

# Multiple and long-term effects of an introduced predatory crab

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**ABSTRACT:** Despite the importance of invasions, few studies have explored their long-term consequences in marine systems or examined multiple types of population-level effects. Initial effects, however, may not persist over longer time frames; effects have been shown to wane in freshwater systems. We combined 14 yr of field surveys (1993 to 2006) with manipulative experiments to examine the potential for multiple effects of a nonindigenous crab *Carcinus maenas* on the native shore crab *Hemigrapsus oregonensis* over time in central California. *H. oregonensis* abundance was negatively correlated with *C. maenas* abundance. However, *H. oregonensis* abundance rebounded to pre-invasion levels once *C. maenas* numbers declined. Other measured changes include a marked decrease in *H. oregonensis* body size and an increase in the proportion of *H. oregonensis* in the high intertidal zone since the arrival of *C. maenas*. These changes in body size and tidal distribution persisted nearly a decade beyond the peak abundance of *C. maenas* and after *H. oregonensis* numbers rebounded. Observed changes in the distribution of the *H. oregonensis* population correspond to shifts in *C. maenas* abundance, and experiments support a causal relationship. Stepwise regression suggests a complex and possibly nonlinear relationship between predictor variables and *H. oregonensis* size and distribution. Overall, our data indicate strong persistent effects on multiple attributes, with a lag in recovery with declining invader abundance, underscoring the potential for long-term effects that are decoupled from year-to-year invasion dynamics.

**KEY WORDS:** Invasion effect · Nonindigenous species · *Carcinus maenas* · Demographic response · Long-term effects · Body size · Intertidal distribution · *Hemigrapsus oregonensis*

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## INTRODUCTION

Nonindigenous species in coastal marine and estuarine systems cause a variety of effects to natural communities and managed habitats (Grosholz 2002). Documented ecological influences include shifts in abundance and habitat use of native species, alteration of habitat structure by ecosystem engineering, changes in community structure, and modification of productivity and nutrient cycling (e.g. Grosholz 2002 and references therein, Castilla et al. 2004, Levin et al. 2006). Coastal invasions also can result in evolutionary effects, such as those documented for morphology and

genetic population structure (Geller et al. 2010). Thus, although the implications of most nonindigenous species have not been evaluated (Ruiz et al. 1999), some species exert strong effects that can be expressed in many different ways.

Among the most commonly reported effects of coastal invasions are changes in the abundance or density of resident populations resulting from predation, parasitism, or competition (e.g. Byers 1999, Grosholz et al. 2000, Torchin et al. 2002). Such cases usually highlight significant numerical responses in populations over relatively short time periods and often soon after colonization. However, initial effects

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on population density may not persist over long time frames; effects have been shown to wane in freshwater and terrestrial systems (Strayer et al. 2006). Few marine studies have spanned time horizons that are necessary to assess long-term or persistent effects of biological invasions on recipient communities.

Studies that evaluate more than 1 population-level effect of marine invaders are also rare. An initial literature review found that only ~6% of 57 marine studies on population-level effects examined more than one type of change in a target population (P. W. Fofonoff pers. comm.). Yet, research on predator–prey interactions, whether native or non-native, identifies that population-level responses of prey can include changes in abundance, size, sex ratio, morphology, fecundity, life history, habitat utilization, activity patterns, and other attributes (e.g. Duffy & Hay 2001, Werner & Peacor 2003, Snyder & Evans 2006). The potential for multiple effects may be greatest when predation risk and therefore numerical responses are strong because the benefits of escaping predators are relatively high. For this reason, introduced predators with strong effects on prey populations may be particularly informative in exploring multiple population-level effects.

In our study we tested for multiple changes in a native prey population through time associated with an introduced marine predator. We combined long-term field measurements with laboratory and field experiments to examine whether the introduced European green crab *Carcinus maenas* (Linnaeus, 1758; henceforth *Carcinus*) affected the abundance and other attributes of the native shore crab *Hemigrapsus oregonensis* (Dana, 1851; henceforth *Hemigrapsus*). A previous study documented that predation by *Carcinus* greatly decreased the abundance of *Hemigrapsus* and other native epifauna and infauna in Bodega Harbor within 3 yr (Grosholz et al. 2000). Using a long-term (14 yr) dataset and experiments at this site, we now examined the broader effects of *Carcinus* on the demography and behavior of the native *Hemigrapsus* population, testing for changes in *Hemigrapsus* size, sex ratio, and intertidal distribution coincident with changes in abundance.

We also examined correlations in the abundance of these 2 species with sea-surface temperature (SST), air temperatures, or rainfall. SST can affect larval development rate (e.g. deRivera et al. 2007), year-class success of crabs (Rosenkranz et al. 2001), the abundance and distribution of nearshore crabs (Attrill & Thomas 1996), and fish and invertebrate community composition (e.g. Collie et al. 2008). Moreover, nearshore temperature fluctuates with upwelling and wind stress, which affect larval delivery (e.g. Roughgarden et al. 1988). Similarly, research has shown lower abundance of *Carcinus* in the intertidal following cold winters

(Broekhuysen 1937, Beukema 1991). Air temperature can interact with other factors to affect suitability and use of the exposed intertidal zone. Rainfall and subsequent outflow from rivers and streams can affect the salinity of estuarine water, as well as the suitability and use of the intertidal zone. While adult *Carcinus* frequently utilize subtidal habitats in other ranges, they are often found intertidally and restricted to estuaries along the eastern Pacific, likely due to predation by native *Cancer* crabs (McDonald et al. 2001, Hunt & Behrens Yamada 2003); therefore, the environmental conditions of the inter-tidal zone are likely to be especially important in this region.

## MATERIALS AND METHODS

**Study site and species.** The present study was conducted in the intertidal zone of Gaffney Point, Bodega Harbor, California (38.316° N, 123.054° W); the site is described in previous studies (Grosholz & Ruiz 1995, Grosholz et al. 2000). This small (<4 km<sup>2</sup>) embayment is flushed for the most part each tidal cycle and receives little freshwater input, so Bodega Harbor's salinity mimics the adjacent ocean. The entrance is protected by a jetty; it is a sheltered harbor with predominantly sandy mud substrate.

*Carcinus maenas*, the European green crab (Decapoda: Portunidae), is a global invader (Carlton & Cohen 2003) native to the Atlantic coast of Europe (Manning & Holthuis 1981). The first established population on the Pacific coast was detected in San Francisco Bay in 1989 and rapidly spread north to Bodega Harbor by 1993 (Cohen et al. 1995, Grosholz & Ruiz 1995). It now inhabits intertidal and shallow subtidal areas from Elkhorn Slough, California, to Queen Cove, British Columbia (Gillespie et al. 2007). While in other regions *Carcinus* occupies a range of habitats and depths, it is primarily found in sheltered bays and often in the intertidal along the west coast of North America, perhaps in response to predation pressure from crabs of the genus *Cancer* (McDonald et al. 2001, Hunt & Behrens Yamada 2003). *Carcinus* exerts a strong influence on bivalves, crabs, and other native benthic species through predation (Grosholz et al. 2000, Grosholz 2005), and it competes with native decapod crustaceans, shore birds, and other animals with overlapping diets (Elner 1981, Cohen et al. 1995, McDonald et al. 2001). In addition, it can alter community structure through the direct and indirect effects of its intense predation (Leonard et al. 1998).

The habitat, range, and diet of the native shore crab *Hemigrapsus oregonensis* overlap broadly with those of *Carcinus*. *Hemigrapsus* inhabits intertidal, muddy shores from Resurrection Bay, Alaska, USA, to the Gulf

of California, Mexico (Smith & Carlton 1975, Jensen 1995). Like *Carcinus*, *Hemigrapsus* is euryhaline and omnivorous, though algae likely constitute a larger proportion of their diet (Jensen 1995). *Hemigrapsus* is smaller than *Carcinus*: typically adult *Hemigrapsus* males grow to 49 mm carapace width (CW) (Jensen 1995), but are typically <30 mm in central California, while *Carcinus* males grow to 105 mm along the west coast of the United States (Grosholz & Ruiz 2003).

**Population data.** To determine the relative abundance and tidal distribution of crabs over time, we set pitfall traps (20 l polyethylene buckets) at Gaffney Point every year from 1993 to 2006. Three traps were set at 50 m intervals parallel to the shoreline along each of 4 transects that were +0.1, +0.4, +0.7, and +1.2 m above mean lower low water (MLLW;  $n = 12$ ). The buckets were buried flush with the substrate surface and acted as passive, unbaited traps. Pitfall traps were checked at ~24 h intervals on 3 consecutive days on spring low tides between 21 May and 14 June each year. We recorded species, gender, and width of dorsal carapace at the widest point for all crabs in the traps. Such traps have been used by many researchers collecting data on relative abundance of mobile organisms (e.g. Kneib 1984, Almeida et al. 2008). While *Carcinus* can potentially eat *Hemigrapsus* in the pitfall traps, this type of predation typically results in obvious remains such as limbs and claws, which we did not observe. In addition, the results for the traps have been calibrated with direct counts of crabs conducted with snorkel surveys in this system (Grosholz et al. 2000).

**Environmental variables.** We explored possible effects of abiotic factors on observed changes in crab populations. We used environmental data collected and archived through the Bodega Oceanographic Observation Node (BOON) to examine possible effects of precipitation and air and sea-surface temperatures on crab numbers, size, and microhabitat use. We examined rainfall (annual mean, minimum, and maximum of monthly totals, and annual total), air temperature (annual mean, standard error, and minimum of mean monthly minima [based on hourly readings] and annual mean, standard error, and maximum of mean monthly maxima), and SST (annual mean, standard error, minimum, and maximum of monthly means of hourly values) for each year (July to June) for each of these 14 measures. We also examined environmental conditions during the 3 d of trapping, using total 3 d rainfall, high and low air temperature, and the same 4 SST measures as above, but for averages of hourly readings. SST data were not collected on the 3 d of trapping in 1999 due to equipment failure, so the missing values for that year were replaced with the mean value for the dataset series.

**Laboratory experiments.** We conducted 2 experiments to test whether correlations observed could be directly attributable to *Carcinus*. First, we examined whether *Hemigrapsus* distribution shifted higher along a slope when *Carcinus* or the larger native crab *Cancer productus* were added to aquaria. We also examined whether *Carcinus* ate more females than males.

Crabs were collected from 24 to 48 h before each experiment. They were kept with conspecifics in holding tanks and supplied with a continuous flow of filtered seawater from Bodega Harbor. Crabs were fed 24 h before each experiment; *Hemigrapsus* were fed crab-food pellets, while *Cancer productus* and *Carcinus* were fed pellets and herring.

For the first experiment, we installed a sheet of 6.3 mm PVC, coated with sand, at an angle in each of two 208 l aquaria, so crabs could distribute themselves along a 1.25 m long slope from 35 cm water depth to 5 cm above the water line. Each aquarium was covered in black plastic, with small flaps we could raise for observations. We used aerated, filtered seawater from Bodega Harbor in the aquaria and exchanged 50% of the water between each trial. For each aquarium and replicate, we used 30 *Hemigrapsus*, 15 males and 15 females. Two aquaria were used for each of 5 replicate trials, including 1 experimental and 1 control aquarium. We divided crabs (10 to 30 mm CW) into 5 mm size groups; each aquarium received the same number per size group. After 3 to 4 h, we tallied the number of *Hemigrapsus* that were occupying each third (deepest, medium, and shallow plus emergent) of the slope. We then added 2 *Carcinus* (56 to 75 mm CW) to 1 of the aquaria, switching which one received these predators after each trial for a total of 5 control plus 5 experimental replicates. Three hours later, we again tallied the number of *Hemigrapsus* along each third of each slope. We repeated the above protocols adding *Cancer productus* (120 to 136 mm) instead of *Carcinus* as the potential predator in 5 additional control and experimental trials. No cannibalism or density-dependent movements were observed during the laboratory or field studies. However, some *Hemigrapsus* were eaten, and others managed to squeeze down to the section of the aquarium below the PVC slope. Therefore, we compared the proportion of total remaining *Hemigrapsus* that occupied the highest third of the slope, the shallow-water plus emergent slope, at the end of the experiment with the proportion that had occupied this highest segment prior to the addition of a predator.

A second aquarium experiment examined whether *Carcinus* preferentially preyed upon female over male *Hemigrapsus*. Each aquarium was filled with filtered seawater over a bottom of 4 cm sand plus 25 clam shells (2.5 to 4.0 cm wide) added for shelter. We added

10 female *Hemigrapsus* of 10 to 16 mm CW, and 10 males matched with female sizes to each of 8 replicate 113 l aquaria. We then recorded predation by 2 *Carcinus*, 60 to 65 mm CW, over 5 h.

**Data analysis.** To examine the intertidal distribution of crabs, pitfall trap data were pooled (combined) across all 3 d and across all 3 buckets within each transect, yielding 1 value for each transect each year. We used these data to calculate the proportion of *Hemigrapsus* that were in the highest transect compared to the total catch. All other data analyses, those on abundance patterns, size, and sex ratio, pooled data from all 12 buckets, yielding 1 value yr<sup>-1</sup> (n = 14). All data were transformed to meet assumptions of normality. We checked residuals to verify that we were not departing from assumptions of homoscedasticity. For all analyses, we excluded *Hemigrapsus* recruits ≤ 7 mm CW because we did not want the annual variation in recruitment to obscure or overemphasize the potential effects of the independent variables. *Hemigrapsus* sizes, minus the recruits, ranged from 8 to 40 mm CW. Excluding recruits never changed the qualitative results. Because crabs grow rapidly during this period, there was a strong positive correlation between Julian Day and the mean *Hemigrapsus* CW even though all collections occurred within a 3 wk period across the years ( $r^2 = 0.46$ ,  $t = 3.21$ ,  $n = 14$ ,  $p = 0.008$ ,  $[CW]^{1/2} = 0.023 \times \text{day} + 3.347$ ). Therefore, to remove the obvious effects of collection date on size, we used the residuals from *Hemigrapsus* carapace width versus Julian Day (for the first of the 3 d of sampling) instead of just CW for all analyses on size.

We performed a principal component analysis (PCA) for parameter reduction of the environmental factors because some combinations of the 21 environmental variables were highly correlated, the number of parameters would exceed the number of replicates if used in a multiple regression, and 21 separate tests for each dependent variable is statistically undesirable. We performed a PCA on 20 of the 21 environmental variables: the 3 d total rainfall was excluded from the PCA because 12 of its 14 values were zero (but rainfall was 3.0 cm in 2005 and 0.03 cm in 2006). Using varimax rotation, 5 components had eigenvalues > 1. The fifth component, however, explained < 10% of the variance in the dataset; it only had 1 variable that loaded strongly (> 0.75) and had many variables that loaded moderately (0.4 to 0.7), so it lacked simple structure. The scree plot was not definitive. Because of the lack of interpretability of Component 5 and the low proportion of variance it explained, we selected the top 4 components for extraction. These 4 components captured 77% of the variation of the original 20 variables, once standardized. Two of the principal components, PC1 and PC2, represent annual air temperature (PC1:

annual mean of mean monthly maxima and minima and minimum of monthly minima; PC2: annual standard error of monthly maxima) and explained 35.9 and 12.3% of the variance in the data, respectively. PC3 represents annual rainfall (PC3: mean of monthly totals and total and maximum rainfall) and explained 17.2% of the variance. PC4 was influenced most by the 3 d sea-surface temperature (PC4: 3 d mean, maximum, and minimum sea-surface temperature) and explained 11.6% of the variance.

We conducted several analyses to identify which factors may affect the 3 dependent variables (1) square-root of *Hemigrapsus* abundance, (2) residual size (from the regression of square-root mean CW vs. Julian Day), and (3) the arcsin[square-root] proportion of the *Hemigrapsus* that were in the highest transect, using the pooled annual data. To identify if these variables changed over time, we conducted change-point analyses (using Change-Point Analyzer 2.0; Taylor 2000) of the 3 dependent variables versus year. Change-Point Analyzer calculates the cumulative sum for each data-point (our 1 value yr<sup>-1</sup>), ordered chronologically, by adding the previous sum (starting at zero) to the difference between the current value and the average. A bootstrap analysis, randomly reordering the original values and calculating the cumulative sums for each repeat reordering, then estimates the confidence level that the change really took place. The magnitude of the change, the maximum minus the minimum, of the cumulative sum values for the bootstrap runs is compared to the magnitude of the change of the dataset in its measured, original order to obtain the confidence level estimate. The process is repeated for each side of a change to determine any secondary changes. The change-point analysis included candidate changes that had a 50% confidence level and identified detected changes that had a 90% or greater confidence level, using 1000 bootstrap runs without replacement. To examine whether the observed shift in *Hemigrapsus* spatial distribution was independent of their decrease in size, we also used a multiple regression with both *Hemigrapsus* size and year as independent variables.

Stepwise multiple regressions examined if the observed changes in the *Hemigrapsus* dependent variables might be influenced by additional factors. We conducted stepwise regressions because the analyses were of an exploratory nature, aimed at determining the potential importance of environmental factors and predators in explaining the variation in the dependent variables that were seen over time. We used the criteria of  $F > 3.84$  to add and  $F < 2.71$  to remove a parameter from these exploratory models. The 4 environmental principal components, *Carcinus* abundance (sqrt) and the abundance of the third most common crab

*Cancer productus* (sqrt) were included as independent factors in the stepwise regressions. We also examined the effect of the environmental principal components and *C. productus* on *Carcinus* abundance.

We used a paired *t*-test to examine whether *Hemigrapsus* moved higher after *Carcinus* or *Cancer productus* were added to sloped aquaria (temporal comparison). We also tested, with a Student's *t*-test, whether a greater proportion of *Hemigrapsus* moved to the highest section in aquaria that received *Carcinus* or *C. productus* than in aquaria that did not (comparison of predator-addition with control aquaria).

We tested whether the percentage of female *Hemigrapsus* changed over the 14 yr of the study or with biotic and environmental factors for females  $\geq 12$  mm CW, using change-point analysis and stepwise multiple regression, respectively. Almost all *Hemigrapsus* females are mature at 12 mm carapace width (authors' unpubl. data). We used the Wilcoxon signed-rank test to identify whether *Carcinus* preferred females as prey in the aquarium experiment described above.

## RESULTS

### Abundance of crabs

*Hemigrapsus oregonensis* abundance exhibited a strong negative relationship with *Carcinus maenas* abundance (Fig. 1; stepwise regression only entered *Carcinus* abundance:  $r^2 = 0.47$ ,  $t = -3.29$ ,  $F_{1,12} = 10.83$ ,  $p = 0.006$ ; the other 5 predictor variables [environmental and *C. productus*] were excluded due to low *F*-values). *Hemigrapsus* abundance averaged 244 when there were few *Carcinus* (2 to 27,  $n = 6$  yr), but just 66.5 when there were many *Carcinus* (35 to 65,  $n = 8$  yr). When *Carcinus* abundance was the dependent variable, none of the predictor variables were retained in the stepwise regression.

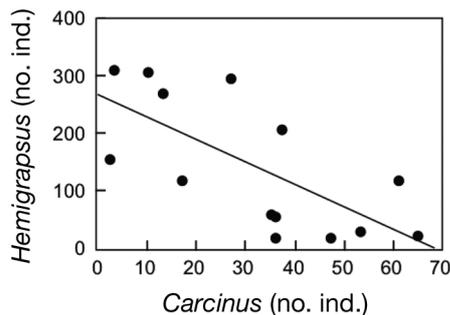


Fig. 1. *Hemigrapsus oregonensis*, *Carcinus maenas*. Number of individuals in pitfall traps (*H. oregonensis* versus *C. maenas*) caught in the same traps each year:  $r^2 = 0.48$ ,  $n = 14$ ,  $y = 265.77 - 3.90x$

The decline in *Hemigrapsus* numbers as a function of *Carcinus* abundance did not translate to a long-term temporal decline, however, likely due to the fluctuating abundance of *Carcinus*, particularly in recent years (Fig. 2a). *Hemigrapsus* abundance declined from 308 in 1993 to 19 in 1998, then increased, with the increase detectable by change-point analysis in 2001 (1st level increase from 8.7 to 13.7 crabs [analysis done on square-root-transformed data], 95% confidence interval: 1997 to 2005, and 94% confidence that a change occurred,  $SD = 4.2$ ). Also detectable in 2001, *Carcinus* abundance declined (Fig. 2b; change-point analysis 4th level effect from 6.9 to 3.7 crabs [square root]: 95% confidence interval: 2001 to 2004, confidence level of change 96%,  $SD = 1.5$ ) following their initial increase, detectable in 1994 (change-point analysis 3rd level effect from 0.8 to 6.9 crabs [square root]: 95% confidence interval: 1994 to 1994, confidence level of change 96%,  $SD = 1.5$ ).

### Decrease in size

*Hemigrapsus* size decreased over time, despite our exclusion of recruits ( $< 7$  mm CW) (Fig. 3, Fig. S1 in the supplement at [www.int-res.com/articles/suppl/m429p145\\_supp.pdf](http://www.int-res.com/articles/suppl/m429p145_supp.pdf); change-point analysis: detectable in 1999 with confidence interval: 1998 to 2006; 2nd level

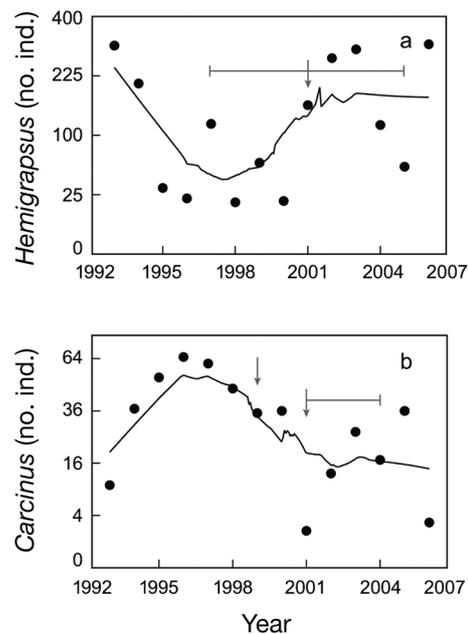


Fig. 2. *Hemigrapsus oregonensis*, *Carcinus maenas*. Number of individuals in pitfall traps per year. (a) *H. oregonensis*, (b) *C. maenas*. Line generated from a Loess smoothing function using Epanechnikov kernels. The times of change indicated by change-point analysis are shown with grey arrows; the confidence interval for each is shown with a grey error bar

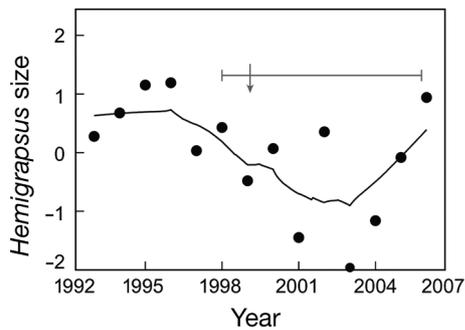


Fig. 3. *Hemigrapsus oregonensis*. Size (residuals of mean carapace width versus Julian Day) in pitfall traps across years, shown with a Loess smoothing line that used Epanechnikov kernels. The time of change indicated by change-point analysis is shown with a grey arrow; the confidence interval is shown with a grey error bar

change from 0.63 to 0.47 mm given Julian Day, confidence level 96%, SD = 0.58). Mean carapace width of *Hemigrapsus* decreased from 14.9 mm in 1993, when *Carcinus* first arrived, to 10.8 mm in 2004, but increased in the last 2 yr of the study. This estimate of the downshift in size is conservative given that we excluded the recruits (<7 mm CW) from the analysis. *Hemigrapsus* size was independent of their abundance ( $r^2 = 0.07$ ,  $t = -0.95$ ,  $F = 0.90$ ,  $df = 13$ ,  $p = 0.361$ ). Stepwise regression examining possible effects of environmental and biotic variables on *Hemigrapsus* size did not enter any predictor variables.

#### Changes in distribution and size of crabs across tidal elevation

The proportion of *Hemigrapsus* in the highest intertidal transect (+1.2 m MLLW) increased over time, detectable in 2002 (Fig. 4a; change-point analysis: 1st level change from 25 to 51% crabs (arcsine square root of proportion), 95% confidence interval: 2001 to 2004, confidence level 96%, SD = 0.13). The proportion increased from 2% in 1993 to 37% in 2004, then declined back to 11% in 2006. This change in tidal height only weakly corresponded to the concurrent decrease in body size ( $r^2 = 0.21$ ,  $t = -1.76$ ,  $F = 3.12$ ,  $df = 13$ ,  $p = 0.103$ ). In addition, a greater proportion of *Hemigrapsus* were trapped in the highest transect through time than was expected due to the decrease in mean size alone (multiple regression: adjusted  $R^2 = 0.36$ ,  $t_{\text{year}} = 2.27$ ,  $p = 0.044$ ,  $t_{\text{size}} = -0.84$ ,  $p = 0.420$ ; whole model  $F_{2,11} = 4.68$ ,  $p = 0.034$ ).

Stepwise regression only entered PC3, with a smaller proportion of *Hemigrapsus* higher in the intertidal in years with greater PC3 values (Fig. 4b;  $r^2 = 0.34$ ,  $t = 2.49$ ,  $F_{1,12} = 6.21$ ,  $p = 0.028$ , other 5 variables

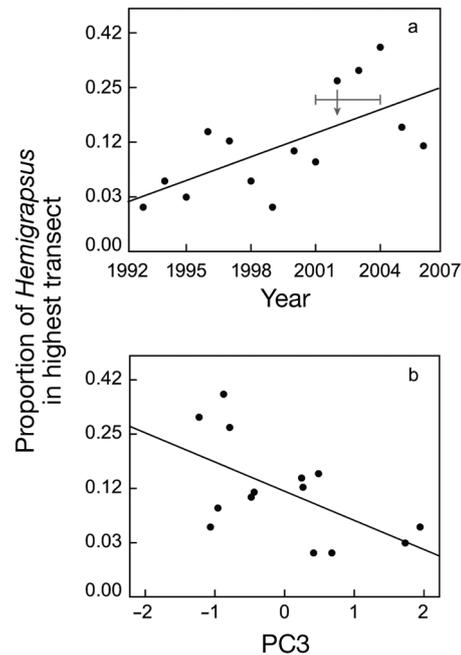


Fig. 4. *Hemigrapsus oregonensis*. Proportions of *H. oregonensis* (arcsine square root) in the uppermost transect versus (a) year ( $r^2 = 0.43$ ,  $n = 14$ ,  $y = 0.025\text{Year} - 50.03$ ) and (b) Principal Component 3 (PC3; mean, maximum, and total annual rainfall;  $r^2 = 0.34$ ,  $n = 14$ ,  $y = -0.094\text{PC3} + 0.341$ ). Numbers on the y-axis are back-transformed to show the proportion of crabs in the highest transect. In Panel a the time of change indicated by change-point analysis is shown with a grey arrow; the confidence interval is shown with a grey error bar

excluded). The rainfall variables, which contributed strongly to PC3, did not explain this trend, however (Table S1, Fig. S2 in the supplement at [www.int-res.com/articles/suppl/m429p145\\_supp.pdf](http://www.int-res.com/articles/suppl/m429p145_supp.pdf);  $r \ll 0.5$  for each); rather, a much weaker contributor to PC3, the standard error in annual SST, was negatively correlated with the proportion of *Hemigrapsus* in the higher intertidal zone (Pearson correlation coefficient  $r = -0.56$ ,  $p = 0.038$ ; Table S1, Fig. S2).

#### Change in distribution in sloped aquaria

In sloped aquaria, an upwards shift in *Hemigrapsus* distribution was attributable to the presence of *Carcinus*. More *Hemigrapsus* used the highest section after *Carcinus* were added (Fig. 5;  $41.0 \pm 10.3\%$  *Hemigrapsus* in the highest section,  $n = 5$ ) than beforehand ( $12.5 \pm 3.0\%$ ; paired  $t$ -test:  $t = -3.03$ ,  $df = 4$ ,  $p = 0.039$ ). In contrast, this difference was not observed in controls ( $18.4 \pm 9.5\%$  after,  $22.1 \pm 11.2\%$  before;  $t = 0.45$ ,  $df = 4$ ,  $p = 0.676$ ). The redistribution of *Hemigrapsus* to the highest third of the aquaria was also less pronounced when *Cancer productus* were added to the sloped

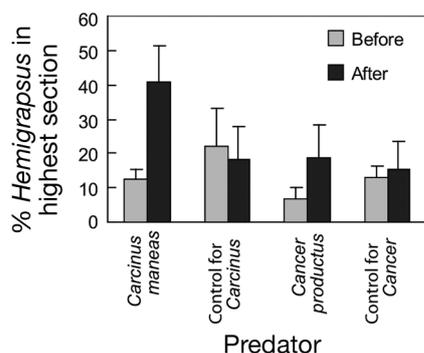


Fig. 5. *Hemigrapsus oregonensis*. Percent of individuals in the highest section of sloped aquaria before versus after addition of larger, predatory crabs (*Carcinus maenas* or *Cancer productus*). Means  $\pm$  1 SE are shown

aquaria instead of *Carcinus* ( $18.9 \pm 9.3\%$  *Hemigrapsus*) compared to beforehand ( $6.4 \pm 3.5\%$ ; paired *t*-test:  $t = -2.32$ ,  $n = 5$ ,  $p = 0.103$ ; *C. productus* controls:  $15.2 \pm 8.4\%$  after,  $13.0 \pm 3.2\%$  before;  $t = -0.35$ ,  $df = 4$ ,  $p = 0.742$ ).

#### Sex ratio

The sex ratio of mature *Hemigrapsus* in pitfall traps, crabs  $\geq 12$  mm CW, did not change over time or with *Carcinus* abundance (change-point analysis did not detect changes over time at the 90% confidence level; stepwise regression did not enter any predictor variables). However, *Carcinus* ate 17 females and 6 males in the preferential predation aquarium experiment, eating more females than males 5 times and more males only once (Wilcoxon signed-rank test:  $Z = -1.80$ ,  $n = 8$ ,  $p = 0.072$ ).

#### Environmental variables

Of the 4 principal components summarizing the environmental variables, only PC3 (mean maximum and minimum annual rainfall) was retained in the stepwise regression for intertidal distribution, and no PCs were retained in the other stepwise regressions (Fig. 4b). Further exploration with Pearson correlation of potential correlations between environmental and crab variables, however, indicated a positive correlation between PC3 and *Carcinus* abundance and a negative correlation between PC3 and *Hemigrapsus* abundance (Table S1, Fig. S2).

Change-point analysis identified a decrease in PC3 detectable in 2000 (1st level from 0.60 to  $-0.60$ , 95% confidence interval from 1995 to 2002, confidence

level = 94%,  $SD = 1.21$ ). Two decreases occurred in PC1 (annual air temperatures), first a decrease in 1998 (1st level from 1.02 to  $-1.00$ , 95% confidence interval from 1998 to 1998, confidence level = 95%,  $SD = 0.47$ ), then another decrease detectable in 2003 (2nd level from  $-1.00$  to  $-0.02$ , 95% confidence interval from 1999 to 2003, confidence level = 92%,  $SD = 0.47$ ). Change-point analysis did not detect (at the 90% confidence level) changes over time for the other principal components of the environmental variables.

#### DISCUSSION

A population of the native crab *Hemigrapsus oregonensis* in Bodega Harbor has changed in multiple ways in the 14 yr since the arrival of the non-native crab *Carcinus maenas* in 1993. The abundance of *Hemigrapsus* was inversely related to changes in *Carcinus* numbers, exhibiting an initial strong decline then rebounding in 2001. The fluctuations in *Carcinus* population size were likely in large part due to variation in recruitment, which recently has been shown for *Cancer magister* along the NE Pacific to be correlated with wind stress (Shanks & Roegner 2007, Morgan & Fisher 2010). Two changes in *Hemigrapsus*, size and intertidal distribution, lagged behind the increase then decrease in *Carcinus* numbers and the subsequent numeric recovery of *Hemigrapsus*. Here, the mean size of *Hemigrapsus* decreased by nearly two-thirds over time. Size increased in the last 2 yr of the study, perhaps indicating a rebound a decade after *Carcinus* numbers started to decline. The tidal distribution of *Hemigrapsus* also shifted dramatically. Between 1993 and 2004, a proportion of *Hemigrapsus*, 18.5 times higher than in 1993, shifted to the highest intertidal zone. While size partitioning across the intertidal occurs in other nearshore crabs (e.g. Orth & van Montfrans 1987, Dumbauld et al. 1993, McMillan et al. 1995) and weakly here, the upward habitat shift was much greater than expected solely from the concurrent decrease in *Hemigrapsus* size.

Three types of factors, as well as their interactions, potentially influenced the shift in population size, body size, and intertidal distribution of *Hemigrapsus*: (1) environmental factors, (2) risk of predation by green crabs, and (3) risk of predation by other predators such as *Cancer productus*. Given the findings on the effect of wind stress on the recruitment of other larval crabs, we expect that wind stress likely affects recruitment of both these crab species (Shanks & Roegner's 2007, Morgan & Fisher 2010). Other environmental factors may be important as well. Annual rainfall (PC3) was correlated with higher *Carcinus* abundance and lower *Hemigrapsus* abundance. Rainfall and *Carcinus* abun-

dance may both play important, perhaps interactive, roles in *Hemigrapsus* populations. Rainfall could affect recruitment of these crabs, the distribution of predators, or the amount of algae available as a food resource to *Hemigrapsus*. Our data, however, are consistent with *Carcinus* being a key driver of the change in *Hemigrapsus*. The correlation with rainfall was not as strong as the correlation between the crab abundances, and it was not retained in statistical models that examined both variables simultaneously.

Similarly, our data best support the hypothesis that predation risk by *Carcinus* influenced *Hemigrapsus* intertidal habitat use, but that intertidal use also may be affected by the variation in SST. There was a clear shift to higher areas in aquaria as a clear response to predation risk by *Carcinus*. *Hemigrapsus* always shifted their distribution to a higher position when *Carcinus* were added to aquaria, but they did not shift in control aquaria or as strongly when the native species *Cancer productus* was added. *Carcinus* and *Cancer productus* remained in deeper water with only brief forays to mid-elevations. *C. productus* eat *Hemigrapsus*, but not as frequently as do *Carcinus* (authors' unpubl. data). Our field measurements and opportunistic observations revealed a large, though variable, number of *Carcinus*, many fewer *C. productus*, and a dearth of other significant crab predators such as predatory fish or birds.

Upward shifts may also be influenced by the trade-offs and interactions between predation risk in the lower intertidal zone, especially in years with many large *Carcinus*, and variably stressful environmental conditions higher in the intertidal or greater recruitment. However, the importance and meaning of the correlations we found between the environmental variables and the distribution of *Hemigrapsus* through the intertidal are unclear. The third principal component was negatively correlated with higher intertidal use and abundance of *Hemigrapsus*. However, the factors that loaded heavily on PC3 (rainfall factors) had low correlation with use of the upper intertidal and instead were more highly correlated with the abundance of *Hemigrapsus* (negatively) and of *Carcinus* (positively).

Rainfall could affect the abundance of crabs in the intertidal indirectly due to weather conditions affecting their recruitment or the distribution of predators, and thus may be connected indirectly to the decreased abundance and use in the upper intertidal of *Hemigrapsus*. The proportion of *Hemigrapsus* in the intertidal was also correlated with the standard error of SST, both negatively with the annual standard error and positively with the 3 d standard error. The variability in SST may reflect more frequent changes in upwelling, which has been shown to affect recruitment

levels in other species (Roughgarden et al. 1988, Connolly et al. 2001). As the pattern of intertidal use was correlated with size, despite our exclusion in data analysis of the smallest crabs, weather and upwelling patterns affecting recruitment and therefore proportion of the population that were young of the year may directly affect the proportion in the upper intertidal.

While *Carcinus* abundance was not retained in models examining potential drivers of the observed decrease in size or microhabitat shift of *Hemigrapsus*, a strong linear relationship with predator abundance would not be predicted if there were a functional or other non-linear response, trait-mediated effects (i.e. behavioral compensation of prey to reduce predation risk), or a time-lagged response (e.g. Sarnelle 2003). For example, if *Hemigrapsus* move higher in the intertidal to seek a potential shallow-water refuge when they encounter aquatic predators and encounters are independent of density because *Carcinus* move more when they are at low densities, the proportion of *Hemigrapsus* using the highest transect would not correlate with *Carcinus* density.

The effects of nonindigenous species can vary in both space and time, and relatively little information is currently available for either dimension in marine systems (Ruiz et al. 1999). For freshwater systems, Strayer et al. (2006) and Strayer & Malcom (2007) suggest that (1) using short-term data on strong initial effects to predict the long-term effects of biological invasions can exaggerate some potential consequences, which are likely to be modulated over time, and (2) long-term studies may reveal more nuanced effects of invasions on native species that develop over time. Our analysis provides further support for this perspective, demonstrating both of these outcomes for a marine invasion.

The observed changes in *Hemigrapsus* body size and habitat use illustrate potentially chronic repercussions of predation by an invader and demonstrate the importance of long-term studies of invasion. Such effects may alter the dynamics of native species when faced with additional perturbations. A multi-year decline in body size could reduce the reproductive potential of the population, as with other crabs and fishes (e.g. Prager et al. 1990, Hines 1991, Berkeley et al. 2004). The shift to higher tidal areas inevitably would have decreased their potential foraging time: because of the inherent longer exposure time, individual *Hemigrapsus* higher in the intertidal must spend more time under the shelter of rocks to prevent desiccation or predation by shorebirds. Therefore, both responses could decrease the likelihood that an affected organism attains numeric or demographic recovery initially or after future predation pressure, especially for populations that are less likely to be supplied from external larval sources. Similar to other studies, especially those

in aquatic systems, the non-lethal consequences of the behavioral changes that result from the threat of predation may be as or even more important than the direct consequences of predation to the population (Peacor & Werner 2001, Preisser et al. 2005).

Previous studies on the effect of temperature on biological invasions suggest that some non-native species will be favored by climate change. Climate change may increase the ranges of species in recipient regions (Dukes & Mooney 1999) and may bring them an advantage locally over natives due to different thermal tolerances (Sorte et al. 2010), earlier and higher recruitment under warmer conditions (Stachowicz et al. 2002), or increased reproductive rates or survivorship (Walther et al. 2009). Similarly, the data here suggest changing climate may serve as a perturbation that interacts with invasion by non-native predators and may mediate the extent or speed of recovery. The abundance of both crabs and the size and habitat use of the native *Hemigrapsus* crabs were correlated with different environmental conditions likely to change due to increases in atmospheric carbon dioxide (Meehl et al. 2007). For example, increased minimum air temperature was correlated with an increased abundance of the non-native crab. Similarly, increased rainfall was correlated positively with the abundance of non-native *Carcinus* and negatively with the native *Hemigrapsus*, and variability in SST was correlated with an increase in the proportion of *Hemigrapsus* using higher intertidal areas. Therefore, warmer or more variable temperatures could increase the success of an invading population as well as extend or exacerbate the longer term repercussions of its predation on native crabs.

Additional examples from terrestrial and freshwater systems demonstrate how non-native species can affect the distribution, habitat displacement, and other behaviors of native species. Such changes have been reported for a variety of non-native arthropods and fishes (Fraser & Gilliam 1992, Gotelli & Arnett 2000, and reviewed by Snyder & Evans 2006). Similarly, studies show that nonindigenous species have had strong effects on the size-frequency distribution, growth rates, and even morphology of natives, often along with other effects (Fraser & Gilliam 1992, Mills et al. 2004, Carroll et al. 2005, Light 2005). Studies of invasions have identified multiple changes to community structure and ecosystem processes as well (Crooks 2001, Levine et al. 2003). For example, Neira et al. (2006) identified physiochemical changes to the habitat due to invasion by hybrid *Spartina* that, in turn, affected the benthic community's species composition and food web structure.

Not only have multiple types of effects been demonstrated on species and community levels, research in other systems is arising that identifies how these

effects last well beyond the initial changes to a recipient community. Changes to the seed bank (Lonsdale et al. 1988, Holmes & Cowling 1997, Drake 1998), soil nutrients (D'Antonio & Vitousek 1992, Corbin & D'Antonio 2004 and references therein), and soil mycorrhizae (Batten et al. 2006, Mummey & Rillig 2006) all have had long-term effects on the population dynamics of native plant populations. The effects of fire ants have not diminished in the decades since their invasion (Gotelli & Arnett 2000). In freshwater systems, population size, recruitment, and growth of native freshwater mussels all stabilized or increased a decade after the zebra mussel invasion, but these measures have not rebounded to pre-invasion levels, and the body condition measure of native mussels remains low (Strayer & Malcom 2007).

In this study we observed changes in abundance, size, and distribution of the native crab *Hemigrapsus* that were evident across a decade. These shifts in the native crab population coincide with the appearance and increase of an invader, and they likely result from increased predation pressure on the native crab. The last 2 yr of the dataset may suggest a recent possible rebound towards pre-invasion states. *Hemigrapsus*, which has pelagic larvae and could have recruited from other less affected populations, showed rapid numeric recovery when *Carcinus* numbers decreased. The *Carcinus* range only extends south to Elkhorn Slough off Monterey Bay and, though in the center of the range, is at very low numbers from just north of Bodega Bay, California, through Vancouver Island, British Columbia, whereas *Hemigrapsus* populations are in high density north and south of the population examined here (authors' unpubl. data). The *Hemigrapsus* population also has increased recently in body size to its original mean and exhibited a partial return to its pre-invasion habitat distribution. Because there were fluctuations throughout, it is premature to say that the 2 data points toward the end of the observation period reflect recovery.

Despite the range of effects that can occur from biological invasions in all systems, analyses of persistence or multiple effects in marine systems are largely lacking. Most studies are limited in scope, both in terms of timeframes and of potential interactions (Ruiz et al. 1999). Only now are broader and long-term studies beginning to emerge, both in marine systems (present study, and for community and habitat changes Crooks 2001, Neira et al. 2005, 2006) and freshwater systems (Strayer et al. 2006, Strayer & Malcom 2007). These long-term studies reveal interesting nuances and trends not identifiable from the shorter ones.

The results of the present study broadly imply that predators could yield sustained effects on prey that affect the structure of communities that are newly

organized due to climate change-related range shifts or invasion or could change the timing and extent of oscillations in population size of predators and prey. Newly colonizing generalist predators could cause sustained population-level effects in resident prey that cause additional stress and decreased reproductive output of prey populations. When prey species are the colonizers due to climate change or other forces, they may not be prevented by predators from establishing self-sustaining populations. This could greatly limit or delay natural spread upstream in response to warming water and limit the number of habitats colonized relative to those with suitable abiotic conditions and within the dispersal range.

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