Environmental stress mediates trophic cascade strength and resistance to invasion

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Abstract. Although much attention has focused on the drivers of trophic cascade strength *among* systems (e.g., habitat type, body size, predator, and prey thermy) comparatively little is known of how trophic cascades change *within* systems, especially with respect to gradients in environmental stress. To address this, we measured the strength of a trophic cascade across an estuarine stress gradient and tested the predictions of "consumer stress model" that suggests sensitivity to stress is greater in mobile consumers relative to sessile prey. We used field observations and experimental manipulations within a central California estuary (Tomales Bay), where higher water temperatures in summer/fall and lower salinity during winter/spring may differentially affect predators (native crabs), meso-consumers (invasive oyster drills), and sessile prey (native oysters). Our results demonstrate that sites with high environmental stress (warmer and lower salinity waters) excluded top predators from the food web, which facilitated high densities of oyster drills and resulted in low oyster survival. In contrast, less stressful sites (cooler and higher salinity waters) had high crab densities leading to reduced oyster drill survival and high oyster survival (an indirect positive effect). Observational data from 14 field sites along both margins of Tomales Bay are consistent with the results of experimental manipulations. This study highlights the importance of environmental stress in mediating within system trophic cascade strength by altering top predator abundance. Our results support the predictions of the consumer stress model and suggest that increasing environmental stress (warming and variable salinity regimes) as a result of climate change may decouple species interactions. Furthermore, warming and extreme low salinities may indirectly intensify the negative effects of non-native species by reducing the biotic resistance provided by native predators.

Key words: biotic resistance; climate change; consumer stress; environmental stress model; estuarine gradient; indirect effect; invasion; *Ostrea lurida*; range limit; tri-trophic interaction; trophic cascade; trophic sensitivity.

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INTRODUCTION

Trophic cascades are the indirect effects of consumers on resources (e.g., plants or basal consumers) via the control of intermediate consumers (Pace et al. 1999). Trophic cascades can determine the structure and function of ecological communities and can alter ecosystem wide properties such as habitat structure, nutrient dynamics, and biogeochemical cycling (Estes and Palmisan 1974, Schindler et al. 1997, Croll et al. 2005, Estes et al. 2011). Much attention has focused on the existence of trophic cascades *among* ecosystem types and the drivers of

cascade strength across systems (Strong 1992, Schmitz et al. 2000, Shurin et al. 2002, Borer et al. 2005). For example, features such as body size, consumer behavior and efficiency, energy flow, and productivity may contribute to the strength of cascading effects (Schmitz et al. 2004, Borer et al. 2005, Shurin and Seabloom 2005, Leroux and Loreau 2008, DeLong et al. 2015). However, the mechanisms underlying variation in the strength of trophic cascades *within* systems remain generally unresolved (Borer et al. 2005).

One driver that may regulate trophic cascade strength within systems is environmental stress (Menge and Sutherland 1987), which is well known to mediate species interactions by altering their direction (i.e., from positive to negative, "stress gradient hypothesis"; Bertness and Callaway 1994), or their magnitude (Sanford 1999). The "consumer stress model" (Menge and Sutherland 1987) predicts increasing stress will reduce the abundance of mobile predators, because they are generally intolerant of stress as compared to sessile basal species (e.g., producers or primary consumers; Menge and Sutherland 1987). Mobile consumers are expected to migrate across habitats and thus behaviorally manage their exposure to stressful conditions. In contrast, sessile prey species are selected for increased tolerance to stress via biochemical adaptation, in part because they possess limited means of behaviorally mitigating stress (Petes et al. 2008). Under less stressful environmental conditions, top-down effects of predators are predicted to dominate the community whereas stressful conditions are expected to attenuate species interactions due to predator emigration or a decrease in foraging activity (Menge and Sutherland 1987). Despite this long held recognition of the importance of environmental stress on species interactions across trophic levels (Dayton 1971, Power 1990, Hunter and Price 1992), the effect of these physical drivers on trophic cascade strength is largely unknown. Moreover, there has been an emphasis in understanding the among system drivers of cascade strength, whereas the within system drivers of cascade strength remain unclear (Borer et al. 2005). This may be due to the difficulty of quantifying stress in a meaningful way across systems and/or the relative rarity of documented cases. A small number of field studies have highlighted how within system trophic cascade strength may

be driven by precipitation (Preisser and Strong 2004), elevation (Preszler and Boecklen 1996), and depth (Shears et al. 2008). Other than these examples, few field studies have examined the influence of environmental stress on within system trophic cascade strength.

Environmental stress may decouple species interactions and thereby alter trophic cascades for at least three related reasons. First, higher trophic levels exhibit greater local extinction risk under increasing stress (Petchey et al. 1999). This greater extinction risk may arise because of low predator population density (Purvis et al. 2000) and/or because larger predator body sizes lead to greater overall resource requirements, which may be limiting under stressful conditions (Cohen et al. 1993, Brose et al. 2006). Second, the abundance of organisms occupying higher trophic levels is more tightly coupled to environmental variables due to higher "sensitivity" (*sensu* Voigt et al. 2003, 2007). Extreme events or trends in climate change may, therefore, first impact higher trophic levels, resulting in local extirpation or decreased abundance. Third, predator and prey responses to stressors, such as temperature, may be asymmetric (i.e., predator response is different than prey response), with systematic variation across trophic levels. For example, predators appear to exhibit lower optimal temperatures for trait performance (e.g., attack or escape velocities; Dell et al. 2014), suggesting that warming beyond predator optima could indirectly benefit prey by reducing predator performance (Kordas et al. 2011) or by inducing predator emigration from the system (Menge and Sutherland 1987).

Habitats that possess strong gradients in environmental conditions (e.g., mountain tops, rivers, rocky shores, estuaries) may offer unique insight into the mechanisms mediating trophic cascades because changes in species abundance and distribution occur predictably in response to environmental gradients. In these systems, environmental change often occurs on the spatial scale of meters to kilometers, which also improves experimental tractability. In particular, estuaries possess strong gradients in environmental conditions (e.g., salinity, temperature, oxygen) that are well known to modify community structure and function (Dauer 1993). Climate change is forecast to alter these conditions, for instance, estuaries are projected to experience increased water

temperatures and increased variation in salinity as a result of extreme storm or drought events (Najjar et al. 2010, Cloern et al. 2011, Min et al. 2011). In addition to strong physical gradients, estuaries also possess large numbers of non-native species (Ruiz et al. 1997, Wasson et al. 2005), suggesting that trophic cascades may involve non-native species, especially when they strongly interact with the native community. For example, native predators may induce a trophic cascade if they prey upon non-native species that would otherwise consume basal native species. Stress gradients may therefore influence the degree to which native species limit the distribution of non-native species (i.e., biotic resistance to invasion; Cheng and Hovel 2010, Kimbro et al. 2013).

We examined the effects of stress along an estuarine environmental gradient on the strength of trophic cascades and biotic resistance to invasion. Using a combined observational and manipulative approach, we test the following hypotheses: (1) native predator abundance is highest at environmentally benign sites and lowest at environmentally stressful sites; (2) native predators, where they are abundant, exert strong predation pressure on non-native meso-consumers; and (3) in the absence of native predators, non-native meso-consumers exert top-down effects upon basal native species.

Methods

Trophic interactions were quantified with observational data and manipulative field experiments along an estuarine temperature and salinity gradient within Tomales Bay, California, USA (located approximately 30 km northwest of San Francisco Bay). In this system, native brown and red rock crabs (*Romaleon antennarium* and *Cancer productus*, respectively) are thought to consume predatory gastropods (invasive *Urosalpinx cinerea* and *Ocenebra inornata*, as well as native *Acanthinucella spirata*). In turn, these gastropods consume the native basal species, the Olympia oyster (*Ostrea lurida*; Kimbro et al. 2009). However, winter/spring low salinity events and summer/fall warm water temperatures may alter these trophic interactions because rock crabs are intolerant of low salinity and higher seawater temperatures (Gross 1957, Sulkin and McKeen 1994, Curtis et al. 2007,
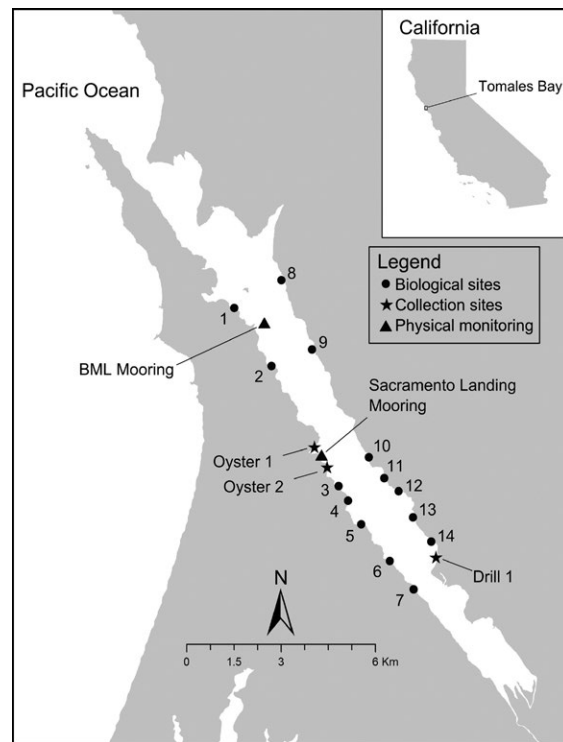

Fig. 1. Map of field sites within Tomales Bay, California, USA. Numbers refer to observational and experimental sites. "Drill 1" refers to collection site for oyster drill tethering experiment. "Oyster 1" and "2" refer to collection sites for the oyster outplant experiment.

2010, Curtis and McGaw 2012). In contrast, the gastropods and oyster are more tolerant of salinity fluctuations and high water temperatures (Federighi 1931, Hanks 1957, Cheng et al. 2015; Cheng et al., *unpublished manuscript*).

Environmental stress

We measured the gradient in environmental conditions in Tomales Bay with a water quality data logger (6920V2, Yellow Springs Instruments, Yellow Springs, Ohio, USA) at an inner bay site (Fig. 1; "Sacramento Landing Mooring"). The data logger was equipped with a surface mounted temperature/conductivity sensor that continuously logged from November 2010 to April 2013 every 15 min. This time series was compared to another data logger at a middle bay site (Fig. 1; "BML Mooring") which was also deployed with a surface mounted temperature/conductivity sensor (SBE37 SIP; Sea-Bird

Electronics, Bellevue, Washington, USA) that continuously logged from February 2011 to April 2013 every 5 min (Bodega Ocean Observing Node; Bodega Marine Laboratory, University of California, Davis, Bodega Bay, California, USA). We focused on time-series data because spot measurements often fail to encapsulate the magnitude and duration of extreme events such as low salinity freshets and heat waves within estuaries (Largier et al. 1997, Cheng et al. 2015).

Field surveys

Observational data were collected from Tomales Bay to assess spatial patterns of predatory crabs, predatory gastropods and oysters. For crab abundance, we deployed baited folding traps (FT-101, Fukui North America, Ontario, Canada) at eight field sites (Fig. 1, Sites 1–3, 7–10, 14) from 2009 to 2013 along the western and eastern margins of Tomales Bay. We conducted additional trapping at three sites along the western margin (Fig. 1, Sites 4–6) from 2011–2013 to further resolve the influence of crabs on the apparent range edge for the nonnative gastropods. Traps were deployed in June–August except for additional sampling in April and May of 2009 and 2010 (N = 429 traps). Within a given year and site, we deployed 5–20 traps (mean = 9.5 traps) with approximately 30 g of anchovy or sardine as bait within each trap for 24 h. Catch was calculated as catch per unit effort (CPUE; crabs caught per trap per 24 h trapping period).

To quantify gastropod and oyster densities, we utilized the same 11 sites as in the crab monitoring from 2011 to 2013 plus additional surveys at three sites along the eastern margin of Tomales Bay in 2011 and 2013 (Fig. 1, Sites 11–13). At each site, we randomly placed 10 0.25 m^2 quadrats along a 30 m transect at 0.0 m mean lower low water (hereafter MLLW; N = 350 quadrats). Within each quadrat, we overturned all rocks and counted all gastropods and oysters. We conducted all trapping and quadrat surveys from June to August in every year, which coincides with the greatest amount of biological activity in this system (B. Cheng, *unpublished data*).

Invasive oyster drill survival

We assessed oyster drill survival by tethering male Atlantic oyster drills (mean shell height

± SD = 22.4 mm ± 1.8) across six field sites (Sites 2–7) in a predator exclusion experiment. A tethering approach evaluates relative survival across sites and allows for snails to forage and hide from predators. Tethered drills were collected from a non-survey site (Fig. 1, "Drill 1") and deployed for 2 weeks over three temporal blocks (6 weeks total) from July to August 2013. At the end of each 2-week deployment, we recovered oyster drills and scored each as alive or dead (oyster drill missing but tether intact). We were unable to locate 4 of 180 tethers (2.2%) and these data points were omitted from further analysis. Oyster drills were tethered using a 0.5 m of braided microfilament line (15 lb test, PowerPro®; Shimano American Corp., Irvine, CA, USA) that was secured to the drills using a slipknot and cyanoacrylate glue. The opposing end of each tether was then secured to the benthos using a 0.45 m PVC stake. Each tether was spaced 4 m apart along a transect at 0.0 m MLLW. Lab experiments indicated that this tethering method did not result in handling mortality and that drills were unable to escape the tether. Lab trials also indicated that both red and brown rock crabs were able to easily manipulate and consume tethered drills. After consumption by crabs in the lab, there was no visible sign of snail shell fragments attached to the tether, but each tether was completely intact. To assess potential handling artifacts within each tethering deployment, five additional tethered drills were placed in a single predator exclusion cage for each site and temporal block (6 sites × 3 temporal blocks × 15 oyster drills = 270). Oyster drills within each cage were treated as exposed drills but with a 0.05 m length of microfilament line and without a PVC stake. These drills were then placed inside cages along with two naturally occurring rocks as habitat. Predator exclusion cages were cylindrical enclosures (21 cm height and 21 cm diameter) made of plastic mesh (3 × 5 mm). Each cage was then secured to the substrate with two 0.45 m rebar posts. During this tethering experiment, we quantified crab abundance at each site following the protocol described above for a total of two trapping sets (total = 20 traps site^{-1}) across the 6 week tethering deployment.

Native oyster survival

We assessed Olympia oyster survival by transplanting adult oysters to five sites (Sites 3–7) within Tomales Bay in a predator exclusion experiment. Native oysters were collected as adults (mean shell height ± SD = 42.5 mm ± 7.6) that were attached to rocks (8–17 oysters per rock) from two non-survey sites in Tomales Bay (Fig. 1, "Oyster 1 & 2"). Experimental units were deployed for approximately 6 months from June to December 2012. Prior to transplantation, we tagged each experimental unit (FTF-69; Floy Tag, Seattle, Washington, USA) and recorded the number of living oysters. We then randomly assigned oysters to sites and to one of three treatments: no cage (predator access), full cage (no predator access; identical to cages used in oyster drill tethering experiment), and partial cage (full cages with two 10 × 15 cm openings). This yielded a total of 150 experimental units (5 sites × 3 treatments × 10 replicates) for a total of 1635 transplanted adult oysters. Five of the experimental units (3.3%) were not recovered and were not included in the statistical analysis. Experimental units were also transplanted to a sixth site (Site 2), but are excluded from this analysis because wave action consistently disturbed the transplanted rocks, causing oyster mortality. Naturally occurring oysters at this site occur on rocks that are larger and more stable.

Statistics

We quantified the relationship between field densities of crabs and gastropods as well as gastropods and oysters using spearman rank permutation tests. We used a permutation approach because data did not meet parametric assumptions and exhibited ties in rank. For each site and year combination, the mean CPUE of native crabs was calculated and compared to the mean density of gastropods (N = 28). The same procedure was repeated for invasive gastropods and native oysters as well as the native gastropod and oyster (N = 35). For all tests, we report the test-statistic rho (ρ) and a P-value based on a distribution of 10,000 simulated test statistics.

We measured the effect of predators on oyster drill and Olympia oyster survival using generalized linear mixed models (GLMMs) with a binomial error distribution and logit link function. For oyster drill survival, we used the 2013 crab CPUE (*R. antennarium* and *C. productus*) as a fixed effect predicting the survival of tethered drills. Analyses with crab densities from the entire 2009–2013 data set yielded similar results as the 2013 data set alone because both data sets are highly correlated. Temporal block was initially treated as a random effect but models estimated zero variance for this term, so data were pooled across blocks. Caged oyster drill survival was excluded from statistical analysis because 100% of caged oyster drills survived, which complicates estimation of model parameters and perhaps more importantly, indicates no handling effect. For the oyster transplant experiment, we modeled the survival of oysters with a fixed effect of 2012 oyster drill density (combined mean *Urosalpinx cinerea* and *Ocenebra inornata* for each site) and cage treatment (no cage, full cage or partial cage). We also modeled a random effect of experimental unit (i.e., each rock that oysters were attached to). For both analyses, combined predator metrics (both native crabs and both invasive oyster drills) were used because separate predictors for each species were positively correlated and statistical models exhibited multicollinearity (variance inflation factors = 2–10), which can lead to inaccurate model parameterization (Graham 2003).

For the oyster drill tethering analysis, the data modeled are in the form of zeroes and ones (binomial distribution with one trial, a Bernoulli distribution) and therefore overdispersion (greater variance than can be explained by a binomial distribution) cannot occur (McCullagh and Nelder 1989). For the oyster survival analysis, the data modeled are in the form of successes (survivors per rock) and failures (mortalities per rock). In this analysis, model overdispersion was evaluated by comparing the ratio of sums of squared residuals to residual degrees of freedom, which suggested that this model was not overdispersed (Ratio = 0.433). For all GLMM models, we used parameter estimates and bootstrapped 95% confidence intervals with 1000 simulations to assess predictor significance. We graphically evaluated model fits with diagnostic plots. All analyses and graphics were performed in R (version 3.2; R Core Team 2015), and the packages "lme4" and "ggplot2".
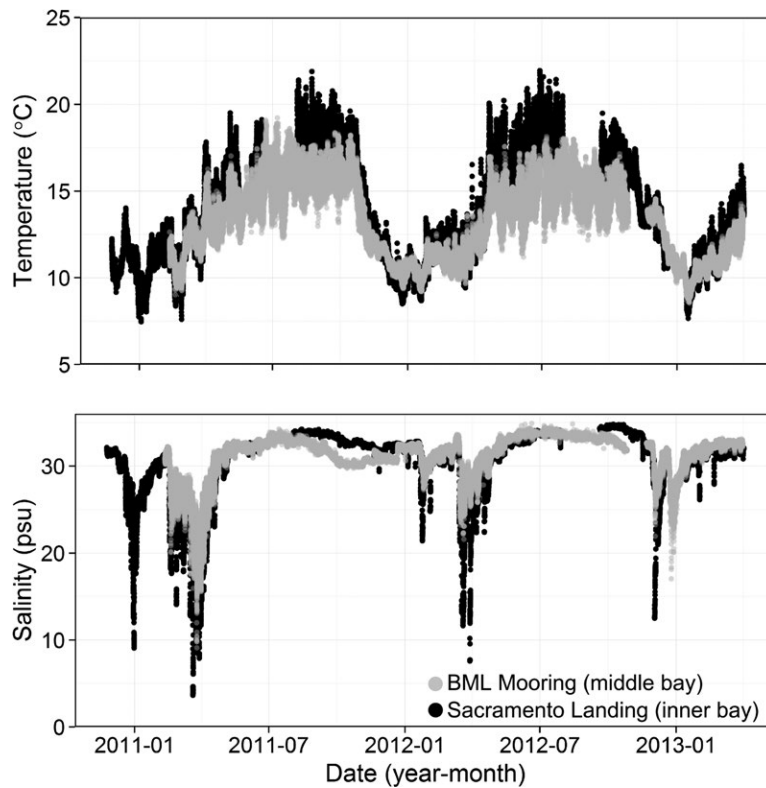
Fig. 2. Tomales Bay time-series data for temperature and salinity from the middle bay (BML Mooring; gray points) and the inner bay site (Sacramento Landing Mooring; black points).

RESULTS

Environmental stress

Time-series data indicate a strong temperature and salinity gradient within Tomales Bay. The inner bay mooring was characterized by consistently warmer summer water temperatures relative to the BML mooring (e.g., July mean water temperature = 17.8 °C vs. 15.3 °C, respectively), but this difference diminished during the winter months (mean February temperature = 11.2 °C vs. 10.9 °C, respectively). Mean salinities between Sacramento Landing and BML only differed slightly (e.g., mean February salinity = 30.1 vs. 31.0 psu, respectively). However, with respect to estuarine organismal physiology, extreme low salinity events play a large role in driving patterns of behavior and survival (Curtis et al. 2007, Curtis and McGaw 2012, Cheng et al. 2015). In this regard, the Sacramento Landing mooring (inner bay) recorded a greater frequency and duration of extreme low salinity events (e.g., 9 events < 10 psu, mean duration = 3.3 h) relative to the BML mooring (3 events < 10 psu, mean duration = 0.4 h). During the dry summer and fall seasons, salinities at both moorings remained high (>30 psu; Fig. 2).

Field surveys

Observational data were consistent with cascading effects of native crabs on oysters. Surveys revealed that brown and red rock crabs were most abundant at middle bay sites (Fig. 3, Sites 1–2, 8–10) and decreased approaching the inner bay. These patterns were consistent along both margins of Tomales Bay. The majority of the catch was comprised of brown and red rock crabs (40.2% and 24.9%, respectively), whereas the remainder was comprised of invasive European green crab (*Carcinus maenas*, 20.0%) and recruiting Dungeness crab (*Metacarcinus magister*, <30 mm carapace length, 14.9%), for clarity the last two species are not plotted. In contrast, quadrat sampling indicated
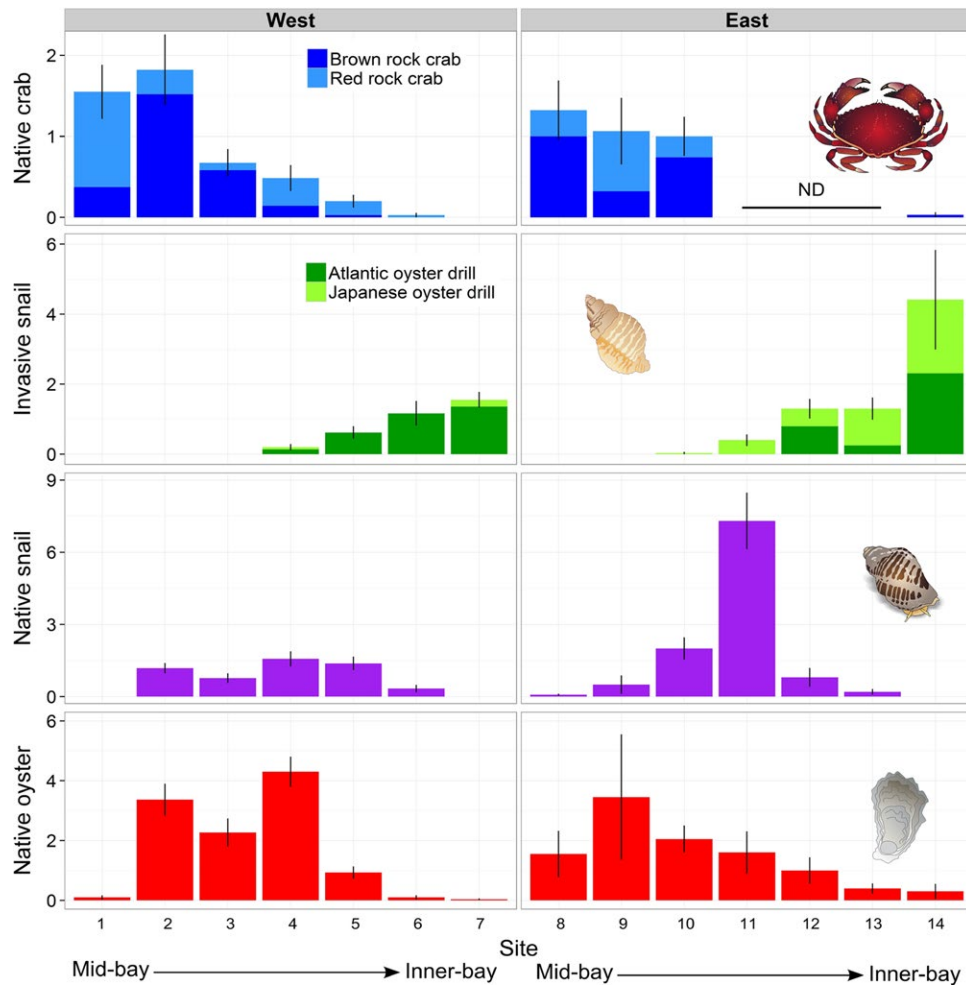
Fig. 3. Species abundance along the western and eastern margin of Tomales Bay (middle bay to inner bay from left to right within each column). Crab abundance is measured as the mean catch per unit effort (CPUE) ± SE for total combined catch. Brown rock crab = *Romaleon antennarium*. Red rock crab = *Cancer productus*. No crab trapping data are available for sites 11–13. Gastropod and oyster abundance is the mean count per quadrat (0.25 m^2) ± SE. For the oyster drills, the standard error is for the combined count of both species. Atlantic oyster drill = *Urosalpinx cinerea*. Japanese oyster drill = *Ocenebra inornata*. Native snail = *Acanthinucella spirata*. Native oyster = *Ostrea lurida*.

that invasive gastropods exhibited increasing densities approaching the inner bay (Fig. 3). The native gastropod varied little across the western margin and exhibited a peak abundance in the mid-bay on the eastern margin. Native oysters were most common at outer and middle bay sites (Fig. 3, Sites 2–4, 8–11) and were nearly absent from sites with the highest oyster drill density (Fig. 3, Sites 6–7, 13–14). As with the Cancrid crabs, gastropod and oyster distributions exhibited consistent patterns along

both margins of Tomales Bay, with the exception of a greater Atlantic drill density on the western margin vs. greater Japanese drill density on the eastern margin (Fig. 3). Spearman rank correlation permutation tests indicate that native crabs were negatively correlated with invasive gastropods (Fig. 4a). Invasive gastropods were also negatively correlated with native oysters (Fig. 4b). In contrast, the native snail was positively correlated with native oysters (Appendix S1, $\rho = 0.74$, $P < 0.001$).
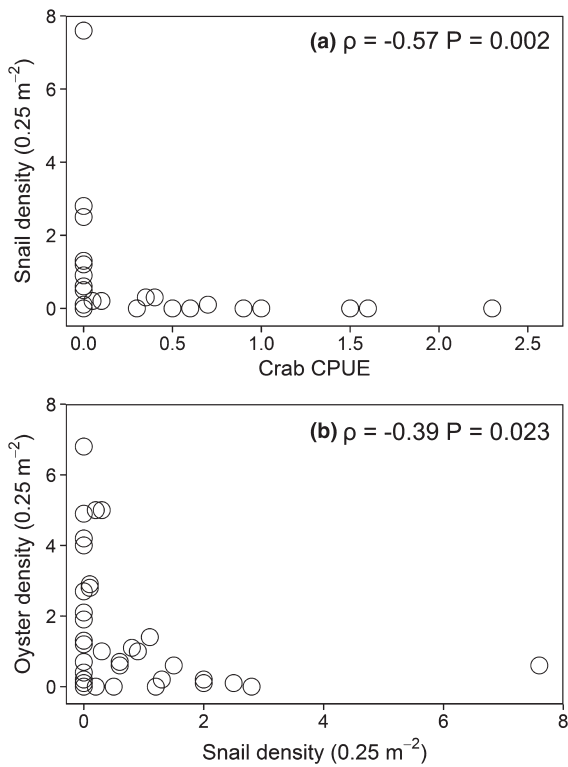
Fig. 4. Mean density per site and year combination between (a) native crabs (brown and red rock crabs combined) and invasive gastropods (Atlantic and Japanese drills combined) and (b) invasive gastropods and oysters. The test statistic (spearman rank ρ) was compared to a permuted data set (10,000 simulations) to calculate each *P*-value.

Invasive oyster drill survival

Invasive oyster drills that were exposed to predators exhibited decreasing survival with increasing density of rock crabs (Fig. 5a; Estimate = −1.48, 95% CI = −2.15 to −0.86). For example, at the site with highest density of rock crabs, survival of predator-exposed snails was 48%, whereas survival was 93% at the site with the lowest density of rock crabs. In total, 176 of 180 (97.8%) predator-exposed tethers (uncaged) and 90 of 90 predator-excluded tethers (caged) were recovered. Of the 176 recovered predator-exposed tethers, 128 were alive (72.7%) and 48 were dead (27.3%). Direct evidence of crushing predators was recovered in some cases where intact tethers had shell fragments attached. Of the caged tethered snails, 100% were recovered alive. In lab trials where tethered
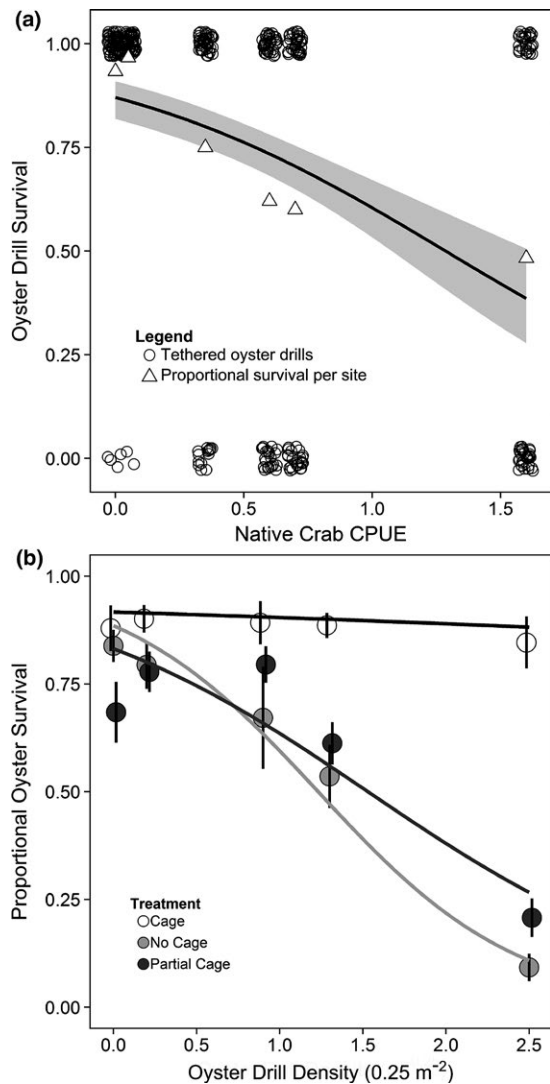

Fig. 5. Results from oyster drill tethering and oyster caging experiments. (a) Atlantic oyster drill survival as a function of native crab density during the tethering experiment. Circles refer to individual tethered oyster drills that were recovered alive (value = 1) or dead (value = 0). Slight random jitter applied for clarity. Triangles refer to the total proportional survival per site. Model prediction is from a binomial GLM (shaded region is 95% confidence interval). Caged oyster drills exhibited 100% survival and are not plotted. (b) Oyster survival (mean proportional survival ± SE) as a function of experimental treatment and oyster drill density. Model predictions are from a GLMM.

oyster drills were exposed to rock crabs, shells were always completely destroyed (10 of 10 trials) whereas tethers were intact.

Table 1. Statistical results from predator caging experiment for oysters. Model estimates are from generalized mixed model with bootstrapped 95% confidence intervals. Reference parameter estimate is full cage treatment (no predator access) at an oyster drill density of zero. All other estimates are in relation to this reference. Model estimates with 95% CI that deviate from zero are in bold and are consistent with other inferential metrics such as Wald Z-tests.

Parameter	Estimate	Lower 95% limit	Upper 95% limit
Full cage (reference)	2.401	1.853	3.014
No cage	−0.359	−1.142	0.487
Partial cage	**−0.803**	**−1.589**	**−0.064**
Oyster drill density	−0.157	−0.557	0.260
Oyster drill density × no cage	**−1.502**	**−2.129**	**−0.946**
Oyster drill density × partial cage	**−0.888**	**−1.481**	**−0.366**

Native oyster survival

Olympia oyster survival decreased with greater oyster drill density, but only in no cage or partial cage plots (Fig. 5b, Table 1, see two-way interactions). At the site with highest oyster drill density (Site 7), only 10.0% (11 of 110) and 20.8% (22 of 106) of native oysters survived in predator access plots (no cage) and partial cage plots, respectively. In contrast, oyster survival in predator exclusion plots (full cage) was 83.5% (86 of 103), at the same site. Survival in predator exclusion plots (full cage) was high across all sites, regardless of ambient oyster drill density (Fig. 5b). When considered without regard to ambient oyster drill density (i.e., when oyster drill density was zero), there was no difference in survival between full cage and no cage plots, but some evidence of decreased survival in the partial cage plots (Table 1, Fig. 5b).

DISCUSSION

Despite the long held recognition that environmental conditions can mediate species interactions (Dayton 1971), we suggest that environmental stress is under appreciated as a driver of trophic cascade strength within ecosystems (e.g., Shurin et al. 2002, Borer et al. 2005, Shurin and Seabloom 2005). Here, we show that trophic cascade strength within a coastal ecosystem is mediated by predator abundance, which is ultimately driven by a predictable and measurable spatial gradient in temperature and salinity stress. Native rock crabs were rarely found in the inner bay region (Fig. 3, Sites 4–7, 11–14) because Cancrids are intolerant of low salinity and high seawater temperatures (Gross 1957, Sulkin and McKeen 1994, Curtis et al. 2007, Curtis and McGaw 2012). In contrast, oyster drills and oysters are tolerant of a broader thermal and salinity range (Cheng et al. 2015; Cheng et al., *unpublished manuscript*), which is consistent with the consumer stress model that suggests mobile consumers are sensitive to stress as compared to their prey (Menge and Sutherland 1987).

Both temperature and salinity likely contribute to preventing crab expansion to inner bay sites throughout the year (Fig. 2; low salinity during winter/spring and high temperature during summer/fall). Although 2.5 °C mean difference between moorings appears to be only a slight difference, small changes in ocean temperature are well known to attenuate predator effects (e.g., Sanford 1999). Furthermore, our inner bay mooring measurement of the gradient is conservative, as it is located at the edge of the oyster drill distribution. Supplemental temperature data from the inner most site 7, reveal a July 2012 mean water temperature of 19.8 °C, which is 4.5 °C greater than the middle bay mooring (B. Cheng, *unpublished data*). In the cooler and higher salinity middle bay, high rock crab abundance results in a trophic cascade with indirect positive effects on oysters. This occurs because crabs significantly reduce oyster drill abundance at high crab density sites (Fig. 5a, 48% survival of Atlantic oyster drills). Although there is potential for crabs to consume oysters and thus attenuate trophic cascade strength due to omnivory, oysters are able to maintain dense populations at high crab density sites due to a habitat and size refuge. Crabs have difficulty foraging on oysters attached to rocks (Kimbro et al. 2009) and previous work may have overestimated crab

omnivory by utilizing unattached seed oysters in lab trials (Grason and Miner 2012). At inner bay sites where crabs are absent or in low abundance, oyster drill survival was high whereas oyster survival was low (Fig. 5b, survival < 25%). Furthermore, observational data from both western and eastern margins of Tomales Bay were consistent with experimental data and demonstrate that oysters were most abundant in the middle bay region where invasive drills were absent and native crabs were common (Fig. 3). Oyster drills were negatively correlated with crabs (Fig. 4a) and negatively correlated with oysters as well (Fig. 4b). In contrast to prior work suggesting that the native gastropod was an important oyster consumer (Kimbro et al. 2009), we found that the native gastropod was positively correlated with oysters (Appendix S1), suggesting that they have weak consumptive effects or little preference for oysters. Although temperature and salinity appear to be the primary drivers of native crab abundance along the estuarine gradient, hypoxia (oxygen depletion) may additionally contribute to the spatial distribution of crabs within Tomales Bay by preventing their utilization of inner bay habitat.

Environmental stress is likely an important driver of trophic cascade strength among and within terrestrial, aquatic, and estuarine/marine ecosystems (Power 1990, Preszler and Boecklen 1996, Moon and Stiling 2004, Shears et al. 2008). Environmental conditions may alter predator abundance (this study; Menge and Farrell 1989) or the local extinction rate of predators (Petchey et al. 1999). For example, during El Niño, heavy precipitation can facilitate the persistence of nematodes that prey upon herbivorous moths that would otherwise consume lupine (Preisser and Strong 2004). Changing environmental conditions may also result in temporal and/or spatial mismatches between predator and prey (Cushing 1990, Winder and Schindler 2004). A mismatch occurs when resource availability is asynchronous with important consumer life history events (such as fledging, reproduction, recruitment, etc.). Mismatches between interacting species may be most common when climate driven phenotypic plasticity is greater in one species than the other (e.g., primary producers vs. consumers; Winder and Schindler 2004). By reducing predator abundance or synchrony among interact-

ing species, environmental stress may generally have the effect of decoupling species interactions and thereby weakening cascade strength. These effects may also extend beyond predator-prey interactions, such as with mutualists (e.g., insect pollinators and host plants) that are differentially sensitive to climate (Harrington et al. 1999), which could result in analogous reductions in the strength of facilitation cascades (Altieri et al. 2007), although this has yet to be tested.

Warming has been shown to strengthen top-down effects in food webs by promoting meso-consumer persistence and consumption rate (Barton et al. 2009, O'Connor 2009, Kratina et al. 2012). However, warming may also attenuate top-down effects because consumer metabolic demands may outpace feeding rates, leading to decreased consumer efficiency and starvation in extreme cases (Rall et al. 2010, Iles 2014). These opposing outcomes may be resolved if the effects of environmental stress (e.g., temperature) are conceptualized as threshold non-linear effects. Short-term stress may result in strengthened interactions as foraging rates increase or if increasing stress results in food webs that are simplified to a few strongly interacting species (Greig et al. 2013). However, once threshold stress levels are surpassed, consumer emigration, or death may ultimately decouple species interactions. Environmental gradients present a useful model to predict food web interactions along a continuum of stress.

Climate change may intensify the impacts of non-native species because they may be more physiologically tolerant of warming and ocean acidification than native species (Sorte et al. 2013). Our study suggests that climate change (warming or more frequent low salinity events) may indirectly facilitate invasive species by reducing the biotic resistance provided by native predators. Estuaries are expected to warm in conjunction with outer coastal habitats (Najjar et al. 2010) which may result in the emigration of native predators to cooler waters. In addition, increased variation in precipitation may produce extreme flood events (Min et al. 2011) which could further expand predation refugia for introduced species such as oyster drills, provided that extreme events are within the tolerance limits of invaders. It is generally assumed that matching environmental conditions

and propagule supply are the primary drivers of high non-native species abundance within estuaries (Ruiz et al. 1997, Wasson et al. 2005). However, estuaries may additionally act as predator refugia for non-native species, where fluctuating and extreme conditions exclude native predators (Hunt and Yamada 2003, Jensen et al. 2007, Cheng and Hovel 2010). Thus, if invasive species are generally more tolerant of changing environmental conditions than their native predators and competitors, climate change could indirectly facilitate the success of invaders by removing their enemies.

Understanding the effects of climate change on species interactions remains one of the central problems in predicting the consequences of ongoing environmental change (Tylianakis et al. 2008, Blois et al. 2013). Although the drivers of trophic cascade strength are complex and consist of a variety of biological determinants, environmental stress is a key component that can mediate the abundance, distribution, and traits of predators, thereby altering cascading effects throughout biological communities. Elucidating the mechanisms underlying trophic cascades is of particular importance due to the systematic loss of predators due to overharvest and habitat loss (Estes et al. 2011). As interacting species (e.g., predator and prey) appear to be asymmetric in their response to stress (Dell et al. 2014), natural gradients may present unique opportunities for understanding how trophic cascades interact with environmental stress and the invasion of non-native species.

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Supporting Information