

RECRUITMENT LIMITATION IN DUNGENESS CRAB POPULATIONS IS DRIVEN BY VARIATION IN ATMOSPHERIC FORCING

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Abstract. Ecologists have long debated the relative importance of biotic interactions vs. abiotic forces on the population dynamics of both marine and terrestrial organisms. Investigation of stock size in Dungeness crab (*Cancer magister*) is a classic example of this debate. We first tested the hypothesis that adult population size was set by larval success. We found that during a five-year sampling period, adult crab population size from Oregon through central California, USA, as measured by the commercial catch, varied directly with the number of terminal-stage larvae (megalopae) returning to Coos Bay, Oregon, four years earlier; adult population size was largely determined (>90% of the variation) by success during the larval stage. We then tested whether biotic interactions or abiotic forces caused the variation in larval success. Most of the variation (>90%) in the number of returning megalopae is explained by the timing of the spring transition, a seasonal shift in atmospheric forcing that drives ocean currents along the west coast of the United States. Early spring transitions lead to larger numbers of returning Dungeness megalopae, while in four other crab taxa, species with very different life history characteristics, early-spring transitions lead to lower numbers of returning megalopae. During the past roughly 30 years, the size of the commercial catch of Dungeness crab is significantly and negatively correlated with the date of the spring transition throughout the California Current system. Long-term variation in the date of the spring transition may explain a major crash in the Dungeness crab fishery in central California, which began in the late 1950s. The data suggest that Dungeness crab population size is determined by variation in larval success and that a significant portion of this variation is due to the timing of the spring transition, a large-scale climatic forcer.

Key words: California Current; *Cancer magister*; density dependence; Dungeness crab; megalopae; recruitment; recruitment-limited; recruitment-regulated; spring transition.

INTRODUCTION

Animal populations can fluctuate dramatically over time. Understanding the causes of demographic variation is a long-standing topic of research and debate in ecology (Bjørnstad and Grenfell 2001). One of the key issues is the relative importance of abiotic vs. biotic control of populations. This topic is especially relevant to marine organisms, because both physical forcing and biotic interactions can have strongly time-varying impacts on population structure. In addition, because many marine organisms have complex life cycles whereby different life history stages are spatially separated, the possible abiotic or biotic controls on a population can be complex. Benthic organisms often produce pelagic propagules or larvae that spend days to months in the plankton. To complete their life cycle, these larvae must make the transition from a pelagic habitat to an appropriate benthic one. If the pelagic stage is long enough (weeks to months), larvae can be

transported substantial distances by ocean currents, probably ensuring that most of the larvae returning to a local population are not offspring of that local population. Marine biologists describe such a population as demographically open, and theory predicts that local recruitment is decoupled from local reproductive output. Instead, local populations depend on input from a larval pool generated by the metapopulation (the sum of local populations within a species' range). Variation in local population demography may be limited by variable rates of these larvae being transported from their pelagic development habitat to the benthos, which is known as a recruitment-limited population. Conversely, populations may be regulated by biotic or abiotic factors affecting benthic juveniles or adults, termed a recruitment-regulated population (Caley et al. 1996). Due to the generally low concentrations of pelagic larvae relative to other zooplankton, variable success during the pelagic stage is likely due to density-independent factors. Once larvae settle to the benthos, however, regulation of the population can be due to density-independent or -dependent factors. Both processes undoubtedly occur to some extent in all marine populations.

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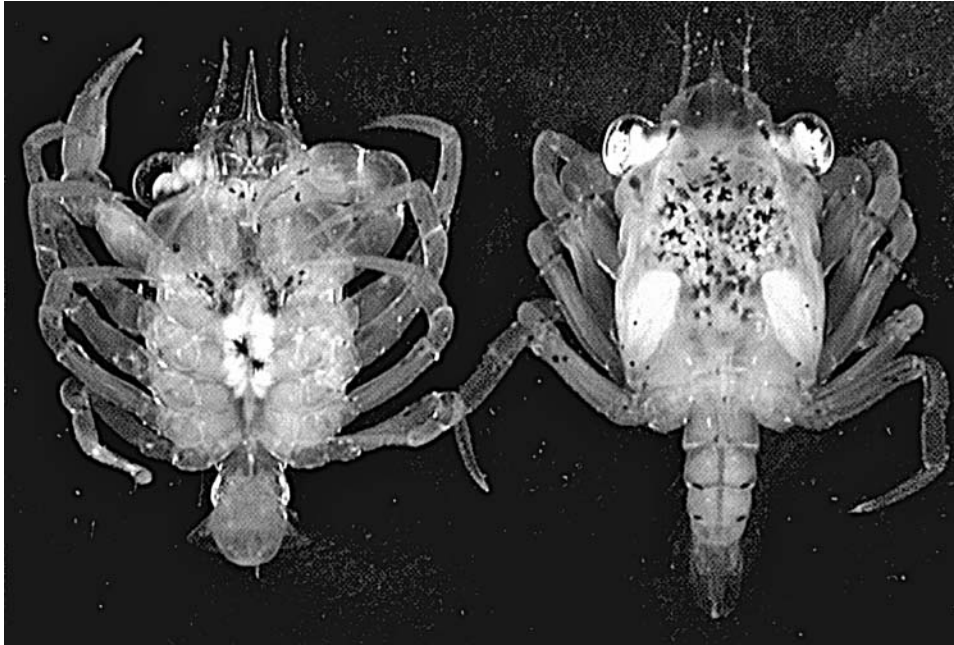


PLATE 1. (Left) Ventral and (right) dorsal views of a *Cancer magister* megalopa. Carapace length is approximately 6 mm. Photo credit: C. Roegner.

In a review of the effects of larval settlement or recruitment on the dynamics of marine populations, Caley et al. (1996) suggest that the key issues to be addressed are: (1) the extent to which recruitment variation in space and time causes variation in the size of the adult population, (2) the causes of variation in the abundance of settlers or recruits, and (3) the relative importance of variation in settlement vs. post-settlement processes in setting the population size.

We investigated these three key issues using the Dungeness crab, *Cancer magister*, as the model organism. The Dungeness crab is a commercially and ecologically important species from the west coast of North America (McKelvey and Hankin 1981, Johnson et al. 1986, Higgins et al. 1997). The fishery on *C. magister* is limited to male crabs >160 mm carapace width (McKelvey et al. 1980). In the California Current system, male crabs generally reach 160 mm by four years of age. The fishery is intense, and currently 80% of the annual catch is obtained within two months of the season opening. By the end of the fishing season, essentially all legal-sized males are caught; thus the annual catch is an accurate measure of the size of the four-year-old year class (Hackett et al. 2003). If the abundance of terminal larvae (megalopae) returning to local populations is variable and post-larval mortality is not large, then the size of an age class should be correlated with the number of settlers (Caley et al. 1996). In the case of *C. magister*, we should find a correlation between the number of returning megalopae and the number of adult male crabs four years later. As we demonstrate below, a strong correlation exists.

A positive stock–recruit correlation infers a recruitment-limited population, leading us to ask what might cause the annual variation in the number of returning megalopae. There are at least two hypotheses: (1) the “larval-production hypothesis” posits that the number of returning megalopae is proportional to the number of offspring produced by the regional population or metapopulation; and (2) the “larval-mortality hypothesis” invokes variable (but density-independent) mortality during the pelagic stage, which leads to variation in the abundance of recruits returning to benthic sites. We tested the first hypothesis by estimating the number of adult female crabs each year from the fishing statistics and correlating this to the annual abundance of megalopae. For the second hypothesis, there are several possible causes for mortality during the pelagic stage, including disease, predation, starvation, and “larval wastage” (i.e., ocean currents carry larvae away from settlement sites). Data describing the variation in mortality due to disease, predation, and starvation during the pelagic larval period are unavailable. However, ocean currents are often driven by climatic variables, and as these data are available, we can examine the effects of mortality due to larval wastage on the rate of recruitment.

To understand how climatic variables and their effect on ocean currents might cause variation in larval success, we review what is known about the larval period of Dungeness crabs. *Cancer magister* larvae hatch near the coast in mid-winter and require about three months to mature (Pauley et al. 1989). As they develop, zoea-stage larvae are found progressively further from

shore (Lough 1974, Reilly 1983). By the megalopal stage (the recruiting form; see Plate 1), larvae are typically found in California Current waters, seaward of the continental shelf, and often >100 km from shore. To survive to adults, megalopae must settle in shallow water, hence, they must migrate from offshore back to the coast (Pauley et al. 1989). In Oregon, megalopae begin returning to shore in mid-April and generally most return by June (Roegner et al., *in press*). Recruitment to coastal and estuarine sites occurs in pulses lasting several days, and this migration is apparently facilitated by some tidally based mechanism over the continental shelf (Johnson and Shanks 2002, Miller and Shanks 2004; Roegner et al., *in press*). Thus, as a first step in their shoreward migration, megalopae must get from the open ocean to the water over the continental shelf, a shoreward migration of some tens of kilometers.

The California Current system is strongly modulated by large-scale atmospheric forcing (Huyer 1983, Hickey and Banas 2003). In winter, downwelling conditions predominate: winds are from the south, the Davidson Current flows northward over the continental shelf while the California Current flows southward seaward of the shelf. In spring, due to seasonal movements of atmospheric high- and low-pressure cells, the winter winds from the south shift to a predominately equatorward direction. This shift is known as the "spring transition," and it instigates a dramatic change in coastal currents (Huyer et al. 1979, Strub et al. 1987). The equatorward winds first stop and then reverse the flow of the Davidson Current. The winds also generate coastal upwelling, and, with this upwelling, the surface waters over the shelf move offshore and are replaced by deeper waters from off the shelf. During the spring transition, waters in the California Current are brought back onto the shelf by the onset of upwelling. In oceanic water, *C. magister* larvae make a typical diel vertical migration between the neuston at night and depths >70 m during the day (G. C. Roegner and A. Shanks, *unpublished data*). The seasonal-upwelling-driven shoreward movement of deeper water from the California Current may transport *C. magister* megalopae from the open ocean onto the continental shelf.

The date on which the spring transition occurs varies annually. We hypothesized that variation in megalopal abundance is related to the timing of the spring transition. With a mid-winter hatching and a three-month larval phase, megalopae are ready to return to shore near the end of March. When the spring transition occurs close to this date, megalopae spend minimum time in the plankton before being transported onto the continental shelf and migrating to shore. Under these circumstances, we predicted annual abundance would be high. In some years the spring transition is delayed by months (Strub et al. 1987), in which case megalopae spend extra months at sea when mortality may decrease their numbers. We hypothesized that the abundance of

megalopae would be low when the spring transition was late.

In our samples, we also enumerated the megalopae of several other crab taxa (*Pagurus* spp., *Hemigrapsus* spp., and Porcellanidae), which have very different life history traits from those of *C. magister*. These taxa spawn twice per year (late winter and spring or summer), the larval period is shorter (40–80 days), and their larvae are primarily found close to shore (<20 km; Lough 1974, Strathmann 1987). At the spring transition, offshore movement of the Davidson Current may carry these larvae away from coastal settlement sites; hence we hypothesized that the timing of the spring transition would have the opposite affect on their recruitment, i.e., low returns when the spring transition was early.

We first demonstrate the strong positive correlation between *C. magister* megalopae returning to Coos Bay, Oregon, and the adult catch four years later. We developed a spawning-stock index based on fisheries catch and used it to test the larval-production hypothesis. We then used cross-correlation of catch and the strength of springtime upwelling and the date of the spring transition to test the larval-mortality hypothesis.

METHODS

Crab megalopae were captured daily from spring and summer 1997 through 2001. In 1997, a stationary zooplankton net set near the mouth of the Coos Bay estuary fished the flood tide (Johnson and Shanks 2002). From 1998 through 2001, we caught megalopae in light traps placed in the small boat harbor in Coos Bay (G. C. Roegner, D. A. Armstrong, and A. L. Shanks, *unpublished manuscript*). For 22 days in 1997 we fished both the zooplankton net and light traps. Using the regression relating the two time series, we estimated the number of megalopae we should have caught in 1997 if we had used the light trap, and these values were used in subsequent statistical analyses. The total number of megalopae captured in each year was used as an index of settling 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 commercial catch landed four years later (the time needed for megalopae to grow to legal-sized crabs) in Coos Bay, Oregon, all of Oregon, Washington, and northern, central, and southern California. The state Fish and Wildlife Offices in Washington and California provided commercial catch data and the Oregon Dungeness Crab Commission provided data for Oregon (Wild and Tasto 1983).

To test the larval-production hypothesis, we developed a spawning-stock index, an estimate of the population size of mature females based on the commercial catch data. Females become reproductive at about two years of age and remain reproductive until they are six or seven (McKelvey and Hankin 1981). Females are not retained in the fishery; we assume that

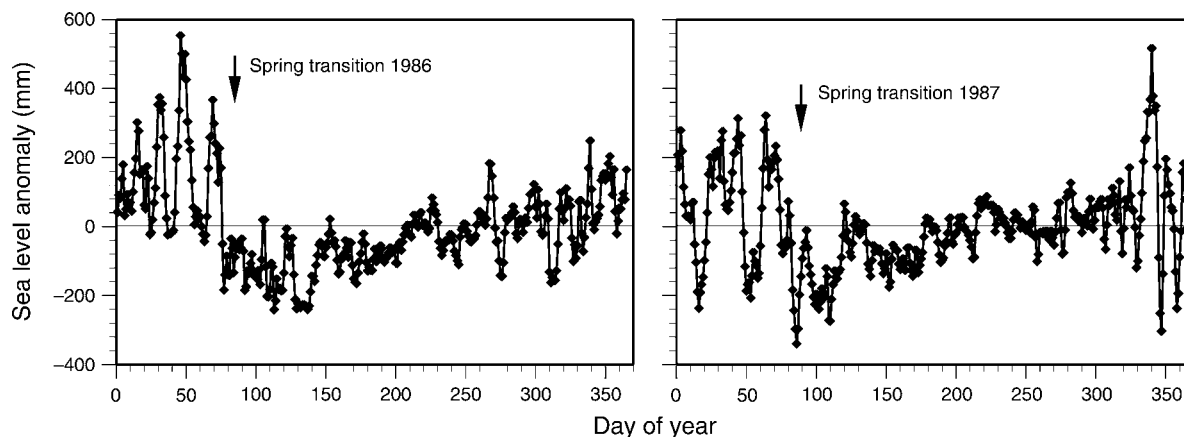


FIG. 1. Determination of the spring transition date from Crescent City, California, USA, sea level data. The spring transition was the date on which the sea level dropped 100 mm below the annual average (e.g., 1986). If winds and sea level fluctuated, we used the date of the drop in sea level after the last return to sea levels typical of winter (e.g., 1987).

fishing mortality is negligible. The sex ratio is essentially 1:1 so the number of males captured in a given year in the fishery, the four-year-olds, should be a good estimate of the number of four-year-old females. We used the catch data from the three years prior to this year and two years after this year to estimate the abundance of female crabs aged seven to five years and three to two years, respectively. To estimate the number of five-year-old females we took the catch data from year₋₁ and decreased this value by an estimate of natural mortality during this period (Higgins et al. 1997). This was repeated for the data from year₋₂ and year₋₃ decreased by two and three years of mortality, assuming a constant natural mortality rate. To estimate the number of two- and three-year-old females we took the commercial catch data from year₊₁ and year₊₂ and increased these values by the estimated amount of mortality they may have experienced during the period from year two or year three to year four. These estimates of the number of females were then summed across the years to generate a spawning-stock index for a given year.

We correlated the spawning-stock index calculated from the commercial catch landed in Coos Bay (e.g., crabs caught within ~30 km of Coos Bay) against the index of settling megalopae to test the hypothesis that variation in the abundance of megalopae was due to the reproductive output of the population. The long larval pelagic phase of this species suggests that local populations are demographically open; the local Coos Bay population likely spawned few of the megalopae returning to the bay. Because local populations are open, a more appropriate estimate of spawning stock size should probably be calculated from a much broader area. We also ran this correlation using spawning stock indices calculated from the commercial catch data for all of Oregon (~500 km of shore), all of Oregon and Washington (~750 km of shore), and all of Oregon, Washington, and northern California (~1200 km of shore).

To test the larval-mortality hypothesis, we compared the index of settling megalopae to the timing of the spring transition and the strength of spring upwelling, two physical variables that may affect the shoreward transport of megalopae. The spring transition is apparent as an abrupt drop from the high coastal sea levels of winter (Fig. 1). The drop in sea level occurs following a period of steady winds from the north (Strub et al. 1987). In some years, upwelling winds trigger the drop in sea level, but then winds reverse and sea level rises back to levels typical of winter (Fig. 1; Strub et al. 1987). The winds can fluctuate one or more times before the spring transition ultimately settles in. 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). If wind and sea level fluctuated, we used the date of the drop in sea level after the last return to sea levels typical of winter (Fig. 1). To determine the date of the spring transition we used sea level data for Crescent City, California, obtained from the University of Hawaii Sea Level Center (*available online*).⁴ The strength of springtime upwelling was estimated from summed monthly averages of the upwelling index for March, April, May, and June. The upwelling index was calculated by the Pacific Fisheries Environmental Laboratory for 42° N (*available online*).⁵

Finally, because our index of settling megalopae is a short time series (only five years), we examined the available fishery and physical time series over longer periods and a broader area. To test for possible relationships between population size and the spawning-stock index, the timing of the spring transition, and the strength of springtime upwelling, we correlated these variables against the size of the commercial catch

⁴ (<http://ilikai.soest.hawaii.edu>)

⁵ (<http://www.pfeg.noaa.gov/pr>)

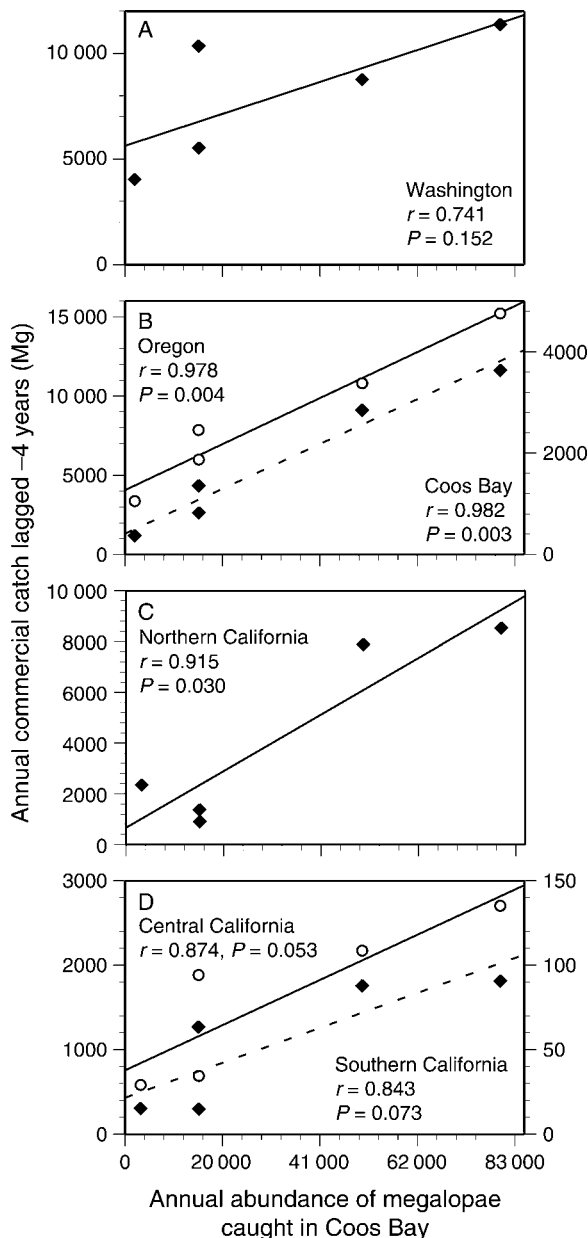


FIG. 2. Commercial catch landed in (A) Washington, (B) all of Oregon and Coos Bay, Oregon (left and right axes, respectively), (C) northern California (Oregon border to Fort Bragg), and (D) central California (San Francisco area) and southern California (Monterey Bay to Morro Bay) (left and right axes, respectively) plotted against the annual abundance of *Cancer magister* megalopae caught in Coos Bay, Oregon. Commercial catch was lagged -4 years to account for growth from megalopae to commercial-sized crabs. Values in each figure are the results of correlations between the lagged annual commercial catch and the annual catch of megalopae in Coos Bay.

(lagged -4 years) landed in (1) Washington, (2) Oregon, (3) northern California (Oregon border to Point Arena), (4) central California (Bodega Bay and San Francisco Bay), and (5) southern California (Monterey Bay south).

Current fishing effort removes essentially all four-year-old crabs, hence, the commercial catch is an excellent measure of this year class (Hackett et al. 2003). We used commercial catch data from years when the fishing effort was similar to current fishing intensity (from the early 1970s for Oregon and California and from the late 1980s for Washington). These data were used to calculate the spawning-stock index as described above, which was cross-correlated against the commercial-catch time series. Because the spawning-stock index is generated from the commercial-catch time series, we would expect significant cross-correlations at small lags. If, however, larval recruitment varies with the size of the spawning stock, then we should see significant cross-correlations at lags of -4 years. The date of the spring transition was determined from coastal sea level data using the methods described above. Data were obtained from sea level monitoring stations in each region in which we ran correlations. The stations were Neah Bay for Washington, Crescent City for Oregon and northern California, San Francisco Bay for central California, and Monterey Bay for southern California. An index of the strength of the springtime upwelling was calculated as described above for each section of the coast (e.g., 48° N, Washington; 42° N, Oregon and northern California; 39° N, central California; and 36° N, southern California).

RESULTS

The annual catch of *C. magister* megalopae settling in Coos Bay, Oregon, varied from 1094 to 79 842 individuals during our five-year study, and this index of settling megalopae was strongly and positively correlated to the commercial catch landed in Coos Bay after a lag of four years (Fig. 2). Adult population size was limited by variation in larval success. We also found significant correlations between the annual catch of megalopae in Coos Bay and the annual commercial catch landed four years later in all of Oregon and in northern California. This correlation was almost significant ($P = 0.053$) for central California (Fig. 2). The catch data from Washington and southern California were not significantly correlated to the abundance of megalopae caught in Coos Bay, although the trend was similar to that seen in the other regions. These significant correlations suggest that not only was adult population size set by larval success, but the factors affecting larval success were very similar over a large area of the coast (~1000 km). The California Current Dungeness crab populations appear to be recruitment-limited.

Increases in the annual catch of megalopae did not, however, lead to proportional increases in the future commercial catch. This can be seen by calculating a per capita recruitment rate into the adult population (commercial catch [in megagrams, or metric tons] landed in Coos Bay divided by the index of settling megalopae; Fig. 3). In 1997, the year in which the fewest megalopae

were caught, this ratio was almost 0.35. In subsequent years, when the index of settling megalopae varied from ~14 000 to almost 80 000 yr^{-1} (10 to almost 100 times larger than in 1997) the ratio was between 0.1 and 0.05. The relationship between returning megalopae and per capita recruitment rate appears to be asymptotic (Fig. 3); a power curve fit to the data is statistically significant ($r = 0.95$, $P < 0.05$, $y = 6.55x^{-0.45}$). As discussed below, these results have bearing on possible density-dependent mortality affecting population size.

The strong correlation between the index of annual megalopae abundance and the size of the commercial catch leads one to question what might be causing the large annual variation in the number of returning megalopae. We found no correlation between our estimate of the spawning biomass of females in a given year and the annual abundance of megalopae caught in the light trap in that year. We tested both the untransformed and log-transformed time series. We then ran cross-correlations between the index of spawning biomass calculated from the commercial catch in each region of the California current (e.g., Washington, Oregon, northern California, central California, and southern California) and the commercial catch in each of those regions (the time series were log-transformed). If the number of returning larvae varies with the spawning biomass of females then we should find significant cross-correlations between the spawning biomass and the commercial catch four years later; no significant correlations were found.

Nor did we find any significant correlations between the strength of the springtime upwelling in Oregon and the index of annual megalopae abundance (untransformed and log-transformed abundances were used) as determined from the light trap data from Coos Bay, Oregon. We extended this analysis by cross-correlating the strength of the springtime upwelling in each region of the California Current against the commercial catch in that region (the catch data were log-transformed). We found no significant cross-correlations at any lag.

We did find, however, that the log-transformed annual abundance of *C. magister* megalopae was significantly and negatively correlated to the date of the spring transition (Fig. 4); recruitment was high when the spring transition was early (March) and low when it was late (May or later). We also found a significant positive correlation between the date of the spring transition and the date on which the first large catch (>100 individuals/d) of *C. magister* megalopae occurred ($n = 5$, $r = 0.962$, $P < 0.008$); large catches of megalopae tended to occur earlier when the date of the spring transition was early.

In addition, annual abundances of *Pagurus* spp., *Hemigrapsus* spp., and Porcellanid crab megalopae were significantly and positively correlated to the timing of the spring transition (Fig. 4); a late spring transition resulted in stronger recruitment. Variation in the spring transition date, a major annual shift in the coastal

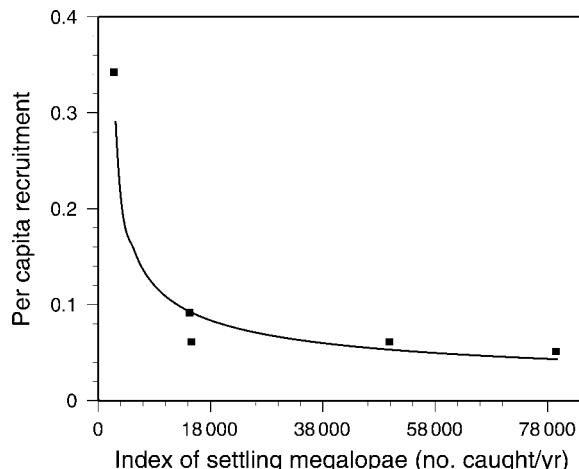


FIG. 3. The per capita recruitment rate (i.e., Coos Bay commercial catch lagged -4 years divided by the index of settling megalopae) plotted against the index of settling megalopae. The curve ($y = 6.55x^{-0.45}$) is significant with $r = 0.95$ and $P < 0.05$.

current regime, explains >90% of the annual variation in the annual abundance of megalopae of *C. magister*, *Pagurus* spp., *Hemigrapsus* spp., and Porcellanid crabs.

The number of megalopae returning to shore determined future commercial catch of Dungeness crabs and the timing of the spring transition determined megalopae abundance; hence we should see a correlation between the timing of the spring transition and commercial catch. Because the spring transition occurs nearly simultaneously from Washington to Point Conception, California (Strub et al. 1987), we predicted we would find negative correlations between the timing of the spring transition and commercial catch over this entire region. Indeed, all correlations were significant. Thus, along the entire West Coast, the date of the spring transition was negatively correlated to the commercial catch and explained from 20% to 70% (average 36%) of the variability in the time series (Fig. 5). Thus, over ~1700 km of coast, variability in the abundance of *C. magister* was significantly correlated to the timing of this major seasonal shift in the California Current system.

We next examined long-term trends in the historical data from San Francisco, where sea level and *C. magister* commercial catch data extend back to 1901 and 1916, respectively. The date of the spring transition varied from day of year 45 (14 February) to 160 (9 June), with high interannual variability. Catch data were log-transformed and lagged -4 years and, to highlight and compare the underlying longer-term patterns, we smoothed both data sets with a nine-year running average. Plotting the smoothed date sets (Fig. 6), we see that peak commercial catches tended to occur during periods when the date of the spring transition was early and low catches occurred when it was late.

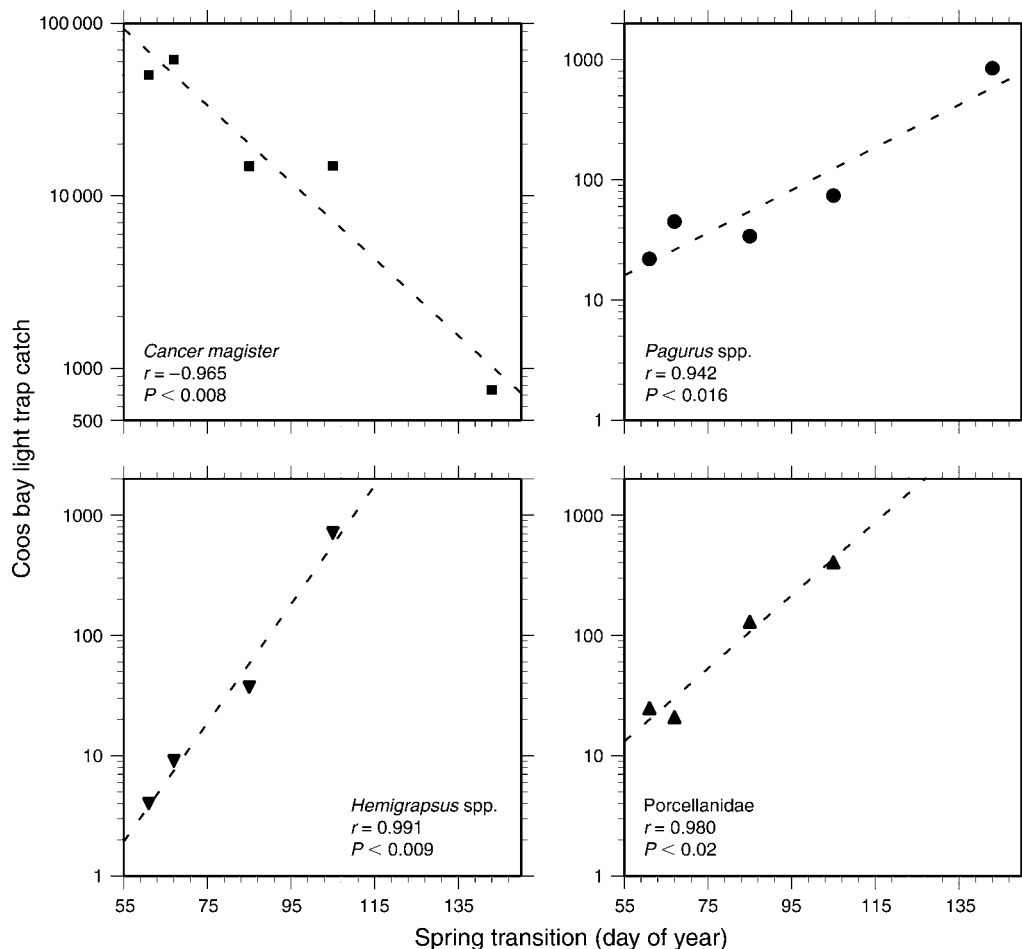


FIG. 4. The relationship between the log-transformed annual abundance of megalopae of four crab taxa caught in Coos Bay, Oregon, and the day of the year of the spring transition, a major seasonal shift in the California Current system. Values in each figure are the results of correlations between the log-transformed annual catch of megalopae and the date of the spring transition.

DISCUSSION

Over a five-year period, >90% of the variation in the size of the four-year-old year class of *C. magister* was explained by the number of megalopae returning to shore. These results address a fundamental question in marine ecology: Is adult population size set by larval or post-larval success? For the Dungeness crab, during this period, population size was clearly limited by the relative success of their larvae during their pelagic development. More surprisingly, the index of settling megalopae determined in Coos Bay, Oregon, was also significantly correlated with the commercial crab catch from the Oregon–Washington border south to around San Francisco, California, suggesting that the factors affecting the annual variation in larval crab recruitment were similar over this entire range.

We hypothesized that the shoreward migration of megalopae from the open ocean onto the continental shelf is a critical event during the larval phase of *C. magister*, and we hypothesized that this shoreward migration occurred as a result of the spring transition

when the California Current moves back onto the continental shelf. We tested this hypothesis by comparing the timing of the spring transition to the size of the annual recruitment of Dungeness megalopae and found that nearly all variation in megalopal abundance can be attributed to the date of the spring transition. When the spring transition was early many more Dungeness crab megalopae returned to shore than when the transition was late. In contrast, crab taxa with larvae that remain close to shore had an opposite relationship, suggesting that they may be carried offshore with the Davidson Current waters during the spring transition. Our results are consistent with the hypothesis, but do not directly test it. Testing would require field sampling of crab larvae before and during the spring transition over several years.

In western Australia, annual variation in the number of returning puerulus (terminal larval stage) of the rock lobster (*Panulirus cygnus*) correlates significantly with the strength of the Leeuwin Current (Caputi et al. 1996). Like *C. magister*, the larvae of the *P. cygnus* hatch over

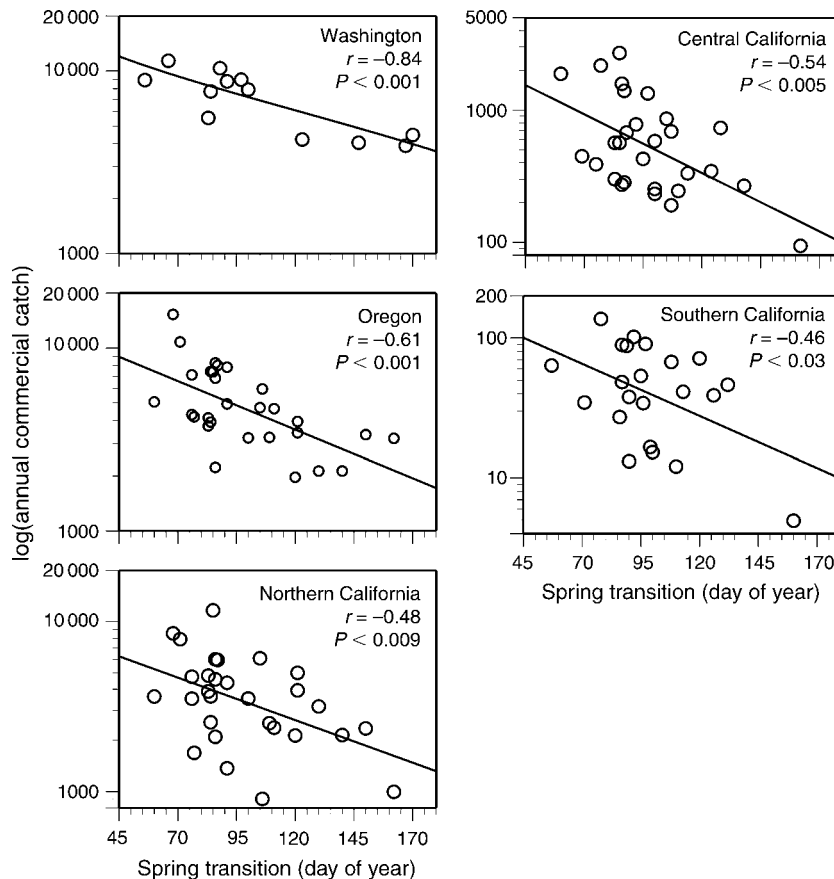


FIG. 5. Log-transformed commercial catch of *Cancer magister* lagged by -4 years (to account for growth from megalopae to commercial crabs; in metric tons prior to transformation) vs. the date of the spring transition for locations along the West Coast. The commercial catch data were limited to periods when the fishing effort was intense enough that catch represents only four-year-old male crabs (early 1970s for Oregon and California and late 1980s for Washington). The date of the spring transition was determined from sea level data in each region. Values in each figure are the results of correlations between the log-transformed annual commercial catch and the date of the spring transition.

the continental shelf and then, during their pelagic development, move steadily offshore (Phillips et al. 1978). By the end of the phyllosomma larval stage, larvae are found at sea and well off the continental shelf. To complete development the puerulus must migrate back to shallow subtidal habitats close to shore, where they settle (Phillips et al. 1978). Shoreward flow increases with increasing strength of the Leeuwin Current, and the size of the annual return of puerulus is directly related to the strength of the Leeuwin Current (Caputi et al. 1996). As with *C. magister*, annual variation in the number of returning larvae appears to be related to variation in currents that will carry the larvae from the open sea toward shore and onto the continental shelf.

When density dependence plays a significant role in population regulation, one typically sees that beyond some level of settlement there is little additional increase in adult population size, i.e., the relationship between settlement and adult population size is asymptotic (Caley et al. 1996, their Case 4C). The relationship we

observed for *C. magister* appears linear over the whole range of observed megalopal abundance (Fig. 2). One could argue that our time series is too short to have captured the full range of variation in either annual megalopal abundance or adult population size; we did not have data in the asymptotic part of the curve. However, in our data the index of settling megalopae varied by almost two orders of magnitude while the Oregon commercial catch varied from slightly less than the 57-year long-term average commercial catch (3357 vs. 3862 Mg) to a record catch in 2005 that was four times larger than the long-term average commercial catch. These results suggest our five-year time series was a broad-enough range of conditions that, if density dependence was regulating the adult population size, we would have found an asymptotic rather than a linear relationship.

The effect of density dependence is clearly seen in the asymptotic relationship between puerulus settlement of *Panulirus cygnus* and the size of the subsequent adult population (Phillips 1986, Caputi et al. 1993). The index

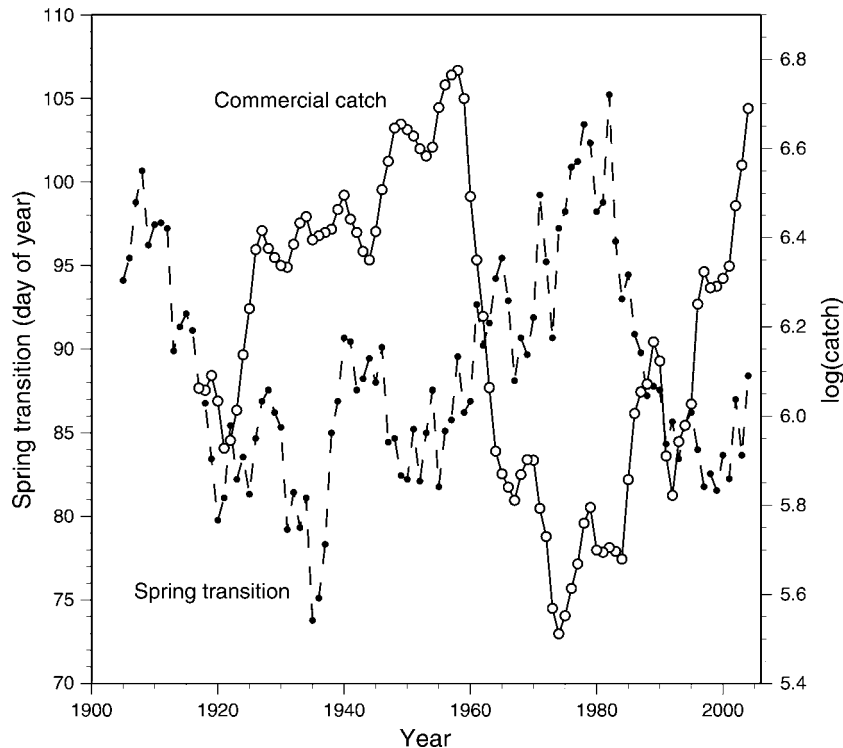


FIG. 6. Date of the spring transition as determined from San Francisco sea level data (solid circles, left-hand axis) plotted with the log-transformed commercial catch of *Cancer magister* (originally measured in metric tons) landed in San Francisco (open circles, right-hand axis). Both time series are smoothed with a 9-year running average, and the commercial catch data were lagged -4 years prior to smoothing.

of puerulus settlement varied from ~10 to 200, but above an index value of around 75 there is no apparent increase in the size of the resulting adult population. This density dependence has been attributed, at least in part, to the limited holding capacity of the nursery reefs (Morgan et al. 1982); at high settlement levels there are too few holes and crevices to provide shelter for all of the new juveniles or there may be an inadequate food supply to support them.

We have not found an asymptotic relationship between megalopal abundance and adult population size in *C. magister*. This may, in part, be due to their habitat. Juvenile and adult Dungeness crabs live on sand or muddy sand bottoms and shelter by burying themselves in the bottom (Morris et al. 1980). In the depth range over which they are found, much of the bottom is sand or muddy sand; habitat and shelter is so abundant that it may not be limiting. Ultimately, there must be some settlement rate at which density-dependent mortality limits the size of the adult population, but this is not apparent in our data.

We found that when megalopal abundance was very low (during 1997), the ratio of commercial catch to the index of settling megalopae (i.e., the per capita recruitment rate) was three to seven times larger than in the subsequent years when the megalopal abundance was much larger. However, in the remaining four years

of sampling, the index of settling megalopae varied by a factor of about six, yet the per capita recruitment rate decreased only slightly (0.075 to 0.050; Fig. 3). The relationship between the abundance of settling megalopae and the per capita recruitment rate appears asymptotic. The initial sharp drop in per capita recruitment with increasing megalopal recruitment suggests a density-dependent effect, but the asymptotic relationship at higher recruitment levels suggests that the strength of this density dependence decreases. Because the time series is short (five years) these conclusions must be considered tentative.

Cannibalism is one of the likely causes of density-dependent mortality of returning megalopae. *Cancer magister* is clearly cannibalistic, with most of the mortality due to juvenile crabs consuming megalopae or early juveniles (Fernandez 1993, 1999, Fernandez et al. 1993); there is no clear evidence that adults consume other adults (Gotshall 1977). Laboratory and field experiments have demonstrated that the first two juveniles stages (J_1 and J_2) are particularly effective predators on megalopae and will also consume, though at a slower rate, other juvenile crabs (Fernandez 1993, 1999, Fernandez et al. 1993). In the field, resident juvenile crabs can consume pulses of settling megalopae within 48 hours (Fernandez et al. 1993, Eggleston and Armstrong 1995). There are several factors that tend to

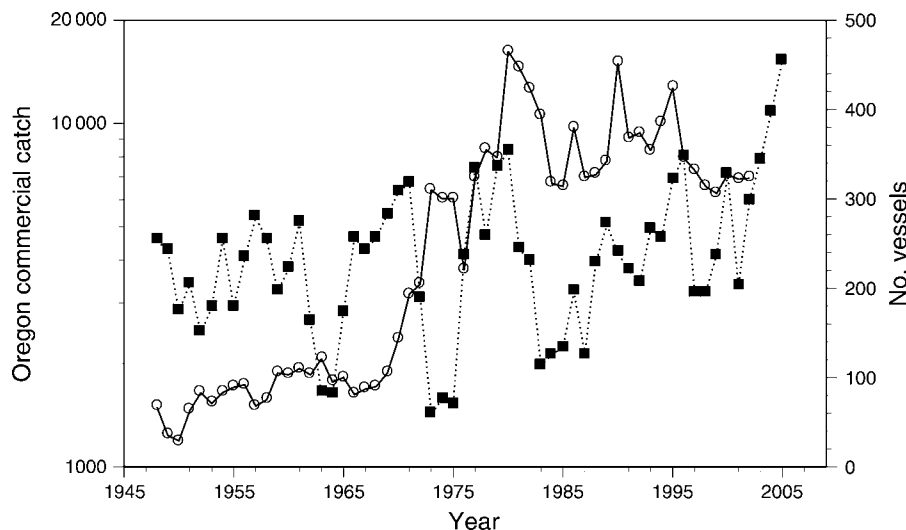


FIG. 7. Oregon commercial crab catch (solid squares; log-transformed [in metric tons prior to transformation]) plotted with the number of vessels fishing for crabs in the Oregon fishery (open circles). Prior to ca. 1980 there was a clear roughly 10-year cycle to crab abundance (significant autocorrelations around a lag of 10 years). After 1980 this cycle is not apparent (no significant autocorrelations at any lag). This change in the pattern of crab abundance may be associated with a large increase in the fishing effort as measured by the size of the commercial crab fishing fleet.

reduce cannibalism. Megalopae are more susceptible than early juveniles crabs (Fernandez 1999), and megalopae molt into juveniles soon after settlement, probably within 24 hours (A. L. Shanks, *personal observation*). The percentage of mortality decreases with increasing megalopae abundance (Fernandez 1999). Most of the annual settlement of *C. magister* megalopae occurs during several brief (two to three days long) pulses (Johnson and Shanks 2002, Miller and Shanks 2004; Roegner et al., *in press*). By swamping the resident crab predators, these pulses may decrease the percentage of mortality due to cannibalism. Apparently due to interference competition between the juveniles, per capita predation on megalopae decreases with increasing juvenile density (Fernandez 1999). As the settlement season progresses, the density of juveniles will generally increase and their effectiveness as predators on megalopae should decrease. This combination of factors may at least in part account for the leveling off in the per capita recruitment rate with increasing annual megalopae abundance.

Historically, researchers have attributed variations in the size of the adult population of Dungeness crabs to the effect of density-dependent negative feedback. For example, Higgins et al. (1997) modeled variations in population size with cannibalism by adults on younger crabs as the driving force: when adult populations are large they consume new recruits, leading eventually to a smaller adult population that has a smaller impact on recruitment. This historical tendency to apply density-dependent models to explain variations in the size of the Dungeness crab population has been motivated by the observation that their populations tend to vary regularly in size with 9 to 10 years between peaks (Botsford and

Wickham 1975, McKelvey et al. 1980). Peaks in the commercial catch in Washington, Oregon, and northern California have been observed about every 10 years starting around 1947 and continuing through about 1977 (Botsford et al. 1989). After the peak in 1977, however, the clear cycling in the commercial catch appears to stop (Fig. 7). Autocorrelations run on the commercial catch data (untransformed and log-transformed) from 1945 to 1977 display significant correlations ($P < 0.05$) at lags around 10 years, but when autocorrelations are run on the data from 1977 to the present there are no significant correlations at any lags.

Intriguingly, the apparent disappearance of the regular periodicity in commercial catch coincides with the rapid build-up in the size of the crab fishing fleet. For example, in Oregon, prior to 1967 there were generally 100 or fewer vessels fishing crab, and these boats deployed <30 000 crab traps (pots). Between 1970 and 1980, the fleet increased to its current size of around 300 vessels, which deploy 110 000–140 000 pots (Fig. 7). During the first roughly 30 years of the fishery, when there was a clear 10-year periodicity to the population size, the number of boats in the fishery fluctuated with the size of the adult population, and this effort lagged the population variations (Botsford et al. 1983); more boats entered the fishery shortly after the peak in population size. From 1975 to the present, this relationship is no longer present. Botsford et al. (1983) present a model, incorporating both density dependence and fishing effort, that lags the peaks in the crab population size. The variation in fishing effort caused variation in the amount of escapement from the fishery. At lower effort some crabs escaped, contributing to the next year's catch (Methot and Botsford 1982); in this

case, catch was in part dependent upon past population size. At high effort there was no escapement and no contribution of animals to the next year's catch. When past dependence was high (low effort) cycles were longer than when past dependence was low (high effort). Since about the mid-1970s the fishing effort has been high, and essentially all of the four-year-old males are removed each year; there is no past dependence. The model suggests that this should lead to shorter cycles. Given the results from the Botsford et al. (1983) model, perhaps the apparent cessation of the 10-year cycle in the Dungeness crab population size is related to the change in the fishing effort in the fishery.

In the late 1950s, the commercial catch in central California dropped dramatically (Wild et al. 1983). This crash was attributed to warmer ocean temperatures from 1957 to 1968, which led to egg failure (Wild et al. 1983). However, by 1969 water temperatures returned to pre-1957 levels, yet commercial catch remained low into the 1980s (Wild et al. 1983). The significant relationship we found between the timing of the spring transition, the return of megalopae to the coast, and subsequent strength of the commercial catch suggests that a period of late spring transitions along the central California coast may have contributed to the crash in the population and the rebound in the 1990s may be due to the earlier spring transitions during this period (Fig. 6).

At least during our five years of sampling, nearly all of the variation in the annual abundance of *C. magister* megalopae could be attributed to one abiotic variable, the timing of the spring transition. Further, the annual variation in the abundance of megalopae explained nearly all of the variation in the subsequent size of the four-year-old year class. Biotic effects such as density-dependent variation in the production of eggs or survival of juveniles apparently played little role in regulating adult population size. The data suggest that *C. magister* populations in the California Current system are recruitment-limited and that recruitment success may vary primarily due to climatic forcing.

Sinclair's (1988) member/vagrant hypothesis states that populations of marine organisms exist where local oceanography ensures that larvae are returned to juvenile or adult habitats. Where oceanographic patterns determine life cycle closure, abiotic variation affecting larvae can generate large interannual variation in year class strength. Our data support this hypothesis and suggest a critical factor for successful recruitment of *C. magister* and other crab taxa in the California Current system is the timing of the spring transition. The life history characteristics of the crab taxa we investigated are typical of many California Current benthic crustaceans and fishes (Shanks and Eckert 2005). On average, shelf/slope species of the California Current spawn during winter, have long larval stages that develop far from shore, and must settle on the shelf or slope. Their larvae are thus pelagic during the spring

transition, when the current system changes dramatically and the change in flow may carry them back to shelf/slope settlement sites. The similarity of their life history characteristics to those of *C. magister* suggests that the timing of the spring transition may influence the larval recruitment of many species in the region. Further, variation in the timing of seasonal shifts in coastal current regimes, both naturally induced or as a possible outcome of global warming, are typical of many areas of the world (Tchernia 1980) and thus may influence recruitment dynamics in many coastal ecosystems.

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LITERATURE CITED

- Bjørnstad, O. N., and B. T. Grenfell. 2001. Noisy clockwork: time series analysis of population fluctuations in animals. *Science* 293:638–643.
- Botsford, L. W., D. A. Armstrong, and J. M. Shenker. 1989. Oceanographic influences on the dynamics of commercially fished populations. Pages 511–564 in M. R. Landry and B. M. Hickey, editors. *Coastal oceanography of Washington and Oregon*. Elsevier, Amsterdam, The Netherlands.
- Botsford, L. W., R. D. J. Methot, and W. E. Johnson. 1983. Effort dynamics of the northern California Dungeness crab (*Cancer magister*) fishery. *Canadian Journal of Fisheries and Aquatic Sciences* 40:337–346.
- Botsford, L. W., and D. E. Wickham. 1975. Correlation of upwelling index and Dungeness crab catch. *Fisheries Bulletin* 73:901–907.
- Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. 1996. Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* 27:477–500.
- Caputi, N., R. S. Brown, and C. R. Chubb. 1993. Regional predictions of the western rock lobster, *Panulirus cygnus*, commercial catch in western Australia. *Crustaceana* 68:245–256.
- Caputi, N., W. J. Fletcher, and C. R. Chubb. 1996. Effect of the Leeuwin Current on the recruitment of fish and invertebrates along the western Australian coast. *Marine and Freshwater Research* 47:147–155.
- Eggleston, D. B., and D. Armstrong. 1995. Pre- and post-settlement determinants of estuarine Dungeness crab recruitment. *Ecological Monographs* 65:193–216.
- Fernandez, M. 1993. Habitat selection by young-of-the-year Dungeness crab *Cancer magister* and predation risk in intertidal habitats. *Marine Ecology Progress Series* 92:171–177.
- Fernandez, M. 1999. Cannibalism in Dungeness crab *Cancer magister*: effects of predatory-prey size ratio, density and habitat type. *Marine Ecology Progress Series* 182:221–230.
- Fernandez, M., D. Armstrong, and O. Iribarne. 1993. First cohort of young-of-the-year Dungeness crab, *Cancer magister*, reduces abundance of subsequent cohorts in intertidal shell habitat. *Canadian Journal of Fisheries and Aquatic Sciences* 50:2100–2105.
- Gotshall, D. W. 1977. Stomach contents of Northern California Dungeness crabs, *Cancer magister*. *California Fish and Game* 63:43–51.
- Hackett, S., M. Krachey, C. Dewees, D. Hankin, and K. Sortais. 2003. An economic overview of Dungeness crab

- (*Cancer magister*) processing in California. California Cooperative Fisheries Investigations Report 44:86–93.
- Hickey, B., and N. Banas. 2003. Oceanography of the U.S. Pacific Northwest coastal ocean and estuaries with application to coastal ecology. *Estuaries* 26:1010–1031.
- Higgins, K., A. Hastings, J. Sarvela, and L. Botsford. 1997. Stochastic dynamics and deterministic skeletons: population behavior of Dungeness crab. *Science* 276:1431–1435.
- Huyer, A. 1983. Coastal upwelling in the California current system. *Progress in Oceanography* 12:259–284.
- Huyer, A., E. Sobey, and R. Smith. 1979. The spring transition in currents over the Oregon Continental Shelf. *Journal of Geophysical Research* 84:6995–7011.
- Johnson, D. F., L. Botsford, R. D. J. Methot, and T. C. Wainwright. 1986. Wind stress and cycles of Dungeness crab (*Cancer magister*) catch off California, Oregon, and Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 43:838–845.
- Johnson, J., and A. L. Shanks. 2002. Time series of the abundance of the post-larvae of the crabs *Cancer magister* and *Cancer* spp. on the southern Oregon coast and their cross-shelf transport. *Estuaries* 25:1138–1142.
- Lough, R. 1974. Dynamics of crab larvae (Anomura, Brachyura) off the central Oregon Coast, 1969–1971. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- McKelvey, R., and D. Hankin. 1981. Comment on cycles in the northern California Dungeness crab population; reply. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1296–1297.
- McKelvey, R., D. Hankin, K. Yanosko, and C. Snygg. 1980. Stable cycles in multistage recruitment models: an application to the northern California Dungeness crab (*Cancer magister*) fishery. *Canadian Journal of Fisheries and Aquatic Sciences* 37:2323–2345.
- Methot, R. D. J., and L. W. Botsford. 1982. Estimated pre-season abundance in the California Dungeness crab (*Cancer magister*) fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1077–1083.
- Miller, J. A., and A. L. Shanks. 2004. Ocean-estuary coupling in the Oregon upwelling region: the abundance and transport of juvenile fish and larval invertebrates. *Marine Ecology Progress Series* 271:267–279.
- Morgan, G. R., B. F. Phillips, and L. M. Joll. 1982. Stock and recruitment relationships in *Panulirus cygnus*, the commercial rock (spiny) lobster of western Australia. *Fishery Bulletin* 80:475–486.
- Morris, R. H., D. P. Abbott, and E. C. Haderlie. 1980. Intertidal invertebrates of California. Stanford University Press, Stanford, California, USA.
- Pauley, G., D. Armstrong, T. P. M. Heun, C. Cordes, and D. Moran. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest): Dungeness crab. Biological Report 82(11.117). U.S. Fish and Wildlife Service, Coastal Ecology Group, Waterways Experiment Station, Vicksburg, Mississippi, USA.
- Phillips, B. F. 1986. Prediction of commercial catches of the western rock lobster *Panulirus cygnus*. *Canadian Journal of Fisheries and Aquatic Sciences* 43:2126–2130.
- Phillips, B. F., D. W. Rimmer, and D. D. Reid. 1978. Ecological investigations of the late stage phyllosoma and puerulus larvae of the western rock lobster *Panulirus longipes cygnus*. *Marine Biology* 54:347–357.
- Reilly, P. N. 1983. Dynamics of Dungeness crab, *Cancer magister*, larvae off central and northern California. Pages 57–84 in P. W. Wild and R. N. Tasto, editors. Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery resource. California Department of Fish and Game, Long Beach, California, USA.
- Roegner, G. C., D. Armstrong, and A. L. Shanks. *In press*. Wind and tidal influences on larval crab recruitment to an Oregon estuary. *Marine Ecology Progress Series*.
- Shanks, A. L., and G. L. Eckert. 2005. Population persistence of California Current fishes and benthic crustaceans: a marine drift paradox. *Ecological Monographs* 75:505–524.
- Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. Washington Sea Grant Program, Seattle, Washington, USA.
- Strathmann, M. F. 1987. Reproduction and development of marine invertebrates of the northern Pacific Coast. University of Washington, Seattle, Washington, USA.
- Strub, P., J. Allen, A. Huyer, and R. Smith. 1987. Large-scale structure of the spring transition in the coastal ocean off western North America. *Journal of Geophysical Research* 92:1527–1544.
- Tchernia, P. 1980. Descriptive regional oceanography. Pergamon Press, Oxford, UK.
- Wild, P., P. Law, and D. McLain. 1983. Variations in ocean climate and the Dungeness crab fishery in California. Pages 175–188 in P. Wild and R. Tasto, editors. Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery resource. California Department of Fish and Game, Long Beach, California, USA.
- Wild, P., and R. Tasto, editors. 1983. Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery resource. California Department of Fish and Game, Long Beach, California, USA.