Jpn. J. Phycol. (Sôrui) 39: 173-178, June 20, 1991

Distributional pattern of *Ecklonia cava* (Phaeophyta) marine forest in the coast of Shima Peninsula, central Japan

Miyuki Maegawa and Washirou Kida

Laboratory of Phycology, Faculty of Bioresources, Mie University, Kamihama 1515, Tsu-shi, Mie Prefecture, 514 Japan

Maegawa, M. and Kida, W. 1991. Distributional pattern of *Ecklonia cava* (Phaeophyta) marine forest in the coast of Shima Peninsula, central Japan. Jpn. J. Phycol. 39: 173-178.

Distributional patterns and intraspecific associations of individuals in *Ecklonia cava* marine forest were studied with special reference to the structure, production ecology and regeneration process using Morisita's I_δ and R'_δ indices. Data were taken by the permanent quadrat method from 1982 to 1985. During a three year cycle, there were periodic yearly changes in the frequency distribution of stipe length i.e. regeneration process. The distributional pattern changed from contagious, through random, to regular distribution with progress of the regeneration process, gap, building and mature phases, respectively. Its pattern of changes was quite similar to that of dominant tree species of terrestrial forests. Severe intraspecific competition was also found between young and adult individuals. The distributional pattern is a result of intraspecific competition for getting light through the regeneration process, according to such a density-dependent function as self-thinning.

Key Index Words: distributional pattern—Ecklonia cava—*intraspecific competition—Phaeophyta-regeneration process—self thinning.*

Ecklonia cava Kjellman (Laminariales, Phaeophyta) has a wide distribution along the central to southern Pacific coast of Japan. It forms a dense and expansive marine forest in the sublittoral zone at a depth of 3-30 m as does *Eisenia bicyclis* Setchell, the latter occupying shallower water than the former. *Ec. cava* is perennial and has the potential to live at least 5 years (Hayashida 1977, Maegawa *et al.* 1988), and therefore population density and structure of this species depend to some extent on the number of recruitments and losses in a growing site.

In our previous papers (Maegawa *et al.* 1988, Maegawa and Kida 1989), we found periodic regeneration of *Ecklonia cava* marine forests and intraspecific competition for getting light by using the permanent quadrat method. Recent ecological research of macroalgal populations have represented a quantitative discipline designed to produce statistically interpretable analyses of biotic distribution and abundance patterns within defined habitats (Dayton *et al.* 1984). Nondestructive measurements, such as utilizing permanently marked sampling locations, provide a powerful method for evaluating the natural changes in dispersion of individuals and intra- and interspecific competition (Littler and Littler 1985).

In general, individuals in the population are distributed according to three fundamental patterns as follows; random, uniform and contagious distributions (Odum 1971). Random distribution is relatively rare in nature, occurring where the environment is very uniform and there is no tendency to aggregate. Uniform distribution may occur where competition between individuals is severe or where there is positive antagonism which promotes even spacing. Contagious distribution with various degrees of clumping represents by far the most common pattern, when individuals are attracted.

A lot of knowledge has been accumulated about the distributional pattern of individuals in land plant populations (cf. Tagawa 1977). However, no experiments have yet been made which allow one to evaluate the probability that in algal populations distributional patterns change in seral stages with the process of regeneration. In this study, we intend to analyze the distributional pattern of individuals in *Ecklonia cava* marine forest with special references to structure, production ecology and regeneration process of the marine forest investigated in our previous papers (Maegawa and Kida 1987, 1989, Maegawa *et al.* 1988). This sort of study will provide the fundamental data for evaluating the intraspecific competition in marine forests.

Materials and Methods

Permanent quadrat experiments for analyzing the distributional pattern were carried out offshore at Hamajima, Shima Peninsula. In May 1982, a 1 m × 3 m quadrat constructed with ropes was set on a flat rocky substratum within the population at a depth of 8 m. The quadrat was divided into 6 small subquadrats for convenience of measuring and mapping. All individuals in the quadrat were marked by tagging sequentially numbered plastic plates (1 cm × 2 cm) around the holdfast for adult plants and plotting the position of individuals on a distribution map for young and small ones. The smallest juveniles marked in this study were 1-3 cm long which could be distinguished from ones of other species.

From the month when the plants were marked, presence or absence of individuals and plant size (stipe length) were measured by means of SCUBA diving. The census in the quadrat was carried out at two- or three-month intervals from 1982 to 1985. Total plants marked in the quadrat for 4 years reached 1000 individuals. Such numerous data enabled us to conduct a comprehensive study of distributional pattern.

Based on the quadrat technique for analyzing the spatial distribution of individuals in a population, there are many indices which express the degree of aggregation or departure from randomness of the distributional pattern. In this study we chose an index of dispersion, I_δ, by Morisita (1959a) and an index of interspecific association, R'_δ, by Morisita (1959b), both of which were influenced neither by the average number of individuals per quadrat nor by the number of quadrats.

In Morisita's I_δ-quadrat size relation, I_δ is a measure of dispersion of individuals in a population which takes the value of unity. When the individuals are distributed at random over the area and the number of individuals is very large, I_δ is almost 1. When the individuals are distributed uniformly over the area, I_δ takes the value smaller than 1. When the distribution of individuals is contagious, I_δ is larger than 1.

In addition, Morisita's index of interspecific association, R'_δ, was also used. We applied this index to analyze the intraspecific correlation between young, small fronds and adult, large fronds in *Ecklonia cava* population in the permanent quadrat, although the R'_δ index was developed for analyzing interspecific association or competition. In Morisita's R'_δ-quadrat size relation, when two species (or groups) are distributed independently of each other, R'_δ is almost 0. When the distributional pattern of two species is attractive or repulsive, R'_δ takes a value from 0 to 1 or from -1 to 0, respectively.

In this study, data for analyzing the distributional pattern were offered from the permanent quadrat experiments. A quadrat (1 m × 3 m) was divided contiguously into 6 groups in size, 0.25 m × 0.25 m, 0.25 m × 0.5 m, 0.5 m × 0.5 m, 0.5 m × 1 m, 1 m × 1 m, 1 m × 2 m for computing the I_δ and R'_δ indices. The number of young and adult individuals were recorded for each subquadrat, and were used for detection of distributional pattern index of I_δ and intraspecific correlation index of R'_δ.

Results

Yearly changes of frequency distribution of the stipe length in the quadrat in June from 1982 to 1985 are shown in Fig. 1. Shaded parts showed the number of plants lost during a period till the following year. In 1982 large fronds with stipe length of more then 20 cm oc-

Fig. 1. Yearly changes in frequency distribution of stipe length of the *Ecklonia cava* population from 1982 to 1985. Shaded portions show the loss by the following year.

cupied greater parts, but in 1983 most of the large fronds in the canopy disappeared and many recruits were produced. In 1984 relatively large fronds which developed in 1983 occupied a large part of the population. In 1985 large fronds formed a dense canopy, showing a similar frequency distribution as in 1982. The population structure in 1983, 1984 and 1985 corresponds to gap, building and mature phase of the regeneration process, respectively, according to our previous paper (Maegawa and Kida 1989).

The number of recruits was controlled by the density of large fronds. After most of the large fronds forming the canopy were lost or drifted out, many recruits were produced and grew to the canopy 1-2 years later. Consequently, the turnover time (regeneration cycle) of the canopy layer of the *Ecklonia cava* marine forest was 3 years.

Fig. 2 shows the dispersion of individuals and the results of analysis of the distributional pattern and the intraspecific correlation of *Ecklonia cava* population in June 1982, which was in the typical mature phase. The distributional patterns were calculated in three groups; young individuals less then 20 cm in stipe length, adult individuals more than 20 cm in stipe length and total individuals. The intraspecific correlation was also computed between young and adult individuals.

Young individuals clearly had a contagious distribution which showed an I_δ value higher than one. It was also noticed that young individuals of *Ec. cava* had a small clump, and the intra-clump distribution was more or less regular. Consequently, the individuals in each clump had a tendency to keep some distance from each other, according to the classification of the distributional patterns by Morisita (1959a). On the other hand, adult individuals showed a regular distribution with a tendency to keep some distance from each other. The distributional pattern of total individuals was random. The intraspecific correlation between young and adult individuals was negative. This result indicates that two groups of young and adult individuals were repulsive to each other.

Fig. 3 shows yearly changes in dispersion of individuals which were recruited in 1983, and distributional patterns in June from 1983 to 1985 of the *Ecklonia cava* population. The dispersion of individuals in 1983, 1984 and 1985 represented the typical phase of gap, building and mature, respectively. In the gap phase in 1983, the distributional pattern was contagious, and thereafter it changed to random pattern of the building phase in 1984. From 1983 to 1984, the population density decreased rapidly as shown in the Fig. 1. Adult individuals in the mature phase in 1985 showed regular distribution. From 1984 to 1985, the population density decreased gradually. It was apparent that the distributional pattern changed with advance of the regeneration process and according to changes of the population density.

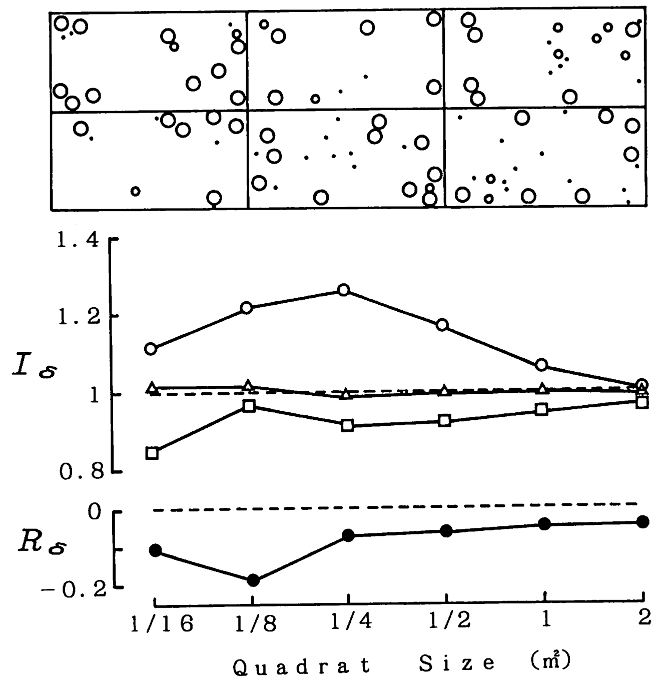

Fig. 2. Analysis of distributional patterns of the *Ecklonia cava* population in June 1982. Upper: Dispersion map of individuals in the permanent quadrat. The size of circles indicates the stipe length; large open circles, adult fronds longer than 20 cm; small open circles, young fronds of 10–20 cm; small solid circles, young fronds shorter than 10 cm. Middle: I_δ-quadrat size relationship for adult fronds (□), young fronds (○), and total fronds (△). Lower: Intraspecific association, R'_δ, between young fronds and adult fronds.

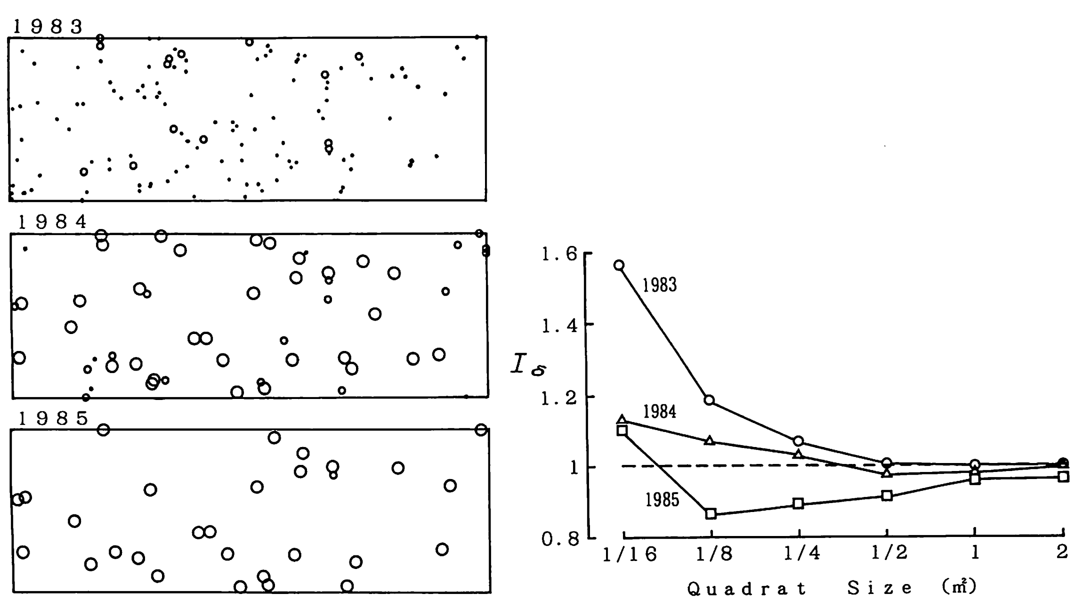

Fig. 3. Changes in the dispersion of individuals and corresponding I_δ-quadrat size relationships with advance of the regeneration process of the *Ecklonia cava* population from 1983 (○) through 1984 (△) to 1985 (□). The size of circles in the dispersion map indicates the stipe length; large open circles, longer than 20 cm; small open circles, 10–20 cm; solid circles, shorter than 10 cm.

Discussion

In this study, we found out that the distributional pattern of the *Ecklonia cava* population changes in accordance with certain principles, and with its density in the regeneration process. In other words, the change in distributional pattern with the process of regeneration is considered partly to be density-dependent. It is noteworthy that the competition between individuals of the same species is one of the most important density-dependent factors in plant communities.

In general, the distributional pattern of recruits in the gap phase is contagious. This is partially because the site available for growth of gametophytes or recruits is restricted by other sessile organisms or by the conditions of substratum, *i.e.* ups and downs of the population floor, and rock, boulder, gravel, or sand. The most important reason for the contagious distribution of recruits is the competition for getting light between young and adult individuals. Germination and growth of the recruits are suppressed by dim light just beneath the adult canopy fronds (Foster 1975, Gerard 1984, Hayashida 1986, Maegawa *et al.* 1988). As a result, the recruits can occupy only small openings where the canopy fronds leave some distance and light intensity is relatively high in the population.

The number of young fronds which fill the gap greatly decreases in the building phase. At this time, a strong intraspecific competition for light occurs according to the growth of each fronds (cf. Maegawa *et al.* 1988). This results in the death of many competitively inferior individuals which may be small and/or shaded, so that few competitively superior individuals survive and grow to canopy fronds. It is a typical model of "self-thinning". Individuals in the clump experience a stronger self-thinning than isolated individuals, so that the dispersion of individuals changes from contagious distribution to random distribution with the growth of fronds.

From the building to the mature phase, adult individuals which have reached sufficient height to form the canopy show a regular distribution, because competition for light is so great that the space occupied by individual fronds in the canopy tends to be nearly equal to each other. Such a change in the distributional pattern of *Ecklonia cava*, contagious to regular through random distribution, is quite similar to that of the dominant tree species of terrestrial forests of Type III by Tagawa (1965), although the period of the regeneration process of a marine forest is extremely shorter than that of a terrestrial forest. There appears to be fundamental similarity in behaviour at the biochemical, physiological population and community levels between at least some seaweeds and terrestrial higher plants, despite basic differences in structure and function as described in Cousens (1985).

It is concluded that one of the most important factors controlling the structure of algal population is the light condition in it as emphasized in our previous papers (Maegawa *et al.* 1988, Maegawa and Kida 1989). The distributional pattern is also a result of intraspecific competition for getting light through the regeneration process, according to such a density-dependent function as self-thinning.

References

Cousens, R. 1985. Frond size distributions and the effects of the algal canopy on the behavior of *Ascophyllum nodossum* (L.) Le Jolis. J. Exp. Mar. Biol. Ecol. **92**: 231–249.

Dayton, P. K., Currie, V., Gerrodette, T., Keller, B. D., Rosenthal, R. and Tresca, D. V. 1984. Patch dynamics and stability of some California kelp communities. Ecol. Monogr. **54**: 253–289.

Foster, M. S. 1975. Regulation of algal community development in a *Macrocystis pyrifera* forest. Mar. Biol. **32**: 331–342.

Gerard, V. A. 1984. The light environment in a giant kelp forest: influence of *Macrocystis pyrifera* on spatial and temporal variability. Mar. Biol. **84**: 189–195.

Hayashida, F. 1977. On age and growth of a brown alga, *Ecklonia cava* Kjellman, forming aquatic forest. Bull. Jap. Soc. Sci. Fish. **43**: 1043–1051.

Hayashida, F. 1986. Synecological studies of a brown alga, *Ecklonia cava*, forming aquatic forest-III. Structure of *Ecklonia cava* population. J. Fac. Mar. Sci. Technol. Tokai Univ. **22**: 159–169.

Littler, M. M. and Littler, D. S. 1985. Nondestructive sampling. p. 161–175. *In* M. M. Littler and D. S.

Littler [ed.], Handbook of Phycological Methods. Cambridge Univ. Press.

Maegawa, M. and Kida, W. 1987. Studies on production structures of *Eisenia bicyclis* and *Ecklonia cava* communities. Jap. J. Phycol. **35:** 34–40 (in Japanese).

Maegawa, M. and Kida, W. 1989. Regeneration process of *Ecklonia* marine forest in the coastal area of Shima Peninsula. Jpn. J. Phycol. **37:** 194–220.

Maegawa, M., Kida, W., Yokohama, Y. and Aruga, Y. 1988. Comparative studies in critical light condition for young *Eisenia bicyclis* and *Ecklonia cava*. Jpn. J. Phycol. **36:** 166–174.

Maegawa, M., Kida, W. and Aruga, Y. 1989. Demographic study of sublittoral brown alga *Ecklonia cava* Kjellman in a coast of Shima Peninsula. Jpn. J. Phycol. **36:** 321–327.

Morisita, M. 1959a. Measuring of the dispersion of individuals and analysis of the distributional patterns. Mem. Fac. Sci. Kyushu Univ. Ser. E. (Biol.) **2:** 215–235.

Morisita, M. 1959b. Measuring of interspecific association and similarity between communities. Mem. Fac. Sci. Kyushu Univ. Ser. E. (Biol.) **3:** 65–80.

Odum, E. P. 1971. Population structure: Internal distribution patterns (dispersion). p. 205–207. *In* E. P. Odum [ed.], Fundamentals of Ecology. W. B. Saunders Company, Philadelphia.

Tagawa, H. 1965. A study of the volcanic vegetation in Sakurajima, southwest Japan II. Distributional pattern and succession. Jap. J. Bot. **19:** 127–148.

Tagawa, H. 1977. Distributional pattern. p. 112–141. *In* S. Ito [ed.], Composition and Structure of Community. Asakurashoten. Tokyo (in Japanese).

前川行幸・喜田和四郎：三重県志摩半島沿岸におけるカジメ海中林の分散構造

漸深帯に大規模な海中林を形成する大型褐藻カジメ (*Ecklonia cava*) の分散構造と種内競争を，森下 (1959a, b) の I'_δ および R'_δ 法により解析した。用いたデータは，1982年から1985年にかけて三重県志摩半島浜島沿岸に設置された永久コドラートから得られた。茎長組成の年変化から，群落更新の周期は3年であることが確かめられた。分析構造は群落更新に伴って変化し，ギャップ相では集中分布，建設相ではランダム分布，成熟相では規則分布であった。このような海中林の分散構造の変化パターンは，陸上における森林の優占種のそれと基本的に同じであった。海中林内では林冠を形成する成体と幼体との間には，厳しい種内競争がみられた。海中林を形成する個体の分散構造は，群落の更新に伴う自己間引きのような密度依存的な作用と光に対する種内競争によって決定されるものと考えられた。（514 三重県津市上浜町1515 三重大学生物資源学部藻類増殖学研究室）