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Phenology of Marine *Enteromorpha compressa* (L.) Greville (Ulvales, Chlorophyceae) Growing along Tidal Levels

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潮位에 따른 海產 綠藻 납작파래 (*Enteromorpha compressa* (L.) Greville)의 生物季節

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ABSTRACT

Phenological study of *Enteromorpha compressa* was conducted monthly from May 1990 to April 1991 in tide pools at three tidal zones of Paekpori, the southern coast of Korea. Although water temperature did not differ significantly among all tidal zones investigated, absence of macroscopic plants during summer was correlated with increasing water temperature. Salinity and suspended particulate matter (SPM) showed statistical differences between high and middle tidal zones, as well as high and low tidal zones. But, the differences in salinity or SPM among tidal zones did not comparatively coincide with the phenological pattern. The frequencies of occurrence of microscopic and macroscopic samples at high tidal zone were always lesser than or equal to those at other zones. At high tidal zone individuals completed the life history at least twice in a year, surviving for about four months, whereas at low and middle tidal zones they completed it once in a year, surviving for about six months.

INTRODUCTION

Seawater temperature fluctuates seasonally, and in many cases affects as a determine factor for seaweeds in geographical distribution. Tolerance to the extreme of temperature can also be an important factor in determing algal distribution on the shore environments (Round, 1981). Growth responses to the temperature are often quite useful in distinguishing the seasonality (Chock and Mathieson, 1978) or in recognizing differences among the characteristic populations (Dawes *et al.*, 1978). In addition, in many cases, salinity can also be an important factor affecting local distribution of marine algae (Wiencke and Lauchli, 1980).

The growth of benthic algae often benefits by increasing amount of various nutrient levels, and the sewage pollution on a beach often results of the rapid growth of green algae *Enteromorpha* and *Ulva* (Clark, 1986). The algae particularly in intertidal zone are subject to wide fluctuations in environmental conditions, and many variations in morphology and mode of reproduction are well recognized (Lobban, 1981). For instance, intertidal algae become very well established in the areas of most favourable to their physiology which give them a competitive advantage over other species in the habitat.

The marine species of *Enteromorpha* are widely distributed in littoral zones of the arctic, temperate and tropical seas, where they grow on rocks, pebbles, woodworks, shells, or some other algae. Most species have a wide range of salinity tolerance, and are found in bays, estuaries, and inland bodies of salt water, and occasionally of freshwater (Taft, 1964). They often grow in the intertidal zone as an autumn-spring annual, particularly common in the areas of polluted waters.

The thalli of *Enteromorpha compressa* are mostly tubular, simple or branched, and cylindrical to compressed. They are attached to substratum by rhizoids from basal cells. The vegetative cells are uninucleate. Each contains a single cup-shaped chloroplast with one or more pyrenoids. The life history is typically of an isomorphic haplodiplontic type, yet sometimes reproducing only by zoospores (Bliding, 1963; Koeman and Hoek, 1982).

Zoosporogenesis in algae is reported to be influenced by light, temperature, nutrients, osmotic shocks and hydrostatic pressure (Shameel, 1973; Dring, 1974). However, the relative importance of these factors for induction of zoospores in *Enteromorphas* is unknown. The seasonality of reproduction is also in question. Some workers observed reproduction throughout the growing seasons (Pringle, 1986), while the others found it limited to winter (Gayral, 1960; Christie and Evans, 1962; Townsend and Lawson, 1972).

The most commonly reported life cycle for members of the genus *Enteromorpha* is an alternation of isomorphic generations (Hartman, 1929; Ramanathan, 1939). Little information is available, however, on the distribution of each phase in relation to local environmental factors. Yamada and Saito (1938) noted that 93% of *E. compressa* fronds investigated discharged zoospores thus to be sporophytes. Arasaki and Shihira (1959) insisted that gametophytes could be located, but they varied with seasons and other environmental conditions.

The objective of this study is to identify spatial and temporal growth pattern of *E. compressa* in intertidal zone. For this, frequency of occurrence in microscopic and macroscopic plants, and length and fertility of individuals were made from three tidal levels during a year.

MATERIALS AND METHODS

Phenological study for *Enteromorpha compressa* was conducted in tide pools at low, middle and high tidal zones of Paekpori (34° 36'N; 127° 47'E), the southern coast of Korea, monthly from May 1990 to April 1991.

In order to clarify exposure duration to air, the height in each tidal level was determined using a surveyer's level and rod; measurements were made for two consecutive days. The change of sea level as time elapsed was compensated with data from tide tables of Yeosu (Anonymous, 1990-1991). Air and water temperatures, salinity, and suspended particulate matter were measured at every collection.

Sampling for a large sample (macroscopic plants), longer than 0.2 cm in length, was made within 100 small quadrats with 10 cm×10 cm, which were set permanently. The quadrat size was determined as minimal area in preliminary sampling. The presence and absense of samples within the small quadrats were tallied at three different levels of tidal zone. These samplings were made 5 replicates at each level. To clarify the phenological changes the investigation was carried out monthly because the algal population did not change rapidly.

Besides, sampling for a tiny sample (microscopic plants), less than 0.2 cm in length observed under the microscope, was made to scrap with a chisel in 1×1 cm^2 area. The 40 cells sampled were selected randomly among the 100 small quadrats. Total number of tiny sampling were made with in 200 cells. Samples collected were put into a vial and brought to laboratory.

The growth of *E. compressa* was measured by thallus length per individual. The fertility was determined by a percentage of fertile individuals to samples of more than 40 individuals. The number of individuals for sample data was determined from a curve of number versus variance depicted from preliminary investigation during the most luxuriant growth of plants.

Differences of environmental factors or phenological data among the tidal leves were tested statistically using a Student's T-test (Sokal and Rohlf, 1981).

Table 1. Height above mean low water, emersion time to air, salinity and suspended particulate matter (SPM) for three tidal zones at Paekpori during the study period

Tidal zone	Height above mean low water (cm)	Emersion time (h/month)	Salinity (‰)	SPM (mg/l)
Low	120	181	28.4-30.5	22-72
Middle	150	282	28.5-30.5	32-82
High	170	364	12.4-26.5	55-125

RESULTS

Three tidal zones were situated to cover the environmental gradients by different emersion time to air, salinity, and suspended particulate matter (Table 1). Heights above mean low water at high, middle, and low tidal zones during this study were about 170, 150, and 120 cm, respectively. Therefore, the longest emersion time to air occurred at high tidal zone, 364 h/month on an average

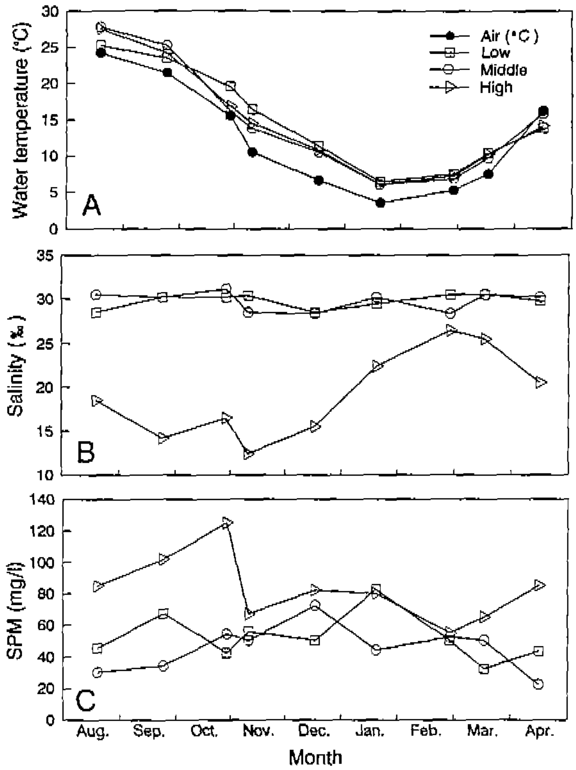

Fig. 1. Changes of mean air temperature, water temperature, salinity and suspended particulate matter (SPM) at low, middle, and high tidal zones, where *Enteromorpha compressa* is growing during the study.

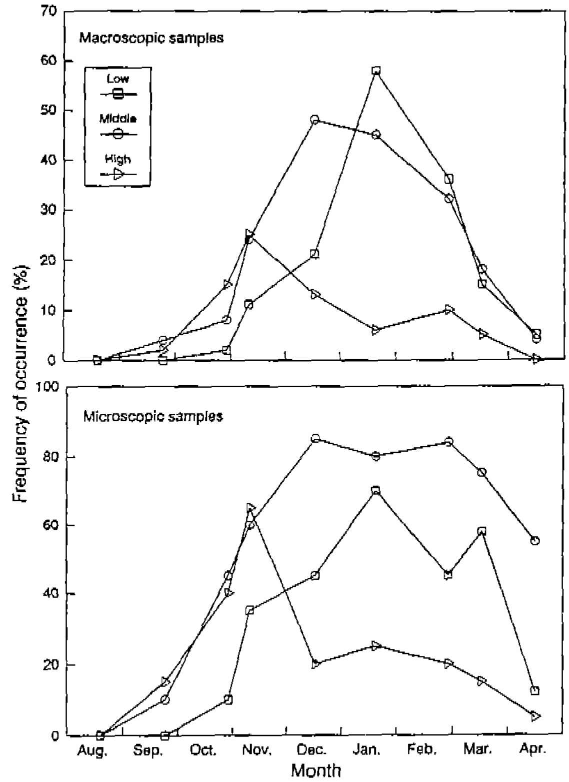

Fig. 2. Frequency of occurrence of *Enteromorpha compressa* for macroscopic (large plants) and microscopic (tiny plants) samples as a percentage of total quadrats at low, middle, and high tidal zones at Paekpori during the study.

and the lowest at low tidal zone, 181 h/month on an average.

Monthly water temperature, salinity, and suspended particulate matter (SPM) were showed in Fig. 1. Water temperature at three tidal levels (low, middle, and high tidal zones) varied from 6.4 to 28.0℃ through out the study period (Fig. 1A), and it was positively correlated with monthly mean value of air temperature ($r=0.96$, $p<0.001$). At all tidal zones, the highest water temperature occurred during August, and the lowest during next January. In general, the water temperature gradually decreased after August to January, followed by a gradual rise. On the basis of T-test the differences of water temperature among those zones in each month were not significant.

The salinity fluctuated throughout the study period, exhibiting a range from 12.4 to 30.5‰ (Fig. 1B). At high tidal zone, it increased gradually from November to next February, but at low and middle tidal zones it was relatively stable throughout the study period. The differences in salinity between low and high tidal zones, and between middle and high tidal zones were statistically significant at $p<0.05$, whereas no significant difference was recognized between low and middle tidal zones.

SPM contents ranged from 22 to 125 mg/*l* (Fig. 1C). Maximum SPM was recorded during October at high tidal zone, followed by a steep decrease. At low and middle tidal zones, comparatively low but recognizable fluctuations were recorded throughout the study period. The differences in SPM on the basis of T-test between low and high tidal zones and between middle and high tidal zones in autumn were statistically significant at $p<0.05$, whereas no significant difference was recognized between low and middle tidal zones.

The frequencies of occurrence of macroscopic samples (above 0.2 cm in length) obtained from quadrat method were shown in Fig. 2. The macroscopic samples were

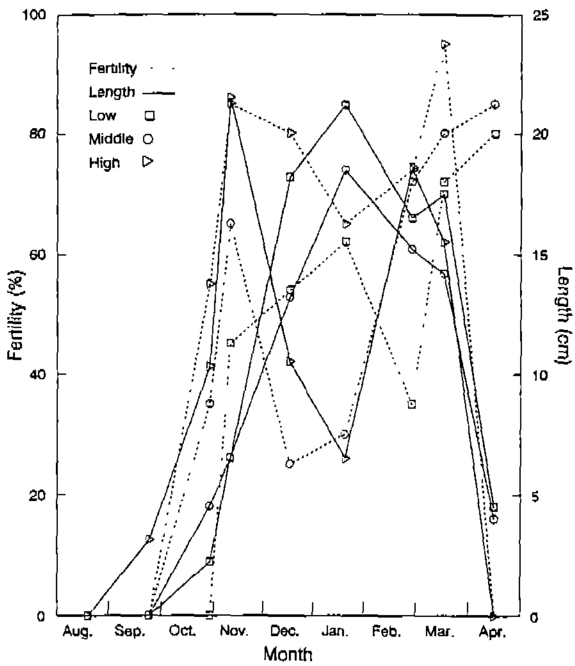

Fig. 3. Growth in length and fertility analyzed by reproductive structures in macroscopic *Enteromorpha compressa* at low, middle, and high tidal zones at Paekpori during the study.

nearly absent during August at both middle and high tidal zones, and from August to September at low tidal zone. However, the frequencies of occurrence of microscopic samples (below 0.2 cm in length) from scraped sampling method indicated that individuals in filamentous form were present at middle and high tidal zones in September and at low tidal zone in October. These filamentous plants appeared to be an early stage of development, eventually growing to macroscopic thalli. At low, middle, and high tidal zones, macroscopic samples occurred in the highest frequency of occurrence in January, December, and November, respectively.

Pearson's product-moment correlation analysis suggested that the frequency of occurrence of macroscopic samples was correlated with water temperature and not with emersion time to air, salinity, and suspended particulate matter. The frequency of occurrence of macroscopic samples negatively correlated with water temperature ($r=-0.84$, $p<0.01$ and $r=-0.79$, $p<0.05$, respectively) at low and middle tidal zones, but it was not significant ($r=-0.37$, $p=0.33$) at high tidal zone.

On the other hand, individuals at high tidal zone showed a growth phenology exhibiting a maximum length both in November and February, but those at middle and low tidal zones had maximum length in January (Fig. 3). At high tidal zone, individuals appeared in September and grew rapidly, reaching the maximum length of about 22 cm on the average in November when approximately 85% individuals were fertile. They decreased in length to about 1.6 cm in January. New germlings appeared again in January and grew to another maximum length in February showing about 18 cm in length and 75% of individuals to be fertile. At low and middle tidal zones, however, no new growth was visible until September. The new plants appeared later in October and grew to a maximum length in about 22 and 18 cm on the average in January. About 62 and 65% of individuals were fertile to liberate swarmers at respective tidal levels. Since March, the length of individuals abruptly decreased, but they maintained relatively high fertility.

Fertile plants released both bi- and quadri-flagellate swarmers at all tidal zones from late October to March of next year, although sexual reproduction was not observed at all tidal zones.

Consequently, at high tidal zone individuals completed the life history at least twice in a year, surviving for about four months, whereas at low and middle tidal zones they completed it once, surviving for about six months.

In comparison of three tidal zones, the water temperature did not differ significantly at all tidal zones investigated. Salinity and SPM showed statistical differences between high and middle tidal zones, and high and low tidal zones, but they were not different between low and middle tidal zones. The frequencies in occurrence of macroscopic and microscopic samples at high tidal zone were always lesser than or equal to those at middle and low tidal zones (Fig. 2), while those between low and middle or high tidal zones were not significantly different.

The differences in salinity or SPM among tidal zones generally occurred during the autumn and did not comparatively coincide with those in frequencies of macroscopic or microscopic samples which appeared from December to March. No differences among the tidal zones regarding substrate type were found, as the substrate generally being rock. SPM contents at high tidal zone were almost always higher than those of low and middle tidal zones, even in autumn. However, the correlations of frequencies of macroscopic or microscopic samples and SPM were not significant at all tidal zones.

DISCUSSION

Environmental factors which may affect the settlement and early growth of their reproductive swarmers are important in relation to the colonization of the algae on substratum and other submerged surface in the sea. The species of *Enteromorpha* occur in intertidal habitat, where the irradiance, temperature, salinity and nutrients are variable. Under such varying environmental conditions, both settlement and germination of the swarmers may also vary, and the algal growth is limited by these factors (Woodhead and Moss, 1975).

Enteromorphas are most common green algae occurring from tide pools to the lower tidal zone (Arasaki and Shihira, 1959). Kapraun (1970) and Kapraun and Flynn (1973) reported that they occurred from autumn to late spring in the vicinity of Taxas and Central America. The absence of macroscopic *E. compressa* in summer at Paekpori, the southern coast of Korea, seems to be correlated with the increase of water temperature. They often grow at intertidal zone as an autumn-spring annual (Fig. 2).

Similarly, Christie and Evans (1962) proposed that the seasonal change of *Enteromorpha* in dominance of occurrence was related to a change of water temperature, when it was dropped below 20℃. In contrast, Zaneveld and Barnes (1965) collected *Enteromorphas* during the summer months. Pringle (1986) found that *E. intestinalis* was present when water temperature was above 10℃, and the swarmers were produced in temperature ranging from 14 to 26℃. Clearly, there is considerable variability in response to temperature on growth of *Enteromorphas*.

The presence of viable microscopic algal filaments of *E. compressa* in the late summer suggests that environmental conditions prevent more rapid growth of the alga.

The species of *Enteromorpha* have been considered a highly salinity-intolerant species, normally occurring in eulittoral zone (Kim *et al.*, 1991). In present investigation, *E. compressa* was found to occur in high tidal zone with lower salinity. Interestingly, the frequency of occurrence of macroscopic samples in middle and low tidal zones with higher salinity and lower suspended particulate matter (SPM) was always greater than or equal to the frequencies found in high tidal zone (Fig. 2).

On the other hand, although water temperature did not significantly vary among high, middle or low tidal zones throughout the year, the statistical differences between tidal zones occur in salinity and SPM (Fig. 1). Since these differences are not common through out the year and occur during autumn months, they probably have little influence on frequency in occurrence or growth and fertility of the alga during winter months. The statistical differences between the high tidal zone and low or middle tidal zones in salinity and SPM are not likely the reason for differences in the frequency in occurrence, length of individuals, and fertility of plants.

Phenology of *E. compressa* also seems to be affected mainly by the water temperature. At high tidal zone, *E. compressa* exhibits a bimodal pattern of seasonality in growth and fertility, showing the peak twice in a year, whereas at middle to low tidal zone once in a year. According to Bliding (1939), *E. compressa* in Sweden becomes fertile from April to October, whereas it liberates swarmers from October to April of next year in this study. It is noticeable that the fertility of *E. compressa* in maximum differs among the three tidal zones by about 85% in high tidal 62% in middle, and 65% in low tidal zones (Fig. 3).

An inverse relationship between seasonal mean of dry weight and ambient temperature was shown by Gaur *et al.* (1982) for *Ulva lactuca* from Veraval coast of India, and by Murthy *et al.* (1978) for intertidal algae at Port Okha in the western coast of India. Mathieson and Burns (1975), Niemeck and Mathieson (1976), and Hansen (1977) had shown that maximum growth of intertidal seaweeds in cold climate was related to an increase of air temperature and day length. However, peak summer temperature resulted to die back of seaweeds.

In temperate climates, subtidal perennial seaweeds grow faster in winter. There is also a winter annual flora of fast growing seaweeds. However, what appears to limit the growth of intertidal seaweeds in temperate climates is the high summer temperature but not the low winter temperature (Murthy *et al.*, 1989).

Kim *et al.* (1991) showed that different species of *Enteromorphas* responded in a different way to temperature changes. *E. linza* was reported to grow best at 15℃, while *E. prolifera* had their maximum growth around 15-20 ℃.

E. compressa requires relatively lower temperature optimum, and exhibits higher growth rates over broad temperature range, so that it had benefit in littoral tide pools where the pronounced thermal changes occur particularly in winter. This shows a similar result of *Ulva lactuca* that the optimum water temperature is 15℃ and the growth is restrained under 25℃ or 5℃ (Fortes and Lüning, 1980). *E. compressa* loses the fronds in summer under 27-30℃, begins to emerge below 20℃ in autumn, and is prosperous under 10-18℃ in the field. Consequently, the temperature can be important to determine the phenology of this alga.

적 요

해산 녹조 납작파래 (*Enteromorpha compressa*)의 조위에 따른 생물계절적 특성을 이해하기 위하여 여천군 돌산도 백포리 해안에서 1990년 5월부터 1991년 4월까지 출현빈도, 길이 및 성숙도를 매달 조사하였다. 수온은 모든 조위간에서 차이가 없었으나 출현빈도의 연중 변동과 높은 상관을 보였다. 염분도와 부유성 고형물질량은 상부와 중부 그리고 상부와 하부 간에 차이가 있었으나 생물계절과는 상관이 없었다. 조간대 상부에서 나타난 본 식물의 출현빈도는 중부와 하부에 비해 대체로 항상 작았다. 또한 상부의 개체들은 조사기간 동안 최소한 2회에 걸친 생활사를 보인 반면에 중부와 하부의 개체들은 약 6개월에 걸쳐 한번의 생활사를 보였다.

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