

Regeneration process of *Ecklonia* marine forest in the coastal area of Shima Peninsula, central Japan

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A regeneration process of the *Ecklonia* marine forest was studied with methods of permanent quadrat and mapping for 6 years. The regeneration process and turnover time were revealed as compared with those of terrestrial climax forests. Three phases of gap, building and maturation were distinguished with reference to structural and dynamic features of the population in the regeneration process. The turnover time (regeneration cycle) of the canopy layer was 3 years. The regeneration process of the *Ecklonia* marine forest was controlled by intraspecific competition for getting light.

Key Index Words: building phase—*Ecklonia cava*—gap phase—mature phase—Phaeophyceae—population dynamics—regeneration—seaweed.

It is considered that the marine climax forest is maintained by dynamic equilibrium, i.e. partial destruction and construction of the canopy. Consequently, the structure and function are stable for many years beyond the life expectancy of the major component individuals. The mechanisms of regeneration (secondary succession) of the marine climax forest are the subject of study attracting ecological interest of some researchers in recent years. However, only a little knowledge was accumulated for the change in population structure of marine forests throughout a long period of study for more than 5 years (TANIGUCHI and KATO 1984, DAYTON *et al.* 1984, KIDA and MAEGAWA 1985). The recent studies of stability and succession emphasize the need for the recognition of appropriate scales in time and space (SUTHERLAND 1981, CONNELL and SOUSA 1983). Particularly, the time scale should be longer than the maximum life span of the major component individuals in the study of population dynamics.

Recently, the regeneration processes of terrestrial climax forests in many countries have been studied intensively. Many authors

have emphasized that tree fall and opening in the canopy play an important role in terrestrial forest regeneration (BRAY 1956, BARDEN 1981, RUNKLE 1981). BRAY (1956) called such an opening the "gap", and the regeneration of terrestrial climax forests takes place mainly in such gaps. The process is named the "gap phase regeneration".

In this study, the regeneration process of marine *Ecklonia* forest was traced with methods similar to the ecological analysis used in terrestrial forests, such as permanent quadrat and mapping. The fundamental properties of structure and regeneration of marine *Ecklonia* forest are comparable well to those of terrestrial forests, in spite of notable differences in the scale of population and the turnover time of the regeneration cycle between them. This kind of information will be useful not only in evolving and examining the theory of succession and stability of marine forest but also in forest conservation and afforestation for its probability of application.

Materials and Methods

Permanent quadrat experiment for analyz-

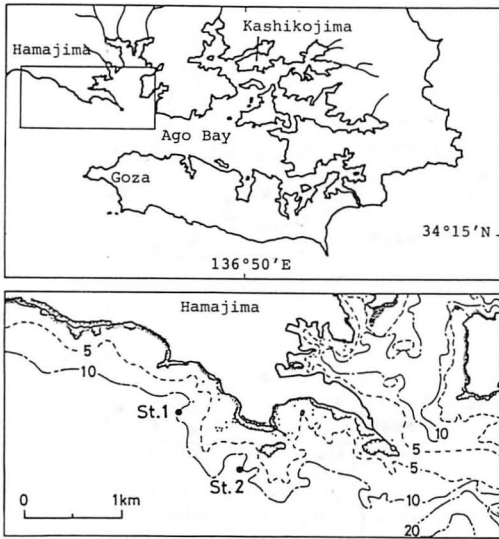


Fig. 1. Maps showing the location of study area.

ing the regeneration process of the *Ecklonia cava* population was carried out offshore at Hamajima (Fig. 1). In May 1982, 2 quadrats of 1 m × 3 m constructed with ropes were set on a flat rocky substratum within a population at a depth of 8 m at Stns. 1 and 2. Each quadrat was divided into 6 small sub-quadrats (0.5 m × 1 m) for convenience of measuring and mapping. All individuals in 2 quadrats 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 through June 1987, presence or absence of individuals and plant size (stipe length) were measured by means of SCUBA diving. The census in the quadrats was carried out 19 times at two- or three-month intervals from 1982 to 1984, and at six-month intervals from 1984 to 1987. Total plants marked in 2 quadrats for 6 years reached 1000 individuals. Such numerous data enabled us to conduct a comprehensive study of the changes in population structure.

Results

Yearly changes of frequency distribution of the stipe length in 2 quadrats in June from 1982 to 1987 are shown in Fig. 2. Shaded parts show the number of plants lost during a period till the following year. The yearly changes in frequency distribution of stipe length in both quadrats showed a similar tendency. In 1982 large fronds with stipe length of more than 20 cm occupied greater parts, but in 1983 most of large fronds in the canopy disappeared and many recruits were produced. In 1984 and 1985 large fronds which developed from recruits in 1982 and 1983 occupied a large part of the population, forming the canopy again. In 1986 most of canopy fronds disappeared and many recruits were produced, showing a similar frequency distribution as in 1983. Frequency distribution in 1987 showed a similar trend as that in 1984. Thus, the number of recruits was con-

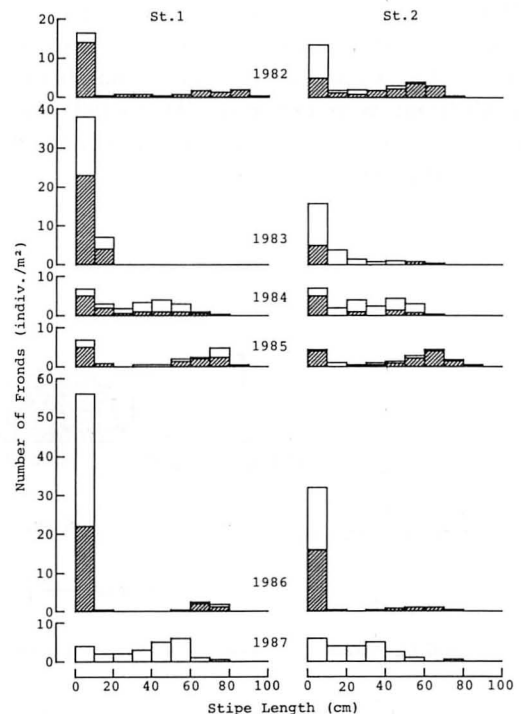


Fig. 2. Yearly changes in frequency distribution of stipe length of *Ecklonia cava* population at Stns. 1 and 2 from 1982 to 1987. Shaded portions show the loss during a subsequent year.

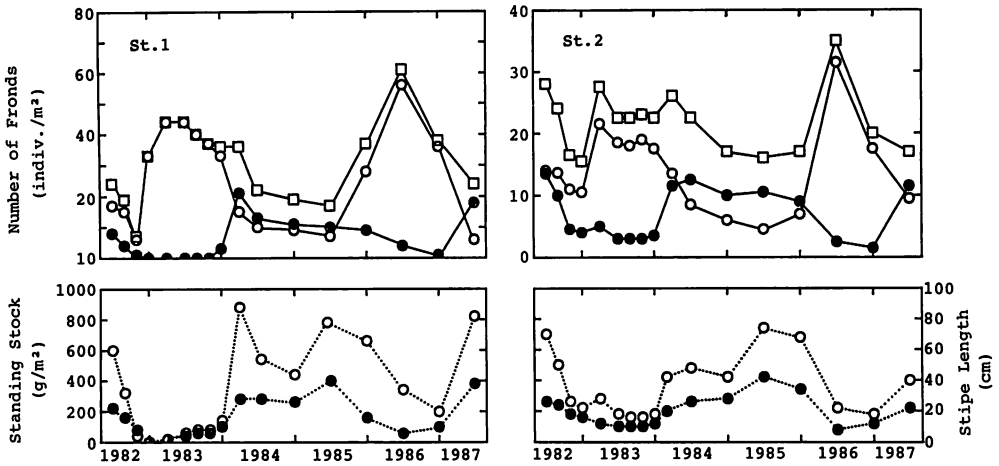


Fig. 3. Changes in the population density of total fronds (—□—), fronds with stipes shorter than 20 cm (—○—), fronds with stipes longer than 20 cm (—●—), average stipe length (---●---), and standing stock (---○---) of *Ecklonia cava* at Stns. 1 and 2 from 1982 to 1987.

trolled by the density of large fronds. After most of 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* marine forest was 3 years. A large number of adult fronds were lost from 1982 to 1983 and from 1985 to 1986, i.e. during the third and the fourth year from germination.

Fig. 3 shows seasonal and yearly changes in the density, standing stock and mean stipe length with advancement of the regeneration process in both populations at Stns. 1 and 2. Standing stock was calculated from the allometric relation between stipe length and total frond weight as indicated in a previous paper (MAEGAWA and KIDA 1984). Mean stipe length is the average for total fronds in the quadrat at every census. Therefore, it is

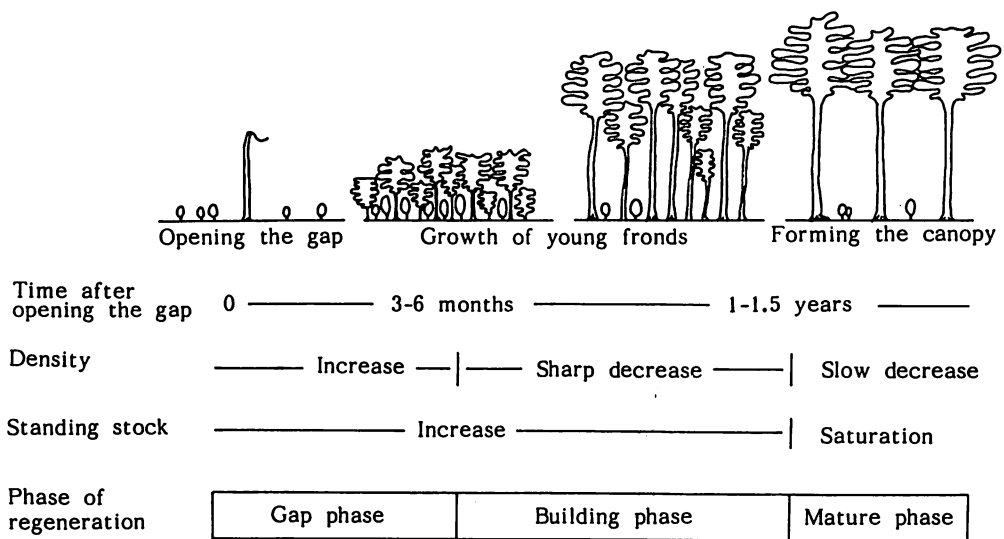


Fig. 4. Schematic diagram of the regeneration process in *Ecklonia cava* population, and changes in the population density and standing stock with advancement of the regeneration process.

a parameter representing the height of the population.

The number of young fronds exhibited periodic changes at intervals of 3 years. The density of young fronds was high in 1983 and 1986 when the density of adult fronds was low, and it was low in 1982, 1984, 1985 and 1987 when adult fronds formed a dense canopy. The maximum density of adult fronds (larger than 20 cm in stipe length) was about 14 individuals/m² which was similar in both quadrats. The changes of standing stock and mean stipe length showed a similar trend: i.e. both were at the peak in 1982, 1984, 1985 and 1987 when the adult fronds formed a dense canopy, and were low in 1983 and 1986 when most of the adult fronds were lost and many recruits were produced in the population. Maximum standing stock and mean stipe length were 0.8 kg/m² and 30–40 cm, respectively.

From the results mentioned above, a schematic diagram of the regeneration process in *Ecklonia* forest was drawn as illustrated in Fig. 4 with summarizing the changes in density, standing stock and regeneration process. Three phases could be distinguished with reference to structural and dynamic feature of the population in the regeneration process. In the first place, the gap is opened by the loss of many large fronds which form the canopy. During the initial 3 to 6 months from gap formation, the density of recruits increases rapidly from winter to spring (gap phase). After the population density reaches the maximum in nearly half a year from gap formation, it decreases rapidly. During this period plants grow rapidly and the standing stock also increases greatly (building phase). Thereafter, the standing stock approaches the maximum (steady state) within 1–1.5 years after gap formation, although it shows winter depression because of decaying old bladelets after the release of zoospores from late autumn to winter. In addition, the population density decreases gradually (mature phase). The mature phase is maintained for about one year. The regeneration process of the *Ecklonia* forest corresponds well to the

typical “gap regeneration” in terrestrial climax forests

Discussion

Recently, long-term ecological researches of seaweeds have been carried out to examine the distribution of species and to analyze the structure of populations or communities. As the result of these studies, the most important factor controlling algal structure was thought to be wave action (SOUSA 1979, DAYTON and TEGNER 1984) and/or grazing by herbivores (EBELING *et al.* 1985, NOVACZEK and MCLACHLAN 1986) which act as external factors. Thus, until now it has been considered that the density and standing stock of marine forests varied irregularly depending on the number of herbivores and the sudden occurrence of storms. In this study, we propose another factor which might be the most important one controlling the population structure of marine forests. It is an intraspecific competition like self-thinning which acts as an internal factor with advancement of the regeneration process. Consequently, structures such as population density and standing stock change periodically at a given interval of the turnover time. The self-thinning is caused originally by the process of getting space and light. Particularly in a dense marine forest, light is the most important limiting factor for growth, and there is a clear advantage to be gained by having light collecting apparatus above that of neighborhood. In our previous papers (MAEGAWA and KIDA 1987, MAEGAWA *et al.* 1987, 1988), it was clear that germination and growth of young fronds were controlled by light intensity on the population floor. The number of young fronds on the population floor play an important role for the regeneration process as major constituents of coming generation.

In the *E. cava* population many recruits, the density of which was 45–60 fronds/m² at Stn. 1 and 25–35 fronds/m² at Stn. 2, were produced in the gap during the period of 3–6 months after the opening was made in the canopy. Difference in the number of recruits was

thought to be caused by the difference of space on the substratum available for germination and growth of young fronds. A large number of recruits as mentioned above decreased rapidly to 10–15 fronds/m² in one year. This decrease in the density supports an evidence of self-thinning which is caused by the changes in the light condition in a population. A large number of recruits germinated too late or grown under dim light beneath neighboring superior recruits are destined to die or lose selectively because they cannot have enough light to grow in the population. On the other hand, several recruits germinated earlier or grown rapidly have a possibility to survive to canopy fronds. Recruits produced densely in the gap tend to increase skewness in size frequency distributions, which is caused for strong intraspecific competition. Recruits are competitively inferior to the established individuals; they may remain small for a long period and be subjected to high mortality. As the result, self-thinning is more active in a dense population with extreme skewness of size distributions, and is one of the most important factors in regulating the structure and density of a plant population developed naturally.

Regeneration of marine climax forests such as *E. cava* populations is usually initiated by the formation of the gap due to death or loss of large canopy fronds. A very small opening formed by loss of one large frond is soon closed by adjacent canopy fronds. Consequently, the regeneration process starts when the assemblage of canopy fronds is lost at the same time and a relatively large opening is formed. In this study, the regeneration process started when the density of canopy fronds with stipes of more than 20 cm long decreased to 2–4 individuals/m². IWAHASHI (1971) also observed that a lot of recruits of *E. cava* occurred when the density of adult plant decreased to 1–2 fronds/m² in the coastal water of Izu Peninsula.

WATT (1947) suggested that terrestrial forest communities have mosaics of patches in which various phases of the regeneration pro-

cess are arranged spatially, and the age of plants in the patch becomes almost even. This phenomenon is called "cyclic succession" or "regeneration complex". WATT's mosaic theory was applicable to various terrestrial forest types (WILLIAMSON 1975, OHSAWA 1981, RUNCKLE 1981, KANZAKI 1984) and is a valuable concept for understanding terrestrial forest structures and regeneration. WATT (1947) distinguished four phases (gap, building, mature, and degeneration) in the course of regeneration. WHITMORE (1982) recognized three phases (gap, building, and mature) in the regeneration process of many terrestrial forests. In this study, three phases (gap, building, and mature) were verified in the regeneration process in *E. cava* forest which is the same as those of terrestrial forests. It is quite interesting that such phases can be distinguished by similar structures and dynamic features of the regeneration process in both terrestrial and marine forests, although there are considerable differences in the scale of a population and/or community and in biological and physiological characteristics of the component species between the two. The most important difference is the turnover time of regeneration, which is 100–200 years or more for terrestrial forests (NAKA 1982, NAKASHIZUKA 1984) while only 3 years for marine *E. cava* forest. Such a short turnover time of *E. cava* forest offers great advantage for this kind of population study as compared with terrestrial forests.

It has been generally observed that there was considerable skewness of age distribution in the *E. cava* population (IWAHASHI 1971, OHNO and ISHIKAWA 1982, KIDA and MAEGAWA 1983). Specifically, young fronds can scarcely grow in a fully developed population in the mature phase. A quadrat sampling method has generally been employed for analyzing the age distribution and for estimating the standing stock of algal populations. When a quadrat is placed within a particular fully developed population which is in the mature phase, large and old canopy fronds may occupy most parts of the popula-

tion, and the mean standing stock in the area may be overestimated. It is considered that many and large scale quadrat methods and/or a long-term observation over the life span of individuals are necessary to estimate a mean size- or age-distribution, standing stock, and regeneration process of marine forests.

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前川行幸・喜田和四郎：三重県志摩半島沿岸域におけるカジメ海中林の更新過程

三重県志摩半島沿岸域のカジメ群落内に、2つの永久コドラートを設置し、1982-1987年の約6年間にわたる個体群動態の調査・解析から、群落の更新過程を明らかにした。永久コドラート内の群落の茎長組成、密度、平均茎長、及び現存量などの規則的な年変化から、更新の周期は3年と考えられた。また、更新のプロセスは典型的なギャップ更新であった。カジメ群落の更新過程は、その構造や機能の面から、3相に分けて考えることができた。林冠を形成する大型個体のまとまった流失により、ギャップが形成され、ギャップ形成後の3-6ヶ月は、幼体の加入量が多く、死亡率もそれほど高くはなく、また、現存量は密度の増加とともに高くなる（ギャップ相）。ギャップ形成後1-1.5年で群落は最大密度となり、幼体の加入量は止まり、その後、密度は急激に減少する。しかし、この時期の現存量の増加は著しい（建設相）。ギャップ形成後1-1.5年で現存量は飽和し、密度減少も緩やかになり、林冠が形成される（成熟相）。カジメ群落の更新過程は、基本的には陸上の森林群落と同じであった。このようなカジメ群落の更新を規制する要因として、群落内の光環境の変化とそれともなう種内競争が考えられた。(514 三重県津市江戸橋2-80 三重大学生物資源学部藻類増殖学研究室)