northern California lagged four years to account for the growth of the megalopae to a legal-sized crab. (C) The day of the year of the spring transition plotted against the annual abundance of megalopae returning to Coos Bay, Oregon. Data are replotted from Shanks and Roegner (2007).

sustainable. A likely explanation for this is that the regulations limit the impact of the fishery on the reproductive output of the population.

Between 1997 and 2001, the annual return of megalopae to the shore as measured by the number of megalopae caught in light traps in Coos Bay, Oregon varied from 1000 in 1997 to nearly 80,000 in 2001. The number of returning megalopae was significantly, positively, and linearly correlated with the commercial crab landings in Coos Bay four years later (fig. 2), and was significantly correlated to landings in all Oregon and Northern California, and was nearly significantly correlated to landings in central California (Shanks and Roegner 2007). These correlations suggested three conclusions: (1) The size of the commercial catch (four-year old year cohort) was set by the relative success of the larvae as measured by the abundance of returning megalopae, (2) Over this range of returning megalopae, there were no obvious density-dependent effects; the relationship was linear, and (3) Whatever was driving the annual success of larvae was a process or processes consistent over a large portion of the West coast.

Off Oregon, larvae hatch in winter and move offshore during development such that by the megalopal stage most larvae are off the continental shelf. The timing of the pulsed return of megalopae to the shore suggests that shoreward transport is due to the internal tides, a hydrographic phenomena characteristic of the shelf (Roegner et al. 2009). Hence, the first step in the shoreward migration of megalopae appears to be transport from waters off the shelf back onto the shelf at which point internal tides could cause shoreward transport. We hypothesized that the spring transition might transport megalopae back onto the continental shelf. The spring transition occurs when winter winds from the south (downwelling favorable) are replaced by spring/summer upwelling favorable winds from the north. During this transition, the Davidson Current, which is present on the shelf during winter is replaced by the California Current moving back onto the shelf and the north winds begin the seasonal cycle of upwelling. These dramatic seasonal changes in the current regime might transport megalopae from waters seaward of the shelf onto the shelf. The spring transition varies from as early as March to as late as July. We hypothesized that if the transition was early (March), Dungeness crab larvae would spend a minimum time in the plankton and the return would be large. In contrast, if the transition was late (June or July) then larvae would spend additional months in the plankton during which a variety of mechanisms might cause increased mortality and the return of megalopae should be smaller. The day of the year of the spring transition was significantly correlated with the number of returning megalopae; when the transition was early, the return was large and, when it was late, the return was smaller (fig. 2). Interestingly, the return of the larvae of several taxa of nearshore or intertidal decapods (Shanks and Roegner 2007) and fishes (Shanks and Pfister 2009), species with larvae that remain close to shore during their development, had an opposite relationship with the date of the spring transition; in these taxa, when the transition was early, the return was low and when it was late, it was higher.

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. Using a light trap (fig. 3) placed in the Charleston small boat harbor in Coos Bay, Oregon crab megalopae were captured daily from roughly the beginning of April through September

Figure 3. Light trap used to sample megalopae in Coos Bay, Oregon. The trap consists of a clear plastic water bottle into which are placed a number of funnels. The light source is a fluorescent lamp powered by an outlet on the dock.

or October (Shanks and Roegner 2007). At the beginning of this study we sampled three replicate traps per day, but we found that the daily catch in these replicates was quite similar and that the greatly increased work required to process three replicates each day was unwarranted (Roegner et al. 2007; Shanks and Roegner 2007). The total number of megalopae captured in each settlement season was used as an index of the abundance of megalopae returning to the coast.

When a daily sample was < 2000 either the entire sample was counted or it was split using standard methods and then counted. Starting in 2007, the daily and annual abundance of megalopae increased dramatically with daily catches during pulses in the range of 10s of thousands of megalopae (5 to 10 liters of megalopae). We could not efficiently count these huge samples. To estimate the number of megalopae, we carefully drained off the water, weighted 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 commercial catch landed four years later. The Oregon Department of Fish and Wildlife provided commercial catch data.

We compared the index of settling megalopae with a variety of climate indices and oceanographic parameters. We correlated the index of settling megalopae to the date of the spring transition. The spring transition is apparent as an abrupt drop from high winter coastal sea levels following a period of steady winds from the north (Strub et al. 1987). As the date of the spring transition, we used the date on which sea level dropped 100 mm below the annual average and stayed there for at least seven days (Strub et al. 1987). We used sea level data for Crescent City, California obtained from the University of Hawaii Sea Level Center (http:/ilikai.soest.hawaii.edu). The strength of winter upwelling was estimated from summed monthly averages of the upwelling index for 42°N (http://www.pfeg.noaa.gov/pr). We correlated the index of settling megalopae with the Pacific Decadal Oscillation (PDO, http://jisao.washington.edu/pdo/PDO.latest), the North Pacific Gyre Oscillation (NPGO, http://eros.eas.gatech.edu/npgo/data/NPGO.txt), the Northern Oscillation Index (NOI, http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/NOIx/noix_download.html?indx=NOI&time=1948+to+present&Submit=Show+List+%28entire+series%29), the East Pacific North Pacific index (EP/NP, http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.CPC/.Indices/.NHTI/) and the North Pacific index (NP, http://www.cgd.ucar.edu/cas/jhurrell/npindex.html). With the NP index we used the sum of the values from December through February, months when this index shows high inter-annual variability (Trendberth and Hurrell 1994). For all other indices we used the sum of the index from January through July, the entire pelagic larval period for Oregon crabs.

Starting in 2007, the return of megalopae increased dramatically. One possible cause of the large jump in

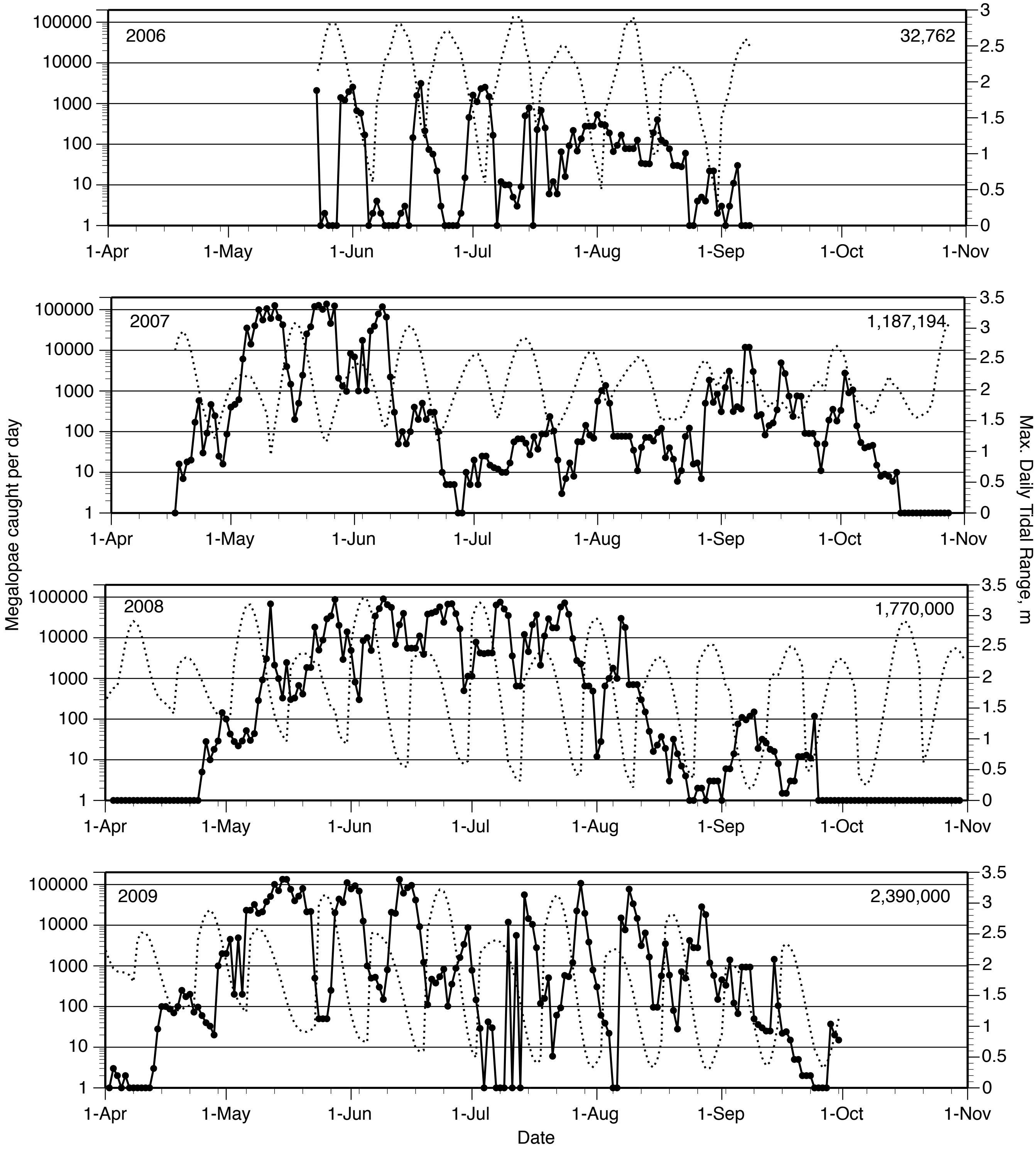

Figure 4. The daily catch of megalopae (solid line and circles) to a light trap in Coos Bay, Oregon during the 2006, 2007, 2008, and 2009 recruitment seasons plotted with the maximum daily tidal range (dotted line). Number in the upper right hand corner of each graph is the total number of megalopae caught each year.

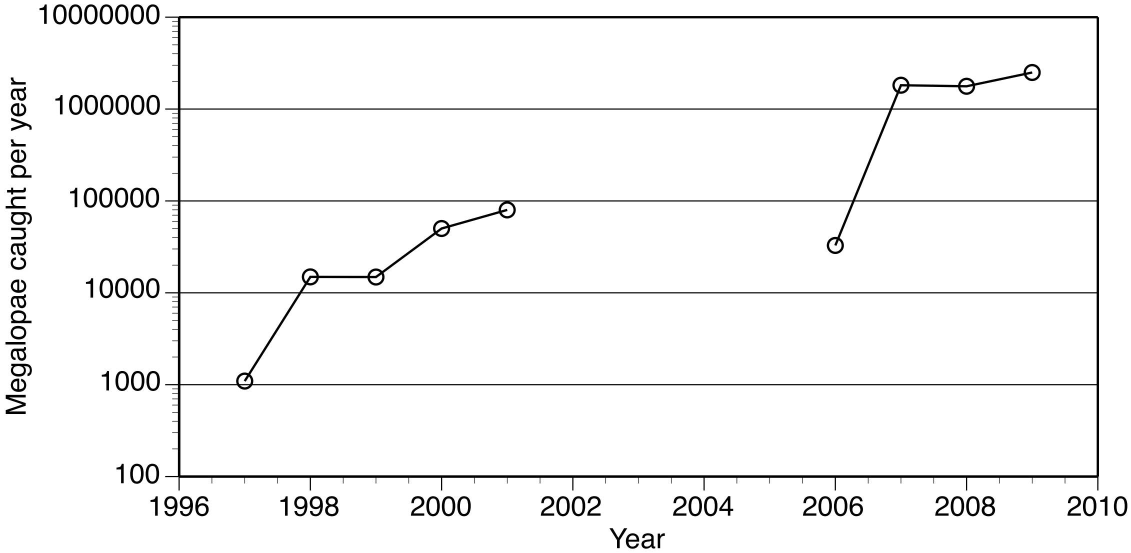

Figure 5. The annual catch of megalopae plotted by year. Prior to 2007, the annual catch ranged from 1000 to 80,000, but from 2007 onward, catch jumped to 1.2 to 2.4 million megalopae.

annual return might be that the at-sea larval growth conditions were better in 2007–2009. If this were the case, we hypothesized that the returning megalopae may be larger in these years than in previous years. To test this hypothesis, we measured the length of megalopae caught on a number of days (about 20) during each recruitment season. Early in the recruitment season, when megalopae were abundant, we measured at least 100 haphazardly-selected animals (i.e., the first 100 animals removed from a sample), but late in the season, when returns were much lower, fewer individuals were available to be measured. In the data from the first six years of sampling, about a quarter of the dates had <100 animals, but in the last three years few dates had <100 animals. During the late season, we either used dates when we could measure at least 10 animals or combined adjacent dates to get at least 10 animals to measure. Length (tip of rostral spine to back of the carapace; DeBrosse et al. 1990) was measured using an ocular micrometer in a dissecting microscope.

One possible consequence of the very high settlement rates of 2007–2009 is that growth rates of juvenile crabs may have been slowed due to intense competition. To investigate this possibility, we measured the sizes (carapace width) of juvenile crabs photographed by an Oregon Department of Fish and Wildlife (ODFW) ROV deployed off Cape Perpetua, Oregon in August of 2007. The average size of these crabs was compared to historical size data for similar aged crabs.

RESULTS

The daily abundance of returning megalopae was highly pulsed (fig. 4). Significant negative cross correlations between the maximum daily tidal range and daily catch, with lags around –1 to –4 days, suggest that peak catches tended to occur between the neap and the spring tides as had been seen previously (Roegner et al. 2007).

In 2006, on the first day of trap deployment, over 2,000 megalopae were caught suggesting that the trap was deployed after the start of the recruitment season. Total catch in the light trap during the first three completely sampled pulses in 2006 averaged around 7,000 individuals suggesting that the first pulse may have been under sampled by about 5,000 animals. In 2007–2009, initial daily catches were between 0 and 10 individuals for at least several days before the first large pulse suggesting that the trap was deployed prior to the beginning of the recruitment season.

The total catch of megalopae in 2006 was similar to catches from previous years, 32,762 megalopae (figs. 4 and 5): given that the start of the season was missed, the annual return of megalopae was probably around 37,000. After 2006, the total annual catch was far larger than in any previous year; total catches in 2007, 2008, and 2009 were 1.2, 1.7, and 2.4 million megalopae, respectively (figs. 4 and 5). During the fortnightly pulses, daily catches ranged from 10s of thousands to > 100,000 individuals. These annual catches were >10X larger than the previous largest annual catch of around 80,000 megalopae (2001). Over nine years of sampling, the total annual return of megalopae varied by a factor of > 1,000 (fig. 5).

Of the last four years of sampling, we have both the annual catch of megalopae and an estimate of the year class strength from the fishery only for 2006 year of megalopae return. Given the past relationship between

TABLE 1
Predicted and observed Oregon commercial catch of Dungeness crab. Predictions were based on the models in Shanks and Roegner (2007) that utilized the date of the spring transition or the total number of megalopae caught in Coos Bay, Oregon during the annual recruitment season (roughly April through September).

Crab fishing year	Date of the spring transition 4 yrs earlier	Oregon predicted catch (lbs) using spring transition date	Oregon predicted catch (lbs) using catch of megalopae	Oregon observed catch (lbs)	Deviation from predicted catch (lbs) (% off)
2005–2006	14 March 2002	27,000,000		27,600,000	–600,000 (2%)
2006–2007	8 May 2003	12,000,000		15,400,000	–3,400,000 (28%)
2007–2008	4 March 2004	28,000,000		12,300,000	–15,700,000 (212%)
2008–2009	13 July 2005	5,500,000		12,500,000	+7,000,000 (127%)
2009–2010	22 April 2006	16,000,000	21,000,000	24,100,000	+8,000,000 or +3,000,000 (33 or 12%)
2010–2011	11 March 2007	26,000,000	>500,000,000		
2011–2012	29 March 2008	18,000,000	>500,000,000		
2012–2013	29 March 2008	18,000,000	>500,000,000		

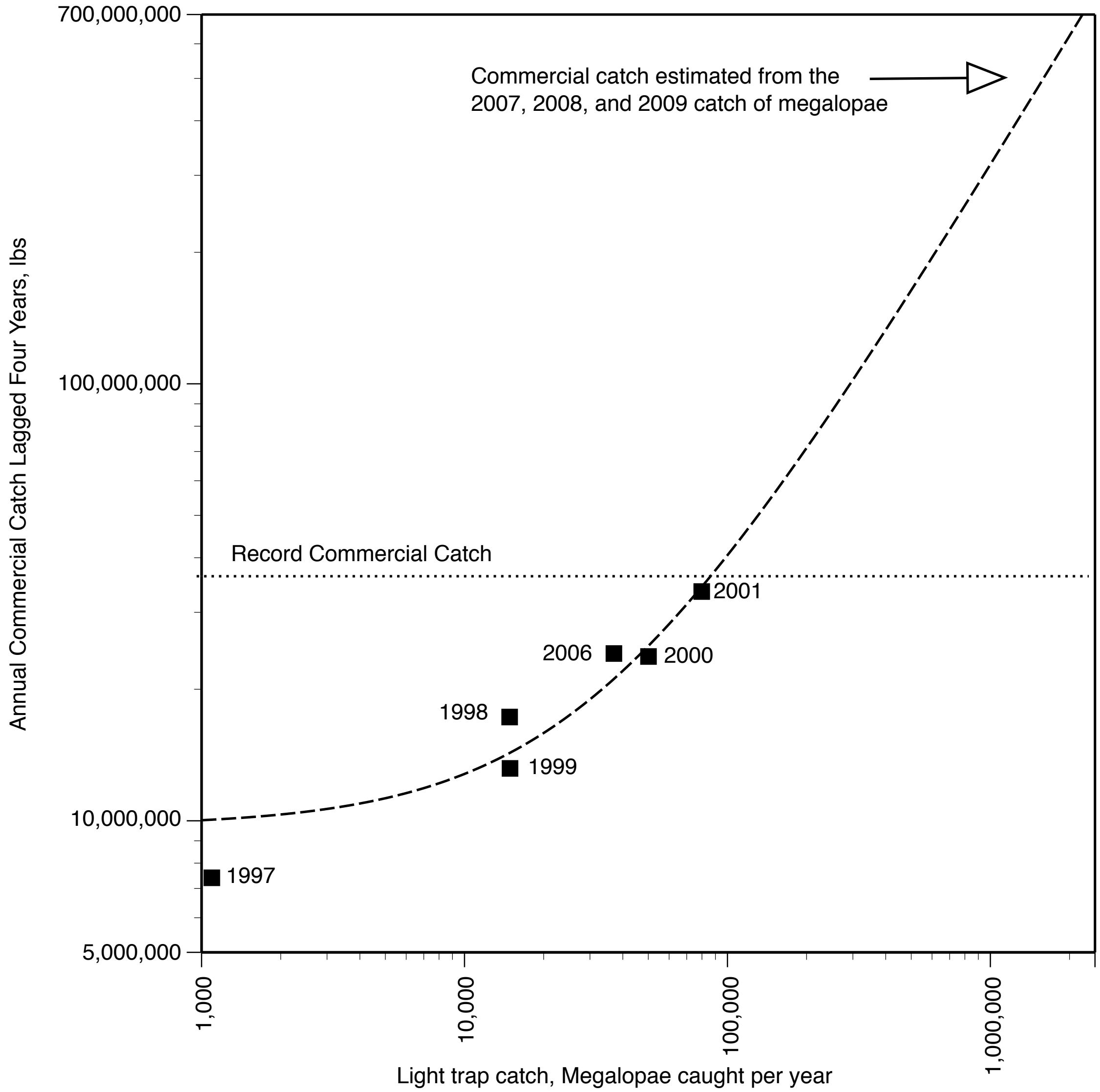

Figure 6. The annual light trap catch of megalopae plotted against the annual commercial catch of Dungeness crabs landed in Oregon lagged four years. From 2007 to 2009, the annual catch of megalopae ranged from 1.2 to 2.4 million individuals. Megalopae that settled during these years have yet to enter the fishery. The arrow indicates the approximate size of the commercial catch if the significant relationship ($R^2 = 0.943$, n=6, $p < 0.01$) for the years 1997 to 2001 and 2006 between the number of returning megalopae and commercial catch were applied. The commercial catch would be > 10 times larger than the current record commercial catch (indicated by the dashed line).

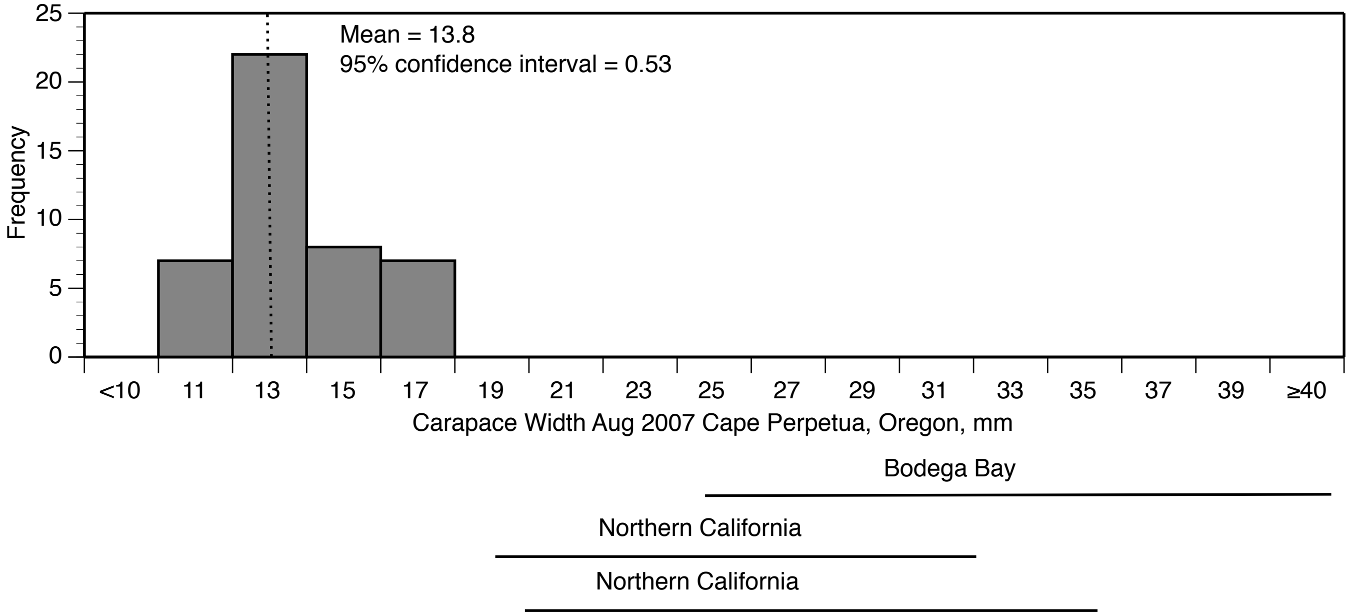

Figure 7. Size frequency distribution of juvenile crabs in August off Cape Perpetua, Oregon. Data are from an ROV video collected by the Oregon Dept. of Fish and Wildlife. The lines below this graph are size ranges for similarly aged juveniles reported in other studies in the California Current (Wainwright and Armstrong 1993).

returning megalopae and commercial catch, the predicted commercial catch generated by the 2006 return of megalopae was 21,000,000 lbs (tab. 1), and the observed commercial catch as of the submission of this paper (1 June 2010) was 22,937,111 lbs. Historically, by this date ≈95% of the annual commercial catch has been landed, suggesting that the total catch for the 2009/2010 fishing season will ultimately be ≈24,100,000 lbs; similar to the catch predicted from the number of returning megalopae. We now have six years in which we have both the total return of megalopae and commercial catch (fig. 6) and the relationship between these two variables remains remarkably strong ($R^2 = 0.932$, n=6, $p< 0.01$). At least within the range of 1,000 to 100,000 returning megalopae, the number of returning megalopae appears to be an excellent predictor of the commercial catch four years later, but will this relationship hold in the future given the recent huge returns of megalopae?

Using the present relationship between returning megalopae and commercial catch, we estimate that the future commercial catches generated by these huge returns of megalopae would be on the order of 500,000,000 lbs (fig. 6). Given that historically the largest commercial catch was 33,000,000 lbs, it is highly unlikely that such large commercial catches will occur; density-dependent effects, mortality due to predation and starvation and reduced growth rates, will likely modify the relationship between returning megalopae and commercial catch. Without systematic sampling of new-recruits as they grow into fishable-sized crabs, we have little evidence that can be used to investigate density dependence.

The 2007 ROV video from ODF&W provides one set of data. The video was shot in August off Cape Perpetua, Oregon. The average density of juveniles was 174 m^{-2} (n= 24, SE = 25, range 25 to 405 m^{-2}). These very high densities could lead to intense competition for food and reduced growth rate of juveniles. Using close-up images from the video, we generated a size frequency distribution of carapace widths (fig. 7). In August, the average juvenile was 13.8 mm wide (95% confidence interval = 0.5 mm), significantly smaller (10 to 20 mm smaller) than the reported sizes of similarly aged new-recruits within the California Current (Wainright and Armstrong 1993). The small size of the 2007 recruits is consistent with the hypothesis that competition for food was retarding their growth. It may take longer than four years for these recruits to enter the fishery.

What might have caused the huge return of megalopae in the last three years? There are at least three possibilities; mortality of larvae due to predation was much lower, growing conditions were much better than in previous years, and ocean currents were highly favorable and returned more larvae to the coast. There is not enough information on the predators of zoeae and megalopae of Dungeness crabs to address the first possibility, but we have some data with which we can investigate the other two potential causes.

If growth conditions during larval development were better during the last three years, then returning megalopae in these years may be significantly larger than in the years with smaller returns. We measured the sizes of megalopae over the recruitment season in 1998, 1999,

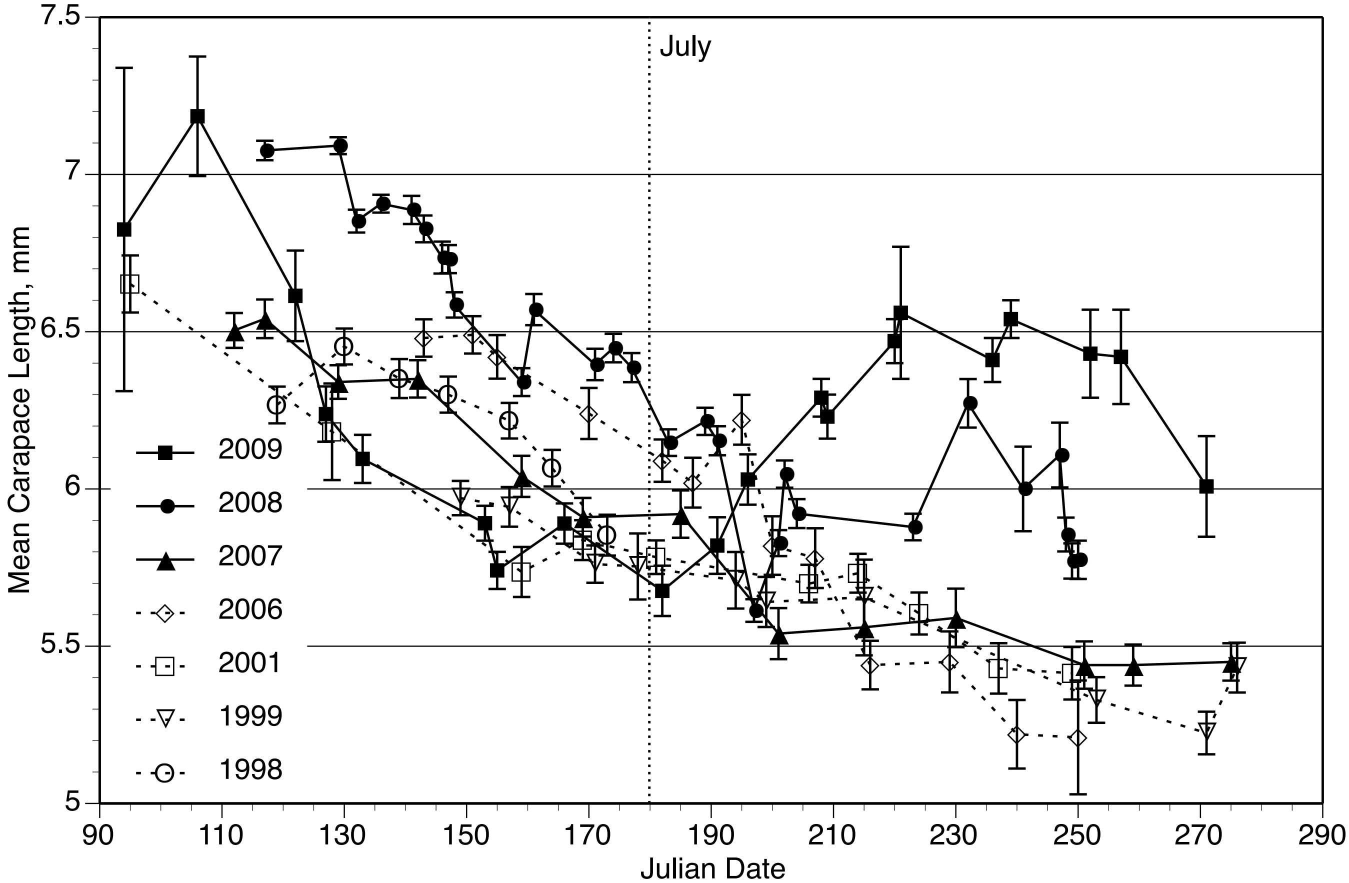

Figure 8. Mean carapace lengths (± 95% confidence interval) of megalopae caught in light traps placed in Coos Bay, Oregon plotted by Julian date. Closed symbols indicate years with very large (> 1 million) annual returns of megalopae and open symbols are years with < 100,000 megalopae returning.

2001, and 2006 through 2009 (1997 and 2000 samples were unavailable). In each year, the largest megalopae were caught at the beginning of the season and returning megalopae decreased in size over the summer (fig. 8). If improved pelagic growth conditions translate into larger returning megalopae, then we would expect to see the size curves from the last three years (closed symbols, fig. 8) located above curves from years with smaller catches (open symbols, fig. 8). The size curve for megalopae from 2007, the first year of huge returns, is co-located with curves for years of lower catch. The curve for 2008 is mostly above curves for the lower catch years, and at the very beginning and toward the end of 2009, megalopae were larger than those from years with lower catches, however, in the middle of the 2009 season, megalopae size was similar to that seen in the years with lower catches. While there are interesting patterns in these data, the results do not clearly support the hypothesis that returning megalopae were significantly larger in years with very high returns than in those with lower returns. If size of returning megalopae is a reflection of pelagic growth conditions then the data do not support the hypothesis that recent huge returns of megalopae were due to improved larval growth conditions.

We investigated a variety of hydrographic and climatic indices that might relate to the ocean transport of Dungeness crab larvae. Shanks and Roegner (2007) found a clear negative relationship between the day of the year of the spring transition and the number of returning megalopae. This relationship held through 2006 ($R^2=0.943$, $n=6$, $P<0.01$), but data points from the last three years of very large catches sit far above this relationship (fig. 9A). The East Pacific/North Pacific (EP/NP) index was negatively related to the number of returning megalopae, the relationship was significant through 2006 ($R^2=0.734$, $n=6$, $P<0.05$), and data points from the last three years sit well above this significant relationship (fig. 9B). Using all the data, the Pacific Decadal Oscillation (PDO) was significantly negatively related to the number of returning megalopae ($R^2=0.532$, $n=9$, $P<0.05$) with the PDO explaining about 50% of the variation in the catch of megalopae (fig. 9C). Using all the data, the summed monthly winter upwelling index was not significantly related to

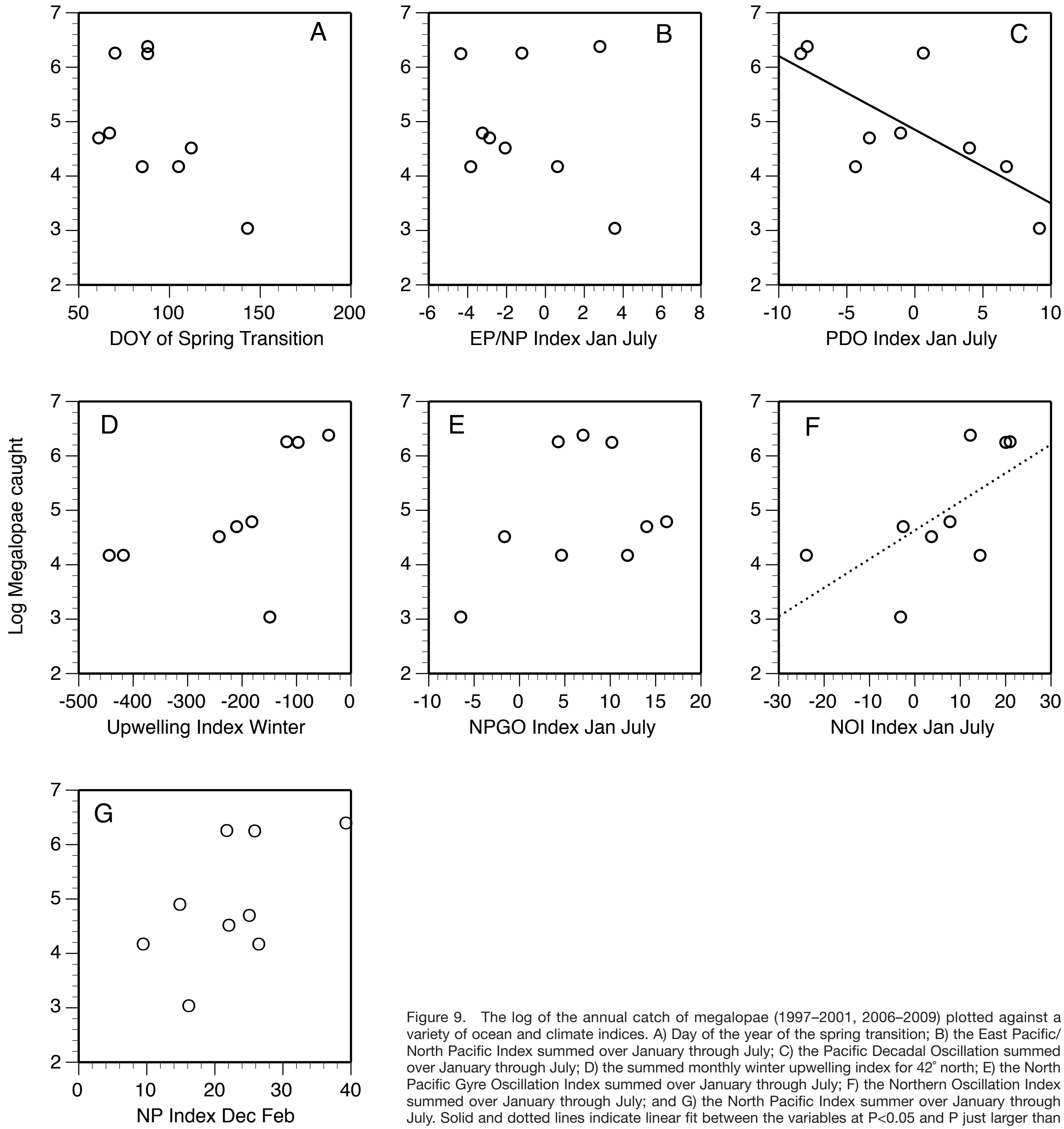

Figure 9. The log of the annual catch of megalopae (1997–2001, 2006–2009) plotted against a variety of ocean and climate indices. A) Day of the year of the spring transition; B) the East Pacific/North Pacific Index summed over January through July; C) the Pacific Decadal Oscillation summed over January through July; D) the summed monthly winter upwelling index for 42° north; E) the North Pacific Gyre Oscillation Index summed over January through July; F) the Northern Oscillation Index summed over January through July; and G) the North Pacific Index summer over January through July. Solid and dotted lines indicate linear fit between the variables at $P<0.05$ and P just larger than 0.05, respectively.

the number of returning megalopae (fig. 9D), with the one outlier point (1997) removed, however, the relationship is highly significant ($R^2=0.782$, $n=8$, $P<0.01$). The remaining indices were positively related to the number of returning megalopae. Neither the North Pacific Gyre Oscillation (NPGO) index nor the North Pacific index were significantly related to the number of returning megalopae (figs. 9E and G), but the relationship between the Northern Oscillation Index (NOI) and the number of returning megalopae was significant at the 0.10 level, but not at 0.05 ($R^2=0.417$, $n=9$, $P=0.060$).

DISCUSSION

In years when the number of returning megalopae was less than about 100,000, the index of returning megalopae has been a good predictor of commercial catch four years in the future. The technique for monitoring returning megalopae, a light trap in Charleston marina, is simple and cost effective. In addition, the time series has revealed fascinating and previously unobserved huge variations in annual larval success.

During the last three years, we have measured annual returns of megalopae in the millions; > ten times more megalopae returned in each of these years than in any previous year and, in fact, during settlement pulses, a day's catch was often larger than the entire annual catch in previous years. How these huge catches relate to the future commercial catch will not be clear until these recruits begin entering the fishery in fishing year 2010/2011, but the size of the commercial catch during the last two fishing seasons (2007/2008 and 2008/2009) offers some indication of what may occur.

We currently have two means of predicting the future commercial catch of Dungeness crabs. We can predict the commercial catch from the number of returning megalopae, but, given the strong relationship between returning megalopae and the day of the year of the spring transition, we can also predict commercial catch from the spring transition date. During the period when we did not have support to maintain sampling, this relationship was used to predict the commercial catch for the 2007/2008 and 2008/2009 fishing seasons (tab. 1). Given the early spring transition in 2004, the 2007/2008 season should have produced a large commercial catch, but the catch was only average. In contrast, the very late spring transition in 2005 (tab. 1) should have produced a very small commercial catch in the 2008/2009 season, but the catch in this year was much larger than predicted.

While we did not have light traps deployed in 2004, we did subjectively monitor recruitment. During this summer, there were vast numbers of megalopae around the docks in Coos Bay and, on sand flats near the docks, there were swarms of juvenile crabs. On a rising tide, at the water's edge, there was a continuous band of juvenile crabs 10 or more cm wide migrating into the intertidal zone to feed. The abundance of megalopae and juveniles suggests that the number of returning megalopae in 2004 was likely comparable to that in the last three years; we strongly suspect that the larval return in 2004 was in the millions. The observed juvenile densities were very high and likely led to stiff competition for food. The juveniles in the Cape Perpetua video were significantly smaller than the size of similarly aged juveniles reported in the literature (Wainright and Armstrong 1993). Off Oregon it typically takes four years for crabs to grow from larvae to commercial sized crabs, but, if densities on the bottom are high, competition may slow growth enough that some recruits may take five years to enter the fishery. The lower than predicted commercial catch in the 2007/2008 fishing season could be due to crabs taking five rather than four years to enter the fishery and the higher than predicted catch in the 2008/2009 fishing season might be due to an influx of five year old crabs that settled in 2004 subsidizing the commercial catch. The current model relationship between the number of returning megalopae and the commercial catch is based upon a four year lag between new settlers and commercial catch; obviously, if it takes four or five years for settlers to enter the fishery this model relationship breaks down and a new model will have to be developed.

The argument presented in the previous paragraph is, obviously, speculative; we will have to wait for the crabs that settled in the last three years to grow and enter the fishery before we can begin to develop an understanding of the relationship between huge settlement events and the size of the commercial catch. In addition, insights from the 2004 settlement event may not be applicable. In 2004, we had one apparently very high settlement year followed probably by a very poor settlement year (2005), but in the current situation we have three very high settlement years (2007, 2008, and 2009) in a row; repeated very strong settlement years would likely exacerbate density-dependent effects.

The most likely relationship between the number of megalopae and the commercial catch is that above some number of returning megalopae the relationship will be asymptotic (Caley et al. 1996). The earlier significant relationship between the number of returning megalopae and the future commercial catch would be the portion of the graph leading to the asymptote and would describe conditions under which the adult population is set by the relative success of the larvae. The current relationship between the huge returns of megalopae and the commercial catch will likely delineate an asymptote and would describe conditions under which settlement is so high that adult population size is not set by the relative success of the larvae, but by the relative success of the recruits; when the returns of megalopae are very high, density dependent effects will likely strongly influence the adult population size. This type of relationship between the annual return of larvae and the eventual size of the commercial catch is exactly what has been seen in the fishery for the Western Australian rock lobster (*Panulirus cygnus*) (Phillips 1986; Caputi et al. 1995). We will not know if this is true until we see how many adults are caught in the future; the first commercial catch from the recent large returns occurs in the 2010/2011 fishing year and will continue for several more years. If the relationship between the number of megalopae returning and the commercial catch is asymptotic then we should be able to predict the commercial catch with this more complete model relationship between number of returning megalopae and the size of the commercial catch.

Density dependent effects can take several forms, e.g., competition for food, increased predation, and the spread of diseases or parasites. The very high densities of recruits seen in the 2007 ROV video off Cape Perpetua, Oregon and their small size suggests that competition for food was reducing their growth rate. Competition for food may eventually lead to starvation or slower growth may lead to a longer period of vulnerability to predators on small crabs. Settling megalopae are preyed upon by young of the year Dungeness crabs (Fernandez et al. 1993; Fernandez 1999) as well as by predators of small crustaceans such as crabs and fish (Armstrong et al. 1995; Visser et al. 2004). Predation on Dungeness crab recruits has received some attention in estuarine habitats (Armstrong et al. 1995; Visser et al. 2004), but studies do not appear have taken place in coastal subtidal habitats. High densities of new-recruits could lead to predators, which do not normally prey on Dungeness crab recruits to target the bounty. This has not been investigated. Very high densities of recruits might also lead to the rapid spread of diseases or parasites, but this has also not been investigated.

What might have caused the amazingly large larval returns of the last three years? Ocean conditions were clearly far more favorable either to the survival of Dungeness crab larvae during their pelagic development or their return to the coast. As pointed out earlier, we know too little about predation on crab larvae to speculate on the contribution of decreased predation as a cause for the large returns of megalopae. We tested the hypothesis that the growing conditions may have been better during the past three years by assuming the sizes of returning megalopae were an indication of growing conditions; larger megalopae would indicate better growing conditions. Megalopae from the last three years were not consistently larger than megalopae from years with lower returns suggesting that, if our assumed relationship between megalopae sizes and growing conditions is correct, then growth conditions during the pelagic phase were not markedly better during the years of huge returns than those with lower returns.

While the size data do not indicate that growth conditions likely varied between years with higher and lower larval returns, the size data are curious. In all years, megalopae were largest at the start of the settlement season and, generally, decreased in size over the course of the spring and summer (fig. 8). It is not clear what might be causing this seasonal size decrease. Off Oregon, larval release is in winter and the larval period is about three months. If larval returns in Oregon are due to larval production from Oregon, then larval returns should end by July, but megalopae continue to settle into October and even November (fig. 4). By July, coastal flow is from the north suggesting that the source of these late summer settlers is to the north. Populations north of Oregon spawn later in the year (Strathmann 1987) and a limited set of measurements suggests that megalopae to the north (Washington and Puget Sound) are smaller than those caught off Oregon (DeBrosse et al. 1990). The very small megalopae caught at the end of the 2006 settlement season were similar in size to those from Puget Sound. The variation in size of megalopae over the settlement season may be due, at least in part, to different larval sources, but why source might affect megalopae size is unknown.

Larval transport may also affect the number of megalopae returning to the Oregon coast. From 1997 through 2006, the timing of the spring transition was clearly related to the number of settlers, suggesting that shoreward transport generated by the spring transition played a substantial role in determining larval success. In the last three years, however, this relationship is no longer true. We investigated the relationship between the number of settlers and a number of ocean and climate indices. Several of these correlations were either significant (summed PDO Jan. – July) or nearly so (summed winter upwelling index, and summed NOI Jan. – July) (fig. 9), and each of these climate or hydrographic variables can be interpreted as indicators of the amount of southward flow along the West coast. The PDO correlates with the amount of water from the North Pacific Drift that enters either the Gulf of Alaska (positive PDO) or the California Current (negative PDO) (Minobe and Mantua 1999); in years when more water is deflected to the California Current the return of megalopae was higher. The summed winter upwelling index indicates both the amount of water forced off- or onshore by the winds, but also the amount of wind-driven north- or southward flow over the shelf; during the winter months, when Dungeness crab larval are pelagic, weaker downwelling-favorable winds (less offshore and northward flow) led to higher numbers of returning megalopae. Positive (negative) values of the NOI tend to be associated with La Niña (El Niño) events, stronger (weaker) upwelling favorable winds along the West coast, and cooler (warmer) sea surface temperatures in the California Current (Schwing et al. 2002); higher returns of megalopae tended to occur when the NOI was more positive indicating more flow from the north. Tentatively—the time series of returning megalopae is short—these correlations suggest that when northward flow during the winter is weak or southward flow during the Dungeness crab larval development period is stronger, more megalopae return to the Oregon coast.

How might north/south flow during the pelagic larval phase affect the number of returning megalopae? Along the Oregon coast, larvae hatch during winter probably within several miles of shore (Wild and Tasto 1983). As development progresses, larvae are found progressively further from shore such that by late zoeae stages they are found seaward of the continental shelf (Wild and Tasto 1983). Early larval stages are, thus, in shelf waters in winter and will be transported northward by the Davidson Current. Northward transport will continue until larvae migrate off the shelf and into the southward flowing California Current present beyond the shelf. The amount of northward vs. southward transport the larvae will experience will be dependent on the amount of time spent in the Davidson Current vs. California Current and current speeds. Given the speed at which drifters are carried northward by the Davidson Current (Austin and Barth 2002), larvae released off Oregon may be transported to Vancouver Island before they migrate seaward of the continental shelf. If larvae experience enough northward transport, they may actually be carried north of the California Current in which case these larvae would settle well to the north of their release site, supplementing the Dungeness crab population along the coast of Vancouver Island. In addition, the amount of southward transport they may experience within the California Current may not compensate for the Davidson Current northward transport, which would again lead to larvae settling to the north of their release point. Whether larvae released in Oregon waters settle to the north or south or settle in Oregon waters may be dependent on the relative transport by the Davidson and California Currents.

The characteristics of the larval stage in Dungeness crabs (e.g., winter spawning, long larval duration, larvae present in the waters over the shelf and beyond, and recruitment to the benthos in spring and summer) are not unique to this species, but are characteristics shared by most shelf/slope species of fish and benthic crustaceans (Shanks and Eckert 2005). Hence, the relative amounts of northward and southward transport as well as processing affecting cross-shelf transport experienced by larvae of these species during their pelagic development may be amongst the critical factors determining the annual larval return at a site.

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