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Effects of periodic air-exposure and nutrients on the competition of *Ascophyllum nodosum* and *Fucus vesiculosus* germlings [1a]

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ABSTRACT

To examine the relationship between competition and environmental factors, the germlings of *Ascophyllum nodosum* (L) Le Jolis and *Fucus vesiculosus* L. were cultured in monocultures and mixtures of the two species under two different exposure and nutrient levels. Both intra- and inter-specific competition were examined in comparison of the mortality and growth of germlings in monocultures and mixtures of the two species. The mortality of germlings increased with increasing density and emergence periods both in the monoculture and mixtures of the two species, and the mortality of *Ascophyllum* was significantly higher than that of *Fucus* both in submerged and emerged treatments. The growth of germlings of both species reduced with increasing density but *F. vesiculosus* always grew faster than *Ascophyllum*. The values of log output ratio were more than 0.1, indicating that *Fucus* 'won' in the competitive battles with *Ascophyllum* under two nutrient- and air-exposure levels. Log output ratio was greater in high than in low nutrients, indicating that the growth of *Fucus* is more enhanced than that of *Ascophyllum* in high nutrients. In the present study, the outcome of inter specific competition between germlings of *Fucus vesiculosus* and *Ascophyllum nodosum* was slightly altered by duration of emergence and nutrient concentration, but not to such an extent as to change the outcome

KEY WORDS: ENVIRONMENTAL FACTORS, GERMLING GROWTH, MORTALITY

INTRODUCTION

Intertidal seaweeds commonly experience desiccation and nutrient limitation stress associated with the tidal cycle (Brawley and Johnson, 1991; Davison and Pearson, 1996). The emersion stress reduces macroalgal growth, photosynthesis, and disrupts cell membranes, and the levels of stress increase with the elevation of shore heights (Schonbeck and Norton, 1980, Dring and Brown, 1982; Mabery and Madsen, 1990). Macroalgal propagules are bottleneck because they are unable to survive in the harsh environmental conditions, and their physiological responses to emergence are clearly related to the subsequent distribution and abundance (Brawley and Johnson, 1991; Vadas *et al.*, 1992; Davison *et al.*, 1993). Generally, dense germlings are able to survive under desiccation condition, where well-spaced individuals would be killed as tested on the shore (Ang and De Wreede, 1992; Andrew and Viejo, 1998) and in simulated tidal regimes in the laboratory (Hruby and Norton, 1979). However, the survival and growth of crowded germlings were negatively correlated, irrespective of monoculture or mixed culture under

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favorable environmental conditions (Reed *et al*., 1991; Creed *et al*., 1996, 1997; Choi and Norton, 2005a; 2005b).

One can reasonably speculate that juvenile and adult macroalgae are more tolerant for the stress than germlings of the species, and the physiological responses of germlings differ between species. Therefore, we could expect that the outcome of competition in mixtures of two species will be changed by the degree of the environmental stressors, such as nutrient depletion and emersion stress. There is evidence that the outcome of competition in mixtures of two species in the adult stage has been altered by temperature, irradiance (Enright, 1979) and nutrient availability (Fujita, 1985; Peckol and Rivers, 1995; Ceccherelli and Cinelli, 1997) but no studies have done in the germling stage.

On many rocky shores in northern Europe, fucoid algae have clear vertical distribution: *Pelvetia canaliculata* from the top shore followed by *Fucus spiralis, F. vesiculosus* and/or *Ascophyllum nodosum* with *F. serratus* at the lowest levels (Lewis, 1964). *F. vesiculosus* and *A. nodosum* have overlapping reproductive period in spring and their mixed stands are occasionally found in the mid intertidal zone (Knight and Parke, 1950). The two species are air-exposed periodically and emersion is an important physical stress. Thus, *F. vesiculosus* and *A. nodosum* are suitable to examine the effect so interactions between varying degrees of desiccation stress and the density of the two competitors. The outcome of competition in mixtures will also be examined with *F. vesiculosus* and *A. nodosum* under two different degrees of desiccation and nutrient sat a wide range of density and frequency. We tested the following hypotheses: 1) Crowding of germlings protects them from desiccation, irrespective of species involved. 2) The outcome of competition can be changed in mixtures of *A. nodosum* and *F. vesiculosus* by emerged stress and nutrient levels.

MATERIALS AND METHODS

1. Study Site

Twenty female and five male plants of *F. vesiculosus* and *A. nodosum* were collected separately from Port St. Mary ledges (N 54° 0', W 4° 44') in May 1999. Receptacles were cut from the male and female plants, washed several times using filtered seawater, dried for 5 h, and submerged in filtered seawater to induce gamete release. After 1 h, the receptacles were removed and clean zygote suspensions were prepared as described by Creed *et al*.(1996).

2. Methods

1) Effects of periodic emersion on the competition of germlings

A total forty-six Petri dishes, each containing 8 slides (2.5 × 2.0 ㎝) and 20 ㎖ of filtered seawater, were prepared and allocated to 23 treatments (Table 1). To achieve the settlement density required (Table 1), four different zygote concentrations (100, 1,000, 5,000 and 15,000 zygotes ㎖) for each species were prepared and 5, 5, 10 and 20 ㎖ of zygote suspensions were in oculated to achieve the log-scale settlement densities (Table 1).

After 24 hours, twelve from 16 slides for each treatment were chosen and four slides were discarded. Of these twelve slides four were used for determining settlement density and eight for the culture experiment. Settlement density was determined after setting up the culture experiment and is shown in Table 1.

Twenty-three slides representing each treatment were put on two steps in each culture tank of four tanks (25 l), continuously submerged and 6 h emerged every 12 h tidal cycle in the artificial tidal tanks as described in detail by Kim *et al*. (2011), and referred to as “submerged” and “emerged” respectively. An emergent period of 6 h was chosen because it is similar to the average submerged/exposed period of the two species on the shore (Schonbeck and Norton, 1978).

Germlings were cultured in culture medium (Kain and Jones, 1964) for a period of 3 weeks at 10 ± 1°C, 16:8 h LD and 120 μmol photons/m^2/s. The culture medium was not changed during the culture period. The final mortality and lengths of the germlings were measured. The lengths of total 25 germlings were measured on each of four replicate slides. In mixtures, the germlings of *Fucus vesiculosus* (hereafter *Fucus*) were clearly distinguished from those of *Ascophyllum nodosum* (hereafter *Asocophyllum*) by the presence of apical hairs. Percentage mortality of germlings was monitored after measuring lengths. One hundred germlings on each slide were counted to determine the mortality of germlings.

To test whether the relative growth of the *Fucus* and *Ascophyllum* in mixtures is altered by the submergence period, Log_{10} output ratios (Fv/An = *Fucus vesiculosus* / *Ascophyllum nodosum*) for mean length was calculated. When intra- and inter-specific competition is equivalent between the two competing species, log output ratio is 0. If relative growth of the two species is not altered by the submergence period, their final log output ratios should overlap between the two submerged conditions.

2) Effects of nutrient on the competition of germlings

The effects of nutrients on the performance of germlings were examined with *Fucus* and *Ascophyllum*. This experiment was set up with the same settlement density of germlings as described above.

Eight 5 l plastic tanks were used, half of which were filled with 2 l of culture medium (Kain and Jones, 1964) and the others with 2 l of filtered (0.25 μm) seawater. Twenty-three slides bearing germlings of different densities and proportions of the two species (Table 1) were put into each tank. Germlings were cultured for a period of 3 weeks at 10 ± 1 ℃, 16:8 h LD, and 120 μmol photons/㎡/s. The media were changed weekly and after three weeks the mortality and lengths of the germlings were measured.

To test whether the relative growth rates of *Fucus* and *Ascophyllum* in mixtures is altered by nutrient conditions, Log_{10} output ratios (Fv/An) for mean length were calculated and the results interpreted as described above.

3) Data analyses

Data were analyzed using one-way and two-way ANOVA. Homogeneity of variances was tested by Cochran's test. Where necessary, data were transformed before analysis to meet the assumptions of parametric tests (Sokal and Rohlf, 1981). The significance of the differences between means was tested with the Tukey HSD test. The regressions for the growth and mortality of germlings were compared with ANCOVA.

RESULTS

1. Effects of periodic emersion on the competition of germlings

The mortality of germlings increased with density and emergence periods both in the monoculture and mixtures (Figure 1). Once compared the mortality over the range of density levels of monocultures, the mortality of *Ascophyllum* was significantly higher than that of *Fucus* both in submerged and emerged treatments (Figure 2, Table 2). For both species, the duration of emergence influenced the mortality of germlings. The results of ANCOVA revealed that the mortality was significantly higher in emerged rather than submerged treatments in both species (*Fucus* : $F_{1,29}$ = 50.89, $p<0.001$; and

Table 1. Various densities (zygotes/㎠) and frequencies used in *Fucus vesiculosus* and *Ascophyllum nodosum* experiment

Ascophyllum	*Fucus*			
	10 (10.3 ± 1.7)	100 (113 ± 8.9)	1000 (1,103 ± 75.7)	7000 (7,112 ± 112.1)
10 (9.8 ± 1.5)	10 + 10 (22.1 ± 2.1)	10 + 100 (118.3 ± 6.7)	10 + 1,000 (1,088 ± 35.4)	10 + 7,000 (7,106 ± 67.8)
100 (106 ± 7.6)	100 + 10 (121 ± 11.9)	100 + 100 (215 ± 23.5)	100 + 1,000 (1,210 ± 56.1)	100 + 7,000 (7,244 ± 98.9)
1,000 (1,023 ± 45.7)	1,000 + 10 (1,043 ± 35.2)	1,000 + 100 (1,145 ± 23.9)	1,000 + 1,000 (2098 ± 45.4)	1,000 + 7,000 (8,188 ± 113.6)
7,000 (7,123 ± 121.9)	7000 + 10 (7,099 ± 98.7)	7,000 + 100 (7,187 ± 132.2)	7,000 + 1,000 (8211 ± 89.8)	

Ascophyllum : $F_{1,29}$ = 71.41, p<0.001). In mixtures, the identification of dead germlings to species was impossible and only total mortality was measured and it was com pared between two emergence treatments. Mortality was significantly higher in emerged compared to submerged treatments (Figure 2, Table 2).

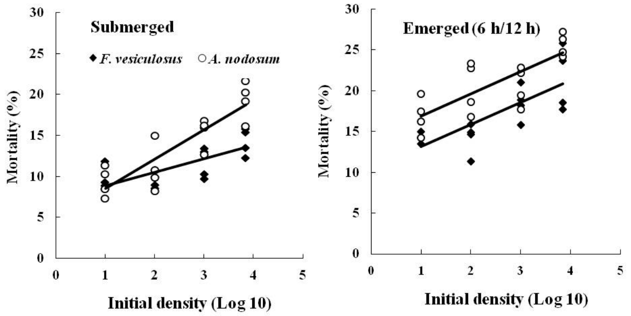

Figure 1. Percentage mortality in monocultures of *Fucus vesiculosus* and *Ascophyllum nodosum* germlings grown at submerged and emerged (16 h/12 h) conditions

The mean length of the two species varied at a wide range of density and frequency of *Fucus* and *Ascophyllum*, and in two submerged treatments. The growth of both species declined with increasing density and duration of emergence (Figure 3). *Fucus* always grew faster than *Ascophyllum* in both monoculture and mixture, and in submerged and emerged treatments (Figure 3). There was a significant difference in mean length between the two species (Table 3). When comparing the effects of density on two species, the growth of *Fucus* rapidly declined with in creasing density compared to *Ascophyllum*.

The effects of duration of emergence on the growth of

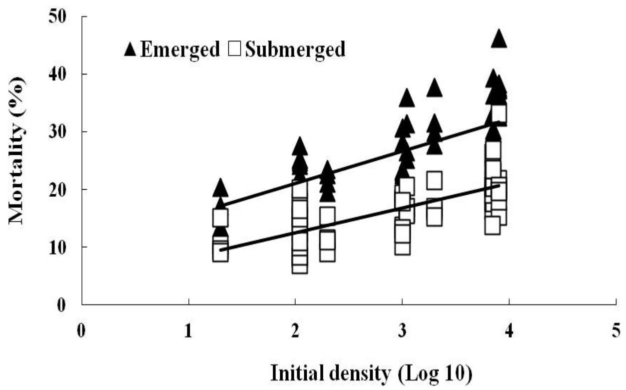

Figure 2. Percentage mortality in mixtures of *Fucus vesiculosus* and *Ascophyllum nodosum* germlings grown at submerged and emerged (16 h/12 h) conditions

germlings were compared for each species. Germlings grew faster in submerged than emerged condition both in monoculture and mixtures over a wide range of density and frequency. In monoculture, the growth of germlings was significantly greater in submerged compared to emerged treatments for *Fucus* was (ANCOVA, $F_{1,29}$ = 152.35, p<0.001), but not for *Ascophyllum* (ANCOVA, $F_{1,29}$ = 0.43, p>0.05). In mixtures, log output ratio was different between submerged and emerged treatments (Figure 4). The values of log output ratio were more than 0.1, indicating that *Fucus* prevailed over *Ascophyllum* in the competitive battles in both treatments. The output ratios of submerged and emerged treatments were separately plotted, showing that the relative growth of the two species was altered by the duration of submergence (Table 4). It was greater in submerged than emerged treatments, indicating that the growth of *Fucus* is more enhanced by submergence than

Table 2. Linear regression equations (p < 0.05) for the mortality of germlings in monoculture and mixture of *Fucus vesiculosus* and *Ascophyllum nodosum* at submerged and emerged (6 h/12 h) treatment

Exposure	Species	Equation	r^2	ANCOVA results
Monoculture				
Submerged	*Fucus*	M = 1.64D + 7.23	0.56	$F_{1,29}$=51.34;
	Ascophyllum	M = 3.58D + 4.95	0.77	(p < 0.001)
Emerged	*Fucus*	M = 2.69D + 10.50	0.60	$F_{1,29}$=44.30;
	Ascophyllum	M = 2.73D + 14.18	0.61	(p < 0.001)
Mixtures				
Submerged	*Fucus* + *Ascophyllum*	M = 4.24D + 4.08	0.50	$F_{1,117}$=110.83;
Emerged	*Fucus* + *Ascophyllum*	M = 5.59D + 9.85	0.45	(p < 0.001)

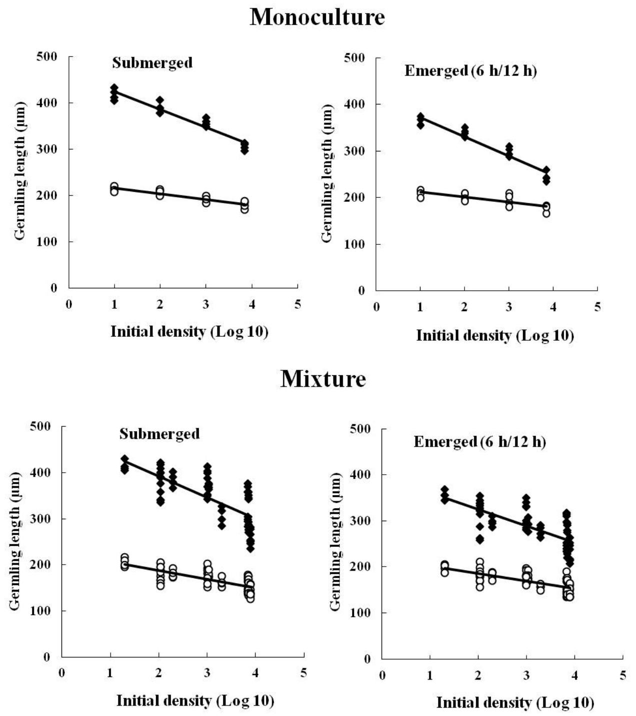

Figure 3. Mean lengths of *Fucus vesiculosus* and *Ascophyllum nodosum* germlings grown in monocultures and in mixtures at submerged and emerged (6 h/12 h tidal cycle) conditions. Germlings were cultured for 3 weeks in the tidal tanks (n=4 replicates).

that of *Ascophyllum* as in monocultures.

2. Effects of nutrient on the competition of germlings

The mortality of *Fucus* and *Ascophyllum* increased with density and nutrient concentration both in the monocultures and the mixtures. In monoculture, the mortality of *Ascophyllum* was significantly higher than that of *F. vesiculosus* in high nutrients but not in low nutrients (Table 5). In monoculture of each species, the mortality of germlings was significantly influenced by nutrient concentration for *Ascophyllum* (ANCOVA, $F_{1,29}$ = 7.23, p<0.05) but not for *Fucus* ($F_{1,29}$ = 0.17, p = 0.68). In mixtures, total mortality of germlings was significantly higher at high than low nutrients (Table 5).

Nutrients influenced the growth of *Fucus* and *Ascophyllum* cultured at different densities and relative frequencies of the two species. Both in high and low nutrients, *Fucus* always grew significantly faster than *Ascophyllum* both in monoculture and mixtures (Table 6), and the effect of density on the growth was greater in *Fucus* than *Ascophyllum*.

In monocultures of each species, the growth of germlings was better in high nutrients for *Fucus* (ANCOVA, $F_{1,29}$ = 196.32, p<0.001), whereas in low nutrients for *Ascophyllum* (ANCOVA, $F_{1,29}$ = 52.82, p<0.001). In mixtures, log output ratio was different between low and high nutrients (Figure 5). The values of log output ratio were more than 0.1, indicating that *Fucus* 'won' in the competitive battles with *Ascophyllum* at both nutrient levels. The output ratios of low and high nutrients were separately plotted, showing that the relative growth of the two species was altered at two nutrient levels (Table 7). Log output ratio was greater in high than in low nutrients, indicating that the growth of *Fucus* is more enhanced than that of *Ascophyllum* in high nutrients.

DISCUSSION

On the mid shore, the vertical distribution of *Ascophyllum* is wider than that of *Fucus vesiculosus* (Lewis, 1964; Schonbeck and Norton, 1978) and the juveniles of the former are occasionally found on the their uppermost areas (Lewis, 1964). In the present study, *Ascophyllum* is likely to benefit when competing with *Fucus* both under periodical emergence and under low nutrient levels. The results well agree with the responses of adult plants. *Ascophyllum* recovers rapidly than *Fucus* when they are resubmerged after desiccation (Brinkhuis *et al.*, 1976; Strömgren, 1977). *Ascophyllum* grows well in summer when nutrient levels are minimal (Mathieson *et al.*, 1976; Vadas *et al.*, 1976; Hardwick-Witman and Mathieson, 1986) and on sheltered shores, where nutrient circulation is less than exposed shores (Lewis, 1964; Keser *et al.*, 1981; Keser and Larson, 1984). In contrast, the growth of *Fucus* is higher in high nutrients than in low nutrients and produces two types of hairs, apical and hyaline, which serve to enhance nutrient uptake at low nutrient concentrations (Schonbeck and Norton, 1978; Galvin, 1988).

Mortality and growth of germlings in monoculture and mixtures of *A. nodosum* and *F. vesiculosus* were density-dependent, indicating that intraspecific- and interspecific competition occurred between germlings, irrespective of cohorts or competitors. The presence of intraspecific and interspecific competition between germlings of the two species were identified with are placement experimental design (density is constant with 500 zygote/㎠ but relative proportion of the two species is changed) by Choi and Norton(2005b). They also reported the facilitation between the two species in the germling stage that *F. vesiculosus* enhanced the survival of *A. nodosum* germlings under stressful field condition. In the present study, germling competition was more severe at higher density than at lower density but positive density effects were not found even in the emerged treatment. Recently, intraspecific and interspecific competition between germlings of *Pelvetia canaliculata* and *Fucus spiralis* were also found in artificial tidal tanks, and *Pelvetia* grew better at 6 h exposure treatment than at continuous submerged treatment (Kim *et al*., 2011). So far, growth responses of germlings were species specific under various environmental conditions and more detailed physiological research for germlings should be performed.

In the present study, the outcome of interspecific competition between germlings of *F. vesiculosus* and *A. nodosum* was slightly altered by duration of emergence and nutrient concentration, but not to such an extent as to change the outcome as found in *F. spiralis* and *P. canaliculata* (Kim *et al*., 2011). There are many stressful environmental factors such as high-temperature and irradiance on the rocky shore, and eutrophication and climate change (i.e., ocean acidification and sea water temperature increase) by human activity, these environmental factors might change seaweed community structure. Thus, to understand tiny germling worlds, we need to study on the growth and survivorship of germlings in order to know the combined effects of various environmental factors. Present results revealed that the responses of germlings to environmental stresses are different between fucoid species but we have to study in detail to understand their distribution on the shore.

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REFERENCES

Andrew, N. L. and R. M. Viejo(1998) Effects of wave exposure and intraspecific density on the growth and survivorship of *Sargassum muticum* (Sargassaceae: Phaeophyta). European Journal of Phycology 33: 251-258.

Ang, P. O., Jr and R. E. De Wreede(1992) Density-dependence in a population of *Fucus distichus*. Marine Ecology Progress Series 90: 169-181.

Brawley, S. H. and L. E. Johnson(1991) Survival of fucoid embryos in the intertidal zone depends upon developmental stage and microhabitat. Journal of Phycology. 27:179-186.

Brinkhuis, B. H., N. R. Tempel and R. F. Jones(1976) Photosynthesis and respiration of exposed salt-marsh fucoids. Marine Biology 34: 349-359.

Ceccherelli, G. and F. Cinelli(1997) Short-term effects of nutrient enrichment of the sediment and interactions between the seagrass *Cymodocea nodosa* and the introduced green alga *Caulerpa taxifolia* in a Mediterranean bay. Journal of Experimental Marine Biology and Ecology 217: 165-177.

Choi, H. G. and T. A. Norton(2005a) Competitive interactions between two fucoid algae with different growth forms, *Fucus serratus* and *Himanthalia elongata.* Marine Biology 146:283-291.

Choi, H. G. and T. A. Norton(2005b) Competition and facilitation between germlings of *Ascophyllum nodosum* and *Fucus vesiculosus*. Marine Biology 146: 525-532.

Creed, J. C., T. A. Norton and J. M. Kain(1996) Are neighbours harmful or helpful in *Fucus vesiculosus* populations? Marine Ecology progress Series 133: 191-201.

Creed, J. C., T. A Norton and J. M. Kain(1997) Intraspecific competition in *Fucus serratus* germling: The interaction of light, nutrients and density. Journal of Experimental Marine Biology and Ecology 212: 211-223.

Davison, I. R., L. E. Johnson and S. H. Brawley(1993) Sublethal stress in the intertidal zone: tidal emersion inhibits photosynthesis and retards development in embryos of the brown alga *Pelvetia fastigiata*. Oecologia 96: 483-492.

Davision, I. R. and G. A. Pearson(1996) Stress tolerance and in intertidal seaweeds. Journal of Phycology 32: 197-211.

Dring, M. J. and F. A. Brown(1982) Photosynthesis of intertidal brown algae during after periods of emersion: a renewed search for physiological causes of zonation. Marine Ecology Progress Series 8: 301-308.

Enright, C. T.(1979) Competitive interaction between *Chondrus crispus* (Florideophyceae) and *Ulva lactuca* (Chlorophyceae) in *Chondrus* aquaculture. Proceedings International Seaweed Symposium 9: 209-218.

Fujita, R. M.(1985) The role of nitrogen status in regulating transient ammonium uptake and nitrogen storage by macroalgae. Journal of Experimental Marine Biology and Ecology 92: 283-301.

Galvin, R. S.(1988) The role of hyaline hairs in *Fucus*. Ph. D. Thesis, University of Liverpool, Liverpool, 303pp.

Hardwick-Witman, M. N. and A.C. Mathieson(1986) Tissue nitrogen and carbon variations in New England estuarine *Ascophyllum nodosum* (L.) Le Jolis populations (Fucales, Phaeophyta). Estuaries 9: 43-48.

Hruby, T. and T. A. Norton(1979) Algal colonization on rocky shores in the Firth of Clyde. Journal of Ecology 67: 65-77.

Kain, J. M. and N. S. Jones(1964) Aspects of the biology of *Laminaria hyperborea* Ⅲ. Survival and growth of gametophytes. Journal of the Marine Biological Association of the United Kingdom 44: 415-433.

Keser, M., R. L. Vadas and B. R. Larson(1981) Regrowth of *Ascophyllum nodosum* and *Fucus vesiculosus* under various harvesting regimes in Marine, U.S.A. Botanica Marina 24: 29-38.

Keser, M. and B. R. Larson(1984) Colonization and growth of *Ascophyllum nodosum* (Phaeophyta) in Marine. Journal of Phycology 20: 83-87.

Kim, B. Y., S. K. Park., T. A. Norton and H.G. Choi(2011). Effects of temporary and periodic emersion on the growth of *Fucus spiralis* and *Pelvetia canaliculata* germlings. Algae 26(2): 193-200.

Knight, M. and M. Parke(1950) A biological study of *Fucus vesiculosus* L. and *F. serratus* L. Journal of the Marine Biological Association of the United Kingdom 29: 439-514.

Lewis, J. R.(1964) The ecology of rocky shores. English Universities Press, London, 323pp.

Maberly, S. C. and T. B. Madsen(1990) Contribution of air and water to the carbon balance of *Fucus spiralis*. Marine Ecology Progress Series 62: 175-183.

Mathieson, A. C., J. W. Shipman., J. R. O'Shea And R. C. Hasevlat(1976) Seasonal growth and reproduction of estuarine fucoid algae in New England. Journal of Experimental Marine Biology and Ecology 25: 273-284.

Peckol, P. and J. S. Rivers(1995) Competitive interactions between the opportunistic macroalgae *Cladophora vagabunda* (Chlorophyta) and *Gracilaria tikvahiae* (Rhodophyta) under eutrophic conditions. Journal of Phycology 3: 229-232.

Reed, D. C., M. Neushul and A.W. Ebeling(1991) Role of settlement density on gametophyte growth and reproduction in the kelps *Pterygophora californica* and *Macrocystis pyrifera* (Phaeophyceae). Journal of Phycology 27: 361-366.

Schonbeck, M. and T. A. Norton(1978) Factors controlling the upper limits of fucoid algae on the shore. Journal of Experimental Marine Biology and Ecology 31: 303-313.

Schonbeck, M. W. and T. A. Norton(1980) The effects on intertidal fucoid algae of exposure to air under various conditions. Botanica Marina 23: 141-147.

Sokal, R. R. and F. J. Rohlf(1981) Biometry, 2nd edn. W. H. Freeman and Co., New York, 859pp.

Strömgren, T.(1977) Short-term effects of temperature upon the growth of intertidal Fucales. Journal of Experimental Marine Biology and Ecology 29: 181-195.

Vadas. R. L., M. Keser and P. C. Rusanowski(1976). Influence of thermal loading on the ecology of intertidal algae. In G. W. Esch & R. W. MacFarlane (eds.), Thermal Ecology Ⅱ (201-212pp.). ERDA Symposium Series (CONF-750425) Augusta.

Vadas, R. L., S. Johnson and T. A. Norton(1992) Recruitment and mortality of early post-settlement stages of benthic algae. British Phycological Journal 27: 331-351.