CHANGES IN PREY MORTALITY: THE EFFECTS OF MULTIPLE PREDATORS AND TEMPERATURE ON CALIFORNIA MUSSELS

By

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ABSTRACT

CHANGES IN PREY MORTALITY: THE EFFECTS OF MULTIPLE PREDATORS AND TEMPERATURE ON CALIFORNIA MUSSELS

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Organisms serve as prey to a variety of predators within natural systems, detecting threats through physical and chemical means. While predator feeding behavior is also affected by the presence of other predators, it is unclear whether differing modes of detection have similar effects on predator feeding behavior. In rocky intertidal zones in northern California, the California mussel (*Mytilus californianus*) is a competitively dominant foundation species consumed by a variety of predators. I quantified the individual and combined effects of ochre star (*Pisaster ochraceus*) and rock crab (*Romaleon antennarium*) predation on mussels by implementing mussel caging experiments at three field sites in northern California and through laboratory feeding trials. I also compared the effects of chemical and physical competitor detection and elevated sea water temperatures on crab and sea star feeding behavior in laboratory feeding trials. I found that in the field mussel predation on vertical surfaces was attributed to seas stars. Further, on horizontal surfaces where mussels were accessible to both predators, predation was dominated by crabs, suggesting that crabs are better competitors and the physical presence of crabs potentially reduces sea star predation. I also found that the chemical detection of crabs increased sea star feeding rates, while physical detection decreased it. Additionally, elevated water temperatures only affected crabs, causing them to increase their feeding rates. Taken together my results suggest that mussels are at greater risk on rocky shores were crabs are present and will likely experience greater predation risk in the future under warmer sea water temperature conditions attributed to climate change.

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CHAPTER 1: EFFECTS OF MULTIPLE PREDATORS ON CALIFORNIA MUSSEL (*MYTILUS CALIFORNIANUS*) MORTALITY ACROSS A NATURAL PREDATOR GRADIENT

INTRODUCTION

Predation is a key factor regulating population dynamics and community structure in natural systems. Studies have shown predators are capable of regulating and limiting prey populations both via consumption (Korpimäki and Kreb 1996, Côté and Sutherland 1997, Sinclair et al. 1998) and through non-lethal modification of prey traits (Pangle et al. 2007). Further, predators can affect populations of species other than their prey through their consumption of prey; examples include, keystone predation (Paine 1966, Estes and Palmisano 1974), exploitative competition (Spiller 1986, Kerfoot and Sih 1987, Kreutzer and Lampert 1999), and trophic cascades (Paine 1980, Carpenter 1985). With the documented importance of predators on prey populations and communities, it is important to consider the mechanisms underlying their effects when attempting to predict their future impacts on natural communities.

While most studies on the effects of predators on prey populations focus on the effects of a single predator (Paine 1966, Estes and Palmisano 1974, Robles et al. 1990, Angerbjorn et al. 1999), most prey species live in environments with many different predators (Sih et al. 1998). Because of this, predators likely interact with one another, particularly if those predators share a common prey species. Studies examining interactions between competing predators have shown their effects can be additive, where the feeding behavior of each predator is not affected by the presence or behavior of the other, resulting in a level of predation equal to the sum of the predation rates of both predators (Travis et al. 1985, Rahel and Stein 1988, Fauth 1990, Spiller and Schoener

1994). Alternatively, interactions between competing predators can alter the interactions between individual predators and their prey and change the level of predation the prey experiences, yielding differing effects on prey populations (Soluk and Collins 1988, Hurd and Eisenberg 1990). One possible outcome is that prey may experience risk enhancement, for example, when prey alter their behavior to avoid one predator and inadvertently make themselves more vulnerable to predation by another (Soluk and Collins 1988, Soluk 1993, Morin 1995, Swisher et al. 1998). Another possible outcome is risk reduction, where prey experience decreased predation due to changes in the interacting predator's behaviors, which cause them to feed less (Soluk and Collins 1988, Ferguson and Stiling 1996, Siddon and Witman 2004). For example, in the presence of lacewings (*Chrysoperla carnea*) aphid (*Aphis gossyypii*) populations are suppressed through predation. However, in the presence of other intraguild predators of aphids like big eyed-bugs (*Geocoris spp*.), damsel bugs (*Nabis spp.*), and the leafhopper assassin bug (*Zelus renardii*) aphid populations increase due to these intraguild predators switching to preying on lacewings, reducing the predation risk of aphids (Rosenheim et al. 1993). These non-additive outcomes are termed multiple predator effects (MPEs; Sih et al. 1998) and have been traditionally studied in freshwater and terrestrial environments; relatively few studies have examined MPEs in marine ecosystems (but see Siddon and Witman 2004, Griffen 2006*a*, 2006*b* for notable exceptions).

Nearshore rocky intertidal ecosystems along the eastern north Pacific comprise large and diverse assemblages of marine organisms (Reaka-Kudla 1997, May 1994). The California mussel (*Mytilus californianus*) is the dominant space competitor on these rocky shores, affecting species diversity in these communities by both displacing other large space-holding organisms (Paine 1966, 1974) and providing habitat for diverse communities of meso- and micro-invertebrates (Suchanek 1985, Seed and Suchanek 1992). *M. californianus* are also a common source of prey for a variety of intertidal predators (Paine 1966, Marsh 1986, Dayton 1971, Hartwick 1973, 1976, Robles et al. 1990, Naverette 1996, Este et al. 2003), including the ochre sea star (*Pisaster ochraceus*), whose consumption of *M. californianus* populations disproportionately contributes to preserving the function and composition of communities in these habitats (Paine 1966, 1969; but see Menge et al. 2016).

Although *P. ochraceus* is an important and well-known predator on *M. californianus*, other intertidal predators may exert consumptive effects on *M. californianus* (Robles et al. 1990, Navarette 1996). One such group of mussel predators are rock crabs in the genera *Cancer* and *Romaleon*. Rock crabs are highly mobile (Robles et al. 1989, Yamada and Boulding 1996) and can be voracious predators of mussels (Robles et al. 1989, Hull and Bourdeau 2017). Rock crabs are also able to traverse various types of substratum quickly in search of food, whereas *P. ochraceus* are much slower, relying on their tube feet to move through their environment. In addition to different levels of mobility, each predator possesses different attack modes (Bourdeau 2009). Sea stars pry open mussels using their tube feed and evert their stomachs into the shell to externally digest mussel tissue, a process that takes considerable time (Feder 1956, 1959, Sanford 2002a, 2002b). Rock crabs, on the other hand, are adept at crushing their prey and will use a combination of crushing, peeling, or snipping to quickly access the tissues within shelled prey (Zipser and Vermeij 1978)

In rocky intertidal habitats in northern California, both *P. ochraceus* and the rock crab *Romaleon antennarium* feed on *M. californianus*. *Pisaster ochraceus* and *R. antennarium* prefer mussels over other intertidal organisms (Landenberger 1968, Roche and Bourdeau, unpublished data) and so it is likely that these two predators interact with one another when searching for prey. Because these predators differ in both mobility and their attack modes on a shared prey, they are a good system for examining MPEs on mussel mortality. To determine the MPEs of rock crabs and *P. ochraceus* on mussel mortality, I did *in situ* caging experiments at three rocky intertidal sites in northern California.

I predicted that the individual effects of predators on mussel mortality would differ, with crabs having a greater impact on mussel mortality than sea stars (Hull and Bourdeau 2017). When these predators encounter one another, I predicted that the presence of sea stars would have no effect on crab foraging, as sea stars likely do not represent a significant competitive threat to crabs, given the latter’s ability to consume mussels at a much greater rate (Hull and Bourdeau 2017). I predicted that sea stars would respond to the presence of crabs by increasing their feeding rates on mussels, in order to consume as many mussels as possible before competitively superior crabs arrive in a mussel bed. Thus, I predicted that both predators in combination would have a greater effect on mussel mortality than the effects of both predators individually (i.e., risk enhancement).

MATERIALS AND METHODS

Study Sites

My study took place at three rocky intertidal locations along the coast of northern California, encompassing Mendocino, Humboldt, and Del Norte counties (Fig. 1). Rocky intertidal habitats in this region are mainly expansive boulder fields with large tidal ranges. In these habitats, mussel beds are located along the top and upper edge of boulders where they occur with macro-algae (*Pelvitiopsis limitata*, *Endocladia muricatea*\and *Pollicipes ploymerus*). Mussel predators, mainly rock crabs (*Cancer productus* and *Romaleon antennarium*) and sea stars (*Pisaster ochraceus*), are found below the mussels, within the matrix of boulders and cobbles. *Pisaster ochraceus* can also be found attached to the vertical surfaces of boulders in the area above the matrix of cobbles, but below the lower limit of mussel beds.

Rock crab and sea star abundances vary across the three study sites (Murie and Bourdeau 2019), with relatively higher densities of both crabs and sea stars at the northern-most site Point St. George [PSG] near Crescent City [41.784778° N, -124.255487° W] intermediate densities of both predators at Devil's Gate [DG] near Cape Mendocino [40.396736° N, -124.378551° W], and lowest predator densities at the southern-most site Belinda Point [BP] near Fort Bragg [39.399092° N, -123.819386° W] creating a north-to-south predator abundance gradient.

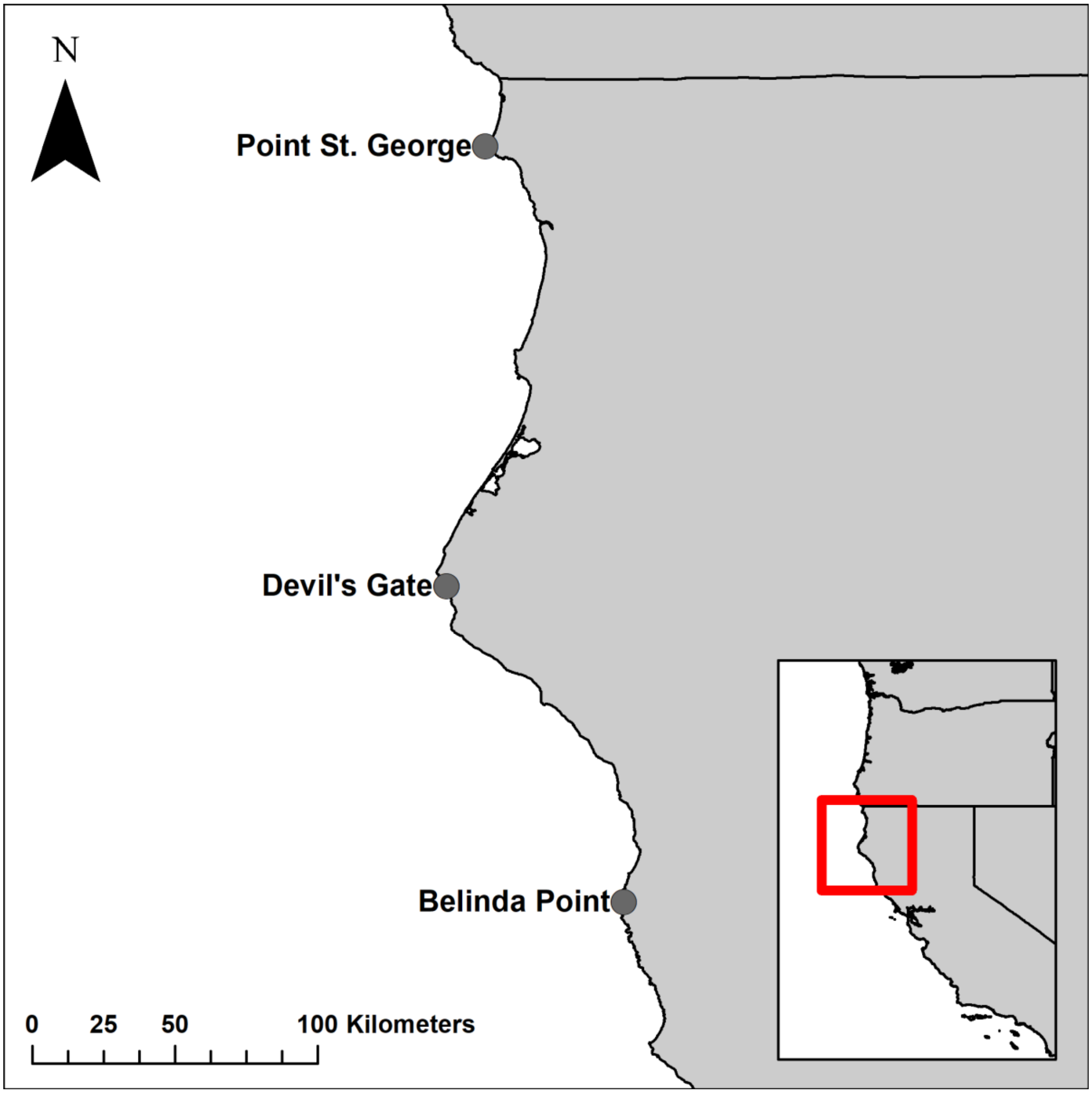

Figure 1. Location of each field site in northern California, USA. Map created in the Geospatial Information System ArcMap (10.6.1).

Crab and Sea Star Density Surveys

To confirm that previously measured crab and sea star densities differed across sites and to determine whether crab and sea star densities differed within sites, I quantified the densities of each predator at each of my three study locations. Using two transects located in the low intertidal zone (characterized by the presence of the kelps (*Alaria*, *Egregia*, *Laminaria*, and *Saccharina spp*. and the red algae *Pyropia*, *Corallina* and *Calliarthron spp.*) at each location, I counted both crabs and sea stars within 1 meter on either side of the transects during two separate tide series. The length of each transect varied across sites as the overall area of each site differed (Table 1). On either side of the transect I searched for both crabs and sea stars, being careful not to flip cobbles or small boulders which might disturb crabs and cause them to move from their original locations. I counted *P. ochraceus* in the cobble field and on the vertical surfaces of rocks, only if vertical surfaces were inside the transect. Once I found a crab or sea star, I marked them with a piece of lumber crayon so I would not accidentally count them again if I either rediscovered them or if they moved. I then calculated the average density (individuals · m^{-2}) of both predators for each sampling events.

Table 1.Transect sampling information at each field site.

Site	Dates	Transect length	Area	Number of Transects
PSG	June 15th, 2019	50 m	100 m^2	2
	August 1st, 2019	50 m	100 m^2	2
DG	June 16th, 2019	75 m	125 m^2	2
	August 2nd, 2019	75 m	125 m^2	2
BP	June 17th, 2019	30 m	60 m^2	2
	July 31st, 2019	30 m	60 m^2	2

Caging Experiment

I did a caging experiment designed to measure the individual and combined effects of crabs and sea stars on mussel mortality at each location. I established 6 spatial blocks (10 x 10 m) at each site in the low intertidal zone. In each block, I created four 15 x 15 cm plots. One plot in each block was located on the vertical surface of a boulder, while the remaining 3 were established horizontally in the cobble field inside each block. I transplanted 30 mussels (shell length = 15.1 - 53.5 mm) into each plot, firmly securing them via plastic (Vexar^{TM}) mesh (0.4 cm^2 openings) to substratum that was cleared of micro- and macro-algae and sessile invertebrates. Mussels were secured in the mesh for three weeks prior to the start of the experiment to allow for byssal thread attachment. After removing the plastic mesh from each plot, I quantified the number of intact, living mussels, removed any dead individuals (gaping with no tissue inside), and assigned each plot to one of four predator treatments. I fitted one mussel plot in the cobble field with a stainless steel fence that was designed to prevent sea star predation but allow access to crabs (Crab plots, Fig. 2A), one on the vertical surface of a boulder without a fence to prevent crab predation but allow access to sea stars (Sea star plots, Fig. 2B), one in the cobble field without a fence to allow access to both predators (MPE plots, Fig. 2C), and one in the cobble field outfitted with a cage (fence plus roof) to prevent predation by either predator (Control plots, Fig. 2D). I ended the experiment after two weeks to ensure that not all mussels were consumed in the plots located at PSG, as this site had the highest density of both predators. Once the experiment ended, I quantified mussel mortality by subtracting the number of intact, living mussels remaining in each plot from the number of living mussels in that plot at the start of the experiment.

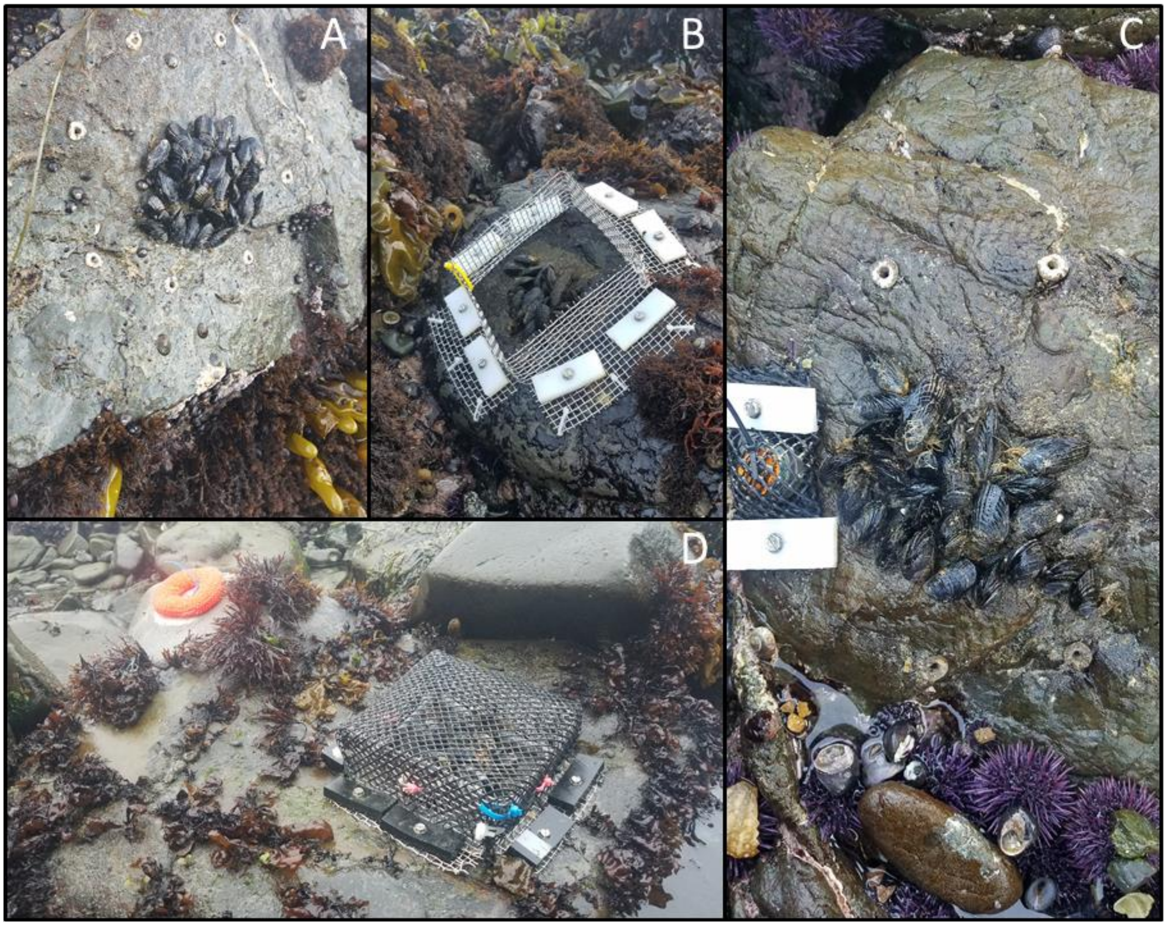

Figure 2. Examples of (A) Sea star plots, (B) Crab plots, (C) MPE plots, and (D) Control plots installed at each site. Note the presence of the Tuffy^{TM} scouring pad in the MPE plot (C).

Mussel Recruitment

To validate the placement of crab and MPE treatments, and to determine if the absence of mussels at lower tidal elevations could be confidently ascribed to predation rather than recruitment limitation, I measured mussel recruitment at each site. In each experimental block, I installed two Tuffy^{TM} scouring pads; one on a vertical surface next to the Sea star plots and one on a horizontal surface in the vicinity of the Crab, MPE, and Control plots. After 104 days, I retrieved both the scouring pads and the transplanted mussels in the control cages from each site and brought them to the Telonicher Marine Laboratory (TML) in Trinidad CA. I cut open each scouring pad and thoroughly rinsed the contents into a large container before pouring it through a 250 µm sieve. This allowed me to remove fine sediment from each sample without losing any juvenile mussels. I then rinsed the samples into the drum portion of a plankton splitter and split each sample. I determined the number of splits for individual samples by examining each split under a dissecting microscope. I stopped splitting samples once a single layer of particles covered the bottom of each petri dish. I then quantified the average number of mussel recruits in the vertical and horizontal scouring pads from each site. I repeated this process for control cages.

Data Analyses

To assess differences in predator density within and among sites I used general linear models (ANOVA) and appropriate post-hoc tests. To test for the effects of predator treatment and site on mussel consumption, I compared a set of generalized linear mixed models (GLMMs) with a Poisson distribution and log link function (*lme4* package, Bates et al. 2014) that included predator treatment, site, and their interaction as fixed factors, and block as a random factor. I used count data representing the total number of mussels consumed in each predator treatment from each site as my response variable for each model. I used maximum likelihood ratio tests (analysis of deviance) to compare full models and reduced models and I used Tukey's test to compare the different levels within fixed factors if fixed factors were shown to significantly affect models. To test the effects of orientation and site on mussel recruitment, I used the same general procedure outlined for examining mussel consumption above with orientation, site, and their interaction as fixed factors, and block as a random factor. I used count data representing the total number of mussels recruited to scouring pads at each site as my response variable. Due to the interaction between site and orientation having a significant effect on mussel recruitment, I analyzed simple effects to explain the interaction. All statistical analyses were done using R (v3.6.1) (R Core Team 2019).

RESULTS

Density Surveys

Prior to analysis, I log-transformed all density data to better fit the assumptions of normality and homogeneity of variances. I found no significant interactive effects of site and predator type on predator density ($F_{2,9}$ = 0.516, P = 0.621). I therefore removed the interaction term from the model and re-ran the analysis using site and predator type as main effects, and found a significant effect of site ($F_{1,10}$ = 63.56, P <0.001) and predator type ($F_{1,10}$ = 8.18, P = 0.021) on predator density. Predator density was highest at PSG, followed by DG, and BP (Table 2A, Fig. 3). Sea star densities were significantly higher than crab densities overall (Table 2B, Fig. 3).

Table 2. Post-hoc comparisons of predator density among sites using Tukey's HSD test.

Comparisons			Difference	Lower	Upper	*P*
A. (Site)	PSG	DG	0.249	0.039	0.458	0.023
	PSG	BP	0.808	0.598	1.017	<0.001
	DG	BP	0.559	0.349	0.769	<0.001
B. (Predator)	Crabs	Sea stars	0.249	0.039	0.458	0.023

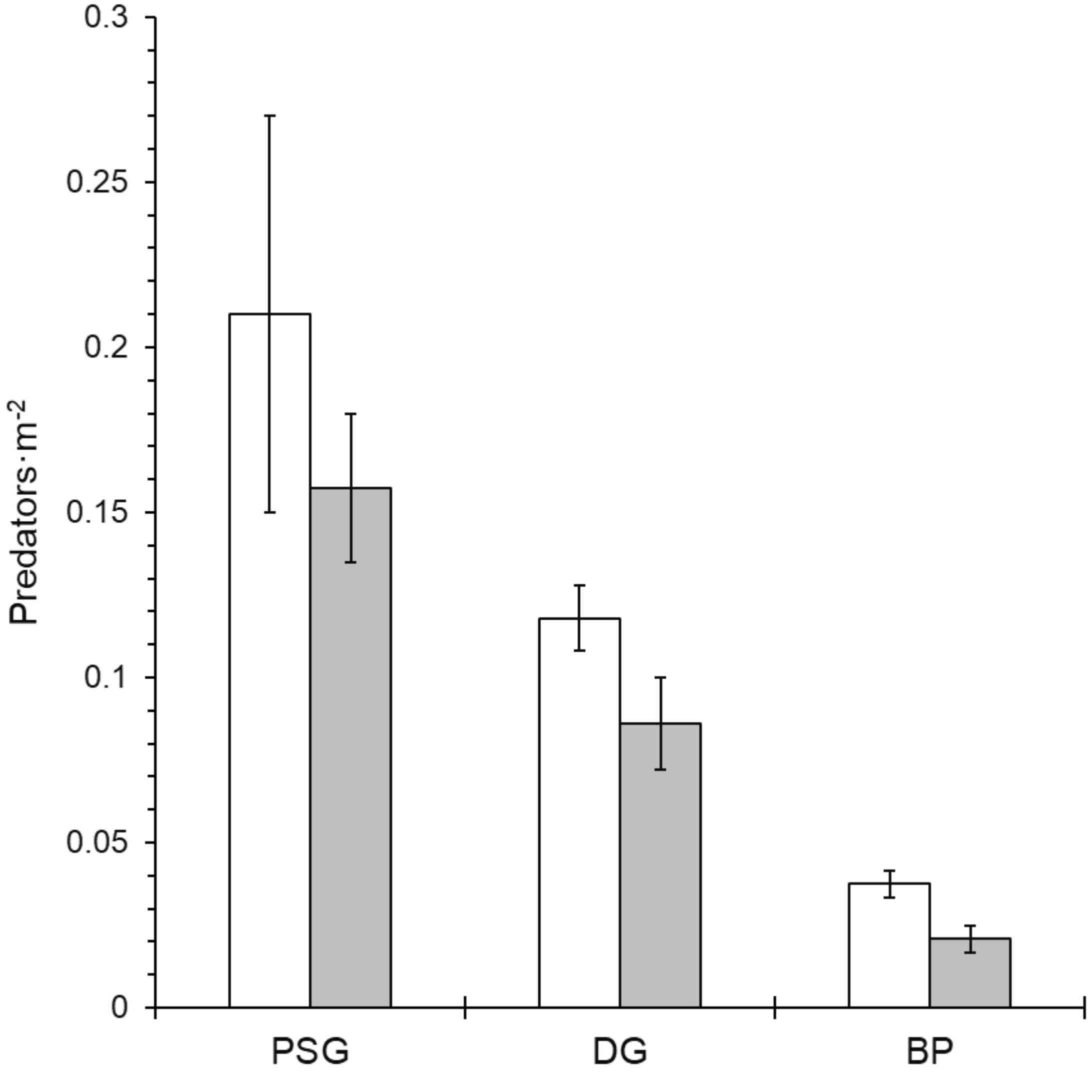

Figure 3. Mean (± 1 SE) density (individuals · m^{-2}) of predators at Point St. George (PSG), Devil's Gate (DG), and Belinda Point (BP). White bars represent sea stars, grey bars represent crabs.

Caging Experiment

I found a significant effect of site (Table 3C), predator treatment (Table 3D), and their interaction on mussel consumption (Table 3B). I found no significant effect of block on mussel consumption (Table 3A). Regarding the effects of site, mussel consumption at PSG was 33% higher than DG and 94% higher than BP, while Mussel consumption at DG was 90% higher than BP (Table 4A, Fig. 4). Additionally, mussel consumption in sea star treatments was 24% higher than both crab and MPE treatments (Table 4B, Fig. 4). Further, at PSG, mussel consumption in sea star treatments was 38% higher than crab treatments (Tukey's, *P* = 0.001) and 37% than MPE treatments (Tukey's, *P* = 0.002). There was no difference in mussel consumption between crab and MPE treatments at PSG (Tukey's, *P* = 0.100) and there was no difference in mussel consumption between predator treatments at DG and BP (Table 5).

Table 3. Results of maximum likelihood ratio test examining differences in generalized linear mixed models for mussel consumption.

Model Comparisons	*d.f.*	AIC	Chi^2	*d.f.*	*P*
A. Treatment + Site + Treatment:Site + (Site|Block)	15	261.13	4.70	6	0.583
Treatment + Site + Treatment:Site	9	253.83			
B. Treatment + Site + Treatment:Site + (Site|Block)	15	261.13	11.92	4	0.018
Treatment + Site + (Site|Block)	11	265.05			
C. Treatment + Site + Treatment:Site + (Site|Block)	15	261.13	22.45	6	<0.001
Treatment + (1|Block)	9	271.57			
D. Treatment + Site + Treatment:Site + (Site|Block)	15	261.13	32.94	6	<0.001
Site + (1|Block)	9	261.56			

Table 4. Post-hoc comparisons of differences in (A) mussel consumption between sites and (B) between predator treatments using Tukey's tests.

Comparisons			Estimate	SE	*Z*	*P*
A. (Site)	PSG	DG	0.48	0.09	5.35	<0.001
	PSG	BP	2.84	0.24	12.02	<0.001
	DG	BP	2.35	0.24	9.81	<0.001
B. (Predator treatment)	Star	crab	0.28	0.10	2.71	0.035
	Star	MPE	0.29	0.10	2.82	0.025
	Crab	MPE	-0.01	0.11	-0.12	1.00

Table 5. Results of maximum likelihood ratio test examining effects of predator treatment on mussel consumption in sites.

Comparisons		*d.f.*	AIC	Chi^2	*d.f.*	*P*
PSG	Treatment + (1|Block)	4	117.92	17.40	2	<0.001
	(1|Block)	2	131.32			
DG	Treatment + (1|Block)	4	87.52	0.28	2	0.870
	(1|Block)	2	83.80			
BP	Treatment + (1|Block)	4	53.16	0.40	2	0.818
	(1|Block)	2	49.56			

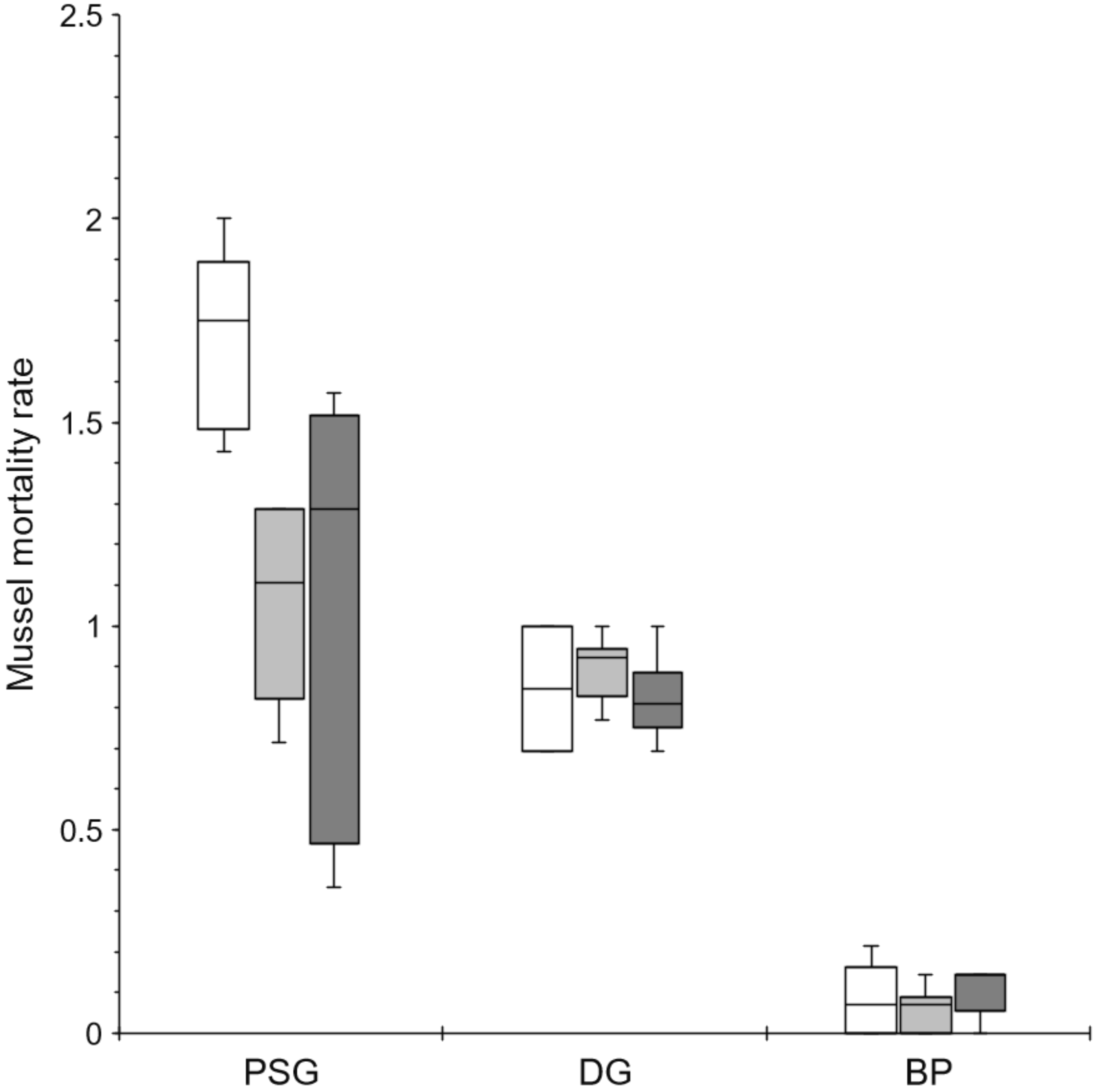

Figure 4. Mussel mortality rate (mussels consumed·day^{-1}) in predator treatments at each site. White bars represent Sea star treatment, light grey bars represent Crab treatment, and dark grey bars represent MPE treatments.

Mussel Recruitment

I found a significant effect of block (Table 6A), the interaction between orientation and site (Table 6B), site (Table 6C), and orientation (Table 6D) on mussel recruitment.

Table 6. Results of maximum likelihood ratio test examining differences in generalized linear mixed models for mussel recruitment.

Model Comparisons	*d.f.*	AIC	Chi^2	*d.f.*	*P*
A. Orientation + Site + Oreintaiton:Site (1|Block)	12	758.26	931.28	6	<0.001
Orientation + Site + Oreintaiton:Site	6	1677.54			
B. Orientation + Site + Oreintaiton:Site (1|Block)	12	758.26	58.61	2	<0.001
Orientation + Site + (1|Block)	10	812.87			
C. Orientation + Site + Oreintaiton:Site (1|Block)	12	758.30	9927.40	9	<0.001
Orientation + (1|Block)	3	10672.50			
D. Orientation + Site + Oreintaiton:Site (1|Block)	12	758.26	672.24	8	<0.001
Site + (1|Block)	4	1414.50			

Effect of orientation on mussel recruitment within sites

I found significant effects of orientation on mussel recruitment within sites (Table 7). At PSG recruitment to horizontal surfaces was 28% greater than recruitment to vertical surfaces and at DG recruitment to horizontal surfaces was 169% greater than recruitment to vertical surfaces (Fig. 5). There was no significant effect of orientation on mussel recruitment at BP, where recruitment was low overall (Table 7).

Table 7. Results of maximum likelihood ratio test examining effects of orientation within sites on mussel recruitment.

Comparison		*d.f.*	AIC	Chi^2	*d.f.*	*P*
PSG	Orientation + (1|Plot)	3	527.14	100.10	1	<0.001
	(1|Plot)	2	625.15			
DG	Orientation + (1|Plot)	3	113.81	95.27	1	<0.001
	(1|Plot)	2	207.08			
BP	Orientation + (1|Plot)	3	116.16	0.01	1	0.926
	(1|Plot)	2	114.17			

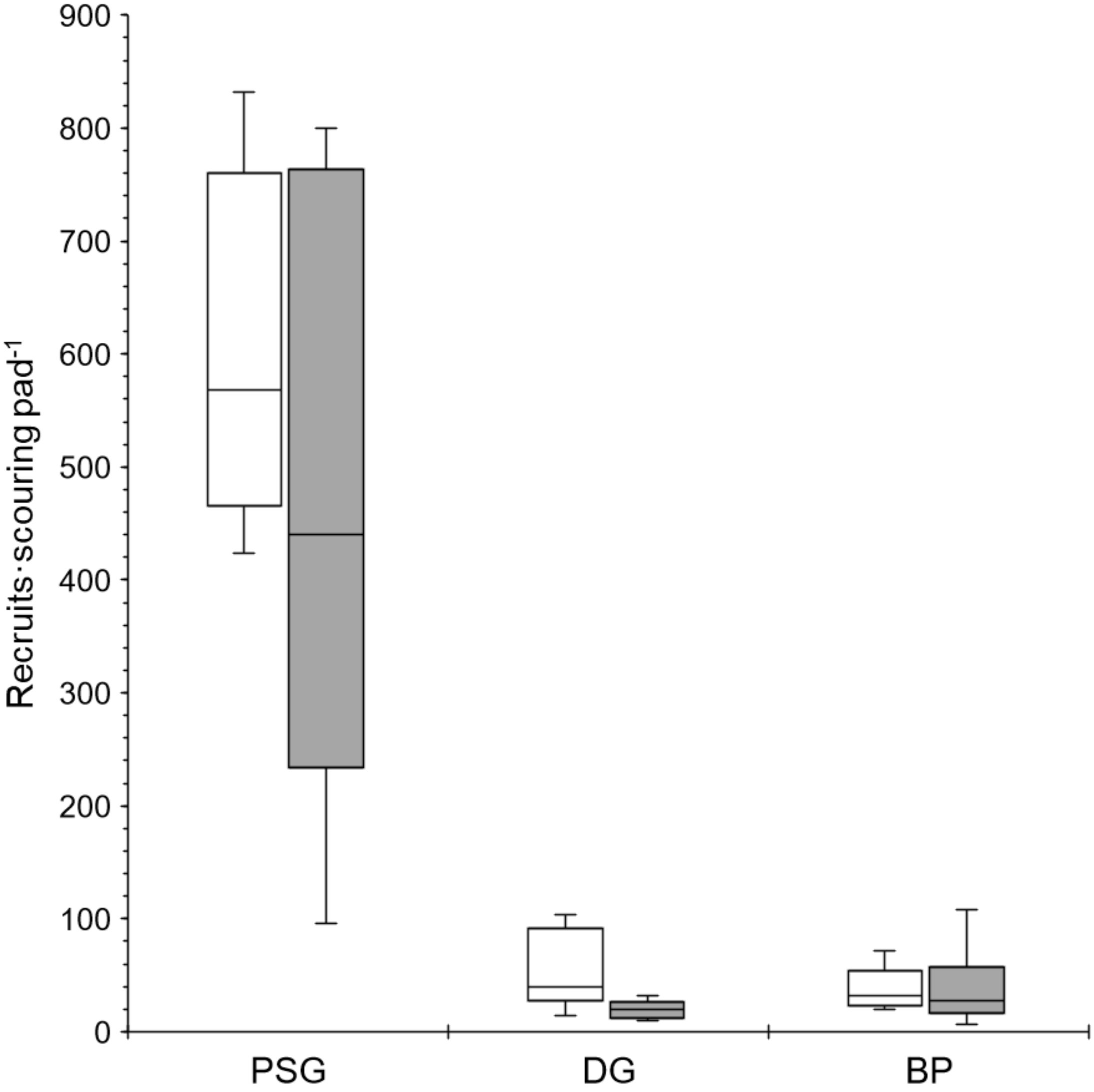

Figure 5. Mussel recruitment at each site. White boxes represent horizontal surfaces within the cobble fields near Crab and MPE treatment plots, grey boxes represent vertical surfaces near Sea star treatment plots.

Effect of orientation on mussel recruitment across sites

I found significant effects of orientation on mussel recruitment across sites (Table 8). Recruitment to horizontal surfaces at PSG was 91% greater at DG and 94% greater than at BP (Table 9, Fig. 5). Additionally, recruitment to vertical surfaces at PSG was 96% greater than at DG and 92% greater than recruitment at BP (Table 9, Fig. 5). There was no difference in horizontal and vertical recruitment between DG and BP (Table 9, Fig. 5).

Table 8. Results of maximum likelihood ratio test examining effects of orientation across sites on mussel recruitment.

Comparison		*d.f.*	AIC	Chi^2	*d.f.*	*P*
Horizontal	Site + (Site|Block)	9	200.07	19.87	2	<0.001
	(Site|Block)	7	215.94			
Vertical	Site + (Site|Block)	9	195.89	15.79	2	<0.001
	(Site|Block)	7	207.68			

Table 9. Post-hoc comparisons of differences in mussel recruitment between horizontal and vertical orientations across sites using Tukey’s tests.

Comparison			Estimate	SE	Z	*P*
Horizontal	PSG	DG	2.60	0.31	8.51	<0.001
	PSG	BP	2.81	0.24	11.89	<0.001
	DG	BP	0.22	0.29	0.75	0.734
Vertical	PSG	DG	3.00	0.34	8.76	<0.001
	PSG	BP	2.61	0.53	4.92	<0.001
	DG	BP	-0.39	0.42	-0.93	0.609

DISCUSSION

I found considerable variation in mussel mortality among my treatments and among sites. Contrary to my predictions, crabs did not consume more mussels than sea stars. In fact, I observed no difference in mussel consumption between crabs and sea stars at both DG and BP and observed greater mussel consumption by sea stars than crabs at PSG. Crab densities and crab predation at BP were significantly lower than crab densities and crab predation at both PSG and DG. However, while crab densities were higher at PSG than at DG, crab predation between PSG and DG did not differ.

Several factors may contribute the observed patterns of mussel consumption by crabs at both PSG and DG, however I suggest that three factors could explain my results. First, rock crab densities are higher at PSG, possibly increasing the likelihood of intraspecific competition among rock crabs. Intraspecific competition has been shown to decrease overall predation in other marine systems (Forrester 1990, Webster and Hixon 2000) and could explain why mussel consumption rates by crabs at PSG were no different than those at DG as larger more aggressive crabs could be utilizing a greater proportion of resources (in this case mussels) and preventing smaller individuals from feeding. Second, several sources of prey like other shelled gastropods (*Calliostoma spp*., *lottia spp.*, *Nucella spp.*, *Tegula spp.*), chitons (*Mopalia* spp., *Tonicella* spp.) and small crustaceans like barnacles (*Semibalanus spp.),* hermit crabs (*Pagurus spp.*) and other smaller crab species (*Hemigrapsus spp*., *Lophopanopeus spp*., *Petrolisthes spp*., *Pachycheles spp*.) were more abundant at PSG compared to DG (personal observations) that could potential serves as an alternative source of prey. If crabs are utilizing these alternative prey sources, this could explain reduced mussel predation in crab treatments in PSG. Finally, if crabs are utilizing these alternative prey sources, they could have become satiated faster during the experiment by consuming a variety of shelled prey (Bernard 1979, Seed and Hughes 1995).

Contrary to my initial prediction that mussel consumption in MPE treatments would exceed both crab and sea star treatments, mussel consumption in MPE treatments was no different than that in the crab treatments. I suspect this pattern occurred because mussel consumption in MPE treatments was primarily due to crabs, which was indicated by the lack of empty shells devoid of tissue that are characteristic of sea star predation. Therefore, at least in horizontal areas where mussels are accessible to both crabs and sea stars, mussel consumption is likely driven by crab predation rather than the combined effects of *P. ochraceus* and crabs as sea stars may be reducing their feeding rates in an attempt to avoid interacting with crabs (see chapter two results).

Mussel mortality within sea star treatments was similar to both crab and MPE treatments at DG and BP, but greatly exceed both crab and MPE treatments at PSG. This was surprising, as I expected mussel mortality in sea star treatments to be less than that in crab treatments given that consumption of mussels via sea stars occurs at a much slower rate than crabs (Hull and Bourdeau 2017). One factor that could be responsible for the observed patterns in sea star predation is sea star density. Given how slow sea stars consume mussels, I would expect the consumption rate of sea stars to be less than that of crabs if both predators were of equal densities, however, on average sea star density was

32.2% higher than crab density across my sites. The higher density of sea stars could explain why mussel consumption via sea stars was similar to mussel consumption via crabs at both DG and BP and greater than mussel consumption via crabs at PSG. Further, this line of thought is reinforced by evidence showing that increased predator density causes increased prey mortality in other systems (Eveleigh and Chant 1982).

An alternative possibility is that sea star feeding rates could be altered due to the presence of abundant crab competitors. Changes in predator behavior due to the presence of competitors have been shown previously to contribute to changes in predation risk experienced by prey. For example, in freshwater systems, higher densities of intraspecific competitors cause the ram's horn snail (*Helisoma trivolvis*) to increase their feeding rates on algae (Sura and Mahon 2011). In marine systems, the presence of American lobsters (*Homarus americanus*) decreases the foraging effectiveness of Jonah crabs (*Cancer borealis*) on green sea urchins (*Strongylocentrotus droebachiensis*) (Siddon and Witman 2004). Additionally, in the eastern north Pacific the presence of *P. ochraceus* inhibits the feeding rates of marine predatory whelks (*Nucella spp.*) on the bay mussel (*Mytilus trossulus*) (Navarrete and Menge 1996). In the case of sea stars at PSG, the observed increase in mussel consumption could be a behavioral response to the presence of crabs (see Fig. 9 in chapter two results). If sea stars face competition from crabs, they may increase their feeding rates to ensure they consume enough mussels before the competitively superior crabs arrive. Such competitive interactions are possible in this system, as mussel recruitment in northern California is much lower than at higher latitudes (Connolly et al. 2001, Sanford and Worth 2010) and mussels are sparser in cobble/boulder fields than on rocky benches in northern California (personal observation), making them a potentially limited resource for these predators at my study sites. While this may explain the observed increase in sea star predation at PSG, it also suggests that this type of response may only be elicited at potentially higher crab densities as this increase in sea star feeding rate was not observed at lower predator densities at DG and BP. At PSG where crab densities were the highest, sea stars may be altering their feeding behavior due to more concentrated crab chemical cues (see chapter two discussion). Regardless, these results show that increases in mussel mortality can be caused by increased predator densities or perhaps by interaction modifications between predators and prey due to the presence of another competitor.

The results from my recruitment experiment suggest that mussel recruitment to horizontal surfaces is greater than recruitment to vertical surfaces at two of my three sites. This is not surprising as vertical environments could be less favorable for juvenile recruitment due to environmental stressors like temperature and wave exposure. For example, it has been shown that increased temperatures can be responsible for increased mortality and the downward vertical shift of mussels and other common intertidal organisms (Harley 2008, 2011) and exposure to strong wave forces can dislodge mussels from substrate (Denny 1987, Carrington 2002). This makes sense as higher tidal elevations are the first to become exposed to air during a low tide and are the last to become submerged during a high tide. For mussels living in these environments this means being exposed to sunlight and air temperatures for longer periods than animals living at lower tidal elevations and running the risk of desiccating. This could also allow terrestrial predators like black oystercatchers (*Haematopus bachmani*), a common predator of mussels (Hartwick 1973, 1976, Miller and Dowd 2019), more opportunity to feed on these mussels as they are immersed for less of the tidal cycle. Additionally, as the tide comes in and out animals living at higher tidal elevations are subjected to crashing waves and floating debris, increasing their chances of becoming dislodged, damaged, or crushed. Further, juvenile mussels may be more susceptible to effects of temperature and wave force, ultimately impacting juvenile mussel mortality (LeBlanc et al. 2005). It has also been shown that mussel larvae will recruit to areas with reduced water velocity first, before redistributing to areas of higher water velocity (Dobretsov and Wahl 2008). Moreover, with horizontal orientations also representing areas of lower tidal elevations in this study, juvenile mussels may avoid these stressors to some degree by recruiting to lower elevations where they can stay submerged longer, stay cool, and decrease the chance of becoming dislodge or damaged by incoming debris. The 100% survival of the caged controls is consistent with this idea – though the cage itself provides significant shading and shelter from wave forces, confounding this inference. While recruiting to these lower horizontal surfaces may mitigate the effects of environmental stressors at higher elevations, juvenile mussels may become more susceptible to predation (Bertness 1985, Lin 1989, Hull and Bourdeau 2017). Therefore, the lack of adult mussels found on horizontal surfaces in the low intertidal zone despite higher recruitment, could be due to predation by crabs, sea stars, and other invertebrate predators, although other biological interactions like competition or abiotic stress like temperature or desiccation cannot be completely ruled out. Future studies would need to incorporate multi-factorial experiments that are designed to test the relative influence of predation and other factors on the mortality of mussel recruits on horizontal surfaces in cobble/boulder habitats.

In intertidal cobble and boulder fields in northern California, the type of predator responsible for mussel predation depends on the habitat mussels are in. On lower horizontal surfaces mussel predation is likely dominated by crabs. This is due in part to crabs being better competitors for prey than sea stars and to the physical presence of crabs potentially causing sea stars to reduce their feeding rates as the addition of sea star predation would have likely increased overall predation on lower horizontal surfaces. On higher vertical surfaces, mussel predation is likely dominated by sea stars. This is because mussels on these surfaces are more accessible to sea stars as crabs are unable to scale these surfaces to reach their prey. Further, increased predation by sea stars in this habitat can be attributed to greater sea star densities, however, the density of crabs within these environments could prompt sea stars to increase their feeding rates causing mussels on higher vertical surfaces to experience an enhanced level of predation risk. Therefore, mussels living in these environments may experience similar levels of predation by both crabs and sea stars, or greater predation by sea stars as both predator density and predator proximity likely play a role in determining the level of predation mussels experience. To better understand the role competitor proximity plays in influencing predator feeding rates, a better understanding of how different modes of competitor detection affect feeding behavior is required to truly understand how multiple predators affect mussel mortality in northern California rocky intertidal habitats.

CHAPTER 2: EXAMINING THE EFFECTS OF COMPETITORS AND ELEVATED TEMPERATURES ON PREDATOR FEEDING BEHAVIOR

INTRODUCTION

Ecological Interaction modifications occur when interactions between species pairs are modified by a third species (Wootton 1993, Golubski and Abrams 2011). Modifications of interactions between consumers and their prey by predators have been commonly documented (Siddon and Witman 2004, Sura and Mahon 2011). For example, spiders with differing attack modes can indirectly affect field communities by reducing the feeding activity of their grasshopper prey (Schmitz and Suttle 2001). When these interaction modifications indirectly affect lower trophic levels, they are known as trait mediated indirect interactions (TMII), or behaviorally mediated trophic cascades (Estes and Palmisano 1974, Wootton 2002, Trussell et al. 2003).

There are many instances of predators indirectly affecting primary producers via trait-mediated effects on herbivorous prey (Losey and Denno 1998, Nelson et al. 2004, Wilkinson et al. 2015, Davis et al. 2017), however less is known about how predators indirectly affect primary consumers via trait-mediated effects on other predator species (Siddon and Witman 2004). These so-called ‘multiple predator effects’ or ‘MPEs’ can be additive, or non-additive; in the latter case either increasing (risk enhancement) or decreasing (risk reduction) the overall mortality on shared prey through changes in predator behavior (Sih et al. 1998). For example, the green sunfish (*Lepomis cyanellus*), a common predator of freshwater isopods (*Lirceus fontinalis*), reduce their feeding rates on isopods by consuming salamander larvae when present; this causes small-mouthed salamander larvae (*Ambystoma barbouri*) to seek refuge from sunfish and thereby reduce their feeding rates on isopods, reducing overall isopod mortality (Huang and Sih 1991). Understanding how predator species interact with each other and indirectly affect the interactions with their shared prey is necessary for predicting prey population dynamics and community structure (Menge et al. 1994, Robles et al. 1995).

Whereas most MPE studies focus solely on the outcome of predator-predator interactions on shared prey, few assess the mechanisms by which MPEs are transmitted. However, it is important to examine the mechanistic bases for MPEs, as predators may not only interact with one another physically, but also chemically (Stauffer and Semlitsch 1993, Eklöv 2000), and the way predators interact with one another may lead to qualitatively different outcomes for prey populations, or the predators themselves. For example, most studies of MPEs only examine the effects of competing predators that are in physical contact with one another (Soluk 1993, Schmitz and Sokol-Hessner 2002, Siddon and Whitman 2004), but do not consider the potential chemically mediated effect predators may have on each other.

The effects of chemical cues on predator-predator interactions are likely to be important. Chemically mediated species interactions are well-studied in aquatic systems, as olfaction is an important source of information gathering for organisms living in a fluid medium (Ferrari et al. 2010). Most notably, the presence of predator chemical cues is a common driver of aquatic predator-prey interactions and is considered responsible for inducing changes in prey behavioral traits (Kusch 1999, Trussell et al. 2003, Richmond and Lasenby 2006, McKay and Heck 2008, Bourdeau 2009, 2010). Just as prey species can sense predators through olfaction, competing predators can sense each other through these means as well (Wissinger and McGrady 1993, Persons and Rypstra 2001, Roozen et al. 2001, Jones et al. 2003, Polo-Cavia et al. 2009). Further, the chemical and physical presence of a predator is likely to alter the behavior of a competing predator in different ways, just as both the chemical and physical presence of predators elicits different responses in prey (Crowl and Covich 1994, Weightman and Arsenault 2002). For example, the detection of predators in aquatic environments via chemical cues can be thought of as a form of remote detection, just like when a terrestrial prey species smells or sees a predator from a distance. In contrast, the physical presence of a predator means close proximity.

Understanding how marine predators affect each other's feeding behaviors and their shared prey through remote and close proximity detection, becomes increasingly important in the context of future predator loss and increases in global ocean temperatures (Harley 2011). For example, decreases in seawater temperature have been shown to decrease the feeding rates of the keystone sea star predator, *Pisaster ochraceus,* on the intertidal mussel *Mytilus californianus* (Sanford 1999), while increased sea water temperatures has been shown to increase the feeding rates of *P. ochraceus* on *M. californianus* (Sanford 2002a). However, when increased sea water temperatures are coupled with increased air temperatures, the feeding rates of *P. ochraceus* on mussels decrease (Pincebourde 2012). The feeding rates of crabs on mussels may be affected differently than those of sea stars by increased seawater temperatures. For example, the metabolic rates of crabs are known to increase with increased sea water temperatures (Leffler 1972, Sanchez-Salazar 1987) and that *P. ochraceus* predation increases with water temperature (Sanford 2002a). At present, we know little about whether increased sea surface temperatures will affect rock crabs and *P. ochraceus* similarly, or if warming effects will be asymmetrical between these two predators.

To examine MPEs by rock crabs and *Pisaster* on mussels, and the behavioral mechanisms underlying these MPEs, I experimentally examined rates of mussel consumption by crabs and sea stars individually and when exposed to the chemical and physical presence of each other under ambient and elevated seawater temperatures. I had several predictions: (1) sea stars will consume fewer mussels than crabs in individual predator treatments: (2) the chemical and physical presence of crabs will cause sea stars to increase their feeding rates; (3) crabs will consume more mussels than sea stars in individual predator treatments and will not be affected by the chemical or physical presence of sea stars; (4) mussel consumption in MPE treatments will be greater than additive predicted values, due to sea stars increasing their feeding rates in the presence of crabs; and (5) mussel consumption rates will be higher in all predator treatment combinations under elevated sea water temperature conditions, due to increased predator metabolism. By investigating multiple predator effects and temperature on mussel consumption by crabs and sea stars, we can begin to understand how these two predators may independently and interactively affect natural mussel populations currently and, in the future, where sea surface temperatures have increased.

MATERIALS AND METHODS

Collection and Maintenance of Study Organisms

I collected rock crabs (*Romaleon antennariu*m; mean carapace width = 93.0 mm ± 12.3 SD, mean weight = 241.1 g ± 98.5 SD) and sea stars (*Pisaster ochraceus*; mean radius = 92.8 mm ± 13.8 SD, mean weight 223.5 g ± 71.5 SD) from Point St. George (PSG; 41.784778° N, -124.255487° W) near Crescent City, CA and mussels from Baker Beach (BB; 41.04928° N, -124.1277° W), near Trinidad, CA. Both collection sites are characterized by large boulder and cobble fields that are partially protected from strong waves by large rocky reefs. PSG was used as my source of predators due to the high relative abundances of both crabs and sea stars, whereas BB was used as my source of mussels due to the presence of large, accessible mussel beds in close proximity to the TML. Crabs, sea stars, and mussels were housed in separate flow-through sea tables at TML to prevent interactions between organisms prior to the start of the experiment.

Estimating Proximity of Predators in the Field

I quantified the distance between individual crabs and sea stars at PSG, BB, and Mussel Rock (MR; 40.34754° N, -124.36440° W), a large boulder field near Cape Mendocino, CA during a low tide series in June 2018. Using a transect tape, I measured the distance (m) between crabs and sea stars by visually locating crabs hiding between cobbles, under boulders, and partially buried beneath mud and sand and their nearest sea star neighbor in a single 10 x 30 m swath in the low intertidal zone at each site. I chose to search for crabs rather than sea stars as crabs are highly mobile and more difficult to spot than sea stars when hiding. Thus, once I found a crab it was easier to find a nearby sea star. When locating crabs, I made sure that I did not disturb the crab by flipping over nearby cobbles or boulders, as this could cause the crab to move from its original location. Once I finished recording the distance between a crab and the nearest sea star, I marked each individual predator with lumber crayon so I would not accidentally measure the distance between them again if I rediscovered them while searching for more crabs. I then calculated the average distance between sea stars and crabs to determine the smallest experimental venue needed to enclose two predators in field-relevant proximity in my experimental replicates (see below).

Laboratory Feeding Experiment

I tested the separate and combined effects of crabs and sea stars on mussel mortality under six levels of predator treatment: (1) two crabs in physical contact with one another (CC); (2) two sea stars in physical contact with one another (SS); (3) two crabs exposed to the chemical presence of sea stars only (S.Cue); (4) two sea stars exposed to the chemical presence of crabs only (C.Cue); (5) crabs and sea stars feeding in physical contact with one another (MPE); and (6) a control with no predators and mussels only. Predator treatments were crossed with two temperature treatments: (1) constant 11.5 °C (Ambient), and (2) constant 16.5 °C (Elevated) (Table 10). The ambient temperature treatment was designed to simulate temperatures near the average annual sea water temperatures at PSG in 2017 (11.6°C ± 1.19 SD, NOAA buoy station 46027, CeNCOOS 2020). I chose a 5°C increase in temperature because marine organisms have experienced temperature increases this high during recent marine heatwaves in the eastern north Pacific (Gentemann et al. 2017). Further, marine organisms are likely to experience more instances of extreme sea water temperatures as warm sea water anomalies become more common in the future due to climate change (Cai et al. 2014, Wang et al. 2017).

Table 10. Design of predator and temperature treatment assignment for laboratory feeding experiments. Plus signs (+) represents predator type, with double plus signs (++) representing two of the tame predator type per treatment. Minus signs (-) represent absence of predator(s). "*Cue*" signifies which predator is generating chemical cue in experimental treatments.

Treatment Combination		Control	SS	CC	C.Cue	S.Cue	MPE
Ambient (11.5 °C)	Sea star	-	++	-	++	*Cue*	+
	Crab	-	-	++	*Cue*	++	+
Elevated (16.5 °C)	Sea star	-	++	-	++	*Cue*	+
	Crab	-	-	++	*Cue*	++	+

Predators were placed in individual flow-through treatment tanks (51 cm x 26 cm x 32 cm) and randomly assigned a given predator treatment. In each cue treatment, feeding predators were physically separated from their respective cue predator with cue water being delivered from individual header tanks (20 cm x 16.5 cm x 15 cm) where cue predators were housed. All treatment tanks received water from header tanks regardless if there was a predator inside the header tank or not. Elevated temperature treatments were achieved by placing three 500-watt aquarium heaters inside elevated sumps (89 cm x 46 cm x 37 cm) while ambient treatments were achieved by using external chillers to cool separate elevated sumps (Fig. 6A). I monitored water temperature inside each treatment tank via a hand-held temperature probe and monitored individual sump temperatures via temperature controllers displaying current sea water temperatures. All sumps producing elevated treatments with aquarium heaters were controlled using the same temperature controllers (Fig. 6A). For all treatment combinations, seawater was gravity-fed from elevated sumps to manifolds that delivered sea water to each header tank, which supplied each treatment tank (Fig. 6B). A total of three sumps were outfitted with their own manifold, that delivered water to four header tanks, with each header tank supplying treatment water to one treatment tank. I randomized the temperature treatments between sumps and predator treatments between replicate tanks at the start of each trial to eliminate any effect of location in my experimental set-up.

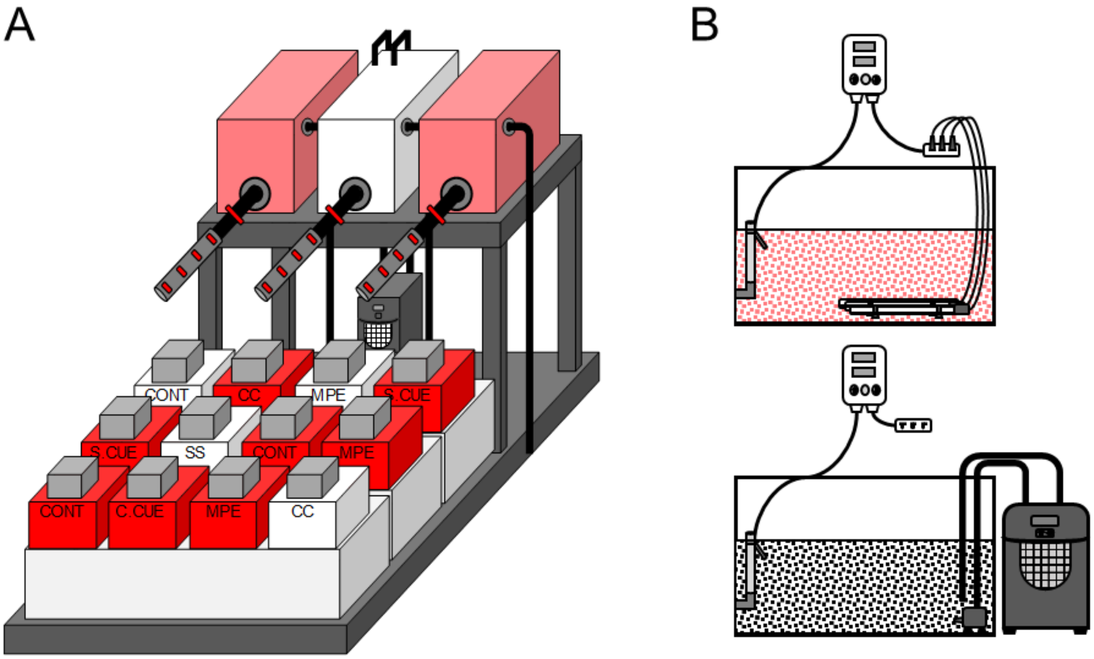

Figure 6. Schematic of (A) an example trials where predator and temperature treatments are randomly dispersed among replicate tanks; and (B) elevated temperature-controlled tanks designed to produce temperature treatments (elevated temperature treatments are depicted in red, ambient temperature treatments are depicted in white).

I performed a power analysis to determine the minimum number of replicates needed to achieve statistical power of 0.8 using an effect size of 0.5 for predator treatment and 0.2 for temperature treatment (Cohen 1988, *pwr2* package, Dean and Voss 1999). Results from the power analysis indicated a minimum of 5 replicates were needed, therefore each treatment combination was replicated 5 times. To replicate each treatment combination 5 times, 6 trials were conducted with 12 replicate tanks per trial.

All predators were sized-matched according to biomass and given three days to feed; with all predators receiving 10 mussels from 3 different size classes: small (25-35 mm), medium (35-45 mm), and large (45-55 mm). Mussels used in each trial were cleaned of all epibionts prior to being placed inside treatment tanks. All predators were fed thawed capelin (*Mallotus villosus*) before being starved for 1 week prior to the start of each trial, which is well beyond the length of time required for gastric clearance in crabs (McGaw and Curtis 2013). Although I was unable to find literature quantifying gastric clearance rates for *P. ochraceus* and given that clearance is quantitatively different than that of crabs, given the external digestion of sea stars, I used a conservative estimate of 1 week. At the end of each experiment, I quantified the number of mussels consumed to assess the separate and interactive effects of predator combinations and temperature on mussel mortality. Whole, intact shells that were pried open and devoid of tissue were attributed to sea star predation, while broken and crushed shells were attributed to crab predation (Fig. 7).

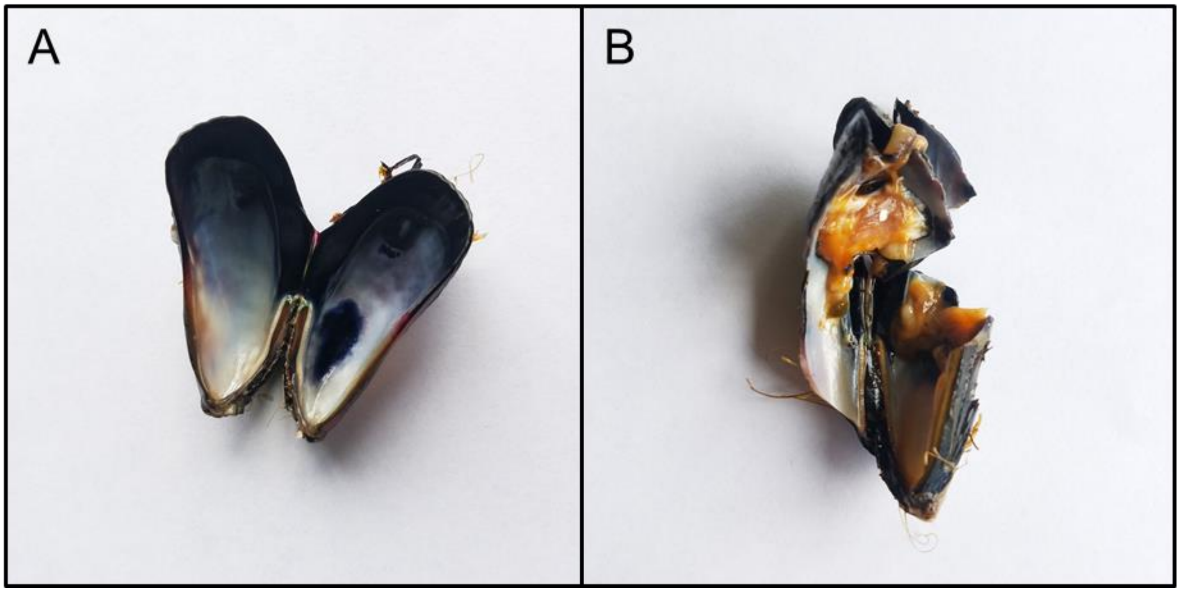

Figure 7. Photographic examples of (A) whole, intact mussel shells with no tissue inside attributed to sea star predation, and (B) broken mussel shells with partially consumed tissue attributed to crab predation.

Data Analyses

I used general linear models and post-hoc comparisons to examine the effects of predator combination, temperature, and their interaction on the per capita mortality rate of mussels (no. mussels lost$\cdot$pred$^{-1}\cdot$day^{-1}) and the effects of predator treatment and temperature on crab and sea star feeding rates. The presence of significant interactions between predator treatment and temperature were further analyzed with simple effects to explain the interaction. I also compared MPE treatments to predicted values from single species treatments using *t*-tests to test for significant non-additive MPEs (Schmitz and Sokol-Hessner 2002). The predicted values were calculated as the mean per capita mortality rate of the two single-species treatments (SS and CC). Therefore, if the mortality rate of MPE treatments was significantly lower than the predicted values, a reduction in risk occurred for mussels in the multiple predator treatment (i.e., risk reduction). Conversely, if the mortality rate of MPE treatments was significantly greater than the values predicted from single species treatments, risk was enhanced by the presence of both predators for mussels (i.e., risk enhancement). Additionally, I compared the consumption rate of mussels from single-species treatments (CC or SS) to the consumption rate of mussels by each predator in MPE treatments, as well the consumption rate of mussels by each predator in MPE treatments between temperature treatments using *t*-tests with Bonferroni-adjusted alpha levels of 0.008 per test. To make consumption rates from single-species treatments comparable to the consumption rates of each predator in MPE treatments I divided the average single-species consumption rates in half to represent the average mussel consumption rate of a single predator in single-species treatments. I was able to make these comparisons due to the contrasting attack modes of both crabs and sea stars, which allowed me to easily determine how many mussels each predator consumed in the MPE treatments (Fig. 7). Control treatments were excluded from all analyses as no mussels in either temperature treatment died over the course of the experiment.

RESULTS

Predator Proximity in the Field

I found that on average, crabs and sea stars were 0.43 m (± 0.34 SD) apart from each other in sampled boulder fields (Fig. 8). At PSG, crabs and sea stars were 0.49 m (± 0.39 SD) apart from each other, and at BB crabs and stars were 0.37 m (± 0.35 SD) apart from each other. Crabs and sea stars had the greatest predator proximity at MR, averaging 0.35 m (± 0.26 SD) between each other. Given the average proximity between crabs and sea stars across and within field sites, the treatment tanks I used for my laboratory feeding experiment were of reasonable size for examining the potential interactions between crabs and sea stars as they were within one SD of the average proximity measured across and in my field sites.

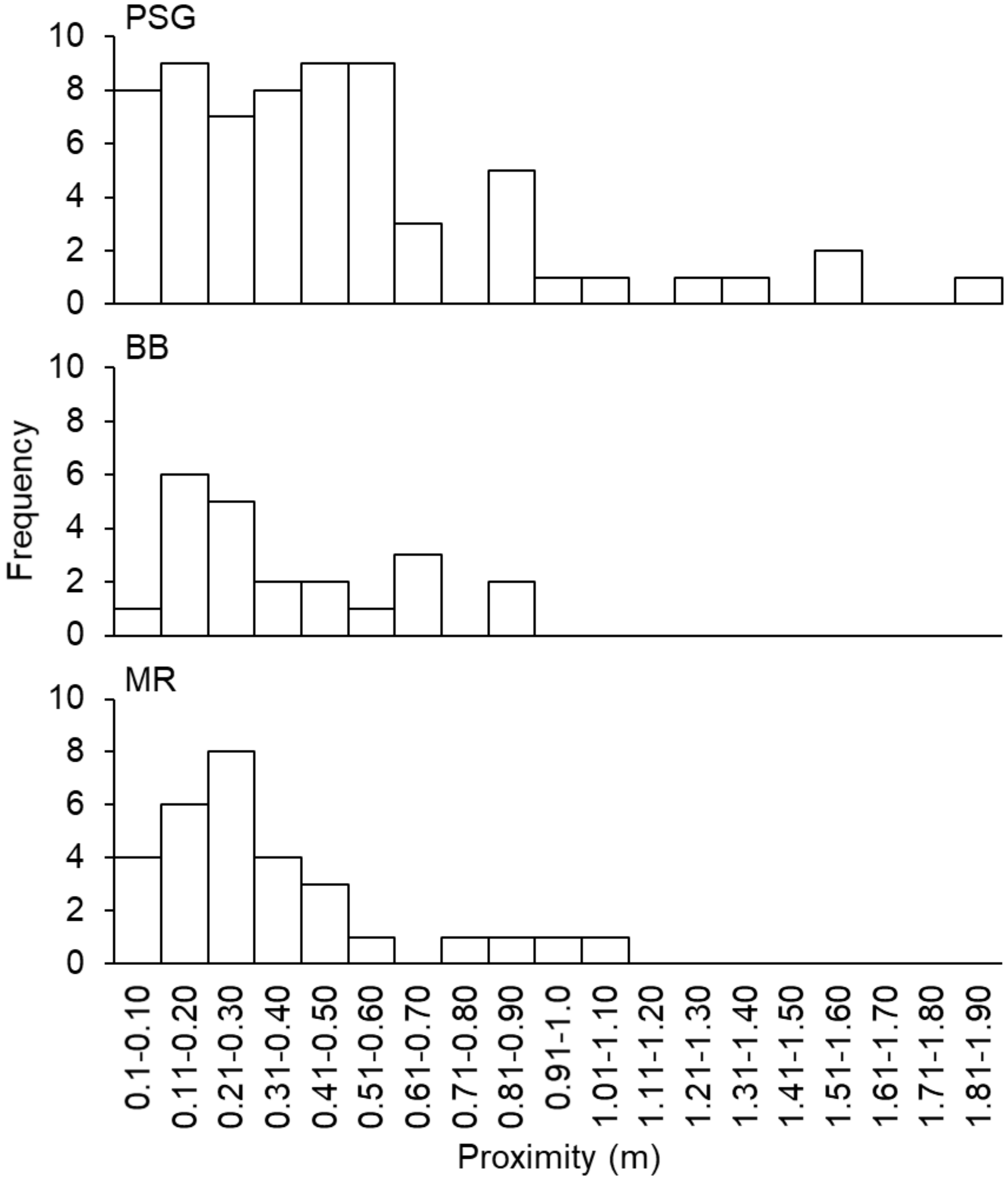

Figure 8. Frequency distributions of crab and sea star proximities (meters) at Point St. George (PSG), Baker Beach (BB), and Mussel Rock (MR).

Effects of Predators and Temperature on Mussel Mortality

The results of my laboratory feeding trials showed a significant effect of predator treatment and a significant interaction between predator treatment and temperature on mussel mortality (Table 11). Per capita Crabs in CC treatments consumed on average 500% more mussels than sea stars in SS treatments, 170% more than sea stars in C.Cue treatments, 66% more than predators in MPE treatments, and 10% more than crabs in S.Cue treatments. Additionally, crabs in S.Cue treatments consumed on average 444% more mussels than sea stars in SS treatments, 144% more than sea stars in C.Cue treatments, and 51% more than predators in MPE treatments (Fig. 9).

Table 11. Results of two-way factorial ANOVA testing the separate and interactive effects of predator (rock crabs and sea stars) presence and temperature on mussel mortality in the laboratory feeding experiment.

Treatment	*d.f.*	SS	MS	*F*	*P*
Predator	4	4.01	1.00	58.21	<0.001
Temperature	1	0.04	0.04	2.03	0.162
Predator:Temperature	4	0.25	0.06	3.66	0.013
Residuals	40	0.02			

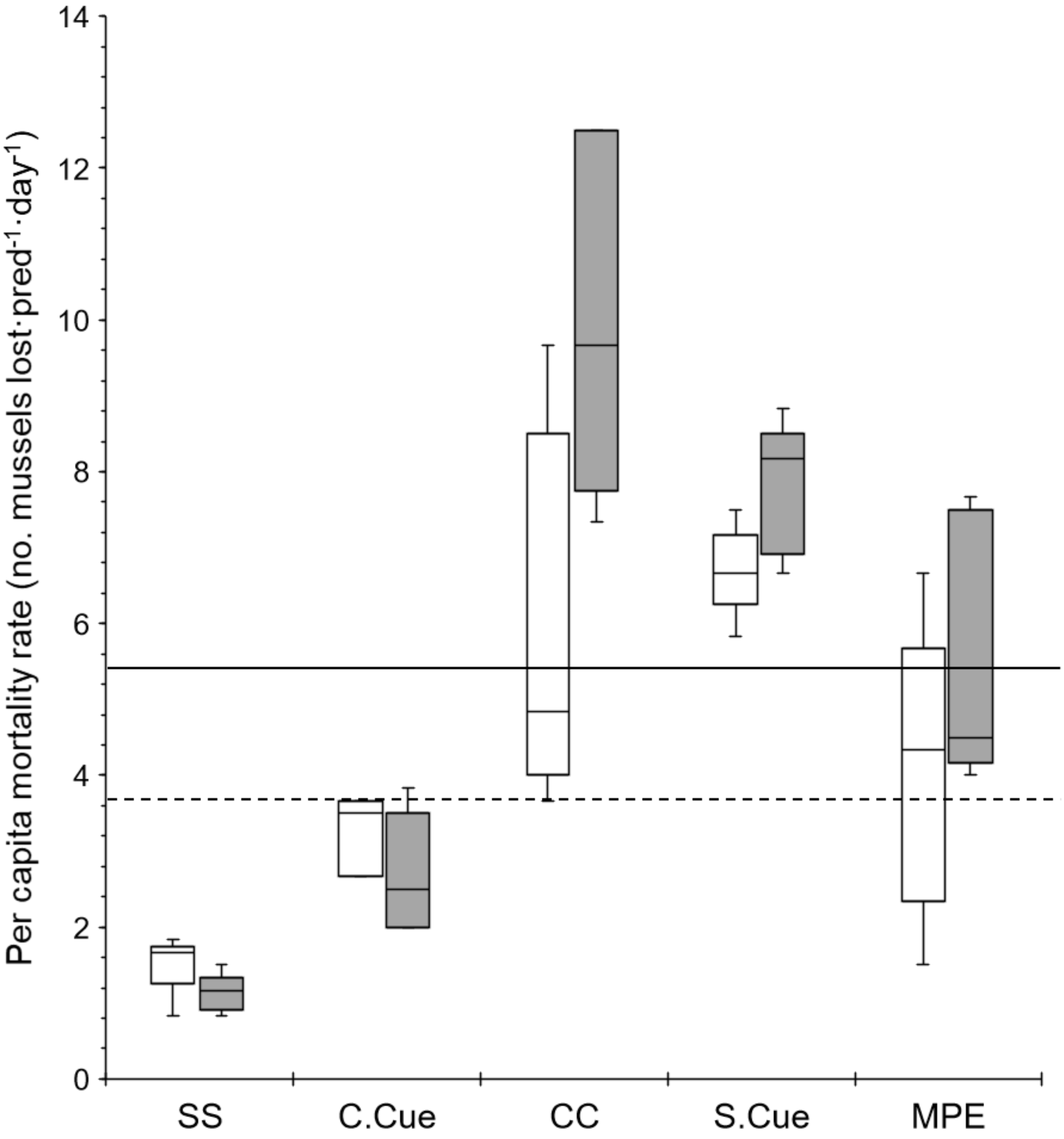

Figure 9. Mean (± 1 SE) per capita mussel mortality rate in predator treatments under both ambient (white) and elevated (grey) temperature treatments. The dashed line represents the predicted ambient MPE value, while the solid line represents the predicted elevated MPE value calculated as the mean per capita mortality rate of the two single-species treatments (SS and CC) in both temperature treatments.

Sea stars in C.Cue treatments consumed on average 123% more mussels than sea stars in SS treatments and consumed 38% fewer than predators in MPE treatments, while predators in MPE treatments consumed on average 261% more mussels than sea stars in SS treatments and 62% more than sea stars in C.Cue treatments.

An analysis of simple effects showed that the temperature effect was significant in elevated CC and S.Cue treatments (Table 12). Crabs in elevated temperature CC treatments consumed 68% more mussels than crabs in ambient CC treatments, while crabs in elevated temperature S.Cue treatments consumed 16% more mussels than crabs in ambient S.Cue treatments. Temperature had no effect on any other predator treatments.

Table 12. Results of simple effects examining the effects of temperature on mussel mortality across predator treatments.

Treatment	*d.f.*	SS	MS	*F*	*P*
SS	1	0.04	0.04	2.68	0.141
CC	1	0.15	0.15	7.23	0.028
C.Cue	1	0.02	0.02	1.87	0.209
S.Cue	1	0.01	0.01	5.39	0.049
MPE	1	0.07	0.07	1.79	0.217

I did not detect a significant difference in mussel consumption between ambient MPE treatments and the value predicted by additive MPEs under ambient conditions (t = 0.371, *d.f.* = 4, P = 0.730, Fig. 8). Furthermore, I did not detect a significant difference in mussel consumption by elevated temperature MPE treatments and the projected elevated temperature treatment value ($t = -0.021$, *d.f.* = 4, $P = 0.984$, Fig. 8), indicating the combined effects of crabs and sea stars on mussel mortality were additive.

Impact of Competitor Presence Under Ambient Temperatures

The results of my ANOVA showed significant effects of predator treatment on predator consumption rates ($F_{4,20} = 14.01$, $P = <0.001$). Sea stars in C.Cue treatments consumed 111% more mussels than sea stars in SS treatments and 52% fewer mussels than crabs in S.Cue treatments. Crabs in CC treatments consumed 289% more mussels than sea stars in SS treatments, while crabs in S.Cue treatments consumed 337% more mussels than sea stars in SS treatments. Additionally, predators in MPE treatments consumed 165% more mussels than sea stars in SS treatments (Fig. 9). There was no significant difference in the number of mussels consumed by crabs in CC treatments versus crabs in S.Cue, sea stars in C.Cue, or predators in MPE treatments. Further, there was no significant difference between the number of mussels consumed by sea stars in C.Cue treatments and predators in MPE treatments, or between crabs in S.Cue treatments and predators in MPE treatments (Table 13).

Table 13. Post-hoc comparisons of differences in mussel consumption between predator treatments under ambient temperature conditions using Tukey's HSD test.

Comparison		Diff	Lower	Upper	*P*
SS	CC	-0.58	-0.87	-0.29	<0.001
	C.Cue	-0.33	-0.62	-0.05	0.018
	S.Cue	-0.65	-0.94	-0.37	<0.001
	MPE	-0.39	-0.68	-0.10	0.005
CC	S.Cue	0.08	-0.21	0.37	0.926
	C.Cue	0.24	-0.05	0.53	0.127
	MPE	-0.19	-0.47	0.10	0.335
C.Cue	S.Cue	0.32	0.031	0.61	0.025
	MPE	0.06	-0.23	0.34	0.976
S.Cue	MPE	0.26	-0.03	0.55	0.084

Impact of Competitor Presence Under Elevated Temperatures

I found significant effects of predator treatment on predator consumption rates ($F_{4,20}$ = 65.90, P = <0.001). Sea stars in C.Cue treatments consumed 138% more mussels than sea stars in SS treatments and 60% fewer mussels than crabs in S.Cue treatments. Crabs in CC treatments consumed 785% more mussels than sea stars in SS treatments, and 272% more mussels than sea stars in C.Cue treatments, while crabs in S.Cue treatments consumed 337% more mussels than sea stars in SS treatments. Additionally, predators in MPE treatments consumed 391% more mussels than sea stars in SS treatments and 106% more mussels than sea stars in C.Cue treatments; while consuming 44% fewer mussels than crabs in CC treatments. There was no significant difference in the number of mussels consumed by crabs in S.Cue treatment versus either crabs in CC treatments or predators in MPE treatments (Table 14).

Table 14. Post-hoc comparison of differences in mussel consumption between predator treatments under elevated temperature conditions using Tukey’s HSD test.

Comparison		Diff	Lower	Upper	*P*
SS	CC	-0.95	-1.15	-0.74	<0.001
	C.Cue	-0.37	-0.57	-0.17	<0.001
	S.Cue	-0.84	-1.04	-0.64	<0.001
	MPE	-0.68	-0.88	-0.48	<0.001
CC	S.Cue	-0.01	-0.30	0.10	0.567
	C.Cue	0.57	0.37	0.78	<0.001
	MPE	-0.26	-0.46	-0.06	0.007
C.Cue	S.Cue	0.47	0.27	0.67	<0.001
	MPE	0.31	0.11	0.51	0.001
S.Cue	MPE	0.16	-0.04	0.36	0.150

I found significant differences in the consumption rate of same-species predators between MPE treatments and single species predator treatments (CC and SS) (Table 16). Sea stars in ambient MPE treatments consumed 82% fewer mussels than sea stars in ambient SS treatments, while sea stars in elevated MPE treatments consumed 88% fewer mussels then sea stars in elevated SS treatments (Fig. 10). Additionally, crabs in elevated MPE treatments consumed 40% more mussels than crabs in ambient MPE treatments (Fig.10). There was no significant difference in mussel consumption rates between sea stars in ambient and elevated MPE treatments, ambient CC and crabs in ambient MPE treatments, and elevated CC and crabs in elevated MPE treatments (Table 15).

Table 15. Results of Welch's t-tests examining differences in sea star and crab consumption rates of mussels in ambient and elevated MPE treatments. The letter (S) represents sea stars in MPE treatments, while (C) represents crabs in MPE treatments. Bonferroni-corrected alpha level of 0.008.

Comparison	*t*	*d.f.*	*P*
Ambient SS - Ambient (S)	4.057	5.959	0.007
Elevated SS - Elevated MPE (S)	7.312	7.310	<0.001
Ambient MPE (S) - Elevated MPE (S)	1.878	6.496	0.589
Ambient CC - Ambient MPE (C)	-0.854	7.433	0.420
Elevated CC - Elevated MPE (C)	-0.320	6.918	0.759
Ambient MPE (C) - Elevated MPE (C)	-2.691	6.839	0.032

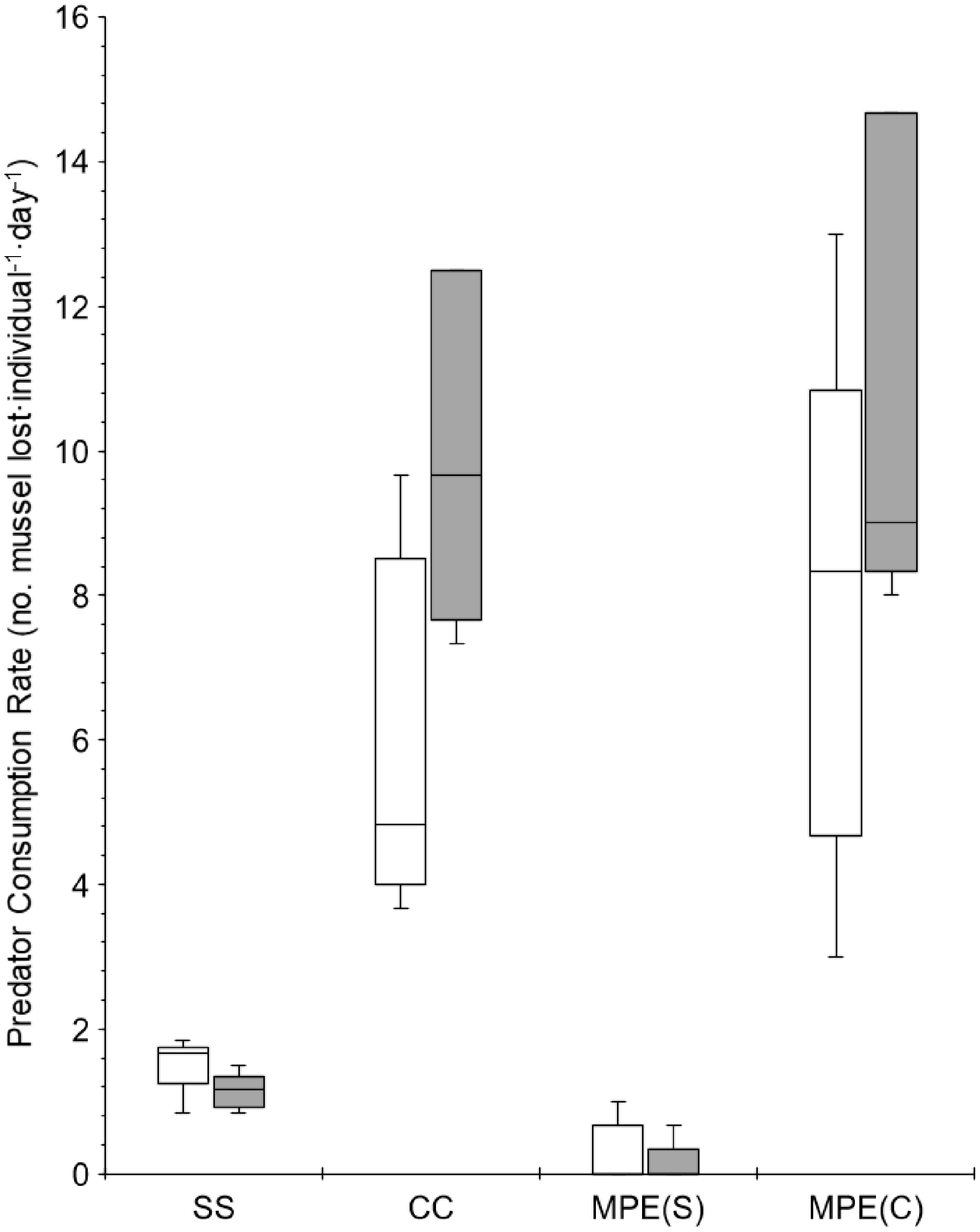

Figure 10. Mean (± 1 SE) per capita mussel consumption rate in predator treatments under both ambient (white) and elevated (grey) temperatures. Letters in parentheses after the treatment names represent the per capita mussel consumption rate of either sea stars (S), or crabs (C) in MPE treatments.

DISCUSSION

In summary, my results show a variety of outcomes for mussel mortality when examining interactions between crabs and sea stars under different temperature conditions (Fig. 11). Regarding sea stars, the exposure to crabs, a likely superior food competitor, produced either risk enhancements or reductions for mussels, suggesting that prey mortality can depend on how competing predators respond to one another depending on their proximity to each other and their mode of detection (chemical or physical). In sea stars, chemically detecting crabs caused them to increase their feeding rates, whereas direct physical interactions caused them to decrease their feeding rates. Additionally, increased temperatures increased mussel predation in crabs and showed that environmental conditions can also greatly influence predator feeding behavior by enhancing predation risk due to the need to satisfy the metabolic needs of predators. While both species are active predators of mussels, physical interactions between the two does not produce risk enhancement for mussels since these predators appear to increase their consumption rates in response to one another.

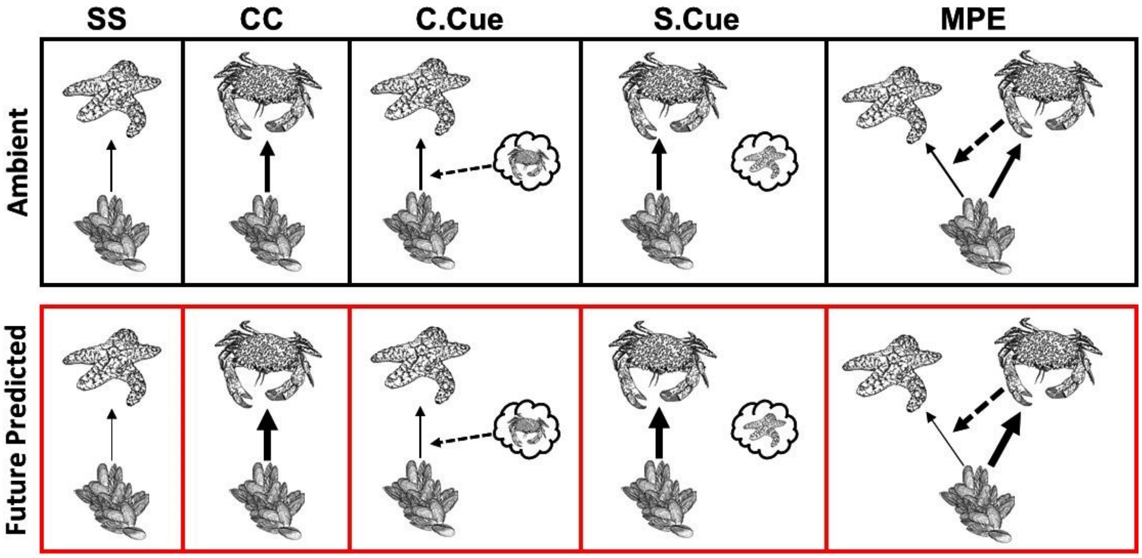

Figure 11. Summary of the effects associated with the rock crab-sea star interactions under different temperature and predator effects. Predators in clouds represent chemical predator cues. Solid black arrows represent direct effects and dashed arrows represent trait-mediated indirect effects (interaction modifications). Arrow thickness is proportional to the magnitude of the interactions.

Contrary to my predictions, the combination of both crabs and sea stars in MPE treatments resulted in no significant increase in mussel mortality rates when compared to my predicted values (ambient = 3.75 mussels·day^{-1}, elevated = 5.85 mussels·day^{-1}), as predators did not appear to increase their consumption rates due to the physical presence of one another. Additionally, there was no effect of temperature on MPE treatments. However, when examining individual mussel consumption rates of each predator within MPE treatments, I found that sea stars reduced their feeding rates in the physical presence of crabs due to a behavioral modification in response to crabs. While these results suggest that mussels may experience a risk reduction from sea stars when the stars are in physical contact with crabs, this does not mean that mussels experience a risk reduction overall when both predators are present; the additional mussel consumption by crabs results in an overall effect of both predators on mussel mortality that is additive.

Most of the variation in mussel mortality was caused by changes in predator behavior, which is a type of interaction modification (Wootton 1993). Sea stars responded to the chemical presence of crabs by increasing their consumption rate of mussels. This may be because crabs are superior competitors (i.e., faster consumers of mussels), so sea stars consume as many mussels as possible when crabs are in the vicinity, but not within close proximity. Conversely, sea stars in physical contact with crabs responded by greatly reducing their consumption rate of mussels, to the point that they consumed significantly fewer mussels than sea stars in the absence of chemical cues from crabs. These results are intriguing, as they suggest that when faced with physical contact by crabs, sea stars reduce their feeding rates in an effort to actively avoid crabs, which can inflict physical damage to sea stars (Appendix A). This type of behavior suggests that sea stars may also recognize crabs as a potential predator and would rather seek refuge away from prey in order to reduce the risk of being attacked, damaged or even consumed by the crabs. Additionally, the only instances of sea stars consuming mussels when in physical contact with crabs during my experiment could have occurred when crabs were already satiated and posed less of a predatory risk to sea stars (Appendix B).

Crabs, on the other hand, displayed very different feeding behaviors than sea stars. Regardless of the type of sea star exposure (chemical or physical), neither had a significant effect on crab consumption of mussels. Although crabs in treatments with two crabs consumed significantly more mussels than both predators together in MPE treatments, further analysis indicated that the number of mussels that crabs consumed when in physical contact with sea stars was no different than that of crabs feeding in the absence of sea stars and their cue. This is unsurprising, as crabs are more mobile and quicker to acquire prey than sea stars and so they may not alter their mussel consumption rates in response to a likely inferior competitor.

Furthermore, crabs consumed more mussels than sea stars in my laboratory feeding experiment, while crabs consumed less than or similar amounts of mussels as sea stars in the field. These differences in mussel consumption between laboratory and field experiments could be due to two reasons. First, mussel consumption by crabs in laboratory feeding trials could be higher due to the absence of alternative prey (Yamada and Boulding 1998) that was otherwise available to crabs in my field experiment. The absence of alternative prey could have caused overall mussel consumption to increase as mussels were the only available source of prey for crabs to consume. Second, by starving both predators for the same amount of time, crabs may have become hungrier than sea stars due to their more rapid metabolism (Padilla-Ramírez et al. 2015). By starving crabs and sea stars for the same amount of time, I could have made crabs hungrier and therefore more aggressive than they normally are in the field, causing them to increase their feeding rates, which could help explain the difference in mussel consumption via crabs between field and laboratory experiments.

Whereas the presence of sea stars did not affect mussel consumption by crabs, warmer temperatures did cause crabs to consume significantly more mussels when feeding alone. Generally, as temperature increases, so too does the metabolism of ectotherms, including crabs (Leffler 1972, Sanchez-Salazar et al. 1987). Additionally, the observed 68% increase in crab feeding rates between 11.5ºC and 16.5ºC is in close agreement with the general physiological rule of thumb that metabolic rate doubles for every 10ºC increase in temperature ($Q_{10} \approx 2$) (Hochachka and Somero 2002). Results suggest that crabs are likely focusing on consuming more mussels to satisfy their metabolic needs than responding to the potential competition from sea stars. This could help explain the interaction between predator treatment type and temperature as the stark differences in mussel consumption rate by crabs between ambient and elevated temperature in the S.Cue and CC treatments far exceeds the change in mussel consumption rates of any other treatment combination. These are the only examples of temperature affecting mussel consumption rates within the entire experiment.

In conclusion, the combination of competitor exposure type and temperature exposure could yield varying levels of predation risk for prey. In my study system, mussels appear to be at greater risk of predation in environments where temperatures are warmer, and crabs are present. This is because the proximity to crabs (but not the direct physical interaction with them) may increase the consumption rates of sea stars, while elevated sea water temperatures may increase the consumption rates of crabs (Leffler 1972, Sanchez-Salazar 1987, Eggleston 1990). However, whether mussels experience greater or reduced predation risk by sea stars may be determined by how sea stars detect crabs within their environment. It is likely that in environments where crabs are dense, we could expect both the chemical and physical detection of crabs by sea stars to be prevalent. Therefore, mussels may experience both risk enhancements and reductions by individual sea stars depending on their proximity to crabs. Conversely, in environments where crab densities are low, I would expect physical contact between both predators to be infrequent, in which case olfaction would likely be the primary mode of crab detection by sea stars resulting in a risk enhancement for mussels. However, with low crab densities it is also likely that the frequency of crab detection by sea stars could also be low as there are less crabs emitting chemical cues, thus resulting in a risk reduction for mussels. A greater understanding of chemical cue structure and residence time is required to determine either effects of low crab densities on sea star mussel consumption. Regardless of the effects of predator exposure type and temperature on either predator separately, when within physical contact with one another the combined effects of both crabs and sea stars appear to be additive.

FINAL CONCLUSIONS

To conclude, I want to revisit the factors likely responsible for driving overall mussel predation in northern California intertidal cobble/boulder fields and describe the level of predation I expect mussels to experience, both currently and in the future, where seawater temperatures have increased due to climate change. Under current conditions, mussel predation is likely being driven by a combination of both crabs and sea stars. In cobble/boulder field sites, where both predators are present, crab predation may additively increase mussel predation above what sea stars already contribute. Further, if crabs are abundant, their chemical presence may increase sea star predation on mussels, leading to risk enhancement, particularly for mussels living on vertical surfaces. However, when crabs are particularly dense, increased physical interactions between crabs and sea stars may reduce sea star feeding rates on mussels, particularly on horizontal surfaces. Therefore, it is likely that mussel mortality on a given shore will depend on a combination of sea star density, crab density, and predator proximity on horizontal and vertical surfaces.

I also predict that the level of predation mussels experience in the future will change. This is because increased sea surface temperatures due to climate change will cause increased crab predation. This increase in crab predation could result in increased overall predation pressure for mussels. Furthermore, climate change will not only increase sea water temperatures, but will also cause sea level rise (Dangendorf et a. 2015, Slangen et al. 2016), potentially making mussels more susceptible to predation by both predators, thereby further increasing the predation risk for mussels and impacting mussel populations. Thus, in northern California where mussels are already recruitment-limited in intertidal cobble/boulder fields compared to other habitats and regions, mussel populations may decrease due to a combination of increased predation, and increased prey accessibility via sea level rise, and climate-induced stress.

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APPENDICES

Appendix A. Evidence of a crab attacking a sea star in an MPE treatment during a pilot laboratory feeding trial.

Appendix B. Evidence of a sea star consuming mussel in an MPE treatment during a laboratory feeding trial.