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Effects of interspecific competition and coastal oceanography on population dynamics of
the Olympia oyster, *Ostrea lurida*, along estuarine gradients

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Effects of interspecific competition and coastal oceanography on population dynamics of the Olympia oyster, *Ostrea lurida*, along estuarine gradients

Abstract

In estuaries, we often see predictable patterns of spatial and temporal variation in both physical and biological factors. This results in an excellent system in which to study variation in population and community dynamics. Longitudinal gradients are heavily influenced by mixing of inputs from the nearshore ocean or rivers. Vertically, tidal elevation on shore is a proxy for a gradient of stress due to factors like aerial exposure or food availability. Consequently, both longitudinal position along the estuary and vertical position on shore can affect demographic patterns of benthic estuarine invertebrates and interactions between species. To this end, I documented demographic factors of the Olympia oyster, *Ostrea lurida*, along both a longitudinal estuarine gradient that is heavily influenced by the nearshore ocean and a vertical elevation gradient in Tomales Bay, California (Chapter 1). Secondly, I investigated the composition and competitive effects of the sessile community on stages throughout oyster life history along these same gradients. I also investigated competitive effects on earlier life stages in San Francisco Bay, California, which has a different estuarine structure and sessile community than Tomales Bay (Chapter 2).

Position along both the longitudinal and vertical gradient in Tomales Bay influenced recruitment and growth but not survival. Increasing water residence time

toward the head of the estuary best predicted recruitment patterns, while a longitudinal food gradient peaking mid-bay best predicted intertidal oyster growth. Subtidal oyster growth did not show significant longitudinal variation. Thus, while benthic and pelagic processes can be coupled in an estuarine system, this link can vary with tidal elevation.

Competition directly affected earlier life history stages but not later stages. In Tomales Bay, size of recruits by the end of their first growing season was significantly reduced but total recruitment was not affected. In San Francisco Bay, we found the opposite pattern such that total recruitment was reduced by presence of competitors but growth was not affected. There was variation in both percent cover and composition of the sessile communities in each bay. These results better our understanding of how variation in habitat characteristics and life history stage together alter demography and species interactions.

Chapter 1: Oceanographic processes influence the population dynamics of Olympia oysters along an estuarine gradient

Abstract

Nearshore ocean and estuarine waters are connected via a range of processes that include estuarine circulation due to freshwater outflow and longitudinal tidal mixing. The longitudinal variation in temperature and salinity that defines estuarine gradients depends on the relative strength of these processes versus freshwater and nearshore inputs. In turn, this spatial structure in habitat influences demographic patterns of benthic invertebrates. We documented recruitment, growth, and mortality of a key benthic estuarine species, the Olympia oyster, *Ostrea lurida*, along longitudinal estuarine and vertical tidal elevation gradients in a bay that only exhibits estuarine circulation in winter such that bay-ocean exchange is dominated by tidal mixing for much of the year. Recruitment increased with increasing residence time from the mouth to the head of the estuary at both intertidal and subtidal heights. However, patterns of growth varied with tidal elevation. Growth of intertidal oysters was correlated with a persistent mid-estuary peak in phytoplankton biomass resulting from gradients in residence time and availability of nutrients imported to the estuary from the adjacent upwelling zone. In contrast, subtidal growth was decoupled from this gradient and was consistently high regardless of position along the estuary. Mortality did not follow any consistent patterns throughout the bay. Results from this study increase our understanding of how nearshore water properties influence estuarine benthic species by documenting multiple demographic factors and showing that the impact of these factors can be dependent on tidal elevation.

Introduction

Estuaries in Mediterranean climates that receive limited seasonal freshwater input are strongly influenced by the influx of nearshore ocean waters. Although longitudinal gradients in water properties will be influenced by freshwater flows during the wet season, in the dry season the estuarine gradient can be strongly influenced by the tidal mixing of coastal waters into the estuary with a strong decline in influence toward the head of the estuary. As a result, areas near the mouth will be dominated by marine waters and strong tidal flushing, while areas near the head will be influenced by riverine inputs and reduced tidal excursion. Low inflow estuaries typical of Mediterranean climates have little to no riverine inputs for much of the year, and so the head of the estuary is dominated by long-residence (aged) waters. Consequently, for these estuaries, tidal mixing is a major determinant for resulting gradients during most of the year (Largier et al. 1997).

Estuarine gradients can strongly influence the demography of benthic estuarine invertebrates (Ruesink et al. 2003, Berger et al. 2006), and so the gradient in water residence controlled by tidal mixing may similarly influence demography. Advection of nearshore ocean waters and subsequent tidal mixing may influence demography. This longitudinal tidal mixing influences water residence time, and, as freshwater inflow weakens in spring, tidal mixing has an even greater effect. As estuaries may serve as retention zones for larvae (Graham and Largier 1997, Sponaugle et al. 2002), these estuary-ocean exchange processes that control water retention can affect larval retention and therefore recruitment both in this estuary and nearby habitats linked by dispersal

(Gaines and Bertness 1992, Roegner 2000, Sponaugle et al. 2002). In low-inflow estuaries, residence time may increase by an order of magnitude from the mouth to the head of the estuary (Largier et al. 1997). However, there is a lack of studies to date that have explored the relationship between recruitment and water residence time.

The tidal flux of nearshore waters into an estuary can also influence growth patterns of benthic invertebrates, especially in estuaries adjacent to coastal upwelling zones. Upwelling results in cold, nutrient-rich nearshore waters which can stimulate primary production to increase benthic invertebrate growth, though associated decreasing temperature may result in slower invertebrate growth (Menge et al. 1997, Blanchette et al. 2007, Menge et al. 2008). Over the course of several days, the nutrients associated with upwelled waters are taken up by phytoplankton blooms that benefit benthic invertebrates. This ageing of upwelled waters is observed nearshore in upwelling shadows or retention zones (Graham and Largier 1997, Vander Woude et al. 2006) and low-inflow estuaries in upwelling regions may serve as similar retention zones where significant phytoplankton concentrations may develop (Kimbrow et al. 2009a). Previous work in estuaries has shown the growth of benthic invertebrate to be coupled with higher phytoplankton due to the import of nutrient-rich or phytoplankton-rich waters into the estuary (Banas et al. 2007, Kimbro et al. 2009a, Escati-Penaloza et al. 2010).

The few studies that have demonstrated this benthic-pelagic coupling have not considered how it influences populations at different vertical tidal elevations on shore. Tidal elevation results in a well established stress gradient of abiotic and biotic factors. Longer immersion time at lower tidal elevations is correlated with greater feeding time, higher growth rates, and less desiccation risk (Barnes and Powell 1953, Suchanek 1978,

Peterson and Black 1987). Biotic factors such as predation and competition can play a greater role at these lower tidal elevations (Connell 1972, Menge and Sutherland 1987). Consequently, demographic patterns along the estuarine gradients may also vary with tidal elevation.

In this study, we document oyster demographic patterns along both longitudinal estuarine and tidal elevation gradients in Tomales Bay, California, a low-inflow estuary where tidal mixing controls nutrient and phytoplankton fluxes for much of the year. We aim to relate the well-described gradient in water properties to patterns of oyster recruitment, growth, and survival at both intertidal and subtidal elevations.

Methods

Study Species and Site

The Olympia oyster, *Ostrea lurida*, is native to eastern Pacific estuaries from Alaska to Baja California Sur, Mexico (Baker 1995, Polson et al. 2009). Olympia oysters grow up to 7 cm on rocks, cobble or other hard substrate, creating beds approximately 0.10 m high within low intertidal and shallow subtidal zones of estuaries (Baker 1995). These oysters are protandrous hermaphrodites that become sexually mature within a year. Females brood developing embryos for 10-14 days. Planktotrophic larvae develop for one to six weeks in the water column before settling on hard substrate in summer and fall (Baker 1995, Carson 2010).

Tomales Bay, CA (38.20° N, 122.90° W) is a low inflow estuary located near an area of strong upwelling with marked wet and dry seasons. It is a long, narrow estuary, approximately 20 km long and 1 - 2 km wide, with strong longitudinal gradients in water

properties and circulation (Hearn and Largier 1997, Largier et al. 1997). Freshwater inflow is negligible during the dry season and so tidal exchange of ocean and estuary waters is the main source of new water mixing into the estuary; its strength determines how far into the estuary nearshore waters are delivered. In Tomales Bay, relatively weak exchange with the ocean allows a sharply increasing gradient of residence time from the mouth to the head of the estuary, despite its small size (Largier et al. 1997). Salinity and temperature follow this same pattern (Hearn and Largier 1997, Largier et al. 1997). Nutrient levels are high at the mouth where mixing of nearshore upwelled waters is strong and levels decrease toward the back of the bay. A persistent phytoplankton maximum occurs in the mid-bay where there are adequate nutrients balanced by sufficient residence time to allow blooms, and intertidal oyster growth reflects this gradient of food availability (Kimbrow et al. 2009a).

We studied oyster populations along estuarine and tidal gradients in Tomales Bay, where this species occurs largely within the mid to lower intertidal zone on rocks and cobbles from +0.5 to -1.0 m MLLW. We used four sites along the west side of the bay located at 6 km, 8 km, 12 km, and 16 km from the mouth (Figure 1.1). These sites were chosen based on previous research in Tomales Bay (Kimbrow et al. 2009a) and also to encompass both the species range and estuarine gradients.

Recruitment

We monitored oyster recruitment at intertidal and subtidal elevations at each site using PVC tiles (10 cm x 10 cm) covered with a cement layer (0.5 cm) to add rugosity and better mimic natural substrate. We attached intertidal tiles vertically to small PVC

crossbar frames alongshore at 0 m MLLW at 5 meters intervals parallel to the water line. At subtidal locations, we attached tiles vertically to PVC frames that were suspended approximately 1.0 m below the surface of a moored buoy immediately offshore of intertidal frames (< 10 m separation from intertidal frames). We brought tiles back to the lab to count recruits under a dissecting microscope and measure them with vernier calipers.

In 2008, we monitored recruitment monthly from August through December. Two sets of 10 tiles were placed at each combination of site and tidal elevation such that one set was left out for two months and another set was brought in at the end of each month. Bimonthly counts were adjusted to provide monthly totals for recruitment. Unfortunately, we lost subtidal tiles at one site (8 km) part way through the experiment, so these data were not available for analysis.

In 2009, we measured recruitment for the entire season from June through November. In addition to the four sites used in 2008, we included an intertidal site at approximately 6.5 km to better describe recruitment at the edge of the oyster range. Ten recruitment tiles were placed at each site and tidal height combination at the beginning of June and retrieved at the end of recruitment season at the beginning of December. Again, subtidal tiles were lost, in this case at the 6 km site, and so data were unavailable for analysis. We did monitor monthly recruitment at 16 km at the intertidal location to compare recruitment between years. Ten tiles were exchanged monthly from May through December.

Growth and Mortality

To monitor oyster growth and survival, we outplanted PVC tiles (10 cm X 10 cm) with lab-reared oysters to sites at both intertidal and subtidal heights. Tiles deployment methods followed recruitment collector deployment methods as described above. We collected adult oysters from Tomales Bay and spawned them in the laboratory, allowing larvae to settle and grow on PVC tiles before being outplanted in the field (see Kimbro et al. 2009a for methods). Tiles were held in large flow through tanks for several months until deployment in summer. We randomly outplanted these tiles amongst sites at both intertidal and subtidal heights following recruitment collector deployment methods above.

In 2008, we randomly assigned tiles with large juvenile oysters (mean size approx. 15 mm, mean density per tile approx. 20) to one of four sites along the bay at either intertidal or subtidal heights. We monitored oysters for growth and survival from August through November 2008, using photos to track individuals. Each month, we measured maximum shell length for all individuals to the nearest millimeter with vernier calipers and counted the total number of oysters for each tile. Subtidal frames with all tiles were lost at the 8 km site.

These oysters were held in large flow through tanks until they were redeployed in June 2009 to measure adult growth and mortality. Tiles with adult oysters (mean size approx. 30 mm, mean density approx. 12) were first grouped by density and size and then randomly distributed among treatment groups. We outplanted tiles at the two mid-point sites (8 km and 12 km) at both intertidal and subtidal elevations. We measured and counted oysters at the beginning of December 2009. These outplanted tiles were also maintained as part of the competition experiment (see Ch. 2), but, because there was no

effect of presence or absence of space competitors, we grouped these tiles yielding $n = 12$ for each site by tidal height combination for 2008 and $n = 18$ for each site by tidal height combination for 2009.

Statistical Analysis

We analyzed the number of oyster recruits using Analysis of Variance (ANOVA) with site and tidal height as fixed factors. We used Cochran's C to test homoscedasticity and normal probability plots to graphically confirm normality (Underwood 1981). If data did not meet assumptions and transformation did not adequately improve data sets, we used nonparametric Wilcoxon and Kruskal Wallis tests or ANOVAs on ranked data. Because one of four subtidal sites was lost each year, we first analyzed recruitment along the broader intertidal gradient that included all sites. Secondly, we analyzed intertidal and subtidal sites together dropping the intertidal site at the same location as the lost subtidal site. In 2008, we analyzed the intertidal gradient using ANOVA on ranked data, and Wilcoxon and Kruskal Wallis to analyze intertidal and subtidal data together. In 2009, we used power transformed data to analyze the intertidal gradient, and log transformed data to analyze intertidal and subtidal data together. We used linear regressions to examine the correlation between recruitment and previously measured values of residence time (Largier et al. 1997) along the bay in each year and at each tidal height. Monthly recruitment in 2008 was analyzed using log transformed data, and a Kruskal Wallis test was used to analyze monthly recruitment in 2009. Finally, we used a Wilcoxon test to test differences in recruitment between years using comparable monthly data from each year for the 16 km site only.

For growth and mortality data, competition was also a fixed factor as part of another experiment, but it was non-significant in all analyses. We analyzed growth data using Analysis of Covariance (ANCOVA), with site and tidal height as fixed factors. All assumptions of ANCOVA were met for both analyses. Growth data in 2008 were analyzed using ANCOVA with density only as a covariate, since initial size of oysters was not a significant covariate. As with recruitment data, we also analyzed intertidal growth data alone to encompass a broader estuarine gradient. However, for the 2009 growth data, we used both density and initial size as covariates. To analyze 2008 mortality data, we used Wilcoxon and Kruskal Wallis tests. For 2009 mortality data, we used ANOVA.

Tukey-Kramer post hoc tests were used for multiple comparisons following ANOVA and ANCOVA. Following Kruskal Wallis tests, Dunn's post hoc test was used for multiple comparisons. All data were analyzed using SAS ver. 9.2, SAS Institute, Cary, N.C.

Results

Recruitment

Intertidal oyster recruitment increased with distance from the mouth of the bay in both years of monitoring, though differences between sites were only significant during 2008, when recruitment was higher (2008 ANOVA: $F_{3,79} = 148.61$, $P < 0.0001$; 2009 ANOVA: $F_{3,39} = 2.46$, $P = 0.0786$) (all Tukey-Kramer $P < 0.05$ for 2008) (Figure 1.2). Although the pattern as not as clear, subtidal recruitment followed the same pattern with distance from the mouth, both in 2008 (Kruskal Wallis, $H = 37.8464$, $df = 2$, $P < 0.0001$)

and 2009 ($P = 0.0334$) (Table 1.1) (Figure 1.3). Recruitment was highly correlated with typical residence time at each site (Largier et al. 1997) in both years and at both tidal heights (Linear Regression: Intertidal 2008 $R^2 = 0.8833$, Intertidal 2009 $R^2 = 0.9623$, Subtidal 2008 $R^2 = 0.8160$, Subtidal 2009 $R^2 = 0.9272$) (Figure 1.4). Subtidal recruitment did not differ significantly from intertidal recruitment in either year (2008 Wilcoxon: $Z = -1.1714$, $P = 0.2414$; 2009: $P = 0.8310$, Table 1.1).

In 2008, monthly intertidal recruitment peaked in September ($F_{3,319} = 15.19$, $P < 0.0001$) (Figure 1.5). In 2009, intertidal recruitment was very low, but peaked in August (Kruskal Wallis: $H = 14.1772$, $df = 7$, $P = 0.0481$). Recruitment in 2008 was approximately 60 times greater than in 2009 when comparing the sum of monthly recruitment at the intertidal 16 km site (Wilcoxon: $Z = -4.4209$, $P < 0.0001$).

Growth and Mortality

The 2008 data revealed interesting patterns in growth rate along the longitudinal estuarine gradient that differed between intertidal and subtidal elevations. At the intertidal elevation, site was the primary factor affecting growth rate ($P < 0.0001$) (Table 1.2), with a significant mid-bay peak in growth rate at the 12 km site, and a decrease toward the mouth (8 km, 6 km sites) and the head (16 km site) (all Tukey-Kramer $P < 0.05$) (Figure 1.6).

Overall, growth rate was higher at the subtidal elevation than at the intertidal elevation ($P = 0.0004$) (Table 1.2), but there was also a significant interaction between site and tidal elevation ($P = 0.0057$) (Table 1.2) (Figure 1.6). Unlike the clear mid-bay peak in intertidal growth, growth rate did not vary significantly among subtidal sites (6

km = 0.142 mm/day, 12 km = 0.155 mm/day, 16 km = 0.142 mm/day). While there was no increase in growth rate at the subtidal elevation at the 12 km site from the intertidal (0.155 mm/day) to the subtidal elevation, growth rates at the 6 km site were 35% greater at the subtidal than intertidal elevation (0.105 mm/day), though this comparison was not significant. At the 16 km site, subtidal growth rates were 65% higher than intertidal growth rates (0.086 mm/day) (Tukey-Kramer $P < 0.05$).

Similar patterns in growth were observed in 2009 such that the intertidal growth rate was greater at the 12 km site than at the 8 km site, and subtidal growth rates were similar between sites. Subtidal growth rate at the 8 km site was 81% higher than intertidal (0.076 mm/day vs. 0.042 mm/day). Growth rates at the 12 km site were relatively similar between tidal elevations (0.080 mm/day vs. 0.074 mm/day). However, in 2009, site and tidal elevation differences were not significant (Table 1.2).

In 2008, there were no differences in mortality rate of outplanted oysters, either by site (Kruskal Wallis: $H = 0.8109$, $df = 2$, $P = 0.6667$) or by tidal elevation (Wilcoxon: $Z = -0.5752$, $P = 0.5651$). However, there was a significant effect of site in 2009 ($P = 0.0019$) (Table 1.3), with greater overall mortality at the 8 km site (62.7%) than at the 12 km site (33.8%).

Discussion

Overall, we found that the extent of influx of nearshore waters into Tomales Bay influences oyster demographic factors along the resulting longitudinal estuarine gradients and some of these patterns vary with tidal elevation. We found that recruitment increased toward the back of the bay, as has been previously observed (Kimbrow 2008). Specifically,

we found that recruitment was strongly correlated with increasing water residence time toward the head of the estuary as mixing declines. Residence time is known to contribute to larval retention, especially when it exceeds pelagic larval duration (Sponaugle et al. 2002). In Tomales Bay, tidal mixing is strong at the mouth of the estuary and weak at the head (Largier et al. 1997, Kimbro et al. 2009a). Accurate estimates of residence time at different points along the main axis of Tomales Bay were developed by Largier et al. (1997) and suggest that residence time is approximately 80 days where our 16 km site is located (Largier et al. 1997) and where recruitment is greatest. Conversely, residence time is only approximately 15 days where we see very little recruitment at our 6 km site (Largier et al. 1997). Olympia oyster larvae may spend from one to six weeks in the water column before they are competent to settle (Baker 1995, Carson 2010). Water residence time far exceeds pelagic larval duration where we see highest recruitment. Thus, our data are consistent with larvae remaining in the water mass in the back of the estuary until they are ready to settle. We infer that larvae released close to the mouth of the estuary are more likely to be advected out of the estuary. The size structure of the oyster population is consistent with this, with an increasing percentage of larger (older) oysters toward the mouth of the bay (Kimbro et al. 2009a).

This study is among the first to show a strong, positive correlation between calculated residence time and recruitment within an estuary (Gaines and Bertness 1992). Ruesink et al. (2003) and Banas et al. (2007) both make reference to higher back bay recruitment in Willapa Bay in the Pacific Northwest and, although specific estimates of residence time are not available, it suggests that this pattern may be found in other estuaries.

Post settlement factors such as predation or competition may also influence recruitment patterns; however, these likely do not drive recruitment patterns in Tomales Bay. Predation by an invasive whelk (*Urosalpinx cinerea*) is actually highest in the back of the estuary (Kimbrot et al. 2009b) where recruitment peaks, and so the highest levels of predation are mismatched from the recruitment pattern shown here. Competition for space or food also likely does not drive this pattern, as presence of other sessile species does not reduce the number of recruits to substrate in Tomales Bay (see Ch. 2).

In addition to high spatial variability, we also found oyster recruitment to be variable both within and between years. Oyster recruitment peaked in September in 2008 and in August in 2009, so there is small variation in when recruitment peaks. Recruitment data from this study as well as from previous years (see Kimbro 2008) indicate that interannual recruitment may be more episodic than even simply variable, with strong recruitment observed every several years. However, the spatial pattern (rank ordering of sites) remained constant between years, despite different levels of recruitment. This pattern was amplified when overall recruitment was higher and when recruitment was measured on a shorter time scale. The shorter time scale likely captured more recruitment than the longer time scale as there was less time for post recruitment processes to come into play to reduce recruit survival. For example, over the six month sampling period in 2009, there was greater opportunity for whelk predation than with the bimonthly sampling periods in 2008. At the 16 km site, predation is especially intense and whelks preferentially prey on small oysters (Kimbrot et al. 2009b), potentially contributing to the greater magnitude of reduction in recruitment at this site than other sites between sampling methods.

We found that the extent of tidal influx of coastal waters also significantly influenced patterns of growth among intertidal oysters along the estuarine gradient. This is due to a persistent peak in phytoplankton biomass occurring 10 - 12 km into the bay, whose underlying mechanisms have been previously documented (Hearn and Largier 1997). Although there are additional mechanisms, the primary forces are a balance between residence time, which increases with distance from the mouth of the bay, and nutrient supply, which decreases along the same axis. Intertidal oyster growth tracked this gradient in phytoplankton biomass, peaking in the middle of the bay, which was in agreement with earlier studies (Kimbrow et al. 2009a). Thus, along an intertidal estuarine gradient, there is clear coupling between benthic and pelagic processes.

In contrast, we found benthic and pelagic processes were decoupled in the subtidal zone; oyster growth did not show significant variation along a subtidal estuarine gradient. Subtidal oyster growth was consistently high along the estuary. This indicates that intertidal oysters toward the mouth and the head of the estuary are likely limited by a combination of feeding time and food concentration relative to their subtidal counterparts. Longer feeding time at lower tidal elevations has been shown to result in greater growth rates in filter feeding animals in intertidal systems (Barnes and Powell 1953, Suchanek 1978, Peterson and Black 1987, Ruesink et al. 2003). Where food concentration is high in the mid bay, oysters do not benefit from having longer subtidal feeding time, such that the concentration observed at this site is potentially saturating for oysters.

In general, we did not find any consistent patterns in mortality along the estuary at any tidal height or between years. In 2009, we did find greater mortality at the 8 km site

than at the 12 km site which may be due to a combination of predation and competition. Kimbro et al. (2009a) suggests that there is greater predation risk at the 8 km site. Other experiments measuring competition have shown that this plays only a minor role in enhancing site differences and does not drive mortality patterns (see Ch. 2). Because there is great physical and biological variation among sites in Tomales Bay, it is likely that different factors contribute to mortality in different parts of the bay.

This study expands our understanding of the importance of connections between the nearshore zone and estuaries for benthic species within estuaries. We found that the advection of nearshore waters and the influence this has on the estuarine gradient significantly influenced the population dynamics of Olympia oysters. However we found that the influence of nearshore waters varied with position along the estuarine gradient as well as the vertical position along the shoreline. In general we found that benthic-pelagic coupling was stronger for the intertidal portion of the population and less so for the subtidal portion. We suggest that this may be a general result for other species that are widely distributed across estuarine gradients.

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Tables

Table 1.1: Analysis of variance of 2009 recruitment. Site and tidal elevation were considered as fixed factors. Bold type indicates results significant at $P < 0.05$.

	2009 Intertidal and Subtidal Recruitment		
Factor	df	F value	P value
Site (S)	2	3.65	0.0330
Tidal elevation (E)	1	0.05	0.8310
S*E	2	3.63	0.0334

*2009 Intertidal and Subtidal Recruitment total df = 56

Table 1.2: Analysis of covariance of growth rate data from 2008 and 2009. Site and tidal elevation were considered as fixed factors. Competition treatment was a fixed factor included as part of separate studies but was not significant. A subtidal site was lost in 2008, so intertidal growth rate was analyzed separately along the broader four-site gradient, then intertidal and subtidal growth rate were analyzed together along a three-site gradient without the intertidal site corresponding to the lost subtidal site. Density was a significant covariate in both years, but initial size was only a significant covariate in 2009. Bold type indicates results significant at $P < 0.05$.

Factor	2008 Intertidal Growth Rate			2008 Intertidal and Subtidal Growth Rate			2009 Intertidal and Subtidal Growth Rate		
	df	F value	P value	df	F value	P value	df	F value	P value
Density	1	5.19	0.0315	1	16.17	0.0002	1	39.79	<0.0001
Initial size	-	-	-	-	-	-	1	54.64	<0.0001
Site (S)	3	13.33	<0.0001	2	12.55	<0.0001	1	2.06	0.1594
Tidal elevation (E)	-	-	-	1	14.54	0.0004	1	2.71	0.1078
Competition (C)	1	2.04	0.1659	1	1.63	0.2065	1	3.38	0.0735
S*E	-	-	-	2	5.70	0.0057	1	1.34	0.2537
S*C	3	2.23	0.1099	2	0.17	0.8406	1	1.85	0.1821
E*C	-	-	-	1	2.14	0.1497	1	0.36	0.5539

*2008 Intertidal Growth Rate total df = 33; 2008 Intertidal and Subtidal Growth Rate

total df = 64; 2009 Intertidal and Subtidal Growth Rate total df = 47

Table 1.3: Analysis of variance of oyster mortality data from 2009. Site and tidal elevation were considered as fixed factors. Competition treatment was a fixed factor included as part of separate studies but was not significant. Bold type indicates results significant at $P < 0.05$.

Factor	2009 Mortality		
	df	F value	P value
Site (S)	1	10.95	0.0019
Tidal elevation (E)	1	2.10	0.1548
Competition (C)	1	0.18	0.6778
S*E	1	0.01	0.9252
S*C	1	3.91	0.0545
E*C	1	0.21	0.6457

* 2009 Mortality total df = 48

Figure Legends

Figure 1.1: Map of sites in Tomales Bay. Sites were located along the west side of the estuary at 6 km, 8 km, 12 km, and 16 km from the mouth. Inset shows location of Tomales Bay along the central California coast north of San Francisco Bay.

Figure 1.2: Intertidal oyster recruitment (mean \pm SE) in 2008 (A) and 2009 (B). Bars with different letters indicate means that are significantly different at $P < 0.05$ in 2008, using Tukey-Kramer post-hoc tests. In 2009, recruitment did not differ significantly between sites ($P = 0.0786$), though there is a strong trend toward the same pattern.

Figure 1.3: Subtidal oyster recruitment (mean \pm SE) in 2008 (A) and 2009 (B). Subtidal recruitment tiles were lost at the 8 km site in 2008 and the 6 km site in 2009. Bars with different letters indicate means that are significantly different at $P < 0.05$ in 2008, using Tukey-Kramer post-hoc tests. In 2009, recruitment did not differ significantly between sites, though a similar pattern persists.

Figure 1.4: Linear regressions between water residence time and mean oyster recruitment. Water residence times for sites 6 km, 8 km, 12 km, and 16 km are from Largier et al. 1997. Recruitment was regressed against water residence time for the intertidal elevation in 2008 (purple diamonds), intertidal elevation in 2009 (blue squares), subtidal elevation in 2008 (red triangles), and subtidal elevation in 2009 (green circles), with trendlines in corresponding colors. Sites are noted in black with arrows along x-axis.

Figure 1.5: Monthly intertidal oyster recruitment at the 16 km site (mean \pm SE) in 2008. Bars with different letters indicate means that are significantly different $P < 0.05$ using Tukey-Kramer post-hoc tests.

Figure 1.6: Oyster growth rate (mean \pm SE) from August through November 2008 in (A) the intertidal zone and (B) the subtidal zone. In each graph, bars with different letters within tidal elevation indicate means that are significantly different at $P < 0.05$ using Tukey-Kramer post-hoc tests.

Figures

Figure 1.1:



Figure 1.2:

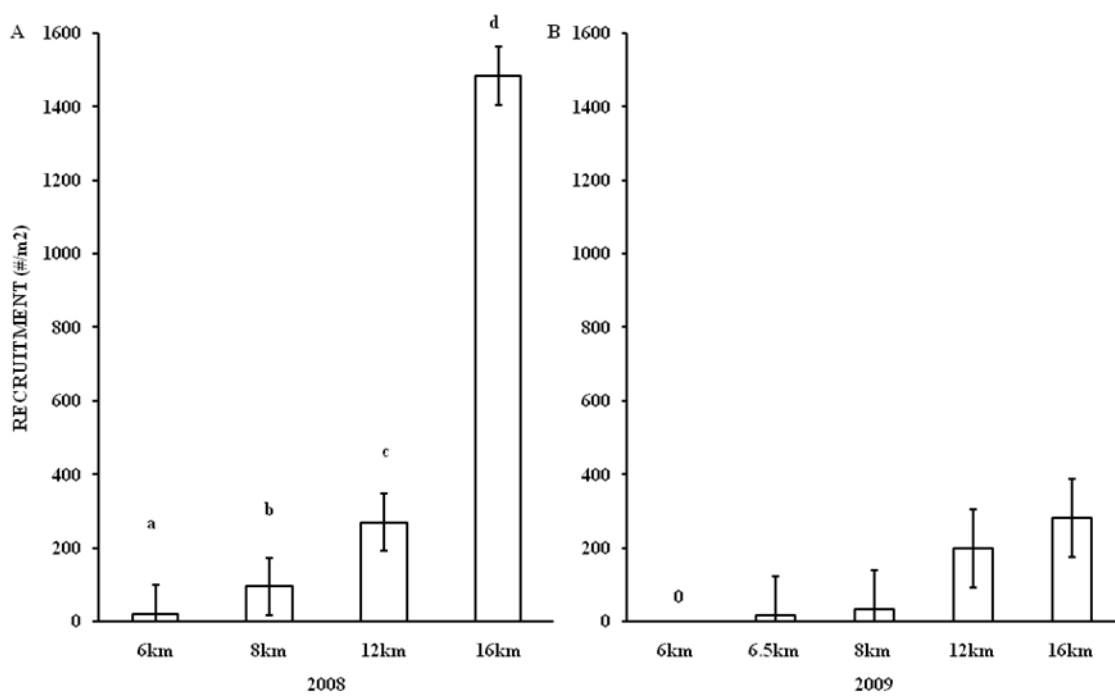


Figure 1.3:

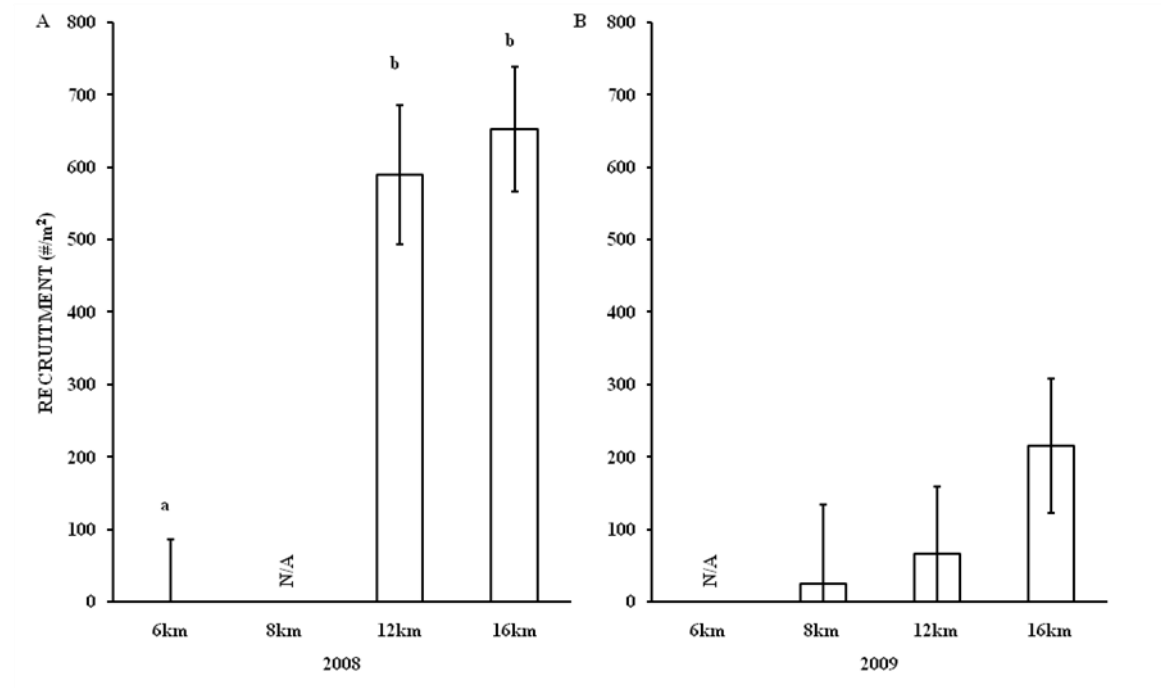


Figure 1.4:

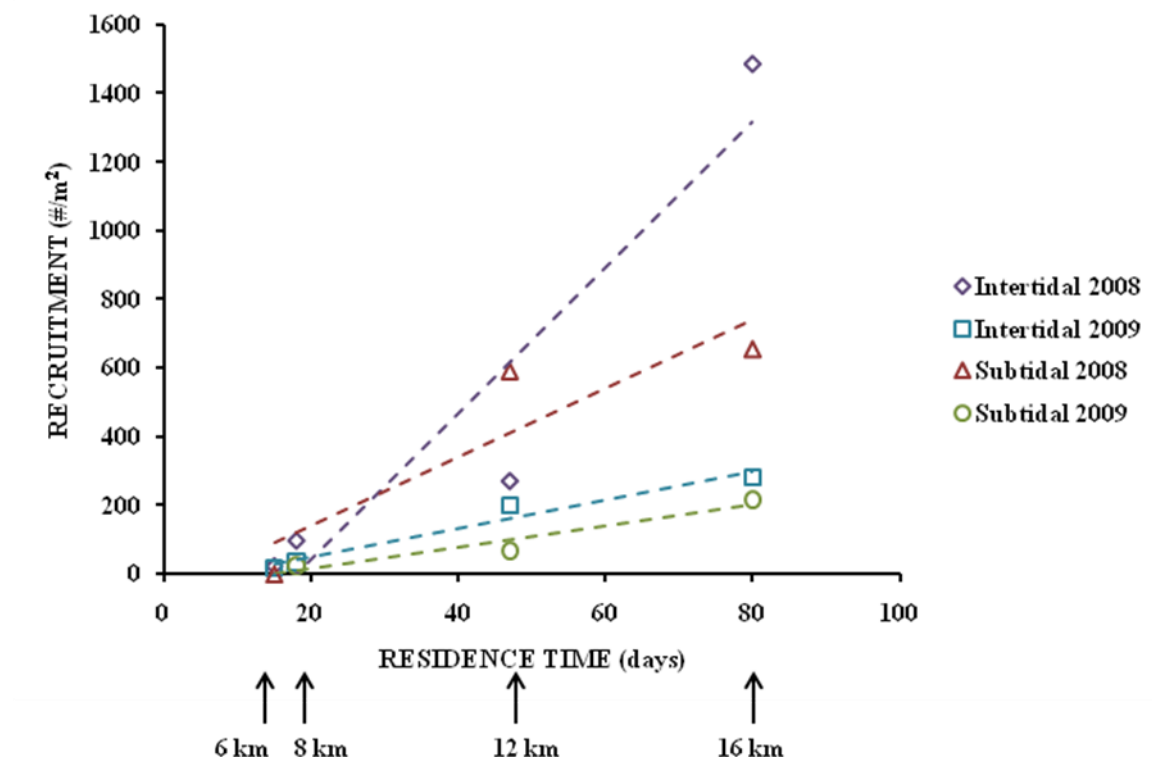


Figure 1.5:

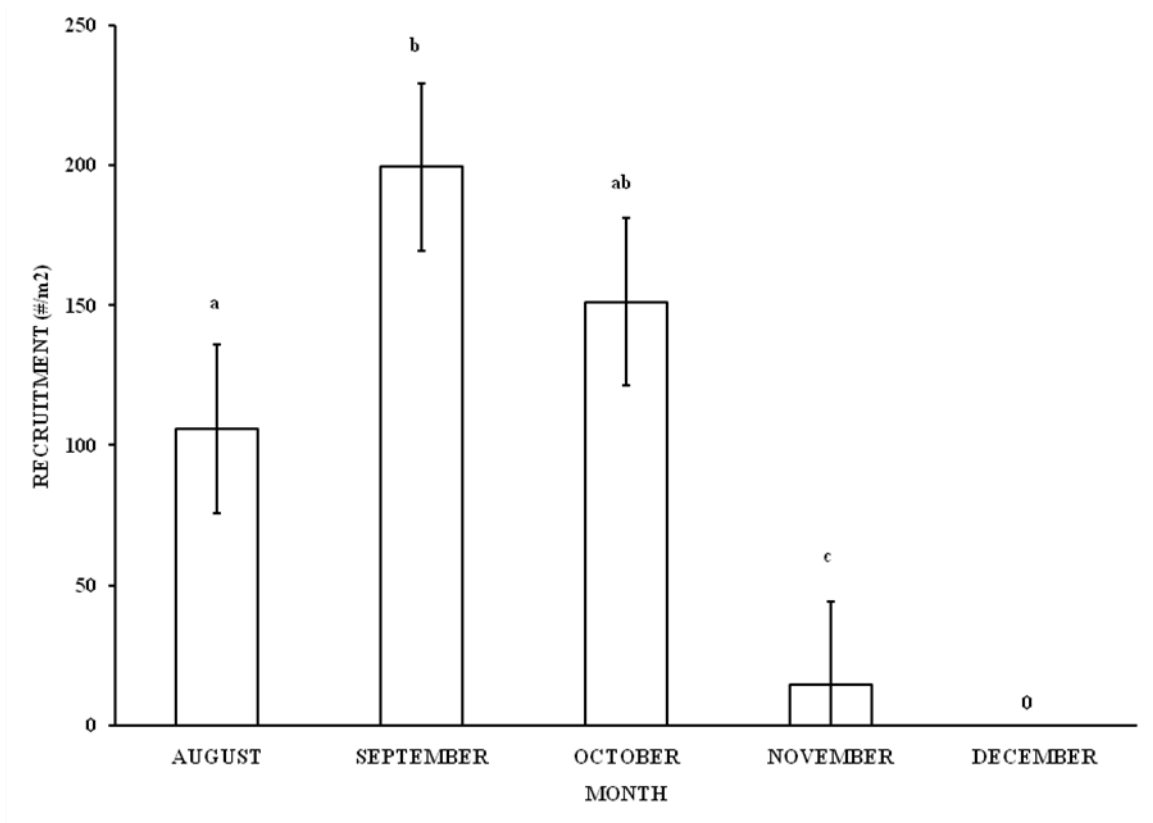
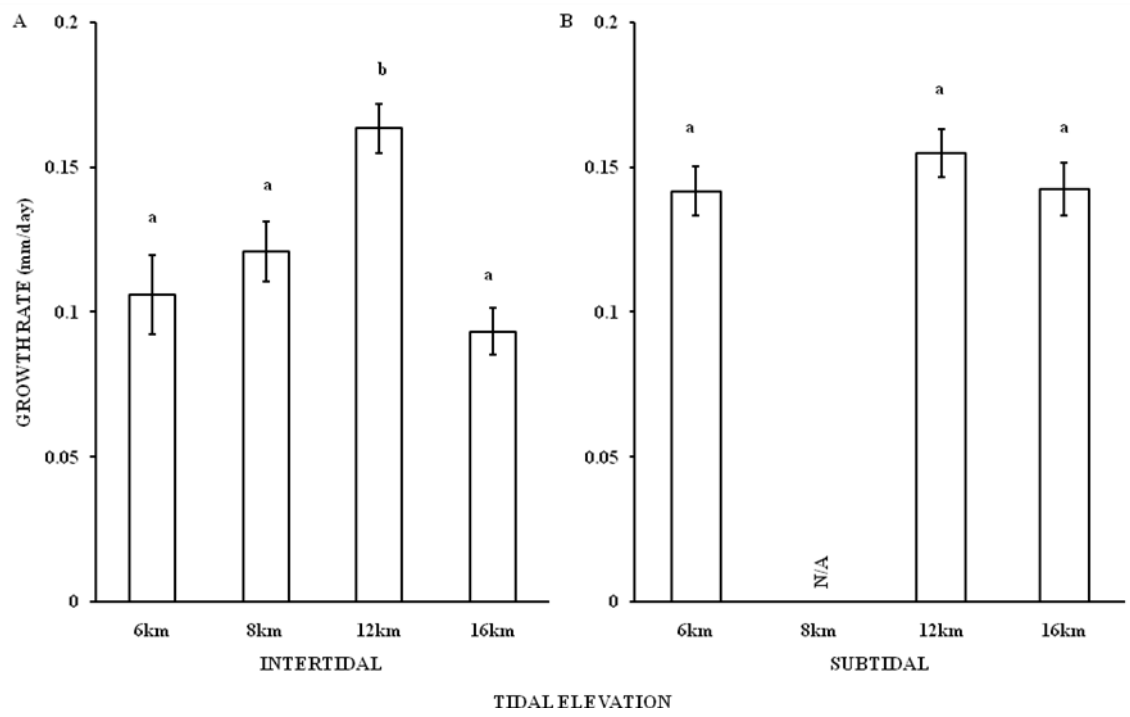


Figure 1.6:



Chapter 2: Competition interacts with life history to variably influence oyster demography along environmental gradients

Abstract

Competitive interactions are widely studied in ecological communities, and their importance may vary along stress gradients as well as with life history stage. In this study, we investigated competitive effects of the sessile community on the native Olympia oyster, *Ostrea lurida*, in two central California estuaries. We explored the cumulative effects of presence of potential competitors on multiple stages of oyster life history: total recruitment, post-recruitment growth, and juvenile and adult growth and mortality. We investigated these demographic variables, as well as the makeup of the sessile community, along estuarine and tidal elevation gradients where both physical and biological factors vary. Despite finding variation in oyster demography and the sessile community along these gradients, there were no effects of competition on juvenile and adult growth and mortality. However, presence of competitors did significantly affect total recruitment in San Francisco Bay and post-recruitment growth of oysters in Tomales Bay. Competitive effects in San Francisco Bay varied along the estuarine gradient, and effects in Tomales Bay varied along the tidal elevation gradient. Although the recruit stage was affected in both bays, results indicate that competitive effects are greater in Tomales Bay. These results better shape our understanding of how variation in habitat characteristics may influence competitive effects on a target species throughout its life history. As the Olympia oyster is currently a species of interest for estuarine restoration, these results may aid restoration practitioners in planning and designing future projects.

Introduction

Interspecific competition has long been considered an important factor structuring ecological communities (Connell 1961), though its relative importance has been debated for decades (Cody and Diamond 1975, Connell 1983, Schoener 1983, Strong et al. 1984, Diamond and Case 1986, Goldberg and Barton 1992, Guerevitch et al. 1992, Gaucherand et al. 2006). In sessile communities, species may compete for resources such as space, nutrients, light, or water (Harper 1977, Buss and Jackson 1979, Buss and Jackson 1981, Sebens 1982, Branch 1984). Theory suggests that competitive interactions become more important along a gradient moving toward less stressful abiotic conditions (Menge and Sutherland 1976, 1987, Bertness and Callaway 1994, Callaway 1998). Competitive interactions may vary along spatial gradients created by changing habitat characteristics or community members, or they may vary along temporal gradients through seasons or different life stages of a target species (Underwood 1984, Etter 1989, Callaway and Walker 1997, Maughan and Barnes 2002). Physical factors in estuaries often exhibit predictable spatial and temporal variation, providing an excellent system to investigate how competitive interactions change along gradients.

In estuaries, the intensity of competition may vary with salinity, temperature, nutrients, or changes in tidal elevation in the habitat. The importance and outcome of competitive interactions have been shown to change along salinity-stress gradients (La Peyre et al. 2001, Crain et al. 2004, Engels and Jensen 2010) and at different nutrient levels (Forqurean et al. 1995, Fong et al. 1996, Pedersen and Borum 1996). Empirical work in intertidal habitats shows increasing importance of competition as tidal elevation

decreases (Connell 1972, Menge and Sutherland 1987), also resulting in greater feeding time, higher growth rates, lower wave intensity, and less desiccation risk (Barnes and Powell 1953, Suchanek 1978, Peterson and Black 1987).

Along these different physical gradients, the suite of dominant species in a community may also shift (Thomsen et al. 2007), leading to variation in competitive interactions with a target species. The composition of these species may vary spatially by tidal elevation and position along an estuary as well as temporally. Further, species identity and abundance may shift seasonally or annually (Mazouni et al. 2001). For instance, shelled species such as mussels and oysters tend to experience greater fouling at lower tidal elevation where there is less physical stress (Jackson 1977). Many soft bodied fouling species such as ascidians, which are often less tolerant of desiccation, tend to increase in abundance at lower tidal elevations, whereas hard bodied organisms such as barnacles or mussels tend to be more prevalent higher in the intertidal zone (Branch 1984). Ascidians and bryozoans have been cited as being better competitors than groups such as algae or barnacles in studies comparing multiple groups (Russ 1982, Nandakumar et al. 1993). Thus, the particular suite of species present may alter how competition affects a target species if these competitors vary in their competitive abilities (Osman and Whitlatch 1995).

The life history stage of the species in question may lead to different outcomes of competitive interactions as the mode of competition may vary. Competition for open space may limit larval recruitment to substrate (Roughgarden et al. 1988, Dalby and Young 1993, Osman and Whitlatch 1995a, Osman and Whitlatch 1995b, Pineda and Caswell 1997), and can prompt larvae to settle elsewhere to avoid certain species

(Grosberg 1981, Young and Chia 1981). Competition for food with or alteration of water flow by other filter feeders may reduce growth rate (Buss 1980, Buss and Jackson 1981, Peterson and Black 1987, Ropert and Gouilletquer 2000) if filter feeders do not differentiate in size or source of food (Dubois et al. 2007, Lefebvre et al. 2009). Overgrowth of a target species may lead to smothering and greater mortality (Connell 1961, Buss and Jackson 1979, Zajac et al. 1989, Hunt and Scheibling 1997), though survival is not always negatively affected by overgrowth (Todd and Turner 1988, Dalby and Young 1993).

To date, few studies have compared competitive effects across multiple stages of life history in sessile species (Callaway and Walker 1997, Schiffers and Tielborger 2006). In terrestrial systems, there are conflicting results in regarding which life stages are most influenced by competition. Some studies report greater effects on earlier life stages, citing the greater vulnerability of small size to stressors (Howard and Goldberg 2001, Horvitz and Schemske 2002). However, other studies have found competitive effects to increase with life stage. These studies suggest that while competitive effects may be present, facilitation is especially important at early stages, resulting in overall neutral to positive neighbor effects at early stages and negative to neutral effects at later stages (Miriti 2006, Schiffers and Tielborger 2006). Results from these studies are mixed as to whether survival or growth is more affected by competition. Asymmetric competition studies have found large plants to disproportionately affect small plants (Weiner and Thomas 1986, Pacala and Weiner 1991). Different species have greatest competitive ability at different life stages (Lamb and Cahill 2006), which may partially explain conflicting results.

Comparative competition studies across life stages are even less common in sessile marine communities, though negative impacts of competition have been shown at most all life stages of sessile marine species. Competition studies tend to focus on either early or late stage aspects of life history rather than looking comparatively across life history of sessile species. For example, Vermeij (2006) focused on competition at earlier life stages of corals, but investigated several potential effects. Competitors affected recruitment through space preemption and overgrowth, but did not affect growth rate, growth strategy, or survival of juveniles. Dalby and Young (1993) investigated how different life stages of ascidians and oysters interact to affect oyster growth and survival in one of the few studies to include multiple stages. Simultaneous recruitment of ascidians and oysters reduced oyster recruitment but not size. When ascidians recruits competed with adult oysters, they decreased oyster survival, but interactions between adult oysters and ascidians resulted in an increase in oyster survival. Overall, ascidians increased adult oyster size. Thus, as in terrestrial plant communities, there seems to be no consensus on when competition has the greatest impact in sessile communities.

To better our understanding of how competitive effects vary with both life history stage and environmental gradients, we examine interspecific interactions between native Olympia oyster populations and the sessile community in central California estuaries. Oysters act as an important model species to investigate competitive effects as they are important both ecologically and commercially. Oysters offer a variety of ecosystem functions; for example, their shell provides habitat that has been shown to increase community richness (Gutierrez et al. 2003, Kimbro and Grosholz 2006, Coen et al. 2007). Competition for space and food with other sessile filter feeders has been of interest both

to ecologists as a factor in decline and recovery of oyster species and to commercial growers as a factor limiting production. To date, only one study has experimentally investigated competitive effects on post-recruitment Olympia oysters, finding decreased juvenile size and survival in a Pacific Northwest estuary (Trimble et al. 2009). One other study investigated competition non-experimentally, concluding little likely impact of competitors on juvenile size and survival (Wasson 2010). These studies find contradictory results for competitive effects on juvenile oysters, and do not investigate multiple phases of life history.

In this study, we investigate the effect of competitors on multiple phases of oyster life history in two central California estuaries. We investigate the cumulative effects of presence of competitors on total recruitment and post-recruitment growth and mortality in San Francisco Bay and Tomales Bay, California, as well as juvenile and adult growth and mortality in Tomales Bay. We explore these demographic variables along both estuarine and tidal elevation gradients where both physical and biological factors, and therefore competitive interactions, may vary.

Methods

Study Species and Sites

Ostrea lurida is the native oyster species on the west coast of North America, and was historically abundant in eastern Pacific estuaries from Alaska to Baja California Sur, Mexico (Baker 1995, Polson et al. 2009). Population levels declined from the mid 1800s through the early 1900s following overharvesting. Other associated factors such as land use change leading to sedimentation and habitat loss as well as the introduction of

nonnative species through oyster transport also contributed to the decline (Kirby 2004, Brumbaugh and Coen 2009, Beck et al. 2009). They can grow up to 7 cm on hard substrate, creating beds approximately 0.10 m high in the intertidal and shallow subtidal zones of estuaries. These oysters act as foundation species as their beds have been shown to increase benthic diversity (Kimbrow and Grosholz 2006). *Ostrea lurida* is a protandrous hermaphrodite that can become sexually mature within a year. Females brood embryos for 10-14 days before releasing larvae to the water column. Planktotrophic larvae then develop for one to six weeks before settling on hard substrate in summer and fall (Baker 1995, Carson 2010).

We studied oyster populations in Tomales Bay, CA (38.20° N, 122.90° W) and San Francisco Bay, CA (37.50° N, 122.25° W) (Figure 2.1). Although Olympia oysters can exist in subtidal areas in many estuaries (Baker 1995), they occur largely within a narrow zone on rocks and cobbles from +0.5 to -1.0 m MLLW in Tomales Bay and San Francisco Bay, though deeper populations may exist.

Tomales Bay is formed by a long, narrow, submerged river valley along the San Andreas Fault, about 20 km long and 1-2 km wide. Located in an area with a Mediterranean climate, Tomales Bay is considered a low inflow estuary (Largier et al. 1997). During the dry season, strong nearshore upwelling occurs and riverine inputs are negligible relative to oceanic inputs. This results in fairly linear gradients along the main axis of the estuary that includes an increase in residence time and salinity and a decrease in nutrient levels toward the back of the bay (Hearn and Largier 1997, Largier et al. 1997). As a result of contrasting gradients in residence time and ocean-derived nutrient inputs, a phytoplankton maximum regularly persists in the middle of the bay during dry

season periods (Hearn and Largier 1997, Kimbro et al. 2009a). Benthic oyster growth in the intertidal tracks this phytoplankton gradient with greater growth associated with the phytoplankton maximum, resulting in coupling between benthic and pelagic processes (Kimbro et al. 2009a). In this study, we used sites located along the west side of the bay at 6, 8, 12, and 16 km from the mouth (Figure 2.1a) based on previous work (Kimbro et al. 2009a) that encompassed the entire range of the oyster population along the estuarine gradient.

San Francisco Bay is a highly urbanized estuary and the largest on the west coast of the United States (Conomos et al. 1985). Due to its Mediterranean climate, San Francisco Bay also has distinct differences between wet and dry parts of the year. The bay has been divided into separate north, central, and south basins, and hydrographic dynamics vary between these sections (Conomos et al. 1985). Approximately 90% of freshwater comes into the North Bay, whereas the South Bay can reach hypersaline levels during dry season extending from late spring to early fall. The Central Bay is most heavily influenced by oceanic inputs relative to the North and South Bays (Smith and Hollibaugh 2006). We chose four sites in San Francisco Bay based on previous research (Grosholz et al. 2008, Zabin et al. 2009) and their location relative to these three regions of the bay. Two sites in San Rafael, CA (SQ and LL) were located close to the physically variable North Bay along the path of major freshwater flow toward the Golden Gate. The other two sites were located in Richmond, CA (FP) in the Central Bay and South San Francisco, CA (OP) in the northwestern South Bay and so were more dominated by oceanic inputs (Figure 2.1b).

Total Recruitment and Recruit Size

In summer and fall of 2009, we investigated the effects of sessile competitors on oyster recruitment in Tomales and San Francisco Bays.

Tomales Bay

In Tomales Bay, we monitored mid intertidal (0 m MLLW) and subtidal (-1.0 m MLLW) recruitment with and without sessile species at three sites along the estuarine gradient: 8 km, 12 km, and 16 km (denotes distance from mouth of bay). In addition, we measured low intertidal (-0.5 m MLLW) oyster recruitment with and without sessile species at the 12 km and 16 km sites to expand the tidal gradient. We monitored oyster recruitment using PVC tiles (10 cm x 10 cm) covered with a cement layer (0.5 cm thick) to add rugosity and mimic natural substrate. At the mid and low intertidal elevations, we attached tiles vertically to PVC crossbar frames at 5 m intervals parallel to the water line at the appropriate tidal elevation. At the subtidal location, we attached tiles vertically to PVC frames that were suspended from moorings at approximately -1 m depth and within 10 m offshore of intertidal tiles. Twenty tiles were placed at each tidal elevation. As sessile species naturally colonized these tiles, tiles were subjected to either a 'removal' treatment where all sessile species (non-oyster) were removed with a toothbrush and forceps or a 'control' treatment with no removals. Every two weeks throughout summer and fall in Tomales Bay, we maintained the removal treatments. At the end of the recruitment season in early December, recruits were counted and measured.

San Francisco Bay

In San Francisco Bay, we measured mid intertidal (0 m MLLW) and low intertidal (-0.5 m MLLW) oyster recruitment with and without other sessile species at the

four sites discussed previously. Small cement bricks (13.5 cm x 13.5 cm) were used as recruitment collectors, and were secured to rebar with cable ties. Our previous work comparing different substrate showed that oyster recruitment did not differ significantly among bricks, shell, and cement. We placed sixteen bricks at 5 m intervals along a transect parallel to shore at each tidal elevation. Sessile species colonized bricks resulting in ambient levels of competition. For eight of the sixteen bricks, we used the same removal treatment described for Tomales Bay where all sessile species (non-oyster) were removed every two weeks in summer using toothbrushes and forceps. The other eight were treated as controls as above. The front of the brick was the experimental surface. Due to reduced recruitment of sessile species during fall, we maintained these treatments monthly. At the end of the recruitment season in early December, recruits were counted and measured.

Juvenile and Adult Growth and Mortality

Tomales Bay

In order to investigate how the presence of other sessile species affected juvenile and adult oyster growth and survival in Tomales Bay, we outplanted 10 x 10 cm PVC tiles lab-reared oysters. These were obtained by spawning adult oysters from Tomales Bay in the lab, allowing larvae to settle onto PVC tiles before being transplanted to the field (see Kimbro et al. 2009a for methods). Tiles were held in large outdoor flow through tanks at ambient food and temperature for several months until deployment in summer. Tile deployment methods followed recruitment collector deployment methods above.

In August of 2008, we randomly assigned tiles with juvenile oysters (mean size approx. 15 mm, mean density per tile approx. 20) to one of four sites along the bay at either mid intertidal or subtidal locations. At each of the eight site and tidal elevation combinations, we outplanted twelve tiles. Sessile species were experimentally removed from six of the twelve tiles at each site and tidal elevation, while the other six tiles acted as controls. We maintained removals every two weeks during low tides using toothbrushes and forceps. Using photos to track individuals, we monitored oysters for growth and mortality from August through November 2008. Longest length of oysters was measured to the nearest millimeter using vernier calipers and total number of oysters per tile was counted in the field. All subtidal tiles located at 8km were lost part way through the experiment.

These oysters were held in the same large flow through tanks with ambient conditions until they were redeployed in June 2009 to measure adult growth and mortality. Tiles of adult oysters (mean size approx. 30 mm, mean density approx. 12) were first grouped by density and size and then randomly distributed amongst treatment groups. We outplanted adult oysters (mean size approx. 30 mm) at the two mid-point sites (8 km and 12 km) at both mid intertidal and subtidal locations. Eighteen tiles were outplanted at each site and tidal elevation combination; nine had natural levels of sessile competition and nine were experimentally maintained with no sessile species present. However, in December 2009, we cleaned the entire tile face of competitive cover so that all oysters could be measured and counted.

Cover of Sessile Competitors on Experimental Tiles

To quantify the relative levels of competition, we monitored the percent cover and composition of all sessile species using an overlay of 25 random points on each tile. In Tomales Bay experimental tiles were surveyed in December of 2008 and 2009. In San Francisco Bay, experimental surfaces were surveyed in December 2009.

Cover of Sessile Competitors on Natural Substrate

We also surveyed the percent cover and composition of sessile species on natural intertidal substrate. To assess cover and composition, we placed a 30 m transect at the same tidal elevation as the experimental tiles. The upper surfaces of ten randomly selected rocks were surveyed using an overlay of 25 random points within a 10 x 10 cm quadrat. In Tomales Bay, we surveyed mid intertidal natural substrate in November 2008, and mid and low intertidal natural substrate in October 2009. We surveyed natural substrate at both the mid and low intertidal elevation between November and December 2009 in San Francisco Bay.

Statistical Analysis

We analyzed the number of oyster recruits and oyster size using Analysis of Variance (ANOVA) with site, tidal elevation, and competition treatment as fixed factors. Cochran's C was used to confirm homoscedasticity and normal probability plots were used to graphically confirm normality (Underwood 1981). Because we did not have low intertidal recruitment collectors at the 8 km site, we analyzed the mid-intertidal and subtidal locations at the 8 km, 12 km, and 16 km sites as the estuarine gradient. We analyzed mid-intertidal, low-intertidal, and subtidal locations at the 12 km and 16 km as

the tidal gradient. We used log transformations for data on total recruitment and recruit size along the estuarine gradient in Tomales Bay and used square root transformations for recruit size in San Francisco Bay to meet parametric assumptions. If transformation did not adequately improve data sets, we used nonparametric Wilcoxon or Kruskal Wallis tests or ANOVAs on ranked data. We analyzed total recruitment and recruit size along the tidal gradient in Tomales Bay, as well as total recruitment in San Francisco Bay, using ANOVAs on ranked data. Percent mortality in Tomales Bay in 2008 was analyzed using Wilcoxon and Kruskal Wallis nonparametric test. We analyzed growth rate data using ANCOVA. In 2008, oyster density was used as a covariate. A regression with growth rate and initial size did not indicate a significant biological reason to include initial size in this data set. In 2009, oyster density and initial size were both used as covariates following significant overall regressions with growth rate.

We used nonparametric Wilcoxon or Kruskal Wallis tests to analyze percent cover of potential competitors on experimental surfaces and natural substrate. Mid intertidal and low intertidal data in Tomales Bay showed no significant differences between tidal elevations in percent cover and composition and this separation by tidal elevation did not aid in explaining oyster patterns, so these data were pooled to test differences among sites. Further, because we found no significant differences between outplanted growth tiles and recruitment tiles within a site in Tomales Bay, these data were pooled for analysis. We also analyzed data from tiles with competitors for community composition; sessile species were broken down into the following taxa: algae, tunicates, bryozoans, barnacles, and other. The 'other' category was generally dominated by sponge or hydroids. Because composition data were both nonparametric and

unbalanced, we used Wilcoxon and Kruskal Wallis tests to make direct comparisons by group rather than using multivariate methods. All data were analyzed using SAS ver. 9.2, SAS Institute, Cary, N.C.

Results

Total Recruitment and Recruit Size

Tomales Bay

In Tomales Bay, total recruitment did not vary with the presence of competitors (Table 2.1). Variation among sites along the estuarine gradient better explained differences seen in Tomales Bay total recruitment ($P = 0.0014$, Table 2.1), with recruitment increasing toward the back of the estuary and peaking at the 16 km site (all Tukey Kramer with 16 km: $P < 0.05$). Number of recruits doubled from the 8 km to 12 km site, and tripled from the 12 km to 16 km site. Overall, there was greater subtidal than intertidal recruitment ($P = 0.0447$, Table 2.1), though there was a significant interaction between tidal elevation and site ($P < 0.0001$, Table 2.1) (Figure 2.2). This revealed that there was equal recruitment across tidal elevation at 8 km and 12 km, and subtidal recruitment was only greater than intertidal recruitment at 16 km (Tukey Kramer $P < 0.05$). Along a broader tidal gradient (mid intertidal, low intertidal, and subtidal) at the 12 km and 16 km sites, site and tidal elevation drove total recruitment patterns ($P < 0.0001$, Table 2.1) more than competitor presence (Table 2.1). At the 12 km site, recruitment was higher at the low intertidal elevation than the mid intertidal and subtidal elevations, while at the 16 km site, recruitment was highest at the subtidal elevation than the mid or low intertidal elevation (all Tukey Kramer $P < 0.05$).

Site, tidal elevation, and competition treatment all contributed to patterns of average recruit size at the end of the recruitment season. The presence of competitors significantly reduced recruit size across the estuarine gradient, regardless of site ($P = 0.0026$, Table 2.2). By the end of the recruitment season, recruits where competitors were absent were almost twice the size of those where competitors were present.

In addition, we investigated recruit size along a tidal elevation gradient from mid intertidal to low intertidal to subtidal at both 12 km and 16 km for a more extensive tidal gradient. At 12 km, there was a significant main effect of competition ($P = 0.0178$, Table 2.2) such that recruits growing without competitors were 1.5 times larger than those growing with competitors. Although there was no significant effect of tidal elevation, there was a trend toward increasing recruit size from mid intertidal to lower intertidal to the subtidal elevation. At 16 km, average size depended on both tidal elevation and competition treatment ($P = 0.0066$, Table 2.2) (Figure 2.3). There was no difference in recruit size with and without competition at either the mid or lower intertidal elevation. At the subtidal elevation, recruits were significantly larger than those at both intertidal elevations ($P < 0.0001$, Table 2.2). Further, there was a significant effect of subtidal competition such that recruits without competitors were over twice as large as those with competitors (Tukey Kramer $P < 0.05$).

San Francisco Bay

In San Francisco Bay, we found significantly more recruits in treatments with competitors removed ($P = 0.0008$, Table 2.3); however, this varied by site ($P = 0.0043$, Table 2.3) (Figure 2.4). Although there was a trend toward greater recruitment without competitors at OP, LL, and SQ, this difference was only significant at SQ (Tukey Kramer

$P < 0.05$). Although there were overall differences in total recruitment at different sites and tidal elevations, the relationship between the two varied (Figure 2.5). Total recruitment varied by tidal elevation at each site ($P = 0.0427$, Table 2.3) such that there were more recruits lower in the intertidal only at LL and SQ (all Tukey Kramer $P < 0.05$). In general, the least recruits were found at FP and the most at LL and OP.

In San Francisco Bay, site was the most important factor determining recruit size ($P < 0.0001$, Table 2.3), and this varied with tidal elevation ($P < 0.0001$, Table 2.3) (Figure 2.6). There was no effect of competitor removals on size. At the mid intertidal elevation, recruits were significantly smaller at OP than at FP and LL (all Tukey Kramer $P < 0.05$). Oysters at OP in the mid intertidal were significantly larger than those at SQ (Tukey Kramer $P < 0.05$). In the lower intertidal, recruits were significantly larger at LL than at FP and SQ and at OP than FP and SQ (all Tukey Kramer $P < 0.05$). Oysters were larger at the lower intertidal elevation at LL, OP, and SQ, although this was only significant at OP (Tukey Kramer $P < 0.05$). At FP, oysters were significantly larger at the mid intertidal elevation (Tukey Kramer $P < 0.05$).

Juvenile and Adult Growth and Mortality

Tomales Bay

In both years, competition had no significant effect on adult growth rate (Table 2.4); however, there was a slight trend toward a higher growth rate in those adult oysters growing without competitors (rate of increased growth: 7.5% in 2008, 36% in 2009). In 2008, growth rate varied by site ($P < 0.0001$, Table 2.4) and by tidal elevation ($P = 0.0004$, Table 2.4), and there was a significant interaction between site and tidal elevation

($P = 0.0057$, Table 2.4) (Figure 2.7). At the intertidal elevation, there was significantly greater growth at 12km than at the 6km site or the 16km site (all Tukey Kramer $P < 0.05$). By contrast, at the subtidal depth, growth rate did not differ significantly by site. In 2009, average growth rates were approximately equal at the subtidal elevation and higher at the 12km site than the 8km site at the intertidal elevation, though this was not significantly different (Table 2.4). Density was a significant covariate for oyster growth both years, such that higher densities were correlated with lower growth (2008: $P = 0.0002$, 2009: $P < 0.0001$, Table 2.4).

In 2008, neither site (Kruskal Wallis: $H = 0.8109$, $df = 2$, $P = 0.6667$), tidal elevation (Wilcoxon: $Z = -0.5752$, $P = 0.5651$), nor competition (Wilcoxon: $Z = -0.5189$, $P = 0.6038$) affected mortality within the bay. However, in 2009, there was a significant effect of site ($P = 0.0019$, Table 2.5) with greater overall mortality at the 8km site than at the 12km site.

Cover of Sessile Competitors on Experimental Tiles

Tomales Bay

In Tomales Bay, percent cover and community composition of sessile competitors were assessed on all experimental tiles at the end of the experiment in December 2008 and at the same time point in December during the 2009 experiment (Figure 2.8). In December 2008, significantly more space was covered on control tiles than on those in the removal treatments (Wilcoxon: $Z = -4.8092$, $P < 0.0001$), with 31% of space occupied on tiles where competitors were not disturbed and only 5% of space occupied on tiles maintained to be free of competition. Total cover did not vary between the intertidal and

subtidal elevation (Wilcoxon: $Z = -0.3181$, $P = 0.7504$). Total percent cover of all species did not vary among sites (intertidal sites, Kruskal Wallis: $H = 1.5772$, $df = 3$, $P = 0.6646$; subtidal sites, Kruskal Wallis: $H = 2.4163$, $df = 2$, $P = 0.2987$). However, there were distinct differences between tidal elevations where bryozoans dominated intertidal tiles (Kruskal Wallis: $H = 33.0574$, $df = 4$, $P < 0.0001$) and tunicates dominated subtidal tiles across all sites (Kruskal Wallis: $H = 11.7188$, $df = 4$, $P = 0.0196$). Bryozoan cover did not differ among intertidal sites (Kruskal Wallis: $H = 2.8596$, $df = 3$, $P = 0.4138$); subtidal tunicate cover peaked at site 12 km (Kruskal Wallis: $H = 7.4629$, $df = 2$, $P = 0.0240$).

In December 2009, control tiles where competitors were not removed had significantly greater cover than at the same time point in 2008 (Wilcoxon: $Z = -6.0708$, $P < 0.0001$), with a mean cover of sessile species of 69% and a maximum of 100% on some tiles. In comparison, tiles in the removal treatment had 14% cover. Control tiles with competitors had significantly greater coverage than those maintained to be free of competitors (Wilcoxon: $Z = 9.8786$, $P < 0.0001$). On control tiles with all competitors present, there were no overall differences among sites in total cover (Kruskal Wallis: $H = 5.6178$, $df = 2$, $P = 0.0603$). However, there was greater coverage on subtidal than intertidal tiles (Wilcoxon: $Z = 2.5161$, $P = 0.0119$). In intertidal locations, the 16 km site had significantly less coverage than other sites (Kruskal Wallis: $H = 35.6164$, $df = 2$, $P < 0.0001$), whereas at the subtidal elevation it had significantly greater coverage than the other sites (Kruskal Wallis: $H = 11.8236$, $df = 2$, $P = 0.0027$). As in 2008, bryozoans dominated intertidal tiles (Kruskal Wallis: $H = 229.0287$, $df = 4$, $P < 0.0001$) and tunicates dominated subtidal tiles bay wide (Kruskal Wallis: $H = 91.5664$, $df = 4$, $P < 0.0001$) (Table 2.6, Figure 2.6). Site 12 km had the greatest cover of intertidal bryozoans

(Kruskal Wallis: $H = 36.0880$, $df = 2$, $P < 0.0001$) and site 16 km had the greatest cover of subtidal tunicates (Kruskal Wallis: $H = 9.1632$, $df = 2$, $P = 0.0102$).

San Francisco Bay

In San Francisco Bay, percent cover and community composition were assessed at the end of the experiment in December 2009 (Figure 2.9). Recruitment tiles in the removal treatment had an average cover of competitors of 31%, which was significantly less than controls with unmanipulated competitor abundance (averaged 54% with a maximum of 100%) (Wilcoxon: $Z = -3.8254$, $P < 0.0001$). There was no significant variation in total cover of competitors among sites (Kruskal Wallis: $H = 7.1625$, $df = 3$, $P = 0.0669$); however, there was significantly greater cover in the mid intertidal (63%) than in the lower intertidal (45%) (Wilcoxon: $Z = -1.9712$, $P = 0.0487$) (Figure 2.9). Overall, algae dominated the sessile communities (Kruskal Wallis: $H = 130.9221$, $df = 4$, $P < 0.0001$); diatoms made up the majority of this group, though macroalgae (*Ulva*, multiple red filamentous species) were present (Figure 2.9). SQ had highest total coverage at the lower intertidal elevation, and OP had the highest total cover in the mid intertidal.

Cover of Sessile Competitors on Natural Substrate

Tomales Bay

In November 2008, there was an average of 46% (± 0.0479 SE) cover on natural substrate at Tomales Bay intertidal sites, with algae dominating (Kruskal Wallis: $H = 39.0752$, $df = 4$, $P < 0.0001$). In October 2009, there was an average of 34% (± 0.0374 SE = tops only) cover across intertidal (mid and lower elevation) sites. Bryozoans and

‘other’ (majority sponge and hydrozoans) dominated the substrate (Kruskal Wallis: $H = 69.3360$, $df = 4$, $P < 0.0001$).

San Francisco Bay

In San Francisco Bay, surveys of natural substrate at LL, SQ, and FP in December 2009 showed an average cover of 66% (± 0.0401 SE), with algae dominating (Kruskal Wallis: $H = 177.0693$, $df = 4$, $P < 0.0001$).

Discussion

Despite significant variation in both the sessile community and in oyster demography throughout the estuary, competitive effects on oysters were minimal at most life stages. We found little effects of competition on juvenile and adult oysters either in terms of growth or survival. However, we found effects of competition at the recruit stage in both bays. In Tomales Bay, we found large effects on growth of oyster recruits during the year in which they settled, and this was consistent regardless of position along the estuarine gradient. In comparison, competitive effects showed greater variation along the tidal elevation gradient, following patterns of percent cover. In San Francisco Bay, we found presence of competitors to decrease total number of recruits rather than recruit size.

Along the estuarine gradient in Tomales Bay, we found that there was no competitive effect on total number of recruiting oysters or larger juvenile and adult growth and mortality rates. However, presence of competitors did significantly affect post-recruitment growth of oysters. At the end of their first growing season, those oysters that settled in space without competitors present were up to twice the size of those that grew with competitors present. Interestingly, this effect did not vary by site along the

estuarine gradient, despite variation in habitat characteristics along this gradient such as phytoplankton biomass (Largier et al. 1997, Kimbro et al. 2009a, Kimbro et al. 2009b). However, importantly for competitive interactions, total cover of competitors did not vary along the estuarine gradient and sites had similar composition of groups of sessile species.

Though composition of groups of species varied by tidal elevation, percent cover seemed to be a better indicator of competitive effect on recruit size along this gradient. Across sites, tunicates dominated subtidal substrate and bryozoans dominated intertidal substrate. These dominant sessile species all potentially compete with oysters for space and food, and also may interfere with oyster feeding by altering water flow. At the 12 km site, total cover did not increase with decreasing tidal elevation. There was an overall competitive effect on size regardless of tidal elevation, indicating that species composition was not a major factor. This site has the highest chlorophyll *a* levels (a proxy for phytoplankton biomass) in the bay (Kimbro et al. 2009a). Although this suggests that filter feeders may not compete for food at this site, when food levels are high competition may become a more important process as competitors are able to grow larger and cover more space (Zajac et al. 1989).

At 16 km, presence of competitors only affected recruit size at the subtidal elevation where cover was much higher than in the intertidal zone (100% vs. 23% cover, respectively). Subtidal 16 km tiles were almost completely encased by a continuous mat of the invasive tunicate *Didemnum*, which likely restricted water flow for feeding to oysters settled underneath (Lenihan 1996). At this site, food levels are low relative to other parts of the bay (Kimbro et al. 2009a). Thus, as well as reduced feeding potential,

these new recruits also likely compete directly for food (Osman et al. 1989). Tidal elevation effects existed regardless of competitive effects. Recruit size mirrored immersion time at this food limited site, as subtidal oysters were significantly larger than those on intertidal tiles.

Bryozoans such as *Bugula* species, *Schizoporella psuedoerrata*, and *Watersipora subtorquata* and tunicates such as *Botrylloides violaceus* and *Didemnum* species dominated the sessile community in Tomales Bay. Bryozoans and tunicates have been found to have strong effects as competitors as compared to other species such as barnacles and oysters (Gappa 1989, Nandakumar et al. 1993, Osman and Whitlach 1995). Had there been more variation in competitor composition along the estuarine or tidal elevation gradient, it is possible that there would have been more variation in effects of sessile species, including facilitation (Osman and Haugsness 1981, Osman 1987, Stachowicz 2001, Bruno et al. 2003). In Tomales Bay, heavy fog generally coincides with day time summer low tides while fall low tides occur in the evening and night, reducing exposure risks along the tidal gradient (Mislán et al. 2009). Consequently, in the intertidal zone in Tomales Bay, we see soft bodied organisms such as tunicates that tend to usually be present only at lower elevations, and do not see as much of a tidal elevation effect on cover and composition as expected (Jackson 1977, Dalby and Young 1993, Bishop and Peterson 2006). At the 16 km site, reduced intertidal cover may be due to greater stress, as this site experiences both reduced food levels and delayed and amplified low tides relative to the rest of the bay.

For recruitment and juvenile and adult growth rate and mortality, competition had no significant effect regardless of cover or composition. Site and tidal elevation were

better predictors. Recruitment increased along the estuarine gradient toward the back of the bay. This follows established patterns of increasing residence time toward the head of the estuary, where water residence time can reach 100 days (Largier et al. 1997). Only one study has investigated Olympia oyster ecology at the larval stage, with a focus on population connectivity patterns (Carson 2010). However, recruitment patterns established in the present study indicate that larvae may become entrained in the back of the bay.

Intertidal growth peaked in the mid bay, following the previously described food gradient along the bay as well as matching previously documented intertidal oyster growth. Thus, intertidal oyster growth depends heavily on the dynamics of this low inflow estuary such that there is coupling between benthic estuarine invertebrate processes and pelagic processes (Kimbrow et al. 2009a). In this study, subtidal oyster growth was uniform along the bay, expanding work by the previous study to show that coupling between benthic and pelagic processes depends on tidal elevation. Subtidal oysters are constantly submerged, allowing more time to feed than intertidal oysters. Consequently, they are less sensitive to spatial variation in food concentration along the estuary. Interestingly, intraspecific competition did impact oyster growth, as increasing oyster density per tile was correlated with lower growth rates. Although not the focus of this study, we expect that these intraspecific effects may have a greater impact in areas with high recruitment (e.g. 16 km) or high numbers of adults (e.g. 12 km (Kimbrow 2008)). Thus, although estuarine and tidal elevation gradients are less relevant to determining interspecific competitive effects on oysters, they both play an important role in determining oyster demographics.

Looking across life history stages, recruit size by the end of the first growing season is seemingly the only aspect of life history significantly affected by competition in Tomales Bay. Lack of competitive effects has been previously reported on settlement as well as adult growth and mortality (Todd and Turner 1988, Dalby and Young 1993, Osman and Whitlatch 1995b, Bullard et al. 2004). Other work investigating competitive effects on multiple phases of life history of both plants and sessile invertebrates have found smaller life stages to have high mortality (Dalby and Young 1993, Howard and Goldberg 2001, Horvitz and Schemske 2002), and, aside from competition, these early, small stages are often cited as being especially vulnerable to factors such as predation and physical stress (Gosselin and Qian 1997, Hunt and Scheibling 1997). It is interesting in this study that it is specifically growth at an early, small stage that is affected, rather than survival.

Competition also affected the recruit stage in San Francisco Bay, but reduced total number of recruits rather than recruit size. Interestingly, algae, specifically diatom species, dominated sessile cover in San Francisco Bay, regardless of their different locations in the bay. Algae may compete for space but not food and have been cited as a less important competitor (Nandakumar et al. 1993), which may explain why recruit size was not affected. Location in the bay and within site was most predictive of recruitment patterns and recruit size. These patterns did not follow regional groupings; for example, LL and SQ, both located on the west side of the bay at the north-central bay boundary, showed very different size patterns indicating that individual site differences are more important. In general, there were both more and larger recruits at the lower intertidal elevation, as the lower intertidal may be less physically stressful for new recruits.

Competition only directly limits *Olympia* oyster populations at the recruit stage in San Francisco and Tomales Bays. While available space for recruitment mattered in San Francisco Bay, competition for food as recruits grew was not likely limiting as the major competitors were diatoms. Conversely, while space for recruitment was not an important limiting factor for oysters in Tomales Bay (especially in light of the large difference in percent cover of competitors between removal and control tiles), higher cover of strong competitor species limited recruit size. These results are in line with previous studies of competitive effects on early life stages of *Olympia* oysters that found a negative effect on recruit size when competitive cover was high and dominated by strong competitors (ascidians) (Trimble et al. 2010), but no effect when competitive cover was very low (Wasson 2010). Though we did not observe any direct effects of competition on later life stages, these stages may still be affected indirectly. Because size is often correlated with first reproduction and overall fecundity (Cole 1954, Kozłowski 1992), reduced recruit size due to competition could potentially have a large effect on oyster populations. Thus, while competition did not directly impact later stages of life history, previous work indicates that early life stage effects may carry over to influence later stages (Pechenik et al. 1993, Franz 1996, Marshall et al. 2003, Marshall and Keough 2004, Podolsky and Moran 2006).

This study will improve the ability of restoration practitioners to prioritize factors and concerns when planning for restoration, and also informs when competition may come into play. Cover of sessile species on natural substrate was lower than on outplanted substrate. If restoration practices require deploying substrate, one may expect to see some competitive effects. Conversely, if a project requires outplanting oyster spat

to supplement the natural population and leads to increased recruitment, competition on natural substrate may not affect oysters. If a site is recruitment limited and restoration efforts include outplanting oysters, waiting to deploy oysters until they are larger would minimize interspecific competition effects. Finally, deploying oysters at medium rather than high densities can reduce interspecific competition to allow higher growth rates.

In conclusion, this study is one of the few to investigate the influence of competition across multiple phases of life history and environmental gradients. It establishes how these competitive effects vary temporally through the life stages of oysters and spatially within estuaries along both tidal and estuarine gradients. Understanding how oysters and other target species respond to the presence of competitors informs restoration practitioners about when to deploy supplemental individuals, where to deploy projects, and when competition may be a structuring force governing the performance of ecologically important species.

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Tables

Table 2.1: Total recruitment along estuarine and tidal gradients in Tomales Bay in 2009.

Bold type indicates results significant at $P < 0.05$.

Factor	Estuarine Gradient			Tidal Gradient		
	df	F value	P value	df	F value	P value
Site (S)	2	6.97	0.0014	1	1.29	0.2592
Tidal elevation (E)	1	4.13	0.0447	2	1.37	0.2594
Competition (C)	1	0.00	0.9758	1	0.03	0.8573
S*E	2	10.60	<0.0001	2	24.55	<0.0001
S*C	2	1.60	0.2061	2	0.43	0.5156
E*C	1	3.19	0.0773	1	0.64	0.5271

Estuarine gradient total df = 112; tidal gradient total df = 118

Table 2.2: Average recruit size at the end of their first growing season along estuarine and tidal gradients in Tomales Bay in 2009. Bold type indicates results significant at $P < 0.05$.

Factor	Estuarine Gradient			12 km Tidal Gradient			16 km Tidal Gradient		
	df	F value	P value	df	F value	P value	df	F value	P value
Site (S)	2	1.99	0.1517	-	-	-	-	-	-
Tidal elevation (E)	-	-	-	2	1.88	0.1740	2	26.40	<0.0001
Competition (C)	1	10.42	0.0026	1	6.48	0.0178	1	4.84	0.0398
S*E	-	-	-	-	-	-	-	-	-
S*C	2	0.57	0.5697	-	-	-	-	-	-
E*C	-	-	-	2	0.14	0.8706	2	6.53	0.0066

Estuarine gradient total df = 42; 12 km tidal gradient total df = 29; 16 km tidal gradient total df = 25

Table 2.3: Total recruitment and average size of recruits in San Francisco Bay in 2009.

Bold type indicates results significant at $P < 0.05$.

		Total Recruitment		Recruit Size	
Factor	df	F value	P value	F value	P value
Site (S)	3	41.34	<0.0001	40.57	<0.0001
Tidal elevation (E)	1	81.66	<0.0001	2.50	0.1172
Competition (C)	1	11.91	0.0008	0.09	0.7710
S*E	3	2.81	0.0427	9.42	<0.0001
S*C	3	4.63	0.0043	1.95	0.1265
E*C	1	3.19	0.0769	0.27	0.6026

*Total recruitment total df = 124; Recruit size total df = 115

Table 2.4: Juvenile (2008) and adult (2009) oyster growth rate per day in Tomales Bay.

Bold type indicates results significant at $P < 0.05$.

Factor	2008			2009		
	df	F value	P value	df	F value	P value
Density	1	16.17	0.0002	1	39.79	<0.0001
Initial size	-	-	-	1	54.64	<0.0001
Site (S)	2	12.55	<0.0001	1	2.06	0.1594
Tidal elevation (E)	1	14.54	0.0004	1	2.71	0.1078
Competition (C)	1	1.63	0.2065	1	3.38	0.0735
S*E	2	5.70	0.0057	1	1.34	0.2537
S*C	2	0.17	0.8406	1	1.85	0.1821
E*C	1	2.14	0.1497	1	0.36	0.5539

*2008 total df = 64; 2009 total df = 47

Table 2.5: Mortality of adult oysters in Tomales Bay in 2009. Bold type indicates results significant at $P < 0.05$.

	2009		
Factor	df	F value	P value
Site (S)	1	10.95	0.0019
Tidal elevation (E)	1	2.10	0.1548
Competition (C)	1	0.18	0.6778
S*E	1	0.01	0.9252
S*C	1	3.91	0.0545
E*C	1	0.21	0.6457

*total df = 48

Table 2.6: Five most common tunicates and bryozoans on experimental tiles in Tomales Bay.

Tunicates	Bryozoans
<i>Ascidia ceratodes</i>	<i>Bugula neritina</i>
<i>Botrylloides violaceus</i>	<i>Bugula stolonifera</i>
<i>Ciona intestinalis</i>	<i>Cryptosula pallasiana</i>
<i>Clavelina huntsmanii</i>	<i>Schizoporella psuedoerrata</i>
<i>Didemnum</i> spp.	<i>Watersipora subtorquata</i>

Figure Legends

Figure 2.1: Map of study sites in Tomales Bay (a) and San Francisco Bay (B). Sites in Tomales Bay are located along the west side of the bay at 6 km, 8 km, 12 km, and 16 km from the mouth. Sites in San Francisco Bay are LL, SQ, FP, and OP.

Figure 2.2: Oyster recruitment (mean \pm SE) at sites along the estuarine gradient in Tomales Bay in 2009 with nonsignificant competition treatment pooled. Recruitment varied along a tidal elevation gradient at different sites. Bars with different letters indicate *within site* means that are significantly different at $P < 0.05$ with Tukey- Kramer post-hoc tests.

Figure 2.3: Average size (shell length) (mean \pm SE) of oyster recruits at 16 km, the site closest to the head of Tomales Bay, in 2009. Average size of recruits varied with tidal elevation and presence of competitor species. Bars with different letters indicate means that are significantly different at $P < 0.05$.

Figure 2.4: Oyster recruitment (mean \pm SE) with and without other sessile species present at different sites in San Francisco Bay in 2009. Bars with asterisks indicate *within site* means that are significantly different at $P < 0.05$.

Figure 2.5: Oyster recruitment (mean \pm SE) at different sites and intertidal elevations in San Francisco Bay in 2009. Bars with asterisks indicate *within site* means that are significantly different at $P < 0.05$.

Figure 2.6: Average size (mean \pm SE) of oyster recruits at each site in San Francisco Bay in 2009. Average size of recruits varied by tidal elevation amongst sites. Bars with asterisks indicate *within site* means that are significantly different at $P < 0.05$.

Figure 2.7: Oyster growth rate (mean \pm SE) from August through November 2008. Bars with different letters within tidal elevation indicate *within tidal elevation* means that are significantly different at $P < 0.05$.

Figure 2.8: Proportional cover of tunicates (white bars) and bryozoans (black bars), the two dominant groups of sessile species, and total cover of sessile species (black diamonds) in Tomales Bay in December 2009.

Figure 2.9: Proportional cover of algae (white bars) and bryozoans (black bars), the two dominant groups of sessile species, and total cover of sessile species (black diamonds) in San Francisco Bay in December 2009.

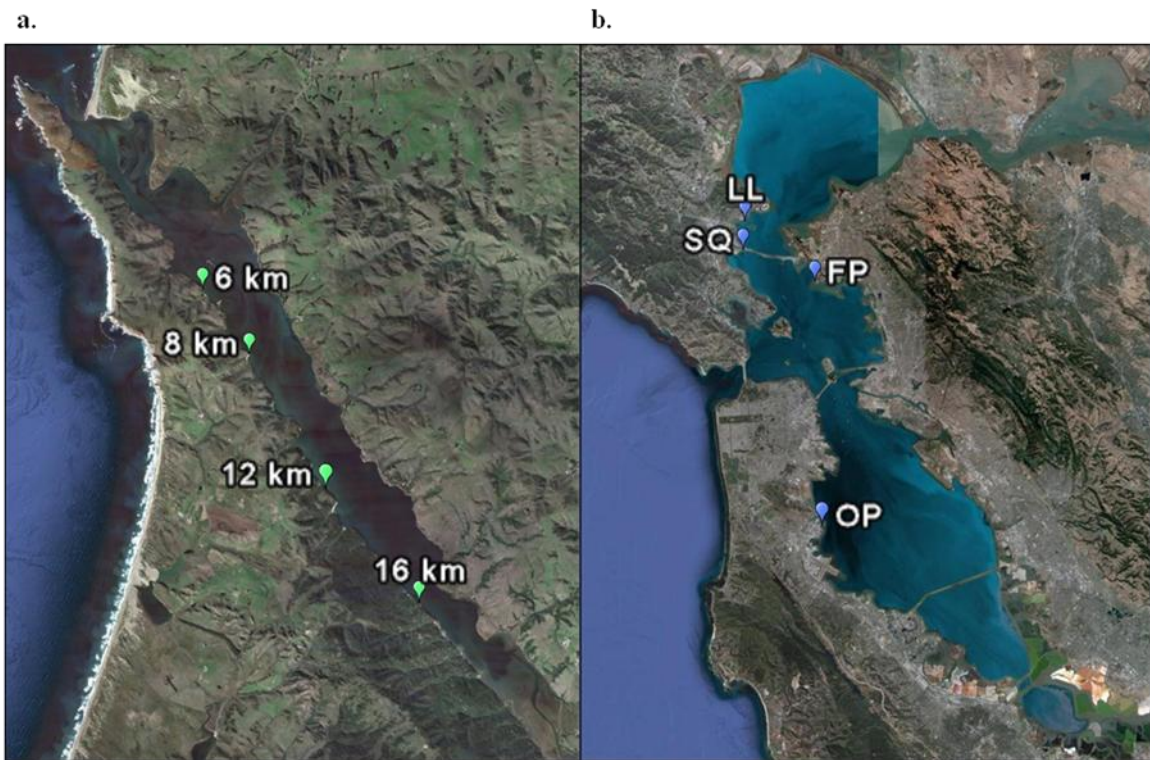
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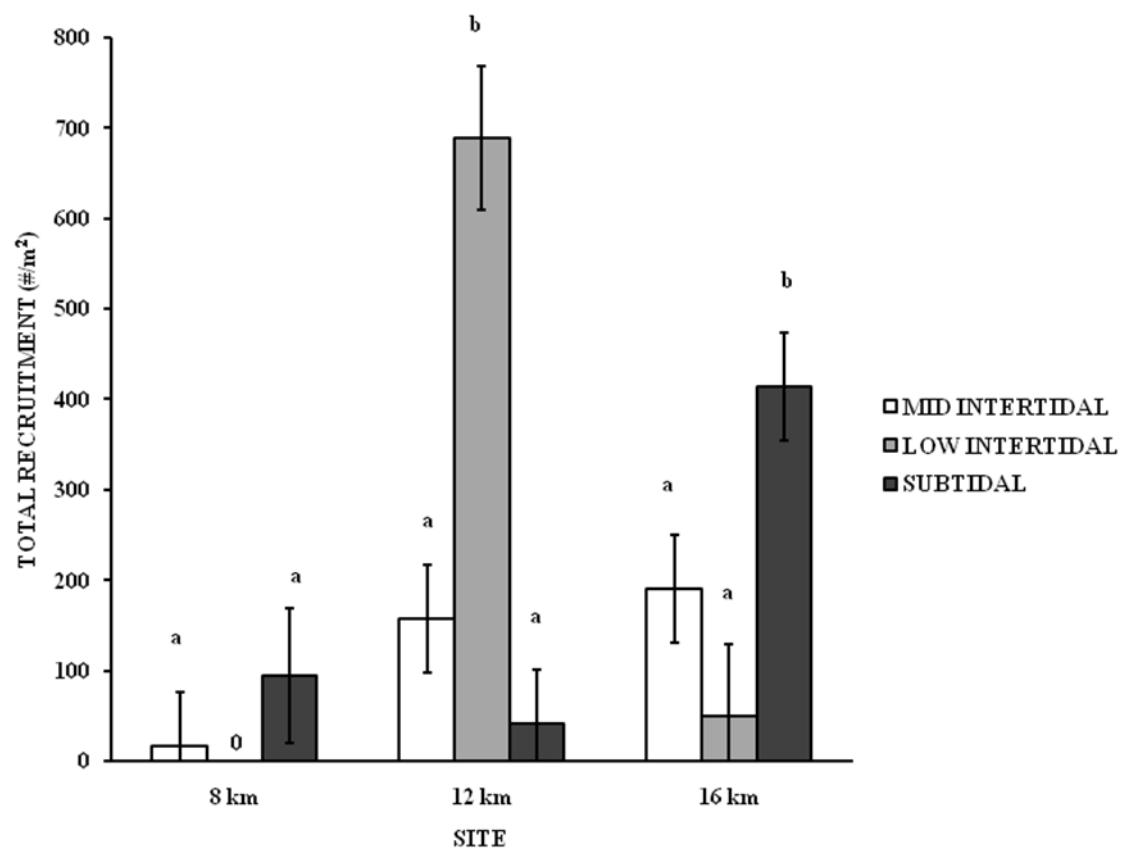


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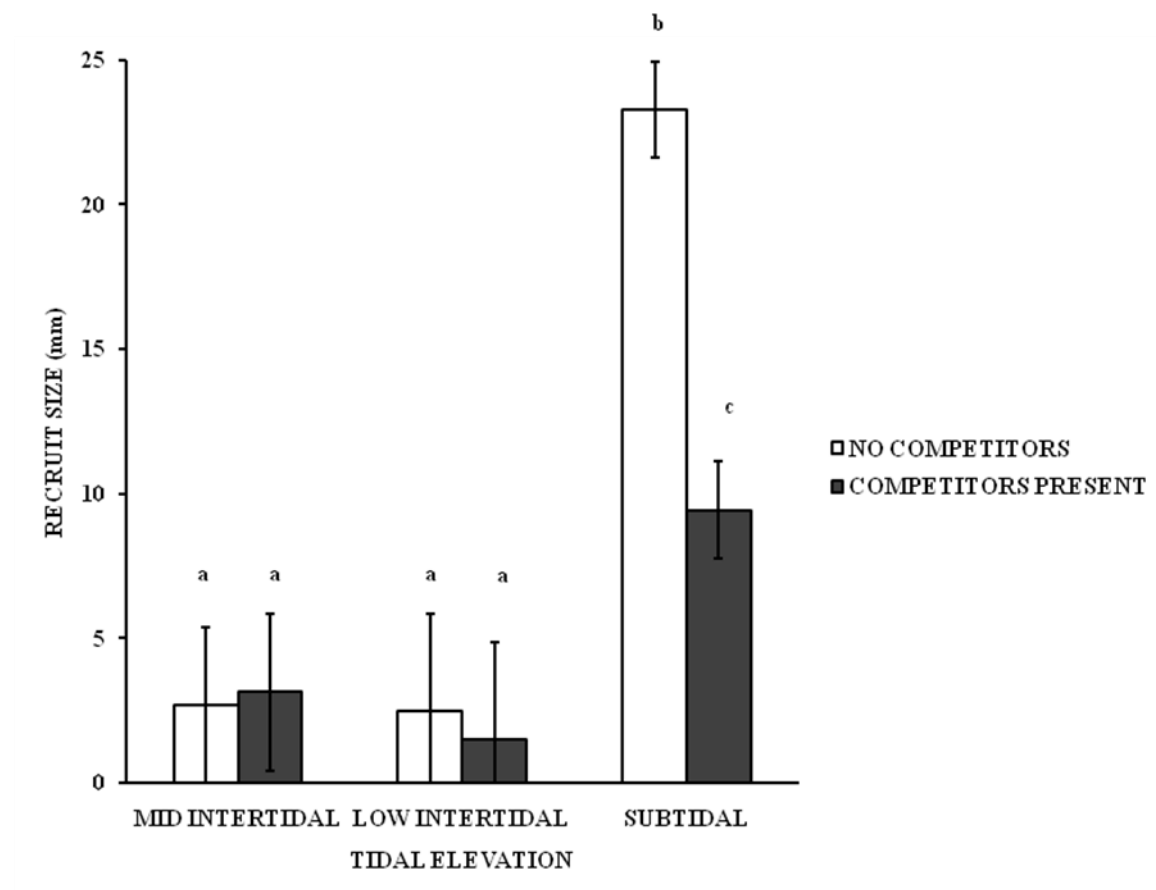


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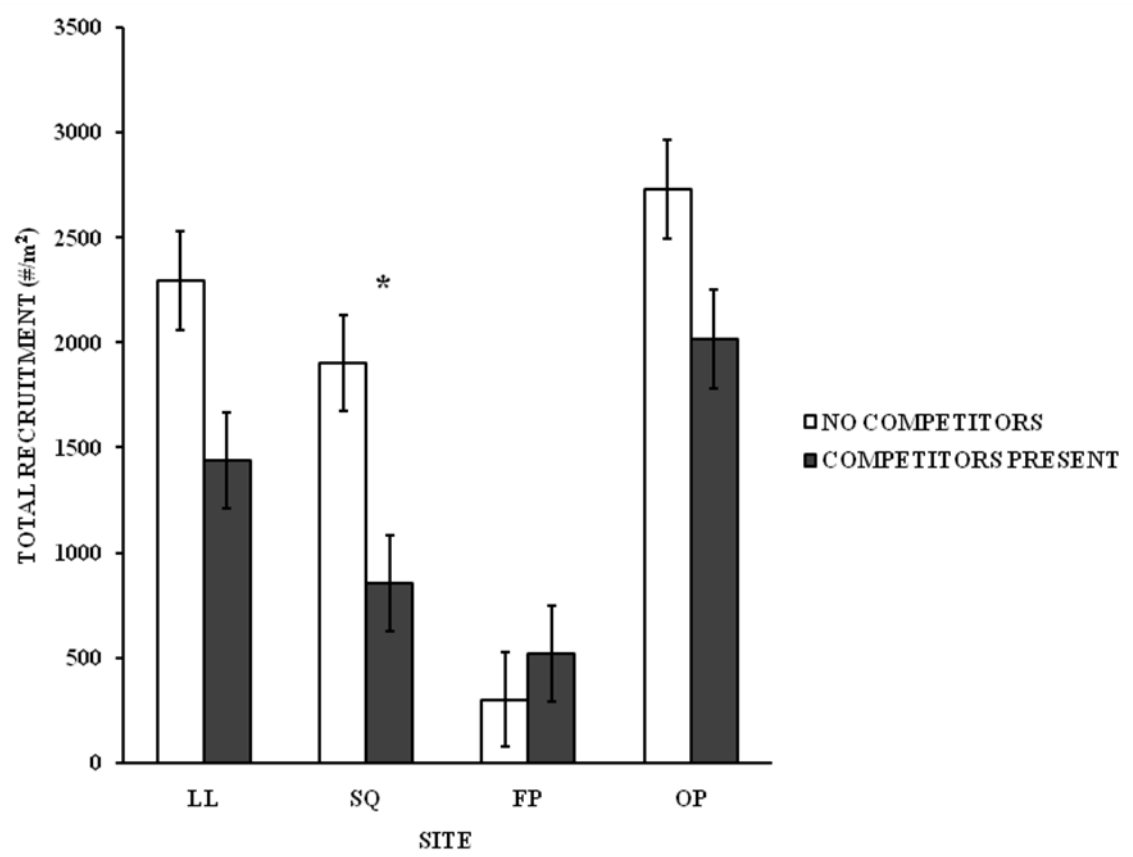


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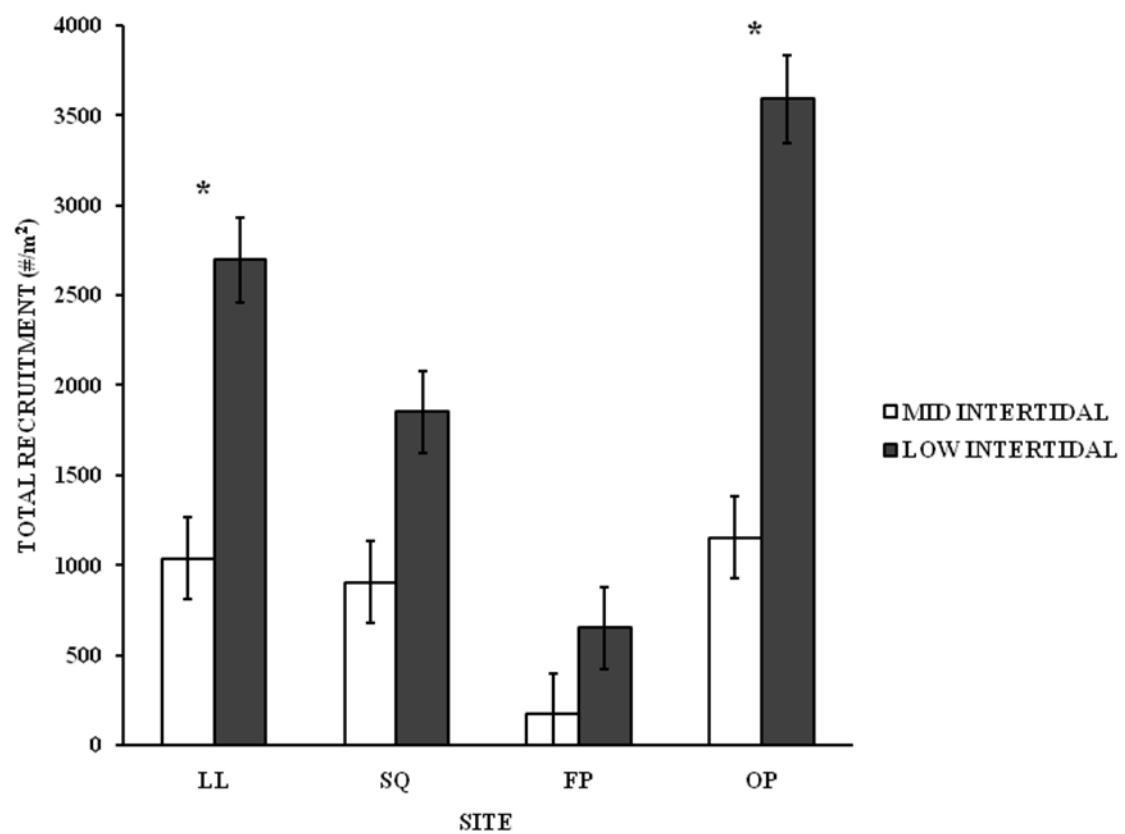


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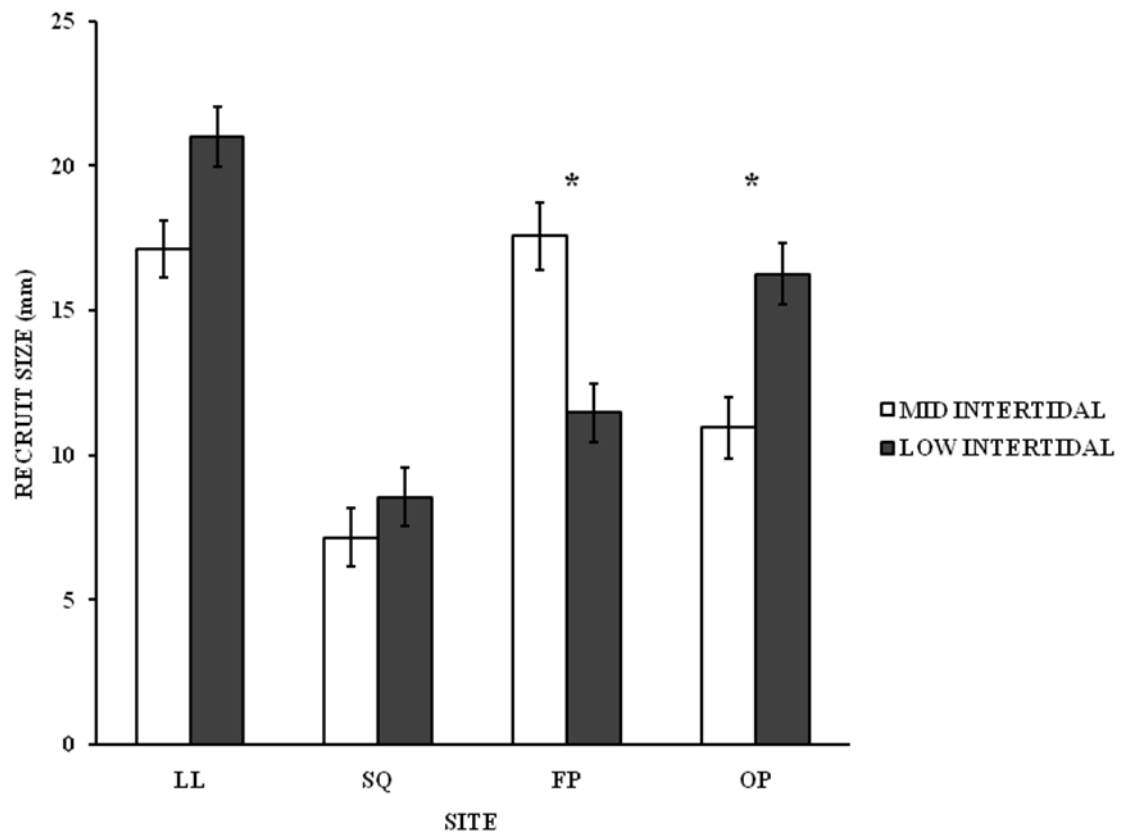


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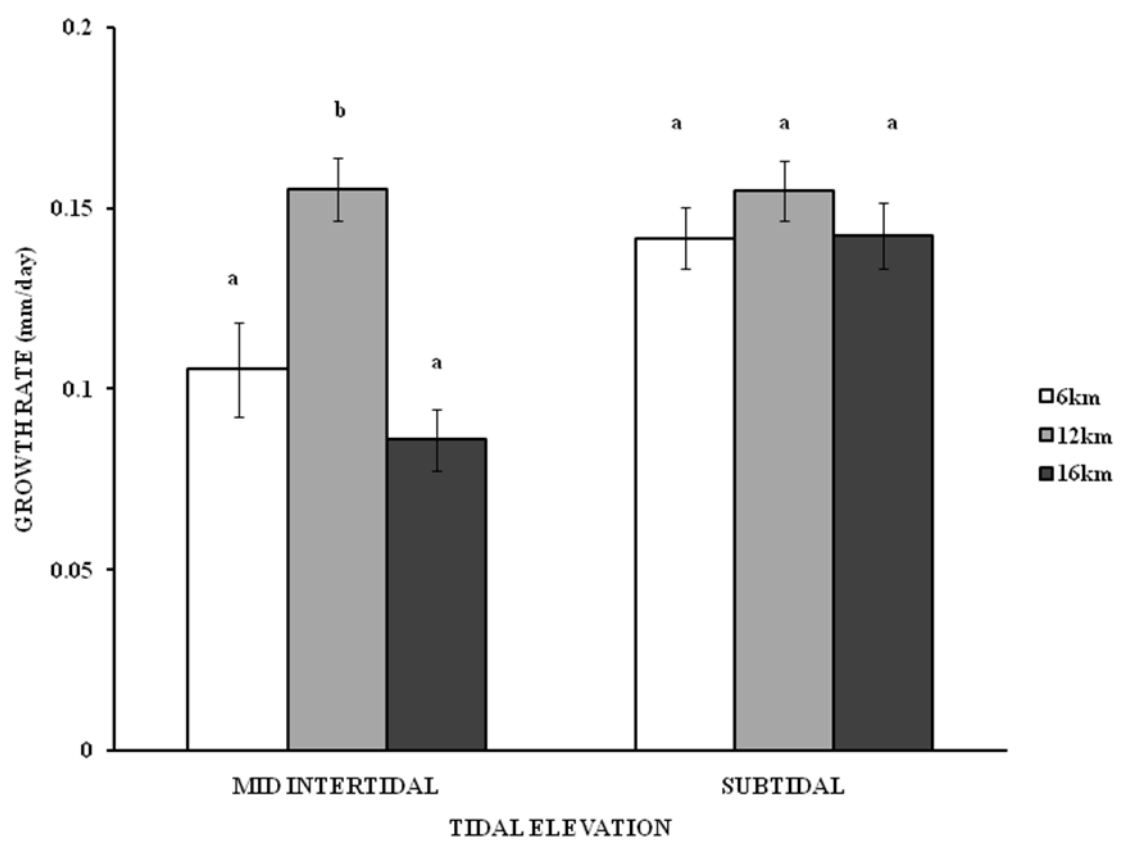


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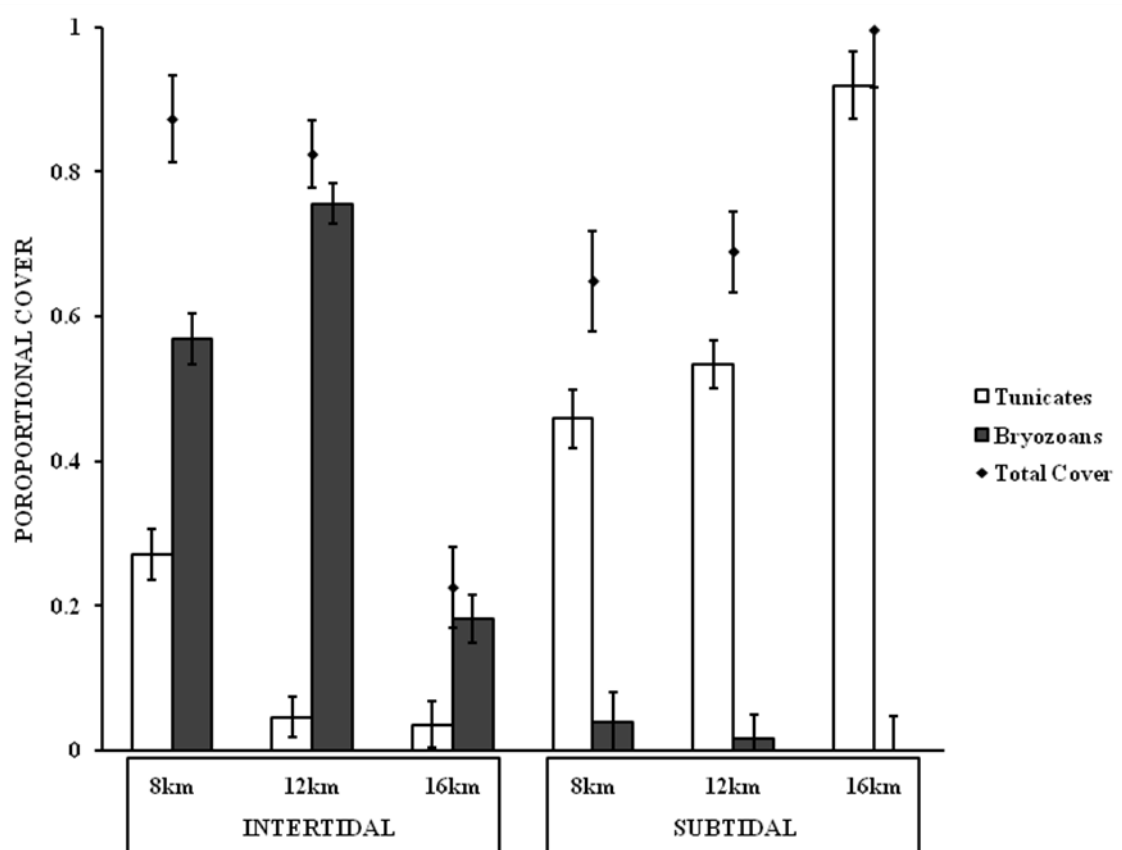


Figure 2.9:

