

Mechanisms of Competition between Canopy-Forming and Turf-Forming Intertidal Algae

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Mechanisms of competition between two canopy algae and an understory alga were investigated by a field manipulative experiment using artificial thalli. The study was carried out in the upper intertidal zone at Nudibranch Point in Vancouver Island, British Columbia, Canada, where two furoids, *Fucus gardneri* and *Pelvetiopsis limitata*, and a turf red alga, *Mazzaella cornucopiae*, were dominant in the algal community. The experiment was designed to test three hypotheses, shading, whiplash, and allelopathy, imposed by potential furoid effects on *M. cornucopiae*. Only the shading effect was significant, indicating that adult furoid thalli reduced *M. cornucopiae* biomass underneath the furoids. Results indicated that reversal of competitive dominance existed between *F. gardneri* and *M. cornucopiae* depending on the life history stage of the competitors. By including the turf alga's effects on the furoids, the well-balanced and non-hierarchical interaction networks among the major macroalgae support the high likelihood of species coexistence in the community.

Key Words: allelopathy, canopy algae, competition, intertidal, macroalgae, shading, turf algae, whiplash

INTRODUCTION

The mechanisms of macroalgal competition have traditionally been recognized as consisting of two basic kinds, exploitative competition and interference competition, although these can be further subdivided (Schoener 1983). Exploitative competition (e.g., consumption, preemption; see Menge (1995) for suggestions for new terms) is an indirect interaction between competitors, and the interaction is always mediated by the resource in short supply (Keddy 1989). Three important resources for macroalgae are light, space and nutrients (Denley and Dayton 1985). In contrast, interference competition (e.g., whiplash, overgrowth) occurs when one individual directly affects another. In this case, a resource (such as space) is not necessarily in short supply, but mortality occurs as a result of physical interference.

However, there are some situations in which both types of competition may occur simultaneously between the same pair of competitors (reviewed by Denley and Dayton 1985). Thus, it is often difficult to identify a single mechanism of competition. For example, exploitative

competition (e.g., shading) can be accompanied by interference (e.g., allelopathic effect). Separation of these mechanisms can be done with an appropriate experimental design, such as a factorial design. Not many such an attempt has been done in the field using macroalgae. As another problem in macroalgal competition, reversals of competitive rank may be common in natural communities (Connell 1983; Schoener 1983). When rank order of competitive superiority is involved, reciprocal tests on both members in a pair are necessary to deal with the problem that asymmetrical competition resulting in the elimination of inferior species is not always the case. To obtain such evidence requires at least two experiments (on each member of a pair), which is rarely done (reviewed by Connell 1983; Denley and Dayton 1985; Underwood 1992).

This manuscript provides an experimental evidence of the effects of intertidal canopy species on an understory turf alga, which were dominant species in a marine algal community in a rocky intertidal zone of the west coast of Vancouver Island, British Columbia, Canada. The underlying hypothesis to be tested is that the taller erect furoids, *Fucus gardneri* and *Pelvetiopsis limitata*, affect the growth of the shorter turf-forming *Mazzaella cornucopiae* by shading, whiplashing (scouring), or by chemical content (e.g., phenolic compounds) whereby the furoids

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allelopathically suppress *M. cornucopiae*. Shading and scouring are commonly reported mechanisms of competition in both subtidal and intertidal habitats (reviewed by Denley and Dayton 1985; Olson and Lubchenco 1990; Paine 1990). A few studies have reported that chemical content of certain algae (including some fucoids) affect other algae by allelopathic influences (McLachlan and Craigie 1966; Carlson and Carlson 1984). The role of major herbivores (i.e., snails and limpets) in algal community dynamics and succession has been covered in separate manuscripts (Kim and DeWreede 1996b; Kim 1997). Thus, this paper deals only with mechanisms of competition shown by the canopy algae.

MATERIALS AND METHOD

Community organization and the location of study site are described in the other manuscript (Kim 2002). A manipulative field experiment was initiated at Nudibranch Point in June, 1994. The experimental design included five treatments using both live fucoid thalli and artificial plants which were attached to a mesh strip and set up on *Mazzaella* turf. The five treatments are as follows: (1) live *Fucus* thalli which test for canopy (shading), scouring (disturbance) and phenolic (allelopathic) effects, (2) live *Pelvetiopsis* thalli testing for the same characteristics as live *Fucus*, (3) 'clear' artificial plants which test only for scouring, but not for canopy nor phenolic effects, (4) 'dark' artificial plants which test for canopy and scouring, but not for phenolics, and (5) a control with neither live nor artificial thalli.

Adult thalli (about 7 cm in length) of *Fucus gardneri* and *Pelvetiopsis limitata* were haphazardly collected (with holdfasts intact) from within the normal vertical range at Nudibranch Point, and were maintained in running seawater tanks. Then, thalli with similar weight (20.5 ± 1.3 (S.D.) g blotted wet weight) were selected, although some trimming was sometimes needed to equalize thallus weight for each experimental unit. Holdfasts and lower parts (~1 cm) of each thallus were placed into twists of 9.4 mm polypropylene rope (5 cm in length) which had both ends melted to prevent untwisting. Vinyl covered wire (1.1 mm in diam.) was tightly wound around the rope to secure the thalli. For the artificial plants, a transparent, flexible plastic sheet (0.55 mm in thickness) was cut to make one type of treatment, 'clear', and an opaque plastic sheet (0.65 mm in thickness) was cut to make a second treatment, 'dark'. Artificial plants (13.5 cm long, 5.7 cm wide for 'blade' area, 1.0 cm wide

for 'stipe') were made by attaching two extra layers of sheet (one of 5.0 cm and the other 8.0 cm long) to the lower part of the artificial plants. In order to attach these extra layers, the margin of each extra layer was sewn with thin monofilament line. Therefore, each artificial plant consisted of a three-layered stipe, a two-layered lower blade and a one-layered upper blade. This construction provided sufficient strength under forceful wave action and mimicked the motion of live plants in the back and forth water flow observed at high tides. Like real fucoid plants, the lower part (about 2.5 cm) of the 'stipe' area of the artificial plant was inserted into the rope and tightened. Vinyl covered mesh (3.5 mm diam.), cross-linked every 2.5 cm x 5.1 cm, was used to hold the treatment plants to the substratum. This mesh is strong and yet malleable enough to bend with the rock substratum (Shaughnessy 1994). Mesh strips were cut so that each was 90 cm x 4 cm, allowing five treatments (including a control for an empty spot) of thalli haphazardly placed 20 cm apart. The ropes in which fucoid thalli and artificial plants were inserted were attached to the mesh strip with an electrician's cable tie. Seven mesh strips (7 replicates) were horizontally attached to the rock substratum at Nudibranch Point where mixed stands of the three species occurred. The orientation of existing live fucoids, which was mostly caused by out-going waves and the slope of rock substratum, was used as an indicator for orienting mesh strips. It was necessary for the treatment thalli to sit on the *Mazzaella* beds in the same direction at every low tide in order to achieve the treatment effects, especially for canopy and allelopathic effects. Attachment sites for mesh strips were chosen where there was an untouched *Mazzaella* bed (by existing fucoids, other algae or barnacles) underneath each treatment thallus. The entire mesh strip was kept in contact with the rock substratum by using either concrete nails or bolts secured at each end and at the middle of the strip.

Artifacts due to using artificial plants, as noted in Connell (1974) and Underwood (1980), were considered. To test for effects on understory *Mazzaella* due to the shade caused by fucoids, replicate light readings (mean \pm S.E., $n = 5$) were taken under the fucoid canopy, 'clear' and 'dark' artificial plants and natural light intensity ('control') using a Licor (LI-185A) quantum photometer. Under no canopy, $2,600 \pm 0.0 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ of light reached the substratum, compared to $12.9 \pm 1.8 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ under *Fucus gardneri*, $13.7 \pm 4.4 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ under *Pelvetiopsis limitata* and $2,650 \pm 6.0 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$

under 'clear' artificial plants. To obtain the 'dark' artificial plant that best mimicked the shade cast by furoid canopies, I haphazardly made eight holes (2.5 mm diam.) on each blade using a hole punch so that $14.3 \pm 4.0 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ of light reached the substratum. Replicate temperature readings were also made under each treatment plant. In the sunny mid-day of June 23, 1994, temperatures under *F. gardneri*, *P. limitata* and 'dark' plants were $18.5 \pm 0.7^\circ\text{C}$, $19.2 \pm 0.9^\circ\text{C}$, $20 \pm 0.4^\circ\text{C}$, respectively. High temperatures under the 'clear' plants (due to a greenhouse effect) were lowered by making twelve holes (3.8 mm diam.) on each blade so that a similar temperature was obtained compared to that of the control ($23.5 \pm 0.5^\circ\text{C}$, $23.1 \pm 0.3^\circ\text{C}$, respectively).

Size class (5 mm difference between classes: size class 1, < 5 mm, size class 2, 5-10 mm, etc.) densities of *M. cornucopiae* blades in 2 x 2 cm quadrats under each treatment plant were measured in the field, and these were then converted to biomass (g) using the regression coefficient (Fig. 1) between size class and wet weight. Data were collected at the beginning (June, 1994) and the end (August, 1994) of the experiment. Sampling was done at the center under each treatment plant. Consequently some portion of the 4 cm² areas sampled probably overlapped with the previously sampled ones. Therefore, a 5 x 2 (Treatment x Time) ANOVA with repeated measures on Time factor and a preplanned multiple comparison with Bonferroni adjusted probability ($p = 0.05 / 4 = 0.0125$) were used for analysis and hypothesis tests. Since it is a repeated measures design, probability values for a multivariate statistic (Wilk's lambda), rather than for univariate statistics, were used for the multiple comparisons. Hypothesis I (shading effect) was tested by comparing *Mazzaella* biomass between 'clear' and 'dark' artificial plants. Hypothesis II (scouring effect) and Hypothesis III (allelopathic effect) were tested by comparing 'clear' vs. control, and 'dark' vs. *Fucus* and *Pelvetiopsis*, respectively. If an effect was significant, a further analysis was done to examine if the effect influenced the size class structure of *M. cornucopiae*. For each size class, an independent t-test was applied to compare the changes in blade density (density after experiment minus density before experiment) between two factors. Since there were six size classes, the t-test was performed six times with a Bonferroni-adjusted probability value ($p = 0.05 / 6 = 0.0083$). The homogeneity of variance was tested using Bartlett's test (Wilkinson *et al.* 1992) and Cochran's test (Winer 1971). The results of both tests were not significant ($p > 0.05$) indicating an equal vari-

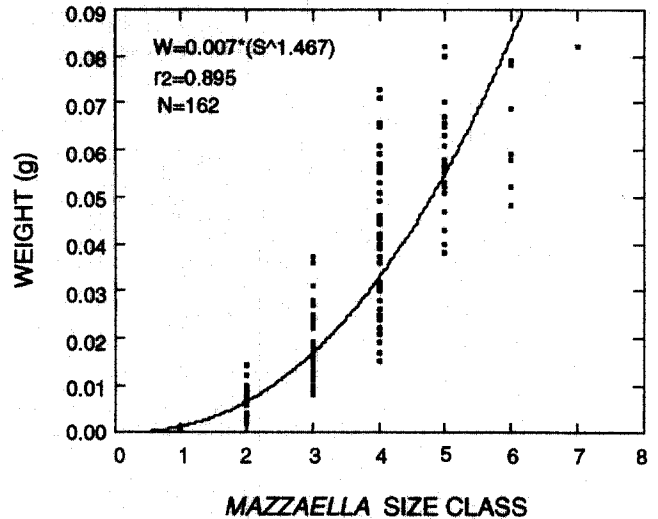


Fig. 1. Relationship between the size class of *Mazzaella cornucopiae* blade and wet weight(g). *Mazzaella* blade height was divided into six 5 mm size classes(SC). SC1 = 1-5mm, SC2 = 6-10mm, SC3 = 11-15mm, SC4 = 16-20mm, SC5 = 21-25mm, SC6 = >26mm.

ance. The residuals were plotted for inspection of normality. A few artificial plants and furoid thalli were partly broken or lost during the two-month experimental period, and these were dropped from the analyses. As a result, a reduction (e.g., to 5) in replicates occurred in certain treatments.

RESULTS

The effects of live furoid thalli and the two types of artificial furoids on *Mazzaella* biomass showed that there were significant differences in biomass of *M. cornucopiae* among the treatments ($p = 0.001$, one-way ANOVA with repeated measures). Biomass (blade wet weight) of *M. cornucopiae* generally decreased during the experimental period (June to August, 1994). The mean biomass for the control decreased by 0.38g (16.8%) per 2 x 2 cm plot (Fig. 2). The *Mazzaella* biomass under the 'clear' artificial plant showed the least reduction (0.14 g, 9.0%), and that under the 'dark' artificial plant had the largest reduction (0.88 g, 50.7%) (Fig. 2).

Of the three hypotheses tested, only the canopy effect (shading) was significant. *Mazzaella* biomass change under the 'dark' artificial plant was significantly greater than under the 'clear' artificial plant, i.e., biomass of *Mazzaella* was affected by reduction of light (Table 1). Reduction of light also caused *Mazzaella* thalli to change color from light greenish red to dark red. The scouring

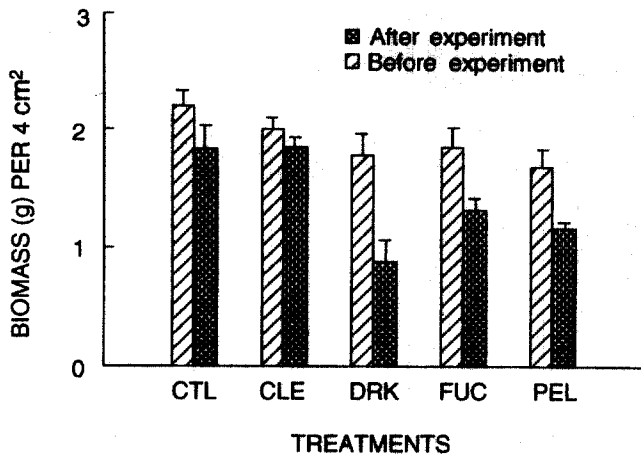


Fig. 2. Changes in *Mazzaella cornucopiae* biomass(g) under each treatment after 2 months. CTL for control, CLE for the clear artificial plants, DRK for the dark artificial plant, FUC for *Fucus gardneri*, and PEL for *Pelvetiopsis limitata*. Data are means +S.E. (n = 5 for CLE, FUC and PEL, n = 6 for DRK, n = 7 for CLE).

effect (hypothesis II), tested by comparing the control with the 'clear' artificial plant, showed no significant difference in biomass change between these two factors, and was thus rejected. The hypothesis of allelopathy, tested by comparing the 'dark' plant with either '*Fucus*' or '*Pelvetiopsis*', was rejected for both fucoids ($p = 0.189$ and $p = 0.374$, respectively), indicating that *Mazzaella* biomass was not affected by allelopathy.

The significance of the canopy effect of fucoids on *Mazzaella* biomass was also analyzed for its potential effect on the size class of the red alga. *Mazzaella* blade densities decreased in all size classes under the canopy of 'dark' artificial blades, whereas the blade densities under the 'clear' artificial blades had a variable change depending on the size classes (Fig. 3). Independent t-tests for blade density changes ('after' minus 'before') between 'clear' and 'dark' plants on each size class indicated that only blades in size class 2 were significantly different ($p = 0.008$) in density between the two treatments.

DISCUSSION

Fucoids did not affect adult *Mazzaella* by scouring (whiplash) or by the presence of chemicals such as phenolic compounds. However, allelopathic effects of brown algae have been noted to be important many years ago when workers studied the antibacterial and anti-algal properties of phenolic compounds in dicty-

Table 1. Results of multivariate statistics as a preplanned multiple comparison for testing three hypotheses. A Bonferroni adjusted probability value ($p = 0.05/4 = 0.0125$) was used to compare each pair of treatments.

	Wilk's lambda	F	df	p
Canopy effect (Clear vs. Dark)	0.541	9.320	2, 22	0.001
Scouring effect (Control vs. Clear)	0.974	0.293	2, 22	0.749
Allelopathic effect (Dark vs. <i>Fucus</i>)	0.859	1.801	2, 22	0.189
(Dark vs. <i>Pelvetiopsis</i>)	0.914	1.029	2, 22	0.374

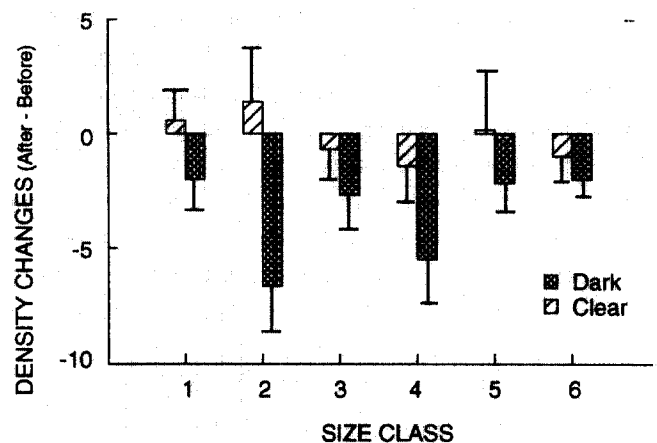


Fig. 3. The effect of fucoid shading on *Mazzaella* size class. Data are means +S.E. (n = 5 for clear and n = 6 for dark artificial plant).

otalean and fuclean algae (McLachlan and Craigie 1966; Fletcher 1975). Schiel and Foster (1986) pointed out the importance of allelopathic effects in determining the dynamics of some communities, and studies have shown that such effects of brown algae (probably due to phenolic compounds) inhibited the abundance of other algae in intertidal (Fletcher 1975) and subtidal (Kennelly 1987) habitats. *Fucus gardneri* and *Pelvetiopsis limitata* are known to contain phenolic compounds of 4.35% and 4.93% dry mass, respectively (Steinberg 1985). However, the biomass of *Mazzaella* underneath real plants (both *F. gardneri* and *P. limitata*) was not significantly reduced when compared to the effect of 'dark' artificial plants; this indicates that further reduction of *Mazzaella* biomass caused by chemicals did not occur. Although it is possible that the whiplashing of fucoids affected the settlement of barnacles and some ephemeral algae in small gaps (5 x 5 cm) cleared in the proximity of the fucoids

(Kim and DeWreede 1996a), fucoids did not affect *Mazzaella* growing within their boundary of scouring. The result of careful field observation of *Mazzaella* around mature fucoid thalli supports this result. The absence of a scouring effect by fucoids may be the result of fucoid size related to *Mazzaella* turf. The fucoids may not have been large enough (Grant 1977; Farrell 1989) to affect adult *Mazzaella* turf.

The reduction of light (to about 0.51% of unshaded condition) by fucoids affected the size class density of *Mazzaella*, with a particularly significant decrease in size class 2 (0.5-1 cm blade length). It is not certain why blade density in this particular size class was significantly reduced. Shading effects on understory species in algal communities have been extensively studied in subtidal kelp communities (Dayton *et al.* 1984; Reed and Foster 1984; Santelices and Ojeda 1984; Kennelly 1989; Dean *et al.* 1989; Reed 1990) and intertidal algal communities (Dayton 1971, 1975; Schonbeck and Norton 1980; Ang and DeWreede 1992). In intertidal habitats shading has sometimes been reported as a positive factor, especially where desiccation is strong (Dayton 1975; Ang 1991). However, in this study light may have been important for *Mazzaella* growth, even when the population declined between June and August 1994, such that shading reduced more biomass than the amount of natural reduction in the control sites. In fact, thalli of *Mazzaella cornucopiae* under the light condition similar to that of under-fucoid-canopy undergo about 74.3% less net photosynthesis than those under the unshaded condition at the same desiccation level (e.g., 10% desiccation) (R. Scrosati, unpublished data). This result confirms that the deleterious effect on *Mazzaella* by fucoid shading could also be effective at other times of the year; thus the effect may be more intense when *Mazzaella* actively grows from February to April (Kim and DeWreede 1996a).

In this study competitive superiority was reversed depending on the developmental stage of the fucoids. *Mazzaella* outcompeted fucoids at the recruitment stage of the fucoids by preempting space (Kim 2002). However, after the recruitment of fucoids, both fucoids inhibited the growth of *Mazzaella* by shading. When a reversal of competitive superiority occurs competitive elimination is less likely (Connell 1983). In his review of field experiments on competition, Connell (1983) reported that only a few studies were sufficiently comprehensive to provide evidence concerning such reversals. A few examples of non-hierarchical competitive networks among marine subtidal animals were shown in Connell

and Keough (1985). Similarly, among macroalgae the direction of competitive overgrowth was reversed in the presence of grazers (Paine 1984; Steneck 1985). Unlike these latter two studies on macroalgae, the change of the direction of competition between *Mazzaella* and the fucoids was due to the difference in morphology and size of these algae.

Is coexistence of the three dominants due to the variation in algal interactions? This research has shown that patterns of interactions among neighbor species are complex yet balanced. The balance in competitive direction (or dominance) between *Mazzaella cornucopiae* and fucoids, as well as the balance in the positive and negative interactions between *M. cornucopiae* and *Fucus gardneri*, enables the persistence of each member in the community (Kim 2002). Looking at their distinctive functional morphology, the shorter turf-forming *M. cornucopiae* probably has a competitive disadvantage over upright and relatively fast-growing fucoids, because the turf-former may have reduced photosynthetic activity limited to the upper portions of the thallus (due to self-shading) and also may suffer nutrition depletion within the turf matrix (Hay 1981). In contrast, *M. cornucopiae* must be the species best adapted to high desiccation and strong wave action among the three dominants. This is due to its water-holding capacity and the fact that self-cushioning thalli exist in a dense turf (Hay 1981; Padilla 1984). *Fucus gardneri* is the only species among the three dominants which also appears in the lower zone (upper-mid intertidal), where it grows up to 3-4 times larger than individuals in these study sites (Kim 2002). Although this alga has a physiological adaptation (i.e., high photosynthetic rate in air) to tidal emergence (Johnson *et al.* 1974; Quadir *et al.* 1979), it still may have some morphological limitation (e.g., relatively wider thallus than *Pelvetiopsis limitata*) to surviving the force of breaking waves. Consequently, the benefit obtained from the positive interaction of *Fucus* with *Mazzaella*, the relatively high recruitment (compared to *Pelvetiopsis*; Kim and DeWreede 1996a) and the facilitation of settlement by barnacles (Kim 1995) are the important parameters which allow *Fucus* to maintain its co-dominance in this community. Natural habitats for *P. limitata* appear to be confined to the upper intertidal, unlike *F. gardneri* (Sousa 1984; Farrell 1989, 1991). In a recent review on fucoid algae by Chapman (1995), there was no information available for the physiological and reproductive ecology of *P. limitata*. However, in this study *P. limitata* seemed to be a relatively better-adapted species to the upper

intertidal zones at Prasiola and Nudibranch Points than *F. gardneri*, because survival and colonization of this alga was not affected by some biological (i.e., the presence of *Mazzaella*; Kim 2002) and physical (i.e., size of disturbance; Kim and DeWreede 1996a) factors.

From a biological perspective, coexistence of these three macroalgae in this community is possible due to the biological adaptation of each species to physical stress, and because the outcomes of their interactions with each other are well-balanced. Thus, competitive elimination is unlikely because competition among the species I studied is symmetric. The data presented in this manuscript provide experimental evidence that detectable biological interactions occur in this community, and that such interactions are important determinants of community dynamics in this upper intertidal habitat.

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