Evolutionary History, Predation, and Coastal Upwelling Interactively Influence Native Oyster Habitat in Tomales Bay, California

By

DAVID LLOYD KIMBRO

B.S. (University of North Carolina, Chapel Hill) 1998

M.S. (University of Caliornia, Davis) 2004

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Ecology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

Dr. Edwin Grosholz

Dr. John Stachowicz

Dr. John Largier

Dr. Louis Botsford

ABSTRACT: Certain structurally complex species such as corals and trees can create habitat that provides the foundation upon which ecological communities are built. Thus, understanding the biotic and abiotic limits of these "foundation species" may provide a means for conserving biodiversity and key ecosystem functions. For my dissertation, I studied native oyster habitat (*Ostrea lurida*) in Tomales Bay, CA, which acts as a foundation species by increasing community species richness and densities. Much of this habitat, however, has been depleted in areas where native crabs and whelks have been replaced by invasive crabs and whelks (Chapter 1). This work shows that in many cases invaders lack a shared evolutionary history and do not recognize each other as predator and prey. Therefore, predator-prey interactions like trophic cascades that normally benefit oysters have been short-circuited. Underlying these potentially important "top-down controls" is a spatial gradient in phytoplankton abundance that is tied to coastal upwelling (Chapter 2). During the summer-upwelling months, the lack of fresh water flowing into the estuary allows the daily pumping of water with each high and low tide (i.e., tidal excursion) to lengthen water residence times as distance from the ocean increases. The tidal excursion's exchange with coastal waters creates a gradient of coastal nutrients that interacts with water residence times to promote consistent phytoplankton blooms in the middle portion of the estuary. These food subsidies influence oyster habitat from the "bottom-up" by allowing juvenile oysters to grow faster in the middle-bay region when compared to oysters in the outer- and inner-bay regions. In addition to phytoplankton, recruitment of oyster larvae is another important bottom-up control (Chapter 3). But the 4-6 week planktonic stage of these larvae allows them to accumulate in the inner bay where residence times are higher. Because high abundances

of recruitment and phytoplankton are decoupled in space and because recruitment is inconsistent, the top-down and bottom-up controls identified in this system interact differently over time. These interactions then create temporally varying gradients of oyster density and size that cannot be understood without simultaneously considering the effects and underlying mechanisms of mortality, growth, and recruitment.

Chapter 1: Lack of historical exposure among native and invasive species disrupts trophic cascades*

ABSTRACT: Although invasive species often resemble their native counterparts, their lack of evolutionary history with species in their invaded range may disrupt native food webs. In a California estuary, native crabs indirectly maintain oyster habitat by both consuming (density-mediated trophic cascade) and altering the foraging behavior (trait-mediated trophic cascade) of the oyster's primary predator, native whelks. In contrast, invasive whelks lack historical exposure to effective crab predators and fail to avoid them, thereby inhibiting trait-mediated cascades. Similarly, the naïvete of invasive crabs prevents them from efficiently consuming adult whelks. Thus, while trophic-cascades allow native crabs, whelks, and oysters to locally co-exist, the replacement of native crabs and whelks by similar looking invasive species results in severe depletion of native oysters. As coastal systems become increasingly invaded, the mis-match of evolutionary histories among invasive predators and prey may lead to further losses of critical habitat that support marine biodiversity and ecosystem function.

---

*Co-authors: Edwin D. Grosholz, Adam J. Baukus, Nicholas J. Nesbitt,

and Nicole M. Travis

Introduction

Trophic cascades indirectly maintain many important basal prey (including hardwood trees, kelps, salt-marsh plants, and scallops) when top predators reduce the foraging of intermediate consumers (e.g., herbivores), either by eating them (density-mediated; Hairston *et al*. 1960; Estes & Palmisano 1974; Paine 1980; Carpenter *et al*. 1985; Polis *et al*. 2000) or by altering their behavior (trait-mediated; Abrams 1995; Trussell *et al*. 2002; Werner & Peacor 2003; Schmitz *et al*. 2004; Preisser *et al*. 2005). Although trophic cascades require that top predators be present, predator presence—alone—may not always be sufficient (Werner & Peacor 2003; Schmitz *et al*. 2004). For example, in density-mediated cascades, a top predator must select and control (i.e., efficiently consume) specific intermediate consumer populations, i.e., those capable of depleting basal prey (Hairston *et al*. 1960; Strong 1992). In trait-mediated cascades, cues of the top predator (e.g., hunting strategy *sensu* Schmitz *et al*. 2004) must be recognized by and cause the intermediate consumer to spend more time and energy hiding rather than consuming basal prey (Abrams 1995; Werner & Peacor 2003).

For trophic cascades that have existed over long periods, the recognition and responses between their top predators and intermediate consumers have likely been influenced by natural selection. Within the context of trait-mediated cascades, an intermediate consumer's historical exposure to a moderately efficient top predator could have selected for individuals that avoid and escape predation by recognizing alarming cues (Vermeij 1982b; Sih 1985; Strauss *et al*. 2007). And for density-mediated cascades, it is reasonable that the top predator's evolutionary history with specific prey (and its own predators) selected a dietary preference, hunting mode, and/or morphological feature that

facilitate hunting the intermediate consumer (Vermeij 1982b). Although the behavior underlying trophic cascades could be learned by individual top predators and intermediate consumers, each animal's capacity for learning would be influenced by the presence/absence of innate morphological or behavioral traits that would increase fitness and ultimately be selected for within a population over time (Berger *et al*. 2001; Smith 2004; Cox & Lima 2006). We therefore suspect that a common feature of long-established cascades, whether trait-mediated or density-mediated, will be that the top predator and intermediate consumer species share an evolutionary history and/or have historical exposure with similar types of predator and prey species.

Because the ongoing movement of species beyond their natural ranges increasingly brings together invasive and native species that may have historically interacted with different predator-prey types, invaders may interfere with or fail to recreate historically important trophic cascades. For instance, an intermediate consumer may not participate in a trait-mediated cascade and may fail to invade a three-level food chain if it is unable to recognize or effectively respond to an unfamiliar top predator (Werner & Peacor 2003; Cox & Lima 2006). This naiveté and unsuccessful invasion should occur if the intermediate consumer experienced little predation or sufficiently different predators in its native range (Cox and Lima 2006). Naiveté, however, could also weaken density-mediated cascades and promote invasion when the foraging traits of top predators are not well matched to novel types of intermediate consumers; such predators may only be capable of or choose to eat small numbers of novel intermediate consumers. In this case, the release of an intermediate consumer from population control could threaten important basal prey including key, habitat-providing foundation species

(Stachowicz 2001). If outcomes of predator-prey encounters are contingent on evolutionary history (Vermeij 2001; Blackburn & Gaston 2005; Vermeij 2005; Strauss *et al*. 2007), then the failure to fit into existing trophic cascades may be an important and underappreciated mechanism by which invasive species affect the organization and diversity of native food webs.

In this study, we investigated whether replacing a native top predator (crab; Fig. 1.1a) and native intermediate consumer (whelk; Fig. 1.1b) with similar-looking invasive species alters established trophic cascades enough to explain why a portion of a California estuary is loosing a historically abundant basal prey (oysters; Fig. 1.1c; see Supplementary Appendices 1.1-1.4 for methods and data underlying Fig. 1.1). Specifically, we manipulated the density of an invasive intermediate consumer (whelk) in the field to test whether this invasion can directly account for oyster mortality being greater in the inner portion of the bay (Fig. 1.1c). Because oysters are maintained in areas where native crabs and native whelks interact, we also manipulated trophic-level numbers in the laboratory to confirm that these oysters indirectly benefit from density- and trait-mediated cascades. By first allowing the intermediate and then the top trophic level to be invaded, we further demonstrate that the absence of trophic cascades from areas where invasive species occur explains why invasive whelks are depleting half of the estuary's oysters. Finally, we infer that the occurrence of at least some trophic cascades depends on the evolutionarily based characteristics of each top predator and intermediate consumer and whether invasions have mis-matched these traits. Since oysters filter estuarine waters (Jackson *et al*. 2001) and provide critical habitat that supports diverse benthic communities (Grabowski *et al*. 2005; Kimbro & Grosholz 2006), the failure of

this estuary's invasive species to participate in established trophic cascades could cause ecosystem-wide consequences.

Methods

Study system and natural histories of predator-prey

We examined how invasive species affect trophic cascades involving a three-level food chain in Tomales Bay, California (38° 07' 17.68" N; 122° 52' 02.86 W). In the middle portion of this estuary, the food chain's top predator is the native rock crab (*Cancer antennarius*, Fig. 1.1a). But the top predator in the inner portion of the estuary is the European green crab (*Carcinus maenas*), which likely invaded in the mid- to late 1990s (Grosholz & Ruiz 1996). Although both crabs actively track prey via water-borne chemical cues (Boulding & Hay 1984; Kaiser *et al*. 1993), their evolutionary histories have selected different diets and feeding strategies that may allow one crab to more efficiently control the consumers of oysters (Grosholz & Ruiz 1996; Behrens Yamada & Boulding 1998). For example, native rock crabs (Cancridae) of all sizes are effective specialist predators because they can crush small gastropod prey as well as 'peel' open large gastropod prey such as the whelks in this study (Behrens Yamada & Boulding 1998). In contrast, the invasive green crab (Portunidae) is a generalist/omnivorous predator that consumes algae, annelids, and mollusks (Grosholz & Ruiz 1996). By preferring to crush rather than peel open their prey, the relatively smaller invasive crab inefficiently consumes adult-sized whelks (Hughes & Elner 1979). Thus, the different evolutionary histories of the crabs may lead to density-mediated cascades and stronger

control of whelk populations in portions of the estuary where native crabs are the top predator.

Similar to the estuary's top predators, its intermediate consumers comprise spatially segregated native and invasive whelks (Fig 1.1b). While the size and diet (barnacles and oysters) of these whelks are similar, their evolutionary histories may have selected different anti-predator behaviors so that only one species may effectively recognize and avoid crab predators. On the coastline and outer reaches of estuaries along the northeast Pacific, native whelk populations (*Acanthinucella spirata*) possess sufficient anti-predator defenses to have co-existed with specialist crab predators (Garth & Abbott 1980; Hellberg *et al*. 2001). But the Atlantic oyster drill (*Urosalpinx cinerea*) that invaded Tomales Bay in the early 20th century originated from a northwest Atlantic estuary (Long Island Sound, USA; J. Carlton, pers. comm.). Because this region's cancrid crabs (i.e., *Cancer irroratus*) occur subtidally and offshore (Williams 1984; Kraemer *et al*. 2007) and because predation by effective blue crabs (*Callinectes sapidus*) is functionally restricted to central and southern estuaries of the Atlantic coast (deRivera *et al*. 2005), it is unlikely that recognizing and avoiding specialist crabs were selected for in the source population of invasive whelks. If the native whelk's anti-predator traits consist of recognizing and avoiding crab cues, then Tomales Bay's segregation of intermediate consumers that differ in predation exposure may cause trait-mediated cascades to occur in some areas (those with native whelks) but not in others (those with invasive whelks).

Direct cause of oyster mortality

Because the invasive whelk is commonly known as the "oyster drill" and because it only occurs in the inner bay, we suspected that invasive whelks are directly causing the high oyster mortality in this region. More physical stress, however, could also explain why oyster mortality is greater in the inner bay than in the middle bay. Consequently, we used a factorial-field experiment to manipulate consumers and physical stress at one inner bay site (Fig. 1.1, open circle) and one middle bay site (Fig. 1.1, open circle). At each site, we randomly assigned 90 rocks with eight living oysters to one of five treatments or cages: invasive-whelk enclosure, consumer exclosure, cage control, shade, and an unmanipulated control (n = 9). All cages were constructed using cylindrical galvanized metal frames that had 25 cm^2 frame openings and a volume of 0.02 m^3. Except for the control and shade, all cages were wrapped in clear plastic mesh (mesh openings = 0.49 cm^2). Treatment bottoms were left open, and frames were held flush to the ground by cable-tying them to rebar poles staked into the ground. To quantify how invasive whelks affect oyster mortality, whelk enclosures received two adult invasive whelks (i.e., mean ambient density/unit area). To create the cage control, two openings (225 cm^2) were cut out of a cage's opposing sides. For shade treatments, we reduced the thermal stress that oysters experience during low tides by covering the frame tops of cages with large black mesh lids (0.56 m^2 with 0.36 cm^2 plastic mesh openings).

Every 10 days, we counted oyster mortality as well as whelk density inside each treatment and depending on the treatment removed (exclosure) or restocked (enclosure) whelks. After ten weeks, we used a two-way univariate Analysis of Variance (ANOVA) and Tukey's post-hoc test to separately compare oyster mortality (proportional mean) and

invasive whelk density (mean for each sampling event) using treatment and site as fixed factors. We also used ordinary least squares regression to assess how well whelk density (log transformed) predicted oyster mortality.

Indirect causes of oyster mortality

To test whether the presence and absence of trophic cascades can explain the high oyster mortality in the inner bay (Fig. 1.1), we used mesocosms to assemble three food webs that represented different areas within the estuary. We then conducted a manipulative experiment with each food web. For all cases, native oysters were the basal prey. In one food web (representing the middle bay), both the top predator and the intermediate consumer were native. In a second food web (transition between middle and inner bay), the top predator was native and the intermediate consumer was invasive. In a third food web (inner bay), both the top predator and intermediate consumer were invasive. Crab-size differences among food webs were minimized by using only adult-sized green crabs (73.87 $\pm$ 1.66 mm) and native crab sizes approximating the observed mean (95.11 $\pm$ 1.94 mm). For each food web experiment, we assigned flow-through mesocosms (1.0 m diameter) at the Bodega Marine Laboratory to one of four treatments: (1) oysters only (basal prey control); (2) oysters and whelks (no trophic cascade possible); (3) oysters, whelks, and non-lethal crabs with restricted claws (trait-mediated cascade possible); (4) oysters, whelks, and lethal crabs with unrestricted claws (density- and trait-mediated cascades possible). While lethal crabs could consume whelks, we prevented non-lethal crabs from consuming whelks by wrapping mesh gloves around their claws. Each mesocosm received 3 gallons of sand and five rocks (~ 225 cm^2) with

3-5 living oysters per rock. All treatments except the basal prey control also received 20 whelks, which represents natural whelk densities. Because whelk behavior affected their susceptibility to predation (i.e., some whelks hid under rocks and climbed up tank walls), every day and evening we quantified the number and location of visible whelks as well as number of whelks consumed by crabs. For visible whelks, we noted whether whelks appeared to be consuming oysters or avoiding crabs by climbing up mesocosm walls. After 6 days, we ended the experiment and quantified oyster mortality. Using the mean of the observational data for days 1-6, we estimated how non-lethal and lethal crabs affected whelk avoidance behavior (number of whelks not visible + high on tank walls) and per capita oyster consumption.

To increase replication, we repeated these experiments in time. Before combining data from separate trials, we used an ANOVA to analyze whether differences among treatment means varied across time. Because we did not find any treatment*time interactions, we combined data for each food web experiment and used ANOVA to test whether response means differed among treatments. For each food web, four responses were analyzed: the mean number of whelks that avoided crabs, the number of whelks consumed by crabs, and the total and per capita number of oysters consumed by whelks. When analyzing the data on whelk avoidance behavior, we used the mean number of whelks consumed in an analysis of covariance (ANCOVA) rather than an ANOVA. Data failing to meet parametric assumptions were either log transformed or analyzed with a non-parametric Wilcoxon/Kruskal-Wallis test.

To assess whether physical conditions and whelk physiology—rather than native crabs—spatially segregate the native and invasive intermediate consumers, we monitored

water conditions at the first middle-bay site (i.e., closest to inner bay) and the nearest inner-bay site (i.e., closest to middle bay and with high oyster mortality). At four-week intervals during the summer (May-August) and winter (November-February) months of 2004-07, we quantified salinity, temperature, and depth with a boat-based CTD profiler (SeaBird Electronics, Inc.) ~100-200 meters offshore of each site. Each site's depth profile was then vertically averaged to obtain temperature and salinity means. Means of the summer and winter months were then averaged to produce seasonal means of temperature and salinity for each site, and these seasonal means were statistically compared using a t-test.

Historical exposure and the matching of predator-prey traits

A separate laboratory experiment was conducted to answer two questions. First, when interacting with different crabs, does a whelk's historical exposure to predation predict the presence of anti-predator behavior and the likely importance of trait-mediated cascades? Second, when interacting with different whelks, does each crab's historically based foraging strategy or size predict its efficiency at consuming whelks and the likely importance of density-mediated cascades?

In this experiment, 15 native and invasive whelks (30 total) were placed in mesocosms similar to those described above, except sediment and rocks were not provided. Each mesocosm was then randomly assigned to one of three predator treatments (n = 10): no crab, native crab, or invasive crab. Every day, we quantified the number and identity of whelks consumed by crabs, noted the crabs' foraging method (i.e., peeling versus crushing), and quantified the number of whelks that avoided crabs by

climbing up tank walls. Each day we minimized the effect of whelk avoidance behavior on crab consumption by returning whelks on tank walls to the bottom of tanks. After 6 days or when whelk density was reduced by 50%, we ended the experiment and averaged the daily observational data. To protect against Type I error rate (Scheiner & Gurevitch 2000) and to determine if the avoidance behavior of both whelk species changed among predator treatments, we conducted a Multivariate Analysis of Variance (MANOVA). Where multivariate analysis indicated a significant effect at $P \leq 0.05$, we used the number of whelks consumed in an ANCOVA and then Tukey's post-hoc test to examine each response variable (i.e., native whelk behavior and invasive whelk behavior) (Underwood 1981). For the whelk mortality data, we also conducted a MANOVA and then used T-tests to assess how total whelk mortality (i.e., predator efficiency) and the mortality of each whelk species varied between native and invasive crabs. Statistical analyses were performed in JMP 5.1 software (SAS Institute, Cary, NC).

Results

Direct cause of oyster mortality

Our field experiment with different cage treatments indicated site by treatment interactions for oyster mortality ($F_{4,77} = 7.95$, $P < 0.0001$) and invasive whelk density ($F_{4,77} = 8.08$, $P < 0.0001$). In the middle bay, the presence of invasive whelks increased oyster mortality compared to the control as expected (Tukey's post hoc test, $t = 3.26$, $P < 0.05$; Appendix 1.5a). The inner bay, however, had high oyster mortality regardless of treatment. This difference between sites resulted because of differences in invasive whelk density across treatments at the two sites (Tukey's post hoc test, $t = 3.26$, $P < 0.05$;

Appendix 1.5b): the consumer exclosures in the inner bay failed to exclude all invasive whelks, and the cage control and shades actually attracted them, presumably by reducing temperature and/or providing a structural refuge from predation. In addition, this experiment coincided with the reproductive stage of invasive whelks, so that by chance the two adult whelks randomly assigned to whelk enclosures often spent more time mating than consuming oysters. Thus, invasive whelk predation was actually lower in whelk enclosures than in cage control or shade treatments and often equaled that of whelk exclosures. To better test the functional relationship between invasive whelk density and oyster mortality, we combined all the treatment values into a single regression and found that invasive whelk density explained more than 60% of oyster mortality variance among treatments (ordinary least squares regression, $R^2 = 0.65$, $Y = 0.76x + 0.19$, $P < 0.001$, Fig. 1.2). Similar functional relationships between invasive whelk density and oyster mortality were observed at both the inner-bay ($y = 0.48x + 0.39$, $R^2 = 0.25$, $P < 0.001$) and middle-bay ($y = 0.65x + 0.17$, $R^2 = 0.27$, $P < 0.001$) site.

Indirect causes of oyster mortality

In our laboratory experiments, whelks consistently consumed more oysters (total and per capita) in the no trophic-cascade treatments (Fig. 1.3c, f, and i). The presence of trophic cascades and reduced oyster mortality, however, depended on whether a food web had native versus invasive crabs and whelks. With native crabs and native whelks, oysters benefited from equally strong density- and trait-mediated cascades (Fig. 1.3c), because lethal crabs consumed whelks (Fig. 1.3b) and non-lethal crabs caused whelks to hide rather than eat oysters (Fig. 1.3a). But a trait-mediated cascade based solely on

whelks recognizing crabs disappeared when native whelks were replaced with invasive whelks (Fig. 1.3d-f), which continued to consume oysters in the presence of non-lethal native crabs. As a result, lower oyster mortality in this food web depended mostly on a strong density-mediated cascade. When native crabs and native whelks were replaced with invasive species (Fig. 1.3g-i), both the trait-mediated cascade based solely on recognition and the density-mediated cascade were eliminated: non-lethal invasive crabs did not alter whelk foraging behavior, and lethal invasive crabs failed to consume enough whelks to reduce both the total and per-capita number of oysters consumed.

During the summer (May-August) and winter (November-February) months from 2004-07, mean water temperature did not statistically differ between an adjacent middle- and inner-bay site (*summer* t-test, t = -0.81, P = 0.20; *winter* t = -0.04, P = 0.97, Table 1.1). Similarly, summer and winter salinities between these two areas of the bay did not differ (*summer* t-test, t = 0.063, P = 0.91; *winter* t = 1.58, P = 0.39).

Historical exposure and the matching of predator-prey strategies

In our separate experiment testing whether whelk recognition of and response to predatory crabs depend on the whelks' evolutionary history, native and invasive whelks responded differently across the predator treatments (MANOVA Wilk's Lambda $F_{4,48}$ = 3.90, P = 0.01, Fig. 1.4a). In comparison to the no-crab treatment, native whelks significantly avoided both native and invasive crabs (ANCOVA $F_{3,24}$ = 3.06, P = 0.05, Number whelks consumed, F = 6.01, P = 0.02; Treatment, F = 4.29, P = 0.03; Tukey's test = 2.50). In contrast, invasive whelks avoided neither crab (ANCOVA $F_{3,24}$ = 3.28. P = 0.18; Number whelks consumed, F = 0.87, P = 0.36; Treatment, F = 1.18, P = 0.32).

Because whelk behavioral responses were minimized, both crab species consumed more whelks in this than in the previous experiment. But by peeling open and crushing their prey, native crabs still consumed more than twice as many whelks as did invasive crabs (MANOVA Wilk's Lambda $F_{6,46} = 7.18$, $P = 0.0001$; t-test = 3.06, $P = 0.005$; Fig. 1.4b); invasive crabs tried consuming whelks only by crushing the apexes of their shell. While native crabs consumed more invasive whelks than did invasive crabs (t-test = 4.07, $P = 0.47$), the size of each crab did not significantly correlate with the number of whelks consumed (native crab = $0.003x + 10.20$, $R^2 = 0.00003$, $P = 0.99$; invasive crab = $0.33x - 19.41$, $R^2 = 0.28$, $P = 0.12$). Despite its statistical insignificance, the relationship between crab size and number of whelks consumed appears more important for invasive than native crabs.

Discussion

Our results show that invasive species can reorganize an estuary's three-level food chain by affecting trophic cascades. We found that the middle region of Tomales Bay has less oyster mortality and more biologically rich oyster habitat than does the inner bay, despite historically receiving less recruitment, because it has not been invaded by non-native whelks (Figs. 1.1-1.2). According to our survey (Fig. 1.1) and laboratory experiments (Fig. 1.3a-c), oysters are also indirectly maintained in this region by trophic cascades involving native crabs and native whelks. In further support of this interpretation, we have found evidence of a density-mediated cascade in the low intertidal zone (< -1.0 m) of middle-bay sites: whelk shells with distinctive native crab predation marks. In addition, at sites with less native crabs, native whelks were equally distributed

in the upper and lower intertidal areas of the oyster zone. But at middle-bay sites with more native crabs, twice as many native whelks were found in the upper than in the lower intertidal oyster zone (Kimbro and Grosholz unpublished work). Such a behavioral shift in habitat use is commonly displayed by prey in other systems, and would allow native whelks to create a trait-mediated cascade by avoiding crabs and consuming barnacles instead of oysters (Power *et al*. 1985; Carpenter *et al*. 1987; Turner & Mittelbach 1990; Gastreich 1999). In contrast, our survey and experimental results (Figs. 1.1-1.3) indicate that the failure of invasive whelks and invasive crabs to generate trait- and density-mediated cascades is causing invasive whelks to deplete oysters in the inner bay.

Because the distinct, non-overlapping distribution of invasive and native whelks throughout the estuary explains why oyster mortality and abundance varies, it is interesting to consider why these whelks remain separated. From distribution patterns throughout their range (Garth & Abbott 1980; Hellberg *et al*. 2001), we assume that native whelks (as well as native crabs) are excluded from the inner bay because they do not tolerate the lower salinity extremes that often occur in the upper estuary during large winter storms (e.g., 12 ppt. in the middle bay versus 6 ppt. in the inner bay; Kimbro unpublished work*)*. Site differences in water salinity or temperature, however, do not adequately explain why invasive whelks are absent from the less physically stressful middle bay (Federighi 1931; Hanks 1957). Alternatively, the absence of a trait-mediated cascade likely prevents invasive whelks from locally co-existing with native crabs in the middle bay. In our laboratory experiments, invasive whelks did not behaviorally respond to native crabs before being consumed (Fig. 1.3d-f and Fig. 1.4a-b). Consistent with the biotic resistance and increased susceptibility hypotheses (Darwin 1859; Elton 1958;

Colautti *et al*. 2004), the invasive whelk's naiveté to native crabs and the ensuing density-mediated cascade likely increase the middle bay's biotic resistance, which can explain why invasive whelks and high oyster mortality do not occur beyond the inner bay.

Consistent with other evidence showing the importance of evolutionary history for predator-prey interactions (Vermeij 2001; Blackburn & Gaston 2005; Vermeij 2005; Strauss *et al*. 2007), the ability of trophic cascades to organize this estuary may ultimately be explained by historical exposure between crabs and whelks. Although our results could be due solely to the species-specific traits of the organisms in this study, three lines of evidence suggest evolutionary history is important. First, not only do native whelks recognize and respond to the presence of non-lethal native crabs, but they also display a behavioral response to non-lethal invasive crabs (Fig. 1.4a). As predicted by Cox and Lima (2006), the historical exposure to native crabs can explain why a general anti-predator behavioral response to smaller but functionally similar invasive crabs has also been selected for in native whelk populations (Garth and Abbott 1980; Hellberg et al. 2001). Invasive whelks, however, generally appear naïve to the threat of crabs—regardless of predator size—because they did not respond to non-lethal native or invasive crabs (Fig. 1.4a). These results and the paucity of effective crab predators in northwest Atlantic estuaries (Williams 1984; deRivera et al. 2005, Kraemer *et al*. 2007) suggest that lower predation pressure did not select for species-specific or general escape responses to crabs within the source population of invasive whelks. Therefore, the evolutionary history of the whelk species accurately predicts the presence of trait-mediated cascades as well as anti-predator behavior to crabs.

A second line of evidence that supports the importance of evolutionary history is that differing foraging strategies (which must be selected for and must evolve through time) lead to differing abilities of native versus invasive crabs to control adult whelks and produce a density-mediated cascade in Tomales Bay. Regardless the size of the crab, prior research (Behrens Yamada & Boulding 1998) and our final laboratory experiment (Fig. 1.4b) suggest that specialist native crabs can effectively control the populations of both native and invasive whelks by peeling open and crushing these relatively large gastropods. But even when whelk avoidance behavior was minimized, generalist invasive crabs still consumed far fewer whelks than did native crabs (Fig. 1.4b). Because invasive crabs consumed whelks only by crushing the shell apex, their ability to consume either whelk appears to be dictated by crab size; higher whelk consumption occurred only when crab sizes were well above modal size classes observed in northeast Pacific and northwest Atlantic populations (Grosholz & Ruiz 1996). Consequently, the invasive crab's historical exposure to other prey has selected a naïve foraging strategy with regards to consuming adult sized whelks (Hughes & Elner 1979). Had Tomales Bay been invaded by a top predator with more effective foraging traits, a density-mediated cascade would also likely reduce oyster losses from the inner bay.

Finally, the evolutionary history of predator-prey pairings also helps to reconcile our results with other studies demonstrating that invasive species do interact to create trophic cascades. In the northwest Atlantic rocky-shore system, the herbivorous snail (*Littorina littorea*) and European green crab (*Carcinus maenas*) are non-native predator-prey that interact to create both density- and trait-mediated cascades benefiting fucoid algae (Lubchenco 1978; Trussell *et al*. 2002). Although these top and intermediate-level

organisms are invaders, they are not naïve to one another since they have interacted both with each other and similar types of predator-prey in their native European range (Vermeij 1982a). We therefore do not believe that every invasive species will fail to participate in trophic cascades. Rather, an invader's effect on food-web dynamics will depend on the types of predator or prey strategies that it historically interacted with. For example, intermediate consumers historically exposed to effective top predators that sit-and-wait before ambushing their prey may more successfully invade food webs with top predators by participating in trait-mediated cascades (Schmitz 2008).

While previous studies of trophic cascades have focused on the impacts of removing top predators via habitat loss or overharvesting, it has recently become clear that these food-web interactions also depend on a predator's identity and hunting strategy (Schmitz *et al*. 2004; Schmitz 2008). Adding to this relatively new focus, our work demonstrates that ecologically replacing native top predators and intermediate consumers with invasive species can dramatically alter food webs by disrupting trophic cascades. All trophic levels within a food web locally co-exist only when top predators and intermediate consumers interact via both density- and trait-mediated cascades. But an invasive intermediate consumer capable of depleting an important foundation species appears to be excluded from the food web, because the invader's naiveté prevents it from recognizing and successfully avoiding a native top predator before being consumed. Thus, echoing the conclusions of previous work on trophic cascades (Byrnes *et al*. 2006; Myers *et al*. 2007), biological invasions (Parker *et al*. 2006), and biodiversity-ecosystem function (Jackson *et al*. 2001; Worm *et al*. 2006), our results suggest that marine food webs can be conserved by protecting native top predators that simultaneously regulate the

foraging of native intermediate consumers (via density- and trait-mediated cascades) and exclude invasive intermediate consumers (via density-mediated cascades). Furthermore, our results counter the argument that native species extinctions at the local and regional scale can be balanced by invasions of functionally similar species (Sax & Gaines 2003), since naiveté can prevent top predators and/or intermediate consumers in invaded food webs from re-creating historically important trophic cascades that maintain biodiversity and ecosystem function (Schmitz 2008).

Acknowledgements

We thank C. Hays, R. Hughes, K. Hultgren, B. Jaffee, E. Sanford, A. Sih, J. Stachowicz, and G. Trussell for comments and ideas that improved this manuscript. S. Attoe, L. Budd, A. Chang, M. Ferner, A. Hettinger, M. Nydam, M. O'Leary, and B. Steves generously provided field assistance. We also thank B. Steves for helping produce the manuscript's figures. This research was supported by grants from the University of California (UC) Marine Council/Coastal Quality Environmental Initiative (to D.L.K.), UC Davis Graduate Group in Ecology (to D.L.K.), National Park Service at Point Reyes National Seashore (to D.L.K.), National Oceanic and Atmospheric Administration (to E.D.G), California Sea Grant (to E.D.G.), National Parks Service-California Cooperative Ecosystem Studies Program (to E.D.G.), Pacific States Marine Fisheries Commission (to E.D.G.), UC Exotic/Invasive Pest and Disease Program (to E.D.G.), and National Science Foundation-Research Experience for Undergraduates (to N.J.N and N.M.T.)

Literature cited

Abrams P.A. (1995) Implications Of Dynamically Variable Traits For Identifying, Classifying, And Measuring Direct And Indirect Effects In Ecological Communities. *American Naturalist*, 146, 112-134

Behrens Yamada S. & Boulding E.G. (1998) Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. *Journal of Experimental Marine Biology and Ecology*, 220, 191-211

Berger J., Swenson J.E. & Persson I.L. (2001) Recolonizing carnivores and naive prey: Conservation lessons from Pleistocene extinctions. *Science*, 291, 1036-1039

Blackburn T.M. & Gaston K.J. (2005) Biological invasions and the loss of birds on islands. In: *Species invasions: insights into ecology, evolution, and biogeography*. (eds. Sax DF, Stachowicz JJ & Gaines SD), pp. 85-110. Sinauer Associates, Sunderland, Mass.

Boulding E.G. & Hay T.K. (1984) Crab Response to Prey Density Can Result in Density Dependent Mortality of Clams Protothaca-Staminea. *Canadian Journal of Fisheries and Aquatic Sciences*, 41, 521-525

Carpenter S.R., Kitchell J.F. & Hodgson J.R. (1985) Cascading Trophic Interactions And Lake Productivity. *Bioscience*, 35, 634-639

Carpenter S.R., Kitchell J.F., Hodgson J.R., Cochran P.A., Elser J.J., Elser M.M., Lodge D.M., Kretchmer D., He X. & Vonende C.N. (1987) Regulation of Lake Primary Productivity by Food Web Structure. *Ecology*, 68, 1863-1876

Colautti R.I., Ricciardi A., Grigorovich I.A. & MacIsaac H.J. (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters*, 7, 721-733

Cox J.G. & Lima S.L. (2006) Naivete and an aquatic-terrestrial dichotomy in the effects of introduced predators. *Trends in Ecology & Evolution*, 21, 674-680

Darwin C.R. (1859) *The origin of species* Literary Classics, New York.

deRivera C.E., Ruiz G.M., Hines A.H. & Jivoff P. (2005) Biotic resistance to invasion: native predator limits abundance and distribution of an introduced crab. *Ecology*, 86, 3364-3376

Elton C.S. (1958) *The ecology of invasions by animals and plants*. University of Chicago Press, Chicago, Illinois.

Estes J.A. & Palmisano J.F. (1974) Sea Otters - Their Role In Structuring Nearshore Communities. *Science*, 185, 1058-1060

Federighi H. (1931) Salinity death-points of the oyster drill snail, Urosalpinx cinerea Say. *Ecology*, 12, 346-353

Garth J.S. & Abbott D.P. (1980) Brachyura: The True Crabs. In: *Intertidal Invertebrates of California* (eds. Morris RH, Abbott DP & Haderlie EC), pp. 594-631. Stanford University Press, Stanford

Gastreich K.R. (1999) Trait-mediated indirect effects of a theridiid spider on an ant-plant mutualism. *Ecology*, 80, 1066-1070

Grabowski J.H., Hughes A.R., Kimbro D.L. & Dolan M.A. (2005) How habitat setting influences restored oyster reef communities. *Ecology*, 86, 1926-1935

Grosholz E.D. & Ruiz G.M. (1996) Predicting the impact of introduced marine species: Lessons from the multiple invasions of the European green crab Carcinus maenas. *Biological Conservation*, 78, 59-66

Hairston N.G., Smith F.E. & Slobodkin L.B. (1960) Community Structure, Population Control, And Competition. *American Naturalist*, 94, 421-425

Hanks J.E. (1957) The rate of feeding of the common oyster drill, Urosalpinx cinerea (SAY), at controlled water temperatures. *Biological Bulletin*, 112, 330-335

Hellberg M.E., Balch D.P. & Roy K. (2001) Climate-driven range expansion and morphological evolution in a marine gastropod. *Science*, 292, 1707-1710

Hughes R.N. & Elner R.W. (1979) Tactics of a Predator, Carcinus-Maenas, and Morphological Responses of the Prey, Nucella-Lapillus. *Journal of Animal Ecology*, 48, 65-&

Jackson J.B.C., Kirby M.X., Berger W.H., Bjorndal K.A., Botsford L.W., Bourque B.J., Bradbury R.H., Cooke R., Erlandson J., Estes J.A., Hughes T.P., Kidwell S., Lange C.B., Lenihan H.S., Pandolfi J.M., Peterson C.H., Steneck R.S., Tegner M.J. & Warner R.R. (2001) Historical Overfishing and the Recent Collapse of Coastal Ecosystems
. *Science*, 293, 629-637

Kaiser M.J., Hughes R.N. & Gibson R.N. (1993) Factors Affecting Diet Selection in the Shore Crab, Carcinus-Maenus(L). *Animal Behaviour*, 45, 83-92

Kimbro D.L. & Grosholz E.D. (2006) Disturbance influences oyster community richness and evenness, but not diversity. *Ecology*, 87(9), 2378-2388

Kraemer G.P., Sellberg M., Gordon A. & Main J. (2007) Eight-year record of Hemigrapsus sanguineus (Asian shore crab) invasion in Western Long Island Sound Estuary. *Northeastern Naturalist*, 14, 207-224

Lubchenco J. (1978) Plant Species-Diversity In A Marine Inter-Tidal Community - Importance Of Herbivore Food Preference And Algal Competitive Abilities. *American Naturalist*, 112, 23-39

Paine R.T. (1980) Food Webs - Linkage, Interaction Strength And Community Infrastructure - The 3rd Tansley Lecture. *Journal Of Animal Ecology*, 49, 667-685

Parker J.D., Burkepile D.E. & Hay M.E. (2006) Opposing effects of native and exotic herbivores on plant invasions. *Science*, 311, 1459-1461

Polis G.A., Sears A.L.W., Huxel G.R., Strong D.R. & Maron J. (2000) When is a trophic cascade a trophic cascade? *Trends In Ecology & Evolution*, 15, 473-475

Power M.E., Matthews W.J. & Stewart A.J. (1985) Grazing Minnows, Piscivorous Bass, and Stream Algae - Dynamics of a Strong Interaction. *Ecology*, 66, 1448-1456

Preisser E.L., Bolnick D.I. & Benard M.F. (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, 86, 501-509

Sax D.F. & Gaines S.D. (2003) Species diversity: from global decreases to local increases. *Trends In Ecology & Evolution*, 18, 561-566

Scheiner S.M. & Gurevitch J. (2000) *Design and Analysis of Ecological Experiments*. Chapman and Hall, New York.

Schmitz O.J. (2008) Effects of predator hunting mode on grassland ecosystem function. *Science*, 319, 952-954

Schmitz O.J., Krivan V. & Ovadia O. (2004) Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, 7, 153-163

Sih A. (1985) Evolution, Predator Avoidance, and Unsuccessful Predation. *American Naturalist*, 125, 153-157

Smith L.D. (2004) Biogeographic differences in claw size and performance in an introduced crab predator Carcinus mamas. *Marine Ecology-Progress Series*, 276, 209-222

Stachowicz J.J. (2001) Mutualism, facilitation, and the structure of ecological communities. *Bioscience*, 51, 235-246

Strauss S.Y., Lau J.A., Schoener T.W. & Tiffin P. (2007) Evolution in ecological field experiments: implications for effect size. *Ecology Letters*, 11, xxx-xxx

Strong D.R. (1992) Are Trophic Cascades All Wet - Differentiation And Donor-Control In Speciose Ecosystems. *Ecology*, 73, 747-754

Trussell G.C., Ewanchuk P.J. & Bertness M.D. (2002) Field evidence of trait-mediated indirect interactions in a rocky intertidal food web. *Ecology Letters*, 5, 241-245

Turner A.M. & Mittelbach G.G. (1990) Predator Avoidance And Community Structure - Interactions Among Piscivores, Planktivores, And Plankton. *Ecology*, 71, 2241-2254

Underwood A.J. (1981) Techniques of analysis of variance in experimental marine biology and
ecology. *Oceanography and Marine Biology Annual Review* 19, 513-605

Vermeij G.J. (1982a) Environmental change and the evolutionary history of the Periwinkle (Littorina littorea) in North America. *Evolution*, 36, 561-580

Vermeij G.J. (1982b) Unsuccessful Predation and Evolution. *American Naturalist*, 120, 701-720

Vermeij G.J. (2001) Community Assembly in the Sea Geologic History of the Living Shore Biota. In: *Marine Community Ecology* (eds. Bertness MD, Gaines SD & Hay ME), pp. 39-60. Sinauer Associates, Inc., Sunderland, MA

Vermeij G.J. (2005) Invasion as expectation: a historical fact of life. In: *Species invasions: insights into ecology, evolution, and biogeography* (eds. Sax DF, Stachowicz JJ & Gaines SD), pp. 315-340. Sinauer Associates, Sunderland, Mass.

Werner E.E. & Peacor S.D. (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology*, 84, 1083-1100

Williams A.B. (1984) *Shrimps, lobsters and crabs of the Atlantic coasts of the eastern United States, Maine to Florida*. Smithsonian Institution Press, Washington, D.C.

Worm B., Barbier E.B., Beaumont N., Duffy J.E., Folke C., Halpern B.S., Jackson J.B.C., Lotze H.K., Micheli F., Palumbi S.R., Sala E., Selkoe K.A., Stachowicz J.J. & Watson R. (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science*, 314, 787-790

Table 1.1. Temperature and salinity of water at adjacent Middle- and Inner-bay sites.

	Mean (±SE) and maximum value of water column temperature (C) for summer months	Mean (±SE) and minimum value of water column temperature (C) for winter months	Mean (±SE) and maximum value of water column salinity (ppt) for summer months	Mean (±SE) and minimum value of water column salinity (ppt) for winter months
Middle bay	Mean = 18.27 (±0.43) Maximum = 19.29	Mean = 12.76 (±0.92); Minimum = 11.95	Mean = 33.10 (±0.42) Maximum = 34.00	Mean = 31.73 (±1.14) Minimum = 27.52
Inner bay	Mean = 19.08 (±0.43) Maximum = 20.74	Mean = 12.81 (±0.92) Minimum = 11.80	Mean = 33.03 (±0.42) Maximum = 34.03	Mean = 30.16 (±1.35) Minimum = 26.58

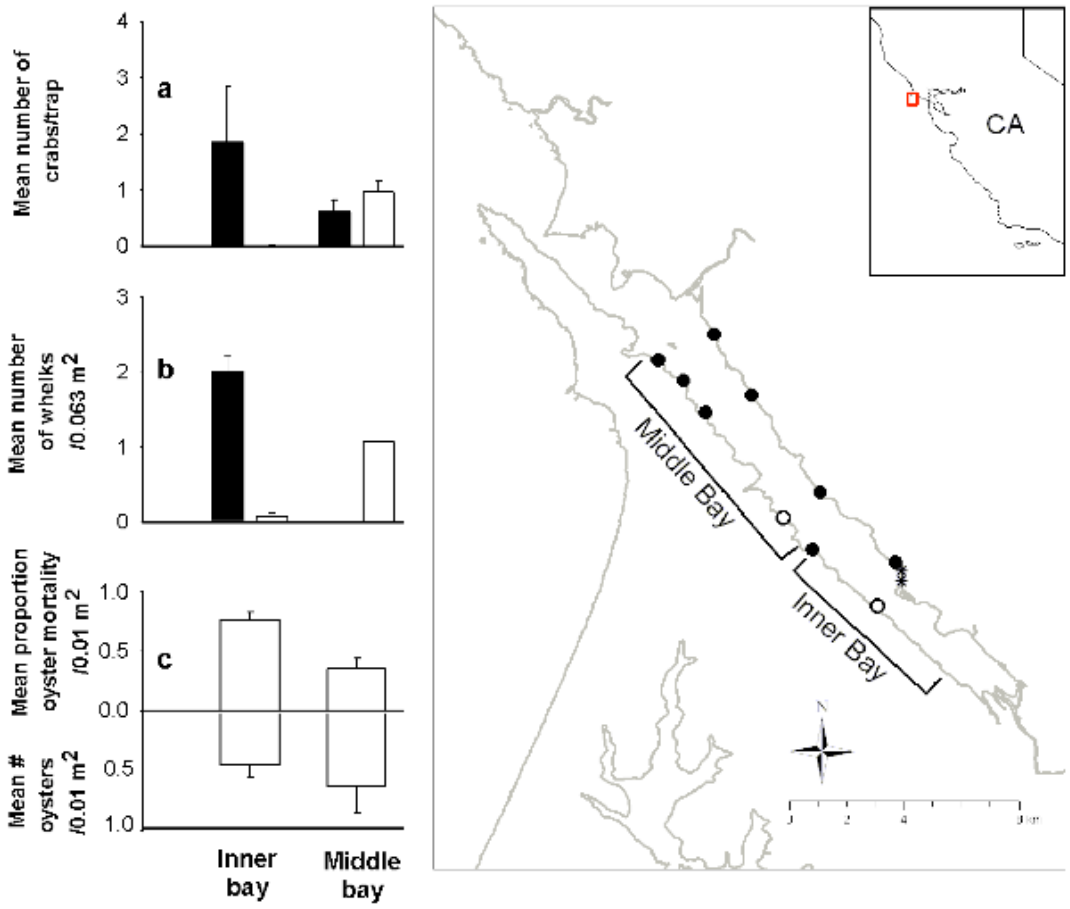


Figure 1.1. Map of research sites in Tomales Bay, CA and histograms showing changes in mean abundance (± SE) of: (a) invasive and native crabs, (b) invasive and native whelks, and (c) native oyster mortality (top) and living oysters from latest survey (bottom) for the inner and middle regions of the bay. Invaders are in closed bars; natives are in open bars. Open circles represent sites that were also used in the field experiment, and asteriks represent sites where only crabs were sampled. Approximately 70% of this estuary's intertidal zone contains the same three-level trophic structure (i.e., crabs, whelks, and oysters), but five kilometers of the inner bay are dominated by invasive crabs (mean size ± SD = 58.41 mm ± 12.09; Fig 1a), invasive whelks (23.79 mm ± 2.94; Fig.

1.1b), and high mortality of native oysters (35.51 mm $\pm$ 8.75; Fig 1.1c). In contrast, 6 km of the middle bay are dominated by native crabs (86.67 mm $\pm$ 25.62), native whelks (22.98 mm $\pm$ 4.70), and low mortality of native oysters (48.03 mm $\pm$ 8.60). Despite historically receiving less oyster recruitment and having fewer adult oysters, the middle bay now has 25% more living oysters than does the inner bay (Fig. 1.1c).

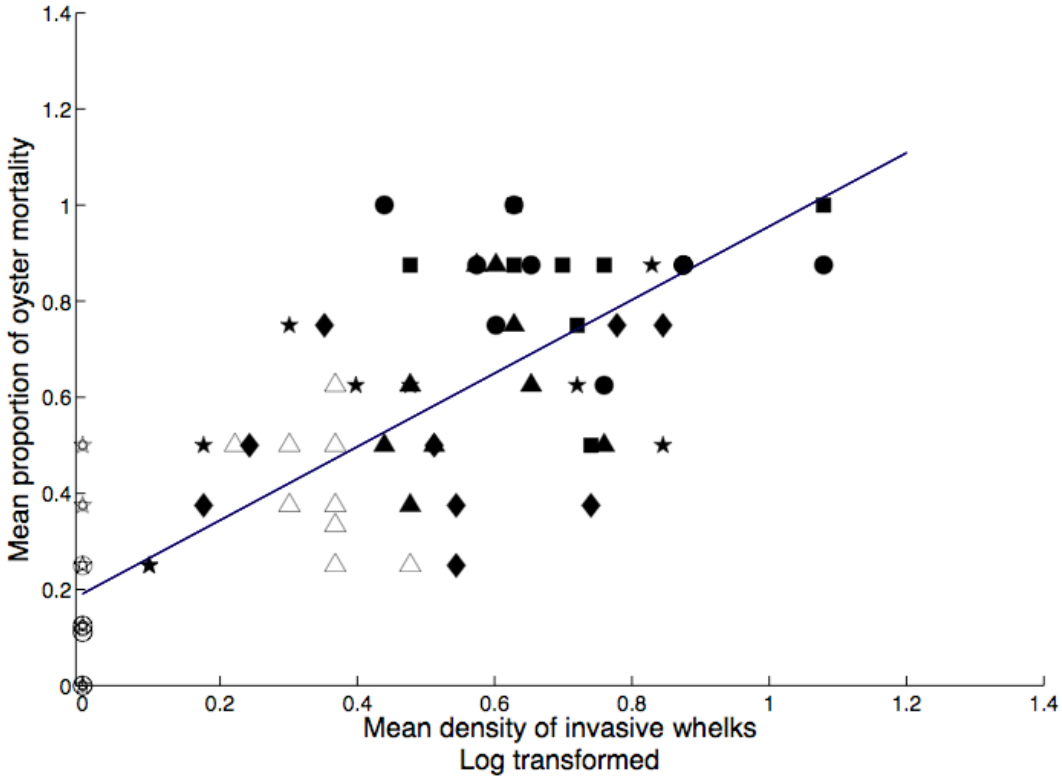


Figure 1.2. Ordinary least squares regression of proportional oyster mortality after ten weeks on mean invasive whelk density over that ten-week period (R^2= 0.64, Y = 0.23x + 0.07). Data taken from a factorial field experiment that used treatment and site as factors. In this plot, markers distinguish treatments [cage control (☐), control (◊), consumer exclosure (*), shade (⍬), and whelk enclosure (Δ)] and color distinguishes sites [inner bay (black symbols) and middle bay (white symbols)].

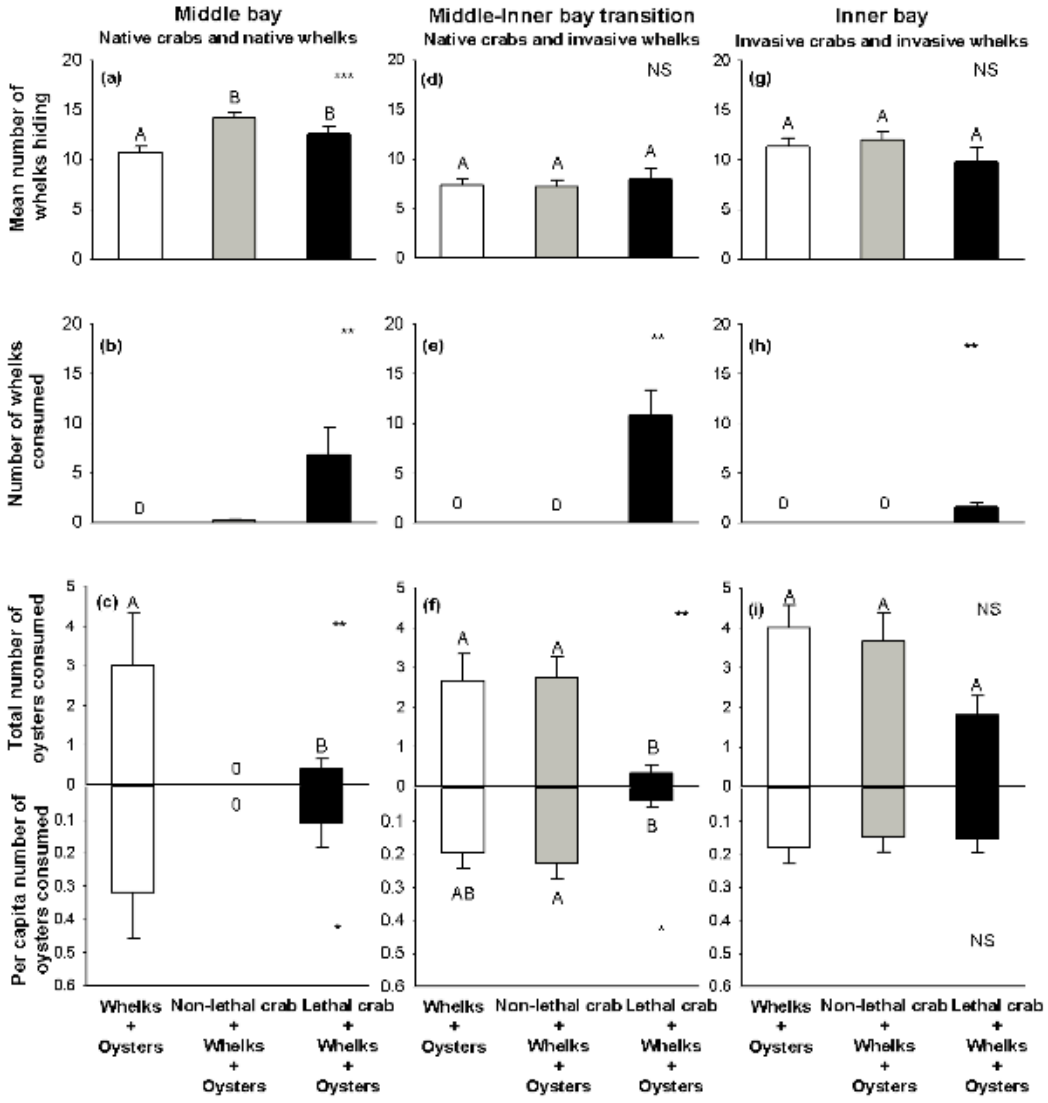


Figure 1.3. Results of three food web experiments with (a-c) native top predator and native intermediate consumer, (d-f) native top predator and invasive intermediate consumer, and (g-i) invasive top predator and invasive intermediate consumer. For each food web experiment, the mean (± SE) of four response variables are presented: (a,d,g) least-squares mean number of whelks hiding, (b,e,h) number of whelks consumed, and (c,f,i) total (upper) as well as per capita (lower) number of oysters consumed by whelks. Significance levels are indicated as follows: *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$; and

NS, not significant (n = 6, except n = 9 for food web with native top and invasive intermediate consumers). Letters above error bars indicate significant differences among the three treatments: whelks and oysters (open bars); non-lethal crabs, whelks, and oysters (gray bars); lethal crabs, whelks, and oysters (black bars). Except for the mean comparison in Fig. 1.3c, which used a t-test, all means were compared using Tukey's post hoc test of means.

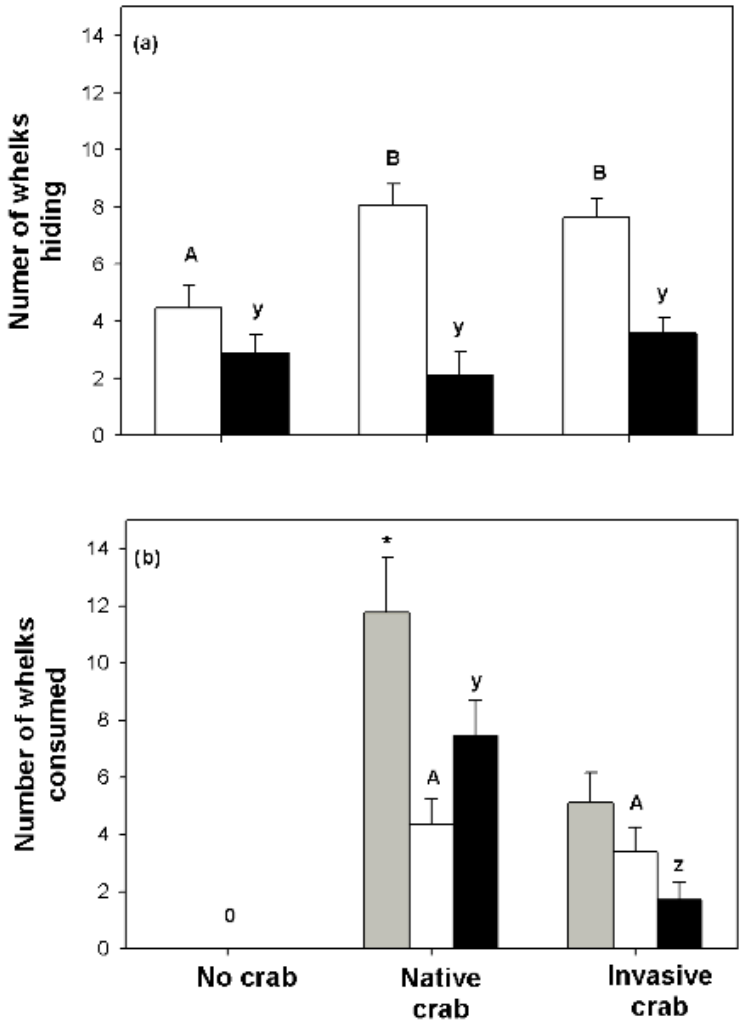


Figure 1.4. Results of (a) least-squares mean number of whelks hiding and (b) crab consumption of whelks when whelk behavior was minimized. In (a), native whelks are open bars and invasive whelks are closed bars. In (b), total number of whelks consumed (gray bars), number of native whelks consumed (white bars), and number of invasive whelks consumed (black bars) are presented.

Appendix 1.1. Summary of field-survey methods used to generate the distribution and abundance data of crabs, whelks, and oysters illustrated in Figure 1.1.

To quantify how the densities of whelks and the mortality of their oyster prey vary throughout the estuary, we conducted four annual intertidal surveys (2003-06) at 6 sites within the middle region of Tomales Bay (6-12 km from the ocean) and 3 sites within the inner bay (13-18 km from ocean) (Fig. 1.1). After selecting equal-sized sites (~300 m) with suitable oyster habitat (intertidal rocks within + 0.5 to –1.5 m MLLW), we divided each site into three –100 m sections perpendicular to the waterline. Each section was then bisected to create high and low intertidal oyster zones paralleling the waterline (six zones/site). In the center of each zone, a 15 m transect paralleling the waterline was established to measure oyster densities. To improve dispersion, each 15 m transect was divided into 7.5 m sub-transects along which we randomly selected three rocks to survey, yielding 6 rocks per transect (36 per site).

For each rock, we centered a 0.01 m^2 quadrat on the top, bottom, and side surfaces and counted living and dead oysters. Using the three quadrats as sub-samples, we generated an average density of living and dead oysters for each rock. By converting a site's mean density of living and dead oysters into proportional abundances, we normalized sites for differences in oyster density and recruitment. On the same randomly selected rocks, we quantified the abundance of native and invasive whelks within a 0.063 m^2 quadrat, and these data were averaged to produce mean whelk densities for each site. Also at these same sites, we sampled crab densities (top predator) by deploying ~ten baited traps spaced at 10 m intervals. After 24 hours, we identified and counted crabs

within each trap. For each site, we calculated a mean density of invasive and native crabs.

To illustrate striking differences of predator identity and oyster demography throughout the bay, we divided the estuary into two regions (i.e., inner and middle bay) and pooled each region's data to show the mean (±SE) abundance for all three trophic levels: native and invasive crabs (Fig. 1.1a); native and invasive whelks (Fig. 1.1b); proportional abundance of oyster mortality (Fig. 1.1c); and mean abundance of living oysters (Fig. 1.1c).

Appendix 1.2. Summary of invasive and native crab catches in the Inner (**a**) and Middle (**b**) regions of Tomales Bay. For each month, we present the Mean number (±SE) of invasive and native crabs caught per trap, the number of sites trapped within each region, and the total number of traps deployed.

a	Mean (±SE) number of invasive crabs/trap	Mean (±SE) number of native crabs/trap	Number of sites trapped	Number of traps deployed
Oct. 2003	0.33 (± 0.42)	0.0 (± 0.0)	2	18
Nov. 2003	1.1 (± 1.85)	0.0 (± 0.0)	1	10
Dec. 2003	0.55 (± 0.50)	0.03 (± 0.09)	4	31
Jan. 2004	0.28 (± 0.42)	0.0 (± 0.0)	3	39
March 2004	8.1 (± 7.77)	0.0 (± 0.0)	4	40
April 2004	10.0 (± 11.51)	0.0 (± 0.0)	1	6
Oct. 2005	0.75 (± 1.05)	0.08 (± 0.21)	2	14
April 2006	0.2 (± 0.21)	0.0 (± 0.0)	2	10
1 May 2006	0.6 (± 0.6)	0.0 (± 0.0)	2	10
15 May 2006	0.17 (± 0.28)	0.0 (± 0.0)	2	12
June 2006	0.08 (± 0.21)	0.0 (± 0.0)	2	12
Aug. 2006	0.0 (± 0.0)	0.0 (± 0.0)	2	12

b	Mean (±SE) number of invasive crabs/trap	Mean (±SE) number of native crabs/trap	Number of sites trapped	Number of traps deployed
Oct. 2003	--	--	--	--
Nov. 2003	1.1 (± 1.29)	0.9 (± 1.73)	1	10
Dec. 2003	0.3 (± 0.67)	2.1 (± 2.36)	1	10

Jan. 2004	0.6 (± 0.97)	0.1 (± 0.31)	1	10
March 2004	2.4 (± 2.37)	0.5 (± 0.53)	1	10
April 2004	--	--	--	--
Oct. 2005	0.0 (± 0.0)	1.71 (± 1.81)	3	21
April 2006	0.16 (± 0.21)	0.84 (± 0.78)	5	25
1 May 2006	0.6 (± 0.62)	0.76 (± 0.59)	5	25
15 May 2006	0.37 (± 0.27)	0.3 (± 0.29)	5	30
June 2006	0.24 (± 0.23)	1.24 (± 1.0)	5	25
Aug. 2006	0.27 (± 0.31)	1.2 (± 1.04)	5	30

Appendix 1.3. Summary of whelk surveys in the Inner (**a**) and Middle (**b**) regions of Tomales Bay. For the results of each annual survey, we present the Mean (± SE) number of invasive and native whelks found per quadrat (0.063 m^2), number of sites surveyed within each region, and the total number of quadrats sampled.

a	Mean (±SE) number of invasive whelks/0.063m^2	Mean (±SE) number of native whelks/0.063m^2	Number of sites surveyed	Number of quadrats sampled
2003*	2.08 (±2.70)	0.0 (±0.0)	2	64
2004	2.46 (±2.18)	0.11 (±0.39)	2	72
2005	2.03 (±1.60)	0.01 (±0.07)	2	71
2006	1.45 (±1.15)	0.19 (±0.48)	3	108

b	Mean (±SE) number of invasive whelks/0.063m^2	Mean (±SE) number of native whelks/0.063m^2	Number of sites surveyed	Number of quadrats sampled
2003*	0.0 (±0.0)	1.31 (±1.67)	2	64
2004	0.0 (±0.0)	0.77 (±0.88)	5	180
2005**	0.0 (±0.0)	0.84 (±0.7)	6	158
2006	0.009 (±0.04)	1.37 (±1.67)	6	213

* This annual survey differed from later surveys by partitioning sites into 2 sections, rather than 3, and selecting 8 rocks per transect. This method yielded 32 rocks per site versus 36.

**Some data lost for two sites.

Appendix 1.4. Summary of annual oyster surveys in the Inner (**a**) and Middle (**b**) regions of Tomales Bay. For the results of each survey, we present Means (± SE) for proportion of oyster mortality and density of living oysters found per quadrat (0.01 m^2), the number of sites surveyed within each region, and the total number of rocks sampled.

a	Mean (± SE) proportional abundance of oyster mortality/0.01m^2	Mean (± SE) abundance of living oysters/0.10m^2	Number of sites surveyed	Number of rocks sampled
2005	0.69 (± 0.23)	1.18 (± 0.25)	2	72
2006	0.83 (± 0.13)	0.46 (± 0.13)	3	108

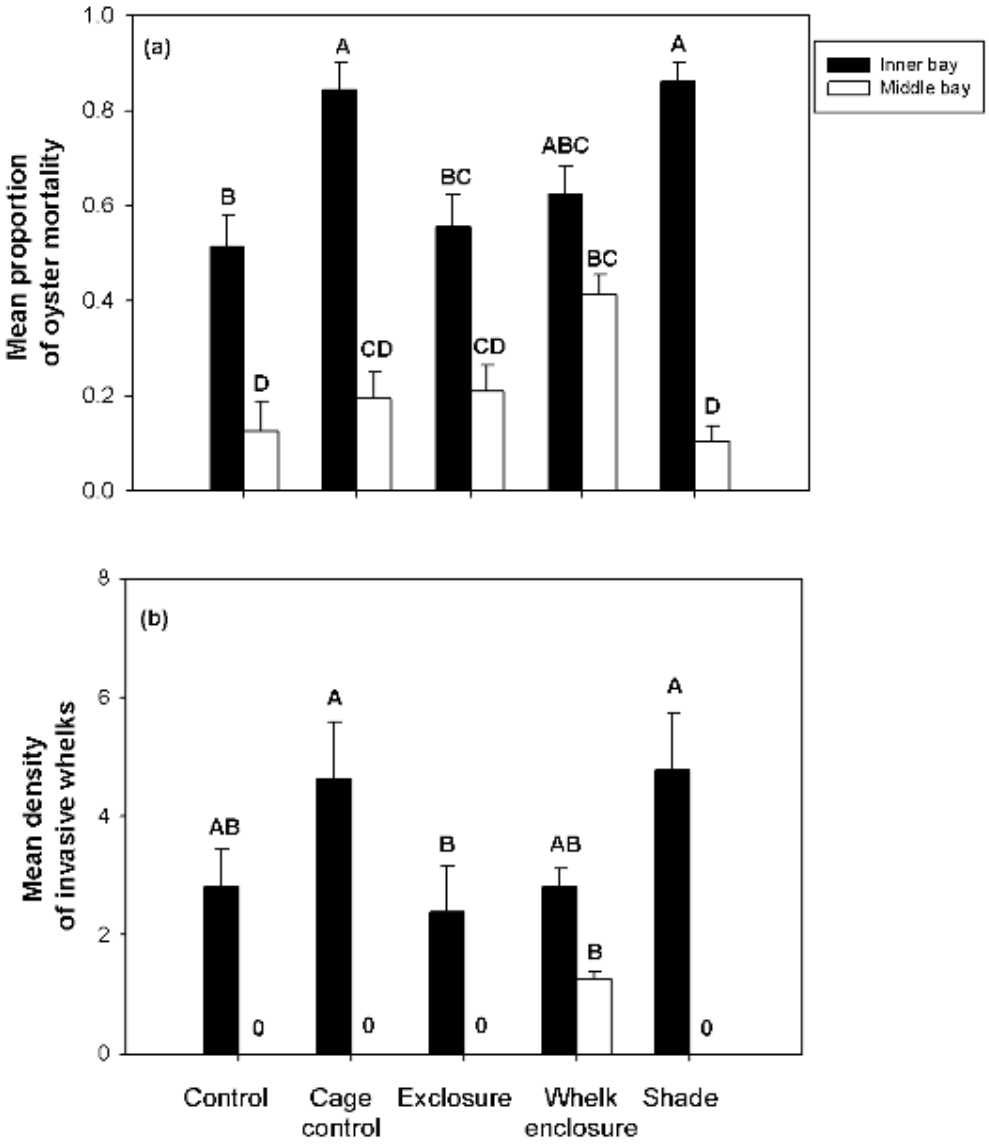
b	Mean (± SE) proportional abundance of oyster mortality/0.01m^2	Mean (± SE) abundance of living oysters/0.01m^2	Number of sites surveyed	Number of rocks sampled
2005**	0.26 (± 0.17)	0.71 (± 0.22)	5	162
2006	0.44 (± 0.13)	0.62 (± 0.22)	6	213

* 2003-04 data did not include relative abundance of dead oysters and are not presented.

** Some data lost for two sites.

*** Data are not included in oyster mortality results if rocks lacked oysters.

Appendix 1.5. Treatment means (±SE) of **(a)** proportional oyster mortality and **(b)** invasive whelk density during a ten week experiment in the inner bay (closed bars) and middle bay (open bars).



Chapter 2: Upwelled nutrients and tidal exchange consistently create phytoplankton blooms that influence oyster growth in a central California estuary.

ABSTRACT: While coastal upwelling often promotes primary production of phytoplankton, intensive upwelling can transport newly generated phytoplankton offshore and make it inaccessible to benthic-suspension feeders along coastlines. In the presence of low-food and cold-water conditions, benthic-invertebrates in upwelling regions may experience lower metabolic rates and less growth than do invertebrates in non-upwelling regions that are characterized by low-food, but warm-water conditions. These observations suggest that the temperature of water better explains size and growth patterns of invertebrates than can the presence of upwelling and primary-production levels. Low-inflow estuaries, however, may predictably enable intensive upwelling and phytoplankton to better explain the growth of benthic-suspension feeders. In a central California estuary that receives little fresh water input during seasonal upwelling, it has been predicted the waters are mixed solely by a tidal exchange gradient that decreases with distance from the ocean. Here, we empirically demonstrate that this tidal-exchange gradient occurs and that it leads to inversely related spatial gradients in coastally-derived nutrients and water-residence times. As a result, seasonal phytoplankton blooms occur in the middle of the bay where intermediate nutrient levels and water-residence times interact, while seasonal temperature maximums occur in the inner-bay where water-residence-times are longer. By out-planting juvenile native California oysters (*Ostrea lurida*) at outer, middle, and inner portions of the bay, we show that phytoplankton better explains the growth of oysters than does water temperature. Thus, benthic invertebrates

within protected embayments of upwelling regions may not conform to the generalization that temperature controls growth.

Introduction

Understanding how nearshore oceanography interacts with benthic population and community dynamics remains one of the outstanding challenges for marine ecology, despite a growing number of studies that link the two (Menge 1992; Wootton *et al*. 1996; Menge *et al*. 2003; Leslie *et al*. 2005; Blanchette *et al*. 2007). In eastern boundary current regions of ocean basins, the growth of benthic suspension feeding invertebrates (e.g., mussels) may be influenced by coastal upwelling (Menge & Branch 2001). During upwelling, along-shore winds create an offshore Ekman Transport of nearshore surface waters, which in turn brings nutrient-rich sub-surface waters up into the euphotic (Mann & Lazier 2006). In response to elevated nutrient concentrations, high rates of primary production occur in the clear light-filled surface waters, resulting in high levels of phytoplankton biomass (Huntsman & Barber 1977). These phytoplankton blooms can enhance the growth and abundance of benthic suspension feeding invertebrates (Menge *et al*. 1997; Menge *et al*. 2003; Dugdale *et al*. 2006).

While coastal upwelling reliably increases nearshore nutrient levels (Chavez *et al*. 2002), it does not always result in phytoplankton blooms (Largier *et al*. 2006), which require photosynthesis to exceed respiration and, further, to do so strongly enough to allow for accumulation in spite of dilution of phytoplankton through mixing (Mann & Lazier 2006). And, in turn, neither can one expect high invertebrate growth to be always associated with upwelling (Phillips 2005; Blanchette *et al*. 2007). Following Largier *et*

al. (2006), the same wind-driven upwelling that delivers nutrients also rapidly mixes water to depth and transports water and phytoplankton offshore. Thus, upwelling alone will not yield phytoplankton blooms (Dugdale *et al*. 2006; Blanchette *et al*. 2007). However, upwelling is neither persistent nor uniform and intense phytoplankton blooms are readily observed at times and locations where aged upwelled water is observed adjacent to active upwelling.

For example, physical features along coastlines interact with upwelling to create predictable bloom patterns in phytoplankton, such as those found in 'upwelling shadows' – areas of weak or zero upwelling downwind of headlands (Graham & Largier 1997; Marin *et al*. 2001; Pitcher & Nelson 2006; Vander Woude *et al*. 2006). During active upwelling, high-nutrient waters upwelled at the headland are advected into adjacent bays, where they are then retained long enough and with weak enough mixing that high levels of phytoplankton develop and persist as long as upwelling persists. Thus, upwelling shadows are a habitat with predictable phytoplankton-rich waters within an intensive upwelling region, with consequences for the growth of intertidal suspension feeders (Graham & Largier 1997; Broitman & Kinlan 2006; Pinones *et al*. 2007).

Similar persistent spatial patterns may develop in semi-enclosed bays where upwelled waters are retained long enough to allow phytoplankton blooms to develop. While previous studies have discussed residence times in these bays (Largier *et al*. 1997), and how exchange is controlled by tides, there has been a lack of studies addressing phytoplankton distributions and the availability of this food to benthic invertebrates (but see Camacho-Ibar *et al*. 2003; Banas *et al*. 2007). In upwelling regions with Mediterranean climates (i.e., wet winters and dry summers) like northern California

U.S.A., the inner portions of many estuaries receive little freshwater input and experience high evaporation during summer months when nearshore upwelling is most intense (Mann & Lazier 2006, Fig. 2.1a). As a result, these "low-inflow estuaries" lack a classical longitudinal salinity gradient and "estuarine circulation" resulting in a retention of water. Nutrient supply to the estuary is dominated by an influx from the ocean, which his controlled by tidal exchange (Largier *et al*. 1997). Since tidal excursion decreases with distance from the mouth of the bay, so do mixing rates and the concomitant increase in residence time can be expected to yield a spatially predictable phytoplankton bloom pattern (Largier *et al*. 1997). The outer bay is characterized by newly upwelled waters and strong tidal mixing, precluding the accumulation of phytoplankton biomass, whereas the innermost bay will characterized by well-aged, nutrient-depleted water unable to support phytoplankton growth in spite of weak mixing (but susceptible to cultural eutrophication if local human activity results in a nutrient flux to these long-residence backwaters; e.g., Boyle *et al*. 2004). In the mid-bay, waters have an intermediate age that matches typical phytoplankton blooms times (Dugdale *et al*. 2006), and mixing dilution rates are low enough to allow for accumulation of phytoplankton (but significant enough to provide the necessary flux of pelagic nutrients to maintain the phytoplankton bloom here).

Here, we investigate whether there is evidence for the above ideas – that the tidal flux of upwelled nutrients to the bay and retention of phytoplankton in the bay indeed result in a characteristic spatial pattern in Tomales Bay, California, USA. Tomales Bay (38°.231 N and 122°.978 W) is a linear basin that is 20 km long and about 1 km wide. It has been tectonically formed and lies on the San Andreas Fault (Hearn & Largier 1997).

This low-inflow estuary receives little river inflow during the summer upwelling season and has a negative hydrological balance due to evaporation exceeding freshwater inflow (Hearn & Largier 1997). Following previous studies (Hearn & Largier 1997; Largier *et al*. 1997), this lack of freshwater input results in opposed gradients of retention time and nutrient availability, with nitrate levels decreasing into the bay and residence times decreasing towards the mouth (Fig. 2.1b).

Secondly, we investigate whether observed phytoplankton patterns have a significant influence in supplying food to benthic invertebrate populations, such as the native oyster, and thus in explaining observed spatial patterns in invertebrate growth. In addition to being important prey at the bottom of food webs, some benthic suspension-feeding invertebrates in low-inflow estuaries (e.g., oysters) also provide habitat that benefits the fitness and diversity of other organisms by ameliorating stress (Bruno & Bertness 2001; Stachowicz 2001). Because the strength of facilitation is often dependent on size or structural complexity of the foundation species (Bruno & Bertness 2001)—and these depend on the rates of recruitment, growth and survival of the foundation species—upwelling can indirectly affect the importance of foundation species. Although the link between coastal upwelling and the growth of foundation species along the outer coast has been examined (Menge & Branch 2001; Blanchette *et al*. 2007; Menge *et al*. 2008) considerably less research has investigated the bottom up effect of oceanography on estuarine foundation species.

Tomales Bay contains a remnant population of native California oysters (*Ostrea lurida*, hereafter Olympia oyster) that still functions as a foundation species despite being over harvested in the early 20th Century (Kirby 2004; Kimbro & Grosholz 2006). But the

oyster's importance as habitat likely varies spatially since oysters appear to be larger in the middle of the bay.

In this study, we test four hypotheses to examine if and why oyster size varies throughout Tomales Bay: (1) Tidal excursion decreases with increasing distance from the mouth of the bay; (2) Phytoplankton biomass (i.e., chl *a*) peaks in the middle of the bay during upwelling months, due to an interplay of nitrate availability and water residence time; (3) Oyster size distributions are skewed toward larger sizes in the middle of the estuary; (4) Levels of phytoplankton biomass influence oyster growth and explain observed differences in oyster size.

Methods

Natural history of Olympia oyster

The Olympia oyster is a protandrous hermaphrodite that is native to eastern Pacific estuaries from Alaska to Baja California Sur, Mexico (Baker 1995). After embryos are brooded within adult oysters for 10-14 days, planktotrophic larvae develop for 4-6 weeks during summer months before settling on hard substrate such as rocks and cobbles (median surface area = 0.7 m^2, Kimbro and Grosholz *unpublished data*). Oysters can grow to ~ 0.06 m in length and often create loose reefs (~ 0.10 m tall) in low intertidal and shallow subtidal portions of estuaries (Baker 1995). Because hard substrate is limited in soft sediment estuaries, oysters compete amongst themselves and with other sessile organisms for space on rocks. At the same time, the biogenic structure of Olympia oysters provides habitat for associate species including amphipods and polychaetes as well as sponges and algae that live on the oysters (Kimbro & Grosholz

2006). Olympia oysters occur across broad areas of shoreline (~20 km) in Tomales Bay with densities up to 40 oysters per 0.063 m^2.

Estimating tidal excursion

To demonstrate that tidal excursion decreases with distance from the mouth, as expected from 1-dimensional mass balance (or continuity) estimates (Largier *et al*. 1997; Harcourt-Baldwin & Diedericks 2006) at each of 3 distances from the mouth we deployed four satellite-tracked surface drifters, encompassing most of the oyster's distribution (distances of 8, 12 and 16km from the mouth). Drifters were drogued between 0.5 and 1.5m and tracked via internal recording Garmin GPS units recording position every 2 minutes; their design is described in detail elsewhere (Davis 1985; Largier 2003). Given that Tomales Bay is well-mixed (Largier *et al*. 1997; Harcourt-Baldwin & Diedericks 2006) with negligible vertical shear in currents, it is expected that these drifter trajectories provide a good measure of currents throughout the water column. For each distance from the mouth, three drifters were equidistantly deployed across the bay (1/4, 12/, and 3/4 of the width), with the fourth one also at half-width. All drifters were deployed in less than an hour during high tide early morning on 2 August 2007. This day was chosen because of the symmetrical tidal cycle (starting with a high tide of 5.8 feet in the morning and ending with a high tide of 5.7 feet in the afternoon). The symmetrical tide allows two observations of excursion (one on flood and one on ebb) and also assessment of tidal residual transport. Tidal range was 5.9 feet on the ebb and 5.8 feet on the flood. Drifters at the 8 km site were deployed around 3:23 am, about 47 minutes after predicted local HW; drifters at 12 km were deployed around 3:51 am, about

69 minutes after predicted local HW; and drifters at 16 km were deployed around 4:10 am, about 86 minutes after predicted local HW. Drifter trajectories are plotted and excursion is calculated as the maximum longitudinal displacement. The small-scale variability in the trajectories also demonstrates small-scale mixing (we only do so qualitatively here).

Physical and biological gradients associated with tidal excursion

To determine the characteristic longitudinal patterns in temperature, salinity and chlorophyll, we conducted monthly boat surveys from 2004 to 2008 in which conductivity-temperature-depth (CTD) profiles were obtained at 10 stations along the estuary (Fig. 2.3) using a SBE19plus CTD (Seabird-Electronic Inc.) fitted with a WETLabs fluorometer. Sampling sites were chosen to repeat those in an earlier study of Biogeochemical Reactions In Estuaries (BRIE) conducted during the late 1980' and early 1990's (Smith *et al*. 1989; Largier *et al*. 1997; http://lmer.marsci.uga.edu/tomales/). Sites were spaced 2km apart and profiles were sampled at 2Hz (approximately 4 values per m). The survey started at the mouth just before slack high tide, and was completed in ~1.5 hours, ending at the station 18km from the mouth about 15-30 minutes after local high tide. We used the Bakun upwelling index (evaluated monthly for latitude 39ºN since 1967; http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/click_map.html) to define seasonality of upwelling for this region (see Fig. 2.1a). Consistent also with this seasonal cycle, we grouped monthly salinity, temperature and chlorophyll-fluorescence data into four seasons: (1) spring transition: March and April, (2) upwelling: May, June, July, and August, (3) fall transition: September and October,

and (4) winter: November, December, January, and February. For each site, all data were then averaged for each station to create seasonal salinity and temperature means ($\pm$ SD).

Water-residence time and nutrient concentrations were not directly sampled. However, salinity and temperature data are good proxies for these parameters. Residence times (T_{res}) for each site were estimated with a bulk (Lagrangian) salt-balance:

$$T_{res} = (S\text{-}S_O)H_{av}/E_{av}S_{av} \qquad \text{(Equation 1)}$$

where S_O represents ocean salinity, S represents the salinity of the specific site, H_{av} represents average water depth along lagrangian trajectory, E_{av} represents the evaporation rate, and S_{av} represents average salinity along the lagrangian trajectory (Largier *et al*. 1997). Salinity values are directly observed and values of 6m and 0.002m/day are used for H and E, respectively (Largier *et al*. 1997). This residence time is a characterization of how long a composite parcel of water has been near-surface and exposed to evaporative loss of freshwater (as well as being exposed to the light that fuels primary production) – in this sense, it is perhaps better thought of as the "age" of the water since it was upwelled. Because this salt-balance assumes steady-state conditions, we estimate residence times only for low-inflow months, i.e., upwelling and fall-transition months, when conditions change slowly and it is reasonable to assume that steady conditions are approximated (Largier *et al*. 1997). Further, we inspected monthly salinity data and river inflow data in these seasons and excluded anomalous months in which inflow was not negligible (e.g., May 2005). As little oyster growth (see chapter 3) and little phytoplankton biomass (except for March 2006, see Appendix 2.1) are observed during winter and spring, our attention is focused on the low-inflow seasons when this simple residence time model is valid.

Nitrate is the limiting nutrient in upwelling systems in general (Dugdale *et al*. 2006), and specifically in this Tomales-Bodega region (Wilkerson *et al*. 2006). Historical data on nitrate concentrations and temperature are available from 1987 to 1995 for all stations in Tomales Bay (Smith *et al*. 1989; http://lmer.marsci.uga.edu/tomales/). Using the expectation that nitrate and temperature are well correlated in recently upwelled waters (Dever *et al*. 2006), due to similar rates of warming and greening of newly upwelled waters, we use these BRIE data to develop a T-N relation that can be used to estimate nitrate concentrations from our monthly observations of temperature during the ocean-dominated summer and fall seasons in Tomales Bay. These data are shown in Appendix 2.2. We fit a quadratic function to the data with $R^2 = 0.6$ in summer and $R^2 = 0.7$ in fall. Further, we also obtain a bi-linear curve that defines the maximum nitrate concentration observed during BRIE for a given water temperature: for water temperatures over 18ºC one expects nitrate below 3 in the upwelling season and below 6 in the fall (and near-zero nitrate when temperatures exceed 22ºC). These expected and maximum possible nitrate values are plotted in Appendix 2.2.

Oyster-size distributions

During the spring of 2006, we surveyed oyster sizes at multiple sites (Fig. 2.5) spanning the entire distribution of oysters in Tomales Bay (6 km – 17 km distance from the mouth of the bay). After selecting equal-sized beaches (~300 meters long) with suitable oyster habitat (intertidal rocks within + 0.5 to –1.5 m MLLW), we vertically divided each beach (relative to horizontal waterline) into three 100m-long sections. Each section's oyster habitat was then horizontally bisected to create a high and low intertidal

oyster zone paralleling the waterline (six zones /site). Within the middle of each high and low oyster zone, a 15 meter horizontal transect was established and then centered in its respective 100m section.

After partitioning each site's oyster habitat, we selected rocks along transects to sample for oyster densities. To avoid selecting rocks clustered at the end of transects, each 15 m transect was divided into two 7.5 m sub-transects. We then marked all rocks occurring within 35 cm of the sub-transects. Each sub-transect's marked rocks were tallied and three rocks were randomly selected to survey, yielding six rocks per transect. For each rock, we centered a 0.01 m^2 quadrat on the top, bottom, and side surfaces and measured the size of all oysters within each quadrat. Using three different non-parametric tests (Wilcoxon/Kruskal-Wallis rank scores, Median rank scores, and Van der Waerden rank scores), we then compared oyster size distributions among sites.

Oyster-growth experiment

To determine whether the spatial distribution of phytoplankton directly affects oyster size and growth, we conducted two different experiments at sites on the western shoreline of Tomales Bay. By spawning adult oysters at the Bodega Marine Laboratory, we were able to settle juvenile oysters onto PVC tiles (0.01 m^2). For the first experiment, we randomly assigned 36 tiles among three sites [sites W2 (8 km), W3 (12 km), and W4 (16 km); n = 9) in July 2006. These sites encompass most of the oyster's distribution, the time of deployment coincides with the season of oyster recruitment, and the tile size is similar to the small cobbles commonly found at these sites (Kimbro and Grosholz *unpublished data*). Before deploying tiles, we marked five oysters per tile with small

numbered tags (Floy Tags Inc., FTF-69 Fingerling Tag-Pennant) and took digital photos of each tile. We then photographed all tiles monthly thereafter, although prior to photos, we removed other sessile invertebrates and algae. Using image analysis software (Metamorph 6.0, Universal Imaging Corporation), we estimated individual growth rates by the change in oyster size between months from July-October 2006.

To better estimate important biotic and abiotic variables at each site where oyster growth was measured, we deployed time-series sensors for chlorophyll fluorescence (WETLabs FLNTUSB-525 sampling every 5 minutes) and water temperature (SeaBird SBE39 sampling every 2 minutes) about 10m offshore of the oyster growth sites. Although most data were of high quality, there was a recurrent spiking problem (repeated data with instrument full-range value of 50 mg/m^3 – values which are too high and also form a distinct second peak in data distributions). As this problem went away after re-installing the anti-fouling wiper blades, this appears to have been the cause of the data problem. However, without confidence that we had removed all spikes, we could not simply calculate the mean value and rather calculated 48-hour median values, which were then used to obtain a monthly mean of chl-a as an estimate of food availability. While tidal fluctuations are not represented in 48-hour-median data, these records do provide a clear signal of variability on time scales sufficiently shorter than the key bloom and upwelling time scales that characterize variations in the food and thermal environments. Finally, we encountered further data problems in loss of the fluorometer at site 16 km during the final month of the 2006 experiment, and failure in data recording at the other two sites for the last two weeks. Thus, we do not have chl *a* data for September-October (Fig. 2.6c), nor temperature data for site 16 km (Figs. 2.6d).

Although the moored fluorometers provide higher resolution of how chl-a may differ among sites, they were different instruments in a different environment (shallow turbid nearshore waters) when compared to the boat-based CTD results. To avoid making invalid comparisons between numbers from the two different fluorescent-sampling procedures, we have not used a standard conversion, but rather just report data in volts which still allows the comparison among sites.

Using a Repeated Measures Univariate Analysis of Variance (ANOVA) with modified degrees of freedom to account for the assumption of sphericity (Quinn & Keough 2002), we first tested whether differences among sites in mean size and growth of oysters depended on time (i.e., sampling month). When significant Site*Time interactions were detected, we then used ANOVA and Tukey's post-hoc comparison of means to test how site means differed within each month. This procedure produced three mean comparisons for oyster growth rates and four comparisons for oyster sizes. Variances involved in all comparisons were homogeneous. To investigate whether oyster growth rate depended on chl *a* and temperature, we used a multiple linear regression of monthly oyster growth rate as the dependent variable versus monthly means of chl *a* and temperature as explanatory variables.

This 2006 experiment was repeated from July-August 2007, except an outer-bay site (6 km) was added. Because this site generally has lower chl *a* values than do middle-bay sites, we felt that this additional experiment would increase the temporal and spatial scope of our results. For this second experiment, we used monthly CTD profile data to estimate mean chl *a* and temperature values rather than the fluorometer and thermistor time series data as in 2006. In addition to monthly chlorophyll fluorescence and

temperature data, we sampled each site on four different days from 30 July to 6 August 2007. All other methods and statistical analyses remained the same as those in the 2006 experiment.

Results

Empirically estimating tidal excursion

In the 13-hour tidal excursion study, the distance that surface drifters traveled decreased as distance from the mouth increased (Fig. 2.2). During a moderate spring tide and calm winds, all drifters at the 8-km site were transported beyond the mouth of the estuary during the ebb tide; two drifters turned about a kilometer beyond the mouth and returned to the bay, one drifter was recovered outside of the estuary, and the fourth drifter was lost outside the estuary. In contrast to this large tidal excursion, drifters released at the 12-km site moved a little over 3 km on the ebb tide, but it appears that the tidal excursion was under-estimated due to drifters snagging on seagrass in shallow waters along the east shore – this was directly observed and it can also be deduced from the fact that the drifters slowed prior to slack water. In the absence of this seagrass snag, it is expected that these drifters would have moved about 4km on the ebb tide. This drift towards the east shore is consistent with a westerly seabreaze that crested the ridge west of the bay only where the ridge was low (personal observations logged during field work). This wind effect was mostly absent for the drifters released at 8km and present but weaker for drifters released at 16km. These drifters released at the 16-km site were transported only 2.5 km and not seen in the seagrass until well after the low-water slack tide. On the subsequent flood tide, 8-km drifters moved back into the bay, with an

excursion of 9-10km. The 12-km drifters remained in the seagrass, while the 16-km drifters moved landward 1-2km before also being snagged by seagrass along the east shore. For all locations landward of 6km (end of complex topography of outer bay; see Hearn & Largier 1997; Largier *et al*. 1997), drifters exhibited smooth tracks with no evidence of small-scale variability, suggesting minimal small-scale eddy mixing during tidal advection. In contrast, drifters that moved beyond the mouth exhibited significant eddy behavior, representing strong eddy mixing of bay waters that were advected beyond the mouth.

Physical and biological gradients

From 2004-08, mean salinity and temperature for the entire estuary varied seasonally, as expected (Largier *et al*. 1997). In the winter and spring-transition months, means of salinity and temperature were relatively low; winter salinity 30.99 $\pm$ 2.24, winter temperature 11.38 ºC $\pm$ 1.02ºC; spring salinity 28.73 $\pm$ 4.18, spring temperature 12.93 ºC $\pm$ 1.42ºC. Summer upwelling and fall transition months exhibited high salinities and temperature: summer salinity 33.29 $\pm$ 1.23, summer temperature 15.59 ºC $\pm$ 3.07ºC, fall salinity 33.59 $\pm$ 0.55, fall temperature 14.30 ºC $\pm$ 2.19ºC. In addition, salinity and temperature varied spatially, as a function of distance from the ocean (Largier *et al*. 1997). Due to the dominant freshwater input at the head of the estuary, salinity decreased with distance from the mouth of the estuary during spring and winter (Fig. 2.4a,d). In the absence of significant freshwater input in summer and fall, salinity remained constant or increased slightly with distance from the mouth of the estuary (Figs. 2.4b,c). For all

seasons except winter, temperature increased with distance from the mouth of the bay (Figs. 2.4e-h) due to the import and heating of upwelled water in the bay.

Chlorophyll *a* concentrations averaged over the entire estuary were highest during the upwelling months (May-August, 16.94 mg/m^3 $\pm$ 11.04 mg/m^3), but still high in the fall-transition months (September-October, 12.24 mg/m^3 $\pm$ 9.79 mg/m^3; Fig. 2.4j,k). During winter and spring, chlorophyll *a* concentrations were low (March-April, 4.20 mg/m^3 $\pm$ 4.08 mg/m^3 and November-February, 5.45 mg/m^3 $\pm$ 3.97 mg/m^3; Fig. 2.4i,l). During summer and fall months, chl *a* concentrations were maximum in the mid-bay (26.86 mg/m^3 $\pm$ 14.69 mg/m^3; 20.40 mg/m^3 $\pm$ 10.30 mg/m^3, respectively). This mid-bay maximum may also be seen in some spring-transition months, when there has been an early decrease in runoff and increase in upwelling (e.g., March 2006), or in some early winter months, when there has been a delay in the onset of runoff (e.g., November 2004; see Appendix 2.1). This summer/fall chl-a spatial pattern is consistent with the longitudinal patterns in residence time (Fig. 2.4b,c) and nitrate concentration (Fig. 2.4f,g). While the outer bay is characterized by newly upwelled high-nitrate waters and short residence times, the inner bay is characterized by very low nitrate levels and long residence. High chl-a levels are found in mid-bay where waters have moderate levels of nitrate and moderate residence times.

Oyster-size distributions

In Tomales Bay, a gradient of oyster-size distributions exists. According to all three nonparametric tests (Wilcoxon/Kruskal-Wallis Tests, ChiSquare = 598.49, $P < 0.0001$; Median Test, ChiSquare = 401.37, $P < 0.0001$; Van der Waerden Test, ChiSquare

= 615.25, P < 0.0001), oyster distributions at Middle-bay sites (i.e., closer to the mouth of the bay) are skewed towards larger sizes (positive values of [Mean-Mean0]/Std0) than are distributions at Inner-bay sites (negative values of [Mean-Mean0]/Std0; Fig 2.5a). For example, sites W1 and E1 have mean (± SD) of 49.71 mm ± 7.98 and 53.71 mm ± 9.65, respectively (Fig 2.5b). In contrast, sites W5 and E4 that are farther from the mouth of the bay have distributions skewed towards smaller oyster sizes (32.97 mm ± 7.08 and 30.92 mm ± 7.17, respectively). In a simple linear regression, mean oyster size is positively correlated with distance from mouth of the bay ($y = -1.97x + 65.49$, $R^2 = 0.84$, P = 0.0006, Fig. 2.5b).

Oyster-growth experiment

During the first experiment (2006), site differences in the mean (± SE) size of oysters varied with time (Repeated Measures ANOVA, Univariate G-G Epsilon $F_{3.85,44.33} = 30.48$, P < 0.001, Fig. 2.6a). Although oyster sizes were similar across sites at the beginning of the experiment ($F_{2,24} = 0.35$, P = 0.71), one month of growth produced oyster sizes at site 12 km that were 50% larger than those of sites 8 km and 16 km ($F_{2,24} = 18.81$, P < 0.001, Tukey's post hoc test = 2.50, Fig. 2.6a). This size difference between sites 8 km and 12 km, however, diminished over time. After four months of growth, sites 8 km and 12 km had equally larger oysters compared to oyster sizes at site 16 km (October $F_{2,23} = 47.46$, P = 0.001, Tukey's post hoc test = 2.50, Fig. 2.6a).

Similar to the oyster size data, differences in the mean (± SE) monthly growth of oysters among sites varied with time (Repeated Measures ANOVA, Univariate G-G Epsilon $F_{3.96,43.59} = 5.15$, P < 0.002). In the first month of the experiment, oyster growth

rate at site 12 km (W3, 0.78 $\pm$ 0.05) doubled that of oysters at sites 8 km (W2) and 16 km (W5) ($F_{2,24}$ = 31.99, P < 0.001, Tukey's post hoc test = 2.50, P < 0.05, Fig 2.6b). But throughout the rest of the experiment, monthly growth increments at site 8 km increased linearly while that of sites 12 km and 16 km did not change. As a result, oyster growth at sites 8 km and 12 km were equally higher than that of site 8 km during the second months ($F_{2,23}$ = 18.66, P = 0.001, Tukey's post hoc test = 2.51) and third ($F_{2,22}$ = 11.98, P = 0.003, Tukey's post hoc test = 2.50).

Fluorescence data indicate that chl *a* was highest at the 12-km site in July-August, and highest at the 8-km site in August-September, although the 12-km site was similar and the 16-km site was much less (Fig. 2.6c). In contrast, water temperature was consistently highest at the 16-km site throughout the experiment (Fig. 2.6d.

When we added an additional site (6 km) and repeated the same experiment from July to August 2007, differences in mean ($\pm$ SE) monthly size of oysters among sites again varied with time (Repeated Measures ANOVA, Univariate G-G Epsilon $F_{3,16}$ = 16.08, P < 0.0001, Fig. 2.6e). At the beginning of the experiment, all sites had equal oyster sizes except for site 6 km, which had slightly smaller oysters (ANOVA, $F_{3,16}$ = 3.61, P = 0.03, Tukey's test = 2.86). One month later, site 12 km had significantly larger oysters than all other sites ($F_{3,16}$ = 12.48, P = 0.0002, Tukey's test = 2.86). During one month, site 12 km oysters also grew significantly more than oysters at all other sites (Welch ANOVA, $F_{3, 8.31}$ = 21.08, P = 0.0003, Tukey's test = 2.86, Fig. 2.6f). In addition to these size and growth differences among means, the ordering of the chl *a* and temperature means also paralleled the corresponding July-August 2006 data (Figs. 2.6g-h). Finally, site 6 km had the lowest chl *a* and temperature means (Figs. 2.6g-h).

A multiple linear regression (MLR) that used chl *a* and temperature as independent variables accounts for 92% of the variance in oyster growth in 2006 (R^2adjusted = 0.87, $F_{2,3}$ = 17.67, MLR P = 0.02). Although increasing chl *a* concentrations significantly explained increasing oyster growth rates ($F_{1,3}$ = 30.53, P = 0.01, Fig. 2.7a), increasing temperatures explained little variation in oyster growth ($F_{1,3}$ = 1.8, P = 0.27, Fig. 2.7b). For July-August 2007, the dependence of oyster growth on chl *a* and temperature in a MLR was similar to that of 2006 (R^2 = 0.99, R^2adjusted = 0.99, $F_{2,1}$ = 521.44, MLR P = 0.03, chl *a*-P = 0.02, Temperature-P = 0.10, Figs. 2.7c-d). Temperature, however, was negatively associated with increasing oyster growth (Fig. 2.7d).

Discussion

Our results show that a low-inflow estuary can be fueled by upwelled nutrients, resulting in spatially and temporally predictable phytoplankton blooms that influence the size structure of estuarine foundation species like native California oysters. Recently upwelled waters that are high in nitrate are imported to the bay (low-inflow estuary) through tidal diffusion. The characteristic longitudinal pattern of residence or "age" of these waters is exhibited as a characteristic longitudinal pattern of phytoplankton concentration with a mid-bay maximum. This is observed in Tomales Bay during the low-inflow summer and fall months. During this period, the outer bay is filled with nutrient-rich coastal waters, but the "age" of these waters is too young and phytoplankton has not been exposed to light long enough for the peak bloom to develop. Further, tidal and eddy mixing is vigorous and nascent blooms are diluted with offshore high-nutrient,

low-chlorophyll waters as quickly as new phytoplankton form. In contrast, the innermost bay receives negligible nitrate from the ocean as the "age" of waters is too old and available nutrients have already been depleted. At the same time, the flux of nutrients from the land is very low due to the absence of freshwater inflow and internal nutrient cycling can only yield low concentrations (Smith *et al*. 1989). In mid-bay (8-14 km from the mouth), an adequate level of nitrate is available and replenished by a reliable tidal flux of nitrate from the ocean. The shallow waters ensure adequate light is available and mixing is weak, so that high levels of phytoplankton can develop before diffusive losses become important. The tidal diffusion of phytoplankton to the outer bay may be large, but here it is rapidly mixed with coastal waters and phytoplankton concentrations remain low. However, the tidal diffusive flux of phytoplankton to the inner bay ensures a persistent but lower concentration of phytoplankton throughout the low-inflow summer and fall. This mid-to-inner flux of particulate organic matter is comparable with that described for Willapa Bay (Banas *et al*. 2007). The difference is that the phytoplankton bloom develops within Tomales Bay, fueled by a tidal influx of high-nitrate waters whereas the phytoplankton bloom develops offshore of Willapa Bay and the bay receives a diffusive influx of particulate organic matter. This scenario may be seen at times for Tomales Bay (e.g., 2004, 2005 – Appendix 2.1), but a record of water temperature at the 2-km site in 1992 suggests that it is unusual to see sufficiently aged upwelled waters at or near the mouth of Tomales Bay (Largier, *unpublished data*).

Responding to the spatial structure of phytoplankton, juvenile oysters grow more quickly in the middle than in the outer or inner bay (Fig. 2.6b,f). These differing growth rates help explain why oyster populations in the middle of the bay comprise larger

individuals while populations in the inner bay consist of smaller individuals (Fig. 2.5a-b). Because smaller oysters are more susceptible to predators (Kimbro unpublished data), higher densities of marine predators coupled with low growth and low recruitment (Kimbro and Grosholz unpublished data) may also explain why oysters are absent from the outer bay (Fig. 2.5a). In addition to being more susceptible to predators, populations of smaller oysters also provide less biogenic habitat for obligate organisms than do larger oysters (Kimbro & Grosholz 2006). Thus, a predictable spatial structure of phytoplankton may allow larger oysters in the middle of the bay to function better as a foundation species resulting in increased intertidal diversity compared with the inner bay.

Underlying these spatial patterns of plankton, oysters and pelagic-benthic coupling is variability induced by variability in the environment, specifically in transport patterns. Variability comes from tide (high-low and spring-neap) and wind (local and offshore) variability. As the tide rises and falls, the longitudinal pattern is compressed and stretched out. In this study, water properties were sampled at high tide and sampling at other phases of the diurnal/semi-diurnal cycle would show a phytoplankton peak closer to the mouth. Given the limited eddy mixing, it is expected that this phytoplankton peak will be advected along the bay as a plug, and these concentrations will only be broken down is water is subjected to the large shears and strong mixing associated with tidal pumping at the mouth (i.e., waters seaward of about the 8-km site). However, there is also a spring-neap cycle in tide range and vigorous mixing near the mouth will influence phytoplankton concentrations over a longer distance as the tidal excursion increases during spring tides. While we only present one set of observations of tidal excursion, this is a deterministic process and tidal excursion estimated for a variety of tidal ranges is

verified by the displacement of isotherms and isohalines in Tomales Bay (Harcourt-Baldwin & Diedericks 2006). In short, one can expect the tidal excursion to vary linearly with tide range, so that one may expect the 4km excursion from the 12-km site to become 6km on a spring tide with range of 7.5 feet and the excursion to be just 2km on neap tide with a range of 2.5 feet (note that even on spring tides, one can expect water at the 12-km site to remain in the bay at low tide and phytoplankton concentrations there to remain intact). Following Largier *et al*. (1997), mixing rates can be expected to vary with the square of the tidal excursion (thus varying nine-fold between neap and spring tides). The effect of these changes in mixing are not quite clear, but will be explored further in a second modeling paper being prepared. While the increased mixing will deliver more nitrate farther into the bay, it will also flush out more phytoplankton from locations deeper in the bay. Following (Chadwick & Largier 1999) observations of cooling of outer San Diego Bay following the spring tide, we expect outer Tomales Bay to contain maximum nitrate load following the big-mixing spring tides and to develop maximum phytoplankton load over the subsequent week, during the weak-mixing neap tides.

Winds are also variable, but less predictably. Their effects can be direct, via winds on the surface of the bay, or indirect, via effects on the coastal ocean. Probably the most important influence is on coastal upwelling and associated sealevel and circulation. When northerly winds are stronger, colder and higher nitrate waters are upwelled along the coast and available at the mouth of Tomales Bay (Dever *et al*. 2006). In contrast, during multi-day calm periods when upwelling relaxes, the coastal waters off Tomales Bay may be “aged upwelled” waters or a combination of this with San Francisco Bay influenced waters (Largier *et al*. 2006), providing a source of waters rich in

phytoplankton which can be tidally mixed into Tomales Bay (cf. Banas *et al*. 2007). Such changes in ambient waters that persist for several days can be expected to be a significant source of variability in the levels and longitudinal pattern of nutrient and phytoplankton levels in Tomales Bay. Another indirect wind effect is lowering of the sealevel during upwelling, and the associated effect of these "wind tides" on the astronomical tides (e.g., Largier 1996). And there may also be significant day-to-day changes in incident light available for photosynthesis.

The direct effect of wind was observed in the drifter experiment (Fig. 2.4). When the cool marine layer crests the ridge west of Tomales Bay, a westerly breeze blows across the bay. The observed drifter tracks suggest that this wind imparts a surface velocity towards the lee shore. While this makes water parcel trajectories more complex, it is expected that the stronger along-bay tidal motions dominate the mixing and residence dynamics of water in Tomales Bay. During strong upwelling winds, there is a significant landward wind along the axis of the bay, which must pile up water at the southern end of the bay. Nevertheless, the bay waters still move landward and seaward with the tide and there is no evidence of increased longitudinal mixing at these times. However, it may be that the regularity of these along-bay winds may be important in maintaining a mixed water column in Tomales Bay, but we cannot assess that with our data.

In spite of various sources of variability (tidal, synoptic meteorology, spring-neap), there is a clear and robust pattern with a mid-bay maximum in phytoplankton availability during the low-inflow months which are also characterized by coastal upwelling. This pattern is also seen in the aggregation of high-frequency fluorescence

data at fixed sites, which captures all of this variability. So, while a single observation may show a spatial distribution that looks different to the characteristic pattern, it appears that the spatial pattern is robust and that this variability is just a variation on the underlying theme: an area of intermediate tidal excursion (i.e., middle bay) hosts seasonal peaks in chl *a* and oyster-size distributions skewed towards largest observed sizes. Our CTD data and oyster size distributions suggest that the tidal excursion gradient illustrated by our drifter study sufficiently explains how coastal upwelling may affect the size of estuarine foundation species like native California oysters.

In this study we did not resolve the plankton community – neither zooplankton consumers nor the phytoplankton producers. A possible limitation of this work is the absence of information on spatial patterns in grazing pressure. Although we did not quantify zooplankton abundance, previous research indicated that estuarine zooplankton abundances within the inner bay (i.e., sites 14 – 18 km) are low when middle-bay phytoplankton peaks occur (Kimmerer 1993). From this it appears that zooplankton-grazing pressure cannot explain why phytoplankton abundance is lower in the inner bay. In contrast, outer-bay waters contain high abundances of neritic zooplankton (Kimmerer 1993) and cultivated oysters (*Crassostrea gigas*) during upwelling. Thus, zooplankton and cultivated oysters (Banas et al. 2007) may cause phytoplankton biomass to be lower in the outer versus the middle bay. While the degree to which grazing pressure explains the outer bay's lower phytoplankton levels remains unaddressed, oysters do not occur in the outer bay and high levels of chl *a* still occur in the middle bay. Consequently, grazing pressure exerts little influence on how tidal excursion and coastal upwelling interactively affect oyster growth in the middle and inner bay.

Concerning phytoplankton, we expect that diatoms are more common in the outer bay and dinoflagellates more common in the inner bay (Cole et al. 1989). In the last month of our field experiment, we began using High Pressure Liquid Chromatography (HPLC) to characterize the community composition of phytoplankton species across our three experimental sites. From these preliminary data, we found consistent levels of diatoms at each site throughout the year. Spatial and temporal peaks in dinoflagellates, however, appear to coincide with higher oyster growth (Kimbro and Waters *unpublished data*). Therefore, phytoplankton composition (i.e., dinoflagellates or a diatom-dinoflagellate mixture) may also account for differences in observed growth rates.

Conclusion

While our study has limitations, one of its strengths is reconciling whether upwelling-generated phytoplankton or temperature more strongly influences the growth of benthic suspension-feeders. Because invertebrate metabolic rates increase with temperature and because upwelling reduces water temperature, it has been argued that the growth and size of suspension feeders is better explained by warmer water temperatures than by upwelling and phytoplankton (Sanford & Menge 2001; Blanchette *et al*. 2007). Increasing water temperature in our study, however, failed to directly affect juvenile oyster growth for two consecutive years (Figs. 2.6-2.7) and appears inversely related to the size structure of oyster populations (2.5a-b). We suggest that physical features that retain upwelled waters, such as upwelling shadows and low-inflow estuaries, may help reconcile our results with those of previous coastal studies.

In the absence of physical mechanisms that retain water, intensive upwelling transports phytoplankton offshore and thereby affects suspension feeders only by reducing water temperature (Blanchette *et al*. 2007; Menge *et al*. 2008). Consequently, suspension feeders at weaker upwelling sites will grow faster than those at strong upwelling sites since they will typically experience warmer temperatures (Blanchette *et al*. 2007) and do not rely on phytoplankton blooms as a primary source of food. However, where phytoplankton is a dominant source of food, one will also observe increased growth with temperature as chlorophyll levels are positively correlated with temperature. So, the growth-temperature link is more general, although it may be that the growth-chlorophyll link is more causative in locations like Tomales Bay. Low-inflow longitudinal bays like Tomales provide a unique example as they have a positive chlorophyll-temperature relationship in the outer bay and a negative chlorophyll-temperature relationship in the inner bay, allowing the separation of temperature and chlorophyll effects.

Within upwelling regions, our study is not the first to demonstrate a benthic-pelagic link between coastal upwelling and estuaries. In fact, Banas *et al*. (2007) recently demonstrated that intermittent upwelling can lead to coastal phytoplankton being imported into and subsidizing a low-inflow estuarine system in Washington, USA – a system also observed in San Quentin Bay, Mexico (Camacho-Ibar *et al*. 2003). In contrast, we have observed a benthic-pelagic link that is more characteristic of bays near persistent upwelling centers, where the bay is subsidized not by particulate organic matter but by dissolved inorganic matter that in turn fuels phytoplankton blooms within the bay. We thus suggest that the benthic-pelagic links between coastal upwelling and low-inflow

estuaries may not be uniform throughout an eastern boundary current region with varying upwelling regimes. Further, these links may change with changes in the upwelling wind climate and/or direct anthropogenic effects on land runoff and nutrient loading to west coast estuaries and bays.

In conclusion, then, prior research has established that energy inputs from coastal upwelling can strongly influence the dynamics of rocky intertidal food webs (Menge 2001 and references therein). More recently, it has even been shown that such inputs can also affect a low-inflow estuarine system (Banas et al. 2007). Complementing these results, our study provides an additional link between coastal upwelling and the population dynamics of an estuarine foundation species. In addition to highlighting an under-appreciated link between upwelling and an estuary, mediated through tidal exchange, our results suggest that caution should be shown in broadly generalizing that the effects of water temperature on suspension-feeder growth trump that of coastal upwelling and food, as suggested by Menge *et al*. (2008).

Acknowledgements

Acknowledgements

We thank C. Hays, R. Hughes, K. Hultgren, B. Jaffee, E. Sanford, A. Sih, J. Stachowicz, and G. Trussell for comments and ideas that improved this manuscript. S. Attoe, L. Budd, A. Chang, M. Ferner, A. Hettinger, M. Nydam, M. O'Leary, and B. Steves generously provided field assistance. We also thank B. Steves for helping produce the manuscript's figures. This research was supported by grants from the University of California (UC) Marine Council/Coastal Quality Environmental Initiative (to D.L.K.),

UC Davis Graduate Group in Ecology (to D.L.K.), National Park Service at Point Reyes National Seashore (to D.L.K.), National Oceanic and Atmospheric Administration (to E.D.G), California Sea Grant (to E.D.G.), National Parks Service-California Cooperative Ecosystem Studies Program (to E.D.G.), Pacific States Marine Fisheries Commission (to E.D.G.), UC Exotic/Invasive Pest and Disease Program (to E.D.G.), and National Science Foundation-Research Experience for Undergraduates (to N.J.N and N.M.T.)

Literature cited

Baker P. (1995) Review of ecology and fishery of the Olympia oyster, Ostrea lurida with annotated bibliography. *Journal Of Shellfish Research*, 14, 501-518

Banas N.S., Hickey B.M., Newton J.A. & Ruesink J.L. (2007) Tidal exchange, bivalve grazing, and patterns of primary production in Willapa Bay, Washington, USA. *Marine Ecology-Progress Series*, 341, 123-139

Blanchette C.A., Helmuth B. & Gaines S.D. (2007) Spatial patterns of growth in the mussel, Mytilus californianus, across a major oceanographic and biogeographic boundary at Point Conception, California, USA. *Journal of Experimental Marine Biology and Ecology*, 340, 126-148

Boyle K.A., Kamer K. & Fong P. (2004) Spatial and temporal patterns in sediment and water column nutrients in a eutrophic southern California estuary. *Estuaries*, 27, 378-388

Broitman B.R. & Kinlan B.P. (2006) Spatial scales of benthic and pelagic producer biomass in a coastal upwelling ecosystem. *Marine Ecology-Progress Series*, 327, 15-25

Bruno J.F. & Bertness M.D. (2001) Habitat modification and facilitation in benthic marine communities. In: *Marine Community Ecology* (eds. Bertness MD, Gaines SD & Hay ME), pp. 201-218. Sinauer Associates, Inc.

Camacho-Ibar V.F., Carriquiry J.D. & Smith S.V. (2003) Non-conservative P and N fluxes and net ecosystem production in San Quintin Bay, Mexico. *Estuaries*, 26, 1220-1237

Chadwick D.B. & Largier J.L. (1999) The influence of tidal range on the exchange between San Diego Bay and the ocean. *Journal of Geophysical Research-Oceans*, 104, 29885-29899

Chavez F.P., Collins C.A., Huyer A. & Mackas D.L. (2002) El Nino along the west coast of North America. *Progress in Oceanography*, 54, 1-5

Davis R.E. (1985) Drifter Observations of Coastal Surface Currents During Code - the Method and Descriptive View. *Journal of Geophysical Research-Oceans*, 90, 4741-4755

Dever E.P., Dorman C.E. & Largier J.L. (2006) Surface boundary-layer variability off Northern California, USA, during upwelling. *Deep-Sea Research Part Ii-Topical Studies in Oceanography*, 53, 2887-2905

Dugdale R.C., Wilkerson F.P., Hogue V.E. & Marchi A. (2006) Nutrient controls on new production in the Bodega Bay, California, coastal upwelling plume. *Deep-Sea Research Part Ii-Topical Studies in Oceanography*, 53, 3049-3062

Graham W.M. & Largier J.L. (1997) Upwelling shadows as nearshore retention sites: The example of northern Monterey Bay. *Continental Shelf Research*, 17, 509-532

Harcourt-Baldwin J.L. & Diedericks G.P.J. (2006) Numerical modelling and analysis of temperature controlled density currents in Tomales Bay, California. *Estuarine Coastal and Shelf Science*, 66, 417-428

Hearn C.J. & Largier J.L. (1997) The summer buoyancy dynamics of a shallow Mediterranean estuary and some effects of changing bathymetry: Tomales bay, California. *Estuarine Coastal and Shelf Science*, 45, 497-506

Huntsman S.A. & Barber R.T. (1977) Primary Production Off Northwest Africa - Relationship to Wind and Nutrient Conditions. *Deep-Sea Research*, 24, 25-33

Kimbro D.L. & Grosholz E.D. (2006) Disturbance influences oyster community richness and evenness, but not diversity. *Ecology*, 87(9), 2378-2388

Kimmerer W.J. (1993) Distribution Patterns of Zooplankton in Tomales Bay, California. *Estuaries*, 16, 264-272

Kirby M.X. (2004) Fishing down the coast: Historical expansion and collapse of oyster fisheries along continental margins. *Proceedings of the National Academy of Sciences*, 101, 13096-13099

Largier J.L. (2003) Considerations in estimating larval dispersal distances from oceanographic data. *Ecological Applications*, 13, S71-S89

Largier J.L., Hollibaugh J.T. & Smith S.V. (1997) Seasonally hypersaline estuaries in Mediterranean-climate regions. *Estuarine Coastal and Shelf Science*, 45, 789-797

Largier J.L., Lawrence C.A., Roughan M., Kaplan D.M., Dever E.P., Dorman C.E., Kudela R.M., Bollens S.M., Wilkerson F.P., Dugdale R.C., Botsford L.W., Garfieldg N., Cervantes B.K. & Koracin D. (2006) WEST: A northern California study of the role of wind-driven transport in the productivity of coastal plankton communities. *Deep-Sea Research Part Ii-Topical Studies in Oceanography*, 53, 2833-2849

Leslie H.M., Breck E.N., Chan F., Lubchenco J. & Menge B.A. (2005) Barnacle reproductive hotspots linked to nearshore ocean conditions. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 10534-10539

Mann K.H. & Lazier J.R.N. (2006) *Dynamics of marine ecosystems: biological-physical interactions in the oceans*. 3rd edn. Blackwell Publishing, Malden, MA, USA.

Marin V.H., Escribano R., Delgado L.E., Olivares G. & Hidalgo P. (2001) Nearshore circulation in a coastal upwelling site off the Northern Humboldt current system. *Continental Shelf Research*, 21, 1317-1329

Menge B.A. (1992) Community Regulation - under What Conditions Are Bottom-up Factors Important on Rocky Shores. *Ecology*, 73, 755-765

Menge B.A. & Branch G.M. (2001) Rocky intertidal communities. In: *Marine Community Ecology* (eds. Bertness MD, Gaines SD & Hay ME), pp. 221-251. Sinauer Associates, Inc.

Menge B.A., Chan F. & Lubchenco J. (2008) Response of a rocky intertidal ecosystem engineer and community dominant to climate change. *Ecology Letters*, 11, 151-162

Menge B.A., Daley B.A., Wheeler P.A., Dahlhoff E., Sanford E. & Strub P.T. (1997) Benthic-pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? *Proceedings of the National Academy of Sciences of the United States of America*, 94, 14530-14535

Menge B.A., Lubchenco J., Bracken M.E.S., Chan F., Foley M.M., Freidenburg T.L., Gaines S.D., Hudson G., Krenz C., Leslie H., Menge D.N.L., Russell R. & Webster M.S. (2003) Coastal oceanography sets the pace of rocky intertidal community dynamics. *Proceedings of the National Academy of Sciences %R 10.1073/pnas.1534875100*, 100, 12229-12234

Phillips N.E. (2005) Growth of filter-feeding benthic invertebrates from a region with variable upwelling intensity. *Marine Ecology-Progress Series*, 295, 79-89

Pinones A., Castilla J.C., Guinez R. & Largier J.L. (2007) Nearshore surface temperatures in Antofagasta Bay (Chile) and adjacent upwelling centers. *Ciencias Marinas*, 33, 37-48

Pitcher G.C. & Nelson G. (2006) Characteristics of the surface boundary layer important to the development of red tide on the southern Namaqua shelf of the Benguela upwelling system. *Limnology and Oceanography*, 51, 2660-2674

Quinn G.P. & Keough M.J. (2002) Experimental design and data analysis for biologists. In: *Experimental design and data analysis for biologists*, pp. i-537

Sanford E. & Menge B.A. (2001) Spatial and temporal variation in barnacle growth in a coastal upwelling system. *Marine Ecology-Progress Series*, 209, 143-157

Smith S.V., Hollibaugh J.T. & Vink S. (1989) Tomales Bay, California - a Case for Carbon-Controlled Nitrogen Cycling. *Limnology and Oceanography*, 34, 37-52

Stachowicz J.J. (2001) Mutualism, facilitation, and the structure of ecological communities. *Bioscience*, 51, 235-246

Vander Woude A.J., Largier J.L. & Kudela R.M. (2006) Nearshore retention of upwelled waters north and south of Point Reyes (northern California) - Patterns of surface temperature and chlorophyll observed in CoOP WEST. *Deep-Sea Research Part Ii-Topical Studies in Oceanography*, 53, 2985-2998

Wilkerson F.P., Lassiter A.M., Dugdale R.C., Marchi A. & Hogue V.E. (2006) The phytoplankton bloom response to wind events and upwelled nutrients during the CoOP WEST study. *Deep-Sea Research Part Ii-Topical Studies in Oceanography*, 53, 3023-3048

Wootton J.T., Power M.E., Paine R.T. & Pfister C.A. (1996) Effects of productivity, consumers, competitors, and El Nino events on food chain patterns in a rocky intertidal†community. *Proceedings of the National Academy of Sciences %R 10.1073/pnas.93.24.13855*, 93, 13855-13858

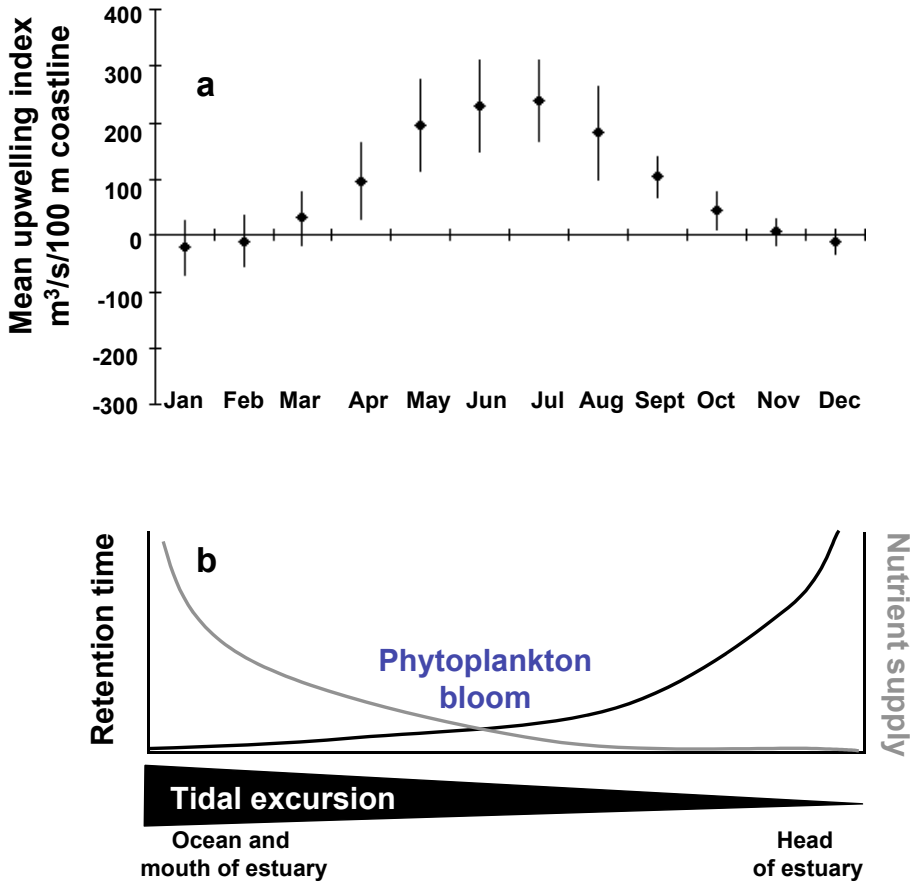


Figure 2.1. (a) Historical upwelling index for 39°N-125°W. Data points represent averages of monthly values from 1967-1991. Data and graph provided by National Oceanic and Atmospheric Administration – Environmental Research Division. (b) Map of hypothetical low-inflow estuary, illustrating how tidal excursion variability may lead to physical gradients that promote phytoplankton blooms during the summer upwelling season.

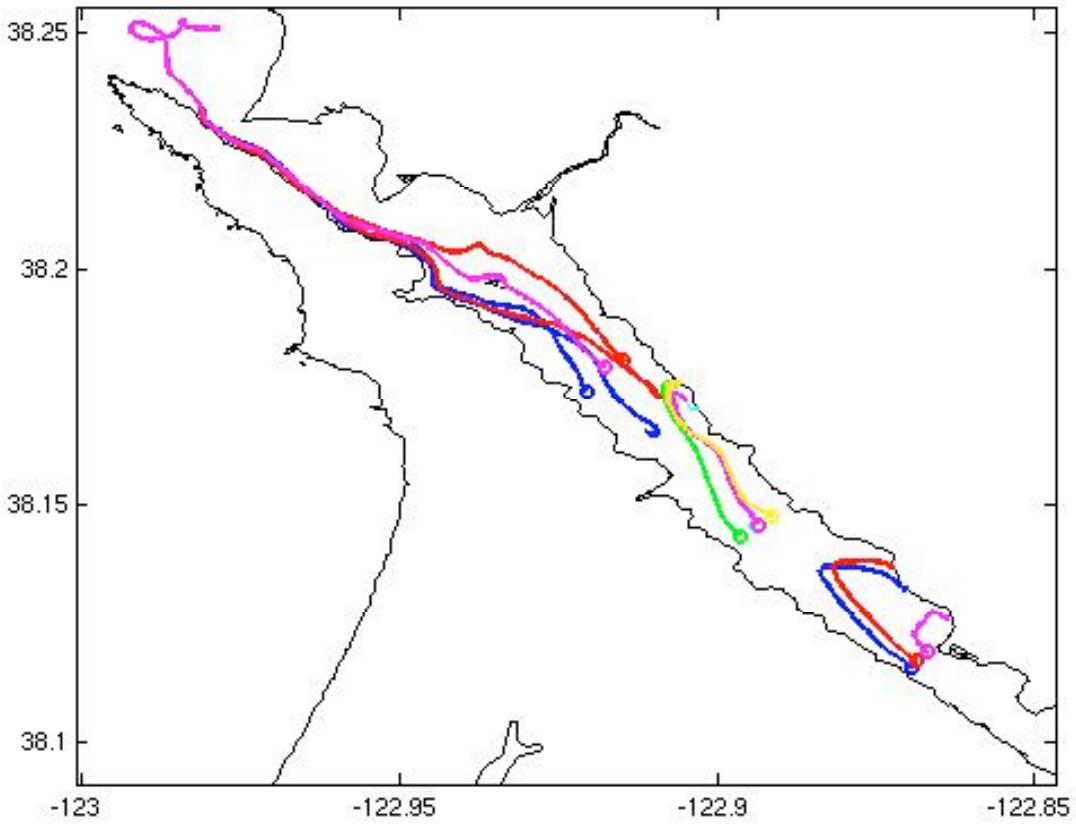


Figure 2.2. Map of empirically measured tidal excursion at three different sites within Tomales Bay: the outer/middle (8 km), middle (12 km), and inner (16 km) portions of the estuary. Tidal excursions were estimated by simultaneously releasing drifters at all sites during slack flood tide (5.8 feet magnitude) at 2:04 am and recovering drifters at the proceeding slack flood tide (5.7 feet) at 3:18 pm. Open circles represent drifter-starting locations. Drifter trajectories were recorded with an embedded GPS unit that recorded drifter positions every two minutes. At each location, four drifters were equidistantly released across the width of the bay.

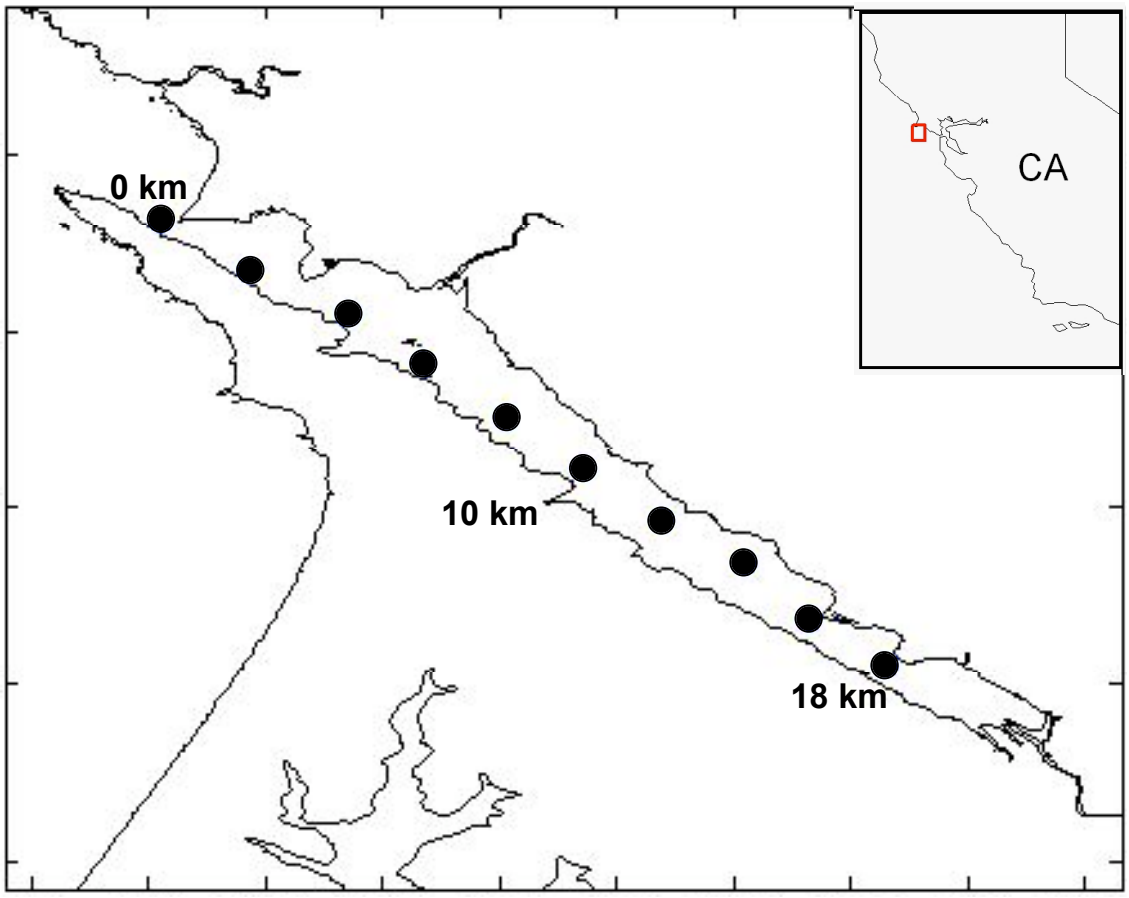


Figure 2.3. Map of ten sampling stations (black dots) located every 2 km from the mouth to the head of Tomales Bay, CA.

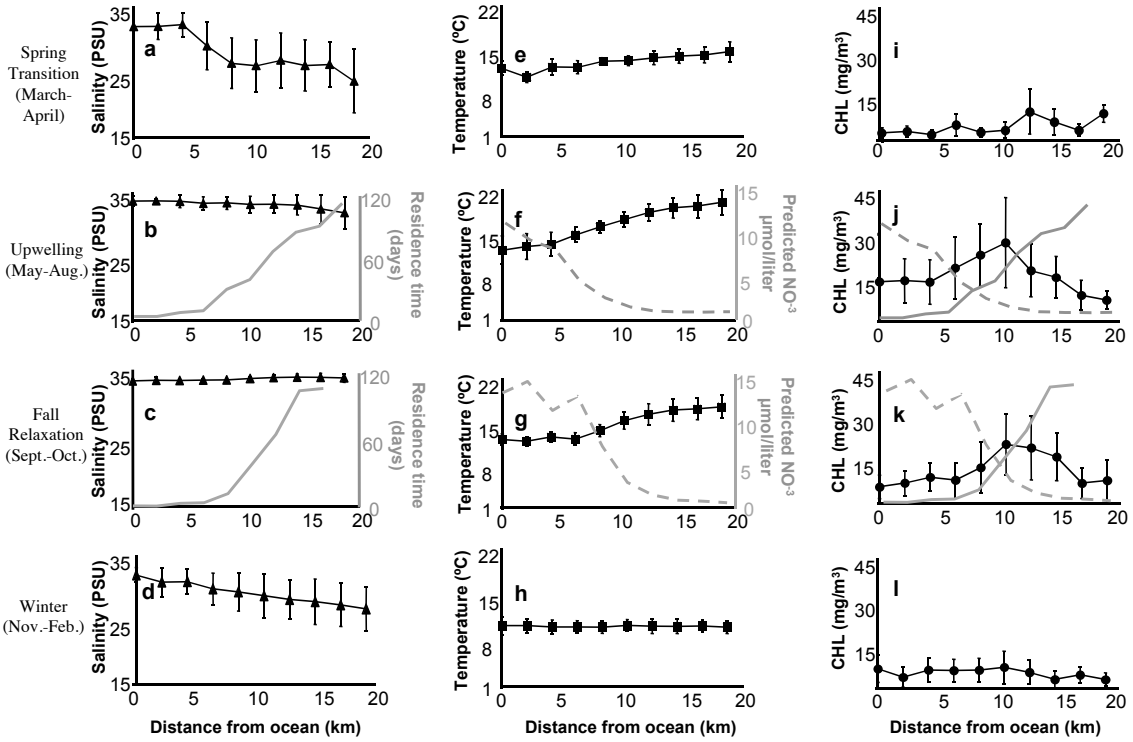


Figure 2.4. Seasonal estimates from 2004-08 of (a-d) mean (± SD) salinity structure represented by black triangles and estimated residence times indicated with gray lines; (e-h) mean (± SD) temperature (black squares) and estimated nitrate concentration (gray dashed line); (i-l) mean (± SD) phytoplankton biomass (chl *a*) across sites. Panel-j incorporates predicted residence time (gray dashed line) and nitrate concentration (gray dashed line) curves to illustrate how they may interactively influence chl *a* concentration in the middle of the bay.

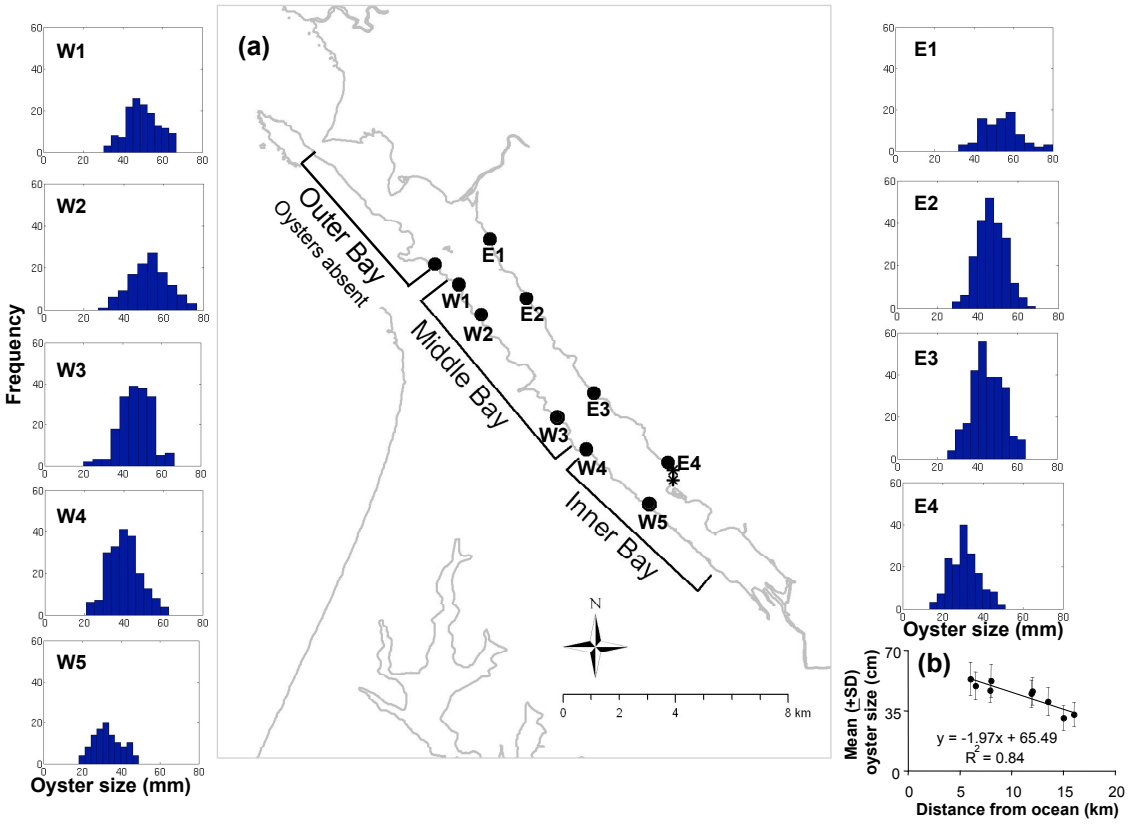


Figure 2.5. (a) Size distributions of oysters throughout Tomales Bay, CA in 2006. (b) Plot of each site's mean (± SD) oyster size versus each site's distance (km) from the mouth of the bay.

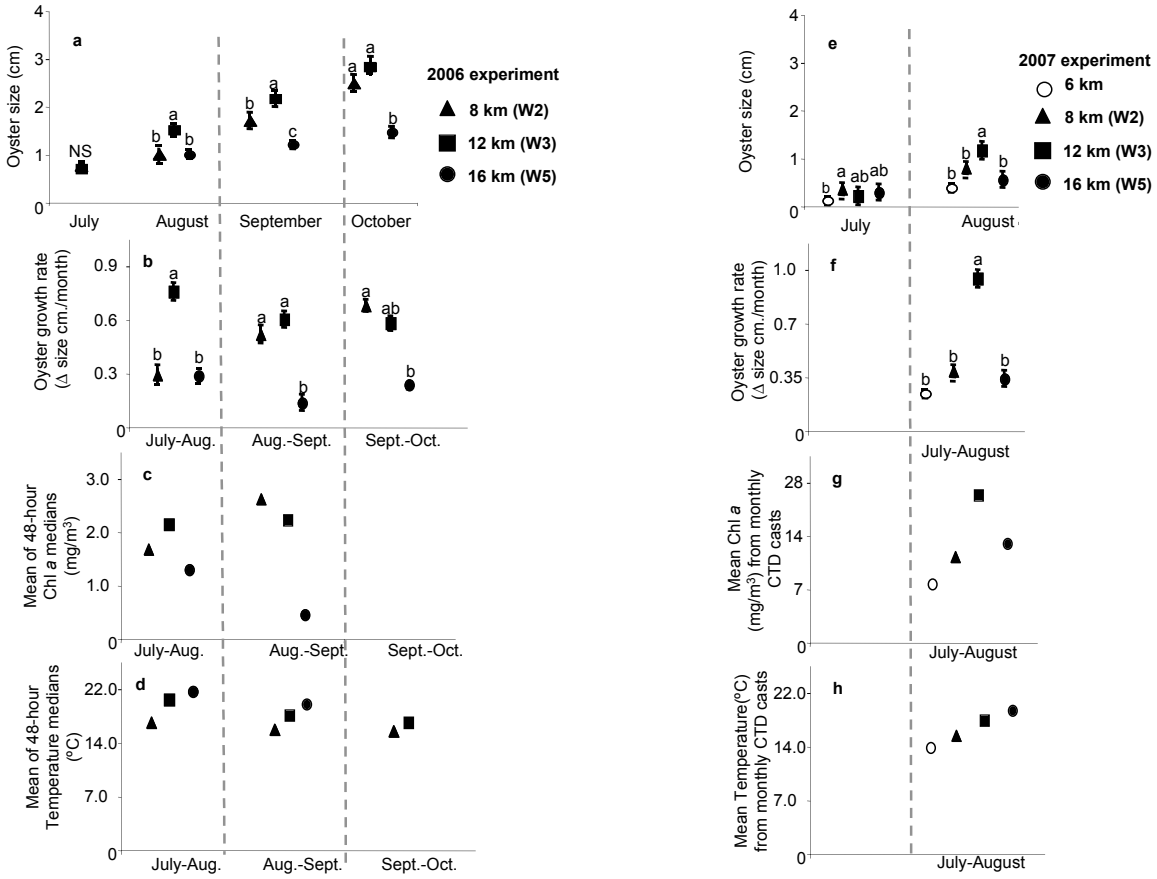


Figure 2.6. Results of oyster-growth experiments from 2006 (a-d) and 2007 (e-h). (a,e) Mean (± SE) oyster size through time at sites within Tomales Bay: 6 km (only 2007 experiment, open circle), 8 km (triangle), 12 km (square), and 16 km (circle) from the mouth of the bay. (b,f) Monthly mean (± SE) of oyster growth at each site through time. (c,g) Mean chl a concentration at each site through time. (d,h) Mean temperature at each site through time. Significant differences among means indicated by differing letters (ANOVA and Tukey's post hoc test).

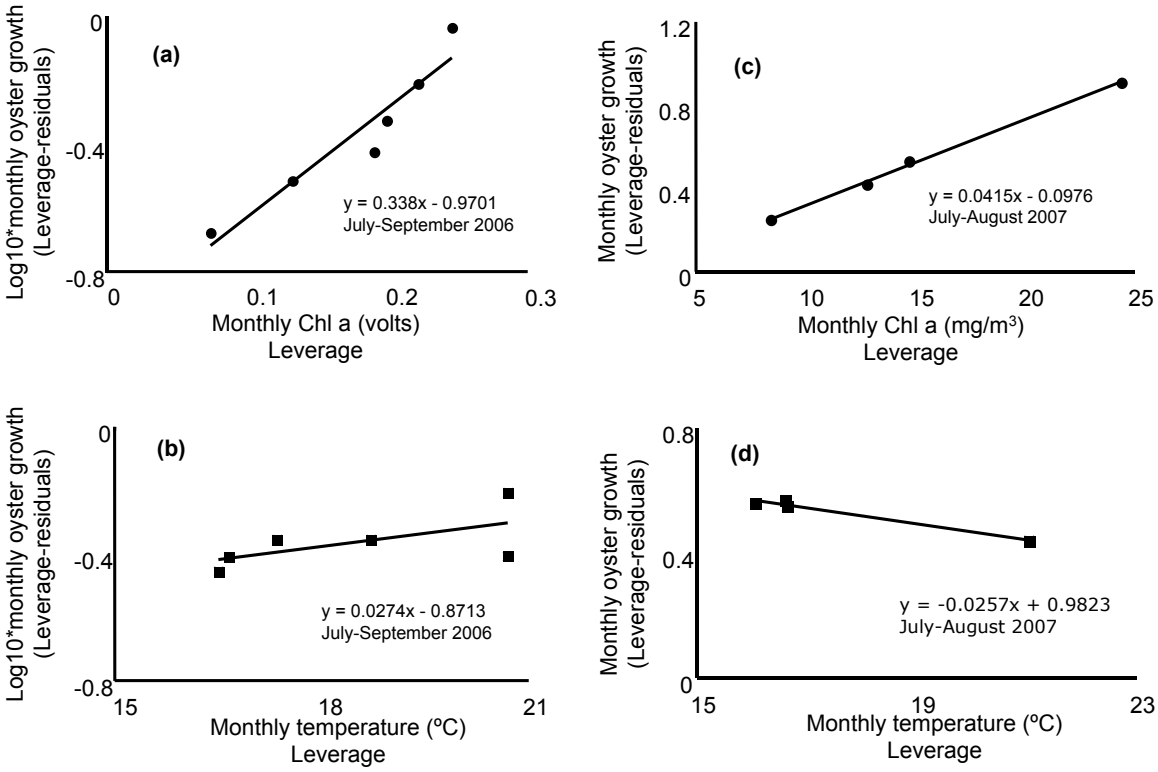
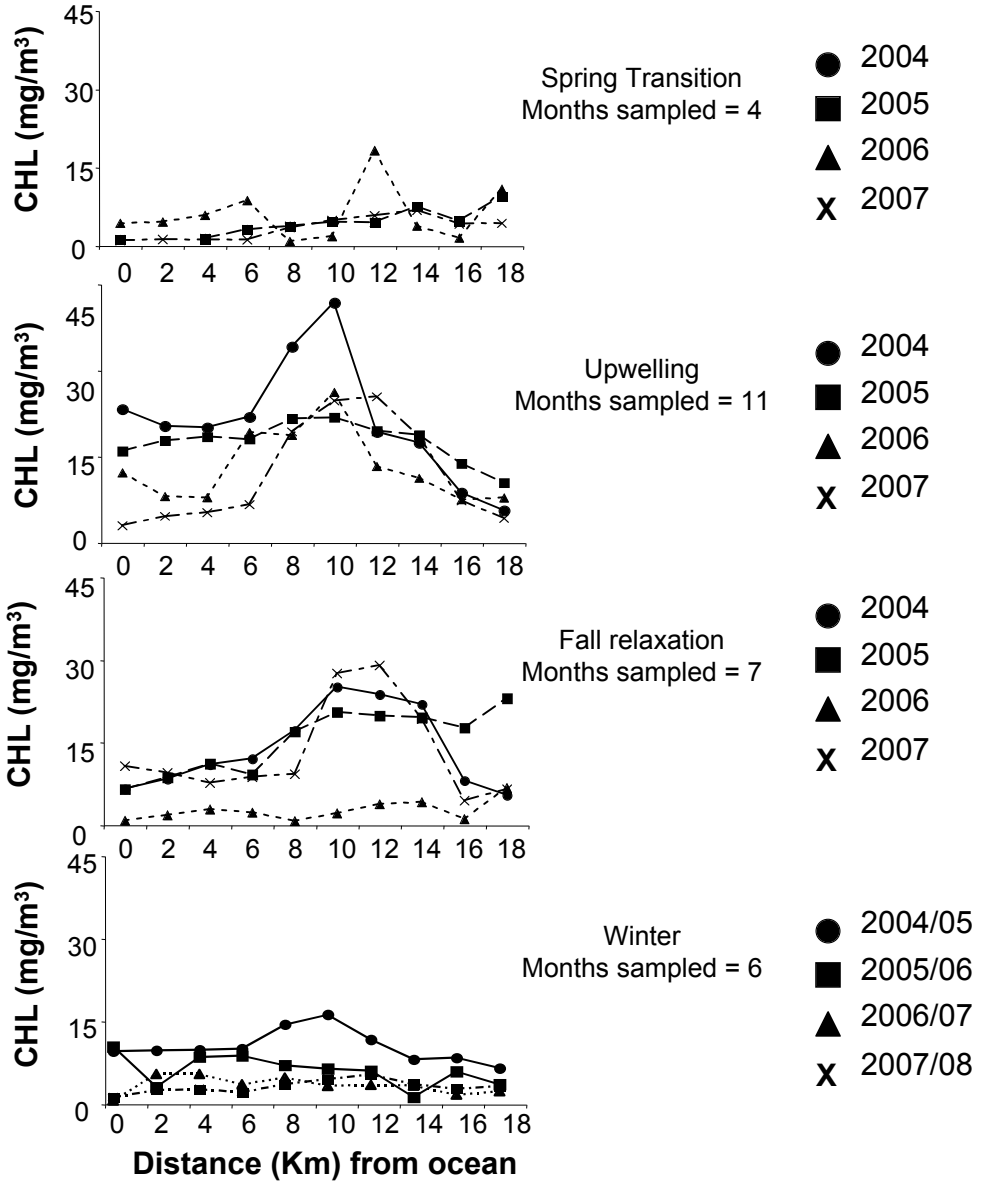
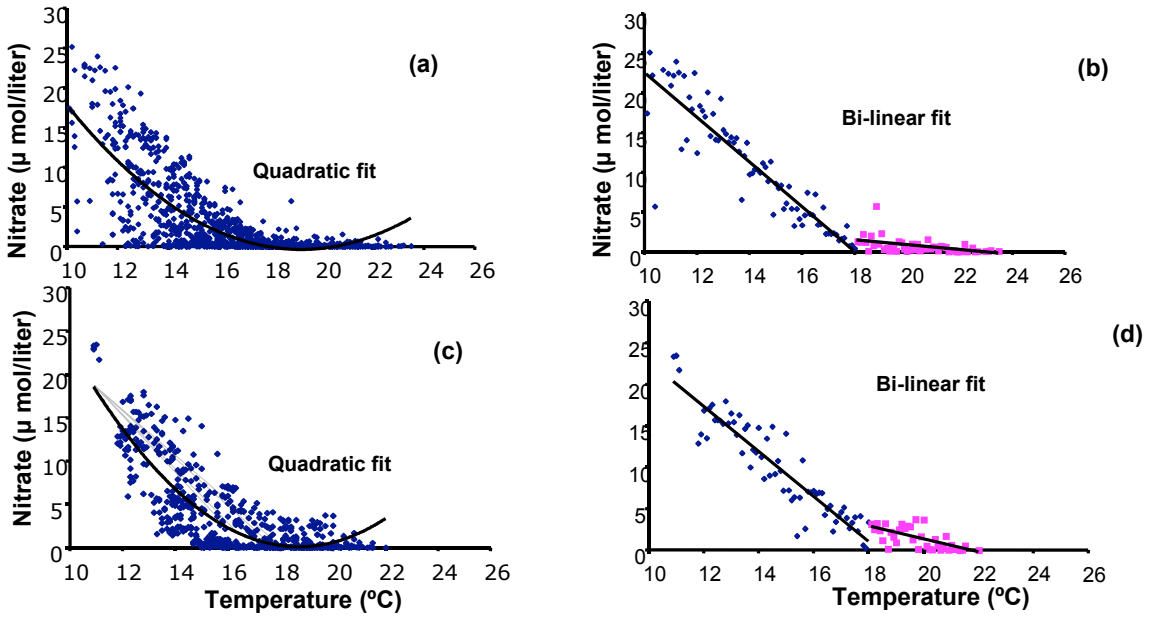


Figure 2.7. Leverage plots of Multiple Linear Regressions that used chl *a* and temperature as independent variables to predict monthly growth of juvenile oysters at each site in 2006 (a-b) and 2007 (c-d).

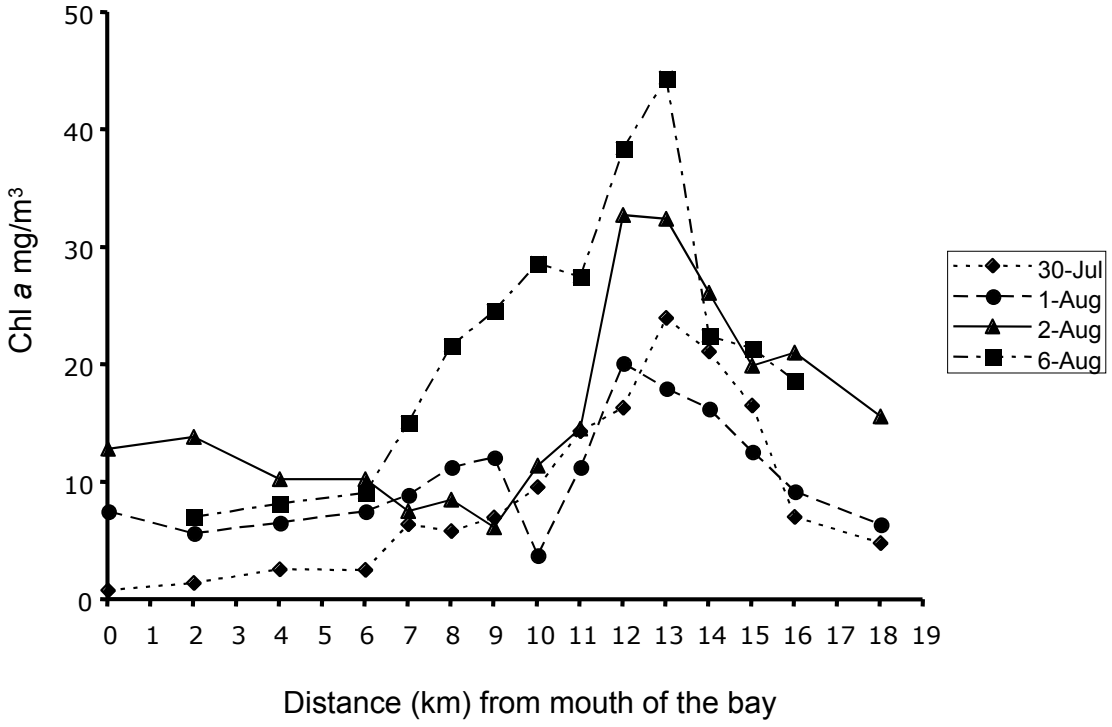


Appendix 2.1. Inter-annual variation in seasonal chl *a* at each site between 2004 and 2008.



Equation	R^2	P-value
Quadratic (a) $Y = 0.22x^2 - 8.27x + 78.97$ (c) $Y = 0.3x^2 - 11.34x + 106.18$	(a) 0.60 (b) 0.72	(a) <0.0001 (c) <0.0001
Bi-Linear (b) Temp.<18.1ºC" Y= -2.82x + 50.82 Temp.>18.1ºC" Y = -0.30x + 6.9 (d) Temp.<18.1ºC" Y= -2.72x + 50.0 Temp.>18.1ºC" Y = -0.79x + 17.10	(b) 0.83. 0.24 (d) 0.86, 0.42	(b) <0.0001, 0.0007 (d) <0.0001, <0.0001

Appendix 2.2. Nitrate versus Temperature in (a-b) upwelling months and (c-d) fall-relaxation months from 1987-1995 in Tomales Bay, CA. Panels (a) and (c) show quadratic fits of entire data set. Panels(b) and (d) show bi-linear fits of maximum observed nitrate concentration versus each observed temperature. Data obtained from http://lmer.marsci.uga.edu/tomales/ (Smith and Hollibaugh, LMER Coordinating committee 1992).



Appendix 2.3. Weekly variation in magnitude and position of chl *a* peak throughout Tomales Bay from 30July-6August 2007. High tides increased each day: 30 July (4.35 ft.), 1 Aug (4.83 ft.), 2 Aug (5.1 ft.), and 6 Aug (5.76 ft.). To increase spatial resolution, chl *a* was sampled every 1 km between sites 6 km and sites 16 km.

Chapter 3: The consequences of larval recruitment, phytoplankton, and predation for native oysters in a central California estuary

ABSTRACT: A growing research trend involves searching for generalities that describe how top-down and bottom-up factors interactively organize natural systems. In biologically productive upwelling-systems, most of this research has focused on open coastlines. Seasonally low-inflow estuaries, however, may also allow upwelling to influence interactions between top-down and bottom-up controls. When upwelling is most intense in central California, a tidal-excursion gradient of a low-inflow estuary creates spatially varying water-residence times that decouple the bottom-up factors of larval recruitment and food for the bay's oyster population. As a result, oyster populations farther from the ocean experience high recruitment-low food conditions and populations closer to the ocean experience low recruitment-high food conditions. While the food-resource gradient is consistent, recruitment appears to be inter-annually episodic. In addition to these bottom-up gradients, native predators in the outer bay and an invasive predator in the inner bay provide two independent top-down controls. Following high oyster recruitment, both productivity differences and native predators interactively explain why the inner bay population has lots of small individuals and why the outer bay population comprises only a few large individuals: food and mortality are relatively low in the inner bay—despite the presence of an invasive predator—, while food and mortality are relatively high in the outer bay. But after a prolonged absence of recruitment, the cumulative effects of invasive predators cause high instantaneous mortality rates of inner-bay oysters. In combination with native predators of the outer

bay, predation causes oyster densities to peak in the middle of the bay. These results suggest that the interplay between bottom-up and top-down factors may be misunderstood in the absence of a long-term, population-level approach. Using this approach, we show that the population variability of an important estuarine foundation species depends on multiple interactions among top-down (mortality) and bottom-up (growth) factors that are sporadically modified from the bottom-up by episodic recruitment.

Introduction

Marine ecologists have developed several conceptual models that illustrate how disturbance, predation, competition, and facilitation locally organize food webs by controlling the distribution and abundance of basal prey (Connell 1961; Menge & Sutherland 1976; Bruno & Bertness 2001; Menge & Branch 2001). The relevance of these top-down controls, however, can be modified from the bottom-up if an insufficient propagule supply produces prey densities that do not support competition, predators, or important facilitator traits (Gaines & Roughgarden 1985; Roughgarden *et al*. 1988; Polis & Hurd 1996; Bruno & Bertness 2001; Menge & Branch 2001; Menge *et al*. 2003). Because basal prey can be locally influenced from the top-down and regionally influenced from the bottom-up, a growing research trend involves searching for generalities that describe how top-down and bottom-up factors interactively organize natural systems (Oksanen *et al*. 1981; Fretwell 1987; Menge & Branch 2001; Menge *et al*. 2003; Hillebrand *et al*. 2007).

In eastern boundary current regions of ocean basins, coastal upwelling winds create one of the most biologically productive habitats (Mann & Lazier 2006). By bringing sub-surface nutrients into the euphotic zone that can support primary production, and by concentrating invertebrate larvae offshore, upwelling —and its relaxation— physically controls the subsidies of phytoplankton and invertebrate larvae into marine food webs. While specific top-down controls may predictably become important when phytoplankton and larval supplies are positively correlated (Menge *et al*. 1997), they may be less predictable when physical factors decouple these two bottom-up controls in space and time (Stapp *et al*. 1999; Menge *et al*. 2003; Yang *et al*. 2008).

One approach that can be used to increase our understanding of top-down/bottom-up interactions involves conducting local-scale experiments at multiple sites that span a large spatial scale, and repeatedly sampling bottom-up factors that vary systematically among sites (Menge *et al*. 2003). Although this approach can identify the presence of potentially important top-down and bottom-up controls, it cannot unequivocally demonstrate how these controls interactively influence population-level patterns of important basal prey. For instance, depending on the type and diversity of predators, both high and low subsidies of basal-prey recruitment can be accompanied by intense predation rates (Hixon & Menge 1991; Menge *et al*. 2003). Similarly, by reducing densities of new recruits and therefore resource competition, predators can increase—rather than decrease—juvenile survivorship since the higher resource levels enhance growth rates through vulnerable size classes (Vonesh 2005).

While most of this top-down/bottom-up research in upwelling regions has occurred along open coastlines, recent research in Tomales Bay, California, USA (38°.231 N and 122°.978 W; see chapters 1 and 2) suggests that estuaries within upwelling regions also warrant an integrated top-down/bottom-up research framework. In Tomles Bay, a native California oyster population (*Ostrea lurida*, Olympia oyster) acts as a foundation species that benefits the estuary by filtering water and by creating biologically-diverse intertidal habitat (Kimbro & Grosholz 2006). In the inner portion of the estuary, the absence of an effective top-crab predator may allow an intermediate-invasive whelk predator (*Urosalpinx cinerea*) to exert top-down control by consuming oysters (Fig. 3.1, see chapter 1). But in the middle of the bay, predatory native crabs create trophic cascades that prevent whelks from consuming oysters. Although these data

identify where predation occurs, they fail to address whether interspecific sessile organisms also influence oysters through competition and/or facilitation and whether any of these top-down controls significantly affect oyster population dynamics.

Meanwhile, underlying these potentially important top-down controls is a spatial gradient in phytoplankton abundance that is tied to coastal upwelling (Fig. 3.1, see chapter 2). During the summer-upwelling months, the lack of fresh water flowing into the estuary allows the daily pumping of water with each high and low tide (i.e., tidal excursion) to lengthen water residence times as distance from the ocean increases (Largier et al. 1997). At the same time, the tidal excursion's exchange with coastal waters creates a gradient of coastal nutrients that interacts with water residence times to promote consistent phytoplankton blooms in the middle of the estuary. These food subsidies cause juvenile oysters to grow more in the middle of the bay and less in the inner bay, where invasive whelks occur. But similar to the data on top-down controls, the data on bottom-up controls remain incomplete: are phytoplankton and oyster larvae abundances positively correlated or are they decoupled? In addition to the lack of knowledge concerning recruitment, it also remains unclear how these subsidies interact with the aforementioned top-down controls to influence oyster population dynamics.

We can refine our predictions regarding how top-down and bottom-up controls interact by investigating population-level patterns comprised of multiple age classes that experience varying levels of mortality, growth, and recruitment. Age distributions are commonly used to estimate population parameters, but this method may be difficult for organisms lacking permanent anatomical features that record age (Smith & Botsford 1998). Although eastern Atlantic oysters (e.g., *Crassostrea virginica*) are amenable to

age-structure methods (Kirby *et al*. 1998), we were unable to age *O. lurida* due to the relatively small size of its anatomical feature that records time: the ligamental area of its shell hinge. Under these circumstances, individual sizes within a population and growth increment data provide an alternative method for estimating population growth and mortality parameters (Barry & Tegner 1990). Using these estimates, we can test inferences regarding the interactions between top-down and multiple bottom-up controls by determining how well growth or mortality at the population level is explained by observed predation interactions and/or resource subsidies.

Here, we use this size-structured approach to investigate how top-down and bottom-up factors affect Tomales Bay's oyster population. This approach involved testing the following six hypotheses: (1) recruitment of oysters temporally matches phytoplankton blooms; (2) the estuary's tidal-excursion gradient and the 4-6 week planktotrophic stage of oyster larvae cause recruitment to peak in the inner portion of the bay where water-residence times are longer; (3) under constant recruitment conditions, a cohort of individual juvenile oysters reaches larger sizes in the middle portion of the bay, where phytoplankton abundances are high; (4) this cohort's density decreases more quickly in areas with invasive whelks and less quickly at sites closer to the ocean; (5) under constant recruitment, competition for space is more intense in the middle of the bay where phytoplankton abundance and oyster growth are high; (6) the observed size-structures and growth trajectories indicate that mortality affects oysters most at sites where invasive whelk densities are high, while growth affects oysters most at sites lacking invasive whelks.

Methods

Natural history of Olympia oyster

The Olympia oyster is a protandrous hermaphrodite that is native to eastern Pacific estuaries from Alaska to Baja California Sur, Mexico (Baker 1995). After embryos are brooded within adult oysters for 10-14 days, planktotrophic larvae develop for 4-6 weeks during summer months before settling on hard substrate such as rocks and cobbles (median surface area = 0.07 m^2, Kimbro and Grosholz *unpublished data*). Oysters can grow to ~ 0.06 m in length and often create loose reefs (~ 0.10 m tall) in low intertidal and shallow subtidal portions of estuaries (Baker 1995). Because hard substrate is limited in soft sediment estuaries, oysters compete amongst themselves and with other sessile organisms for space on rocks. At the same time, the biogenic structure of Olympia oysters provides habitat for associated species including amphipods and polychaetes as well as sponges and algae that live on the oysters (Kimbro & Grosholz 2006). Olympia oysters occur across broad areas of shoreline (~20 km) in Tomales Bay with densities up to 40 oysters per 0.03 m^2.

Site description

To quantify and examine demographic patterns of Olympia oysters, this study used six sites within the middle region of Tomales Bay (6-12 km from the ocean) and three sites within the inner bay (13-18 km from ocean, Fig. 3.1). Eight of these sites were chosen to create four east-west pairs of sites (E1,W1; E2,W2; E3,W3; E4,W4) that span the oyster's entire distribution at nearly equal spatial intervals: 6 km, 8 km, 12 km, and

16 km from the mouth of the bay. Site W3.5 was added towards the end of the study to improve our estimates of inner-bay patterns.

Oyster recruitment

We began monitoring oyster recruitment in August of 2002 by deploying seven-0.02 m^2 PVC tiles at five-meter intervals in the intertidal of one inner bay site. Three of these tiles were removed after two weeks and 4 of these tiles were removed after one month. We measured oyster recruitment to each of these tiles under a dissecting microscope in the laboratory. We used a t-test to assess which time interval captures more oyster recruitment within one site.

Based on the 2002 recruitment results, we used smaller PVC tiles (0.01 m^2) and added seven more sites to quantify spatial patterns in summer oyster recruitment from 2003 to 2005. These seven additional sites were chosen to create four east-west pairs of sites (E1,W1; E2,W2; E3,W3; E4,W4) that span the oyster's entire distribution at nearly equal spatial intervals: 6 km, 8 km, 12 km, and 16 km from the mouth of the bay (Fig. 3.1). Because we observed zero recruitment between the summers of 2003 and 2005, in 2006 we began monitoring recruitment in all seasons using bricks for settlement surfaces instead of PVC tiles. From March 2006 – August 2006, this monitoring occurred every month. After August 2006, these bricks were monitored every three months until August 2007.

In the summer of 2007, five additional bricks were added to each east-west site at a larger spatial interval of 15 meters. Oyster recruitment to these bricks was monitored every two months from June-October 2007. To assess whether post-settlement predation

by intertidal organisms such as whelks and crabs influences intertidal recruitment patterns, we also deployed PVC tiles on floating collectors to only west-side sites. Each of these collectors used one PVC tile that was attached to four-1.0 meter PVC arms, which were oriented at ninety degrees to each other. These arrays were maintained in the water column at ~ 1.0 remained off the benthos, away from benthic predators, constantly submerged, and oriented towards the benthos. We deployed two of these subtidal collectors at 5 sites on the western side of the bay (W1, W2, W3, W3.5, and W4; Figure 3.1). Two additional western sites (W2.5 and W3.5) were added, producing a distribution of collectors along the western shoreline at 6 km, 8 km, 10 km, 12 km, 14 km, and 16 km. Every two months from Aug 2007 to May 2008, we quantified oyster recruitment to the frames and flower-pots before cleaning them and returning them to the water.

For each year that recruitment occurred to the intertidal collectors, we calculated the mean recruitment of the entire bay. For the 2007 intertidal-collector data, we also calculated the mean recruitment of each pair of east-west sites and used ordinary least squares regression (OLS) to quantify how recruitment varied across stations (i.e., 6 km - 16 km. OLS was also used to quantify how recruitment to subtidal collectors m below the surface with a surface float and a concrete mooring, so that the tiles varied among stations.

Densities and individual sizes of an oyster cohort

Because the size structure of a population is influenced by growth, mortality and recruitment, we manipulatively tested whether location within Tomales Bay influences an

oyster cohort's density and size through time when recruitment is held constant. Before beginning this experiment, we spawned adult oysters under controlled conditions in the Bodega Marine Laboratory. Larval oysters were then settled onto PVC tiles (0.01 m^2). These tiles could easily be out-planted into the field, and therefore, allowed us to obtain demographic data using juvenile oysters of the same age, size, and initial densities.

Because oysters naturally recruit to adult populations during summer months (Baker 1995), we randomly assigned and out-planted 64 tiles to eight sites (8 tiles/site) in August 2005 (Fig. 3.1). These eight sites were chosen to create four east-west pairs of sites (E1,W1; E2,W2; E3,W3; E4,W4) that span the oyster's entire distribution at nearly equal spatial intervals: 6 km, 8 km, 12 km, and 16 km from the mouth of the bay. At each site and within the middle of the oyster-tidal zone (-0.2 m MLLW), we deployed tiles by fastening them to concrete bricks with cable ties. To orient the tile-bricks perpendicular to the ground, we cable-tied the tile-bricks to 0.5 meter rebar poles that were hammered into the ground. Before deploying tiles in August 2005, we marked five oysters per tile with small numbered tags (Floy Tags Inc., FTF-69 Fingerling Tag-Pennant) and took digital photos of each tile.

To determine how interspecific competition for space or interspecific facilitation influences oyster density and size, tiles were randomly assigned to interspecific-removal (all sessile organisms other than oysters removed) and control (no removal) treatments and were then photographed monthly thereafter until August 2006. From August 2006 to May 2007, tiles were photographed every three months. Collectively, these data describe how oyster size and density (individually and as a cohort) changed over 21 months as a function of location and competition.

Because of seasonal patterns in water temperature, salinity, and food (i.e., chl *a*; Smith *et al*. 1989) we divided our data into 7 three-month intervals and used Repeated Measures-Univariate Analysis of Variance (ANOVA) to analyze how oyster density (and then size) changed as a function of competition/facilitation (removal or control) and side of the bay (east or west). Since gradients in temperature, salinity, and chl *a* that encompass the oyster's distribution are continuous, we used each site's distance from the mouth of the bay as a covariate rather than using site as a discrete variable (Cottingham *et al*. 2005). To comply with parametric assumptions, we first tested each dependent variable for homogeneity of variances among all four distances from the mouth of the bay and then the two sides of the bay. When necessary, we satisfied assumptions by using Log, Log10, or power transformations. In addition, we also used modified degrees of freedom (Univariate G-G Epsilon) to comply with the sphericity assumption of Repeated Measures ANOVA (Quinn & Keough 2002). When significant independent variable*time interactions were detected, we used ANCOVA to test how the independent variables affected oyster density (and then size) at each time interval. We included independent variable and covariate (station) interactions as important biological effects in the model (Quinn & Keough 2002). For both oyster density and size, data from the previous time interval were used as an additional covariate.

Following the ANCOVA at each time step, we used ordinary least squares regression (OLS) to illustrate how the functional relationship between oyster density (and then oyster size) and station changed between linear and quadratic over time. In the presence of significant main effects or interactions, separate functional relationships were plotted for competition and/or side of the bay. For the OLS analyses, we used R^2 and a

partial-F statistic (Quinn & Keough 2002) to determine whether linear or quadratic fits best describe the functional relationships.

To investigate whether predation or high temperatures during low tides explain why juvenile oysters experience high mortality at sites closest to the mouth of the bay (see Results), we conducted a manipulative experiment at site W2. Before beginning the experiment, oyster larvae were settled on to PVC tiles in the laboratory (see methods above) and 18 tiles were randomly assigned among control, predator-exclosure, and shade treatments. For the controls, tiles were fastened to concrete bricks and were oriented perpendicular to the ground. The predator-exclosure tiles were placed in hardware cloth boxes (0.0005 m^3 and mesh openings = 0.49 cm^2), while the shade tiles were only covered by a hardware-cloth top (0.01m^2). Oyster densities were quantified at the beginning (Aug 2004) and at the end of the experiment (September 2004). With initial densities as a covariate, we used ANCOVA and Tukey's post-hoc test to compare how oyster mortality varied among treatments.

Oyster-population surveys

Each spring between 2003-06, we surveyed oyster densities and sizes at multiple sites in Tomales Bay (Fig. 3.1) to determine how population-size structure varies over space and through time. After selecting equal-sized beaches (~300 meters long) with suitable oyster habitat (intertidal rocks within + 0.5 to –1.5 m MLLW), we divided each beach into three-100 m long sections perpendicular to the waterline. Each section's oyster habitat was then horizontally bisected to create a high and low intertidal oyster zone paralleling the waterline (six zones /site). Within

the middle of each high and low oyster zone, a 15 meter horizontal transect was established and then centered in its respective 100 m section.

After partitioning each site's oyster habitat, we selected rocks along transects to sample for oysters. To avoid selecting rocks clustered at the end of transects, each 15 m transect was divided into two 7.5 m sub-transects. We then marked all rocks occurring within 35 cm of the sub-transects. Each sub-transect's marked rocks were tallied and three rocks were randomly selected to survey, yielding six rocks per transect and 36 rocks per site. For each rock, we centered a 0.01 m^2 quadrat on the top, bottom, and side surfaces and measured oyster density and sizes within each quadrat. Using the three quadrats as sub-samples, we generated an average density of oysters for each rock.

If oysters were not present on a transect, we extended our search in order to improve our estimates concerning a site's size distribution. This extended search involved lengthening transects and prolonging our rock sampling until at least 20 oysters per transect were measured. Oyster densities at some sites, however prevented us from measuring the sizes of at least 20 oysters per transect. The 2003 annual survey differed from later surveys by partitioning sites into 2 sections, rather than 3, and selecting 8 rocks per transect. This method yielded 32 rocks per site versus 36.

For individual oyster size and then density, we used ANCOVA to test how each dependent variable changed as a function of year (discrete) and station (continuous covariate). We included the interaction between these two variables in our model because we feel it represents a potentially important biological effect (Maxwell et al. 1993, Quinn and Keough 2002). When the year*station interaction was significant, we used ordinary least squares (OLS) regression to examine the functional relationship

between station and each dependent variable. By comparing values of R^2 and employing a partial-F statistic (Quinn and Keough 2002), we also determined whether a linear or quadratic model best fits these functional relationships.

Estimation model

To determine whether differences in population-size structure occur primarily because of bottom-up (growth) or top-down (mortality) forces, we created a size-structured estimation model that assumed constant recruitment among all sites. In this model, the oyster density and size data obtained from the tiles were treated as proxies for each site's natural population. From these proxy data, we then calculated an individual growth parameter for each site as a series of linear growth segments with the standard deviation of sizes a fixed fraction of the mean through 7 time steps. Based on our inspection of the growth trajectories and frequency of data sampling, these time steps comprised months 0, 3, 6, 9, 12, 15, and 18. For all sites and time steps (i), we calculated mean oyster size (l_i), standard deviation ($sigma_i$), and ratio of standard deviation to mean (coefficient of variation, S_i). After inspecting the distribution of observed S_i among all sites, we used the median value as constant model parameter for S.

With site-specific growth trajectories and a constant S parameter, the estimation model then exhaustively searched for the rate of instantaneous mortality (M) that most likely underlies the size structure of each site during 2006. To perform this exhaustive search, the model assumed constant recruitment and mortality. Constant recruitment was achieved by adding 1000 oyster recruits of the smallest size class into each population at months 0, 12, and 24, 36, and 48 (August). These simulated recruitment events coincide

with the timing of natural recruitment events (Baker 1995, see *Oyster recruitment* results below). At each subsequent 3-month time step, the estimation model then applied a constant mortality rate. A range of constant mortality rates for the model to exhaustively search was calculated from the proxy data by using the known initial oyster densities (N_0) on tiles at each site and equation (1), which assumed that each site's instantaneous mortality did not vary with size.

(1) $N_0 \exp^{-M} = (N_3+N_6+N_9+N_{12}+N_{15}+N_{18} / N_0+N_3+N_6+N_9+N_{12}+N_{15})$,

To reach an equilibrium-state for the particular time at which each site's population structure was observed (spring, see *Oyster population surveys*), recruitment, growth, and M were continued until month 57 (spring). Because our natural population-size structures were observed each spring, the model assessed which value of M interacts with each site's growth trajectory and S-parameter to produce an estimated population-size distribution the best fits each site's observed size-distribution. Best fits for M were determined by minimizing the separation statistic of Schnute and Fournier (1980) without their multiple of two (equation 2):

(2) $\sum = O_l * \ln(O_l/P_l)$,

where O_l and P_l are the observed and predicted number of individuals at length l. Although our observed growth trajectories do not extend beyond month 18, our monitoring of adult oysters at each site indicated that oysters grow asymptotically and

increase in size very little after month 18. Thus, we held oyster size constant after month 18.

Results

Oyster recruitment

At site W4 during August 2002, more oyster larvae settled onto PVC tiles (0.02 m^2) when tiles were left in the field for one month (1071.0 $\pm$ 117.20) versus tiles that were left in the field for two weeks (281.67 $\pm$ 161.86; t-test = -3.69, P = 0.01). In addition, monthly oyster recruitment to PVC tiles at this site was considerably higher in August (1071.0 $\pm$ 117.20 per 0.02 m^2) than in September (44.33 $\pm$ 135.33 recruits per 0.02 m^2; T-test = 5.73, P = 0.002).

During the summers of 2003-2005, we observed zero recruitment onto PVC tiles. In May and August of 2006, we observed small recruitment at one site (Fig. 3.2a). But multiple sites did not receive modest levels of recruitment again until October 2007. During this recruitment event, recruitment generally increased with distance from the mouth of the bay, but the functional relationship between recruitment and station distance differed between intertidal and subtidal recruitment collectors (Fig. 3.2b). However, because oysters settled onto the PVC frames and concrete flower-pots, we were unable to standardize oyster recruitment per unit area for the subtidal data. As a result, we do not compare the actual number of observed recruits between the intertidal and subtidal collectors.

Densities and individual sizes of an oyster cohort

When we experimentally deployed oysters of known size, density, and age, a four-way interaction among time, station, competition, and side of bay interactively influenced oyster density (Repeated Measures ANOVA-Wilks' Lambda, $F_{42,237.97}$ = 1.92, P = 0.001; 4-way interaction $F_{2.03,111.61}$ = 5.32, P = 0.006). But as discussed below, initial density (covariate) and the interaction between station and side of the bay accounted for most of the variation at each time step. Before the experiment began in August 2005 (month 0), we randomly assigned tiles such that oyster densities did not differ among stations (y = 0.02x + 1.62, R^2 = 0.02, P = 0.31, Table 3.1, Fig. 3.3a). After including the previous time period's oyster density as a covariate (i.e., August density was the covariate for November density), we found that November (month 3), February (month 6), and May (month 9) oyster densities decreased less as station distance from the mouth of the bay increased (Table 3.1). Based on the results of our additional experiment at site W2, juvenile oyster mortality was significantly reduced only when predators were excluded (ANCOVA $F_{3,7}$ = 4.04, P = 0.05; Treatment F = 5.60, P = 0.04; Initial density F = 4.67, P = 0.07, Tukey's = 2.94).

Between November 2005 and May 2006, these significant factors caused oyster densities to be asymptotically higher as distance from the mouth of the bay increased (Fig. 3.3b-d, Table 3.3). But by August 2006 (month 12) on the eastern shoreline, changes in oyster density were no longer associated with station (Tables 3.1-3.2a, Fig. 3.3e). And in November 2006 (month 15) and February 2007 (month 18), the same results were also observed for oyster densities on both shorelines (Table 3.1). Consequently, the relationship between oyster density and station at

months 15 and 18 appeared slightly unimodal on the eastern shoreline and remained asymptotic on the eastern shoreline (Figs 3.3f-g).

Throughout the course of this cohort experiment, only month 3 contained a significant interaction or effect involving competition (Table 3.1). Despite a significant 3-way interaction at month 3 between station, competition treatment, and side of bay (P = 0.04, Table 3.1), an independent analysis of the east and west sides of the bay indicated that only station and initial density were significantly related to oyster density (Table 3.2). Thus, competition did not strongly influence oyster density throughout our study.

Competition also did not influence the size of oysters. Instead, oyster sizes differed among stations and between sides of the bay, and these differences changed with time (Repeated Measures ANOVA-Wilks' Lambda, $F_{42,181.69} = 3.87$, $P < 0.0001$; station*time $F_{1.55,66.5} = 27.21$, $P < 0.001$; bay side*time interaction $F_{1.55,66.5} = 21.67$, $P < 0.001$). Before the experiment began, slightly smaller oysters were unintentionally assigned to stations farther from the mouth of the bay (Month 0, $y = 0.004x + 0.27$, $R^2 = 0.06$, $P = 0.05$, Table 3.4, Fig. 3.3h). By November 2005 (month 3), station and side of the bay interactively influenced oyster size (Table 3.4). On the eastern shoreline, the larger oysters at sites closer to the mouth of the bay created an asymptotic relationship between size and station (Fig. 3.3i, Tables 3.2 and 3.3). But on the western shoreline, larger oysters in the middle of the bay created a slight unimodal relationship between size and station (Tables 3.2- 3.3, Fig 3.3i). After using these oyster-size patterns as covariates, we found that oyster size changed very little between November 2005 and February 2006 (month 6) on the eastern shoreline

(Table 3.2 and 3.4). Meanwhile, oyster size on the western shoreline increased at sites closer to the mouth of the bay (Tables 3.2 and 3.4). These size changes —and lack thereof on the eastern shoreline— maintained the asymptotic and unimodal patterns of oyster size versus station that were observed in November 2005 (Fig 3.3j).

By May 2006 (month 9) and August 2006 (month 12), only previous size and station were significantly related to changes in oyster size (Table 3.4). Because increases in oyster size were inversely related to station distance, oyster sizes of the whole bay became asymptotically higher as station distance decreased during May 2006 (Fig. 3.3k, Table 3.3) and then linearly higher as station distance decreased during August 2006 (Fig. 3.3l, Table 3.3). By November 2006 (month 15), changes in oyster size were significantly influenced only by the covariate of August 2006 sizes (Table 3.4); adult oyster size was inversely related to stations (Fig 3.3m and Table 3.3). Greater changes in oyster size at sites closer to the mouth of the bay the following winter (Table 3.4) reinforced the inversely linear relationship between oyster size and station that was observed in month 15 (Fig. 3.3n).

Oyster-population surveys

Oyster densities changed with distance from the mouth of the bay (ANCOVA $F_{7,938} = 36.72$, $P < 0.0001$) and this relationship also changed through time (Year*Station $F_{3,938} = 19.94$, $P < 0.0001$, Fig. 3.5b). In 2003, oyster density linearly increased with increasing station distance (oyster density = $0.27x - 0.67$, $R^2 = 0.05$, $F_{1,94} = 5.45$, $P = 0.02$). While this weakly positive linear relationship grew

statistically stronger in 2004 (oyster density = 0.31x – 1.88, R^2 = 0.25, $F_{1,265}$ = 88.50, P < 0.0001), distance again explained little variation (R^2 = 0.07) in oyster density during 2005 (oyster density = 0.09x – 0.20, $F_{1,260}$ = 19.34, P < 0.0001). By 2006 oyster density was highest at station 12 km, which lead to a unimodal relationship between density and station (oyster density = $-0.03x^2 + 0.01x + 0.77$, R^2 = 0.09, $F_{2,318}$ = 14.94, P < 0.0001).

For four years, individual sizes within each oyster site significantly declined with increasing distance from the mouth of the bay (ANCOVA $F_{7,5116}$ = 729.11, P < 0.0001). Figure 3.4 illustrates how individual oysters are distributed across size classes for all sites and years. Although individual oyster sizes within sites consistently declined as distance from the mouth of the bay increased, the nature of this relationship changed among years (Year*Station $F_{3,5123}$ = 14.326, P < 0.0001, Fig. 3.5a). In 2003, oyster size linearly declined with distance from the mouth of the bay (2003 size = -1.15x + 38.85, R^2 = 0.11, $F_{1,999}$ = 124.08, P < 0.0001). But when more sites throughout the oyster's distribution were sampled from 2004-2006, the relationship between individual size and station was no longer strictly linear, as oyster size did not decrease until after station 12 km (2004 size = $-0.24x^2 – 1.76x$ + 59.5, R^2 = 0.29, Partial-$F_{1,1476}$ = 57.85, P < 0.0001; 2005 size = $-0.36x^2 – 1.76x + 62.55$, R^2 = 0.40, Partial-$F_{1,1167}$ = 127.79, P < 0.0001; 2006 size = $-0.24x^2 – 1.77x + 63.67$, R^2 = 0.39, Partial-$F_{1,1479}$ = 122.84, P < 0.0001).

Size-structured estimation model

From the proxy population data, site-specific growth trajectories of individual oysters ended at three different maximum sizes (Fig. 3.6a, Table 3.5). The highest maximum size values were reached by three sites closest to the mouth of the bay: E1, W1, and W2. The next largest maximum size value was attained by sites E3, W3, and E2. Finally, the smallest maximum size value observed in this study was reached at sites E4 and W4. Among all of these sites, the median observed S-value was 0.20.

Using these site-specific growth trajectories, a constant recruitment rate, and the range of constant mortality observed in the cohort study (Fig. 3.6b, Table 3.5), our preliminary model estimated that the instantaneous rate of mortality (M) of oysters unimodally varied with distance from the mouth of the bay (Fig. 3.7) such that mortality was low at station 12 km and high at stations 6 km, 8 km, and 16 km ($y = 0.03x^2 - 0.06x + 1.23$, $R^2 = 0.78$, $F_{2,4} = 7.88$, < 0.0001).

Discussion

In Tomales Bay, CA, a tidal-excursion gradient creates spatially varying water-residence times that decouple the bottom-up factors of larval recruitment and food for the bay's oyster population (Largier *et al.* 1997). As a result, oyster populations farther from the ocean experience high recruitment-low food conditions and populations closer to the ocean experience low recruitment-high food conditions (Figs. 3.1 and 3.2). While the food-resource gradient is consistent, recruitment appears to be inter-annually episodic (Fig. 3.2a). In addition to these bottom-up gradients, native predators in the outer bay and an invasive predator in the inner

bay provide two different top-down controls (Fig. 3.1). During a period of high recruitment, both bottom-up gradients and the native predators in the outer bay adequately explain the individual sizes and densities of oysters throughout the bay (Fig. 3.5). But after a prolonged absence of recruitment, a high instantaneous rate of mortality in areas with invasive whelks (inner bay) and native predators (outer bay) causes oyster densities to peak in the middle of the bay (Figs. 3.5).

Although our results demonstrate that spatial variation in food availability creates consistent differences in oyster growth patterns among sites (Fig. 3.6a), our results also demonstrate that the second bottom-up factor of recruitment is highly variable and poorly understood (Fig. 3.2). For instance, by monitoring the timing of recruitment from 2002-2007, we are fairly confident that simulating August recruitment events is appropriate in our estimation model (months 0, 12, and 24, 36, and 48). But our relatively short time-series of oyster recruitment inhibits us from knowing the degree to which consistent, annual recruitment events in the estimation model are inappropriate (Fig. 3.2a). In addition, the recruitment results failed to illustrate how our model should vary recruitment levels among sites. For example, intertidal-oyster recruitment asymptotically increased with distance from the ocean, and this gradient suggests that stations 12 km and 16 km receive equally high recruitment levels (Fig. 3.2b). In contrast, subtidal-oyster recruitment exponentially increased with distance from the ocean, and this gradient suggests that station 16 km receives far higher recruitment than any other station (Fig. 3.2b).

While the subtidal-recruitment pattern closely matches that predicted from water-residence times if oyster larvae behave as passive water particles (Largier et al. 1997), we

are still uncertain about the degree to which recruitment levels are low at stations 6 km and 8 km. This uncertainty arises from the oyster-cohort study clearly showing that post-settlement mortality is extremely high at these stations (Figs. 3.3 and 3.6). In fact, subsequent experiments involving predator exclosure and shading treatments suggest that this mortality is caused by predators such as the lined shore crab (*Pachygrapsus crassipes*) and the bat star (*Asterina miniata*). Therefore, our monthly sampling intervals may underestimate recruitment at stations 6 km and 8 km if most of the recruits are consumed in less than a month. Because our size-structured estimation model assumed consistent and constant recruitment conditions, our estimates of population-mortality levels are certainly inaccurate. The effects of this assumption should be experimentally and quantitatively addressed.

A second limitation of this study concerns our assuming constant mortality in the estimation model. Although an oyster cohort's density decreased continuously at sites W4 and E4 (station 16 km) densities at the remaining six sites ceased to decrease and remained relatively constant by month 6 (Fig. 3.3a). Within these six sites, densities decreased more sharply at sites E1, W1, E2, and W2 (stations 6 km and 8 km) in the first three months than did densities at sites E3, W3 (station 12 km). These size-dependent mortality patterns that vary spatially conflict with another assumption of our estimation model and increase the uncertainty of our model's conclusion regarding how mortality affects the size structure of oyster populations in Tomales Bay.

In response to the two limitations of this estimation model, a revised model could incorporate the annual size-distribution data from 2003-2005. Beginning with the simulated recruitment of the 2002 cohort and using the site-specific growth trajectories,

this model could exhaustively search for the instantaneous mortality rates of each cohort that allow an estimated-size distribution to best fit each site's observed-size distribution for each year (i.e., 2003-2006). In combination with AIC, this revised model could then examine whether the additional parameters of age- and size-dependent mortality increase our understanding of oyster-population dynamics and whether these cohort effects change as time since observed recruitment increases (i.e., 2002 recruitment event).

Despite the limitations of our study, it still provides several insights into how top-down and multiple bottom-up controls can interactively influence population-level patterns of an important estuarine species. First, the environmental stress model (ESM) predicts that under high levels of recruitment and intermediate levels of stress, interspecific competition will be an important top-down control for marine populations (Menge & Sutherland 1976; Menge & Branch 2001). At station 12 km in our study, the stress from reduced salinity during winter months is intermediate, food concentrations are high, and predation is relatively low (see chapters 1 and 2). At station 16 km, salinity often reaches lower and more stressful levels, food concentrations are low, and recruitment of interspecific competitors for space is high (Chang and Kimbro *unpublished data*). Nevertheless, interspecific competition for space did not affect oyster densities or sizes at either of these stations in our cohort study (Tables 3.1 and 3.4).

Due to the effects that intertidal grazers can have on sessile invertebrates (Stachowicz & Whitlatch 2005) and to the high densities of chitons and limpets at stations 12 km and 16 km (Appendix 3.1), we hypothesize that theses intertidal consumers may reduce interspecific competition by inhibiting the recruitment and growth of competitors in the intertidal oyster zone. Furthermore, we hypothesize that

competition at station 12 km may have occurred intraspecifically rather than interspecifically. There, high food levels during August promote the highest observed growth rates immediately following settlement. This high growth may in turn lead to self-thinning, high post-settlement oyster mortality, and adult crowding that minimize the sizes adult oysters attain. In contrast, adult oysters at stations 6 km and 8 km grow to larger sizes not because they receive more food, but because the relatively higher mortality of juvenile oysters produced low adult densities that minimized adult crowding and intraspecific competition.

A second insight from our study pertains to another top-down prediction of ESM, which suggests that stress and predation pressures are inversely related (Menge & Sutherland 1976; Menge & Branch 2001). While this principle historically provided useful community- and population-level predictions, its usefulness may be diminishing as humans continue to move species beyond their natural ranges (Cohen & Carlton 1998; Ruiz *et al*. 2000). Because many successful invasions involve physiologically tolerant organisms, physically stressful environments that historically lacked predators may now have their empty predator niches being filled by invasive species. For example, our previous results (see chapter 1) and our size-structured estimation model illustrate that the effects of invasive whelks can strongly alter oyster-population dynamics in a stressful region of Tomales Bay where predation by native predators was historically absent. Thus, biological invasions may alter a fundamental prediction of ESM by decoupling the inverse relationship between stress and predation.

Our study also provides a direction for future research on bottom-up control of estuarine systems in upwelling regions. Despite their life-history differences, both

phytoplankton and invertebrate larvae are often retained behind coastal promontories and may jointly influence coastal invertebrate populations over the same spatial and temporal scale (Menge *et al*. 1997). But in sheltered estuaries whose circulation is driven primarily by tidal excursion, water residences become longer with increasing distance from the ocean. The differences in life histories between phytoplankton and invertebrate larvae may interact with water residence times to decouple food and larval recruitment subsidies, leading to more complex predictions of how top-down and bottom-up factors influence invertebrate populations. In this case, increasing residence time is associated with higher recruitment but lower phytoplankton abundance. In addition, the recruitment of some invertebrates may be less consistent than the occurrence of food subsidies. Consequently, future top-down/bottom-up research should consider estuaries in upwelling regions, and whether the underlying physical gradients of the estuary predictably decouple subsidies of food and larval recruits.

In conclusion, while most top-down/bottom-up research in marine systems has focused on how upwelling influences coastal food webs (Menge *et al*. 1997; Menge & Branch 2001; Menge *et al*. 2003), our results suggest that upwelling can also influence how top-down and bottom-up factors interact in low-inflow estuaries. Moreover, the tidal exchange of these estuaries may interact with upwelling to decouple phytoplankton and larval invertebrate subsidies through space. Regardless of the level of recruitment and even with lower ambient phytoplankton abundances, marine predators likely limit the density but enhance the size of estuarine basal prey towards the mouth of the bay. In contrast, increasing recruitment, higher phytoplankton abundances, and the presence of a trophic cascade suggest higher densities of slightly smaller oysters are governed

predominately from the bottom-up. Finally, the decreasing subsidy of phytoplankton and increasing subsidy of recruitment in the inner bay maintained very high densisites of the smallest observed oysters even in the presence of an invasive predator. With the loss of recruitment subsidies, however, the effect of invasive whelks largely controls oyster demography.

While the scope of our results is restricted to one California estuary, our conclusions may generally apply to many other estuaries in upwelling regions with Mediterranean climates (i.e., wet winters and dry summers). In these systems, which lack dry season input of nutrients from watershed sources and instead are subsidized by nutrient inputs from nearshore upwelling, phytoplankton abundance may peak in the outer and middle portions of estuaries (Banas *et al*. 2007, see chapter 2). In addition to a similar food-resource gradient, these low-inflow estuaries would also be predicted to have a similar gradient in water-residence time. High residence time in the inner portion of these estuaries may result in accumulation and high rates of settlement of planktonic larvae. Moreover, many of these estuaries contain or are close to major shipping ports and many have the same invasive whelk (Carlton 1992). As a result, their inner portions likely have an invasive-predation gradient that is similar to or more extreme than that of Tomales Bay. Therefore, it is plausible that the density and size-structure of sessile invertebrate populations in many low-inflow estuaries are governed by similar interactions between top-down and bottom-up factors.

Acknowledgments

I thank R. Hughes, J. Stachowicz, M. O'Farrell, L. Botsford, and E. Grosholz for

comments and ideas that improved this manuscript. S. Attoe, A. Baukus, L. Budd, A. Chang, M. Ferner, R. Hughes, B. Kordas, N.Nesbitt, A. Newsom, M. O'Farrell, M. O'Leary, J. Sones, and B. Steves generously provided field assistance. I also thank B. Steves for constructing the size-structured estimation model. This research was supported by grants from the University of California (UC) Marine Council/Coastal Quality Environmental Initiative (to D.L.K.), UC Davis Graduate Group in Ecology (to D.L.K.), National Park Service at Point Reyes National Seashore (to D.L.K.), National Oceanic and Atmospheric Administration (to E.D.G), National Parks Service-California Cooperative Ecosystem Studies Program (to E.D.G.), Pacific States Marine Fisheries Commission (to E.D.G.), and UC Exotic/Invasive Pest and Disease Program (to E.D.G.).

Literature cited

Baker P. (1995) Review of ecology and fishery of the Olympia oyster, Ostrea lurida with annotated bibliography. *Journal Of Shellfish Research*, 14, 501-518

Banas N.S., Hickey B.M., Newton J.A. & Ruesink J.L. (2007) Tidal exchange, bivalve grazing, and patterns of primary production in Willapa Bay, Washington, USA. *Marine Ecology-Progress Series*, 341, 123-139

Barry J.P. & Tegner M.J. (1990) Inferring Demographic-Processes from Size-Frequency Distributions - Simple-Models Indicate Specific Patterns of Growth and Mortality. *Fishery Bulletin*, 88, 13-19

Bruno J.F. & Bertness M.D. (2001) Habitat modification and facilitation in benthic marine communities. In: *Marine Community Ecology* (eds. Bertness MD, Gaines SD & Hay ME), pp. 201-218. Sinauer Associates, Inc.

Carlton J.T. (1992) Introduced marine and estuarine mollusks of North America: An end-of-the-20th Century perspective *Journal Of Shellfish Research*, 11, 489-505

Cohen A.N. & Carlton J.T. (1998) Accelerating invasion rate in a highly invaded estuary. *Science*, 279, 555

Connell J.H. (1961) Influence Of Interspecific Competition And Other Factors On Distribution Of Barnacle Chthamalus Stellatus. *Ecology*, 42, 710-&

Cottingham K.L., Lennon J.T. & Brown B.L. (2005) Knowing when to draw the line: designing more informative ecological experiments. *Frontiers in Ecology and the Environment*, 3, 145-152

Fretwell S.D. (1987) Food Chain Dynamics: The Central Theory of Ecology? *Oikos*, 50, 291-301

Gaines S. & Roughgarden J. (1985) Larval Settlement Rate - a Leading Determinant of Structure in an Ecological Community of the Marine Intertidal Zone. *Proceedings of the National Academy of Sciences of the United States of America*, 82, 3707-3711

Hillebrand H., Gruner D.S., Borer E.T., Bracken M.E.S., Cleland E.E., Elser J.J., Harpole W.S., Ngai J.T., Seabloom E.W., Shurin J.B. & Smith J.E. (2007) Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 10904-10909

Hixon M.A. & Menge B.A. (1991) Species-Diversity - Prey Refuges Modify the Interactive Effects of Predation and Competition. *Theoretical Population Biology*, 39, 178-200

Kimbro D.L. & Grosholz E.D. (2006) Disturbance influences oyster community richness and evenness, but not diversity. *Ecology*, 87(9), 2378-2388

Kirby M.X., Soniat T.M. & Spero H.J. (1998) Stable isotope sclerochronology of pleistocene and recent oyster shells (Crassostrea virginica). *Palaios*, 13, 560-569

Largier J.L., Hollibaugh J.T. & Smith S.V. (1997) Seasonally hypersaline estuaries in Mediterranean-climate regions. *Estuarine Coastal and Shelf Science*, 45, 789-797

Mann K.H. & Lazier J.R.N. (2006) *Dynamics of marine ecosystems: biological-physical interactions in the oceans*. 3rd edn. Blackwell Publishing, Malden, MA, USA.

Menge B.A. & Branch G.M. (2001) Rocky intertidal communities. In: *Marine Community Ecology* (eds. Bertness MD, Gaines SD & Hay ME), pp. 221-251. Sinauer Associates, Inc.

Menge B.A., Daley B.A., Wheeler P.A., Dahlhoff E., Sanford E. & Strub P.T. (1997) Benthic-pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? *Proceedings of the National Academy of Sciences of the United States of America*, 94, 14530-14535

Menge B.A., Lubchenco J., Bracken M.E.S., Chan F., Foley M.M., Freidenburg T.L., Gaines S.D., Hudson G., Krenz C., Leslie H., Menge D.N.L., Russell R. & Webster M.S. (2003) Coastal oceanography sets the pace of rocky intertidal community dynamics. *Proceedings of the National Academy of Sciences %R 10.1073/pnas.1534875100*, 100, 12229-12234

Menge B.A. & Sutherland J.P. (1976) Species-Diversity Gradients - Synthesis of Roles of Predation, Competition, and Temporal Heterogeneity. *American Naturalist*, 110, 351-369

Oksanen L., Fretwell S.D., Arruda J. & Niemela P. (1981) Exploitation Ecosystems in Gradients of Primary Productivity. *American Naturalist*, 118, 240-261

Polis G.A. & Hurd S.D. (1996) Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *American Naturalist*, 147, 396-423

Quinn G.P. & Keough M.J. (2002) Experimental design and data analysis for biologists. In: *Experimental design and data analysis for biologists*, pp. i-537

Roughgarden J., Gaines S. & Possingham H. (1988) Recruitment Dynamics in Complex Life-Cycles. *Science*, 241, 1460-1466

Ruiz G.M., Fofonoff P.W., Carlton J.T., Wonham M.J. & Hines A.H. (2000) Invasion of coastal marine communities in North America: Apparent patterns, processes, and biases. *Annual Review Of Ecology And Systematics*, 31, 481-531

Smith B.D. & Botsford L.W. (1998) Interpretation of growth, mortality, and recruitment patterns in size-at-age, growth, increment, and size frequency data. In: *Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management* (eds. Jamieson GS & Campbell A), pp. 125-139. National Research Council Canada

Smith S.V., Hollibaugh J.T. & Vink S. (1989) Tomales Bay, California - a Case for Carbon-Controlled Nitrogen Cycling. *Limnology and Oceanography*, 34, 37-52

Stachowicz J.J. & Whitlatch R.B. (2005) Multiple mutualists provide complementary benefits to their seaweed host. *Ecology*, 86, 2418-2427

Stapp P., Polls G.A. & Pinero F.S. (1999) Stable isotopes reveal strong marine and El Nino effects on island food webs. *Nature*, 401, 467-469

Vonesh J.R. (2005) Egg predation and predator-induced hatching plasticity in the African reed frog, Hyperolius spinigularis. *Oikos*, 110, 241-252

Yang L.H., Bastow J.L., Spence K.O. & Wright A.N. (2008) What can we learn from resource pulses? *Ecology*, 89, 621-634

Table 3.1. ANCOVA results for mean oyster density at each three-month time step.

	Time 0		**Time 3**		**Time 6**		**Time 9**	
Indep. variable	F (dfNum. ,dfDen.)	P-value	F (dfNum. ,dfDen.)	P-value	F (dfNum. ,dfDen.)	P-value	F (dfNum. ,dfDen.)	P-value
Full model	0.43 (7,57)	0.87	13.53 (8,56)	<0.0001	12.39 (8,56)	<0.0001	19.68 (8,56)	<0.0001
Station	0.83 (1,1)	0.36	57.84 (1,1)	<0.0001	25.41 (1,1)	<0.0001	16.71 (1,1)	<0.0001
Side	0.12 (1,1)	0.73	0.04 (1,1)	0.84	0.55 (1,1)	0.46	0.21 (1,1)	0.65
Comp.	0.01 (1,1)	0.94	0.87 (1,1)	0.36	1.17 (1,1)	0.28	1.28 (1,1)	0.26
Station* Side	0.43 (1,1)	0.52	0.13 (1,1)	0.72	0.17 (1,1)	0.68	0.26 (1,1)	0.61
Station* Comp.	1.04 (1,1)	0.31	0.10 (1,1)	0.76	0.05 (1,1)	0.83	0.001(1,1)	0.97
Side* Comp.	0.01 (1,1)	0.93	0.83 (1,1)	0.37	1.94 (1,1)	0.17	0.76 (1,1)	0.39
Station* Comp.* Side	0.43 (1,1)	0.51	4.41 (1,1)	0.04	3.59 (1,1)	0.06	2.15 (1,1)	0.15
Time			35.63	<0.0001	50.10 (1,1)	<0.0001	48.37	<0.0001
	Time 12		**Time 15**		**Time 18**			
Full model	16.75 (8,55)	<0.00 01	24.41 (8,55)	<0.0001	28.39 (8,55)	<0.0001		
Station	10.71 (1,1)	0.002	3.60 (1,1)	0.06	3.19 (1,1)	0.08		
Side	1.84 (1,1)	0.18	0.16 (1,1)	0.69	1.34 (1,1)	0.25		
Comp.	0.15 (1,1)	0.70	1.76 (1,1)	0.19	0.02 (1,1)	0.88		
Station* Side	4.15 (1,1)	0.05	2.34 (1,1)	0.13	5.97 (1,1)	0.02		
Station* Comp.	0.10 (1,1)	0.75	0.47(1,1)	0.50	0.14 (1,1)	0.71		
Side* Comp.	0.41 (1,1)	0.53	0.04 (1,1)	0.83	0.59 (1,1)	0.44		
Station* Comp.* Side	1.63(1,1)	0.21	1.10 (1,1)	0.30	0.50 (1,1)	0.48		
Time	32.49 (1,1)	<0.00 01	65.17	<0.0001	78.92 (1,1)	<0.0001		

Table 3.2. Summary of ANCOVAs that were conducted for (a) oyster densities and (b) oyster sizes at particular time steps with a significant interaction involving side of the bay .

a.	**Time 3 (east)**		**Time 3 (west)**		**Time 12 (east)**		**Time 12 (west)**	
Indep. variable	F (dfNum.,dfDen.)	P-value	F (dfNum.,dfDen.)	P-value	F (dfNum.,dfDen.)	P-value	F (dfNum.,dfDen.)	P-value
Full model	10.88 (4,28)	<0.0001	17.66 (4,27)	<0.0001	28.23 (2,29)	<0.0001	42.75 (2,29)	<0.0001
Station	29.46 (1,1)	<0.0001	30.49 (1,1)	<0.0001	0.24 (1,1)	0.63	15.95 (1,1)	0.0004
Comp.	0.02 (1,1)	0.88	2.23 (1,1)	0.15				
Station * Comp.	2.04 (1,1)	0.16	3.40 (1,1)	0.08				
Time 0	7.25 (1,1)	0.01	32.27 (1,1)	<0.0001				
	Time 18 (east)		**Time 18 (west)**					
Full model	45.06 (2,29)	<0.0001	71.61 (2,29)	<0.0001				
Station	0.02 (1,1)	0.89	3.60 (1,1)	0.07				
Time 0	63.92 (1,1)	<0.0001	48.94 (1,1)	<0.0001				

b.	**Time 6 (east)**		**Time 6 (west)**	
Indep. variable	F (dfNum.,dfDen.)	P-value	F (dfNum.,dfDen.)	P-value
Full model	102.10 (2,29)	<0.0001	65.72 (2,27)	<0.0001
Station	0.70 (1,1)	<0.41	14.84 (1,1)	0.0007
Time 3	125.15 (1,1)	<0.0001	101.18 (1,1)	<0.0001

Table 3.3. Summary of indicators (R^2, p-value, Partial-F statistic) used to evaluate whether a linear or quadratic line best describes the functional relationship between (a) oyster density and station and (b) oyster size and station at each time step.

(a) Oyster density				
Time	Linear OLS R^2 P-value	Quadratic OLS R^2 P-value	Partial F-statistic test of quadratic P-value	Equation of best fit
3	0.41 <0.0001	0.44 <0.0001	3.38 (2,62) P < 0.025	$Y = 0.009x^2 + 0.10x + 0.13$
6	0.45 <0.0001	0.49 <0.0001	5.21 (2,62) P < 0.01	$Y = 0.01x^2 + 0.10x + 0.03$
9	0.44 <0.0001	0.49 <0.0001	5.77 (2,62) P < 0.01	$Y = 0.01x^2 + 0.10x + 0.03$
12 (east)	0.24 0.004	0.38 0.001	6.02 (2,29) P = 0.007	$Y = 0.02x^2 + 0.08x + 0.27$
12 (west)	0.61 <0.0001	0.71 <0.0001	9.78 (2,29) P = 0.0006	$Y = 0.02x^2 + 0.12x - 0.29$
15	0.37 <0.0001	0.47 <0.0001	11.41 (2,62) P < 0.0001	$Y = 0.03x^2 + 0.21x + 0.004$
18 (east)	0.22 0.007	0.31 0.005	3.65 (2,29) P = 0.04	$Y = -0.01x^2 + 0.07x + 0.21$
18 (west)	0.55 <0.0001	0.67 <0.0001	10.6 (2,29) P = 0.0004	$Y = -0.02x^2 + 0.12x - 0.30$
(b) Oyster size				
3 (east)	0.32 0.0006	0.51 <0.0001	12.0 (2,30) P = 0.0002	$Y = 0.017x^2 - 0.04x + 2.07$
3 (west)	0.02 0.51	0.66 <0.0001	59.67 (2,30) P < 0.0001	$Y = -0.02x^2 + 0.02x + 1.78$
6 (east)	0.34 0.0005	0.45 0.0002	5.95 (2,29) P = 0.007	$Y = -0.02x^2 - 0.06x + 2.87$
6 (west)	0.19 0.02	0.70 <0.0001	43 (2,27) P < 0.0001	$Y = -0.04x^2 - 0.02x + 3.19$
9	0.33 <0.0001	0.41 <0.0001	8.46 (2,59) P = 0.0006	$Y = -0.02x^2 - 0.09x + 4.08$
12	0.40 <0.0001	0.42 <0.0001	2.6 (2, 53) P = 0.08	$Y = -0.02x + 0.78$
15	0.40 <0.0001	0.45 <0.0001	1.67 (2, 53) P = 0.20	$Y = -0.01x + 1.47$
18	0.63 < 0.0001	0.65 <0.0001	3.0 (2,51) P = 0.06	$Y = -0.05x + 2.08$

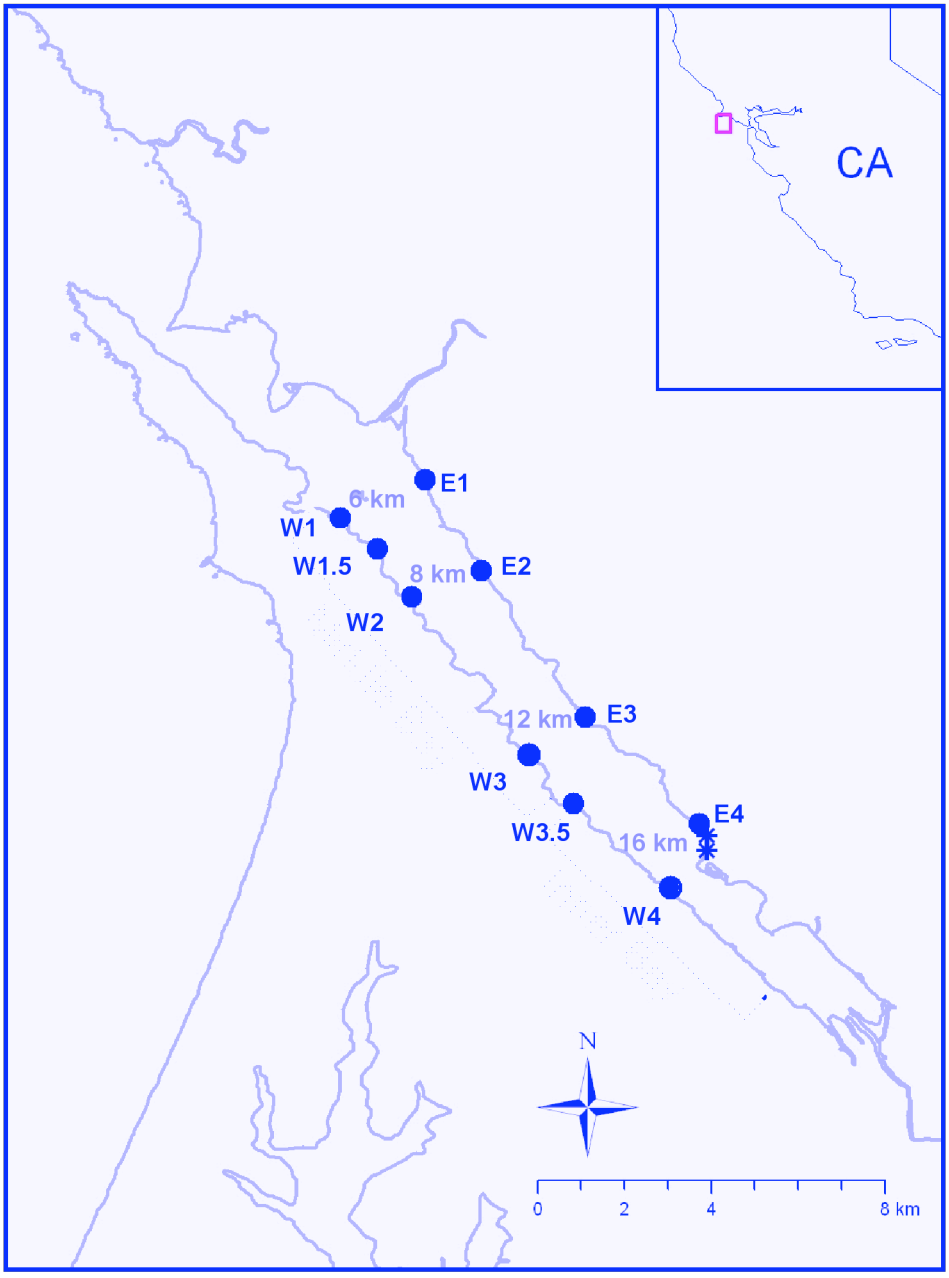
Table 3.4. Summary of ANCOVA results for oyster sizes at each time step. Factors used in the model at each time step were determined by a Repeated Measures ANCOVA that included time, all main effects, and all possible interations (see Methods and Results).

Time	Indep. variable	F (dfNum., dfDen.)	P-value	Time	Indep. variable	F (dfNum., dfDen.)	P-value
0**	Full model	1.57 (3,61)	0.21	**3**	Full model	6.55 (4,59)	0.0002
	Station	4.19 (1,1)	0.05		Station	8.41 (1,1)	0.005
	Side	0.03(1,1)	0.87		Side	8.48 (1,1)	0.005
	Station* Side	0.44 (1,1)	0.51		Station* Side	5.35 (1,1)	0.02
					Time 0	1.38 (1,1)	0.25
6	Full model	97.15 (4,57)	<0.0001	**9**	Full model	92.49 (4,57)	<0.0001
	Station	8.89 (1,1)	0.004		Station	13.80 (1,1)	0.0005
	Side	9.77 (1,1)	0.002		Side	0.21 (1,1)	0.65
	Station* Side	8.22 (1,1)	0.006		Station* Side	0.35(1,1)	0.56
	Time 3	214.71 (1,1)	<0.0001		Time 6	168.61 (1,1)	<0.0001
12	Full model	42.02 (4,51)	<0.0001	**15**	Full model	55.33 (4,49)	<0.0001
	Station	4.82 (1,1)	0.03		Station	3.13 (1,1)	0.08
	Side	0.97 (1,1)	0.33		Side	0.03(1,1)	0.86
	Station* Side	0.32 (1,1)	0.57		Station* Side	0.68 (1,1)	0.41
	Time 9	47.29 (1,1)	<0.0001		Time 9	82.06	<0.0001
18	Full model	99.05 (4,48)	<0.0001				
	Station	47.45 (1,1)	<0.0001				
	Side	2.89 (1,1)	0.12				
	Station* Side	0.01 (1,1)	0.93				
	Time 15	82.57 (1,1)	<0.0001				

**= transformed to 0.5 power

Table 3.5. Summary of the oyster growth increments, standard deviations, and coefficient of variations for each site that were used in the size-structured estimation model.

Site	**Month 0**	**Month 3**	**Month 6**	**Month 9**	**Month 12**	**Month 15**	**Month 18**
	Mean size Standard deviation C.V.	Mean size Standard deviation C.V	Mean size Standard deviation C.V	Mean size Standard deviation C.V	Mean size Standard deviation C.V	Mean size Standard deviation C.V	Mean size Standard deviation C.V
W1	0.52 0.07 0.14	1.40 0.25 0.17	2.00 0.35 0.18	2.93 0.59 0.20	4.48 0.28 0.06	5.32 0.48 0.09	5.51 0.20 0.04
W2	0.44 0.10 0.23	1.78 0.36 0.20	2.94 0.43 0.15	3.65 0.50 0.14	5.10 0.87 0.17	5.41 1.09 0.20	5.63 1.15 0.20
W3	0.50 0.11 0.22	1.95 0.37 0.19	2.78 0.58 0.21	3.28 0.76 0.23	4.37 1.01 0.23	4.50 1.12 0.25	4.62 1.15 0.25
W4	0.45 0.13 0.29	1.37 0.36 0.26	1.77 0.41 0.23	2.30 0.47 0.20	3.46 0.70 0.20	3.52 0.90 0.26	3.44 0.71 0.21
E1	0.52 0.10 0.19	1.61 0.47 0.29	2.50 0.49 0.20	3.63 0.72 0.20	4.90 1.26 0.26	5.13 1.47 0.29	5.89 1.04 0.18
E2	0.46 0.08 0.17	1.50 0.29 0.19	1.91 0.44 0.23	2.45 0.50 0.20	3.71 0.89 0.24	4.37 0.95 0.22	4.36 0.86 0.20
E3	0.46 0.07 0.16	1.71 0.36 0.21	2.37 0.48 0.20	2.94 0.64 0.22	3.89 0.77 0.20	4.28 1.00 0.23	4.39 1.03 0.23
E4	0.46 0.09 0.20	0.86 0.23 0.27	1.14 0.25 0.22	1.68 0.35 0.21	3.06 0.49 .0.16	3.19 0.59 0.18	3.22 0.49 0.15



Figur 3.1. Map of Tomales Bay, CA that illustrates intertidal-research sites (black font and circles) and mid-channel stations (gray font). During the upwelling season, phytoplankton blooms are observed between stations 8 km – 12 km. At stations E2, W3, and E3, native predatory crabs may indirectly benefit native oysters by consuming the oyster's predator, native whelks (see chapter 1). At stations W3.5, E4, and W4, the absence of native crabs allows invasive whelks to consume oysters.

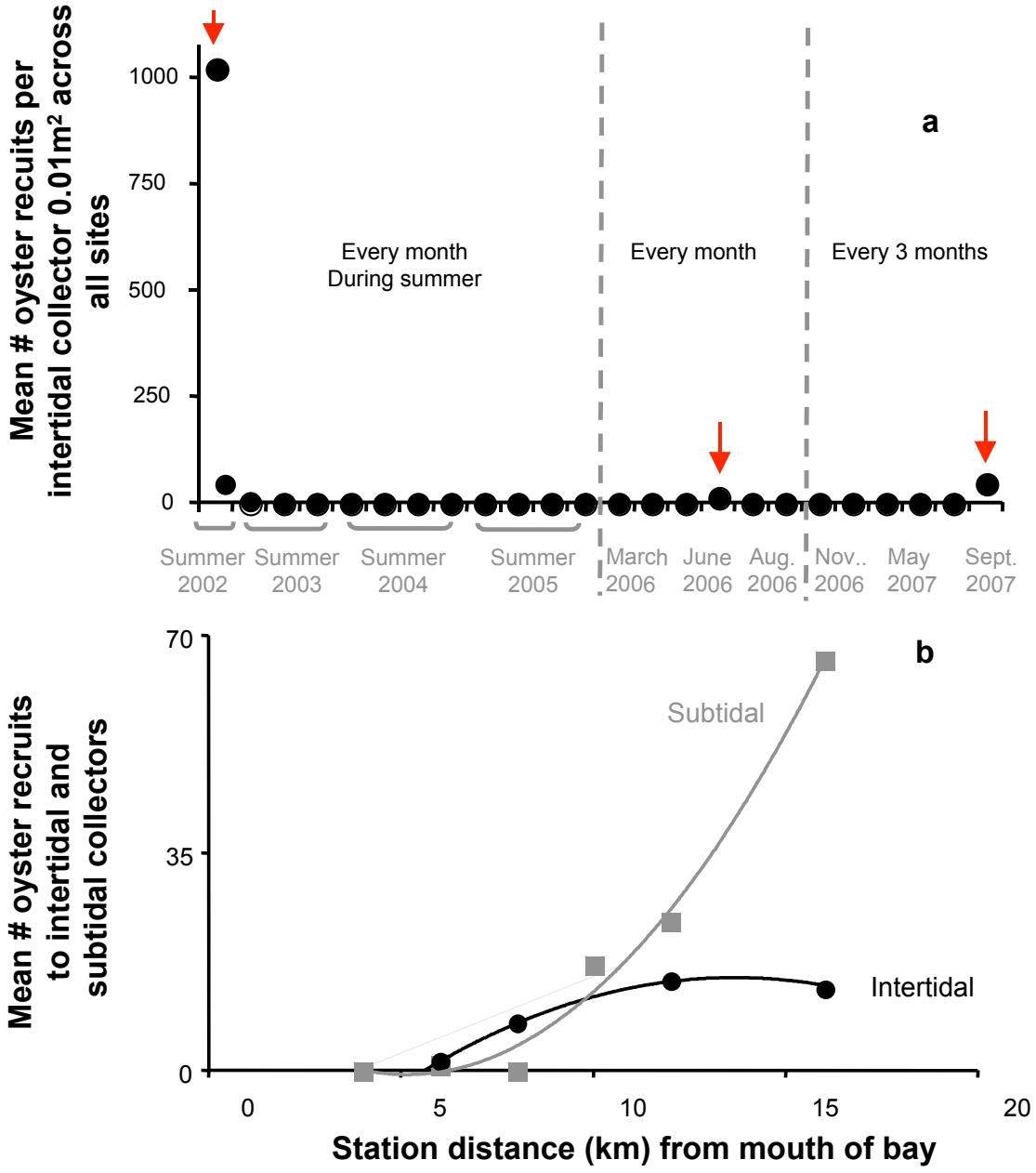


Figure 32 (a) Averaged across all sites, a time series of oyster recruitment to intertidal collectors from August 2002 to October 2007. Recruitment data of 2002 represent only one site. Arrows indicate observed recruitment events (b) Number of oyster recruits observed on intertidal (black circles) and subtidal collectors (gray squares) versus distance from the mouth of the bay in October 2007.

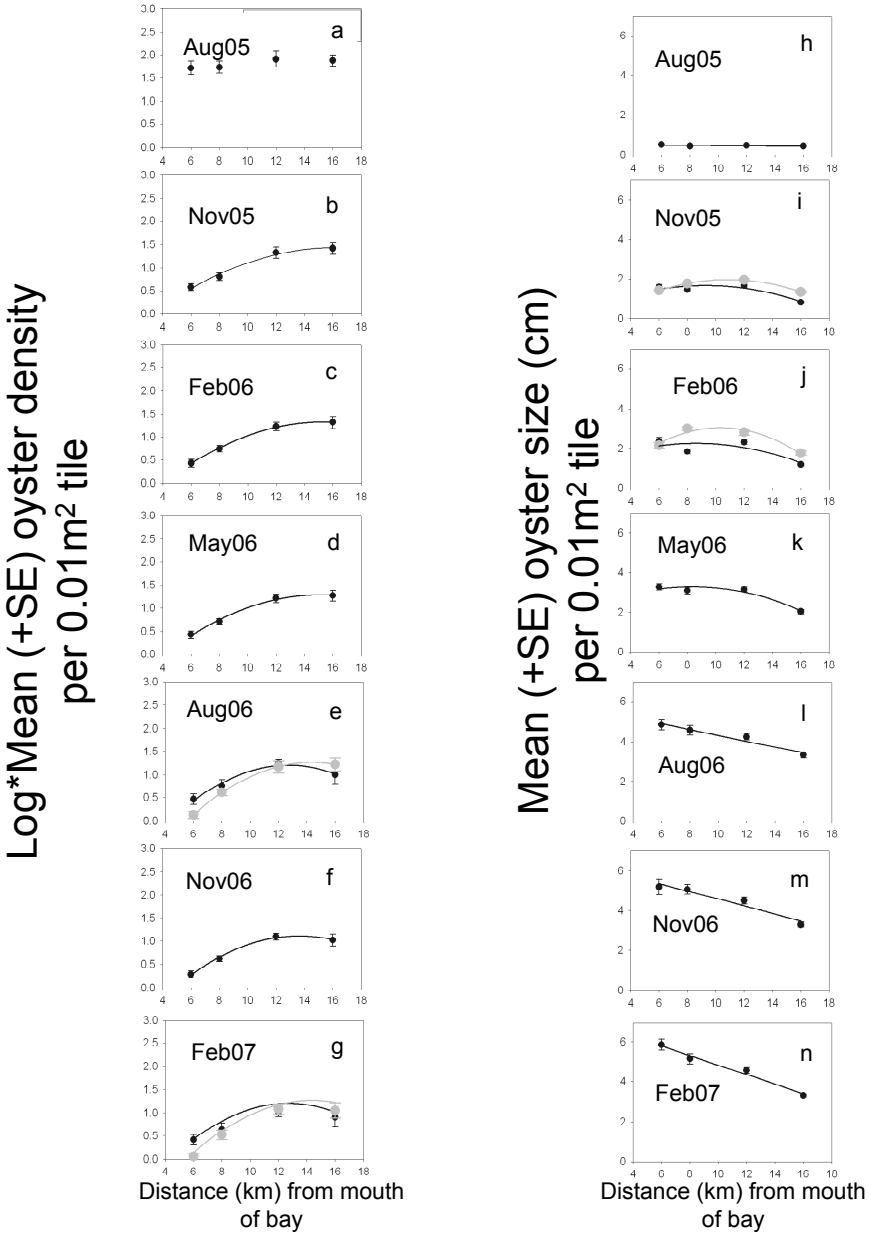


Figure 3.3. (a) Mean (±SE) oyster density and (b) mean (±SE) oyster size of an oyster cohort versus distance from the mouth of the bay. Each panel (a-n) represents a 3-month time step from August 2005 to February 2007. Oyster density data (panels a-g) are log-transformed. For time steps with significant effects of side of the bay, gray lines represent west-side sites and black lines represent east-side sites.

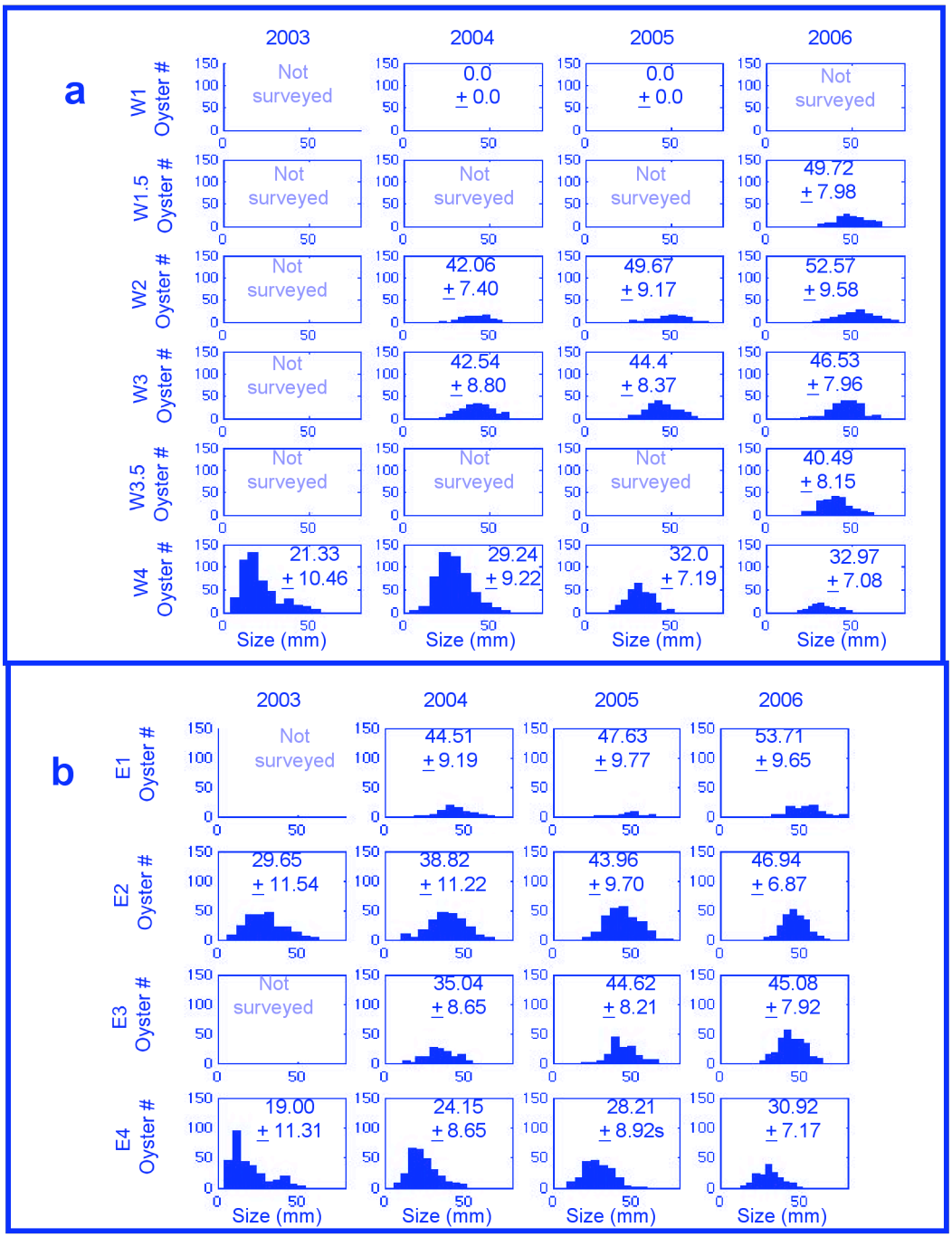


Figure 3.4. Annual-spring survey results of oyster size distributions at research sites from (a) the west side and (b) the east side of Tomales Bay from 2003 to 2006. For each site and year, the mean (±SD) oyster size is included with its respective size distribution.

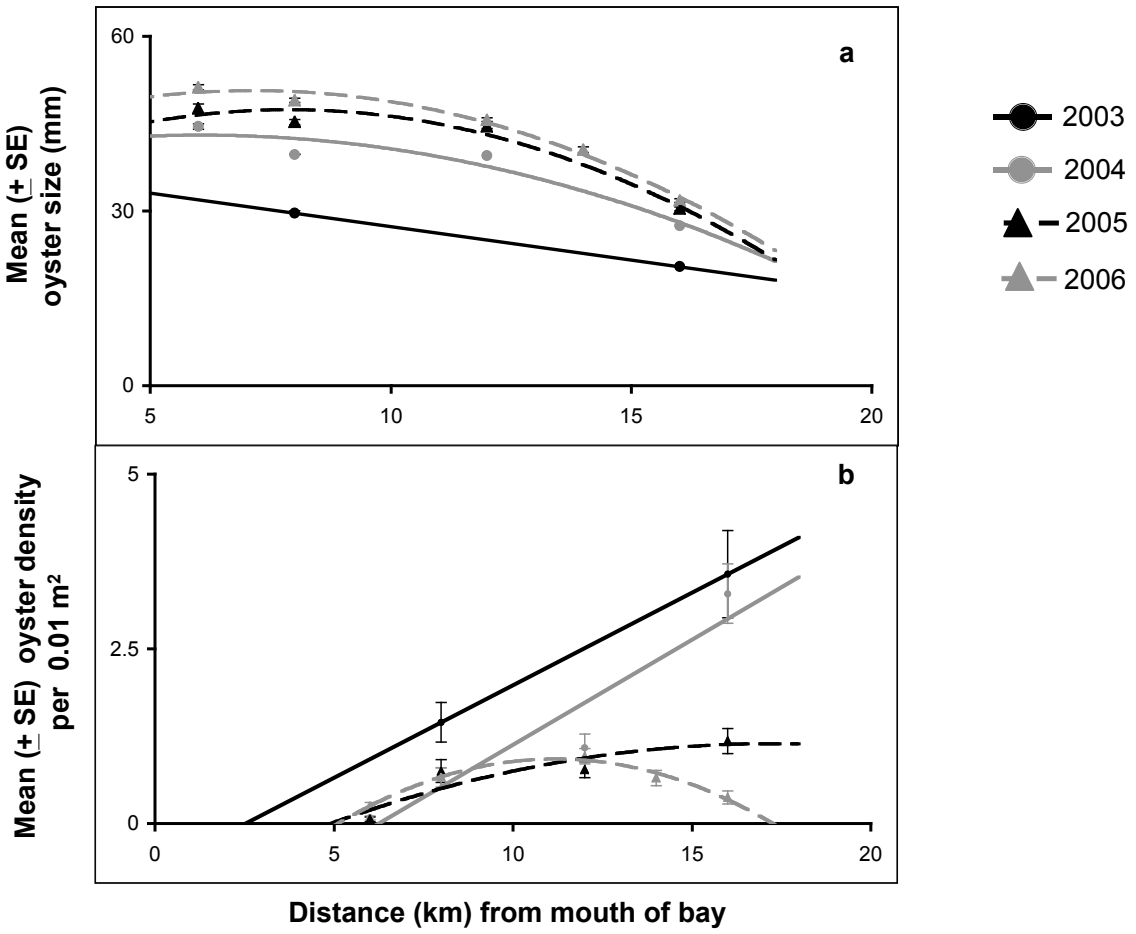


Figure 3.5. Annual-spring survey results illustrating (a) the mean size of individual oysters and (b) the mean density of oysters versus distance from the mouth of the bay from 2003 to 2006.

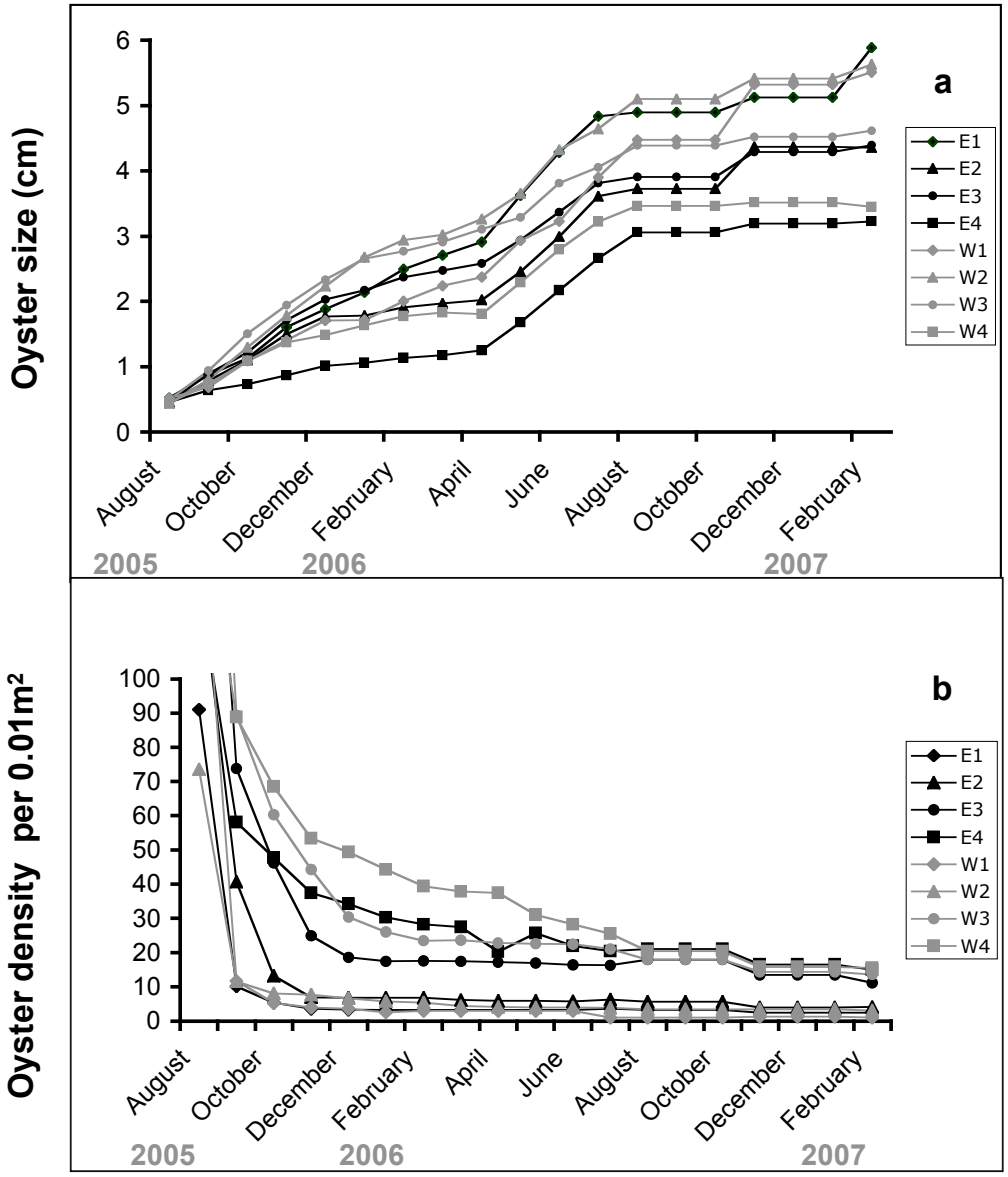


Figure 3.6. Summary of oyster cohort experiment illustrating (a) mean oyster size and (b) mean oyster density for each station from August 2005 to February 2007. In the estimation model, data from months 0, 3, 6, 9, 12, 15, and 18 were used as proxies for natural population data at each site.

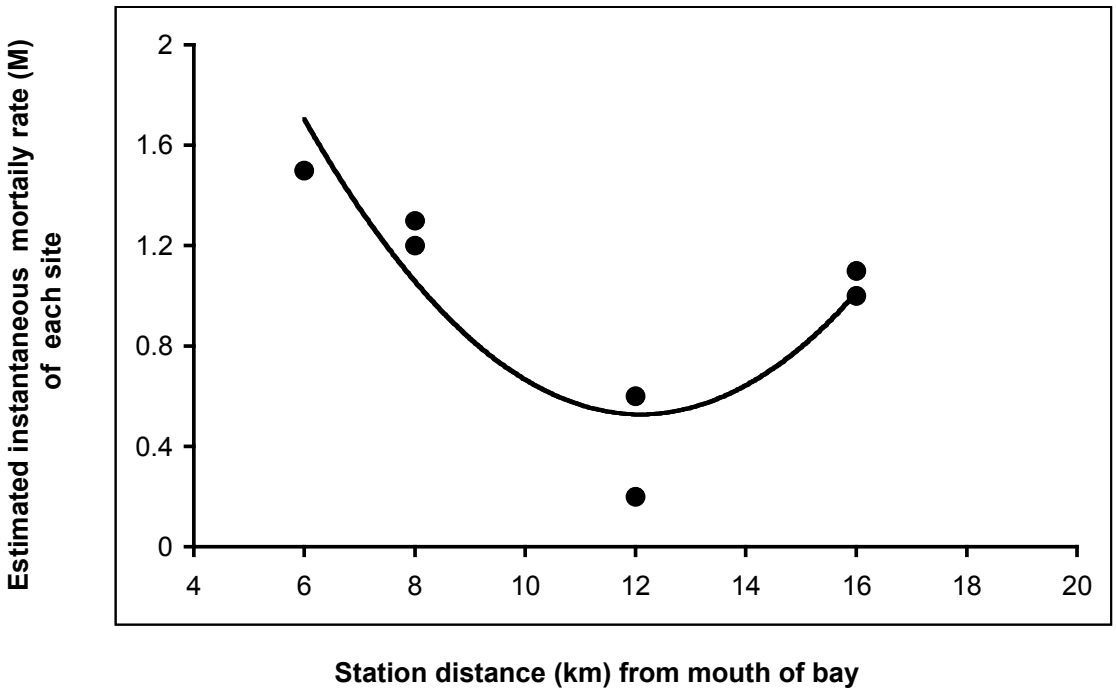
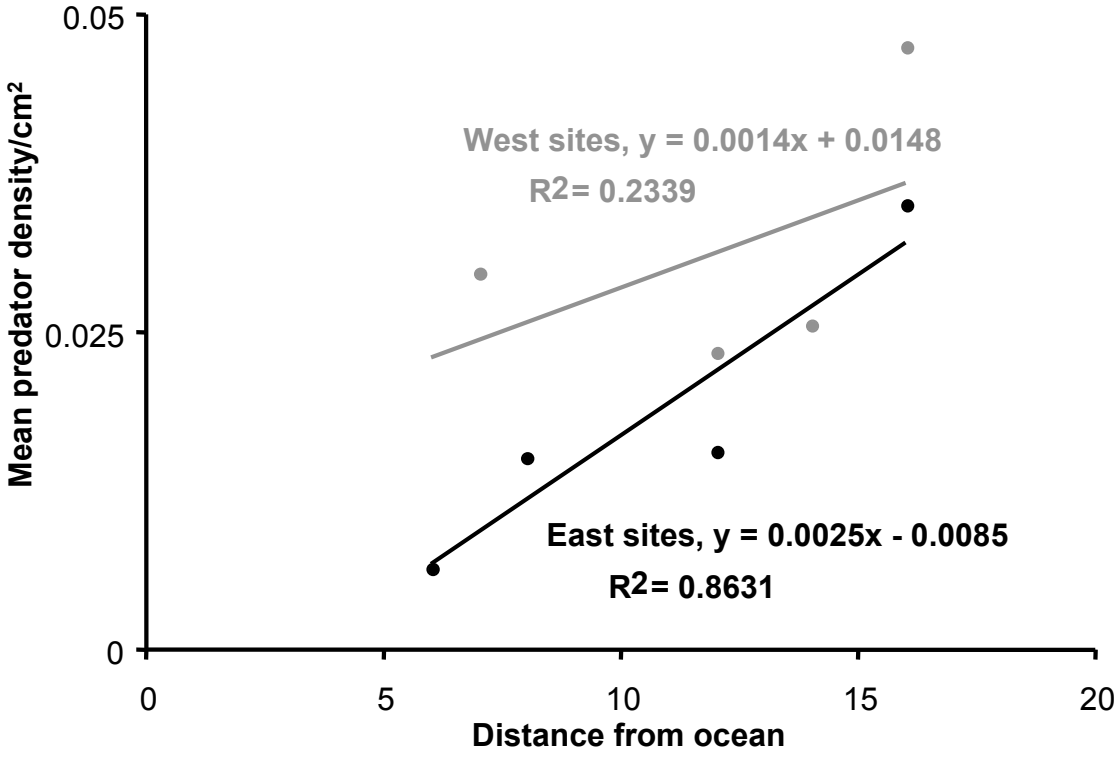


Figure 3.7. Results of size-structured model that illustrate how estimated instantaneous mortality rates vary over distance from the mouth of the bay.



Appendix 3.1. Mean density of chitons and limpets (standardized per unit area of rock sampled) during the spring of 2006.