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Short communication

Biofilm: A crucial factor affecting the settlement of seaweed on intertidal rocky surfaces

Sang Rul Park [a], Yun Hee Kang [b], Chang Geun Choi [c,*]

[a] University of Texas at Austin Marine Science Institute, 750 Channel View Drive, Port Aransas, TX 78373, United States
[b] Marine Research Institute, Pusan National University, Busan 609-735, Republic of Korea
[c] Department of Ecological Engineering, Pukyong National University, Busan 608-737, Republic of Korea

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ABSTRACT

We hypothesized that the presence of biofilm accelerated the settlement of dominant seaweed species and maintained high levels of species richness by regulating the blooming of particular species on an intertidal rocky shore. The coverage and species richness of macroalgae on sterile and cleared substrates (225 cm^2) were measured to investigate the effects of biofilm on the settlement of macroalgae in intertidal zones at Noryang, Songmoon, and Sangnam in Gawngyang Bay on the southern coast of the Korean peninsula. Green algae coverage on cleared substrates was significantly higher than that on sterile substrates at both Noryang and Songmoon during the study period. This suggests that the presence of biofilm enhances the settlement of green algae by providing various habitat structures and, consequently, may lead to serious 'green tide' events. However, the coverage of algae other than green algae and algal species richness on cleared substrates remained high at Sangnam during the experimental period. Biofilm facilitated the settlement of macroalgae and inhibited the blooming of specific algae by inducing inter-specific space competition. Therefore, biofilm plays an important role on seaweed assemblages on intertidal rocky shores by accelerating the settlement of seaweed.

1. Introduction

Anthropogenic and natural disturbance is often observed on rocky shores. In particular, physical disturbances such as wave exposure, sediment loads, desiccation, and human activities (e.g., tramping, harvesting) play key roles in the seaweed community structure of rocky intertidal shores by making new space available and alleviating resource competition (Schiel and Foster, 1986; Milazzo et al., 2004; Airoldi et al., 2008). Thus, disturbance may be extremely important in maintaining heterogeneity and rates of change in community structures and dynamics (Sousa, 2001). The recovery patterns and processes of seaweed communities following disturbance have been the focus of study by marine ecologists and phycologists for more than a century, as they imply shifts in community structure (Hobbs and Huenneke, 1992; Chapin et al., 2000). According to the model of succession proposed by Connell and Slatyer (1977), the establishment of species in the later stages of succession is facilitated by the early succession species. The early colonists are enhanced by the presence of biofilm, which may affect the settlement of microorganisms (Michael and Smith, 1995). Therefore, successful settlement of the planktonic stages of benthic plants is very important in the establishment and maintenance of benthic plant populations.

Biofilm, formed by organic material and microorganisms such as diatoms and bacteria, serves as an attractive substrate for the settlement of benthic organisms (Wahl, 1989; Wieczorek and Todd, 1998). Many studies have focused on the settlement and metamorphosis of invertebrate larvae on biofilm (Todd and Keough, 1994; O'Connor and Richardson, 1998; Rahim et al., 2004). For seaweed species, the settlement of the zoospores of the ephemeral algae *Ulva* was affected by biofilm made from organic material (Joint et al., 2007). The macroalgal biomass on natural substrates with propagules has been shown to be higher than that on sterile substrates (Eriksson et al., 2006). The propagules allow for the massive recruitment of bloom-forming algae and thereby may control population dynamics and dominance patterns in macroalgal blooms (Lotze et al., 2000).

In this study, experiments were conducted on gently sloping rocky intertidal shores at three locations with distinct features in seaweed community structure. Green algae bloomed frequently at Noryang on the southern coast of the Korean peninsula. There were only two dominant species (*Ulva pertusa* and *Ulva linza*), which

* Corresponding author.
E-mail address: cgchoi@pknu.ac.kr (C.G. Choi).

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caused "green tides" in the lower intertidal zone. At Songmoon, the algal community was dominated by four species: *U. pertusa* and *Ulva compressa* dominated the lower and upper intertidal zones, respectively, and two turf-forming algae (*Chondracanthus teedii* and *Chondracanthus intermedia*) dominated the middle intertidal zone year-round. In contrast, at Sangnam, the dominant species of algae varied with season, and species diversity was relatively high. The main species were *U. pertusa* and *U. linza*, and secondary species were *Hizikia fusiformis, Sargassum thunbergii, Ectocarpus arcuts, Sytosiphon lomentaria, Ishige okamurae, Polysiponia morrowii, Porphyra* sp., *C. teedii, C. intermedia, Chondrus crispus, Corallina pilulifera, Chondria carassicaulis,* and *Gelidium divaricatum*. Based on the seaweed community structure at each location, we tested the following hypotheses in five zones at three locations on intertidal rocky shores: the presence of biofilm (1) accelerates the settlement of dominant seaweed species, (2) regulates the extent of green algal blooms on intertidal rocky shores, and (3) supports high levels of species richness at sites where species richness and species diversity are high.

2. Materials and methods

We carried out experiments on intertidal rocky shores at three locations (Noryang, 34°56′N, 127°52′E; Songmoon, 34°56′N, 127°51′E; Sangnam, 34°49′N, 127°49′E) in Gawngyang Bay on the southern coast of the Korean peninsula from January 1999 to December 2000. Commercial shellfish and fishery aquaculture (e.g., mussel, oyster, and seaweed) was actively conducted in Gawngyang Bay. The tidal regime is semidiurnal, with an approximately 2.5-m tidal range, and the system is identified as mesotidal, with two tides per day (Tide Tables for the Coast of Korea, National Oceanographic Research Institute of Korea). Salinity (PSU) usually ranged from 30 to 33, but decreased to 20 during periods of rainfall due to the input of freshwater from the Sumjin River. Water temperatures varied from 7.4 °C during winter to 28.9 °C during summer.

The experiment was initiated in January 1999 in all zones except for the mid-intertidal zone at Songmoon, where experimentation began in April 1999. Experimental units were composed of sterile substrates and cleared substrates. In the intertidal zone at each location where dominant species occurred, twenty 15 × 15-cm plots were set up. The corners of the plots were marked using a hammer drill and anchor bolts to facilitate plot re-location. Plots were separated by at least 2 m to minimize the effects of experimental treatment on adjacent plots. All plots were cleared by hand chiseling to remove macroscopic algae. Half of the plots were heat-sterilized to remove biofilm and the propagule bank. Although all macroscopic algae on cleared plots were removed, the biofilm was not completely removed and could still be observed. To examine the treatment effects, clearing and heat sterilization were conducted at each sampling event after the percentage cover of each species had been measured. The cleared plots and sterile plots were rechecked to remove macroscopic organisms the next day following disturbance. After a day and a week, the presence of biofilm in a sub sample of both plots was determined using a light microscope. Biofilm covered by considerable diatoms was observed on cleared plots after a day following disturbance. One week later, we observed biofilm on cleared plots with a naked eye. Unfortunately, it was not possible to identify species level or density due to the limitation of non-destructive sampling. We measured the coverage of all macroalgal species on each plot monthly in the field using a 225-cm^2 stainless frame with 100 subplots. Recorded algal cover included only those thalli whose holdfasts were in the plot. The percent cover of each species was estimated using an efficient and accurate visual estimation method (Dethier et al., 1993). Species richness (number of species) was extracted monthly from the coverage data of each plot only at Sangnam, where the species richness was relatively high.

All values are reported as means ± 1 SE. To achieve normality and homogeneity of variance, the percent cover and species richness were arcsine-transformed and log-transformed, respectively. Significant differences in the percent cover of algal groups or dominant species between substrate types (the effects of biofilm) and among sampling times at each location were tested using a two-way ANOVA with time as a block. When significant differences among treatments were observed, a Student–Newman–Keuls (SNK) *post hoc* test was performed. Statistical significance was set at the alpha < 0.05 level. All data analyses were performed using SPSS (version 12.0).

3. Results

Significant differences were found in the settlement of macroalgae on sterile and cleared substrates throughout the experimental period (Figs. 1–3, Table 1). The coverage of green algae (e.g., *U. pertusa* and *U. linza*) was significantly ($p < 0.001$) higher on cleared than on sterile substrates at Noryang, where green algae dominated year-round (Fig. 1). It was notable that green algal coverage on cleared substrates was high even when there was no algal settlement on sterile substrates. Green tides occurred twice a year during the experimental period, and the maximum percentage of green algae recorded on cleared and sterile substrates reached 93 and 75%, respectively. The mean percentage on cleared substrates was 3.6 times higher than that on sterile substrates.

At Songmoon, algal settlement was strongly influenced by treatment and tidal height (Fig. 2, Table 1). After disturbance, the species that had previously dominated each zone were observed, and they ultimately dominated; these were opportunistic algae such as *U. pertusa, U. compressa*, *C. teedii*, and *C. intermedia*. In the upper intertidal zone, the coverage of *U. compressa* on cleared substrates was significantly ($p < 0.001$) higher than that on sterile substrates throughout the experimental period (Fig. 2A). During the study period, *C. teedii* was the conspicuous species in the mid-intertidal zone (Fig. 2B). Although the peak coverage of *U. linza* was observed during June–July 2000 (data not shown), this species disappeared in less than 1 month. The mean coverage of *C. teedii* was ca. 20% throughout the experimental period. In the lower intertidal zone, the percent cover of *U. pertusa* was about seven times higher on cleared substrates than on sterile substrates, ranging between 0 and 60% (Fig. 2C).

Results from Sangnam contrasted with those from the two locations described above. Here, two green algae (*U. pertusa* and *U. linza*)

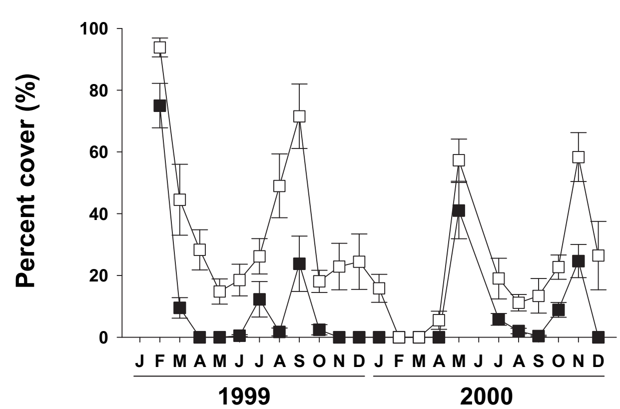

Fig. 1. Percent cover of green algae (*Ulva pertusa* and *Ulva linza*) on sterile (solid squares) and cleared (open squares) substrates at Noryang. Data represent means ± SE ($n = 10$).