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Linking ocean conditions to year class strength of the invasive European green crab, *Carcinus maenas*

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Abstract Once a non-native species arrives and survives in an area, its long-term persistence depends on its recruitment success. If conditions are not favorable for recruitment it will ultimately disappear. The European green crab (*Carcinus maenas*) has a 6 year life span and has persisted at low densities in Oregon and Washington coastal estuaries for the past 12 years. We show here that after the arrival of the strong founding year class of 1998, significant self-recruitment to the Oregon and Washington populations occurred only in 2003, 2005 and 2006. Warm winter water temperatures, high Pacific Decadal Oscillation and Multivariate ENSO (El Niño Southern Oscillation) Indices in March, late spring transitions and weak southward shelf currents in March and April are all correlated with the these strong year classes. Cold winter water temperatures, low Pacific Decadal Oscillation Indices, early spring transitions and strong southward (and offshore) currents in March and April are linked to year class failure. Right now, green crabs are still too rare to exert a measurable effect on the native benthic community and on shellfish culture in Oregon and Washington. However, if their numbers were to increase, we would be able to predict the arrival of strong year classes from ocean conditions and alert managers and shellfish growers of possible increases in predation pressure from this invader.

Keywords Year class strength · El Niño · Pacific decadal oscillation · Spring transition · California current system · Temperature limitation

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Introduction

Inter-annual variations in ocean temperature and current patterns have profound effects on coastal ecosystems, and therefore commercial fisheries landings. The warming of surface waters and the suppression of effective upwelling during El Niño events are linked to low nutrients, low productivity and crashes in fish stocks such as Peruvian anchovies, California sardines and Oregon Coho salmon as well as low meat content in oysters (Schoener and Fluharty 1985; Peterson et al. 2006). Inter-annual variation in the direction of coastal currents can affect the recruitment of species with planktonic larvae. When surface currents are moving off-shore during the critical time when larvae are competent to settle, a

whole year class of recruits can be lost (Cowen 1985; Pringle 1986; Ebert et al. 1994). El Niño events have been linked to the northern range expansions of marine invertebrates and fishes (Schoener and Fluharty 1985; Pearcy and Schoener 1987). For example, the mole crab *Emerita analoga* established ephemeral populations on the west coast of Vancouver Island and even on Kodiak Island, Alaska when larvae drift north from source populations further south (Hart 1982; Schoener and Fluharty 1985; Pearcy and Schoener 1987). These populations persist for a few years and then disappear until the next incursion of larvae from the south.

While strong northward moving coastal currents during major El Niño events can result in the temporary northern range expansions of native species, these currents also have the potential to extend the ranges of non-native species. Genetic analysis of Oregon populations of the Eastern mud crab, *Rhithropanopeus harrisii*, supports the hypothesis that larvae from this invader were transported from San Francisco Bay to Oregon estuaries during strong El Niño events (Petersen 2006). El Niño events during the 1990's likewise facilitated the northern range expansion of the invasive European green crab, *Carcinus maenas*, in the northeastern Pacific. A well established population of green crabs was first documented in San Francisco Bay around 1990 (Cohen et al. 1995; Grosholz and Ruiz 1995) and within a decade, the species expanded its range to the west coast of Vancouver Island (Jamieson et al. 2002). From age class analysis of *C. maenas* sightings along the coast and from the arrival of 0-age green crabs in Bodega and Tomales Bay in 1993 and in Oregon and Washington estuaries in 1998, we estimate that there were 3 range expansions to date: from San Francisco to Humboldt Bay, California in 1993; to Oregon estuaries in 1995 or 1996 and to Washington and the west coast of Vancouver Island, British Columbia in 1998 (Grosholz and Ruiz 1995; Miller 1996; Jamieson et al. 2002; Behrens Yamada et al. 2005). Each of these range expansions is linked to unusually high coastal sea levels during the first 4 months of the year (ftp://ilikai.soest.hawaii.edu/islp/slpp.anomalies June 18, 2009) which in turn imply stronger poleward coastal currents. For example, currents off Newport, Oregon averaged 40 km/day in a poleward direction

from January 1 through February 23, 1998 (Kosro 2002). Given a larval duration of around 2 months at 12°C (Dawirs et al. 1986), these velocities, if spatially uniform, would be strong enough to transport larvae from source populations in California and Oregon to the west coast of Vancouver Island and beyond (>2,000 km), as opposed to only ~400 km in a non- El Niño year. Ongoing measurements show that displacements by poleward coastal currents since the 1997/1998 El Niño have been significantly weaker. Weaker currents, combined with very low densities of *C. maenas* in northern California (Grosholz and Schlosser, personal communication) and no evidence of recruitment in our southern Oregon site from 1999 to 2002, suggest that the chances of California populations "seeding" Oregon and Washington estuaries in recent years would have been low. We thus assume that 0-age green crabs appearing in Oregon and Washington estuaries, and on the west coast of Vancouver Island after 1998, were locally produced (Behrens Yamada et al. 2005; Behrens Yamada and Gillespie 2008).

Once a species arrives and survives in an area, its persistence depends on successful recruitment into the population. If conditions are not favorable for recruitment within the lifespan of the colonists, the local population becomes extirpated. Factors acting at different levels influence the temporal and spatial pattern of juveniles recruiting to a population. For species with planktonic propagules, large scale water temperature and currents factors during the critical early life history stages contribute to overall larval availability, while smaller scale factors, such as local wind and tidal forcing, and larval behavior, affect settlement into the adult habitat (Cowen 1985). Finally, post-settlement factors such as desiccation, salinity stress, competition and predation can limit the number of juveniles entering the breeding population. Hjort (1926) found that ocean conditions experienced by larvae often determine year class strength. While post-settlement events do play a role, they can be over-shadowed by large-scale ocean conditions during larval development. For example, Shanks and Roegner (2007) found that commercial landings of Dungeness crabs (*Cancer magister*) are tightly correlated to the abundance of megalopae (last larval stage) 4 years earlier and to ocean conditions during the larval rearing period. In the present study,

we look for a similar correlation between ocean conditions early in the year and the year class strength of 0-age *Carcinus maenas* at the end of their first growing season.

Cold winters have been linked to high mortality of adults and poor recruitment of *Carcinus maenas* in Europe and Maine while warm winters are typically followed by strong year classes of 0-age crabs (Berrill 1982; Beukema 1991). Warm temperatures early in the year would increase the developmental rate of eggs and larvae and may increase survival of larvae and newly-settled crabs. In addition to warm temperatures, currents favorable to shore-ward transport of larvae during the settlement phase are also needed for successful recruitment. The first zoea stage of *C. maenas* swims to the surface, soon after hatching, and rides an ebbing tide from the estuary to the nearshore (Queiroga et al. 1997). There they feed, grow and undergo vertical migrations. When the megalopae are competent to settle, they migrate to the surface, ride a flood tide back to shore, settle and metamorphose into the first crab stage (Queiroga 1998). Queiroga et al. (2006) found that both tidal amplitude and wind patterns play a role in returning *C. maenas* megalopae to Portuguese estuaries. Transport of megalopae to estuaries by tidal currents was enhanced when winds were blowing from the south and the surface water was advected onshore. Thus currents systems capable of retaining larvae in the nearshore during the rearing phase and returning the megalopae to the estuary are critical for the successful local recruitment of young *C. maenas*.

We propose that recruitment of megalopae, and the subsequent development of the 0-age class, of *Carcinus maenas* in Oregon and Washington are linked to winter water temperatures and current patterns during late winter and spring when larvae rear in the nearshore and settle from the plankton. Specifically, we are looking for correlations between year class strength from 1998 to 2008 for 4 Oregon and 2 Washington estuaries and four measures of ocean condition: (1) local mean winter water temperatures for Coos, Yaquina and Willapa Bay, (2) large-scale indices of temperature and sea-level variability (El Nino and the Pacific Decadal Oscillation), (3) dates of annual spring transitions off the Oregon coast and (4) intensity and direction of the mean alongshore currents off Newport, Oregon in March and April.

Methods

Sampling for the 0-age class

Sampling effort focused on 6 estuaries in Oregon and Washington: Coos, Yaquina, Netarts Tillamook, Willapa and Grays Harbor (Fig. 1). We used baited crayfish traps (21 cm by 37 cm) with 6 cm openings and 0.5 cm mesh in all estuaries as well as pitfall traps at the Stackpole site in Willapa Bay where green crabs have been sampled by this method since 1998. Pitfall traps are water-filled 5-gallon buckets buried into the sediment so that their rims are flush with the surface of the sediment. They trap actively foraging crabs of any
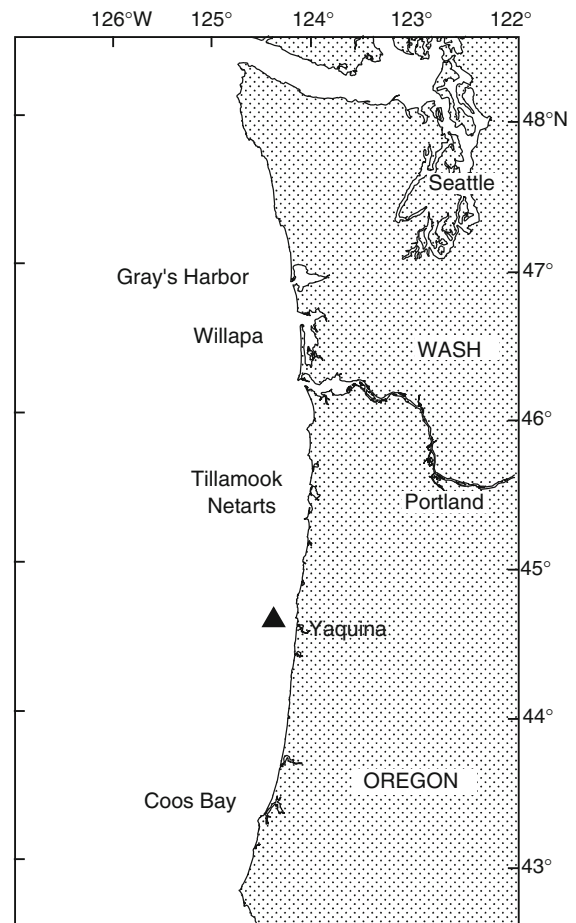

Fig. 1 Study sites in Oregon and Washington. The location of Station NH-10 is indicated by a triangle

size. Since megalopae settle in the upper intertidal (Zeng et al. 1999), all traps were deployed in the high intertidal, typically within *Spartina* or *Scirpus* beds, between late August and early October to document the arrival of 0-age *Carcinus maenas*. These young crabs are easily distinguished from older crabs by their green coloration and small size (30–55 mm in carapace width). Since *C. maenas* is still rare in Oregon and Washington, we do not typically detect the 0-age crabs until they are large enough to enter traps. The only time we observed crabs smaller than 20 mm was in June 1998, after the strong El Niño cohort settled.

We cut fish carcasses into sections and placed them into commercial bait containers (15 × 8 cm). Holes (0.5 cm) in the sides and lids of the containers allow bait odors to diffuse. One bait container with fresh bait was placed in a trap and left for one tidal cycle (∼ 24 h). We retrieved the traps at low tide, identified all crabs and other by-catch to species and noted the sex, carapace widths (CW) and color of the abdomen of all *Carcinus maenas*. *C. maenas* were measured between the tips of their fifth anterio-lateral spines using digital calipers. Native crabs and other by-catch were released while *C. maenas* were removed and frozen. Since densities were low, catch per unit effort (CPUE) of 0-age *C. maenas* for each estuary and year was expressed as number of individuals caught per 100 traps (Table 1). Minimum number of traps set at

the end of the growing season was typically between 50 and 100 traps per estuary.

Age class analysis

Since we did not systematically sample for 0-age *Carcinus maenas* in all the Oregon estuaries prior to 2002, nor in Willapa Bay in 2004, we supplemented our catch data with year class analysis to determine whether *C. maenas* recruited in a particular year to a particular estuary. We compiled all available data of crabs retrieved from the estuaries and noted the size, sex, carapace condition and date of capture. Using the results from a growth study of marked crabs (Behrens Yamada et al. 2005), we estimated the age of each crab at time of capture and thus the year it would have settled from the plankton. For example, we trapped in Coos Bay every year, but did not sample at the appropriate times in 1999, 2000 and 2001 to intercept 0-age crabs. If recruitment to the population had occurred in those years, we would have trapped 1, 2 and 3 year old crabs in subsequent years. But since all the crabs we trapped in Coos Bay prior to 2003 could be attributed to the 1998 year class, we concluded that *C. maenas* did not recruit into the Coos Bay population from 1999 to 2001 and entered "(0)" in Table 1. On the other hand, for Tillamook Bay we entered "p" for 1999 and 2000 because those year classes were

Table 1 *Carcinus maenas*. Relative abundance of 0-age crabs in Oregon and Washington estuaries

Estuary/Site	Number of 0-age *Carcinus maenas* per 100 traps										
	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
Grays harbor WA	**100**	2	1	1	0	**(0)**	(0)	**3**	**2**	0	
Willapa WA	**76**	2	4	4	0	**10**	(0)	**77**	**8**	0	0
Tillamook OR	**125**	p	p	2	0	**17**	10	**17**	**32**	0	0
Netarts OR	**139**	(0)	(0)	6	0	**15**	0	**92**	**65**	0	0
Yaquina OR	**192**	20	31	p	1	**7**	7	**14**	**20**	3	2
Coos Bay OR	**65**	(0)	(0)	(0)	0	**1**	0	**5**	**32**	7	1
Number of estuaries	**6**	5	5	5	6	**6**	6	**6**	**6**	6	5
Average	**116**	4.8	7.2	2.6	0.17	**8.33**	2.83	**34.7**	**26.5**	1.67	0.6
Log10 (average) year class strength	**2.07**	0.68	0.86	0.41	−0.77	**0.92**	0.45	**1.54**	**1.42**	0.22	−0.22

Catches are given as # of 0-age crabs per 100 traps at the end of their first growing season (late August–early October). Typically a minimum of 50–100 traps were deployed for one tidal cycle or one day. When no catch data for 0-age crabs were available, we deduced the presence (p) or absence (0) of a cohort from age class analysis of adults in subsequent years. The 4 highest ranked years for year class strength are indicated in bold

present in subsequent samples and were also found by shellfish growers.

Water temperature measurements

Two sources of local water temperature data for Oregon and Washington were investigated: (1) National Oceanic and Atmospheric Administration (NOAA) weather buoys anchored offshore from northern California to Washington, and (2) stations inside Coos, Yaquina and Willapa estuaries. We used the long-term surface temperature data from the buoy stations to get a general pattern of north–south variation in monthly ocean surface temperature in the upper meter. Data summaries are provided by the NOAA National Data Buoy Center (http://www.ndbc.noaa.gov/maps/North west.shtml June 18, 2009).

Since the nearshore weather buoys often break down during winter storms, we used stations close to the mouth of estuaries for determining interannual variation in winter water temperature for the duration of our monitoring program. Specifically, we wanted to know during which years winter water temperatures were >10°C, the critical temperature below which green crabs are not able to molt and larvae cannot develop (Berrill 1982; deRivera et al. 2007). For Coos estuary we used surface temperature readings from Valino Island in South Slough for which continuous data exist from 1999. Gaps in data were filled from readings taken at Charleston Bridge, an adjacent site closer to the mouth of Coos Bay. These data were obtained from the National Estuarine Research Reserve System Central Data Management Office (http://cdmo.baruch.sc.edu June 18, 2009). For Yaquina Bay we obtained data from a sonde attached to the Hatfield Marine Science Center dock, 1 meter off the bottom. This station samples the salt wedge and thus would reflect conditions experienced by brooding female *Carcinus maenas* and larvae rearing in the nearshore ocean more closely than other stations in the Yaquina estuary. For Willapa Bay, we used surface water readings for Bay Center and supplemented data gaps with readings from the adjacent Oysterville station or indicated "est." in Table 2. For each of the three estuaries we calculated the mean winter water temperatures from December to March (Table 2). Temperature data were not available for the other three estuaries.

Interannual indices: pacific decadal oscillation and El Niño

Two widely recognized modes of large-scale interannual ocean variation are the El Niño/Southern Oscillation (ENSO) (e.g. Philander 1989) and the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997; Zhang et al. 1997). El Niño varies most energetically on time scales of 2–5 years, is forced by variations in the tropical Pacific, but has effects which are felt along the west coasts of North and South America. As an index of the time variation of ENSO, we use the Multivariate ENSO Index (MEI) as provided by the National Oceanic and Atmospheric Administration (http://www.cdc.noaa.gov/people/klaus.wolter/MEI/ table.html June 18, 2009). The Pacific Decadal Oscillation is based upon the most energetic pattern of variation (empirical orthogonal function) in sea surface temperature for the extratropical North Pacific, above 20°N. Although based on conditions outside the tropics, its spatial pattern is similar to that of El Niño, and its monthly temporal variation is significantly correlated with El Niño and the MEI. Seasonal averages of the PDO have been characterized as having reversals on decadal time-scales, although recent reversals have been more frequent. The seasonally averaged PDO has been used to define multi-decadal physical "regimes" whose covariation with abundances of certain marine species or even ecosystems has been explored (Mantua et al. 1997; Mantua 2004; deYoung et al. 2004; Peterson et al. 2006), although the very limited number of cycles of variation (degrees of freedom) means the significance is uncertain. Here, we use the monthly values of the index as provided by Mantua (http://jisao.washington.edu/pdo/PDO.latest June 18, 2009), without additional low-pass filtering. We find the late winter/early spring (March) PDO is most strongly correlated with the recruitment data; this timing is similar to the findings for alongshore current (March–April) and to the date of the spring transition, described below. The March MEI is also most strongly correlated.

Determining spring transition

Winters in the north-eastern Pacific are characterized by winds blowing from the south, resulting in downwelling (surface waters transported onshore, sea-level raised toward the coast, weak vertical stratification

Table 2 Relationship between *Carcinus maenas* year class rank, winter water temperature for three estuaries, Pacific Decadal Oscillation Index for March, day of spring transition and alongshore currents for March and April

Year	Log10 average year class strength	Mean water temperature December–March (°C)			Pacific decadal oscillation for March	Day of spring transition (Day 94 ±)	Alongshore currents for March and April (cm/s)
		Willapa	Yaquina	Coos			
1998	**2.07**	**9.9**	**11.2**	**–**	**2.01**	**108 (+14)**	**−9.3**
1999	0.68	8.1	8.8	–	−0.33	91 (−3)	−15.2
2000	0.86	8.3	9.7	9.8	0.29	79 (−15)	−21.4
2001	0.41	7.8	9.6	9.7	0.45	69 (−25)	−17.2
2002	−0.77	8.0	9.4	9.6	−0.43	76 (−18)	−31.5
2003	**0.92**	**9.2**	**11.0**	**10.9**	**1.51**	**127 (+33)**	**−3.9**
2004	0.45	8.6	10.1	10.4	0.61	68 (−26)	−26.1
2005	**1.54**	**8.7**	**10.1**	**10.3**	**1.36**	**145 (+51)**	**−8.1**
2006	**1.42**	**8.3**	**9.8**	**9.9**	**0.05**	**111 (+17)**	**−5.8**
2007	0.22	8.4 est.	9.5	9.8	−0.36	71 (−23)	−23.5
2008	−0.22	7.7 est.	8.4	8.8	−0.71	88 (−6)	−18.0
Correlation of physical variables							
Winter water temperature for Yaquina					$r^2 = 0.846$	$r^2 = 0.216$	$r^2 = 0.219$
					$p < 0.001$	$p = 0.150$	$p = 0.147$
Pacific decadal oscillation for March						$r^2 = 0.365$	$r^2 = 0.349$
						$p = 0.049$	$p = 0.065$
Day of spring transition							$r^2 = 0.695$
							$p = 0.001$

Gaps in the temperature record are indicated by "est." Variations from the long term average day for the spring transition (4 April, or Day 94) are indicated in parentheses. Strong year classes of 0-age crabs were correlated with warm winters, high PDO indices, late spring transitions and weak along-shore currents to the south. The 4 highest ranked years for year class strength are indicated in bold. Physical variables were regressed against each other with significant correlations ($p < 0.05$) indicated by bold

over the shelf, and so northward, weakly-sheared shelf currents). During the summers winds blow from the north and push surface water offshore, causing deeper, colder water to be upwelled, isopycnals to tilt upward toward the coast, and sea level to drop at the coast, resulting in a southward coastal jet, strongest near the surface. The "spring transition" is the usually sudden shift from the winter to the summer pattern (Huyer et al. 1979), which occurs on average around April 4 off Oregon, but with a standard deviation of 25 days (Kosro et al. 2006), so that it can fall anytime between March and June. The date of the spring transition to upwelling was estimated off Newport by examining the subtidal sea level records at South Beach Oregon (adjusted for fluctuations in atmospheric pressure), as well as the alongshore current, and its vertical shear measured at the NH-10 current meter (Fig. 1). When sea-level dropped persistently below its long-term average and the alongshore currents became

equatorward and sheared, the spring transition was said to have occurred (Kosro et al. 2006). These dates and the number of days they varied from the long-term average of April 4 are shown in Table 2.

Current measurements

Horizontal currents in the water column 18 km off Newport, Oregon, have been measured nearly continuously since 1998 with an acoustic Doppler current profiler located at station NH-10 near 44° 38.8′ N, 124° 18.4′ W, moored near-bottom at the 81 m isobath (Kosro 2003; Kosro et al. 2006). These data have been interpolated vertically to 2 m depth intervals, interpolated in time across brief temporal gaps during mooring turnarounds, and low-pass filtered using a cosine-Lanczos filter with 46 h half-power point. They have also been rotated to axes aligned along the principal axes of current variability,

22/112°T, which are taken to represent alongshore and across-shore components respectively. Near-surface measurements contaminated by side-lobe reflection, usually shallower than 10 m, were eliminated. In addition, near-surface currents in the region were measured since 1997 using an array of SeaSonde HF surface current mappers, operating near 12 MHz (Kosro 2005), which provided time-series maps of horizontal currents at about 0.6 m. These data, after correcting for seasonal vertical shear, were used to bridge a gap in the current meter data during December 1997 through April 1998. Monthly averages of alongshore current at 12 m depth were computed for comparison with other data.

Regression analysis

Catches of 0-age *Carcinus maenas* from the 6 estuaries were recorded, averaged by year and Log10-transformed. The 4 years ranking highest for year class strength were indicated in bold (Tables 1, 2). Mean winter water temperatures for three estuaries, March PDO, day of spring transition and alongshore currents were also tabulated (Table 2). Regression analyses were carried out on Log10-transformed catch data for each estuary versus each of the four measures of ocean conditions (Table 3). Since we lacked winter water temperature measurements for three of the estuaries, we regressed year class strength

Table 3 *Carcinus maenas.* Regressions of log10 year class strength for six estuaries against four measures of ocean condition

Estuary	Local winter water temperature	PDO for March	Day of spring transition	Currents March–April
Grays Harbor	**(Willapa Temp.)** $r^2 = 0.441$ $p = 0.036$ $N = 10$	$r^2 = 0.359$ $p = 0.067$ $N = 10$	$r^2 = 0.122$ $p = 0.322$ $N = 10$	$r^2 = 0.192$ $p = 0.205$ $N = 10$
Willapa Bay	**(Willapa Temp.)** $r^2 = 0.462$ $p = 0.021$ $N = 11$	$r^2 = 0.690$ $p = 0.002$ $N = 11$	$r^2 = 0.633$ $p = 0.003$ $N = 11$	$r^2 = 0.593$ $p = 0.006$ $N = 11$
Tillamook Bay	**(Yaquina Temp.)** $r^2 = 0.680$ $p = 0.006$ $N = 9$	$r^2 = 0.710$ $p = 0.004$ $N = 9$	$r^2 = 0.388$ $p = 0.073$ $N = 9$	$r^2 = 0.520$ $p = 0.028$ $N = 9$
Netarts Bay	**(Yaquina Temp.)** $r^2 = 0.451$ $p = 0.024$ $N = 11$	$r^2 = 0.564$ $p = 0.008$ $N = 11$	$r^2 = 0.606$ $p = 0.005$ $N = 11$	$r^2 = 0.654$ $p = 0.003$ $N = 11$
Yaquina Bay	(Yaquina Temp.) $r^2 = 0.296$ $p = 0.104$ $N = 10$	$r^2 = 0.418$ $p = 0.043$ $N = 10$	$r^2 = 0.119$ $p = 0.328$ $N = 10$	$r^2 = 0.277$ $p = 0.118$ $N = 10$
Coos Bay	(Coos Bay Temp.) $r^2 = 0.003$ $p = 0.880$ $N = 9$	$r^2 = 0.171$ $p = 0.206$ $N = 11$	$r^2 = 0.217$ $p = 0.149$ $N = 11$	$r^2 = 0.301$ $p = 0.081$ $N = 11$
Pooled Estuaries	**(Yaquina Temp.)** $r^2 = 0.438$ $p = 0.027$ $N = 11$	$r^2 = 0.587$ $p = 0.006$ $N = 11$	$r^2 = 0.426$ $p = 0.029$ $N = 11$	$r^2 = 0.607$ $p = 0.005$ $N = 11$

All regressions were positive with significant regressions ($p < 0.05$) indicated in bold. N indicates the number of years for which data sets were available
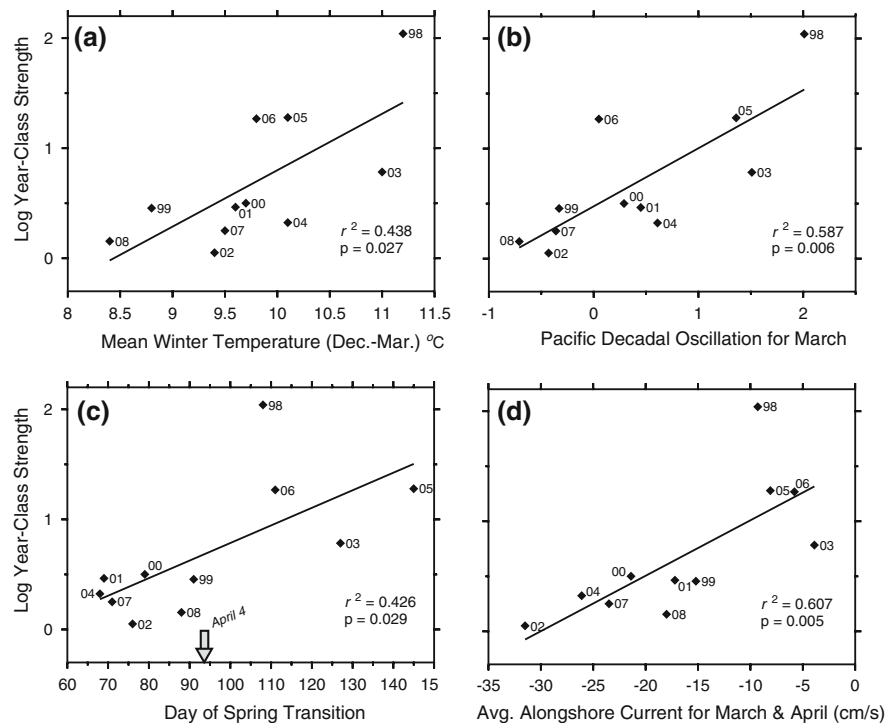
for Grays Harbor against Willapa temperature and
those for Tillamook and Netarts against Yaquina
temperature (Table 3). In addition to the individual
regressions, we also performed regressions on pooled
catches from the 6 estuaries against each of the 4
physical measures. Since the Yaquina Bay water
temperature data set was the most complete, and
reflected the same inter-annual trends as that of the
other two estuaries, we used it in the pooled estuaries
analysis (Tables 2, 3; Fig. 2a). The four physical
variables are not independent (Table 2). While a
multi-parameter regression can be computed, the
limited degrees of freedom (11 yearly data values)
would limit the added benefit of such an analysis.

Results

Inter-annual year class strength

The arrival of new year classes of *Carcinus maenas*
in the six estuaries was synchronous. Catches of
0-age crabs was highest in 1998 and 2005 and lowest
in 2002 and 2008 (Table 1). An average of one 0-age
crab was caught per trap in 1998 but none in 2002
and 2008. Even though over 3300 traps were

deployed in Washington and Oregon in 2002, only
one 0-age crab was trapped in Yaquina Bay. The
trend of poor recruitment after 1998 was reversed in
2003, when half of the estuaries showed catches of at
least ten 0-age crab per 100 traps. 2005 was even a
better year with both Netarts and Willapa Bay
exhibiting catch rates of over 70 crabs per 100 traps,
very similar to what was observed in 1998. The
2006 year class was well represented in Oregon but
not in Washington and 2007 and 2008 showed no
0-age crabs north of Yaquina Bay (Table 1).

Water temperature and March Pacific Decadal
Oscillation (PDO)

Long-term weather buoy data show that ocean surface
water temperatures on the west coast of North
America vary widely with location and season but
show a persistent decrease with increasing latitude (http://
www.ndbc.noaa.gov/maps/Northwest.shtml June 18,
2009). Super-imposed on these latitudinal and season
patterns is an inter-annual variation that can vary by
as much as 3°C for any given season (Landry et al.
1989; McGowan et al. 1998). For example, mean
January water temperature at a buoy off Newport,
Oregon was 12.4°C in 1998 and 9.6°C in 1999 (Kosro

et al. 2006). Long-term monthly mean water temperature measurements from weather buoys in the off-shore and nearshore ocean show that average monthly mean water temperatures do not drop below 10°C off Coos Bay, Oregon but north of Newport they do (http://www.ndbc.noaa.gov/maps/Northwest.shtml June 18, 2009). Thus, during an "average" year, one could expect Carcinus maenas larvae to develop year-round south of Newport. During El Niño years, that boundary would shift northward into Washington and the west coast of Vancouver Island (Jamieson et al. 2002).

Winter water temperatures in the estuaries reflect the same latitudinal trend as the nearshore ocean, in that the two Oregon estuaries are generally >1°C warmer than Willapa Bay (Table 2). During the winter, estuarine stations tended to be ∼0.5°C colder than adjacent near-shore stations (http://www.ndbc.noaa.gov/maps/Northwest.shtml June 18, 2009). All three estuarine stations exhibit the same inter-annual trend with 1998 and 2003 having the warmest and 2008, the coldest winters (Table 2).

Since PDO is a measure of temperature variation that covaries basin-wide, it is notable that the March PDO is very strongly correlated with the local Yaquina Bay water temperatures ($r^2 = 0.85$, $p < 0.001$). For both measures, 1998 was the warmest and 2008, the coldest year (Table 2; Fig. 2 a, b). Moreover, the state of the PDO and of ENSO covaried strongly for March from 1998–2008 ($r^2 = 0.71$, $p = 0.001$).

Spring transition and alongshore currents

The date of the spring transition is a measure of the duration of winter conditions of poleward average winds and currents; the average date is April 4. The earlier the transition, the sooner is the change to offshore Ekman transport in the surface layer, driven by winds from the north. In a similar way, the average March and April alongshore current velocity is a measure of the strength of the coastal currents and the timing of their change in direction. Since these two measures describe different aspects of the same ocean conditions they are significantly correlated ($r^2 = 0.70$; $p = 0.001$). The year 2002 not only had an early spring transition, but was also a year of highly anomalous, large-scale southward flow referred to as the "subarctic invasion" (Huyer 2003; Kosro 2003).

On the other hand, 1998, 2003, 2005 and 2006 had late spring transitions and weak average alongshore currents in March–April (Table 2; Fig. 2c, d).

Regression analysis

When the estuaries were pooled, year class strength of 0-age Carcinus maenas showed a significant positive regression with all four measures of ocean condition (Table 3; Fig. 2a, b, c, d). The years 1998, 2003 and 2005 consistently ranked high while the years 2002, 2007 and 2008 ranked low. Winter water temperatures and March PDO in 1998, 2003 and 2005 were above 10°C and above 1 respectively, suggesting that early larval development was possible during these years (Table 2; Fig. 2a, b). However, this was not the case in 1999, 2002, 2007 and 2008 when winter water temperatures remained below 10°C and March PDO values were negative. When the spring transition occurred before April 4, as it did in 1999, 2000, 2001, 2002, 2004 2007 and 2008, or when currents in March–April were strongly southward on average (>10 cm/s or >8 km/d) (same years), the year class strength of C. maenas was poor (Table 3; Fig. 2c, d). On the other hand, when the spring transition occurred after the middle of April, as it did in 1998, 2003, 2005 and 2006, or when March–April average alongshore currents were weak (same years), year classes were strong (Table 2; Fig. 2c, d). Year class strength in 2005, a year with a strongly delayed spring transition (Kosro et al. 2006) was especially good, with Willapa and Netarts exhibiting record highs (Table 1). Likewise, the best year for recruitment was 1998, following the very strong northward (and shoreward) currents of the 1997-98 El Nino.

While inter-annual variation in ocean conditions early in the year correlated significantly with coast-wide recruitment of 0-age Carcinus maenas at the end of their first growing season, not all estuaries responded equally. The estuaries in the middle of the range, Willapa, Tillamook and Netarts were the most sensitive in showing significant regression with three to four of the measures of ocean condition (Table 3). Yaquina Bay and Grays Harbor exhibited significant regressions with winter water temperature and March PDO respectively, while Coos Bay was the least responsive with no significant regressions (Table 3).

Discussion

Favorable ocean conditions during larval development and settlement are critical to the persistence of any benthic species with planktonic larvae, including the invasive *Carcinus maenas*. While *C. maenas* in Oregon and Washington are still too rare for their larvae to be detected during routine plankton sampling programs (Shanks and Peterson, personal communication), several lines of evidence suggest that in years when 0-age *C. maenas* are abundant, that settlement of larvae occurs around March and April. When we held female green crabs in the laboratory at 12°C, they released eggs in November and early December and produced viable larvae in mid February. At similar temperatures and abundant food, these larvae would have settled as megalopae two months later. In April of 1998, Heath Hampel, a shellfish grower in Coos Bay, alerted biologist to the settlement of "thousands" of small *C. maenas* sheltering under oyster shells. We subsequently followed that strong year class in Coos Bay and the other estuaries and found that growth was very rapid, averaging 14 mm in carapace width by the end of June, 32 mm by the end of July, and 47 mm at the end of their first growing season in September (Behrens Yamada et al. 1999, 2005). A bioenergetics model for green crabs in Willapa Bay, Washington supports the view that 0-age green crabs can attain a carapace width of 50 mm in about 5 months (McDonald et al. 2006). Thus crabs attaining 50 mm CW in September would have settled out from the plankton around March or April. In cooler years, settlement would occur later. The mean carapace width of Oregon and Washington 0-age crabs at the end of their first growing season was 44 mm and varied from 35–51 mm between estuaries and years (Behrens Yamada unpublished data). In the Dutch Wadden Sea, where water temperatures remain below 10°C for 6 months, the earliest settlers arrive in late June and attain a carapace width of 20 mm before their first winter (Klein Breteler 1976; Beukema 1991). In Oregon and Washington, where nearshore and estuarine temperatures typically remain below 10°C for only 0–4 months *C. maenas* larvae would develop 2–3 months earlier and thus would first settle from March to May. Local winter temperature, date of spring transition, current data as well as large scale indices like PDO and MEI from 1998 to 2008 all

suggest that March and April are critical times for determining year class strength in *C. maenas* in Oregon and Washington estuaries.

Our analysis uses the very complete data set off Newport, Oregon (winds, sea level, and midshelf currents through the water column) to estimate the date of the spring transition there, assuming that it represents the variation at all sites studied. While the spring transition is characterized as a large-scale event with alongshore length scales of 500–2,000 km (Strub et al. 1987), evidence for shorter scale variability is also known (Henson and Thomas 2007).

We found that warm water temperatures during winter and early spring are linked to strong year classes in *Carcinus maenas* in Oregon and Washington. The same pattern has also been observed in Europe and Maine (Beukema 1991; Berrill 1982). Green crabs do not grow and larvae cannot develop if water temperatures remain below 10°C (Berrill 1982; deRivera et al. 2007). This physiological temperature limitation could explain why we only observed strong year classes in Willapa Bay in 1998, 2003 and 2005 when mean water temperatures in March averaged above 10°C. In 2002 and 2008, when water temperatures in Coos, Yaquina and Willapa Bay never rose above 10°C during the entire winter months, virtually no young green crabs were trapped in any of the 6 estuaries. We hypothesize that warm winters and springs speed up development, thus allowing earlier settlement and increased survival and growth of newly-settled crabs. The observation by Klein Breteler (1975) that newly recruited *C. maenas* in the first settlement wave in the Dutch Wadden Sea grew and survived significantly better than those in subsequent waves supports this view.

Warm winters and early springs, however, do not explain all the variation associated with year class strength. Water temperatures in Coos and Yaquina Bay during the winter of 2004 were just as warm as in 2005, but year class strength was significantly poorer. This discrepancy is linked to an unusually early spring transition (9 March) and strong southward currents during March and April 2004 and an unusually late spring transition (25 May) and weak southward currents in 2005. It appears that the longer the winter circulation pattern persists during the prime settlement period, the greater the chances for larvae to be maintained closer to the coast, and the greater the chances of them being carried onward to

their estuarine recruitment grounds by any combination of the numerous proposed mechanisms for cross-shore transport (see Shanks 1995 for a review), including wind relaxations (Roughgarden et al. 1991; Wing et al. 1995), Ekman transport (Roegner et al. 2002), selective tidal stream transport (Forward and Tankersley 2001), or transport by non-linear internal waves (Shanks 1983), possibly in a multistage process. The spring transition, initiated by the onset of substantial offshore Ekman transport at the surface, presumably moves plankton away from the coast. Shanks and Roegner (2007) found that the final larval stages of the native crabs *Pagurus* spp., *Hemigrapsus* spp., and Porcellanids entered Coos Bay in greater numbers during years of late spring transitions. The larvae of these three species and those of *C. maenas* rear in the nearshore (Shanks and Roegner 2007; Queiroga 1996). Thus for these species, the chances of larval transport back to the estuary would decrease once the summer upwelling patterns starts. In addition, numerous reports have been made of offshore species being found nearer to shore during El Niño years (Connolly and Roughgarden 1999; Peterson et al. 2002). Our finding that 1998 produced the strongest year class suggests that the 1997-98 El Niño provided both alongshore and onshore transport which promoted larval retention and recruitment.

While offshore transport of larvae by the upwelling circulation makes return to the coast more difficult, it is not impossible. It has long been hypothesized that larvae could use vertical migration between vertically sheared currents–offshore surface Ekman layer and onshore deeper return flow, or equatorward surface flow and poleward deeper flow (e.g. poleward undercurrent)–to maintain location in the larger scale circulation, analogous to selective tidal stream transport in estuaries (e.g. Queiroga and Blanton 2005). In addition, Shanks and Brink (2005) show from field measurements near the coast that upwelling/downwelling do not always lead to offshore/onshore transport of larvae, depending upon larval vertical distribution and behavior. A recent study by Morgan et al. (in press) supports this observation. The larvae of 45 species of crustaceans remained close to shore throughout their development during the peak of the upwelling season.

While the overall recruitment of 0-age green crabs was strongly correlated with ocean conditions, the estuaries in the middle of the range, Willapa,

Tillamook and Netarts exhibited the strongest correlation, while Coos Bay, at the southern range, showed no significant correlations with any of the measures of ocean condition. This asymmetry is suggestive of a metapopulation model whereby larvae might be transported 50–300 km north from their source during a non-El Niño year. The observation that the Coos Bay population did not receive recruitment from 1999 to 2002, and that Yaquina Bay (140 km to the north) did, would support this view.

Evidence from other parts of the world where *Carcinus maenas* has established self-perpetuating populations suggests that moderate water temperatures and current patterns that favor larval retention nearshore are the keys to success. In addition to the critical lower temperature of 10°C needed for molting and larval development, the critical upper temperature appears to be 18°C, above which females cannot successfully brood their eggs (Crothers 1967). Thus it is not surprising that none of the *C. maenas* introductions into tropical waters resulted in the establishment of permanent populations (Carlton and Cohen 2003). While *C. maenas* populations in Oregon and Washington have not expanded significantly within the last 12 years, those in sheltered inlets on the west coast of Vancouver Island, British Columbia are thriving (Behrens Yamada and Gillespie 2008). Recent surveys by Fisheries and Oceans Canada show average densities of over 10 and 20 crabs per trap in Winter Harbor, Quatsino Sound and in Pipestem Inlet, Barkley Sound, respectively (Gillespie, personal communication). These densities are two orders of magnitude greater than what we observe in Oregon and Washington estuaries, even though *C. maenas* arrived in Oregon earlier than on Vancouver Island (Behrens Yamada et al. 2005). Two factors on the west coast of Vancouver Island would contribute to larval retention: poor flushing of the inlets and a gravity driven coastal current that flows north from the Strait of Juan de Fuca past the northern tip of Vancouver Island. This northward-flowing current hugs the shore of Vancouver Island year-round and acts as a cross-shore barrier to the sea-ward transport of organisms (Thomson et al. 1989). Larvae would thus tend to be retained close to shore and less likely to be transported out to sea, in contrast to the case in Oregon and Washington after the spring transition.

A counter example to larval retention is found on the western shores of South Africa and Namibia

where the north-flowing Benguela current is characterized by strong coastal upwelling (Boyer et al. 2000). Under upwelling favorable winds, Ekman transport would transport larvae in the surface waters offshore. While a large *Carcinus maenas* population has persisted in the docks of Table Bay Harbor in Cape Town since the early 1980s, no major range expansion has occurred in over 20 years, despite the presence of a favorable wave-sheltered bay and lagoon with abundant shellfish prey just 90 km to the north (Robinson et al. 2005).

In summary, young *Carcinus maenas* established strong year classes in Oregon and Washington estuaries only during years with warm winters, high March PDO or MEI indices, late spring transitions and weak average southward currents during March and April. While future studies are needed to elucidate the mechanisms contributing to these correlations between ocean conditions and year class strength, we can make predictions. So far *C. maenas* has remained relatively rare in Oregon and Washington estuaries. This could change, particularly if we were to experience a series of strong El Niños, a positive PDO fluctuation or an increase in the incidence of late spring transitions as observed in 2003, 2005 and 2006. When either condition occurs, we will be able to predict year class strength from ocean conditions and alert managers and shellfish growers of possible increases in predation pressure from this invader.

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