



A short-term response of macroalgae to potential competitor removal in a mid-intertidal habitat in Korea

Baek Jun Kim, Hyuk Je Lee, Seungshic Yum, Hyun Ah Lee, Yong Ju Bhang, Sang Rul Park, Hyun Jin Kim & Jeong Ha Kim*

Department of Biological Science, Basic Science Institute, Sungkyunkwan University, Suwon 440-746, Korea

*Author for correspondence; Tel: 82-31-290-7009. Fax: 82-31-290-7015. E-mail: jhkimbio@skku.ac.kr

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Abstract

Interspecific interactions among three dominant macroalgae, *Pterocladia capillacea* (Rhodophyta), *Hizikia fusiformis* (Heterokontophyta) and *Chondracanthus intermedius* (Rhodophyta), were experimentally investigated on the rocky mid-intertidal zone of Sungsan, Jeju Island, Korea from March 1998 to June 1999. Each of the potentially competing species was removed in permanent plots (20 × 20 cm), and percent covers of non-manipulated species were measured by an image analyzing method using a digital camera. *Pterocladia capillacea* was the most abundant during all seasons, except for winter. Its abundance was lowered by the removal of the turf-forming alga *C. intermedius*, indicating that turf had a positive effect on *P. capillacea*. Conversely, there was a negative effect of *P. capillacea* on the abundance of *C. intermedius*. Interactions between *C. intermedius* and *P. capillacea* can probably be explained as a consequence of the water-trapping ability of the former and the canopy-forming ability of the latter. There was, however, no apparent effect related to *H. fusiformis* since the abundance of this alga remained low. This study supports that both negative and positive effects between same pair of species could be common depending on the morphological differences of algae and particular habitat conditions.

Introduction

Interspecific interactions among marine benthic algae have been considered as a fundamental force to understanding dynamics in marine macroalgal communities. Thus, in natural communities, patterns of algal interaction have often turned out more complex due to other biotic factors, such as the presence of herbivores, algal life history, morphology, and seasonality (Olson & Lubchenco, 1990; Dudgeon et al., 1999). The majority of previous researches has, however, shown that the outcome of interaction is often one-directional, which means species A outcompetes species B, or A has a positive effect on B, even though the necessity of reciprocal test to detect an interactive effect in both directions has been suggested (Denley & Dayton, 1985; Olson & Lubchenco, 1990; Kim, 1995). The presence of both negative (i.e., competition) and positive (i.e., facilitation) effects between the same pair of species has rarely been reported. If this is the case, the

result can theoretically cause the exclusion of one species. This extreme outcome of interaction, however, is not common in natural communities, because the coexistence of species is maintained by other factors, such as consumers, other algal species, disturbance, or the changes in interaction strength with season or life history stages. In this study we report an example of both negative and positive effects occurred between the same pair of species of intertidal macroalgae and discuss its implication for the community structure.

Although positive interactions have been investigated less frequently than competition in marine benthic organisms, their possibility and relevance have been discussed theoretically by some ecologists (Connell & Slatyer, 1977; Vandermeer, 1980; Connell, 1983; Dethier & Duggins, 1984; Bertness & Callaway, 1994). Some positive interactions occur as a consequence of the direct beneficial influence of one species on another (Dayton, 1975; Brawley & Johnson, 1993; Kim, 2002a); others occur as a con-

sequence of negative interactions that are manifested indirectly through other species (Kastendiek, 1982; Dethier & Duggins, 1984; Hay, 1986; Kim, 1997). In physically stressful habitats (e.g., intertidal zones under desiccation stress), positive interactions (e.g., neighbor habitat-amelioration; Bertness & Callaway, 1994) rather than competition may be a particularly important factor leading to species coexistence in a community.

The present work is the first report regarding the interspecific interactions of marine benthic macroalgae on Korean shores. The aim of this study is to investigate a short-term response of macroalgae to the press effect of potential competitor removal in a three species-dominated intertidal community. The three dominants used in the experiment differed in their morphology, upright and turf-forming, and coexisted in an apparently space-limited community in the mid-intertidal zone of Jeju Island, Korea.

Study site and organisms

The study site is located at Sungsan on Jeju Island, South Korea (33° 27' N, 126° 56' E; Fig. 1). The rocky shore of Jeju Island, mostly consisting of volcanic rocks, supports the most diverse marine intertidal flora in Korea, probably due to exposure to low levels of pollutants and the influence of a mixture of the warm Kuroshio current with the relatively cold Yellow Sea current (Lee & Lee, 1982; Kim, 1991; Park et al., 1994). Along the rocky coast at Sungsan, the intertidal zone stretches over 60 m at low tides, and has a gentle slope with many shallow tide pools. The shoreline is exposed to moderate wave action due to a barrier effect by nearby Woo Island. The tidal regime usually exposes the habitat for prolonged period (about 4–6 hours a day) during daylight hours except for winter months when low tides mostly occur in the evening.

The mid-intertidal zone at Sungsan is dominated by three macroalgae, *Pterocladia capillacea* (Gmelin) Bornet (Gelidiales, Rhodophyta), *Chondracanthus intermedius* (Suringar) Hommersand comb. nov. (Gigartinales, Rhodophyta) and *Hizikia fusiformis* (Harvey) Okamura (Fucales, Heterokontophyta). Both *P. capillacea* and *H. fusiformis* are upright, fleshy algae and their sizes at maturity in this site are 5–7 cm and 6–10 cm, respectively. However, thallus size of *H. fusiformis* at the site was variable depending on tidal height and slope, and plants >20 cm are common. *Chondracanthus intermedius* is a turf-forming

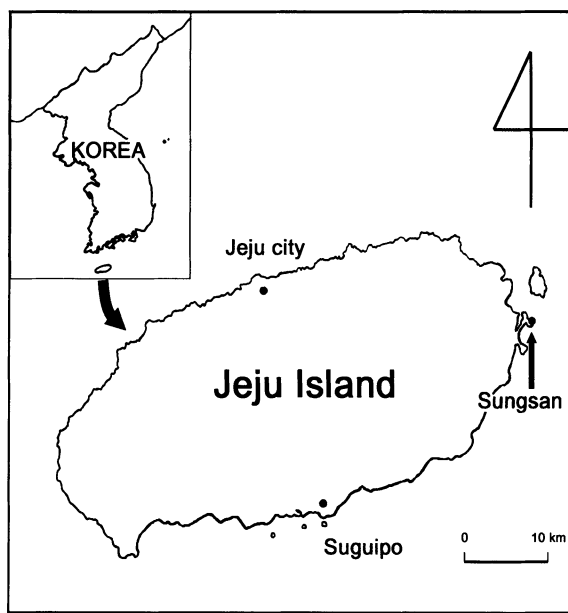


Figure 1. Map of the study site in Jeju Island, Korea.

alga (< 1 cm in turf thickness) and its branched flat thalli grow horizontally on the rock surface. This alga sometimes grows together with *Gigartina teedii* (Roth) Lamouroux and *Caulacanthus okamurae* Yamada in this habitat. Other algae occurred less frequently or seasonally in the experimental plots, including *Sargassum thunbergii* (Mertens ex Roth) Kuntze, *Gloiopeltis complanata* (Harvey) Yamada, *Gelidium amansii* (Lamouroux) Lamouroux, *Chondrus ocellatus* Holmes, *Ulva conglobata* Kjellman, crustose coralline algae and benthic diatoms. Percent covers of these algae in the plots hardly reached >7% for the study period, except for *S. thunbergii* appearing in a substantial amount from a few plots. We recorded their abundance, and then removed them at every sampling time to focus on the interactive effects among the three dominants.

Materials and methods

A permanent transect line (6 m in length) was established along a gently sloped portion of the shore where the three species of macroalgae occurred in a mixed stand. Anchor bolts were placed into the substratum to mark both ends of the line. The line was marked at every 30 cm to position 20 permanent plots (20 × 20 cm) alternately placed on the upper and the lower sides of the line. We assumed that effects of experimental treatment on the adjacent plots were

not significant, because plots were placed alternately along the line with a 10 cm gap between the marked points and the edge of the next plot. By using the same transect line hooked to the anchor bolts, plots could be relocated at each sampling time.

Plots were randomly assigned to one of 4 treatments with 5 replicates per treatment. The treatments included: (1) *Hizikia fusiformis*-removal, (2) *Pterocladia capillacea*-removal, (3) *Chondracanthus intermedius*-removal and (4) undisturbed controls. For the treatment effects, each species was continuously removed on sampling dates which were distributed over intervals of 2–3 months. Other species, which usually occurred in low abundance, were also removed from all the plots. Plants were removed by scraping using a small flat screw driver, and care was taken not to affect the remaining species. Percent coverage of remaining species was visually estimated on a computer monitor using Adobe Photoshop (version 5.0) after photographing all plots in the field using a digital camera (Kodak DC260 zoom). For accurate assessment of percent covers of understory species, such as *C. intermedius*, extra photos were taken after laying the canopy aside. Visual estimation of cover in the lab rather than in the field (Dethier et al., 1993; Kim & DeWreede, 1996a) allowed us more time for the assessment of percent coverage with a greater accuracy and repeatability.

Percent cover data were analyzed for treatment effects using an one-way ANOVA on each sampling date, followed by Tukey's HSD tests if the results of ANOVA were significant. Data were arcsine-transformed prior to analysis to provide variance homogeneity. We did not perform a test for normality since the sample size was low ($n = 5$) and because ANOVA is generally robust against violation of the assumption of normality in the case of equal sample size (Keppel, 1991). All data analyses were done using SPSS (version 6.1).

Results

Effects of one species removal on the abundance of remaining species under each experimental condition are shown in Figure 2. Effects of the treatments on the percent covers of each seaweed are presented in Figure 3. *Pterocladia capillacea* was the most abundant alga in control plots and comprised 30–60% cover during the study period except for February, 1999 when cover dropped to ~20% (Fig. 2D). *Chondracanthus*

intermedius cover decreased to 10% from June to October, 1998; however, cover of this alga slightly increased in February, 1999, as *P. capillacea* cover declined. Mean percent covers of *Hizikia fusiformis* were low (< 10%) except for the first sampling date (Fig. 2D). Although the abundance of the three species was similar at the beginning of the experiment (March, 1998), both *C. intermedius* and *H. fusiformis* became less abundant than *P. capillacea*, as shown in control plots.

Among the three macroalgae, the interaction between *P. capillacea* and *C. intermedius* showed an interesting result. In the *Chondracanthus*-removal plots, percent covers of *P. capillacea* were relatively lower than those in the control plots, except for February, 1999 (ANOVA, $F_{(2,12)} = 3.954$, $p = 0.048$ for October, 1998; Fig. 3B). This result supports the hypothesis that *C. intermedius* has a positive effect on the abundance of *P. capillacea*. Conversely, in the *Pterocladia*-removal plots, percent covers of *C. intermedius* were significantly higher than those in the controls (ANOVA, $F_{(2,12)} = 4.543$, $p = 0.034$ for October, 1998; $F_{(2,12)} = 6.042$, $p = 0.015$ for April, 1999; $F_{(2,12)} = 18.768$, $p < 0.001$ for June, 1999; Fig. 3C). This result indicated that *P. capillacea* had a negative effect on *C. intermedius*. Therefore, both positive and negative effects occurred between the two species. Percent covers of *H. fusiformis* were higher in the *Pterocladia*-removal plots than in the control and the *Chondracanthus*-removal plots in October, 1998 (ANOVA, $F_{(2,12)} = 5.663$, $p = 0.019$; Fig. 3A).

Discussion

The present study represented short-term responses of neighbor species to the effects of potential competitor removal in a rocky mid-intertidal habitat. The interaction pattern between *Pterocladia capillacea* and *Chondracanthus intermedius* showed an opposite effect on each other, which could be explained by the morphological characteristics of the algae. Turf-forming algae with fast vegetative propagation have been shown to inhibit erect algae by space preemption (Sousa et al., 1981; Airoidi, 1998; Kim, 2002a). However, in this study the positive effect of the turf-forming *C. intermedius* on the upright *P. capillacea* might result from habitat-amelioration (Bertness & Callaway, 1994). The potential advantages of being a neighbor of turf algae can be explained as follows: less desiccation pressure because of the moisture-trapping ability of

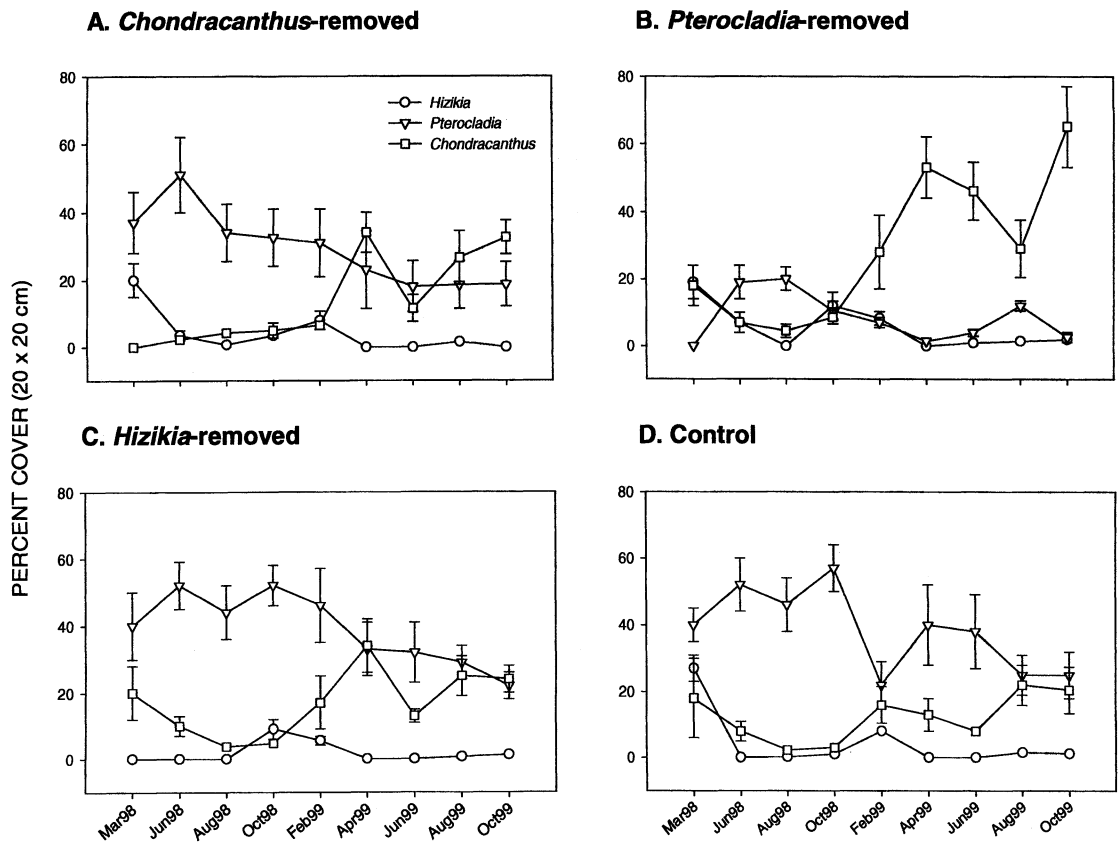


Figure 2. Changes in the percent cover of each alga under each treatment. Data are means \pm SE of 5 replicates.

turf (Hay, 1981; Padilla, 1984) and a buffering effect of the turf against wave impact (Kim, 2002a). It seems obvious that dense turf forms are particularly resistant when exposed to desiccating conditions since gaps between the compact thalli trap a substantial amount of water. This characteristic of turf may lead to better photosynthetic performance compared with non-turf morphology (Hay, 1981). However, the ability of turf algae to ameliorate desiccating habitat conditions by enhancing the growth rates and survivorship of neighboring species has not been well documented. In a previous study on the interspecific interaction between *Fucus gardneri* P.C. Silva and *Mazzaella cornucopiae* (Postels et Ruprecht) Hommersand in the upper intertidal zone of western Canada, the survivorship of *F. gardneri* growing close (about 2 cm) to the turf-edge of *M. cornucopiae* was enhanced in comparison with that of other microhabitat conditions (Kim, 2002a). Kim (2002a) claimed that this could be the result of a potential benefit of *Mazzaella* turf ameliorating microhabitat conditions through lessening desiccation stress or buffering wave impact, or both. In this study, thalli of *C. intermedius* form a dense turf, unlike the com-

pact upright fronds of *M. cornucopiae*, by growing close to the substratum as creeping fronds. Therefore, it seems unlikely that the thin (usually <1 cm in thickness) *C. intermedius* turf can provide a buffer against wave impact. Rather, this alga may improve microhabitat conditions for other seaweeds by retaining moisture and reducing desiccation stress. This explanation is supported by the fact that the positive effect of *C. intermedius* on *P. capillacea* became weak during winter when desiccation was less severe.

The negative effects of *Pterocladia capillacea* on *Chondracanthus intermedius* might be due to shading since highly branched thalli of *P. capillacea* form an effective canopy that reduces the amount of irradiance that reaches the understory *C. intermedius* turf. Although there is no information available on the irradiance requirement for *C. intermedius*, it is apparent that when this species co-occurred with *P. capillacea* it showed inhibited growth even during its active growing season, February–June, 1999 (Fig. 3C). Also, it was observed that the abundance of *C. intermedius* under the canopy was often much less than that occurring in nearby open areas (B. J. Kim, pers. obser.).

Other possibilities for the mechanism of the negative effect of *P. capillacea* on *C. intermedius* might be whiplash and allelopathy. A few reports have claimed that some small sized intertidal algae, such as *Fucus gardneri* or *Pelvetiopsis limitata* (Setchell) Gardner (about 7–8 cm in height at maturity), did not affect neighboring species by whiplash (Grant, 1977; Farrell, 1989; Kim, 2002b). *Pterocladia capillacea* in this habitat grows up to a similar size as these fucoids, but this alga is lighter because of its thinner thallus; therefore, the whiplashing effect by *P. capillacea* would not be strong enough to affect *C. intermedius*. Allelopathic effects might be possible since thalli of the two species were usually in contact when emergent, however there is no evidence that either species produces allelochemical.

No influence of *Hizikia fusiformis* on either *P. capillacea* or *C. intermedius* and vice versa was detected in this study because *H. fusiformis* abundance remained low regardless of the treatment throughout the study period. Except for the first sampling date, we found most of *H. fusiformis* thalli were < 1 cm. This small thallus size might be in part due to the influence of commercial harvesting by local people who use this alga as a foodstuff (Lee & Kamura, 1997).

The occurrence of both positive and negative effects between the two macroalgae provides an interesting ecological implication. Denley & Dayton (1985) suggested that an experimental approach for interspecific competition should accommodate an experimental design for detecting reciprocal effects, rather than simply the effect of species A on species B. According to the results in this study, it is clear that *Chondracanthus intermedius* enhances the abundance of *Pterocladia capillacea*, which then competitively inhibits the former. If so, will the positive and negative effects of these species on each other result in *P. capillacea* increasingly outcompeting *C. intermedius* and excluding the turf-forming alga from the local community? However, our observations suggest that exclusion does not occur since both species appear to coexist in the intertidal habitat. There are many factors that may potentially lead to coexistence; unpredictable perturbation, herbivory, seasonality of the species, life history traits. Although herbivores may switch the competitive dominance of macroalgae through their differential food preferences (Lubchenco, 1983; Kim & DeWreede, 1996b), in this experiment we found few major herbivores, such as limpets and snails, in our plots except for a few crabs and polychaetes. Moreover, *P. capillacea* is not collected by people un-

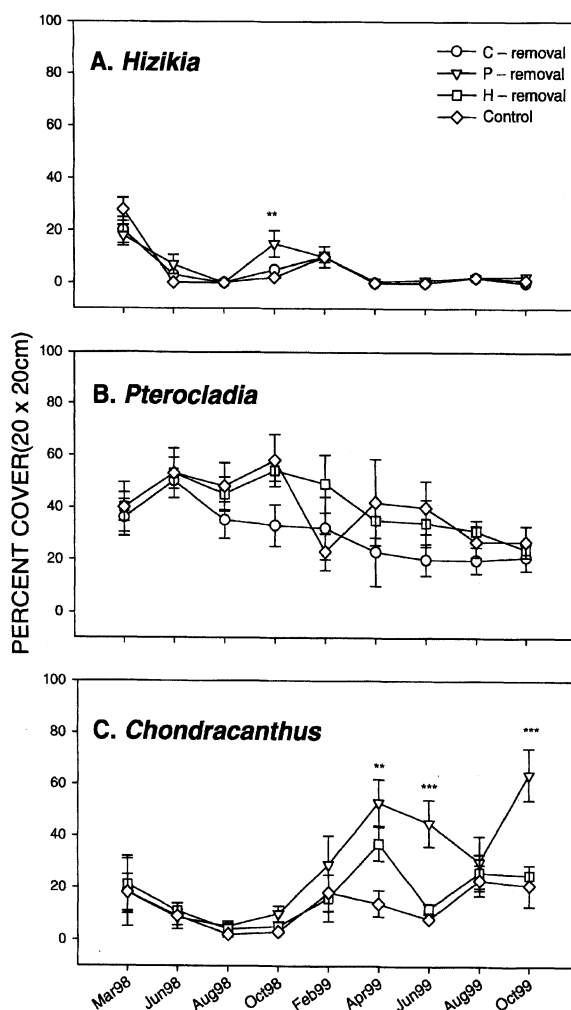


Figure 3. Effects of the treatments on the percent covers of each alga. C-removal: *Chondracanthus intermedius* removed; P-removal: *Pterocladia capillacea* removed; H-removal: *Hizikia fusiformis* removed; Control: no alga removed. Data are means \pm SE of 5 replicates. * for <0.05, ** for <0.025, *** for <0.01.

like *H. fusiformis*. The most likely explanation for the coexistence of these species at Sungsan would be the difference in their seasonality. The abundance of *P. capillacea* decreased in March, 1998 and February, 1999 when *C. intermedius* showed peaks in its abundance (Fig. 2D).

This study presents a possible example of a reciprocal interaction between two morphologically distinct macroalgae, and may be extended to other sets of macroalgae and to other habitats. Together with experimental evidence for the mechanisms underlying these interactions, the information regarding the two species will be useful for understanding the dynamics of large-scale algal assemblage in this habitat.

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References

- Airoidi, L., 1998. Roles of disturbance, sediment stress, and substratum retention on spatial dominance in algal turf. *Ecology* 79: 2759–2770.
- Bertness, M. D. & R. Callaway, 1994. Positive interactions in communities. *TREE* 9: 191–193.
- Brawley, S. H. & L. E. Johnson, 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.
- 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. & R. O. Slatyer, 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.
- Dethier, M. N. & D. O. Duggins, 1984. An 'indirect commensalism' between marine herbivores and the importance of competitive hierarchies. *Am. Nat.* 124: 205–219.
- Dethier, M. N., E. S. Graham, S. Cohen & L. M. Tear, 1993. Visual versus random-point percent cover estimation: 'objective' is not always better. *Mar. Ecol. Prog. Ser.* 96: 93–100.
- Denley, E. J. & P. K. Dayton, 1985. Competition among macroalgae. In Littler, M. M. & D. S. Littler (eds), *Ecological Field Methods: Macroalgae. Handbook of Phycological Methods*. Cambridge University Press. New York: 511–530.
- Dudgeon, S. R., R. S. Steneck, I. R. Davison & R. L. Vadas, 1999. Coexistence of similar species in a space-limited intertidal zone. *Ecol. Monogr.* 69: 331–352.
- Farrell, T. M., 1989. Succession in a rocky intertidal community: the importance of disturbance size and position within a disturbed patch. *J. exp. mar. Biol. Ecol.* 128: 57–73.
- Grant, W. S., 1977. High intertidal community organization on a rocky headland in Maine, U.S.A. *Mar. Biol.* 44: 15–25.
- 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.
- Kastendiek, J., 1982. Competitor-mediated coexistence: interactions among three species of benthic macroalgae. *J. exp. mar. Biol. Ecol.* 62: 201–210.
- Keppel, G., 1991. *Design and Analysis: A Researcher's Handbook*. Prentice Hall. New Jersey.
- Kim, J. H., 1995. *Intertidal Community Structure, Dynamics and Models: Mechanisms and the Role of Biotic and Abiotic Interaction*. Ph.D. Thesis. The University of British Columbia, Vancouver, BC, Canada.
- Kim, J. H., 1997. The role of herbivory, and direct and indirect interactions, in algal succession. *J. exp. mar. Biol. Ecol.* 217: 119–135.
- Kim, J. H., 2002a. Patterns of interactions among neighbor species in a high intertidal algal community. *Algae* 17: 41–51.
- Kim, J. H., 2002b. Mechanisms of competition between canopy-forming and turf-forming intertidal algae. *Algae* 17: 33–39.
- Kim, J. H. & R. E. DeWreede, 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. & R. E. DeWreede, 1996b. Distribution and feeding preference of a high intertidal littorinid. *Bot. mar.* 39: 561–569.
- Kim, Y. H., 1991. Marine algal resources in Cheju Island. *J. Cheju Studies* 8: 137–156.
- Lee, Y. P. & S. Kamura, 1997. Morphological variations of *Hizikia fusiformis* (Harvey) Okamura (Sargassaceae, Pheophyta) from the western coast of the north Pacific. *Algae* 12: 57–72.
- Lee, Y. P. & I. K. Lee, 1982. Vegetation analysis of marine algae in Jeju Island. *Proc. Coll. Natur. Sci., SNU* 7: 73–91.
- Lubchenco, J., 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity and plant escapes during succession. *Ecology* 64: 1116–1123.
- Olson, A. M. & J. Lubchenco, 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.
- Park, S. H., Y. P. Lee, Y. H. Kim & I. K. Lee, 1994. Qualitative and quantitative analyses of intertidal benthic algal community in Cheju Island: 1. Species composition and distributional patterns. *Korean J. Phycol.* 2: 193–203.
- Sousa, W. P., S. C. Schroeter & S. D. Gaines, 1981. Latitudinal variation in intertidal community structure: the influence of grazing and vegetative propagation. *Oecologia* 48: 297–307.
- Vandermeer, J., 1980. Indirect mutualisms: variations on a theme by Stephen Levine. *Am. Nat.* 116: 441–448.

Note added in proof

No Korean material has been examined for the basis of recently suggested taxonomic revisions (Santelices & Hommersand, 1997), hence we have retained current usage.