

Biological and physical ocean indicators predict the success of an invasive crab, *Carcinus maenas*, in the northern California Current

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ABSTRACT: An introduced population of European green crabs *Carcinus maenas* was established in San Francisco Bay (California, USA) prior to 1989. Subsequently, their larvae were likely carried northward into the embayments of Oregon, Washington (USA), and British Columbia (Canada) by the unusually strong Davidson Current during the winter of the El Niño of 1997–1998. Since this colonizing event, green crabs in Oregon and Washington have persisted at low densities. In this study, we show that after the arrival of the strong founding year-class of 1998, significant recruitment to the Oregon and Washington populations has occurred, but only in 2003, 2005, 2006 and 2010. Warm winter water temperatures, high positive values of the Pacific Decadal Oscillation (PDO) and Multivariate ENSO (El Niño Southern Oscillation) indices in March, weak southward shelf currents in March and April, a late biological spring transition, and high abundance of subtropical copepods are all strongly correlated with strong year-classes. We hypothesize that northward transport of larvae from California by coastal currents during warm winters is the mechanism by which the larvae are delivered to the Pacific Northwest. Among the best indicators of northward flow (and green crab recruitment) were the date of ‘biological spring transition’, the sign of the PDO, and the biomass of southern copepod species, which indicate (1) stronger northward flow of coastal waters during winters, (2) relatively warm winters (sea surface temperature >10°C), which enable larvae to complete their development in the near-shore, and (3) coastal circulation patterns that may keep larvae close to shore, where they can be carried by tidal currents into estuaries to settle.

KEY WORDS: European green crab · California current system · Pacific Decadal Oscillation · El Niño · Alongshore currents · Plankton community structure · Year-class strength · Recruitment

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INTRODUCTION

The European green crab *Carcinus maenas* has been introduced to many areas of the world, but self-sustaining populations have persisted only in temperate regions where water temperatures are warm enough (>10°C) for the larvae to develop, yet cool enough for the females to successfully incubate their

eggs (<18°C) (Crothers 1967, Berrill 1982, deRivera et al. 2007). These 2 isotherms broadly define the global distribution of native and introduced populations of European green crabs (Behrens Yamada 2001, Hidalgo et al. 2005, Compton et al. 2010). Confirmed sightings of this species in tropical regions such as Panama, Brazil, Madagascar, the Red Sea, Sri Lanka, Myanmar, and Hawaii did not result in self-

sustaining populations, whereas those introduced to temperate regions of the western North Atlantic, south-east Australia, Tasmania, South Africa, the north-eastern Pacific, and Argentina have prevailed (Behrens Yamada 2001, Carlton & Cohen 2003, Hidalgo et al. 2005). Along the west coast of North America, an introduced population of green crabs was established in San Francisco Bay prior to 1989 (Cohen et al. 1995, Grosholz & Ruiz 1995). From there, their larvae were carried northward via coastal currents to northern California, Oregon, Washington (USA) and British Columbia (Canada), during the 1990s (Behrens Yamada et al. 2005). At this time, El Niño-like conditions dominated the oceanography of the California Current (Trenberth & Hoar, 1996), and transport to the north was stronger. In April 1998, a shellfish grower in Coos Bay reported the settlement of 'thousands' of small green crabs sheltering under oyster shells. We subsequently followed that strong year-class in Oregon and Washington estuaries and learned that this cohort grew rapidly, attaining 32 mm carapace width (CW) by the end of July, and 47 mm CW the end of their growing season in September 1998. Sexual maturity was attained during their first year at CW ~35 mm (Behrens Yamada 2001). From a mark-recapture study we learned that crabs can attain 70 and 85 mm CW during their second and third growing season, respectively, and that longevity is ~6 yr (Behrens Yamada et al. 2005), similar to that observed in Maine, USA (Berrill 1982).

While ocean temperature may limit where green crabs can persist on a large geographical scale, inter-annual variation in ocean conditions can limit their local temporal success, especially those conditions that are related to larval survival and their subsequent transport on-shore (Queiroga et al. 2006). Cold winters in Europe and Maine are linked to high mortality of adult and poor recruitment of young of the year (age-0) green crabs, while warm winters are typically followed by strong year-classes of age-0 green crabs (Berrill 1982, Beukema 1991). Warm temperatures early in the year would increase the developmental rate of eggs (Glude 1955) and larvae and may enhance the survival of larvae and young crabs. In addition to warm temperatures (>10°C), for successful development, larvae also need water circulation patterns that are favorable for onshore transport when they are ready to settle. The first zoea larvae swim to the surface and ride an ebbing tide from the estuary to the near-shore (Queiroga et al. 1997) where they feed, undergo vertical migrations, and develop into megalopae larvae. When the megalopae are competent to settle, they rise to the surface

and ride a flood tide back to shore, settle and metamorphose into the first crab stage (Queiroga 1998). On the Portuguese coast, transport of megalopae to 2 estuaries was enhanced when winds were blowing from the south and surface water was advected on-shore (Queiroga et al. 2006). Thus, in the green crab's native range, current patterns capable of retaining larvae in the nearshore during the rearing phase, and returning the megalopae to estuaries, are critical for the successful recruitment of young green crabs.

Similar circulation patterns are found in Oregon and Washington estuaries. Warm winters and late transitions to the beginning of the spring/summer coastal upwelling season benefit the recruitment of young green crabs, while cold winters with water temperatures <10°C and an early start to the upwelling season resulted in year-class failure (Behrens Yamada & Kosro, 2010). In summary, at least 2 conditions must be met before larvae can settle and establish a new year-class in northern waters: (1) relatively warm winters (sea surface temperature [SST] >10°C) for larvae to complete their development in the nearshore (deRivera et al. 2007), and (2) coastal circulation patterns that keep larvae close to shore such that they can ride tidal currents into estuaries when they become competent to settle (Queiroga et al. 2006).

This study builds on previous research by Behrens Yamada & Kosro (2010) in predicting green crab year-class strength, by using an additional 6 yr of data on the abundance of juvenile green crabs in Oregon and Washington estuaries and by evaluating additional ocean indicators that are used in salmon forecasting (Peterson et al. 2014). Our previous paper examined year-class strength patterns using data on winter water temperature from Yaquina Bay, the Pacific Decadal Oscillation (PDO) for March, the date of spring transition (when seasonal upwelling is initiated), and the strength of coastal currents during March and April. These indicators showed that conditions that lead to year-class success of green crabs in Oregon and Washington estuaries include warm winter water temperatures, a positive PDO, a late start to the upwelling season, and northward currents. Conversely, year-class failures were associated with cold winter temperatures, negative PDO, late onset of the upwelling season, and southward currents. In the present study, we again compare year-to-year variations in the abundance of juvenile green crabs in Oregon and Washington estuaries using additional physical and biological indices: ocean surface water temperatures in mid-shelf waters 5 nautical miles off Newport, winter PDO, Oceanic El Niño index (ONI), wind-based physical spring transition,

upwelling indices, biomass of 'southern' and 'northern' copepods, the date of biological spring transition, and copepod community index.

MATERIALS AND METHODS

Sampling for age-0 crabs

On the West Coast of North America, European green crabs are most abundant in wave-protected soft sediment habitats such as those found in estuaries and inlets (Cohen et al. 1995, Behrens Yamada & Gillespie 2008). Since 1998, green crabs were monitored in 4 Oregon estuaries: Coos, Yaquina, Netarts, and Tillamook, and 2 Washington estuaries: Willapa Bay and Grays Harbor (Fig. 1) (Behrens Yamada et al. 2002–2014, 2005, Behrens Yamada & Kosro 2010). These estuaries vary in size from 11 km² (Netarts) to 240 km² (Willapa) and include ocean-dominated mudflats such as Willapa and Netarts, as well as deep draft estuaries including Coos and Yaquina (Table 1) (Cortright et al. 1987, Hickey & Banas 2003).

The Grays Harbor site was discontinued after 2009 due to cost constraints. Of specific interest were the samples taken at the end of the summer and early fall to target young-of-the-year, or age-0 crabs, after their first growing season on the mudflats. These young crabs are easily distinguished from older crabs by their green coloration and small size (30–55 mm CW). Traps were deployed in the upper marsh, comprising vegetation such as *Scirpus* sp., between late August and early November where age-0 green crabs were found to be most abundant (B. R. Dumbauld pers. comm.). The same sites were sampled with traps each year using identical methods (for trapping locations, see Behrens Yamada et al. 2014 and other annual reports between 2002–2014 available at <http://ir.library.oregonstate.edu>).

We used cylindrical Frabill crayfish traps (diameter = 21 cm diameter, length = 37 mm, mesh size = 0.5 cm). The funnel-like openings at either end were expanded to 5 cm diameter. We used egg-shaped commercial bait containers (15 × 18 mm) with 0.5 cm holes drilled into the sides to allow bait odors to diffuse. Fresh or frozen fish carcasses were cut into sections and placed into bait containers. Each trap received a bait container and was pinned down to the soft substrate with thin metal stakes. Traps were evenly spaced ~10 m apart, parallel to the marsh-bare mudflat interface, and retrieved after ~24 h. Native crabs and other by-catch were identified to species, counted and released (Behrens Yamada

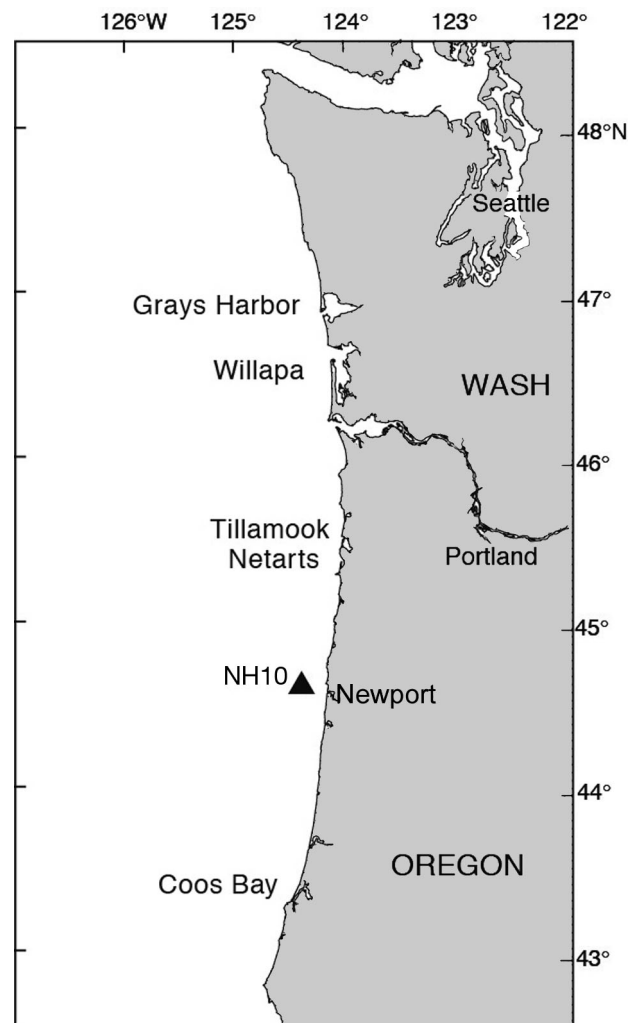


Fig. 1. Study sites in Oregon and Washington, USA. The location of NH10 is indicated by a triangle. Newport designates the location of Yaquina Bay. Sampling site NH5 is halfway between NH10 and Newport

2014). Green crabs were measured between the tips of their fifth antero-lateral spines using digital calipers, sexed, the hardness or molt condition noted, and then destroyed.

A minimum number of 50–100 of crayfish traps per estuary were set in most years. Estuaries were also sampled from spring to summer using collapsible Fukui fish traps (dimensions = 63 × 46 × 23 cm, mesh size = 1.6 cm), with wide, slit-like openings to target adult crabs >40 mm CW, with the goals of obtaining relative density estimates and determining population age structure (Behrens Yamada et al. 2005, Behrens Yamada & Gillespie 2008). Since we did not sample for age-0 green crabs in all estuaries every year, we supplemented our catch data with age class analysis to determine whether green crabs

Table 1. Relative abundance of age-0 *Carcinus maenas* in Oregon and Washington estuaries. Catches are given as the number of age-0 crabs per 100 trap-days (min of 50–100 trap-days per estuary) at the end of their first growing season (late August to early November). When no catch data for age-0 crabs were available, we deduced the presence (p) or absence (-) of a cohort from age class analysis of adult crabs in subsequent years. The 5 years with highest year-class strength are shaded

Site	Catch (no. per 100 trap-days)																
	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014
Grays Harbor, WA	100	2	1	1	0	-	-	3	2	0	0	0	12	0	0	0	0
Willapa, WA	76	2	4	4	0	10	-	77	8	0	0	0	0	0	0	0	0
Tillamook, OR	125	p	p	2	0	17	10	17	32	0	0	0	0	0	0	0	1.5
Netarts, OR	139	-	-	6	0	15	0	92	65	0	0	2	30	0	0	0	25.7
Yaquina, OR	192	20	31	p	1	7	7	14	20	3	2	0	5	0	0	0	2.1
Coos Bay, OR	65	-	-	-	0	1	0	5	32	7	1	0	4	1	0	-	1.5
No. of estuaries	6	5	5	5	6	6	6	6	6	6	5	6	5	5	5	4	5
Average year-class strength (no. catches)	116	4.8	7.2	2.6	0.17	8.33	2.83	34.7	26.5	1.67	0.6	0.33	10.2	0.2	0	0	6.16
Log ₁₀ (average year-class strength + 1)	2.068	0.763	0.914	0.556	0.068	0.970	0.583	1.553	1.439	0.426	0.204	0.124	1.049	0.079	0	0	0.855

recruited to a particular estuary in a particular year. Age class analysis was based on growth rates of individually tagged age-0 crabs and on shifts in size peaks of the strong 1998 cohort over time (Behrens Yamada et al. 2005, Behrens Yamada & Gillespie 2008). For example, Coos Bay was not sampled for age-0 crabs with crayfish traps in 2013, but the trapping of adults with Fukui traps during the summer of 2014 did not produce any 1 yr old crabs that could be attributed to the 2013 cohort (Behrens Yamada et al. 2014). Thus, we entered '0' in Table 1. Since green crab densities in Oregon and Washington coastal estuaries were low, abundance estimates of age-0 crabs from each estuary and year were multiplied by 100 and expressed as number of individuals caught per 100 trap-days.

Water temperature indicators

We obtained water temperature data for the months between December–March for stations inside Coos, Yaquina, and Willapa estuaries. For Coos estuary, we used surface temperature readings from Valino Island in South Slough (<http://cdmo.baruch.sc.edu>), for Yaquina Bay, data were obtained from a sonde attached to the Hatfield Marine Science Center dock, 1 m off the bottom (maintained by the Environmental Protection Agency, Newport), for Willapa Bay, we used surface water readings for Bay Center (Washington Department of Ecology). All study sites in the 3 estuaries are located within 8 km of these stations. For each of the 3 estuaries we calculated the mean winter water temperatures from December to March. Winter ocean temperature (November–March) was measured in the top 20 m at NH5, 5 miles (9 km) west of Newport, using a SBE-25 CTD (Seabird) during bi-weekly oceanographic cruises (Peterson et al. 2014) (Table 2).

Basin-scale indices

Two widely recognized modes of large-scale inter-annual ocean variation are the El Niño /Southern Oscillation (ENSO) (Philander 1989) and the PDO (Mantua et al. 1997, Zhang et al. 1997). El Niño, which varies most energetically on a period of 2–5 yr, is forced by variations in the tropical Pacific but has effects which are felt along the west coasts of North and South America. We used the 6 mo (January–June) average of the ONI (available at www.cpc.ncep.noaa.gov) as an index of El Niño activity. The

PDO is based upon the most energetic mode of SST variability in 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 ONI (Newman et al. 2003). 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, Peterson & Schwing 2003, deYoung et al. 2004, Mantua 2004, Peterson et al. 2014), 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>). For both of these basin-scale indices we use values averaged for December–March for PDO, and January–June for ONI, as well as the monthly index for March, as prior regression analysis indicated that this month explained the most inter-annual variation in green crab year-class strength (Behrens Yamada & Kosro 2010).

Day of physical spring transition and upwelling indices

Off the coast of Oregon, the start of coastal upwelling in springtime often occurs as a well-defined event called the 'spring transition' (Huyer et al. 1979), marked by a drop in coastal sea level, the uplifting of previously level or downwelled isopycnals, and the spin-up of a southward, vertically sheared current with strongest equator-ward flow at the surface. The average date of the spring transition is April 4 but with a wide standard deviation of 25 d (Kosro et al. 2006). The date of the spring transition was estimated from ocean data collected near Newport (as in Behrens Yamada & Kosro 2010) by examining atmospherically adjusted coastal sea level at the South Beach tide gauge, current and current shear at the mid-shelf NH10 current meter mooring (44.65° N, 124.3° W, 81 m water depth) (Fig. 1) and, when available, water column temperature measurements at NH10; this estimate is hereafter referred to as the 'ocean-based' spring transition.

The date of spring transition was also estimated from daily values of the Bakun Upwelling Index (Bakun 1973), an approach which estimates up-

welling in $\text{m}^3 \text{s}^{-1}$ per 100 m of coastline. We used the index for 45° N, 125° W, the latitude of Newport, Oregon. If wind forcing is upwelling-favorable on average for a given day, the index has a positive sign, and if downwelling, a negative sign. Daily values from 1 January are cumulated day by day (and are usually negative throughout the January–March winter downwelling season). Following the method of Bograd et al. (2009), the spring transition is taken to be that date when a minimum is reached and subsequent cumulative values become less negative (i.e. when seasonal upwelling becomes more dominant than downwelling and the summer upwelling season has begun); these values are listed as the 'wind-based' physical transition day (Table 3). The date of fall transition is estimated similarly, with the date on which the upwelling season has ended indicated as the date when cumulative values have reached a maximum. The date of spring transition is subtracted from the date of fall transition to estimate the length of the upwelling season (Table 3). The upwelling anomaly for April and May were also tabulated.

Alongshore current measurements

Horizontal currents 12 m below the surface have been estimated at the mid-shelf NH10 mooring (Fig. 1) (near 44° 38.8' N, 124° 18.4' W, bottom depth = 81 m), 10 miles (16 km) from shore, when available, or from high frequency radar surface current mapping observations, adjusted for vertical shear (Behrens Yamada & Kosro, 2010). All currents have been subtidally smoothed with a 46 h half-power filter and rotated to the alongshore direction determined from the principal axis of variability (22° T). The 12 m depth was chosen as the shallowest consistently reliable depth available from the upward-looking, near-bottom Acoustic Doppler Current Profiler deployments.

Biological indicators

Between 1996–2014, zooplankton samples were collected at fortnightly intervals along the Newport Hydrographic Line (NH5; 44.6° N, 124.2° W), located 5 miles (9 km) offshore of Newport. Samples were collected using a plankton net (diameter = 0.5 m, mesh = 202 μm) hauled vertically from a few meters above the sea floor to the sea surface. The volume of water filtered during each net tow was estimated using a TSK flowmeter. In the laboratory, copepods

were enumerated by species and developmental stage following methods outlined in Hooff & Peterson (2006). Counts were converted to biomass using length-to-mass regressions and standardized to units of mg carbon m^{-3} . Based on their water-mass affinity, copepod species were classified into 2 general groups: (1) 'northern cold water species', which include *Calanus marshallae*, *Pseudocalanus mimus* and *Acartia longiremis*, which dominate the coastal species assemblages of the Gulf of Alaska and Bering Sea, and (2) 'southern warm water species' which include *Acartia tonsa*, *Calanus pacificus*, *Calocalanus* spp., *Clausocalanus* spp., *Corycaeus anglicus*, *Ctenocalanus vanus*, *Mesocalanus tenuicornis* and *Paracalanus parvus*, which dominate the coastal zooplankton species assemblages off central and southern California. The biweekly copepod biomass data were monthly averaged, and the seasonal cycle was removed by subtracting the average biomass for each month (based on averaging monthly data over the entire 1996–2014 time series). Biomass anomalies were calculated as the $\log_{10}(x + 0.01)$, where x represents the ratio of the monthly copepod biomass (mg C m^{-3}). In Table 4 we report anomalies averaged over May–September, of the 'northern' and 'southern' species, and the day of the year of the 'biological spring transition', i.e. the sampling date when the copepod community had transitioned from a 'southern community', which dominates during winter, to a 'northern community', which dominates during the summer. Note that these indices indicate the dates when a 'northern community' or 'southern community' has arrived at Newport. They will always lag the dates of physical transition as well as other physical indicators because the physical indices describe only the day when, for example, upwelling has begun, not when a biological signal is first noted.

We characterized the copepod community index from an ordination (non-metric MDS), using PC-ORD (McCune & Grace 2002). A 2-axis solution was obtained with the x-axis accounting from nearly 70% of the variance (Keister & Peterson 2003). We define the x-axis scores for each sampling date as the 'copepod community index'. As with the biomass data, the seasonal cycle is first removed, then monthly anomalies calculated using the entire data set as a climatology.

Regression analysis

Regressions were performed on data pooled (Tables 2 to 4) across all estuaries ($n = 5$ –6) and data from individual estuaries. The mean catches of age-0

Carcinus maenas from individual estuaries from 1998 through 2014 are presented in Table 1 and Fig. 2. Catches from the estuaries were averaged by year, +1 added to each value (in order to include the 2 'zero' data from 2012 and 2013), then \log_{10} -transformed to account for the log-normality of many biological variables (Table 1). Regressions were run between the log year-class and the following indicators: Yaquina Bay water temperature (December–March), near-shore ocean temperature (November–March), PDO index (December–March), March PDO index, Oceanic Niño index (January–June), and the March Oceanic Niño index (Table 2). Similar regressions were carried out with the 2 estimates of physical spring transition, the 2 upwelling indicators, alongshore currents for March and April (Table 3), and the 4 biological indicators of ocean conditions (Table 4). Regressions were also run on catch data for each of the 6 estuaries to rule out the possibility that any one estuary was driving overall patterns (Table 5). Log year-class strength for each of the individual estuaries was regressed against the 4 original indicators (local water temperature, March PDO, ocean-based day of spring transition and alongshore currents), and ocean surface water temperature, southern copepod biomass, northern copepod biomass, biological spring transition and copepod community index. Winter water temperatures were not available for all the estuaries; thus, we used Willapa Bay temperature for Grays Harbor, and Yaquina Bay temperature for Netarts and Tillamook (Table 5).

Since many of the physical and biological variables are not independent of each other, there was little value in carrying out multivariate analysis. The p-values in this paper assume no serial correlation of the data. In reality, a small serial correlation is present (year-class strength + 1 is autocorrelated at 0.2 after 1 yr and 0.04 after 2 yr), somewhat lowering the degrees of freedom and raising the effective p-values (Davis 1976, Sciremammano 1979, Aschan & Ingvaldsen 2009). Integral time scales for the effective degrees of freedom are only weakly affected (sample interval = 1 yr; integral time scale = 1.0–1.1 yr for most correlations, with the greatest change observed for copepod community index, which increases to 1.3 yr, all considering lags of –3 to 3 yr). No formal procedures have been used to adjust for possible artificial skill which arises from multiple hypothesis testing. Because the true separate and joint probability distribution functions are unknown for the variables considered here, we also estimated confidence intervals for the correlations using the bootstrap method (Efron & Tibshirani 1986) of computation on an

Table 2. Regressions of *Carcinus maenas* ($\log_{10} + 1$) year-class strength (no. of catches per 100 trap-days) against 6 temperature indicators: mean Yaquina water temperature ($^{\circ}\text{C}$) between December–March, Ocean water temperature ($^{\circ}\text{C}$) in the upper 20 m of NH5 between November–March, Pacific Decadal Oscillation (PDO) index during December–March, PDO for March, mean Oceanic Niño index (ONI) between January–June, and ONI for March. Mean values for each variable between 1998–2014 are also shown. N: number of years for which data sets are available. The 5 years with highest year-class strength are shaded. Bold in the bottom shaded area indicates the 2 forcing terms which most strongly predict the year-class strength. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Regressions significant at $p < 0.005$ are shaded; those significant at $p < 0.001$ are **bold**

Year	Average year class strength	\log_{10} (av. year class strength + 1)	Mean Yaquina water temp. Dec–Mar	Ocean water temp. Nov–Mar	PDO Dec–Mar	PDO Mar	ONI Jan–Jun	ONI Mar
1998	116	2.068	11.2	12.27	5.07	2.01	1.08	1.33
1999	4.8	0.763	8.8	10.31	-1.75	-0.33	-1.10	-0.89
2000	7.2	0.914	9.7	10.12	-4.17	0.29	-1.13	-1.05
2001	2.6	0.556	9.6	10.22	1.86	0.45	-0.42	-0.43
2002	0.17	0.068	9.4	10.08	-1.73	-0.43	0.23	0.16
2003	8.33	0.970	11.0	10.70	7.45	1.51	0.33	0.51
2004	2.83	0.583	10.1	10.85	1.85	0.61	0.20	0.08
2005	34.7	1.553	10.1	10.60	2.44	1.36	0.37	0.31
2006	26.5	1.439	9.8	10.61	1.94	0.05	-0.38	-0.52
2007	1.67	0.426	9.5	10.04	-0.17	-0.36	0.02	-0.07
2008	0.6	0.204	8.4	9.33	-3.06	-0.71	-1.05	-1.16
2009	0.33	0.124	8.9	10.19	-5.41	-1.59	-0.21	-0.54
2010	10.2	1.049	10.1	11.01	2.17	0.44	0.70	0.99
2011	0.2	0.079	9.3	10.02	-3.65	-0.69	-0.77	-0.95
2012	0	0	8.7	9.62	-5.07	-1.05	-0.42	-0.41
2013	0	0	9.5	10.09	-1.67	-0.63	-0.38	-0.63
2014	6.16	0.855	9.2	9.47	1.24	0.97	-0.27	-0.48
r			0.72	0.74	0.71	0.83	0.50	0.58
95% CI			0.48–0.90	0.41–0.94	0.40–0.85	0.61–0.94	0.00–0.84	0.15–0.87
r^2			0.51	0.55	0.50	0.69	0.21	0.33
p			0.0012**	0.0007***	0.0015**	<0.0001***	0.0404*	0.0156*
N			17	17	17	17	17	17

ensemble of subsamples, with replacement. The Matlab routine bootci was used, with bias correction and accelerated percentile method, to estimate the range of correlations expected to encompass 95% of values.

RESULTS

Inter-annual year-class strength

Similar abundance patterns of age-0 *C. maenas* were found among the 5 estuaries, i.e. a good year (one with high crab abundance) in one estuary is typically a good year in all the others (Table 1, Fig. 2). Young crabs were most abundant in 1998 with average catches of over 100 individuals per 100 traps. The next highest catches were in 2005 and 2006 with averages of over 20 individuals per 100 traps. The years 2003, 2010 and 2014 showed some moderate recruitment in most of the estuaries. Recruitment failure was observed in 2002, and 2011–2013.

Water temperature indicators

The winter water temperatures for Coos, Yaquina and Willapa and for the offshore NH5 were highly correlated ($p < 0.0001$); Coos Bay, on average, was consistently 0.1°C warmer than Yaquina Bay, whilst Willapa Bay was 1.4°C cooler than Yaquina Bay. Since the Yaquina Bay water temperature data set is the most complete, and reflects the same inter-annual trends as the other 2 bays, it was used in the pooled estuary analysis (Table 2). Winter surface ocean temperatures at NH5 were consistently 0.7°C warmer than inside Yaquina Bay. In Yaquina Bay, winter water temperatures were $>10^{\circ}\text{C}$ in the years 1998, 2003–2005, and 2010, and cold in 2008 and 2012 (Table 2). NH5 temperatures were $<10^{\circ}\text{C}$ only in 2008, 2012 and 2014. The 2 PDO indicators and the 2 ENSO indicators are strongly correlated to Yaquina Bay and NH5 temperatures and to each other ($p < 0.001$ in all cases). Both PDO indicators are positive (warm) in 1998, 2001, 2003–2006, 2010 and 2014, and negative (cold) in 2008, 2009, and 2011–2013. The 2

Table 3. Regressions of *Carcinus maenas* year-class strength (no. of catches per 100 trap-days) against 5 physical factors related to circulation patterns of: ocean-based physical spring transition (day of year with offset from the average day [April 4] in parentheses) wind-based physical spring transition, upwelling anomaly between April–May, length of upwelling (no. of days), and alongshore currents (cm s^{-1} ; negative values denote south-flowing currents) between March–April. Mean values for each variable between 1998–2014 are also shown. N: number of years for which data sets are available. The 5 years with highest year-class strength are shaded. nd = data not available. ** $p < 0.01$. Significant regression ($p < 0.01$) indicated by shading

Year	\log_{10} (average year class strength + 1)	Ocean-based physical spring transition day	Wind-based physical spring transition day	Upwelling anomaly Apr–May	Length of upwelling	Alongshore currents Mar–Apr
1998	2.068	108 (+14)	83	-14	191	-9.3
1999	0.763	91 (-3)	88	19	205	-15.2
2000	0.914	79 (-15)	134	-36	151	-21.4
2001	0.556	69 (-25)	120	2	173	-17.2
2002	0.068	76 (-18)	84	-12	218	-31.5
2003	0.970	127 (+33)	109	-34	168	-3.9
2004	0.583	68 (-26)	113	-27	177	-26.1
2005	1.553	145 (+51)	142	-55	129	-8.1
2006	1.439	111 (+17)	109	-14	195	-5.8
2007	0.426	71 (-23)	70	9	201	-23.5
2008	0.204	88 (-6)	87	0	179	-18.0
2009	0.124	88 (-6)	82	-5	201	-20.7
2010	1.049	100 (+6)	95	-35	161	-11.9
2011	0.079	119 (+25)	105	-36	153	nd
2012	0	114 (+20)	123	-35	161	nd
2013	0	98 (+4)	97	-21	164	-13.0
2014	0.855	134 (+40)	129	-37	133	-9.8
r		0.39	0.23	-0.22	-0.16	0.65
95% CI		0.01–0.69	-0.36–0.68	-0.68 to -0.17	-0.66–0.37	0.33–0.83
r ²		0.15	0.05	0.05	0.03	0.42
p		0.12	0.38	0.40	0.54	0.0091**
N		17	17	17	17	15

ENSO indicators show warm temperatures in 1998 and 2010 and cold temperatures in 1999, 2000, and 2008 (Table 2).

All regressions of \log_{10} year-class strength of age-0 green crabs against each of the 6 temperature indicators were significant (Table 2, Fig. 3a,b). Of these, winter ocean temperature and March PDO were the best predictors of green crab year-class strength, explaining 55 and 69% of the annual variation, respectively (Table 2). The same patterns were observed for individual estuaries, with the exception of local temperature for Coos Bay (Table 5).

Day of spring transition and upwelling indices

No significant regressions were found between *Carcinus maenas* year-class strength and (1) either of the 2 estimates of the date of physical spring transition, or (2) strength of upwelling in spring or the length of the upwelling season (Table 3). Considering data from each estuary individually, significant regressions between year-class strength and the day

of ocean-based spring transition were observed in both Willapa and Netarts Bay ($r^2 = 0.6$, $p < 0.01$) (Behrens Yamada & Kosro 2010); however, by 2014, only Netarts Bay exhibited this relationship (Table 5).

Alongshore currents

Regressions analyses for green crab year-class strength against alongshore currents for March–April revealed a significant correlation. Weaker March–April average south-flowing currents (i.e. when the northward current contributes more to the average), corresponded to stronger year-class strength (Table 3, Fig. 3c). Of the 6 individual estuaries, 2 exhibited the same pattern with an additional 2 showing significance at $p = 0.051$ (Table 5).

Biological indicators

Green crab year-class strength is strongly positively correlated with southern (subtropical) copepod

Table 4. Regressions of *Carcinus maenas* year-class strength (no. of catches per 100 trap-days) against 4 biological indicators used in salmon forecasting. Mean values for each variable between 1998–2014 are also shown. N: number of years for which data sets are available. The 5 years with highest year-class strength are shaded. ***p < 0.001

Year	Log ₁₀ (average year class strength + 1)	Southern copepod biomass (mg C m ⁻³)	Northern copepod biomass	Biological spring transition (day of year)	Copepod community index
1998	2.068	0.6	-0.77	263	0.78
1999	0.763	-0.23	0.03	134	-0.82
2000	0.914	-0.21	0.14	97	-0.82
2001	0.556	-0.21	0.14	79	-0.77
2002	0.068	-0.23	0.27	108	-0.98
2003	0.970	0.09	-0.14	156	-0.19
2004	0.583	0.2	0.04	132	-0.14
2005	1.553	0.55	-0.86	238	0.58
2006	1.439	0.07	-0.02	180	0.04
2007	0.426	-0.07	0.12	81	-0.66
2008	0.204	-0.23	0.24	64	-0.94
2009	0.124	-0.18	0.14	65	-0.81
2010	1.049	0.21	0.15	169	-0.21
2011	0.079	-0.14	0.42	82	-0.68
2012	0	-0.18	0.38	125	-0.78
2013	0	-0.2	0.26	91	-0.83
2014	0.855	-0.02	0.25	162	-0.29
r		0.82	-0.83	0.88	0.88
95% CI		0.54–0.95	-0.95 to -0.65	0.65–0.96	0.65–0.97
r ²		0.67	0.69	0.77	0.78
p		<0.0001***	<0.0001***	<0.00001***	<0.00001***
N		17	17	17	17

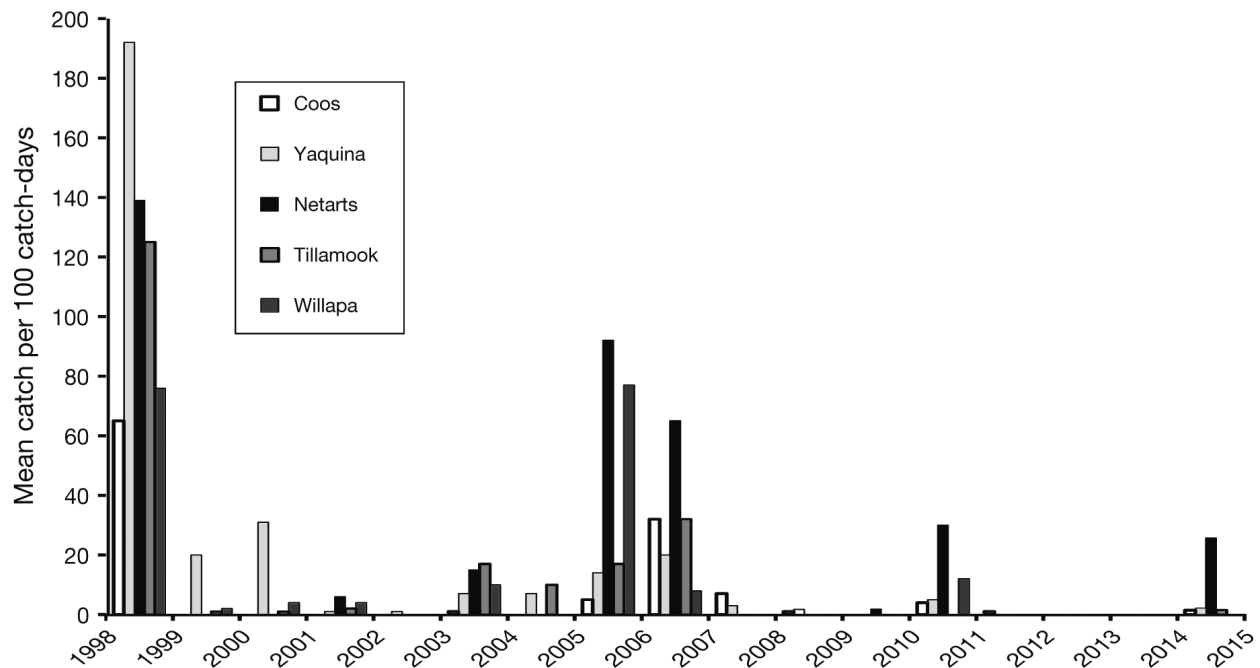


Fig. 2. Year-class strength (mean no. of catches per 100 trap-days) of age-0 *Carcinus maenas* between 1998–2014 in Oregon and Washington estuaries

Table 5. Regressions of *Carcinus maenas* ($\log_{10} + 1$) year-class strength for 6 estuaries against 8 physical ocean indicators: local winter temperature (measured in Willapa, Yaquina, and Coos Bay), ocean water temperature in the upper 20 m of NH5, Pacific Decadal Oscillation (PDO) index for March, day of ocean-based physical spring transition, alongshore currents between March–April, southern and northern copepod biomass, day of biological spring transition, and copepod community index. All regressions, with the exception of Northern copepod biomass, are positive. Significant regressions ($p < 0.05$) are indicated by shading. Bold values are the regression-squared values for the significant correlations. N: number of years for which data sets are available

Estuary	Local winter water temp. (°C)	Ocean temp. at NH5	PDO March	Ocean-based day of spring transition	Alongshore currents Mar–Apr	Southern copepod biomass	Northern copepod biomass	Biological spring transition	Copepod community index
Grays Harbor	(Willapa temp.)								
r ²	0.43	0.73	0.36	0.13	0.21	0.44	0.54	0.56	0.49
p	0.028	0.0009	0.051	0.28	0.16	0.026	0.01	0.008	0.016
N	10	10	10	10	10	10	10	10	10
Willapa Bay	(Willapa temp.)								
r ²	0.53	0.56	0.58	0.18	0.40	0.64	0.76	0.68	0.66
p	0.0009	0.0006	0.0004	0.09	0.012	0.0001	0.0001	0.0001	0.0001
N	17	17	17	17	15	17	17	17	17
Tillamook Bay	(Yaquina temp.)								
r ²	0.61	0.56	0.62	0.11	0.3	0.62	0.66	0.65	0.77
p	0.0006	0.0014	0.0005	0.22	0.051	0.0005	0.0002	0.0003	0.0001
N	15	15	15	15	13	15	15	15	15
Netarts Bay	(Yaquina temp.)								
r ²	0.40	0.35	0.52	0.36	0.59	0.61	0.50	0.69	0.73
p	0.007	0.013	0.0011	0.011	0.0008	0.0002	0.0014	0.0001	0.0001
N	17	17	17	17	15	17	17	17	17
Yaquina Bay	(Yaquina temp.)								
r ²	0.39	0.51	0.54	0	0.13	0.39	0.54	0.50	0.45
p	0.01	0.002	0.0012	0.855	0.21	0.0093	0.0012	0.0022	0.0043
N	16	16	16	16	14	16	16	16	16
Coos Bay	(Coos temp.)								
r ²	0.07	0.38	0.25	0.11	0.26	0.50	0.38	0.49	0.59
p	0.34	0.0082	0.04	0.2	0.051	0.0016	0.009	0.002	0.0003
N	15	17	17	17	15	17	17	17	17
Pooled estuaries	(Yaquina temp.)								
r ²	0.51	0.55	0.69	0.15	0.42	0.67	0.69	0.77	0.78
p	0.0012	0.0007	0.0001	0.12	0.009	<0.0001	<0.0001	<0.00001	<0.00001
N	17	17	17	17	15	17	17	17	17

biomass, day of biological spring transition, and the copepod community index, and negatively correlated with northern (subarctic) copepod biomass (Table 4). Individual estuaries exhibited the same patterns (Table 5). The biological spring transition (the day of the year when the plankton community had shifted from winter to summer species) and the copepod community index are the strongest predictors of green crab year-class strength of all the indicators, accounting for 77 and 78% of the inter-annual variability, respectively.

DISCUSSION

Favorable ocean conditions during the larval development and settlement are critical for the success of many benthic species, including green crabs. Large-scale factors such as water temperature and ocean currents 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, Queiroga et al.2006).

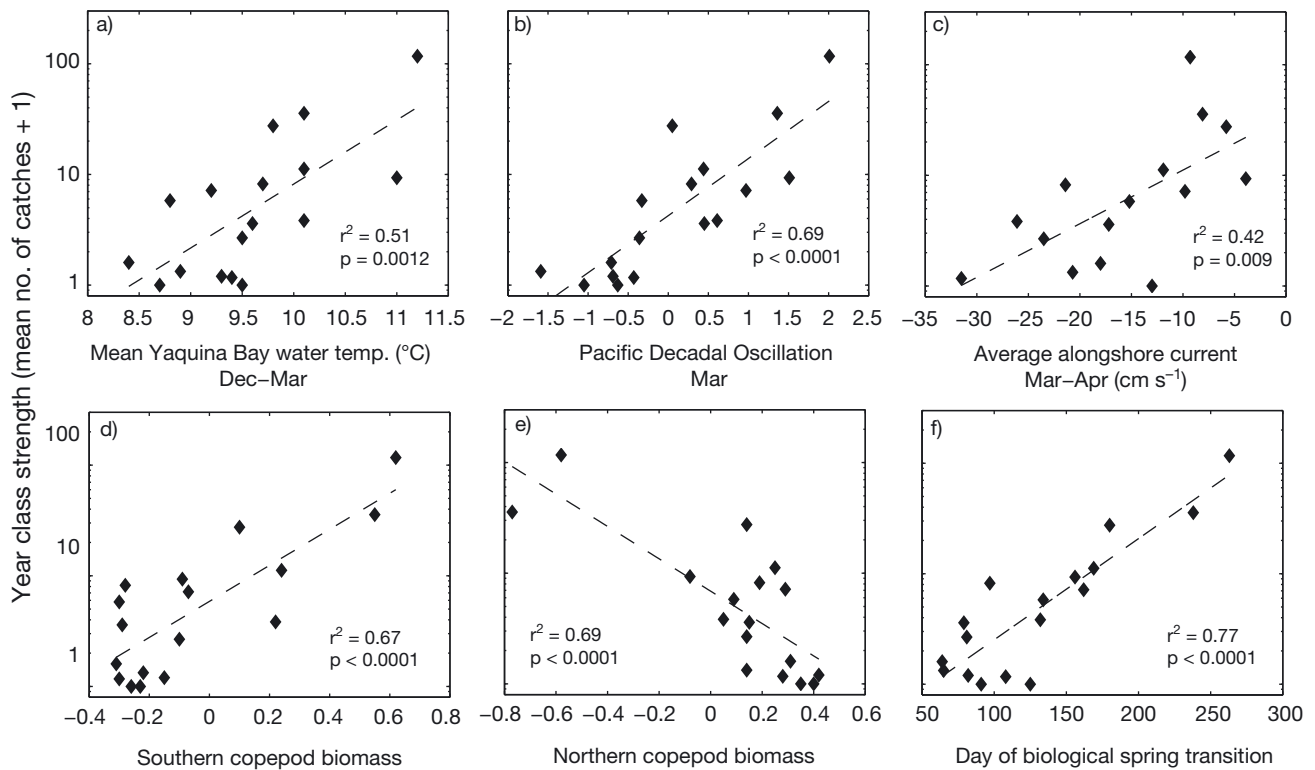


Fig. 3. *Carcinus maenas* year-class strength as a function of ocean indices. The logarithm of average catch data (mean no. of catches + 1) for the 6 estuaries were regressed against (a) mean winter water temperature (December–March) for Yaquina Bay, (b) Pacific Decadal Oscillation index for March, (c) average alongshore currents (cm s^{-1}) during March and April, (d) southern copepod biomass, (e) northern copepod biomass, and (f) day of biological spring transition

For example, Shanks (2013) found that commercial landings of Dungeness crabs *Cancer magister* are tightly correlated to the abundance of megalopae (last larval stage) 4 yr earlier and to ocean conditions during the larval rearing period. Similarly, the abundance of age-0 green crabs in Oregon and Washington estuaries during the fall is strongly correlated to ocean conditions during the previous winter and spring, when their larvae, presumably, develop in the near-shore and return to the estuaries to settle.

Several lines of evidence suggest that, during the years when age-0 green crabs are abundant, settlement of larvae occurs from late winter to early spring: (1) Gravid females held in the lab produced viable zoea larvae in mid-February (Behrens Yamada 2001). (2) During the warm winter of 2010, Shanks (2013) found early-stage green crab zoea in January, February and early March in Coos Bay. Under favorable conditions, these larvae would settle 2 mo later from March to May. (3) In April of 1998, ‘thousands’ of newly settled crabs were discovered among oyster shells in Coos Bay (H. Hampel pers. comm.). Individuals from that year-class averaged 47 mm CW in the fall (Behrens Yamada et al. 2005). (4) A bioenergetics

model for green crabs in Willapa Bay, Washington supports the view that age-0 crabs can attain 50 mm CW in ca. 5 mo (McDonald et al. 2006). Thus, crabs attaining 50 mm CW in September would have settled out from the plankton in March or April.

In our previous study, encompassing data from 1998–2008, we detected significant correlations between *C. maenas* year-class strength, and winter water temperature, March PDO, the ocean-based date of spring transition and alongshore currents during March and April (Behrens Yamada & Kosro 2010). We hypothesized that during warm winters, when larvae were present in the plankton, delayed upwelling and weak south-flowing currents during the spring would allow *C. maenas* larvae, rearing in the near-shore, to be carried back into the estuaries by tidal currents. Six more years of data confirm this hypothesis. All 6 indices associated with winter surface temperature show significant correlations with age-0 green crab year-class strength. This additional data improved the regressions between year-class strength and Yaquina Bay winter water temperature ($r^2 = 0.44$ – 0.51) and March PDO ($r^2 = 0.59$ – 0.69), confirming that winter water temperature indices re-

main important and robust predictors of green crab recruitment success in Oregon and Washington estuaries. The same pattern of strong year-classes following warm winters has also been observed in Europe and Maine (Beukema 1991, Berrill 1982).

The 2 indices related to circulation patterns, the ocean-based physical day of spring transition and alongshore currents during March and April, were significantly correlated with green crab year-class strength from 1998 to 2008 (Behrens Yamada & Kosro 2010). However, by 2014, the ocean-based day of physical spring transition became insignificant, and alongshore currents during March and April dropped in significance from explaining 61 to 42% of the inter-annual variability in recruitment success. These observations are not surprising because winter water temperatures (with the exception of 2010) were low in recent years. Since larvae do not develop below 10°C, it would not matter how favorable the currents are for on-shore transport, i.e. if it is too cold for larvae to develop, there will not be a new year-class.

With the addition of the new biological (copepod) indicators, the original conclusions are strengthened. Data on relative abundance of copepod species seem to have greater explanatory power because the larvae of green crabs, like copepods, are planktonic; drifting with ocean currents; thus, copepods alone can serve as indicators of the origin and presence/absence of specific water types. Indeed, copepod species within these 'northern' and 'southern' groups are often referred to as 'indicator' or 'sentinel' species, because changes in their abundances are typically indicative of a substantial shift in circulation patterns as well as ecosystem structure (Fager & McGowan 1963).

Recent work has shown that anomalies of northern and southern copepod species biomass off Oregon and the copepod community index are significantly correlated with alongshore currents estimated from sea level data (Bi et al. 2011) and from a regional ocean modeling system (ROMS) model (Keister et al. 2011); thus, these copepod indices themselves indicate the strength of the California Current. Therefore, it should not be surprising that they are correlated with green crab recruitment. Furthermore, the positive correlations with the PDO and ONI certainly suggest that each of those data sets indicate transport of different water types into the California Current as first proposed by Hooff & Peterson (2006). Hooff & Peterson (2006) suggest that when the PDO and ONI are negative, southward flows in the California Current are strong and the bulk of the water entering the

coastal branch of the Northern California Current (NCC) is from the north (southern British Columbia or coastal Gulf of Alaska), whereas when the PDO is positive (and when the ONI is positive), flows are weaker and more water of offshore and subtropical origin feeds the NCC (see also Chelton & Davis 1982). Given the strong correlations with copepods and the recruitment of green crabs to Oregon and Washington estuaries, our copepod indices can serve as early warning indicators of success or failure of a new year-class of green crabs.

Given that, of all indicators, the copepod indices and the biological spring transition were the strongest predictors of green crab year-class strength, we suggest that ocean conditions and transport processes associated with the shift in copepod species with season may be mechanistically linked to year-class strength of *C. maenas* larvae. The reason for this is that the copepod indicators alert us to when a new water type has arrived at Newport. Changes in transport indicators (PDO, SST, and ocean currents) suggest only changes in physical forcing; however, the biological response is not instantaneous, and there will be a time-lag (potentially several months) between when the changes in physical forcing occur and the time in which the biological response is observed.

The degree to which the source of larvae to the estuaries and bays of Oregon and Washington is local or distant (i.e. from bays and estuaries in the south, in California) remains to be clarified. Clearly, larvae were transported north during the 1990s and continue to be transported north in winter depending on the strength of the Davidson Current. However, we know of at least one instance when green crab larvae were produced locally in Coos Bay, Oregon. A. L. Shanks (unpubl.) took monthly plankton samples in Coos Bay, Oregon, from August 2009 to December 2010 and observed early-stage green crab zoea in January, February, and early March 2010. Densities peaked in mid-February, ranging from 50–145 zoea m⁻². While local recruitment of green crabs within the Oregon and Washington estuaries is possible during warm ocean conditions, more detailed studies are needed to assess the relative contribution of the 2 larval sources.

Finally, we note that our results are consistent with work performed elsewhere on the ecology of green crabs. Temperature limitations for larval development (>10°C), egg incubation (<18°C), and physiological tolerance of adults (~0–35°C) roughly set the potential geographic range of *Carcinus maenas* (Crothers 1967, Berrill 1982, Behrens

Yamada 2001, Carlton & Cohen 2003, Hidalgo et al. 2005, deRivera et al. 2007, Compton et al. 2010). In its native range in Europe and North Africa, as well as in eastern Australia, this potential range has been realized (Carlton & Cohen 2003, Garside et al. 2014). On the east coast of South America and on the west and east coasts of North America, green crabs are still expanding their range. The potential range of green crabs on the east coast of South America extends from Southern Argentina to southern Brazil (Carlton & Cohen 2003, Hidalgo et al. 2005). While green crabs in Argentina were first discovered near the town of Camarones in 2003 (Hidalgo et al. 2005), it is now believed that this species was first introduced to Puerto Deseado, an important oil shipping port, 250 km to the south. North-flowing currents would facilitate the northern transport of larvae. Abundances in Camarones has increased, and by 2011 their range expanded 70 km north of Camarones to Cobo Raso. Recent (May 2015) unconfirmed sightings have been reported from Puerto Madryn, ~200 km north of Camarones (F. J. Hidalgo pers. comm.). Up until 2010, green crabs in British Columbia were restricted to the inlets on the west coast of Vancouver Island. However, in 2011 and 2012, satellite populations were discovered on the Central British Columbia coast around Bella Bella. As of 2014, green crabs had not reached Haida Guaii nor had they penetrated into the inland sea between Vancouver Island and the mainland (Gillespie et al. 2014). On the North American Atlantic coast, green crabs were first discovered in New York in 1817 and they slowly spread northward, reaching Nova Scotia around 1960 (Carlton & Cohen 2003). The recent introduction of a new genotype from a colder source population to Nova Scotia has resulted in a new wave of range expansions into the Gulf of St. Lawrence and into Placentia Bay, Newfoundland (Blakeslee et al. 2010). This species is presently expanding its range on the west coast of Newfoundland (C. H. McKenzie pers. comm.). While a green crab population has persisted in Table Bay Harbor in Cape Town, South Africa, since the early 1980s, no major range expansion has occurred in over 30 yr, despite the presence of favorable wave-sheltered bays and lagoons with abundant shellfish prey just 90 km to the north (Robinson et al. 2005, C. L. Griffiths pers. comm.). The north-flowing Benguela current off South Africa and Namibia is characterized by strong upwelling (Boyer et al. 2000). Under upwelling favorable winds, Ekman transport would transport larvae in the surface water offshore, thus creating a barrier to

dispersal into those favorable habitats. These examples, and our observations on the Oregon and Washington coasts, confirm the important roles that temperature and currents play in limiting the success of this global invader.

Acknowledgements. Catch data for age-0 European green crabs were compiled from Washington Department of Fisheries and Wildlife data files, publications by S.B.Y. and P.M.K., and from status reports for *Carcinus maenas* in Oregon and Washington for 2002–2014 prepared by S.B.Y. for the Pacific States Marine Fisheries Commission. We thank A. Randall for her dedication in helping to produce the nearly continuous data set for Willapa Bay. Additional help was provided by Justin Ainsworth, Summer Knowlton, Bruce Kaufmann, P. Sean McDonald, Joel Prickett, and Wendy Sletton. Chuck's Seafood of Charleston, Oregon, provided most of the bait for the traps. We thank the staff and faculty of the Oregon Institute of Marine Biology for their hospitality while sampling in Coos Bay and the Oregon Department of Fish and Wildlife for allowing their shellfish samplers to help with the trapping effort in Netarts and Tillamook Bay. We thank Erika Anderson, William Percy and 4 anonymous reviewers for commenting on earlier versions of this manuscript. This research was supported, in part, by the Pacific Marine Fisheries Commission (S.B.Y.) and, through the U.S. Global Ocean Ecosystem Dynamics program, by the National Science Foundation and National Oceanic and Atmospheric Administration (PMK, WP); this is U.S. GLOBEC contribution #752. W.T.P. also received support from the NOAA/NMFS Stock Assessment Improvement Program and NOAA/NMFS Fisheries and the Environment Program. P.M.K. also received funding from NANOOS/IOOS.

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*Editorial responsibility: Steven Morgan,
Bodega Bay, California, USA*

*Submitted: February 17, 2015; Accepted: July 19, 2015
Proofs received from author(s): September 17, 2015*