

## Patterns of Interactions among Neighbor Species in a High Intertidal Algal Community

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Three dominant rocky intertidal macroalgae, the fucoids *Fucus gardneri* and *Pelvetiopsis limitata* (Phaeophyta) and the red alga *Mazzaella cornucopiae* (= *Iridaea cornucopiae*) on the west coast of Vancouver Island, British Columbia, Canada were used in a series of field experiments to examine interspecific interactions. These experiments showed complex patterns which included an interchange of negative (inhibition) and positive (facilitation) interactions depending on neighbor distance. Less fucoid recruitment occurred in the plots with greater percent cover of a turf-forming red alga, *M. cornucopiae*. However, experimentally removing *Mazzaella* turf (the turf was considered to be "blocking" fucoid recruits or "shading" growing recruits) did not increase recruitment. This result indicated that there may be another factor(s) involved in the survivorship of juvenile fucoids in the turf-removed plots. Morphological differences in adult plants between *Mazzaella* and the two fucoids resulted in another type of interaction; these began when fucoids successfully settled and grew nearby or within the red algal turf. By monitoring microhabitat at the individual plant level for two years, I found that survivorship of fucoid recruits showed different species-specific patterns. The patterns also varied as the microhabitat changed from *Mazzaella* turf edge to open space. For *F. gardneri*, longevity respectively goes from low to high to intermediate with increasing distance from the turf edge. In contrast, longevity of *P. limitata* at all distances tested was similar. A reason for greater longevity of *F. gardneri* individuals at edge microhabitats may be that these sites have one side open to light and nutrients and another site that buffers them from desiccation and wave impact. In the *Mazzaella-Fucus* interaction, neighbor distance was a key factor in determining whether the outcome of the interaction would be competition or facilitation (or protection). This study provides experimental evidence that detectable biological interactions occur in this upper intertidal algal community where physical conditions are usually severe, and also indicates the importance of small scale examination in understanding macroalgal interactions in intertidal habitats.

**Key Words:** competition, facilitation, fucoid, intertidal, macroalgae, microhabitat, neighbor distance, turf algae

### INTRODUCTION

Species interactions are fundamental in producing community structure and dynamics. Marine ecologists exploring direct and indirect interactions between marine benthic organisms have reported many such interactions. The usefulness of experimentally testing hypotheses with regard to the roles of species interactions in determining the distribution and abundance of marine organisms has been reviewed (Connell 1974, 1983; Paine 1977, 1990; Schoener 1983; Denley and Dayton 1985; Olson and Lubchenco 1990). Despite criticism of the nature and design of some of the experiments (Dayton and Oliver 1980; Underwood and Denley 1984),

such studies have been considered effective for the development of realistic models of the structure and dynamics of natural communities (Connell 1974, 1983; Dayton and Oliver 1980; Denley and Dayton 1985).

Typically ecologists have focused on negative interactions (e.g., competition) while positive interactions (e.g., facilitation or protection) have received less attention and are ignored in some current models of community organization (Connell and Slatyer 1977; Menge and Sutherland 1987; Tilman 1994; but see Bertness and Callaway 1994). This trend is not unique to marine benthic algal ecology. Thus, current reviews on competition of marine benthic macroalgae indicate the necessity of more experimental data on (1) the variability of mechanisms of competition with changing life-history stages of competitors, (2) variable environmental conditions, and (3) positive interactions, to improve our understanding

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of the role of species interactions in structuring algal assemblages (Paine 1990; Olson and Lubchenco 1990).

The outcome of competitive interactions may depend on such plant traits as morphological type and life history stage, and also on the mechanism of competition (Olson and Lubchenco 1990). For example, if the interaction is preemption of space, then larger size, spreading habit, and the ability to perennate may afford competitive dominance. If interference is involved, rapid lateral growth, ability to raise the growing edge off the substratum and production of toxins are traits that may affect the outcome of an interaction (Olson and Lubchenco 1990). However, the above relationship between traits and competitive dominance may not be straightforward, and sometimes the outcome of competition may be strongly affected by other biological interactions (e.g., herbivory) or physical effects (Connell 1975; Lubchenco and Gaines 1981; Hawkins and Hartnoll 1983; Paine 1990).

Although positive interactions have been investigated less frequently than competition in marine benthic organisms their possibility and relevance have been discussed theoretically by many ecologists (Connell and Slatyer 1977; Vandermeer 1980; Connell 1983; Dethier and Duggins 1984; Sousa 1984; Bertness and Callaway 1994). Some positive interactions occur as a consequence of direct beneficial influences of one species on another (e.g., Dayton 1975; Brawley and Johnson 1993); others as a consequence of negative interactions acting indirectly through other species (indirect commensalism) from the same trophic level (e.g., Duggins 1981; Kastendiek 1982) or from a different trophic level (e.g., Dethier and Duggins 1984; Hay 1986). Particularly in a physically stressful habitat (e.g., upper intertidal zones), positive interactions (e.g., neighbor habitat-amelioration; Bertness and Callaway 1994) rather than competition may be an important factor for the coexistence of various species in a community.

There is no study which examines the variation of positive interactions along microhabitat gradients (e.g., neighbor distance in the case of neighbor habitat-amelioration) in marine intertidal zones. The concept of neighbor distance has been most studied in terrestrial plant communities (Fawcett 1964; Mack and Harper 1977; Turkington and Harper 1979; Lindquist *et al.* 1994). In marine habitats the importance of biological interactions in small patches has been invoked in a few studies (Connell 1972; Paine 1990). Connell (1983) stated that for organisms that compete for space, and in particular clon-

al plants and attached colonial animals, competition occurs mainly between neighbors. In the context of these experiments, neighbor distance was measured as a parameter to test if the outcome of algal interactions was affected by the distance between two interacting species.

This study investigates how algal interaction patterns change due to the developmental stages of the competitors and the neighbor distance between morphologically distinct species. Both manipulative and non-manipulative field experiments were designed to address the two questions or hypotheses. First, does the turf-forming red alga, *Mazzaella cornucopiae*, affect the recruitment of the fucoids? Second, does *M. cornucopiae* affect the post-recruitment survivorship of the fucoids? The concept of neighbor distance was applied to evaluate the outcome of interaction among benthic macroalgae.

## MATERIALS AND METHODS

### The study site and organisms

The study areas are located in the rocky intertidal zones at Prasiola Point and Nudibranch Point in Barkley Sound, near Bamfield Marine Station, on the west coast of Vancouver Island, British Columbia, Canada (48°49' N, 125°10' W). The two sites are about 0.4 km apart and both are exposed to intermediate waves from the northwest and stronger waves from the west; both sites have a similar flora and fauna (see below). All experiments were conducted in the upper zones between 3.4 m and 4.2 m above Lowest Normal Tide (LNT: Canadian Chart Datum).

The algal community is dominated by three perennial macroalgae, *Mazzaella cornucopiae* (Post. & Rupr.) Hommersand (= *Iridaea cornucopiae*, Gigartinales, Rhodophyta), *Pelvetiopsis limitata* Gard. and *Fucus gardneri* L. (both Fucales, Phaeophyta). The thallus of *M. cornucopiae* is 2-3.5 cm in length and grows as a dense turf on the rock substratum. The two morphologically similar fucoids are erect and usually 4-7 cm in length at maturity in the study sites. However, the thallus of *F. gardneri* is wider than that of *P. limitata* (e.g., width of the base of top dichotomy for non-reproductive plants with 5-6 cm in thallus length: 6.13±1.11 (S.D.) mm for *F. gardneri* and 2.49±0.70 (S.D.) mm for *P. limitata*). *Fucus* has 'wings' on the both sides of its midrib whereas *Pelvetiopsis* has a more terete thallus without both 'wings' and midrib. *Mazzaella cornucopiae* appears to propagate vegetatively although carposporangial and tetrasporangial blades are found seasonally. Vegetative

ingrowth from existing turfs is common (Olson 1985, R. Scrosati unpublished data, J.H. Kim personal observation). The two fucoids generate recruits by zygotes (see Chapman 1995 for references) even though fucoids have a potential to regenerate vegetatively from wounded thalli (McCook and Chapman 1992).

These macroalgae comprise the uppermost algal zone apart from some ephemeral algae, such as *Porphyra* spp. and benthic diatoms, that appear further up the shore in the spring. The three macroalgae occur in well-mixed or in mono-specific stands depending on wave-exposure. Other stands of *Mazzaella cornucopiae* occur in extremely wave-exposed sites where the alga *Lessoniopsis littoralis* (Tilden) Reinke and the invertebrate *Pollicipes polymerus* Sowerby characteristically occur. Fucoid stands, on the other hand, are found in relatively more wave sheltered sites. Nonetheless, sites for all experimental plots and sampling were done in areas where mixed stands of the three macroalgae predominated. Due to the morphological similarity of the two fucoids, experiments largely focused on the interactions between *M. cornucopiae* and the two fucoids. Additional species in the community are described elsewhere (Kim and DeWreede 1996a).

Barnacles are abundant in the community. The dominant species is *Balanus glandula* Darwin, whereas *B. cariosus* Pallas and *Chthamalus dalli* Pilsbury occur less frequently. The abundant herbivores in the community are limpets, primarily *Lottia digitalis* Rathke and a few *L. pelta* Rathke, and snails, primarily *Littorina* sp. (Boulding et al. 1993). Mussels, primarily *Mytilus edulis* L., occur infrequently.

#### Experiment 1: The relationship between *Mazzaella* cover and fucoid recruitment

In August of 1991 sixteen permanent plots (20 x 20 cm) were randomly established at Prasiola Point. Concrete nails were used to mark at least 3 corners of each plot. These permanent plots were monitored at two-month intervals using a 20 x 20 cm quadrat divided into 400 squares (each 1 cm<sup>2</sup>) by monofilament line. Percent cover and exact location of *Mazzaella cornucopiae* turf was determined by mapping the squares that had > 50% cover of blades; in this way the squares with < 50% were dropped so the estimation is balanced for overestimation. The position of the fucoids was also mapped using this technique, and size class and reproductive condition were also noted. At each sampling date it was possible to recognize newly recruited individual fucoids and thus this method enabled us to follow individual fucoid thalli

from birth to death. The sixteen plots initially, and continuously, received four treatments (*Mazzaella*-removed, *Fucus*-removed, *Pelvetiopsis*-removed, and the control). Because there were no significant treatment effects between the control and either *Fucus*-removed or *Pelvetiopsis*-removed plots (Kim 1995), *Fucus* recruits used for analysis were collected from the control and *Pelvetiopsis*-removed plots, and *Pelvetiopsis* recruits were from the control and *Fucus*-removed plots. Monitoring was done until October of 1993.

Statistical analyses were done using SYSTAT, version 5.2.1 for Macintosh, (Wilkinson et al. 1992). The Pearson Product Moment Correlation between the number of recruits (log-transformed) and percent cover of *Mazzaella* was calculated for both fucoids. The significance of the correlation coefficients was assessed using Fisher and Yates' tables (1963).

#### Experiment 2: Effects of pruning *Mazzaella* turf on fucoid recruitment

Correlations found in Experiment 1 do not necessarily indicate a cause and effect relationship, so we conducted a manipulative field experiment to test the hypothesis that removing *Mazzaella* turf enhances recruitment of *Fucus* and *Pelvetiopsis*. The experimental units consisted of two levels of *Mazzaella* pruning; (1) "total pruning" - cutting whole *Mazzaella* blades, leaving only their hold-fasts, (2) "partial pruning" - cutting the upper part of the blades and leaving 1 cm of the bottom, and (3) "control" - no pruning. The different levels of *Mazzaella* pruning were done to test if the dense turf physically blocked fucoid propagule arrival. The different heights of *Mazzaella* blades were used to simulate different levels of 'blocking' recruits and 'shading' growing recruits. At Prasiola Point, 8 permanent transect lines (about 1 m each) were marked by placing concrete nails at both ends of each line. Using 10 cm intervals on the transect line, I numbered all potential plots for treatments on both sides of the transect line. Treatments were assigned by randomly choosing three plots (10 x 10 cm) per line. The position of individual fucoid plants was mapped using a 10 x 10 cm quadrat with subdividing lines (comprising 100 1 x 1 cm subplots); this enabled me to obtain both the number of fucoid recruits and percent cover of *M. cornucopiae* in each plot on every sampling date. The experiment was initiated in June, 1993. Data were collected in October, 1993, and February and April, 1994.

I found a correlation between *Mazzaella* percent cover and fucoid recruitment (Fig. 1), so I first examined the

relationship between the pruning treatment and *Mazzaella* cover as independent variables. The first step in this analysis was a test for homogeneity of slopes, which can be determined by examining the interaction term of a regression, using the pruning treatment and percent cover as independent variables and the parameter values as dependent variables. In all 6 cases (3 sampling dates and 2 species), the probability value for the interaction term was not significant ( $p > 0.05$ ), so we then conducted ANCOVA's with the pruning treatment as an independent variable and *Mazzaella* cover as a covariate. Analyses were done using the BMDP2V statistical package.

### Experiment 3: Effects of *Mazzaella* turf on post-recruitment survivorship of fucoids

While Experiment 1 was designed to test the effect of *Mazzaella cornucopiae* on the recruitment stage of both fucoids, this experiment tests its effects on post-recruitment survivorship of the fucoids. Non-manipulative field monitoring for the sixteen permanent plots (the same plots used in Experiment 1) at Prasiola Point was done from August, 1991 to October, 1993. Using the quadrat with subdividing lines described previously, the co-ordinates of *M. cornucopiae* turf and individual fucoid plants in each plot were tape-recorded in the field and then mapped on a sheet. The life span of individual fucoids was obtained by following individual thalli from recruitment to disappearance. Individuals recruited or found after August, 1992, were not included in the analysis because their complete life span could not be followed. Using the map, the distance between each fucoid thallus and the nearest *M. cornucopiae* was measured. However, because the edge of the *Mazzaella* turf changed over time due to vegetative growth or decline, the distance from each fucoid to the turf was not always the same in bimonthly samples. For this reason, I calculated the mean distance for each fucoid over its life span from distance values measured bimonthly and used these values for analysis. The life span and the mean distance for each fucoid were plotted to investigate their relationship.

For data analyses I divided the distance between the *Mazzaella* turf and the fucoid recruits into three groups based on the pattern of *Fucus* life span along with the neighbor distance (Fig. 2). The three distance groups include 'CONTACT' for those growing within the turf (or 0 cm from turf), 'CLOSE' for those growing between 0.3 and 0.7 cm from the turf, and 'FAR' for those grow-

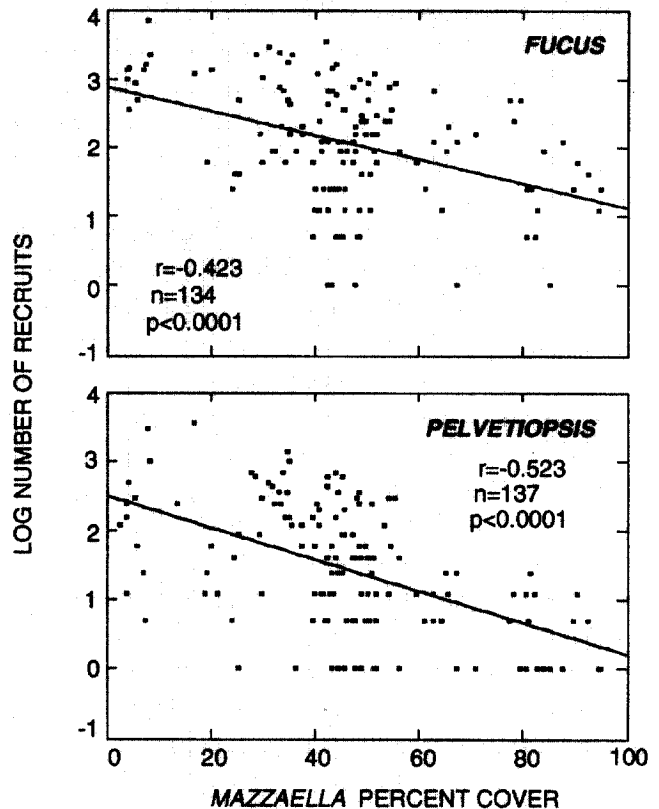


Fig. 1. Correlations of *Mazzaella cornucopiae* percent cover and number of fucoid recruits.

ing  $> 2$  cm from the turf. To avoid violation of the ANOVA assumption, homogeneity of variance was checked by Cochran's C test and Fmax test (Winer 1971), and all longevity data were log-transformed prior to analysis. One-way ANOVA was used to test the difference among the distance groups for each fucoid species. Tukey's HSD test was also used when ANOVAs were significant. Student's t-test was used to compare the life span (months) of *Fucus gardneri* and *Pelvetiopsis limitata* in the same distance group. SYSTAT (Wilkinson et al. 1992) was used for all data analyses.

## RESULTS

### The relationship between *Mazzaella* cover and fucoid recruitment

Lower recruitment of *Fucus gardneri* occurred in the plots where greater *Mazzaella cornucopiae* cover existed (Pearson Product-Moment Correlation,  $r = -0.423$ ) (Fig. 1). *Pelvetiopsis limitata* showed the same relationship to *Mazzaella* cover ( $r = -0.523$ ) (Fig. 1). Both correlations were significant (*Fucus*,  $F(1,132) = 28.73$ ,  $p < 0.0001$ ; *Pelvetiopsis*,  $F(1,135) = 50.84$ ,  $p < 0.0001$ ).

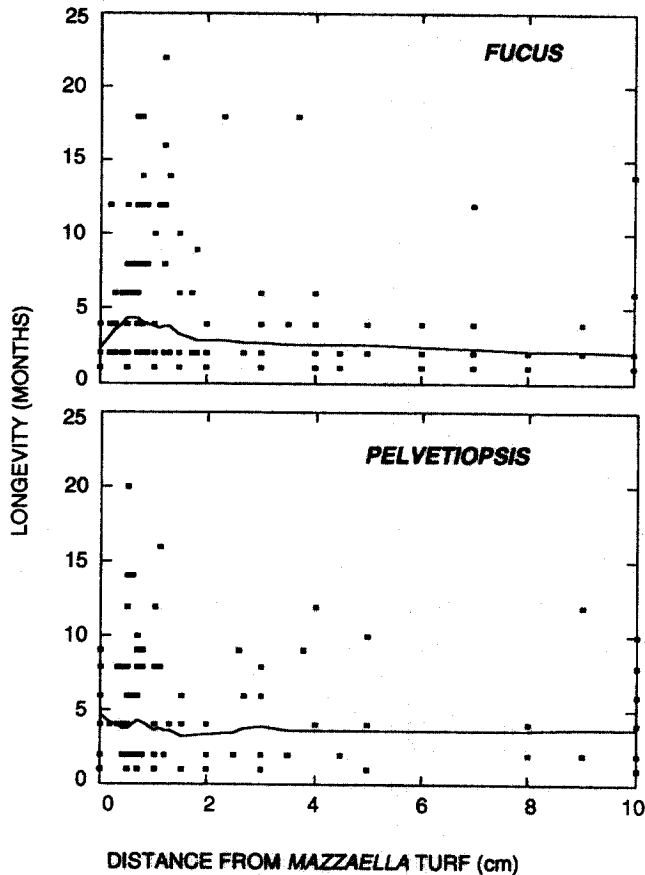


Fig. 2. The effect of *Mazzaella cornucopiae* turf on fucoids after recruitment stage. Curves are the weighted average of plots.

#### Effects of pruning *Mazzaella* turf on fucoid recruitment

Pruning *Mazzaella* blades resulted in a significant reduction of percent cover of this alga in most plots, particularly in the 'total pruning' plots. The difference in percent cover between the total pruning plots and the partial pruning or control plots was about 24% at the first sampling date. This difference became minor at the later sampling dates as *Mazzaella* blades regrew (Fig. 3). This indicated that the pruning treatment was only effective at the early sampling date, October 1993, which was four months after initiation.

The results of ANCOVA, with *Mazzaella*-pruning treatment as an independent variable and *Mazzaella* percent cover as a covariate, showed that the pruning-treatment term was not significant for any sampling date, while the *Mazzaella* percent cover term was significant ( $p < 0.05$ ) in every case (Table 1). In other words, the number of fucoid recruits adjusted by the effect of *Mazzaella*

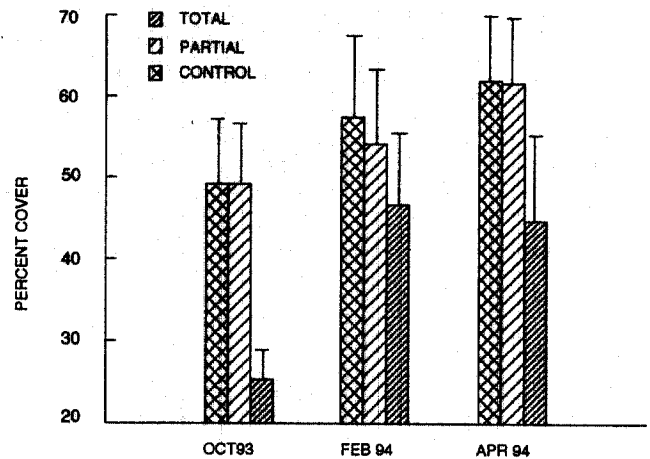


Fig. 3. The effect of pruning *Mazzaella cornucopiae* blade on *M. cornucopiae* percent cover in the same experimental plots (10 x 10 cm).

cover (Fig. 4; B) was not significantly ( $p > 0.05$ ) changed by the pruning treatments at any sampling date. Therefore, removing *Mazzaella* turf canopy which was considered responsible for 'blocking' or 'shading' recruits (from the results of Experiment 1) did not significantly increase the fucoid recruitment in this manipulative experiment.

#### Effects of *Mazzaella* turf on post-recruitment survivorship of fucoids

The presence of *Mazzaella* turf influenced the survivorship of the two fucoid species differently (following fucoid recruitment). The mean life span of *Fucus gardneri* recruited within the turf was relatively short (2.2 months). However, as the mean distance between individual *F. gardneri* and turf became greater, *Fucus* life span showed a sharp increase and reached a peak (5.4 months) at a distance of about 0.5 cm from the edge of the turf (Fig. 2). The mean life span then decreased gradually (to 3.6 months) to a distance of approximately 2 cm, and at  $> 2$  cm the changes in life span were relatively small. In contrast, the longest mean life span of *Pelvetiopsis limitata* (5.0 months) was found in the individuals within *Mazzaella* turf. However, the life span as related to neighbor distance changed irregularly (Fig. 2).

The results of one-way ANOVA and a post hoc test, comparing the life span of the three distance groups, indicated that for *Fucus gardneri* the life span of the 'close' group (0.3-0.7 cm) was significantly higher than that of either the 'contact' (within turf or 0 cm) or the 'far' ( $> 2.0$  cm) group (Table 2). The life spans in the 'contact' and 'far' groups was not significantly different.

**Table 1.** Results of ANCOVA on fucoid recruitment in the three different *Mazzaella* pruning plots. Three treatments are 'total pruning', 'partial pruning' and no pruning(control), see text for details. The ANCOVA was applied to each sampling date. The covariate is *Mazzaella* percent cover in each plot(M-cover).

Source of variation	df	October 1993			February 1994			April 1994		
		MS	F	p	MS	F	p	MS	F	p
<i>Fucus</i>										
Treatment	2	3.48	1.51	0.242	1.60	0.90	0.419	0.07	0.03	0.967
M-cover	1	23.12	10.02	0.004	34.29	19.2	0.000	20.06	9.41	0.005
Error	23	2.31		1.78		2.13				
<i>Pelvetiopsis</i>										
Treatment	2	2.23	0.84	0.444	0.19	0.12	0.889	0.60	0.51	0.608
M-cover	1	11.67	4.42	0.047	14.12	8.78	0.007	21.18	17.87	0.000
Error	23	2.64		1.61		1.19				

 NUMBER OF FUCOID RECRUITS PER 100 cm<sup>2</sup>

**Fig. 4.** The effect of *Mazzaella cornucopiae* pruning on fucoid recruitment. A. number of fucoid recruits actually occurring in the plots. B. number of fucoid recruits adjusted by *Mazzaella* percent cover(the covariate) in each plot at each sampling date. These values were used in the ANCOVA. Data are means +S.E. of 9 replicates. PT for *Pelvetiopsis limitata* in the total pruning plots, PP for *P. limitata* in the partial pruning plots, PC for *P. limitata* in the control plots; FT,FP and FC for *Fucus gardneri* in the respective plots.

However, in *Pelvetiopsis limitata* the life span of all three groups was similar (5.0, 4.6, 4.3 months for 'contact', 'close', 'far', respectively). When comparing the two

fucoid species for their life span with the same distance group, there was no significant difference between the two species in any distance group (independent t-test at  $p = 0.05$ ). However, the mean life span in the 'contact' group was notably different (2.2 months for *Fucus* and 5.0 months for *Pelvetiopsis*;  $p = 0.004$  at  $df = 20$  if pooled variances were used), although this difference was not statistically significant if separate variances were used (as suggested by Wilkinson *et al.* 1992 because of the severely unequal sample sizes,  $n = 16$  and 6, respectively).

## DISCUSSION

### The complexity of algal interactions among the three dominants

The results presented here provide an example of bi-directional interactions, in which competitive dominance is reversed depending on the developmental or life history stage of the competitors. Space preemption by *Mazzaella cornucopiae* reduced the number of recruits of both *Fucus gardneri* and *Pelvetiopsis limitata* within its turf. However, once the fucoids had successfully recruited, they formed a canopy thus reducing *Mazzaella* biomass by shading.

The preemption of suitable space by a turf-forming species, and the subsequent reduction of settlement of other morphological forms, has been reported by many authors (Lubchenco 1978; Hruby and Norton 1979; Ambrose and Nelson 1982; Chapman 1984; Kennelly 1987). From this literature the mechanisms by which the *Mazzaella* turf prevented recruitment of fucoids are outlined as follows: (1) the physical occupation of space by turf may reduce the area available for settlement by fucoid propagules, or (2) the turf may outcompete juve-

**Table 2.** Comparison of longevity among the distance groups in each species and between *Fucus gardneri* and *Pelvetiopsis limitata* at each distance group. Means are number of months.

	CONTACT (0 cm)			CLOSE (0.3-0.7 cm)			FAR (>2.0 cm)			One-way ANOVA
	Mean	SE	N	Mean	SE	N	Mean	SE	N	<i>p</i>
<i>Fucus</i>	2.19	0.95	16	5.42	0.53	52	3.57	0.51	56	0.004
<i>t</i> -test( <i>p</i> )		0.086*			0.322			0.175		
<i>Pelvetiopsis</i>	5.00	1.50	6	4.62	0.51	53	4.25	0.56	44	0.831
Tukey's HSD on <i>Fucus</i>										
			CONTACT	CLOSE			FAR			
	CONTACT		1.000							
	CLOSE		0.008	1.000						
	FAR		0.405	0.031	1.000					

\*Separate variances are used due to the severely unequal sample sizes (Wilkinson *et al.* 1992)

nile fucoids for light or nutrients. However, the experimental removal of turf did not significantly increase recruitment of either *Fucus* or *Pelvetiopsis*. This was an unexpected result even though there were slightly more fucoid recruits in the "total-pruning" plots than in the control plots. This result implies that there must be another factor(s) involved in the survivorship of juvenile fucoids in turf-removed plots. Relatively stronger desiccation and increased wave impact resulting from turf removal may be factors. These will be discussed in the next section.

Morphological differences between adult plants of *Mazzaella* and the two fucoids resulted in another set of competitive interactions when fucoids successfully settled nearby or within the red algal turf. Olson and Lubchenco (1990) documented that competitive interactions change as the developmental stages of competitors change. In our study as fucoids grew (> 3 - 4 cm) they formed a canopy and reduced the understory biomass of *Mazzaella* due to light interception. A similar case has been reported by Lubchenco (1983). She found that in the absence of grazers *Enteromorpha* outcompeted *Fucus* germlings early in succession by the former's faster growth rate. However, when grazers of *Enteromorpha* were effective *Fucus* became established and dominated *Enteromorpha*. Thus in the long term *Fucus* excluded *Enteromorpha* from the rock surface by preempting space. In the upper intertidal communities at Nudibranch Pt. and Prasiola Pt., successful fall recruitment of both fucoids within *Mazzaella* beds (Kim and DeWreede 1996a) could be possible due to *Littorina* sp. preference for *Mazzaella* (Kim and DeWreede 1996b). The intensity of this preferential feeding may be increased in the summer months when snail densities are higher (Kim and

DeWreede 1996b). In any case, summer decline of *Mazzaella* populations opens up free space for fucoids which have their recruitment peak in October (Kim and DeWreede 1996a). These series of coincident events change the direction of competition and the outcome. Thus, when the fucoids settled successfully nearby or onto *Mazzaella* turf and grew up, they formed a canopy and inhibited the growth of *Mazzaella* (Kim 2002). This indicates that the outcome of competition is reversed, and adds another complexity in understanding algal interactions in this community.

#### The mechanism of positive interaction and neighbor distance

The relatively high survivorship of *Fucus* growing at the edge of the *Mazzaella* turf provides evidence of direct facilitation by neighboring species: potentially limiting physical stresses are ameliorated. A possible explanation for the different longevity patterns of *Fucus* and *Pelvetiopsis*, with respect to distance from *Mazzaella*, is based on the hypothetical relationships between competitive interactions and physical stresses (Fig. 5). Individual plants of *Fucus* and *Pelvetiopsis* recruiting and growing within the *Mazzaella* turf may encounter less desiccation because of the moisture-holding ability of the red algal turf (Hay 1981; Padilla 1984). As the fucoids mature, they may have limited space for holdfast expansion because of *Mazzaella*'s preemption of space. This increases the susceptibility of fucoids to wave impact, and this lethal factor is probably more detrimental to *Fucus* which has relatively wider thalli than *Pelvetiopsis*. This assumption is partly confirmed by calculating friction drag of the two fucoids using the formula and the coefficient values given by Denny (1995). For example, at

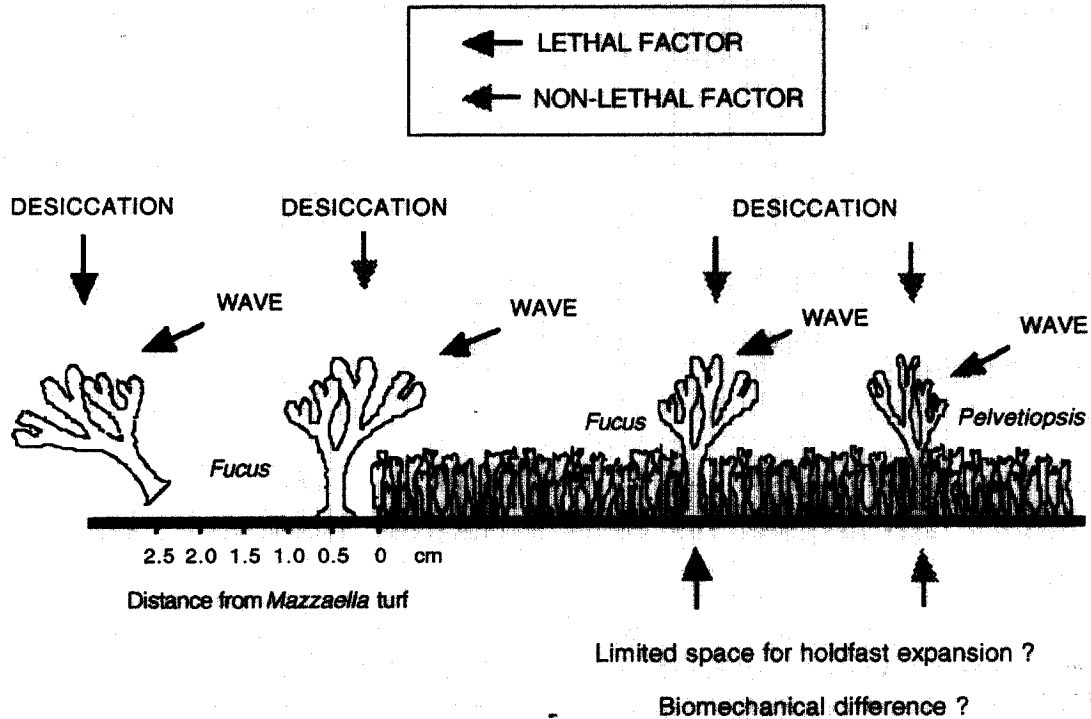


Fig. 5. Diagram of potential factors affecting fucoid mortality (See DISCUSSION for further explanation).

the water velocity of 3.2 m/s and with a surface area of 0.001 m<sup>2</sup>, the calculated friction drag for *F. gardneri* is 0.351 and 0.227 for *P. limitata*. By considering that *Fucus* has a generally greater surface area than *Pelvetiopsis*, the difference in drag between the two fucoids will be even greater.

It has been found that the competitive outcomes among macroalgae are sometimes influenced by local (microhabitat) physical conditions (e.g., desiccation, wave action) (Padilla 1984). Thus, the short life span of *Fucus* within *Mazzaella* turf may be a result of competition coupled with physical stress. The microhabitat conditions at the turf edge can be ameliorated by *Mazzaella*'s buffer against wave impact and also by sufficient moisture from turf, thus no competition for space apparently occurs. However, at a distance > 2 cm, both desiccation and wave impact can be lethal for *Fucus*. I suggest a model for *Fucus gardneri* survivorship in relation to the distance from the primary space-holder, *Mazzaella cornucopiae*, and with respect to the two limiting factors, competition and physical stress (Fig. 6). Competition is probably effective only if the two species are in contact. The intensity of competition then drops suddenly as the neighbor distance increases. At the same time physical stresses gradually increase as the distance between the two species increases. The highest survivorship of *Fucus*

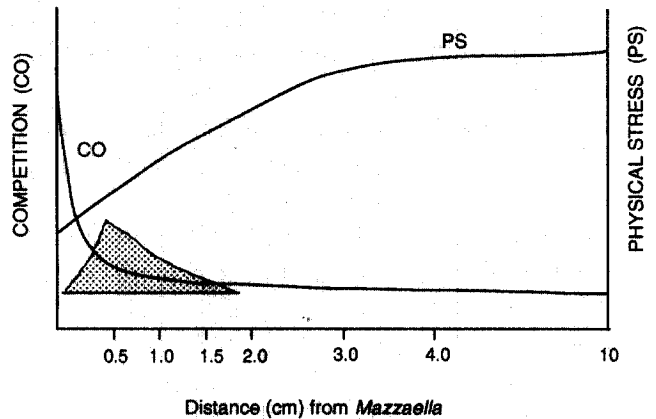


Fig. 6. The survivorship curve of *Fucus gardneri* in relation to the changing effects of competition and physical stress with distance from the edge of a *Mazzaella* turf. The shaded area represents the possibility of *Fucus* survival.

occurs at the point (or distance) where the combined effect of the two factors is minimal.

The effect of *Mazzaella* on post-recruitment survival of *Fucus*, as shown by this study, suggests three important factors in structuring this algal assemblage. First, direct positive interactions may be common and predictable forces in natural communities and in physically harsh environments in particular. The mechanism of the interaction found in this study is an example of neighbor



habitat-amelioration (Bertness and Callaway 1994). This can be differentiated from the results of Paine (1980) and Dethier and Duggins (1984), which showed empirical evidence of positive indirect interactions and feedback mechanisms in food webs. In some harsh intertidal habitats there is limited evidence that neighbor species improve deleterious habitat conditions (e.g., severe heat and desiccation pressure) and facilitate recruitment of barnacles (Bertness 1989) and mussels (Bertness and Grosholz 1985). Dayton (1975) reported an example of direct positive interaction between macroalgae, and suggested that larger overstory algae (e.g., *Hedophyllum*) protected smaller understory species from desiccation or radiation damage.

Second, the concept of neighbor distance, which was first introduced in terrestrial plant interactions (Fawcett 1964; Turkington and Harper 1979), should be adapted to marine benthic algal interactions albeit with a modified mechanism. Since no belowground competition exists among benthic algae, the outcome of algal interactions is solely dependent upon morphological form and thallus size (Hay 1981; Paine 1984). This is particularly true if the limiting resource is space, or if the competition is by interference. This study confirms the idea that for organisms which compete for space, and in particular clonal ones such as plants and some sessile animals, competition occurs mainly between neighbor species (Connell 1983). In addition, neighbor distance in this upper intertidal habitat determined which factor(s) is (are) responsible for the fate of an individual plant. Thalli of *Fucus gardneri* encountered different biotic and abiotic factors (competition to protection to physical stress) as neighbor distance increased. Consequently, the survival of a *Fucus* thallus in this high intertidal site, which features intermediate to strong wave action, occurs at a certain optimal distance (e.g., 0.5 cm) from its neighbor. Therefore, the presence of a *Fucus* population is partially dependent on the presence of *Mazzaella cornucopiae*, especially in the case where *Fucus* increases its population size toward sites with conditions more extreme (e.g., higher tidal height, more wave-exposed) than its normal habitat.

Third, the importance of interactions on a small spatial scale in this community should be noted. Paine (1990) pointed out that interaction mechanisms on a small (< 2 m<sup>2</sup>) scale are important in understanding the nature of algal assemblages. The range of spatial scales at which one species affected another was surprisingly small (< 2 cm). This should be considered in designing field experi-

ments for detecting species interactions of small organisms. Brawley and Johnson (1993) reported that microclimate was an important predictor of the likelihood and spatial pattern of survival of settled larvae, reproductive propagules, and other microscopic stages in the life histories of organisms growing in intertidal and other water-stressed (desiccating) environments. It is certain that relevant spatial scale is mainly determined by the size of organisms interacting (this applies only to sessile organisms) and the severity of physical stresses.

Bertness and Callaway (1994) proposed that positive interactions during succession and recruitment, as well as among established adults, are unusually common in harsh physical environments for the simple reason that primary space-holders frequently buffer neighbors from potentially limiting stresses. In this perspective, the *Mazzaella-Fucus* interaction in a stressful environment with strong wave force and desiccation deserves increased empirical attention, and should be incorporated into models of community organization in harsh habitats like the upper intertidal zone.

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## REFERENCES

- Ambrose R.F. and Nelson B.V. 1982. Inhibition of giant kelp recruitment by an introduced brown alga. *Bot. Mar.* 25: 265-267.
- Bertness M.D. 1989. Intraspecific competition and facilitation in a northern acorn barnacle population. *Ecology* 70: 257-268.
- Bertness M.D. and Grosholz T. 1985. Population dynamics of the ribbed mussel, *Geukensia demissa*: the cost and benefits of an aggregated distribution. *Oecologia* 67: 192-197.
- Bertness M.D. and Callaway R. 1994. Positive interactions in communities. *TREE* 9: 191-193.
- Boulding E.G., Buckland-Nicks J. and Van Alstyne K.L. 1993. Morphological and allozyme variation in *Littorina sitkana* and related *Littorina* species from the Northeastern Pacific. *The Veliger* 36: 43-68.
- Brawley S.H. and Johnson L.E. 1993. Predicting desiccation stress in microscopic organisms: the use of agarose beads to determine evaporation within and between intertidal

- microhabitats. *J. Phycol.* **29**: 528-535.
- Chapman A.R.O. 1984. Reproduction, recruitment and mortality in two species of *Laminaria* in southwest Nova Scotia. *J. Exp. Mar. Biol. Ecol.* **78**: 99-109.
- Chapman A.R.O. 1995. Functional ecology of fucoid algae: twenty-three years of progress. *Phycologia* **34**: 1-32.
- Connell J.H. 1972. Community interactions on marine rocky intertidal shores. *Ann. Rev. Ecol. Syst.* **3**: 169-192.
- Connell J.H. 1974. Field experiments in marine ecology. Pages 21-54 in R. Mariscal, editor. *Experimental Marine Biology*. Academic Press. New York.
- Connell J.H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: Cody M.L. and Diamond J.M. (eds), *Ecology and evolution of communities*. Belknap, Cambridge. pp. 460-490.
- Connell J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* **122**: 661-696.
- Connell J.H. and Slatyer R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* **111**: 1119-1144.
- Dayton P.K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol. Monogr.* **45**: 137-159.
- Dayton P.K. and Oliver J.S. 1980. An evaluation of experimental analyses of population and community patterns in benthic marine environments. In: Tenore K.R. and Coul B.C. (eds), *Marine benthic dynamics*. University of South Carolina Press. pp. 93-120.
- Denley E.J. and Dayton P.K. 1985. Competition among macroalgae. In: Littler M.M. and Littler D.S. (eds), *Ecological field methods: macroalgae. Handbook of phycological methods*. Cambridge University Press. New York, New York, U.S.A. pp. 511-530.
- Denny M. 1995. Predicting physical disturbance: mechanistic approaches to the study of survivorship on wave-swept shores. *Ecol. Monogr.* **65**: 371-418.
- Dethier M.N. and Duggins D.O. 1984. An "indirect commensalism" between marine herbivores and the importance of competitive hierarchies. *Am. Nat.* **124**: 205-219.
- Duggins D.O. 1981. Interspecific facilitation in a guild of benthic marine herbivores. *Oecologia* **48**: 157-163.
- Fawcett R.G. 1964. Effects of certain conditions on yield of crop plants. *Nature* **204**: 858-860.
- Hawkins S.J. and Hartnoll R.G. 1983. Grazing of intertidal algae by marine invertebrates. *Oceanogr. Mar. Biol. Ann. Rev.* **21**: 195-282.
- Hay M.E. 1981. The functional morphology of turf-forming seaweeds: Persistence in stressful marine habitats. *Ecology* **62**: 739-750.
- Hay M.E. 1986. Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. *Am. Nat.* **128**: 617-641.
- Hruby T. and Norton T.A. 1979. Algal colonization on rocky shores in the Firth of Clyde. *J. Ecol.* **67**: 65-77.
- Kastendiek J. 1982. Competitor-mediated coexistence: interactions among three species of benthic macroalgae. *J. Exp. Mar. Biol. Ecol.* **62**: 201-210.
- Kennelly S.J. 1987. Inhibition of kelp recruitment by turfing algae and consequences for an Australian kelp community. *J. Exp. Mar. Biol. Ecol.* **112**: 49-60.
- Kim J.H. 1995. Intertidal community structure, dynamics and models: mechanisms and the role of biotic and abiotic interactions. Ph.D. Thesis. The University of British Columbia, Vancouver, British Columbia, Canada.
- Kim J.H. 2002. Mechanisms of competition between canopy-forming and turf-forming intertidal algae. *Algae* **17**: 27-33.
- Kim J.H. and DeWreede R.E. 1996a. Effects of size and season of disturbance on algal patch recovery in a rocky intertidal community. *Mar. Ecol. Prog. Ser.* **133**: 217-228.
- Kim J.H. and DeWreede R.E. 1996b. Preferential feeding by a littorinid: Implications for its role in an upper intertidal algal community. *Bot. Mar.* **39**: 561-569.
- Lindquist J.L., Rhode D., Puettmann K.J. and Maxwell B.D. 1994. The influence of plant population spatial arrangement on individual plant yield. *Ecol. Appl.* **4**: 518-524.
- Lubchenco J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *Am. Nat.* **112**: 23-39.
- Lubchenco J. 1983. Littorina and Fucus: effects of herbivores, substratum heterogeneity and plant escapes during succession. *Ecology* **64**: 1116-1123.
- Lubchenco J. and Gaines S.D. 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Ann. Rev. Ecol. Syst.* **12**: 405-437.
- Mack R.N. and Harper J.L. 1977. Interference in dune annuals: spatial pattern and neighborhood effects. *J. Ecol.* **65**: 345-363.
- McCook L.J. and Chapman A.R.O. 1992. Vegetative regeneration of *Fucus* rockweed canopy as a mechanism of secondary succession on an exposed rocky shore. *Bot. Mar.* **35**: 35-46.
- Menge B.A. and Sutherland J.P. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Nat.* **130**: 730-757.
- Olson A.M. 1985. Early succession in beds of the red alga, *Iridaea cornucopiae* Post. & Rupr. (Gigartinaeae): Alternate pathways. M.S. Thesis, Oregon State University, Corvallis, Oregon, USA.
- Olson A.M. and Lubchenco J. 1990. Competition in seaweeds: linking plant traits to competitive outcomes. *J. Phycol.* **26**: 1-6.
- Padilla D.K. 1984. The importance of form: differences in competitive ability, resistance to consumers and environmental stress in an assemblage of coralline algae. *J. Exp. Mar. Biol. Ecol.* **79**: 105-127.
- Paine R.T. 1977. Controlled manipulations in the marine intertidal zone and their contributions to ecological theory. *Spec. Pub. Aca. Nat. Sci. Phil.* **12**: 245-270.
- Paine R.T. 1984. Ecological determinism in the competition for

- space. *Ecology* 65: 1339-1348.
- Paine R.T. 1990. Benthic macroalgal competition: complications and consequences. *J. Phycol.* 26: 12-17.
- Schoener T.W. 1983. Field experiments on interspecific competition. *Am. Nat.* 122: 240-285.
- Sousa W.P. 1984. Intertidal mosaics: Patch size, propagule availability and spatially variable patterns of succession. *Ecology* 65: 1918-1935.
- Tilman D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75: 2-16.
- Turkington R. and Harper J.L. 1979. The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. I. Ordination, pattern and contact. *J. Ecol.* 67: 201-218.
- Underwood A.J. and Denley E.J. 1984. Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. In: Strong D.R., Simberloff D., Abele L.G. and Thistle A.B. (eds), *Ecological communities: Conceptual issues and the evidence*. Princeton University Press, New Jersey, U.S.A. pp. 151-180.
- Vandermeer J. 1980. Indirect mutualisms: variations on a theme by Stephen Levine. *Am. Nat.* 116: 441-448.
- Wilkinson L., Hill M.A. and Vang E. 1992. *SYSTAT: Statistics, version 5.2.1* ed. SYSTAT. Evanston, Illinois, USA.
- Winer B.J. 1971. *Statistical principles in experimental design*. McGraw-Hill. New York, New York, USA.

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