

Prey productivity effects on the impact of predators of the mussel, *Mytilus californianus* (Conrad)

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Abstract

The relationship of increasing prey productivity, a measure incorporating prey settlement and body growth, to changes in the relative impact of two predator groups, birds and the sea star, *Pisaster ochraceus* (Brandt) on a competitively dominant mussel, *Mytilus californianus* were examined. The purpose of this experiment was twofold, 1) to determine if the separate effects of each predator group on prey abundance increased as prey productivity increased and 2) to determine if the relative impacts of the two predator groups diverged as prey productivity increased. In this experiment, the separate impact of each predator group increased with increasing prey productivity. However, the relative impact of each predator group did not diverge with increasing prey productivity. Unlike previous studies that suggested with increasing prey productivity the relative effect of two predator groups should diverge, this experiment suggested that communities can have more redundant predator groups than originally thought. The results of an analysis using a proportional hazards model suggested that despite increasing prey productivity, birds and the sea star were equal in their ability to curb population increases by *M. californianus*. These results highlight the need to carefully consider what type of species to species comparisons to make when attempting to discern the relative roles of different predator groups in a community.

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1. Introduction

The impact of predators on species composition in a community comprises a central research area in

ecology. Two studies that helped clarify the impact of predators on a community were those by Paine (1966) and Menge and Lubchenco (1981). These studies suggested a single (Paine, 1966) or multiple predator species (Menge and Lubchenco, 1981) could maintain species diversity by preying on competitively dominant prey. Based partly on the results of earlier studies (Lubchenco and Menge, 1978; Menge, 1976; 1978), and their work in Panama Menge and Lubchenco (1981) suggested these different types of pre-

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dation, termed keystone (Paine, 1969) and diffuse (Robles and Robb, 1993) predation, were functions of the physical conditions associated with a geographic location. In temperate regions, they suggested moderate abiotic stresses (e.g. wave stress) resulted in a community where at least one predator, for example *Pisaster ochraceus*, could impact local prey populations. In tropical regions, they suggested relatively benign physical conditions promoted an environment where multiple predator species could persist and ultimately affect species composition in a community.

However in California, Robles and Robb (1993) observed over a spatial scale of 1 km, a diverse algal turf community that was maintained by diffuse and keystone predation on the competitively dominant mussel *Mytilus californianus*. Over the relatively small spatial scale used in their study, diffuse predation occurred where the lowest mussel recruitment and wave exposure was observed, keystone type predation occurred where the highest mussel recruitment and wave exposure was recorded (Robles and Robb, 1993; Robles, 1997). This suggested the impact of different predators on a community were related to wave exposure and local rates of settlement. In particular, the results of Robles and Robb (1993) supported previous studies that postulated a link between settlement and the strength of post-settlement processes in marine communities (Gaines and Roughgarden, 1985; Roughgarden et al., 1985, 1988). These studies proposed that increased settlement could affect predation rates (e.g., Gaines and Roughgarden, 1985), since with an increase in settlement more prey would be available to support a higher biomass of predators (Oksanen et al., 1983; Leibold, 1996). Hence, measurements of settlement variation could potentially be used to predict the intensity of predation in a community.

It has been suggested, that with increases in productivity of a competitively dominant prey, at least one predator should begin to have a disproportionately larger effect on prey survivorship relative to other predators in the same system (Menge et al., 1994). In the *Pisaster–Mytilus* interaction this presumably occurs because *P. ochraceus* has a greater numerical response and increased rate of predation, relative to other predator groups, in response to increases in prey productivity (Menge et al., 1994; Robles et al., 1995; Robles and Desharnais, 2002). Although previous studies have demonstrated that other intertidal predators (e.g. ma-

rine gastropods and arthropods) can also affect prey survivorship (Kitching et al., 1959; Ebling et al., 1964; Fairweather, 1987; Robles and Robb, 1993; Robles and Desharnais, 2002), in the intertidal systems of the U.S. West coast it appears that relative to other invertebrate predators, *P. ochraceus* has a larger effect on prey populations at increased levels of prey productivity (Menge et al., 1994; Robles and Desharnais, 2002).

The other predator group examined in this study, birds, is not normally considered when assessing the impact of different predators on intertidal prey populations (Meese, 1993). As an active endotherm, birds must consume a large number of calories on a daily basis (Cayford and Goss-Custard, 1990; Wootton, 1997). As such, in the face of increased prey productivity, there is the potential for this predator group to increase its foraging rate in accordance with prey productivity to take advantage of a now abundant resource (Cayford and Goss-Custard, 1990; Wootton, 1997). Such an increase in foraging rate may allow birds, relative to *P. ochraceus*, to have an equal effect on survivorship of a competitively dominant prey despite increases in prey productivity (Wootton, 1997).

I describe an experiment in which I examined the impact of two predator groups, *P. ochraceus* and coastal birds, on survivorship of the mussel *M. californianus* across experimental plots where *M. californianus* displayed variation in prey productivity. In this study prey productivity was defined by rates of settlement density and rates of body growth. In addition to settlement rate, body growth provided a second factor by which to determine the relative effect of predators on prey populations since rapidly growing prey can quickly move out of the size stages vulnerable to many predators (Norris and Johnstone, 1998; Bologna and Heck, 1999). The two questions addressed by this study were: can variations in prey productivity be used to predict changes in the separate impact of two predator groups and does the relative impact of those groups diverge as prey productivity increases?

2. Materials and methods

2.1. Study site

This study was conducted at two locations along the west coast of North America, Vandenberg Air

Force Base (hereafter V.A.F.B.), Lompoc, CA, U.S.A. (34°42'N, 120°36'W) and Sandford Island, BC, Canada (48°53'N, 125°20'W). The intertidal zone at V.A.F.B. is comprised of sandstone benches that extend out towards the water from the base of cliffs. *Mytilus californianus* predominates in the mid-intertidal zone at V.A.F.B. The algae *Corrallina californica*, and *Mazzeala splendens*, and the colonial polychaete, *Phragmatapoma californica*, cover the low intertidal zone. The barnacle *Balanus glandula* and the alga *Pelvetia pelvetiopsis* are present in the upper intertidal. Tides at V.A.F.B. are mixed semidiurnal with a maximum amplitude of 2.5 m.

Sandford Island is a large rocky island located within Barkeley Sound on the west coast of Vancouver Island. Typical of most rocky intertidal communities in the Pacific Northwest, *M. californianus* is abundant in the mid-intertidal zone on Sandford. The algae *Corallina vancouveriensis*, *Laminaria setchellii*, and *Halosaccion gladiiforme* cover the low intertidal zone. The barnacle *Semibalanus cariosus* and an overstory of the alga *Fucus distichius* cover the upper intertidal zone. Tides around Sandford are mixed semidiurnal with a maximum amplitude of 3.9 m.

Both *P. ochraceus* and the birds focused on in this study; the glaucous winged gull, *Larus glaucescens* (Nauman), the western gull *Larus occidentalis* (Audubon), the black oystercatcher, *Haematopus bachmani* (Audubon) and the northwestern crow *Corvus caurinus* (Baird) can be found at these sites throughout the year. Peak abundances of each species occur from late May to early October (C. Garza, personal observation). Although both predator groups have been reported to forage on mussels (Feder, 1959; Paine, 1966, 1969; Frank, 1982; Marsh, 1986; Meese, 1993; Robles et al., 1995; Wootton, 1997), the impact of bird predation on mussel populations is not as well documented as that of *P. ochraceus* (Meese, 1993).

2.2. Measurements of prey productivity

In order to characterize average prey productivity at each site-by-shore-level combination, I measured mussel settlement and body growth at the upper and lower ends of the mussel bed at each site. At Sandford and V.A.F.B. each tidal level studied were approximately 1.5 and 2.0 m above mean lower low water

(MLLW). In order to measure settlement density, I bolted 12 settlement plates at each site-by-shore-level combination. Each plate measured 25 × 45 cm and consisted of green Astroturf attached with Z-SPAR™ marine epoxy to gray PVC backing. Astroturf mimics the byssal threads of adult mussels, which are the preferred settlement habitat of juvenile mussels (Bayne, 1964).

Settlement plates were collected monthly for 2 years prior to any experiments at V.A.F.B. At Sandford settlement plates were collected every month from May to September. Owing to the hazards involved in reaching Sandford in winter, collections were only made every 2 months from November to March for the 2 years leading up to my experiments. The settlement plates were taken back to the lab where the number of settlers was counted in three, 5 cm² quadrats that had been etched into each plate. Average settlement density was calculated after counting. I used the identification techniques of Martel et al. (1999) to identify juvenile *M. californianus* that settled onto the plates.

Settlement data were analyzed with an ANOVA model. Settlement rate average across month for each year served as the dependent variable while site, shore level, and sampling year were treated as fixed independent variables. Previous observations at both sites (C. Garza, personal observation; C. Robles, personal communication) suggested that the prey population typically foraged on by predators during their peak period of activity, May–September, derives from settlement pulses that occur from mid-fall to early spring. Hence, settlement data from the October to April sampling were used in the analysis.

On April 15 and June 25, 1999, I began measuring mussel growth by transplanting 10 clumps of mussels, each containing 10 mussels, both to the lower and upper edges of the mussel beds at V.A.F.B. and Sandford. Plastic vexar mesh (mesh size 0.75 cm², Naltex Corp.) was bolted over the top of each clump to keep each clump in place and serve as a barrier to predators. Mussels used in this experiment were no bigger than 5 cm in total length. A small alphanumeric tag was attached to each mussel and a small notch was made in the posterior shell edge prior to transplantation. A distinctive ridge normally forms beyond this notch as the shell grows and allows for easy measurements of shell growth with no noticeable negative

effects on shell growth (Menge et al., 1994). At the end of 6 months changes in shell length were measured and the average change in shell length was calculated from each clump. Mussel growth was analyzed with an ANOVA model. Average change in shell length served as the dependent variable, while site and shore level were treated as fixed independent variables.

2.3. Measurements of predator abundance

In order to characterize predator abundance and activity in relation to variations in prey productivity, I measured *P. ochraceus* abundance and bird foraging effort across each site-by-shore-level combination. I measured *P. ochraceus* abundance along three, 10-m long transects laid parallel to each shore level. This resulted in a total of six transect lines at each site. Across each transect line *P. ochraceus* abundance was measured 10 times within 0.25 m² quadrats at 1 m intervals. I conducted monthly surveys for 2 years leading up to any experimental manipulations at V.A.F.B. At Sandford, observations were made monthly from May to October and every 2 months from November to March. Abundance data were analyzed with an ANOVA model in which *P. ochraceus* abundance averaged across months within each year served as the dependent variable. Site, shore level and sampling year served as fixed independent variables. In this analysis all data came from months May to October, a time frame during which, historically, *P. ochraceus* has been observed to actively forage within the mussel beds (Paine, 1969; Robles et al., 1995; C. Garza, personal observation). During winter months the majority of the *P. ochraceus* population recedes to lower shore levels and remains inactive until early summer (Robles et al., 1995).

Unlike *P. ochraceus*, birds rarely reach the abundances recorded for invertebrate predators in the intertidal. However, a single bird has a high daily caloric requirement and must consume a large number of items on a daily basis (Wootton, 1997). Thus, bird abundance may underestimate their potential impact on a prey population relative to invertebrate predators. To address this potential inequality between predators I measured the amount of time, during a 5 h observation period, that an individual bird allocated to foraging on mussels as opposed to, for example, other prey

items such as barnacles and gastropods. This measurement provided an estimate of how much foraging pressure was placed on mussels within each of the site-by-shore-level combinations during a single low tide.

Foraging activity was recorded at each site and across each shore level with a 10 × 100 Bausch and Lomb™ spotting scope. Bird observations were conducted from May to October of 1998. Previous observations at each site suggested that these months represented peak foraging times for birds in the intertidal (C. Garza, personal observation). Bird data were analyzed with an ANOVA model in which minutes allocated to foraging on mussels by birds averaged across months served as the dependent variable. Site and shore level served as fixed, independent variables in the model.

2.4. Mussel survivorship experiment

During July and August 1999 I conducted an experiment to determine how the separate and the relative effect of each predator on prey survivorship varied across the four site-by-shore-level combinations. On May 15 and July 15, 1999 I transplanted 24 clumps comprised of 51 mussels to the upper and lower ends of the mussel bed at both V.A.F.B. and Sandford. Mussels in each clump ranged from 2 to 9 cm in total length. These lengths represented the range of size classes commonly encountered by predators at each site (C. Garza, personal observation). Each clump was transplanted by placing a sheet of plastic vexar mesh (mesh size 0.5 cm²) over the top and then sealing the edges with six steel bolts and 3 cm diameter washers. After 2 weeks the mesh was removed and one the of six treatments, each replicated four times, was then randomly assigned to each clump. The six treatments consisted of no predators present, birds excluded, *P. ochraceus* excluded, an open control plot, and two cage controls. Two cage controls were required because of different cage designs used to measure the separate effects of birds and *P. ochraceus*. No post-transplant mortality was recorded prior to the assignment of treatments.

The predator exclusion cage consisted of a vinyl covered wire letter basket turned upside down. Holes were drilled into the rock and the cages, each measuring 29 × 34 × 7.5 cm, were then attached to the

substrate using wall anchors, bolts, washers, and heavy gauge copper wire (Wootton, 1997). Vexar mesh, 0.5 cm^2 , was attached along the top and the sides of each cage to keep birds from reaching mussels through large openings present on the top and the sides of the cage. Occasional scrapings of the cages removed fouling organisms and although not measured, potentially helped prevent changes to the hydrodynamic regime inside the cage. The bird exclosures resembled the no predator treatment, except for a $15.0 \times 4.0 \text{ cm}$ opening at one end of the cage that allowed access by *P. ochraceus* but was low enough to the substrate to prevent entrance by birds. Cutting off two ends of the basket and, removing some of the structural wiring, created the control for the no predator and no bird treatment, control 1. This left the basic frame of the basket and openings that allowed access by birds and *P. ochraceus* to the mussels underneath. High tide observations by divers at each site confirmed foraging activity by *P. ochraceus* in the treatments and controls. Low tide observations confirmed foraging activity by birds in treatments and controls.

P. ochraceus was excluded with a different cage design. Four 1.5 cm diameter all-thread rods, 15 cm in length, were screwed into steel wall anchors set into holes that had been drilled in the rock. Four panels of galvanized steel hardware cloth were then attached to the all-thread with plastic cable ties. This created an open top cage with vertical panels that measured $29 \times 34 \times 15 \text{ cm}$. Presumably the open top and large mesh size did not restrict water flow. *P. ochraceus* was excluded from the cage by bending over the top of each panel to create an overhang. The bottom lip of each panel was then sealed with four bolts and 3 cm diameter washers. The control for this cage gave both predators access and consisted of two vertical panels attached to three lengths of all-thread that formed a right angle, control 21. Mussel per capita survivorship was measured every 2 days, July 1–28 at V.A.F.B and August 1–28, 1999 at Sandford.

2.5. Statistical analyses of survivorship data

In this experiment the separate impact of each predator was analyzed with a three-way ANOVA model. In the model the independent variables were treatment, site, and shore level. Per capita survivor-

ship, across the six treatment groups, at the end of the experiment was the dependent variable. Prior to analysis all data were visually inspected and met assumptions of normality via a measure of Kurtosis ($N=96$, $G=1.126$). In this model the variable of interest was the three-way interaction. A significant three-way interaction would suggest, in regards to survivorship, that each of the sites by shore level combinations behaved differently from one another, with respect to predation effects. In the survival model, this would then permit the analysis of relative predator impacts as a function of each of the sites by shore level combinations.

To analyze the relative impact of each predator on mussel survivorship, I used Cox's proportional hazards model (Muenchow, 1986; Pyke and Thompson, 1986; Fox, 1993; Petraitis, 1999). Standard analyses of relative predator impacts on survivorship over time involve the use of repeated measures ANOVA. However, one main assumption of repeated measures ANOVA is that over time, data are normally distributed; often survivorship data are not (Fox, 1993). Proportional hazards models are robust enough to analyze nonparametric data (Lee, 1992). Furthermore, unlike proportional hazards models, standard ANOVAs cannot analyze right-censored data; data from individuals whose actual time of death during a survivorship experiment is unknown. Often ecologists discard right-censored data either thinking they have little to offer or that their analyses are terribly complex (Fox, 1993).

Cox's proportional hazards model can be described as a modified multiple linear regression comprised of independent variables that over time act multiplicatively upon a hazard function. The hazard function $H(t)$ may be defined as:

$$H(t) = \log_e \frac{hi(t)}{ho(t)} \\ = \beta_1(x_1 - x_{1i}) + \dots + \beta_p(x_p - x_{pi})$$

In this equation the hazard function is interpreted as a relative risk. The term $hi(t)$ represents the risk of mortality for an individual with a given set of values x_1, \dots, x_{pi} , while $ho(t)$ represents the risk for an individual who has an average value for every variable. This ratio can be used to compare the relative risk for individuals with different values of the inde-

pendent variables (Lee, 1992). The β 's are the regression coefficients and are calculated using a maximum likelihood method with the Newton–Raphson iteration method (Lee, 1992).

In the model, treatment (reduced to *P. ochraceus* versus birds) and location (i.e. site by shore level combinations) were independent variables. In the model, the treatment variable comparison consisted of an analysis of the relative impact of the bird and *P. ochraceus* predator groups. The location variable comparisons was comprised of four groups, Sandford low, V.A.F.B. low, Sandford high and V.A.F.B. high across which per capita mussel survivorship could be analyzed. The response variable used in this analysis was per capita mussel survivorship as a percent of the initial density in a predator treatment or at a location.

In a proportional hazards analysis, the model assigns one of the groups in each variable as the group whose values approximate the average for the variable. This value, termed the favorable group (Lee, 1992), serves as the denominator in the hazard ratio and represents the group in which the lowest mortality is observed or expected. Thus, the hazard function reflects the force of mortality in the unfavorable groups relative to the favorable group. In the predator treatment comparison the denominator was mussel survivorship in the *P. ochraceus* group, while for location, mussel survivorship at V.A.F.B. high shore level was the denominator. Chi-square (χ^2) tests were then used to test for significant differences between groups within a variable. I also examined the potential interaction between variables to determine whether the hazard function was dependent upon any potential interaction between predator treatment and location.

3. Results

3.1. Measurements of local prey productivity

Mussel settlement and body growth differed over the four site-by-shore-level combinations. Over the course of my surveys the Sandford low received the highest average number of settlers, approximately 16 per 0.5 cm² (Fig. 1). The low shore level at V.A.F.B. received an average of nearly 11 settlers per 0.5 cm² (Fig. 1). Sandford high received an average of 4 settlers per 0.5 cm² (Fig. 1). On average V.A.F.B. high re-

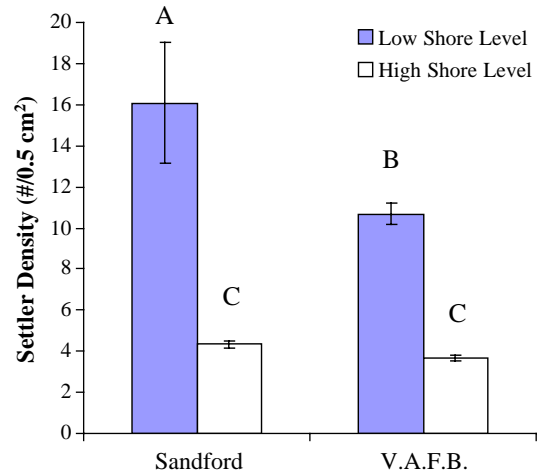


Fig. 1. Average mussel settlement across the four site by shore level combinations. Data was collected between 1997 and 1998. Bars not connected by the same letters represented significant differences by Tukey's HSD. All averages are \pm S.E., $N=132$.

ceived the fewest settlers, 3.67 settlers per 0.5 cm² (Fig. 1). In the ANOVA model there were no significant interactions with the year variable (Table 1). There was a significant interaction (Table 1, Fig. 1) between site and shore level. Tukey's honestly significant difference (HSD) test of the site-by-shore-level interactions suggested a significant difference between means ($\alpha=0.05$, $Q=2.6042$). The post hoc rankings suggested Sandford low received the most settlers followed by V.A.F.B. low (Fig. 1). Sandford and V.A.F.B. high received equal numbers of settlers (Fig. 1).

Average mussel growth was highest at Sandford low, intermediate at V.A.F.B. low and least at both of the high shore levels (Fig. 2). On average, mussels at Sandford low showed the greatest average shell growth, increasing in length by an average of 4.8 mm. There was a significant interaction between site and shore level (Table 2, Fig. 2). Tukey's HSD suggested a significant difference between interaction means ($\alpha=0.05$, $Q=2.3053$). Mussels at Sandford low showed more growth than V.A.F.B. low (Fig. 2). Mussels at Sandford and V.A.F.B. high demonstrated equal growth rates (Fig. 2); however, both were significantly less than Sandford and V.A.F.B. low (Fig. 2). Post hoc analyses of the settlement and growth data (Figs. 1 and 2) suggested the ranking of prey productivity in the site by shore level combina-

Table 1

ANOVA of mussel settlement by site, shore level and sampling year

Source of variation	df	MS	F	P
Site	1	1276.060	7.583	0.007
Shore level	1	2112.500	12.554	0.001
Year	1	178.395	1.060	0.305
Site*Shore level	1	1292.955	7.684	0.006
Site*Year	1	11.945	0.665	0.416
Shore level*Year	1	222.058	1.320	0.253
Site*Shore level*Year	1	211.265	1.256	0.265
Error	124	168.270		

tions was Sandford low>V.A.F.B. low>Sandford high=V.A.F.B. high.

3.2. Measurements of local predator abundance/activity

Average predator abundance and activity increased, qualitatively, in a similar fashion as prey productivity. An ANOVA of sea star density demonstrated a significant three-way interaction between shore level, site and year (Table 3). However, this was due to similar numeric changes in sea star abundance at Sandford high and V.A.F.B. low between years 1 and 2 of my surveys as wells as an

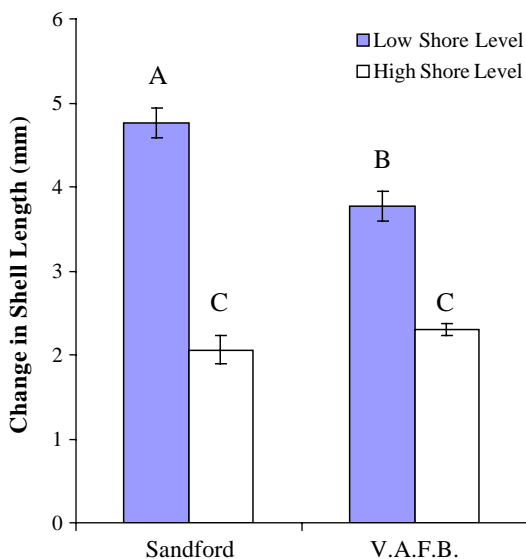


Fig. 2. Average mussel growth, measured as an increase in shell length, across the four site by shore level combinations. Bars not connected by the same letters represent significant differences by Tukey's HSD. All averages are \pm S.E., $N=400$.

Table 2

Two-way ANOVA of mussel growth by site and shore level

Source of variation	df	MS	F	P
Site	1	0.5720	0.109	0.7415
Shore level	1	429.0059	81.742	<0.0001
Site*Shore level	1	66.7066	12.711	0.0004
Error	292	5.248		

increase in sea star density at Sandford low between years 1 and 2 (Fig. 4). Over the course of my surveys the highest average density for *P. ochraceus* was recorded at Sandford low in year 2 (6.2 sea stars per 0.25 m² Fig. 3). The next highest average density of sea stars was observed at V.A.F.B. low in year 1 (0.97 sea stars per 0.25 m², Fig. 3) and Sandford high, (0.7 sea stars per 0.25 m²) in years 1 and 2 (Fig. 3). Tukey's HSD suggested a significant difference ($\alpha=0.05$, $Q=3.0401$) among the interaction means with the following ranking of sites with respect to sea star density: Sandford low>V.A.F.B. low=Sandford high>V.A.F.B. high (Fig. 3).

The average amount of time birds concentrated their foraging efforts on mussels increased in the same direction as prey productivity across the four site-by-shore-level combinations. (Fig. 4). Birds at Sandford low allocated more of there time to foraging on mussels at 7.5 min per bird (Fig. 4). The second highest average number minutes allocated to foraging on mussels by birds was observed at V.A.F.B. low 3.8 min per mussel (Fig. 4). Birds at Sandford and V.A.F.B. high displayed a near equivalent average number of minutes foraging on mussels, 2.7 and 2.8 min, respectively (Fig. 4). Increased numbers of gastropods and barnacles offered a more abundant resource at higher shore levels than mussels, which become patchy in their distribution (Robles and

Table 3

ANOVA of sea star density by site, shore level and sampling year

Source of variation	df	MS	F	P
Site	1	943.180	218.629	0.000
Shore level	1	1071.731	248.427	0.000
Year	1	140.781	32.633	0.000
Site*Shore level	1	743.523	172.348	0.000
Site*Year	1	129.902	30.115	0.000
Shore level*Year	1	204.419	47.384	0.000
Site*Shore level*Year	1	92.173	21.366	0.000
Error	858	4.314		

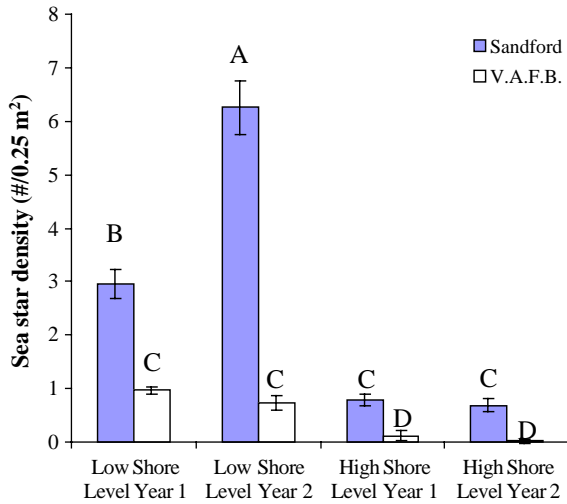


Fig. 3. Average number of sea stars across the site by shore-level by year combinations. Bars not connected by the same letters represent significant differences by Tukey's HSD. All averages are \pm S.E., $N=866$.

Desharnais, 2002), hence more time was allocated to foraging on these readily available prey items at higher shore levels (C.Garza personal observation). There was a significant interaction between site and

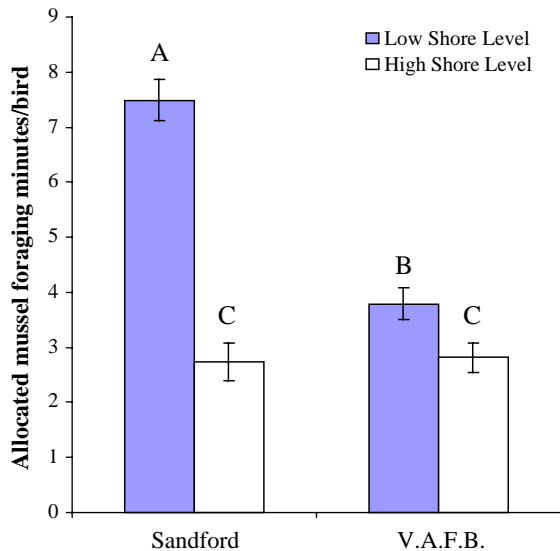


Fig. 4. Average number of minutes spent by birds foraging on mussels at each site by shore level combination between May and October of 1998. Bars not connected by the same letters represent significant differences by Tukey's HSD. All averages are \pm S.E., $N=183$.

Table 4

Two-way ANOVA of minutes allocated to foraging on mussels by birds

Source of variation	df	MS	F	P
Site	1	60.169	10.802	0.001
Shore level	1	161.108	28.922	0.000
Site*Shore level	1	78.051	14.012	0.000
Error	179	5.570		

shore level (Table 4). Tukey's HSD demonstrated a significant difference among the interaction means ($\alpha=0.05$, $Q=2.5933$) and suggested the following ranking of sites according to the amount of time devoted by birds to foraging on mussels: Sandford low > V.A.F.B. low > Sandford high = V.A.F.B. high (Fig. 4).

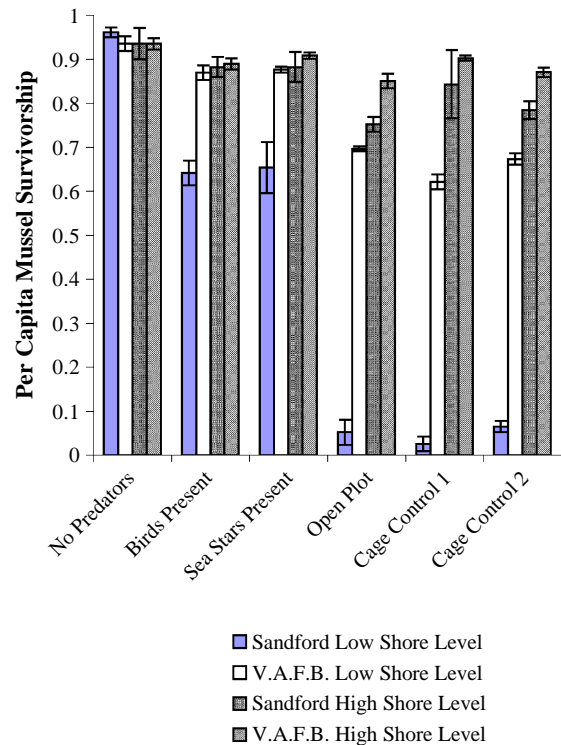


Fig. 5. Mussel survivorship by treatment, $N=96$, across the four site by shore level combinations. Values represent the average proportion of mussels \pm S.E. surviving to the end of the 30-day experiment. Bars are arranged in decreasing value of prey productivity (prey settlement and growth), at each of the site by shore level combinations. Cage control 1=control for bird exclusion. Cage control 2=control for sea star exclusion.

Table 5

ANOVA of mussel survivorship by site, shore level and predator treatment

Source of variation	df	MS	F	P
Site	1	1.034	620.346	0.000
Shore level	1	1.907	1144.471	0.000
Treatment	5	0.379	227.260	0.000
Site*Shore level	1	0.673	404.087	0.000
Site*Treatment	5	0.099	59.260	0.000
Shore level*Treatment	5	0.202	121.488	0.000
Site*Shore level*Treatment	5	0.054	32.542	0.000
Error	72	0.002		

3.3. Survivorship experiment

The separate effect of each predator on average mussel survivorship increased as prey productivity increased (Fig. 5). A three way interaction between site, shore level and treatment (Table 5) suggested the separate effects of each predator group differed by each of the site by shore level combinations with respect to predator treatment. The largest observed effect of each predator group on average mussel survivorship was at Sandford low (0.66 and 0.67 survivorship in the bird and *Pisaster* groups, respectively). Within the remaining three experimental plots average mussel survivorship within each of the predator treatment groups measured between 0.95 and 0.99 (Fig. 5). There were no cage effects evident in the experiment (Fig. 5).

Because the ANOVA model suggested there were significant differences among the predator treatments and the controls (Table 5, Fig. 5) the only treatment effects analyzed in the hazard model were between *P. ochraceus* and the bird group. The objective of the model application was to ascertain, via an index and

Table 7

Effect likelihood ratio test of the main effects, predator treatment and location, in the Cox's proportional hazards model

Source of variation	df	χ^2	P
Predator treatment	1	0.071	0.7909
Location	3	101.802	0.0000
Predator treatment*Location	3	1.905	0.5922

Statistics are represented as χ^2 analysis, in which the two levels of the treatment, bird versus *P. ochraceus*, on mussel survivorship are tested. The location factor incorporates survivorship across the four sites by shore level combinations.

after confirming differences among the treatment groups, the magnitude with which the relative impact of the two predator groups could vary with changes in prey productivity. Another comparison to the controls would only serve as a secondary confirmation that there were differences between the control and predator treatment groups. Thus, in the model, the primary effects examined, via the predator treatment and location variable, were the relative impacts of the *P. ochraceus* and the bird groups and the relative impact of the four site by shore level combinations on mussel survivorship.

The calculated hazard function suggested that over the course of the experiment, that an individual's risk of survival in either of the predator treatment groups was equal (Table 6). A non-significant χ^2 analysis of the two predator groups within the treatment variable (Table 7) suggested the mortality imposed by either predator was equal in this experiment. However, in looking at the risk of mortality to mussels as a function of location, at Sandford low relative to V.A.F.B. high, mussels were 2.76 times more likely to be preyed upon at Sandford low (Table 6). Relative to V.A.F.B. high mussels at V.A.F.B. low were 2.23

Table 6

Relative mussel survivorship as calculated by Cox's proportional hazards model

Relative risk comparison	β	S.E.	Risk ratio
Birds/ <i>Pisaster</i>	−0.021	0.081	0.979
Sandford low/Vandenberg high	1.014	0.104	2.757
Vandenberg low/Vandenberg high	0.803	0.176	2.234
Sandford high/Vandenberg high	0.044	0.131	1.045
Bird/ <i>Pisaster</i> * Sandford low/Vandenberg high	0.044	0.103	1.045
Bird/ <i>Pisaster</i> * Vandenberg low/Vandenberg high	−0.234	0.176	1.022
Bird/ <i>Pisaster</i> * Sandford high/Vandenberg high	0.115	0.131	0.991

Risk ratios exceeding one suggest a relatively stronger effect on survivorship due to the numerator (e.g. birds). Risk ratios <1 suggest a relatively stronger effect on survivorship due to the denominator (e.g. *P. ochraceus*). β represents the regression coefficient for the proportional hazards model.

times more likely to suffer predator-induced mortality (Table 6). Finally the risk of mortality at Sandford high to V.A.F.B. high was equivalent as evidenced by the calculated risk ratio of 1.04 (Table 6). A χ^2 analysis revealed a significant difference in the risk of mortality between locations (Table 7).

A further review (Table 6) of the risk ratio values of near one for each interaction suggested that mussel mortality was not weighted towards the effect of the predator treatments at any of the site by shore level combinations. This was confirmed by a non-significant χ^2 value term for the overall interaction term, which further suggested that prey survivorship was more dependent upon location rather than the predator treatment variable (Table 7). In summary, across the site by shore level combinations, the separate effects of each predator increased with increasing prey productivity but their relative effects on prey survivorship remained the same (Fig. 5).

4. Discussion

Across sites that demonstrate increasing prey productivity, Menge et al. (1994) suggested that the relative effects of two or more predators on prey populations should diverge, with one predator having a relatively larger impact on prey survivorship. This assertion is based in part on a study in which they compared the relative effects of the whelk, *Nucella emarginata*, and *P. ochraceus* on mussel survivorship in Oregon (Menge et al., 1994). They concluded, that as prey productivity increased, *P. ochraceus* had a relatively larger impact because it was better able to maintain predation pressure due to its shorter handling times, particularly in regards to larger mussels, and its ability to remove more than one prey item at a time (Menge et al., 1994). This observation complemented previous theoretical predictions and experimental evidence that suggested predation intensity should increase as prey productivity increases (Hagen and Mann, 1992; Menge, 1992; Navarrete and Menge, 1996; Abrams and Roth, 1997; Robles, 1997; Hochberg and van Baalen, 1998; Bologna and Heck, 1999).

In this study, the separate impact of each predator in this study increased with increasing prey productivity (Fig. 5). This probably occurred as a result of numerical increases by *P. ochraceus* (Fig. 3) and

increased foraging rates on mussels by birds (Fig. 4). What is of some surprise, given previous observations with *P. ochraceus* (Menge et al., 1994), is that relative to the other predator group, birds, and with increasing prey productivity that its effect on prey survivorship did not become disproportionately larger (Table 6). These results also suggest a synergistic effect of the two predators on per capita survivorship, particularly at Sandford low (Fig. 5). A previous experiment (Garza, 2001) suggests this occurs because each predator forages on specific size ranges within each of the clumps. On average birds consumed the largest mussels (60–90 mm) from each transplant clump while sea stars foraged on medium (35–50 mm) mussels within each. Within each of these size ranges, predators consumed equal numbers (Garza, 2001). Once mussels within each predators preferred size range were depleted, they ceased foraging within the clump. Because numbers of mussels within medium and larger size ranges were equal, the effect on per capita survivorship was equal between the two predator treatments and non-additive on total per capita survivorship (Garza, 2001). In open plots once these larger mussels were consumed, smaller mussels (10–25 mm) may have lost a protective canopy from predators (Robles and Desharnais, 2002) such as the whelk, *N. emarginata*, that were not considered in the caging experiments. Thus a larger than expected effect on total survivorship was observed in this experiment, particularly at Sandford low (Fig. 5).

The different results obtained by these experiments were most likely due to differences in the organisms used in each study. This study differs from some previous efforts in that both predator groups, birds and *P. ochraceus*, could effectively deal with highly productive prey. Though relative to *P. ochraceus*, bird abundance can at times appear exceedingly low, their high consumption rates and short handling times can allow birds to have an impact on mussel abundance despite increases in prey productivity. Thus, in this experiment, the predators were essentially equal in their ability to effectively forage with increasing prey productivity.

Additionally, unlike *P. ochraceus*, birds employ foraging methods that may, on average, allow them to forage on mussels that fall above the maximum size typically accessible to *P. ochraceus*. These methods include breaking open mussel shells (oystercatcher

and crows), swallowing whole mussels and breaking down the shell in the gizzard (gulls) to slicing the adductor muscles and then removing the mussel from its shell (oystercatchers). In contrast, physical constraints often prevent *P. ochraceus* from foraging on mussels larger than 6 cm in length (Paine, 1976; McClintock and Robnett, 1986). Previous studies have also suggested that birds may concentrate their foraging efforts on large prey (Cayford and Goss-Custard, 1990; Norris and Johnstone, 1998; Hilgerloh and Siemoneit, 1999). Since birds must maintain the high metabolic rate of an active endotherm, a large prey item should be more energetically profitable (Norris and Johnstone, 1998).

The result of this experiment highlights the need to carefully consider what type of species comparisons to make when estimating the relative impact of different predator groups on a prey population. Had I made a different comparison (e.g. *P. ochraceus* to *N. emarginata*), it is conceivable I may have incorrectly concluded *P. ochraceus* had the largest impact on the competitive dominant in this community when in fact, over the same period, birds could have had a similar impact. Over the time scales and localities investigated in this study, it would appear that despite increasing prey productivity, birds and *P. ochraceus* are equal in their ability to prevent spatial dominance by mussels in the rocky intertidal. Although differences exist between this study and others (Fairweather, 1987; Hagen and Mann, 1992; Menge, 1992; Abrams and Roth, 1997; Robles, 1997; Navarrete and Menge, 1996; Hochberg and van Baalen, 1998; Bologna and Heck, 1999), one aspect is similar: that increased prey productivity, whether through heightened settlement and recruitment or growth or both elicited a higher total magnitude of predation at a local scale.

Determining the relative role of multiple predator species poses an important challenge to ecologists. The concept of a keystone predator that plays an important ecological role has entered into the strategies of wildlife managers who wish to allocate resources towards protecting specific species (Mills et al., 1993; Navarrete and Menge, 1996). However, as evidenced by this current study, one may arrive at conflicting results regarding the relative impact of a specific predator depending upon what other groups of predators it is compared to. Although challenging, what will be needed to further disentangle the relative

effects of predators in marine communities, are studies that examine the simultaneous effects of multiple predator guilds such as those conducted by Menge and Lubchenco (1981) and Robles and Robb (1993).

Concordantly an attempt must also be made to identify other local physical and biological factors, such as wave action, temperature and prey density that can also affect the separate and relative impact of different predator groups on a community. Although not specifically tested here, these factors, in addition to variation in prey productivity, can have additional effects on the relative impacts of different predator groups in marine communities that are not easily discerned in this study (Sanford, 1999; Robles and Desharnais, 2002). Only when studies that can incorporate these factors simultaneously are attempted, will ecologists be able to identify, more completely, the suite of processes that regulate the relative impact of different predator species on the structure of ecological communities.

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