

## Ecological Studies of *Eisenia bicyclis* (KJELLMA) SETCHELL and *Ecklonia cava* KJELLMAN

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This study was designed to examine the ecological characteristics of two brown algae, *Eisenia bicyclis* and *Ecklonia cava*, and the marine forests formed by these species. These species are widely distributed along the Pacific coast of central Japan and are important algae both ecologically and economically. Wherever the water conditions and substratum are suitable, both species form dense, expansive marine forests, 1-3 m in height. *Ei. bicyclis* usually grows in shallow water down to 8-10 m in the sublittoral zone. *Ec. cava*, on the other hand, occupies deeper water of 4-25 m or more.

Allometric relationships between stipe length or diameter and weight of stipe, blade, and total frond were examined to obtain useful analytic characters for measuring the population structure.

The regeneration of both marine forests were studied with the 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. The three phases of gap, building and mature were distinguished by reference to the structural and dynamic features of the population in the regeneration process. The turnover time was 5-6 years for the *Ei. bicyclis* population and 3 years for the *Ec. cava* population.

The analysis of distributional patterns and production structures of *Ei. bicyclis* and *Ec. cava* populations suggested that there was significant intraspecific competition for getting light between the canopy fronds and recruits involving the same age groups. Young fronds of these species were growing under considerably low light conditions on the population floor. Critical light conditions for young *Ei. bicyclis* and *Ec. cava* were examined on the population floor.

The daily compensation light for young *Ei. bicyclis* and *Ec. cava* was calculated with mathematical models based on photosynthesis-light equations and natural light conditions. The estimated daily light compensation point did not conflict with the observed critical light under *in situ* light conditions. It was clear that young *Ec. cava* fronds can grow under lower *in situ* light intensity in deeper water than young *Ei. bicyclis* fronds.

The demography was studied mainly for the *Ec. cava* population. The Weibull frequency distribution was used to analyze the factors regulating mortality from the survivor curve. The average life span of *Ec. cava* was 16.5 months, and the maximum life span was 5 years, as indicated in life table.

**Key words:** *Eisenia bicyclis*, *Ecklonia cava*, population structure, production, demography

### Introduction

The two species of brown algae, *Eisenia bicyclis* (KJELLMAN) SETCHELL and *Ecklonia cava* KJELLMAN (Laminariaceae), have wide distribution along the coast from central to southern Japan (Fig. 1). *Ei. bicyclis* is distributed from south of Iwate Prefecture to Kyushu Island facing the Pacific coast, and from Tsuruga Bay to Kyushu Island facing the Japan Sea. On the other hand, *Ec. cava* is distributed from Chiba Prefecture to Mie

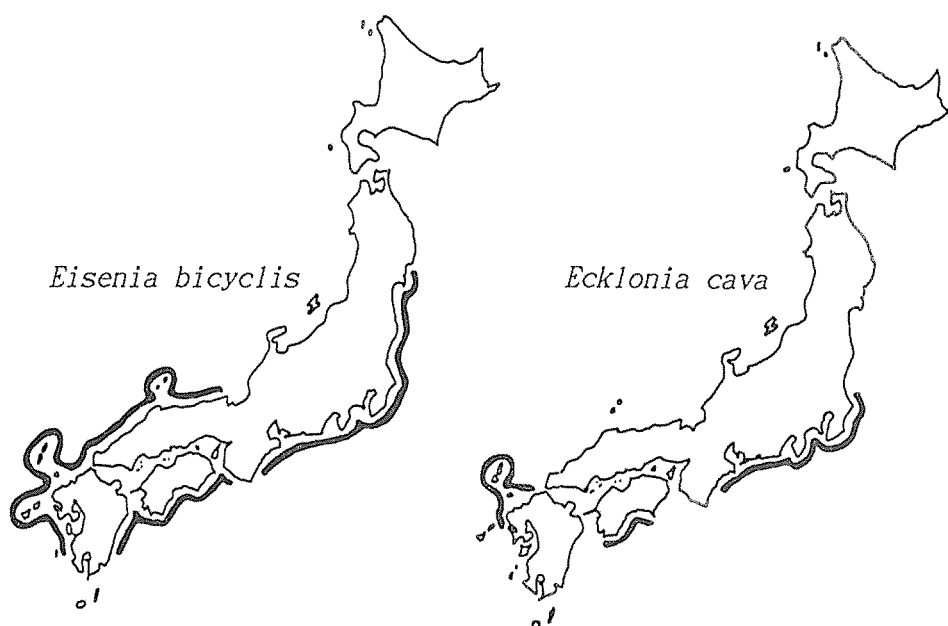


Fig. 1. Distributions of *Eisenia bicyclis* and *Ecklonia cava* around the coasts of Japan.

Prefecture, south of Shikoku Island and north of Kyushu Island. Where the distributional area of both species overlaps, *Ei. bicyclis* usually grows in shallow water down to 8–10 m in the sublittoral zone, and *Ec. cava* occupies deep water, 4–25 m or more. These species are perennial and usually grow attached to solid substratum anchored into place by fibrous holdfasts, and form dense populations called marine forests 1–3 m in height (Plate 1).

The life cycles of both species are similar, and show typical ones of Laminariaceae. Fig. 2 shows the life cycle of *Ec. cava*, and Fig. 3 shows morphological changes of both species through the growth. Young sporophytes (macroscopic generation) germinate from winter to spring. In the early stage during one year from germination, the shapes of both intact young fronds were similar (Fig. 3), although *Ei. bicyclis* has a wrinkled blade and *Ec. cava* has a smooth blade. After one year from germination, the primary blade of *Ei. bicyclis* decays, and the top of stipe forks and many bladelets are produced on the both sides of the forks (cf. Fig. 3). *Ec. cava* grows without apparent changes in the fronds' proportion from the young to adult stage. In summer after 1.5 years from germination, sori involving the zoosporangia are produced on both surfaces of the bladelet in both species. Liberated zoospores develop to female and male microscopic gametophytes (Fig. 2). The female gametophytes consist of only two or three cells, and male gametophytes consist of three or more cells in a row. Within one month both gametophytes mature and make eggs and sperms, respectively. Fertilized eggs grow to 1–3 cm of visible size embryo in late winter to spring after 1–2 months from fertilization. The maximum life span of *Ei. bicyclis* and *Ec. cava* sporophytes are more than 7 years for the former and 5 year for the latter<sup>1,2)</sup>.

*Ei. bicyclis* and *Ec. cava*, which are the major primary producers in shallow water, play an important role both ecologically and economically in the coastal ecosystem. Therefore, considerable knowledge has been accumulated on their distribution, growth and population structures from an ecological point of view<sup>1,3–19)</sup>.



**Plate 1.** Marine forests of *Eisenia bicyclis* at a depth of 3 m (upper), and *Ecklonia cava* at a depth of 7 m (lower), in the coast of Shima Peninsula, Mie Prefecture.

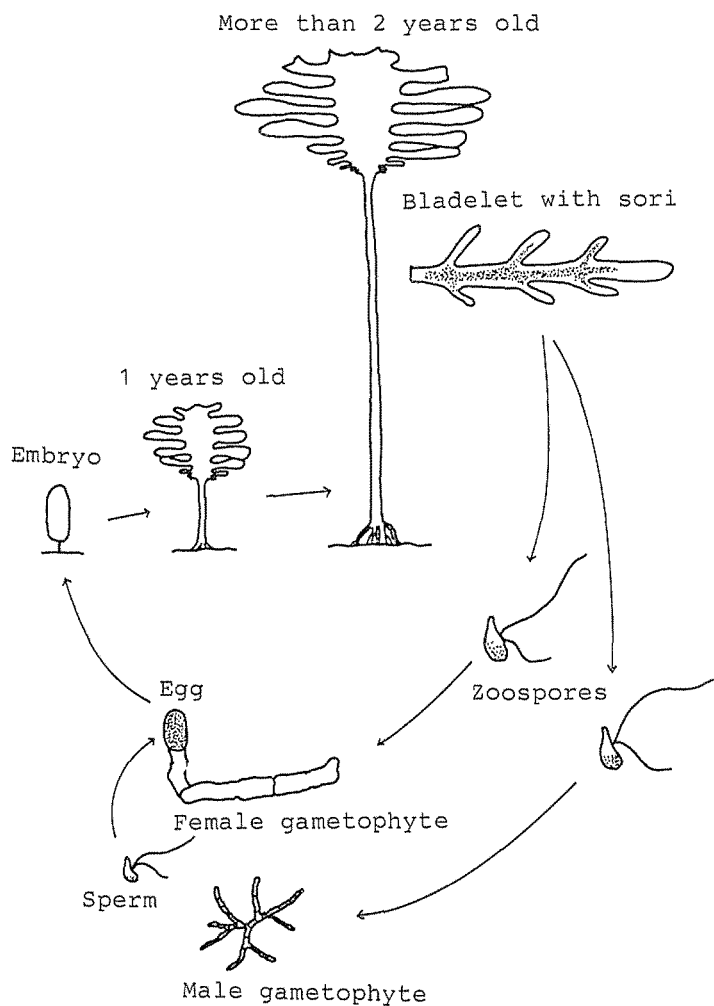


Fig. 2. Life cycle of *Ecklonia cava*.

Recently several studies on their photosynthesis and respiration<sup>2,20-22)</sup>, estimating the primary production<sup>9,23,24)</sup> and production ecology<sup>22,25)</sup> were reported. However, little attention has been paid to population dynamics<sup>2),7)</sup>. Population dynamics is the study of changes in the number of organisms in populations and of the factors influencing them<sup>26),27)</sup>. The study of population dynamics is greatly important, not only for the ecological field but also for fisheries and commercial fields in order to provide fundamental data for management and conservation of marine bioresources.

*Ei. bicyclis* and *Ec. cava* are perennial algae, and their populations are maintained by alternating each age group<sup>14,24)</sup>. Both marine forests are regarded as climax stages in the successional process of sublittoral algal vegetation<sup>28)</sup>. Thus, it was thought that the yearly changes in population density or biomass were scarcely little and were in fairly stable equilibrium in such marine forests<sup>9,29)</sup>. Recently, KIDA and MAEGAWA<sup>14)</sup> and TANIGUCHI and KIRO<sup>24)</sup> drew attention to the fact that there were dynamic changes in age groups and structure according to the advancement of the regeneration process in these populations. In addition, it is thought that one of the most

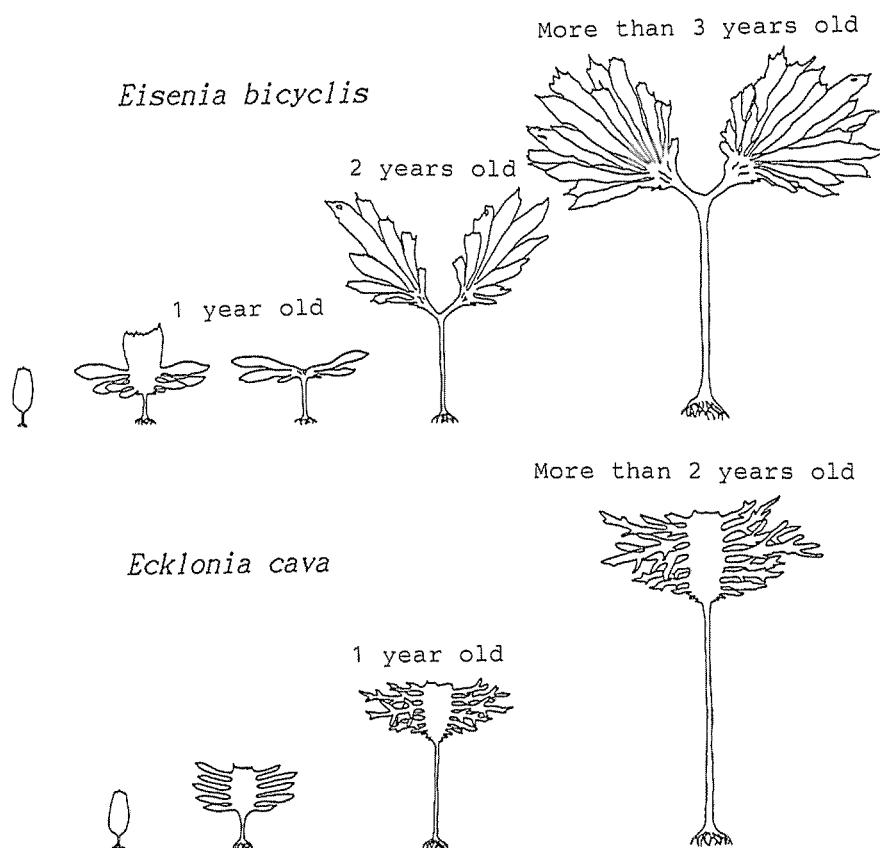


Fig. 3. Morphological changes in *Eisenia bicyclis* and *Ecklonia cava* with growth of fronds.

important factors controlling the structure and regeneration process are the changes in light condition and intraspecific competition in these populations<sup>25,30)</sup>.

Until now many factors such as the stability of substratum, wave action, water temperature and grazing by herbivours have been thought to play an important role in controlling the population structure of *Ei. bicyclis* and *Ec. cava*<sup>24,28)</sup>. Many investigations with their respects to such physical and biological factors controlling the population structure have been made for another marine kelp forests<sup>31-37)</sup>.

The structure of the plant community is dependent upon both the interactions between organisms in the community and the physical nature of the environment. CONNELL<sup>38)</sup> suggests that interaction of competition and biological disturbance provides most of the organization in natural communities. The structural significance of competition for getting light and/or space on algal populations has been shown in various marine communities<sup>36,39-41)</sup>. In most cases where competitive interactions prevail, the algal assemblage is characterized by high abundance of a few competitively superior species that are frequently long-lived and inhibit invasion.

The competition for getting light plays an important role in structuring many terrestrial plant communities<sup>26,42)</sup>. There are, however, a few studies for algal population with such viewpoints of population dynamics<sup>36)</sup> and intra- and interspecific competition for light<sup>2,43,44)</sup>. The competition for light may be more drastic in marine forests than in terrestrial forests, because light intensity and quality are altered greatly by both

the vegetation and the water in the sea. Many aspects of the marine forest light environment remain yet undefined.

In my study area, *Eisenia* and *Ecklonia* marine forests are distributed expansively on the solid substratum in the sublittoral zone. Both species are exclusively dominant macrophytes inhibiting the scarce understory of other algae. For analyzing such populations similar methods used in land climax forests can be applicable, although there are considerable differences in the scale of the population and/or community, and in biological and physiological characteristics of the components between the two. The structure of submerged algal vegetation is in many ways comparable to terrestrial forests<sup>45)</sup>.

In terrestrial forests, the often long-lived species which form the highest canopy can monopolize light and thus alter understory vegetation<sup>26)</sup>. In subtidal algal communities along the coast from central to southern Japan facing open sea, *Ei. bicyclis* and *Ec. cava* are the most abundant and widely distributed, and play an important role in the subtidal ecosystem. However, only a few studies of both marine forests have been experimentally conducted for evaluating the algal competition for getting light, and the effects of the canopy on understory algae<sup>2,46)</sup>.

This study was undertaken to examine the characteristics of two brown algae, *Ei. bicyclis* and *Ec. cava*, with reference to ecological points of view. I will reveal the differences between both species and marine forests ecologically and physiologically, with reference to light condition and production. Particularly, a factor controlling the difference in vertical distribution, *i.e.* *Ei. bicyclis* in shallow water and *Ec. cava* in deep water, will be one of the most important subjects. All these results will be explained and discussed in the following chapters: Chapter I, Distribution and Growth; Chapter II, Light and Production; Chapter III, Demography; Chapter IV, Conclusion.

## Chapter I. Distribution and Growth

### 1. Introduction

*Ei. bicyclis* and *Ec. cava* have wide distribution in the temperate coastal area from central to southern Japan (Fig. 1). Comprehensive research on taxonomy, population structure, age distribution, growing pattern, etc., has been accumulated in various areas by many authors, such as Matsushima Bay<sup>17,24)</sup>, Miura Peninsula<sup>11)</sup>, Izu Peninsula<sup>8)</sup>, and Shikoku Island<sup>15)</sup>. From the results of these studies it was revealed that the population density and frond length of these species varied with the physical and biological circumstances, which were characterized in their growing locality. For example, stipe length of adult *Ei. bicyclis* is long (about 100 cm for adult) in the coast of Izu Peninsula and Shima Peninsula<sup>12,13)</sup>, while short (50–60 cm) in Matsushima Bay. For *Ec. cava*, stipe length is long (200–300 cm) in the east coast of Izu Peninsula, and is short (80–100 cm) in other areas. It was also reported that there might be 2 or 3 variations of blade types in *Eisenia* in Japan<sup>47,48)</sup>. In addition, growing depth and density of both species varies even in nearby areas around the coast of Izu Peninsula<sup>8)</sup>. Therefore, I primarily intended to observe and examine the variability in population structures of both species, from inland to open sea waters, from shallow to deep waters concerning their distribution under natural condition in my study area.

For terrestrial forests, there are some standard measuring characters and age characters such as the height of tree, DBH (the diameter of breast height),  $D^2H$  ( $DBH^2 \times \text{height of tree}$ ), the annual ring, etc. which are greatly useful for analyzing the structure and growth patterns of forests<sup>49)</sup>. I intended to search for such

characters by using allometric method for *Eisenia* and *Ecklonia* populations. There have been, however, only a few studies in allometry for macrophytes from an ecological point of view<sup>31,50,51</sup>.

It is thought that the climax marine forest was maintained by dynamic equilibrium, *i.e.* partial destructions and construction of the canopy. Consequently, the structure and function are stable for many years beyond the life expectancy of the major component individual. The mechanisms of the regeneration process (secondary succession) or stability of the climax marine forest are the subjects of study attracting ecological interest of some researchers in recent years. However, little knowledge was accumulated for the population dynamics of *Ei. bicyclis* and *Ec. cava* throughout a long study period for more than 5 years<sup>2,14,17</sup>. The recent studies of stability and succession emphasize the need for the recognition of appropriate scales in time and space<sup>52,53</sup>. Specifically, the time scale should be longer than the maximum life span of the major component individual in the study of population dynamics.

Recently, regeneration processes of climax terrestrial forests in many countries have been studied intensively<sup>54</sup>. Many authors have emphasized that tree fall and opening in the canopy play important roles in terrestrial forest regeneration<sup>55–59</sup>. BRAY<sup>55</sup> called such an opening the “gap”, and the regeneration of climax terrestrial forests takes place mainly in such gaps, and its process is named the “gap phase regeneration”. In such forests, intrastage phases expressing a mosaic structure would be seen. This phenomenon in which various phases of regeneration are arranged spatially is called “cyclic succession” or “regeneration complex” by WATT<sup>60</sup>.

In this study, I intend to trace the regeneration processes of both marine forests 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 *Eisenia* and *Ecklonia* marine forests are comparable well to those of terrestrial forests, in spite of the notable differences in the scale of population and the period of turnover time of the regeneration cycle between them. Information of this kind 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.

Recent ecological researches of macroalgae have represented a quantitative discipline designed to produce statistically interpretable analyses of biotic distribution and abundance patterns within defined habitats<sup>36,61</sup>. Nondestructive measurement, by utilizing permanently marked sampling locations, provides a powerful method for evaluating the natural changes in dispersion of individuals and intra- and interspecific competition<sup>62</sup>. The ultimate object of this study in distributional pattern is to obtain sufficient understanding to explain why the individuals existed in a particular pattern at a specific time and place. An adequately large number of samples must be taken for proper statistical treatment, and this requires that the method is rapid and simple to use.

Several methods have been proposed to find the distributional patterns of plant individuals. Some of these were based on the data obtained from quadrats<sup>63,64</sup>, and others are based on the spacing methods<sup>65</sup>. A lot of knowledge has been accumulated about the distribution of individuals in land plant populations with using these methods<sup>66</sup>. The changes in distributional pattern found in seral stages of terrestrial forests was studied in detail by TAGAWA<sup>67</sup>. However, no experiments have yet been made which allow one to evaluate the probability that distributional pattern changes with the seral stage in algal population and with the process of regeneration. I intend to examine the distributional pattern of individuals for both plant populations with special references to the stratification and the regeneration process of marine forest. This sort of study will provide the fundamental data for analyzing the intraspecific competition in marine forests.

## 2. Materials and Methods

### a) Study Area

The main study area for the distribution and growth research was around the coast of Shima Peninsula, Mie Prefecture, central Japan (Fig. 4). To compare the locality of distributional characteristics, another two study areas, Toshi Island near the mouth of Ise Bay and Kii-Nagashima southwest of main study area, were selected. In these areas rocky substrata distribute widely to the extent of 30–40 m in depth. *Ei. bicyclis* and *Ec. cava* populations form a dense, expansive marine forest along the coast exposed to the open sea wave action throughout the year.

*Ei. bicyclis* usually grows in shallow water down to 8–10 m in the sublittoral zone, and *Ec. cava* occupies

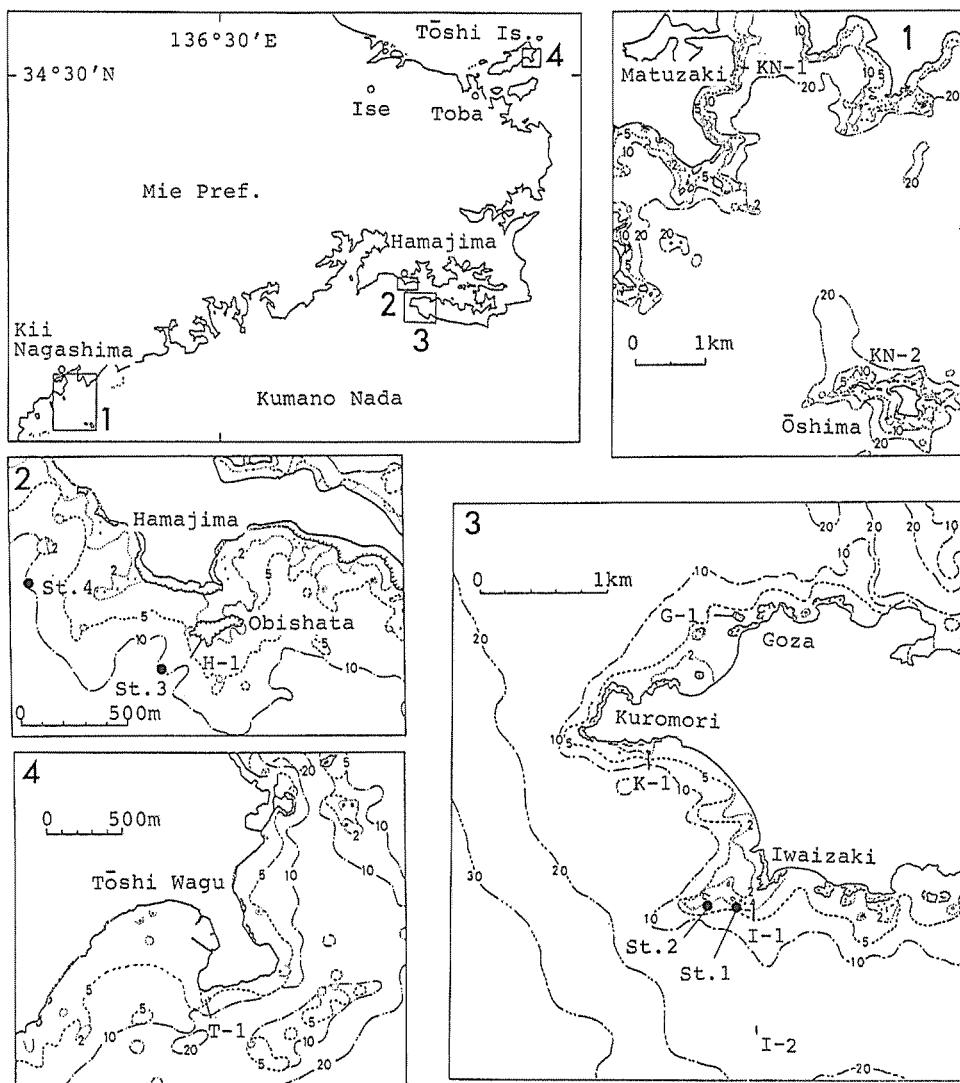


Fig. 4. Maps showing the location of surveyed areas.

KN-1, 2, H-1, I-1, 2, K-1, G-1, T-1; belt transects. Sts. 1–4, permanent quadrats.



deeper water of 4–25 m or more. On a flat and solid substratum both species can grow to adulthood and form a dense canopy. However, on a sharp slope and loose substratum such as boulder, adult plants are absent and can grow only young and small plants less than one year old. *Ec. cava* also forms a dense marine forest from 8 to 15 m on a flat and solid substratum, although in deeper water more than 15–20 m in depth they are small and do not grow to adulthood.

In both well developed marine forests the understory vegetation was scarce. Only a few species of *Chlamidophora repens* OKAMURA, *Zonaria diesingiana* J. AGARDH and *Codium mamillosum* HARVEY were seen on the community floor. It was also noted that herbivores were scarce; particularly, sea urchins which affect the structure and stability of algal community in many ways<sup>68–70</sup>) existed few in my study areas.

For sampling the materials and quadrat study in growth analysis and regeneration, I sought the areas in which each marine forest made reasonably homogeneous canopy compositions around Shima Peninsula. In addition, these areas had to be wide enough to decrease variability within and between samples. In consideration of these criteria, I chose two suitable study areas; south of Iwaizaki for *Ei. bicyclis* and south of Hamajima for *Ec. cava*, where each marine forest was fully developed monopolistically at a depth of 2–4 m for the former, and 7–10 m for the latter.

#### b) Belt Transect

From June to August in 1981 and 1982, belt transect researches were carried out to observe and examine the characteristics of vertical distribution of *Ei. bicyclis* and *Ec. cava* marine forests, as well as the properties of substratum. Study sites were around the coast of Shima Peninsula from the mouth of Ago Bay to the open sea, Toshi Island near the mouth of Ise Bay and around the coast of Kii-Nagashima (Fig. 4). In these areas a 100 m belt transect was extended from the seashore out to the open sea. I also chose the study site in which the end of the belt transect reached more than 10 m in depth where *Ec. cava* made a homogeneous population. Furthermore, a 50 m belt transect was set south of Iwaizaki, where the end of the 100 m belt transect did not reach to 10 m in depth.

Along the belt transect topographical profile of the substratum, frequency distribution of stipe length and population density of both species growing in a width of 30 cm and a length of 2 m were measured continuously. The topographical profile was recorded by an echo sounder. The depth was measured with a water pressure depth gauge, and allowance was made for the height of the tide at the time of diving, correcting all measurements to meters below ELMS (extreme low water spring). Stipe length was measured ranging from the top of the holdfast to the growing point located at the bottom of primary blades.

#### c) Allometry

Various sizes of 150–250 fronds were randomly sampled from south of Iwaizaki at 3–4 m depth for *Ei. bicyclis*, and from offshore at Hamajima at 7–8 m depth for *Ec. cava* at intervals of two or three months from March 1983 to March 1984. In the laboratory, each sample was divided into three parts: holdfast, stipe and blade. Then, the following dimensions usable for allometric analysis were measured: stipe length and diameter, dry weight of stipe and blade, number of growth rings for both species, and additionally fork length for *Ei. bicyclis*. The dimensions for holdfast were not measured because of technical difficulties in tearing off the holdfast from substratum without wounding, particularly for *Ei. bicyclis*. The stipes and blades divided were dried preliminarily outdoors for several hours, thereafter dried at 85°C for 12 hours and weighted.

In some species of Laminariaceae and Sargassaceae the concentric zones were found in a longitudinal or transverse section of the stipes and holdfasts. Methods of determining the age by counting these zones have been developed by the following authors: PARKE<sup>71)</sup> for *Laminaria saccharina* (L.) LAMOUR; BAARDSETH<sup>72)</sup> for *Alaria esculenta* (L.) GREV. KAIN<sup>73)</sup> for *Laminaria hyperborea* (GUNN.) FOSLIE; HAYASHIDA<sup>1)</sup> for *Ecklonia cava* KJELLMAN and YOSHIDA<sup>74)</sup> for *Sargassum ringgoldianum* HARVEY. As for *Ei. bicyclis*, ARASAKI<sup>47)</sup> suggested that the concentric zones observed in the transverse section of the stipes have a possibility of being used for an age character. In this study, all fronds collected were provided for age determination. A transverse disk cut in thickness of 0.5–1 mm was taken from just above the holdfast for young fronds and 2–3 cm above the holdfast for adult ones of both species for age determination. It was easy to count the first, second, and third ring with the naked eyes, but it was difficult to count more rings because those closely approached the cortex which involved photosynthetic pigments.

It is sometimes observed that adult *Ei. bicyclis* fronds growing just below the intertidal zone have shorter stipes and longer forks than those in deep areas<sup>75,76)</sup>. *Ec. cava* may also have a similar tendency in that stipe length of adult fronds varies with increase in water depth. So, various sizes of fronds were collected from the following depths: 2, 4 and 8 meters for *Ei. bicyclis*; 5, 7 and 17 meters for *Ec. cava*. Thereafter, the relationships between growth depth and stipe length were examined in each age group.

#### d) Permanent Quadrat

Permanent quadrat experiments for analyzing the regeneration process and the distributional pattern were carried out south of Iwaizaki for the *Ei. bicyclis* population (St. 1 and St. 2), and offshore at Hamajima for the *Ec. cava* population (St. 3 and St. 4). In May 1982, two quadrats of 1 m × 3 m constructed with ropes were set on a flat rocky substratum within each population at a depth of 4 m for *Ei. bicyclis* and 8 m for *Ec. cava* (Fig. 5). Each quadrat was divided into 6 small subquadrats for convenience of measuring and mapping. All individuals in the 4 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.

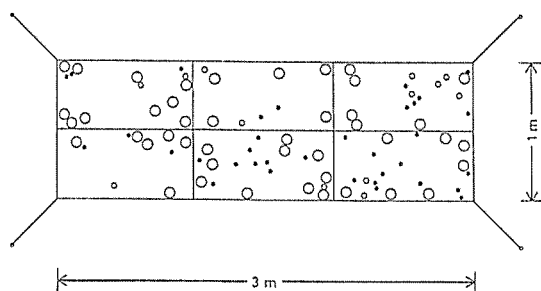


Fig. 5. Permanent quadrat and dispersion of *Ecklonia cava* fronds in June 1982 at St. 3. The size of circles indicates the length of stipes; large open circles, higher than 20 cm; small open circles, 10–20 cm; small solid circles, lower than 10 cm. Permanent quadrat is divided into 6 subquadrats.

From the month when the plants were marked through June 1986, 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 nineteen times at two- or three-month intervals from 1982 to 1984, and at six-month intervals from 1984 to 1988.

Total plants marked in the 4 quadrats for 6 years reached 2000 individuals. Such numerous data enabled me to conduct a comprehensive study of population dynamics.

#### e) Dispersion of Individuals

Individuals in the population are distributed according to three fundamental patterns as follows: random, uniform and contagious distributions (Fig. 6). 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 attracting.

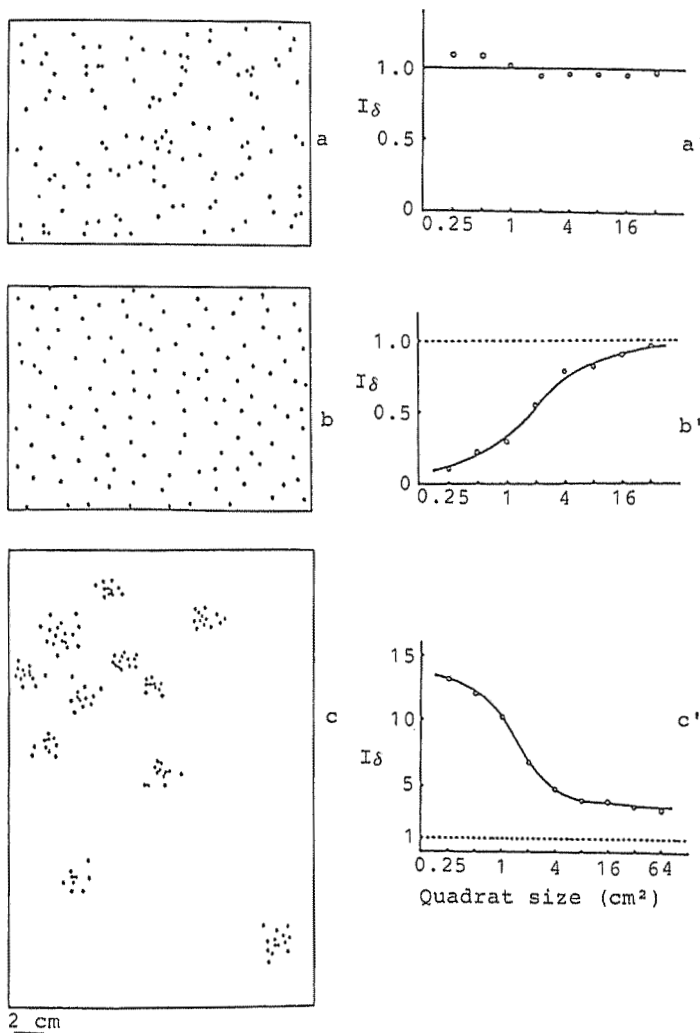


Fig. 6. Dispersion maps of individuals (left) and corresponding  $I_\delta$ -quadrate size relations (right). a and a', random distribution; b and b', uniform distribution; c and c', contagious distribution with small clumps.

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 of individuals<sup>63)</sup>. However, some indices change with the increase or decrease of the quadrat size taken as the sampling unit. Therefore, in this study I chose an index of dispersion,  $I_\delta$ , by Morisita<sup>63)</sup> and an index of interspecific association,  $R'_\delta$ , by Morisita<sup>64)</sup>, both of which were influenced neither by the average number of individuals per quadrat nor by the number of quadrats.

$I_\delta$  was computed by the following equation:

$$I_\delta = q \times \delta = q \sum_{i=1}^q n_i(n_i - 1) / N(N - 1),$$

where  $n_i$  is the number of plant individuals occurring in the  $i$ -th subquadrat ( $i = 1, 2, \dots, q$ ), and  $N$  is the total number of individuals sampled.

In Morisita's  $I_\delta$ -quadrat size relation,  $I_\delta$  is a measure of dispersion of individuals in a population which takes the value of unity as shown in Fig. 6. If the individuals are distributed at random over the area and the number of individuals is very large,  $I_\delta$  is almost 1 (Fig. 6, a and a'). When the individuals are distributed uniformly over the area,  $I_\delta$  takes the value smaller than 1 (Fig. 6, b and b'). If the distribution of individuals is contagious,  $I_\delta$  is larger than 1 (Fig. 6, c and c'). I applied this index to *Ei. bicyclis* and *Ec. cava* populations in the permanent quadrats in this study.

In addition, Morisita's index of interspecific association,  $R'_\delta$ , was also used.  $R'_\delta$  represents the correlation between two groups.  $R'_\delta$  is given in the following equation:

$$R'_\delta = 2 \sum_{i=1}^q s_{xi} n_{yi} / (\delta_x + \delta_y) N_x N_y - 2 / (\delta_x + \delta_y) q,$$

where  $n_{xi}$  and  $n_{yi}$  respectively indicate the number of individuals of the group  $x$  and  $y$  growing in the  $i$ -th subquadrat,  $N_x$  and  $N_y$  are respectively the total number of individuals of the group  $x$  and  $y$  which were sampled in all the quadrats, and  $\delta_x$  and  $\delta_y$  are the  $\delta$  of group  $x$  and  $y$ , respectively.

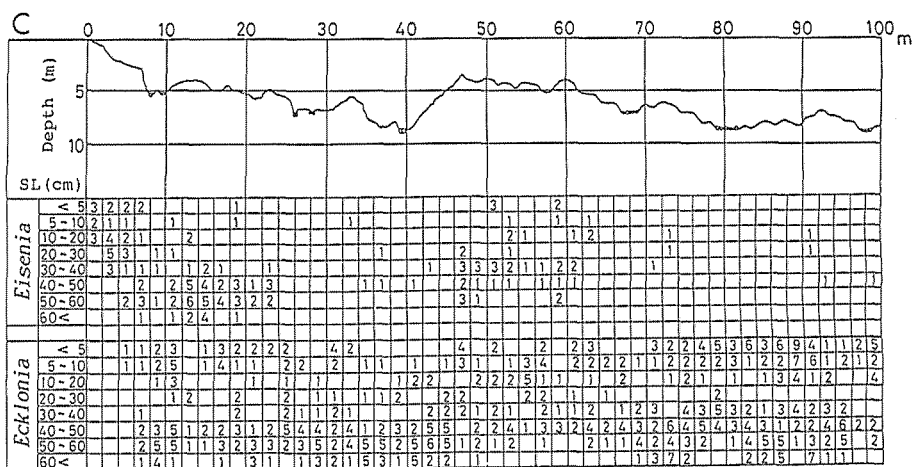
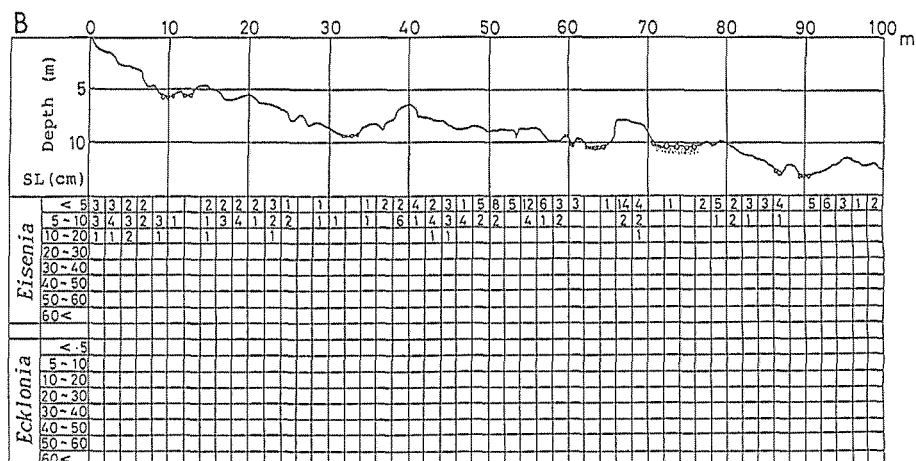
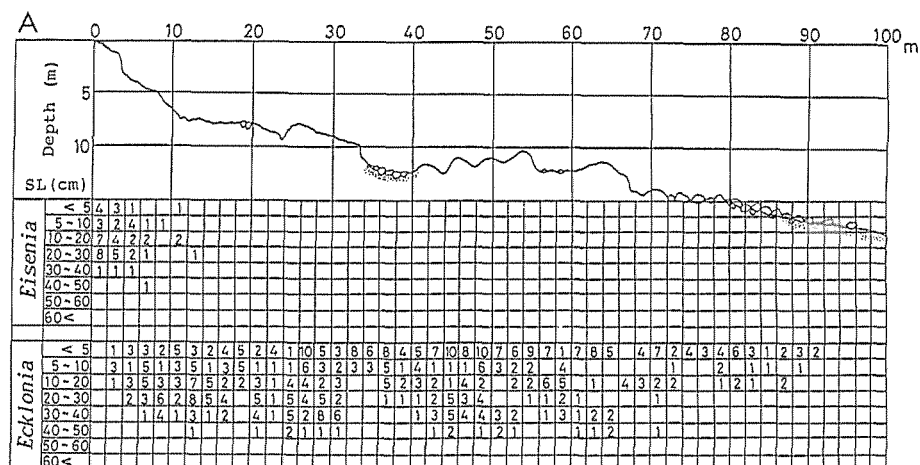
I intended to analyze the intraspecific relation between young, small fronds and adult, large fronds in *Ei. bicyclis* and *Ec. cava* populations in the permanent quadrats, although the index  $R'_\delta$  was developed for analyzing interspecific association or competition. In Morisita's  $R'_\delta$ -quadrat size relation, if two species (or groups) are distributed independently of each other,  $R'_\delta$  is almost 1. If the distributional pattern of two species is attractive or repulsive,  $R'_\delta$  takes a value from 0 to 1 or from  $-1$  to 0, respectively.

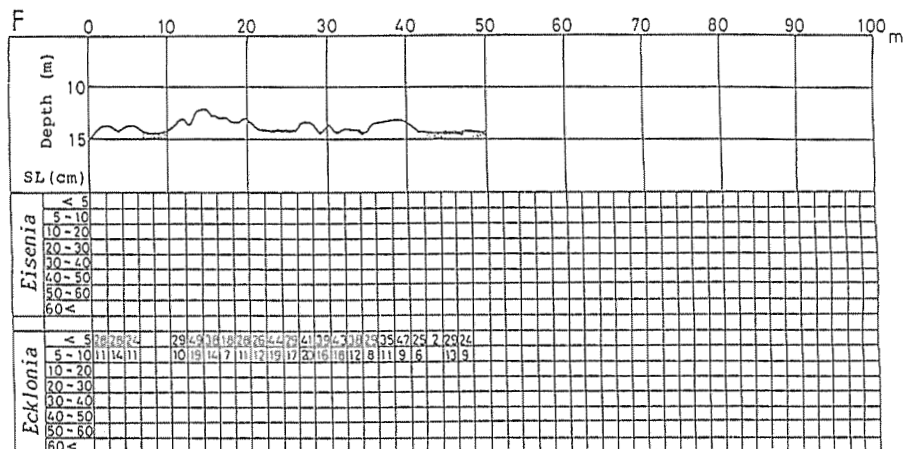
In this study, data for analyzing the distributional pattern were offered from the permanent quadrats experiments. A quadrat ( $1 \text{ m} \times 3 \text{ m}$ ) was divided contiguously into 6 groups in size,  $0.25 \text{ m} \times 0.25 \text{ m}$ ,  $0.25 \text{ m} \times 0.5 \text{ m}$ ,  $0.5 \text{ m} \times 0.5 \text{ m}$ ,  $0.5 \text{ m} \times 1 \text{ m}$ ,  $1 \text{ m} \times 1 \text{ m}$ ,  $1 \text{ m} \times 2 \text{ m}$  for computing the  $I_\delta$  and  $R'_\delta$  indices. The number of young and adult individuals was recorded for each subquadrat. Values of  $I_\delta$  were used for detection of the distributional pattern of each group and total individuals in a population. Values of  $R'_\delta$  were used for detection of the intraspecific competition between young and adult plants.

### 3. Results and Discussion

#### a) Vertical Distribution

The profile diagrams of substratum and the distribution of *Ei. bicyclis* and *Ec. cava* are shown in Fig. 7, A-H.





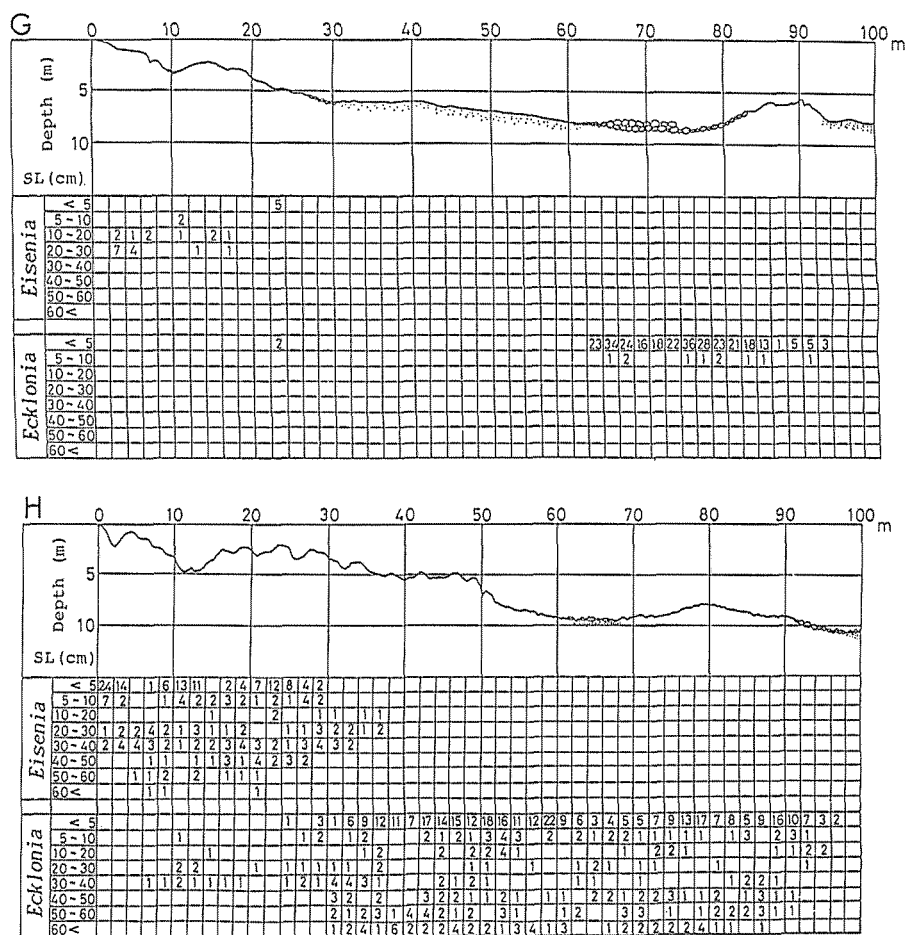


Fig. 7. Profile diagrams of substratum and distribution of *Eisenia bicyclis* and *Ecklonia cava* on the belt transect. Numerals in the figure show the number of fronds in each 2 m  $\times$  0.3 m quadrat along the belt transect.

- A; KN-1, Kii Nagashima
- B; KN-2, Oshima Island, Kii Nagashima
- C; H-1, Hamajima
- D; K-1, Kuromori
- E; I-1, Iwaizaki
- F; I-2, off shore of Iwaizaki
- G; G-1, Goza, Zizoubana
- H; T-1, Toshi Wagu

Each diagram in the lower part represents a frequency distribution of stipe length of both species growing in a width of 30 cm and a length of 2 m which corresponds to the upper profile. In the topographical profile the kind of substratum, such as rock, boulder and sand, is also illustrated. The upper line in each diagram shows 0 m of ELWS (extreme low water springs).

Fig. 7,A shows the result in the coast of Kii-Nagashima. This station is characterized by sheltered wave action and relatively steep slope. Distribution of *Ei. bicyclis* was restricted near the seashore above 7 m, and

large fronds more than 50 cm in stipe length was absent. *Ec. cava* was also distributed from 3 m to 17 m on the solid substratum, and made a dense marine forests. Where the bottom consisted of boulders, large fronds were absent. On the sandy bottom both species could not grow. In the coast of Oshima Island off Kii-Nagashima (Fig. 7,B) exposed to the severe wave action, only *Ei. bicyclis* was distributed on the rock for all the vertical extent down to 18 m. This is the typical pattern of distribution in the area directly facing open sea.

In the coast of Shima Peninsula in Figs. 7,C-E, the profile of the bottom shows moderate ups and downs to the depth of 20 m or more, and the wave action is not so severe. At these stations, *Ei. bicyclis* was distributed from just below the intertidal zone to the depth of 8–10 m, while *Ec. cava* occupied the zone from 4 m to 15 m or more in depth. The homogeneous marine forest was formed from 2 to 4 m in depth for *Ei. bicyclis* and from 8 to 12 m in depth for *Ec. cava*. In deep areas of 13–14 m only small fronds of *Ec. cava* grew densely and adult fronds were absent (Fig. 7,F).

Near the mouth of Ago Bay (Fig. 7,G), characterized by slight wave action and relatively turbid water, the density of *Ei. bicyclis* in particular decreased, and only small fronds grew at a depth of 6–9 m.

In the coast of Toshi Island sited in the mouth of Ise Bay (Fig. 7,H), dense marine forests of both species grew in the area facing the open sea. *Ei. bicyclis* distributed in shallow water above 5 m in depth and *Ec. cava* occupied the deep water more than 4–5 m in depth. Both species of *Ei. bicyclis* and *Ec. cava* were bordered clearly at a depth of 4–5 m as compared with other study areas.

The lower limit of *Ei. bicyclis* ranged from 3 m to 10 m below ELMS in this study. This result was comparable well with those of other areas: 5 m in Matsushima Bay, Miyagi Prefecture<sup>9)</sup>; 3–4.5 m in the coast of Miura Peninsula, Kanagawa Prefecture<sup>11)</sup>; and 7–10 m in the coast of Izu Peninsula, Shizuoka Prefecture<sup>8)</sup>. The lower limit of *Ec. cava* was confirmed by diving to be 25 m or more in depth. This result is in agreement with these of OKAMURA<sup>77)</sup> and IWAHASHI<sup>8)</sup>.

TAKAMA<sup>11)</sup> pointed out, however, that the range of vertical distribution of each species varied with local characteristics such as these in an inland sea or in an open sea area. In this studies the lower limit of *Ei. bicyclis* was shallow (3–5 m) in the inland sea near the mouth of the bay (Fig. 7,G), while deep (8–10 m) in the coast facing the open sea with moderate wave action as indicated in Figs. 7,C-E. Specifically, it was distributed to the depth of 13 m or more in the area exposed to severe wave action in Kii-Nagashima Oshima (Fig. 7,B). SUTO<sup>78)</sup> also suggested that *Ei. bicyclis* could extend its growth area to deeper waters when *Ec. cava* was absent. This is the typical pattern of vertical distribution in the area directly facing the open sea with severe wave action. It is clear that the vertical distributional pattern varies with locality, depending on the degree of wave action, topography of substratum, competition with herbivores<sup>17)</sup> in each place. However, factors characterizing the structure of marine forests of these two species could not be examined by the belt transect measurements in this study.

The stability of substratum controls the community structure and life forms of the algae growing there as indicated by the detailed investigations of KATADA and KONNO<sup>28)</sup>, SOUSA<sup>40)</sup>, LIEBERMAN *et al.*<sup>79)</sup> and LITTLER and LITTLER<sup>80)</sup>. In my study, it was also apparent that the frequency distribution of stipe length varied in close relation to the stability of substratum consisting of solid rock, boulder or sand as mentioned above.

## b) Growth Pattern

An allometric relation was examined between the stipe length, stipe diameter,  $D^2H$  (diameter<sup>2</sup> × stipe length) and weight of stipe, blade and total fronds for *Ei. bicyclis* and *Ec. cava*. Figs. 8 and 9 show the seasonal



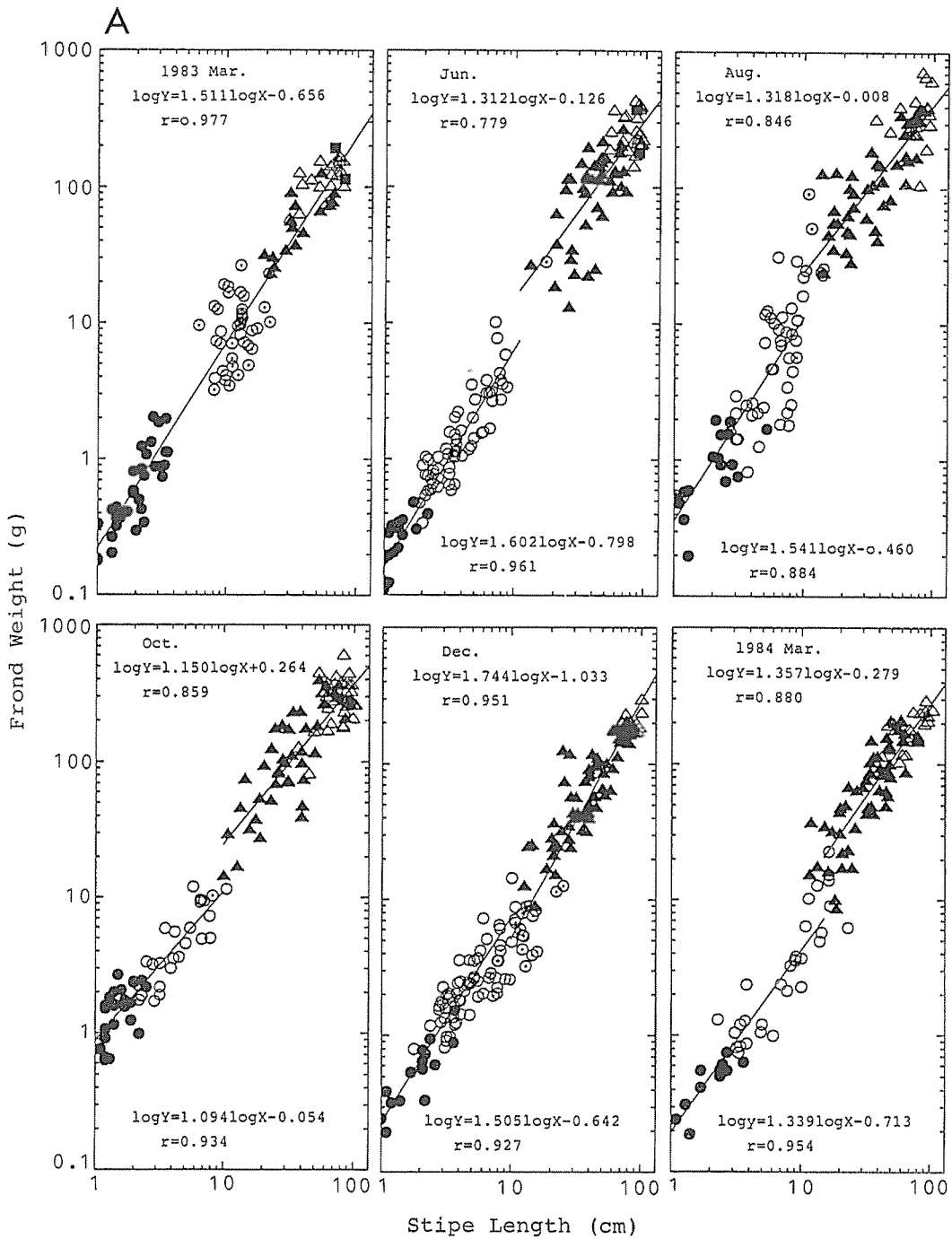
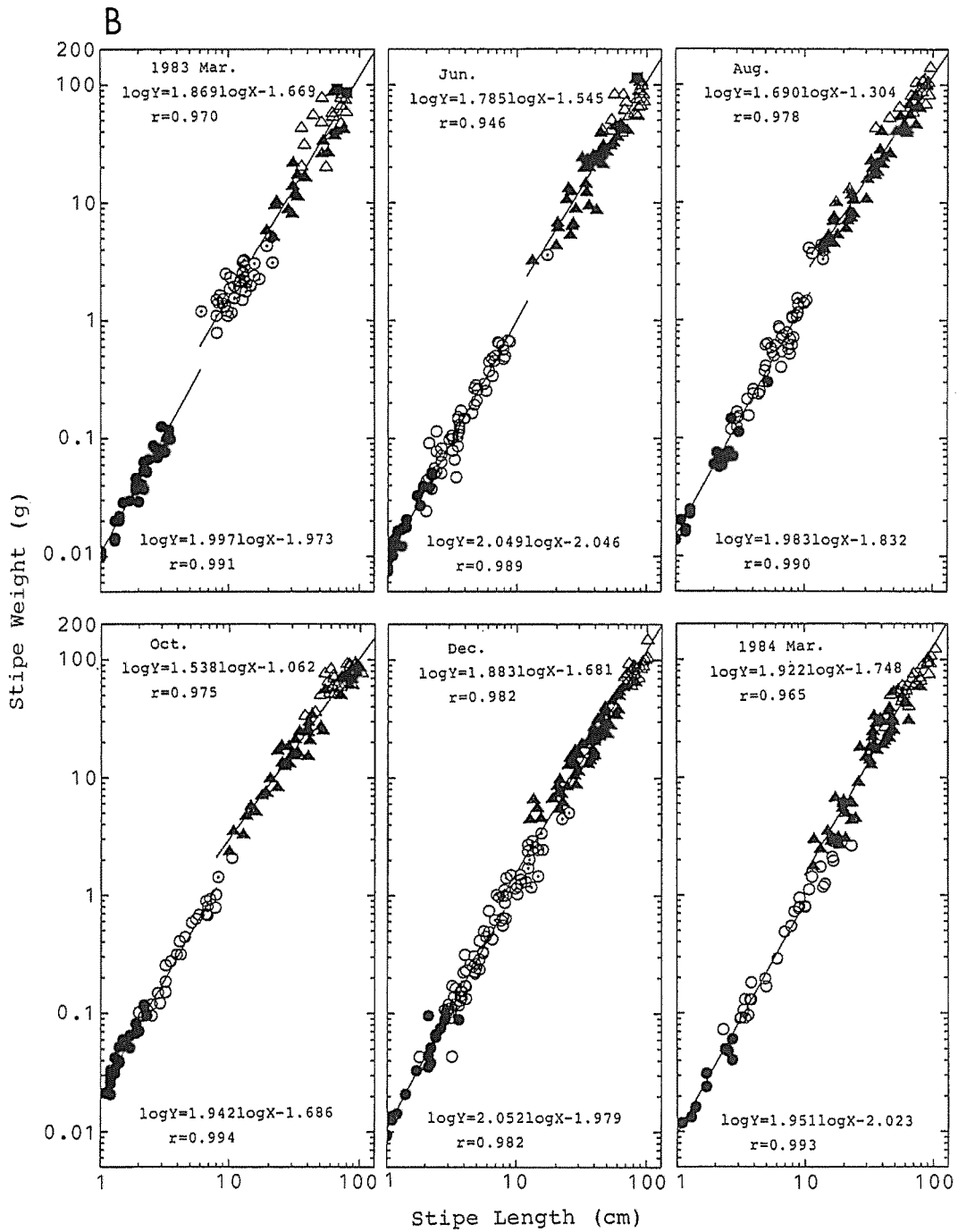
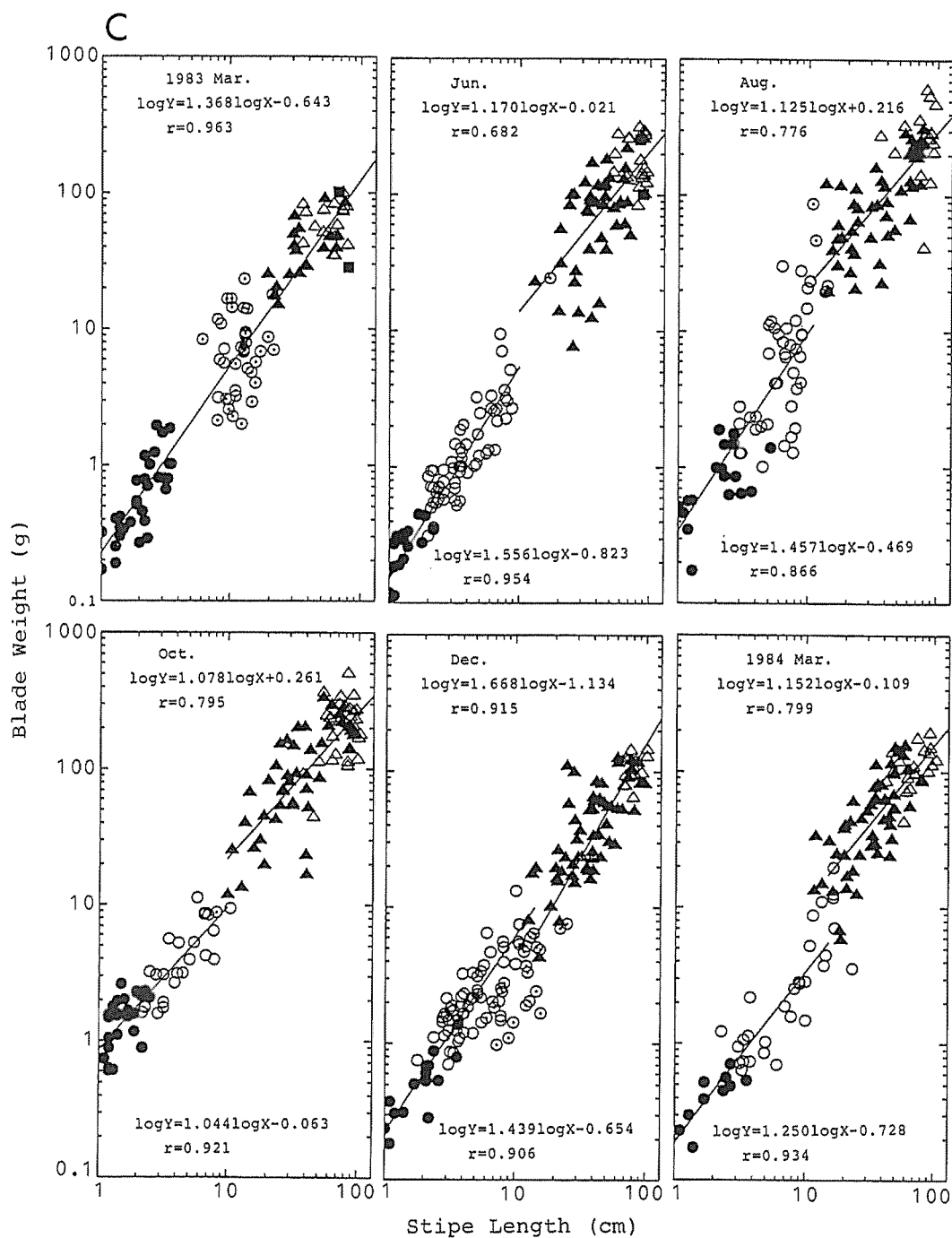


Fig. 8. Seasonal changes of the allometric relation of *Eisenia bicyclis* from March 1983 to March 1984. Regression equations and correlation coefficients are shown together. Symbols show fronds with no ring (●), one ring (○), one ring with fork stipe (⊙), two rings (▲), three rings (△) and four rings (□).

A; Stipe Length-Frond Weight    B; Stipe Length-Stipe Weight    C; Stipe Length-Blande Weight





changes in allometric relations between the stipe length and the weight of fronds, blade and stipe for both species. In these figures various types of symbols show the age groups classified by the number of growth rings. Zero to four growth rings for *Ei. bicyclis* and zero to three rings for *Ec. cava* were counted throughout the year, and the number of growth rings increased with the elongation of stipe length.

As for *Ei. bicyclis* (Fig. 8,A-C), the allometric lines were discontinuous because of remarkable changes in its form through the growth of individuals, *i.e.* a primary blade produced at the young stage was lost and the upper part of stipe forked after 1 to 1.5 years from germination (cf. Fig. 3). So, the two allometric lines were calculated for two groups from 0 to 1 year old and more than 2 years old. The correlation coefficients in the groups from 0 to 1 year old were always higher than those in the group more than 2 years old in every combinations of the parameters in allometric analyses. The tests for significant differences of slope and position of allometric lines between two groups were carried out after ITO<sup>81)</sup>.

Fig. 8,A shows seasonal changes in the allometric relation between stipe length and frond weight of *Ei. bicyclis*. In April, the non-ring group germinating from winter to the beginning of spring was clearly distinguished from other ring groups and reached 3.5 cm in stipe length. Almost of all the fronds with one ring have already forked. From April to June, the one-ring group with fork grew up to the two-ring group. Individuals grown up to more than 2 cm in stipe length formed the first growth ring. Therefore, from April to June fronds in each age group formed another growth ring. From August to December, each age group showed no marked changes, and the range of stipe length was shorter than 3 cm for the non-ring group, from 3 to 10 cm for the one-ring group, from 10 to 50 cm for the two-ring group, and longer than 50 cm for the three- or more ring group. In December, fronds with stipes longer than 3 cm began to fork in the one-ring. Consequently, *Ei. bicyclis* began to fork in December and completed to fork in April after almost one year from germination. This result corresponds well to the reports by ARASAKI<sup>47)</sup>, NISHIKAWA and YOSHIDA<sup>82)</sup> and KOJIMA<sup>10)</sup>.

Fig. 8,B shows the seasonal changes in the allometric relation between stipe length and stipe weight of *Ei. bicyclis*. The allometric lines were also discontinuous because of remarkable changes in its form through the growth of fronds. However, the discontinuity of two allometric lines was smaller than that observed between stipe length and frond weight, although the two lines had statistically a significant difference. There are no remarkable seasonal variations in allometric relations between stipe length and stipe weight throughout the year, and the correlation coefficient showed high values more than 0.97.

On the other hand, the seasonal changes in the allometric relation between stipe length and blade weight showed notable discontinuity except for one observed in April 1983 (Fig. 8,C). Specifically, allometric lines obtained for the age groups with fork more than two years old showed remarkable changes throughout the year and had relatively lower correlation coefficients than those between stipe length and weight of frond and stipe. Consequently, the main reason for discontinuity observed in allometry was the drastic changes in blade weight when *Eisenia* fronds forked.

As for *Ec. cava* (Fig. 9,D-F), allometric lines were continuous, because *Ec. cava* grew up from the young to adult stage without apparent changes in the proportion of fronds, being different from *Ei. bicyclis* (cf. Fig. 3).

Fig. 9,D shows the seasonal changes in allometric relations between stipe length and frond weight of *Ec. cava*. Juveniles with the non-ring group which germed from winter to the beginning of spring appeared in April. These juveniles grew up rapidly and reached 10 cm in stipe length in June. The range of stipe length was from 10 to 30 cm for the one-ring group and more than 30 cm for two- and three-ring groups. Two groups with two and three growth rings were not distinguished very clearly from one other, although fronds with relatively long

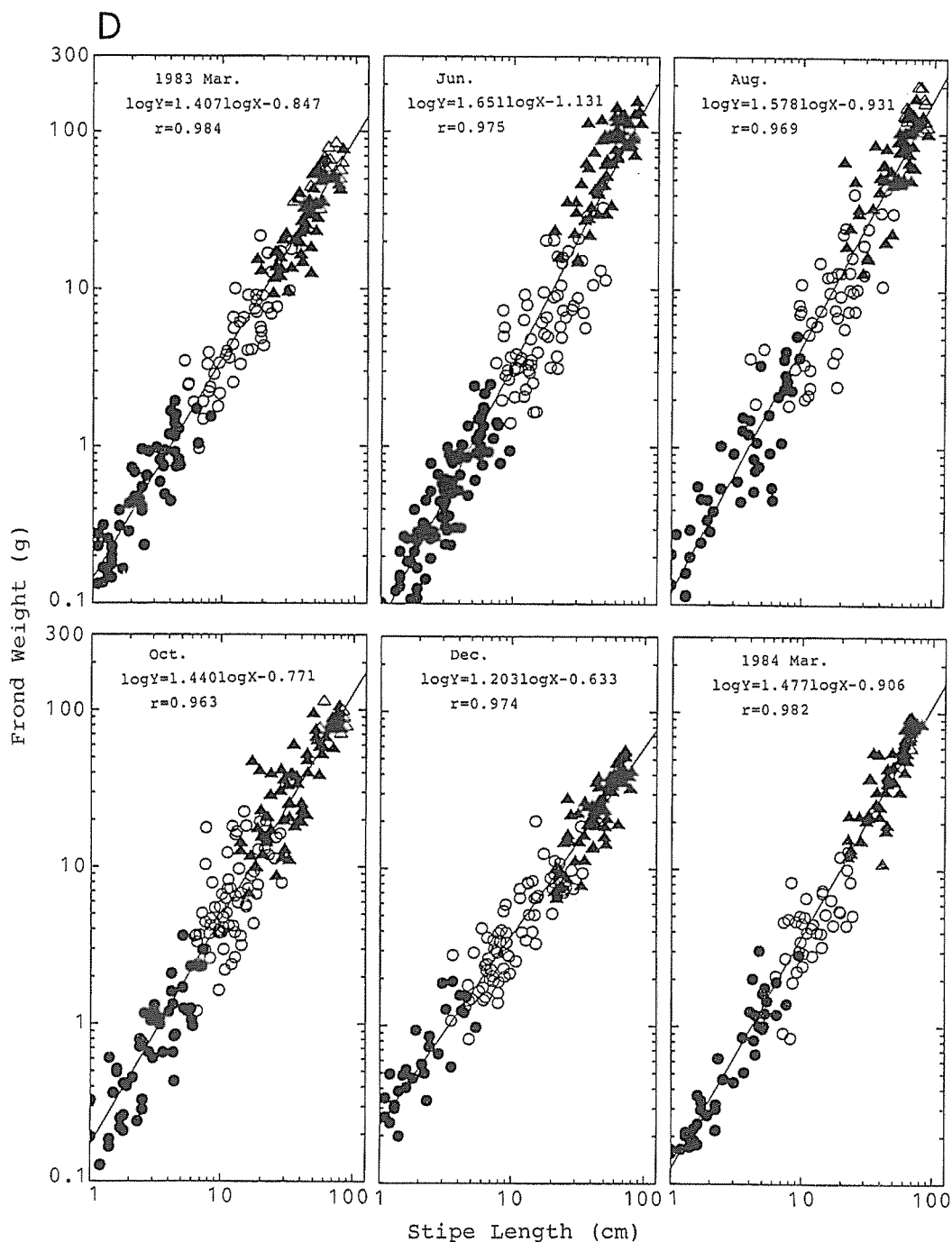
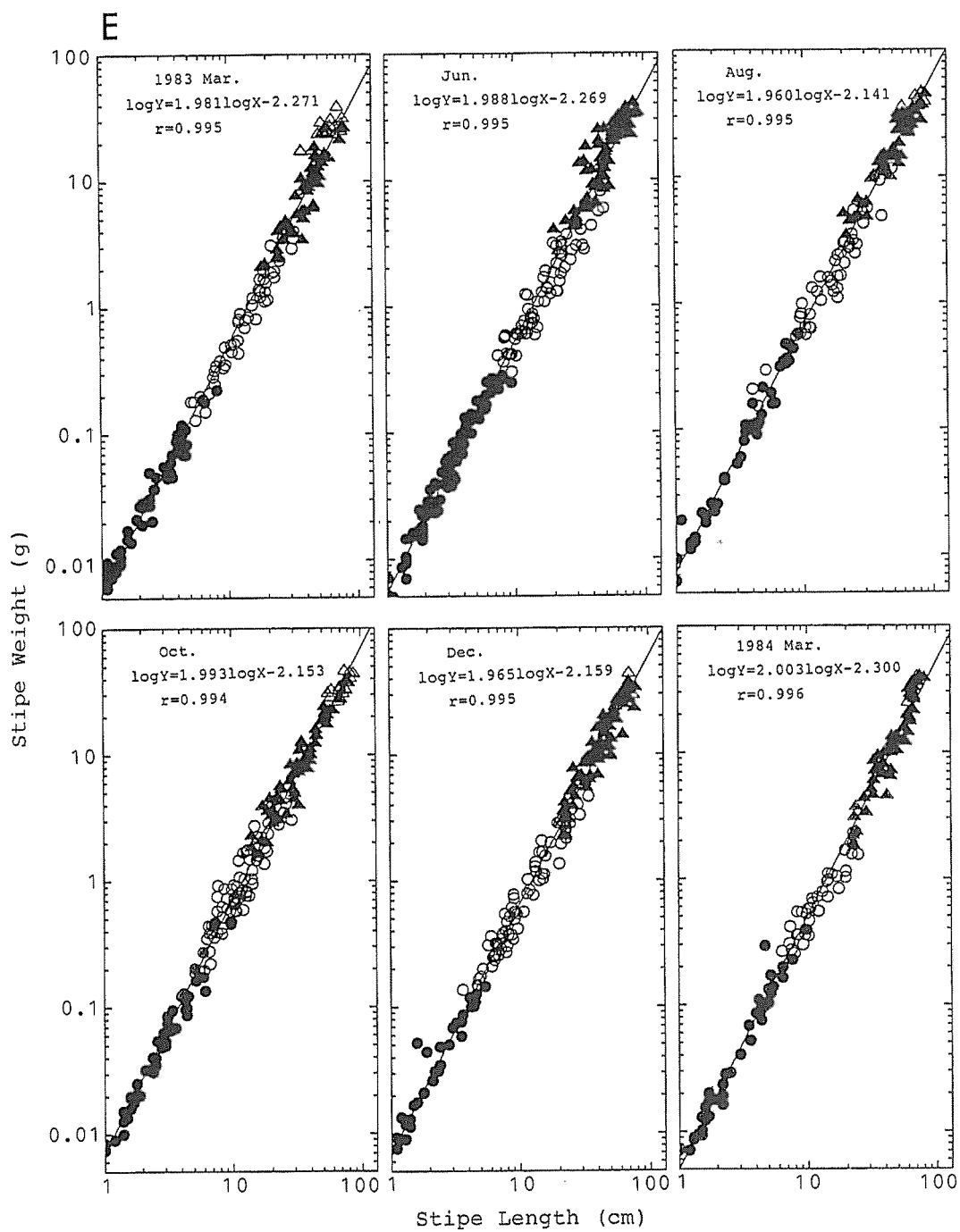


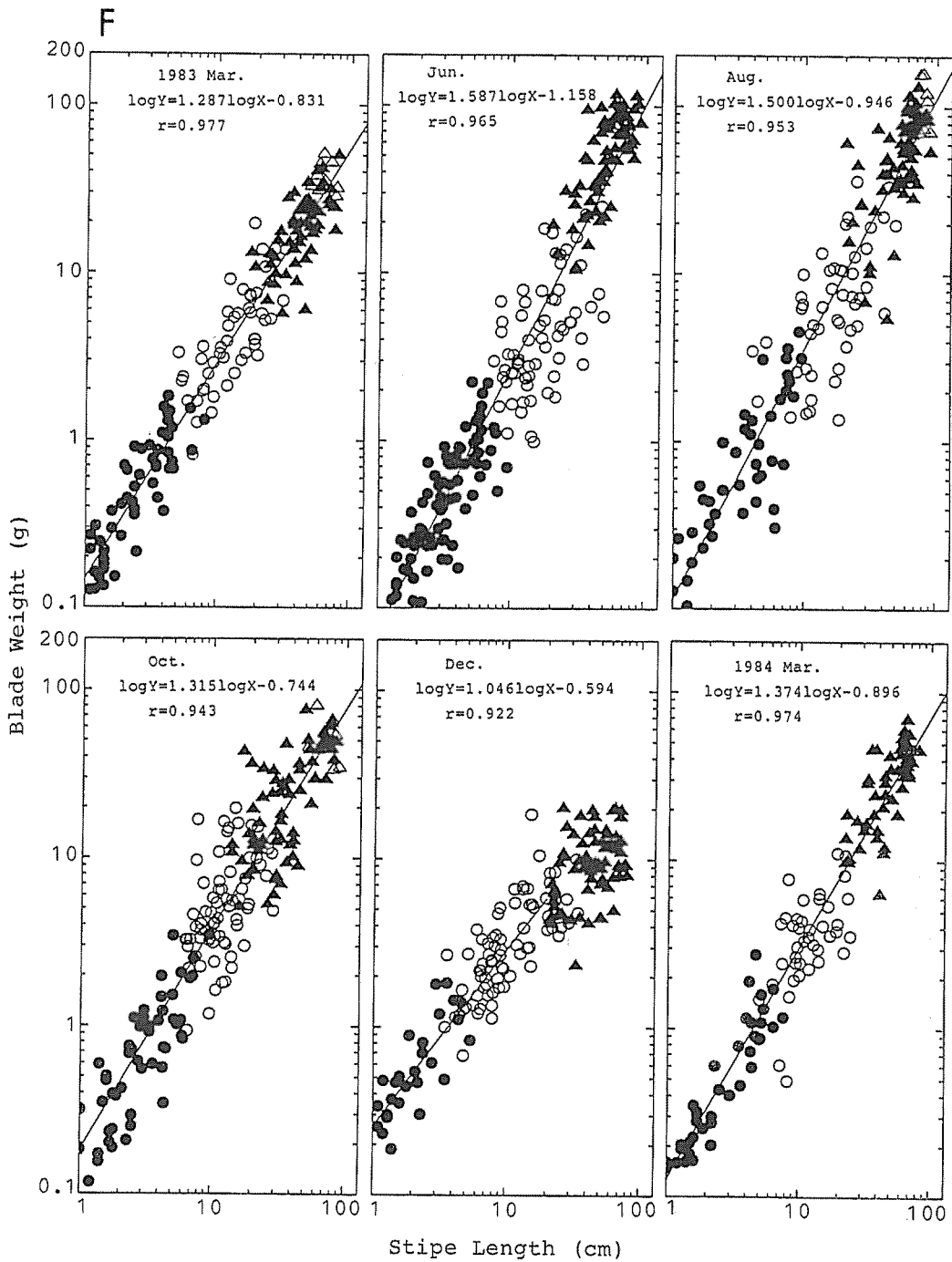
Fig. 9. Seasonal changes of the allometric relation of *Ecklonia cava* from March 1983 to March 1984. Regression equation and correlation coefficients are shown together. Symbols show fronds with no ring (●), one ring (○), one ring (▲) and three rings (△).

D; Stipe Length-Frond Weight

E; Stipe Length-Stipe Weight

F; Stipe Length-Blande Weight





stipes had a tendency to belong to the three-ring group. From June to October, the range of stipe length in each age group showed no marked changes. In December, the non-ring group had a stipe length shorter than 5 cm, and the fronds with stipe length from 5 to 10 cm joined the one-ring group. Therefore, in December each age group was in the process of developing one additional growth ring. In April 1984, the formation of growth rings was completed, and the recruits with non-rings appeared again. The distributional pattern of each age group in April 1984 were almost the same as the previous April. Furthermore, there was no significant difference between the allometric lines in April 1983 and April 1984 in the test of differences in slope and position by Ito's<sup>81)</sup> method.

Fig. 9,E shows the seasonal changes in the allometric relation between stipe length and stipe weight of *Ec. cava*. The allometric line was also continuous because of no remarkable changes in their form through the growth of fronds, being different from *Ei. bicyclis*. There were no remarkable seasonal variations in the allometric relation between stipe length and stipe weight throughout the year, and the correlation coefficient showed high values more than 0.97. Conversely, the allometric relation between stipe length and blade weight showed notable seasonal variations in values of the slope and the position (Fig. 9,F), and the correlation coefficient was lower than those between stipe length and weight of frond and stipe.

Similar to other species of Laminariaceae, sporophytes of *Ei. bicyclis* and *Ec. cava* exhibit distinct seasonal changes in growth, i.e. growth cycle<sup>6,30)</sup>, standing stock and net production<sup>9,22)</sup>, and photosynthetic activity<sup>21)</sup>. The growth cycles of both species were almost similar. Based on the biometric studies by HAROUN *et al.*<sup>83)</sup>, the following 4 periods were distinguished in the annual growth cycle of the *Ec. cava* blade: (1) period of active formation of new primary blades and bladelets in winter; (2) period of active growth of bladelets in spring; (3) period of thickening of bladelets and development of sori from late spring to summer; and (4) period of decay of old bladelets during autumn. As the result the standing stock reached the maximum in mid-summer and minimum in mid-winter. The rate of net production, however, reached a maximum in mid-spring and a minimum in late summer<sup>23)</sup>. In this study, allometric lines between stipe length and stipe weight were almost the same throughout the year, while the allometric lines between stipe length and blade weight exhibited remarkable seasonal changes in both species. Consequently, the seasonal changes in standing stock were mainly due to the changes in blade weight.

Figs. 10 and 11 show the allometric relations between stipe diameter,  $D^2H$  and weight of frond, stipe, and blade for *Ei. bicyclis* and *Ec. cava*, respectively. All the analyses were done with the data of June 1983. For *Ei. bicyclis* (Fig. 10,G-H), there were clear allometric relations which were exhibited by two lines in all combinations of parameters. Correlation coefficients were nearly at the same levels more than 0.95 in the groups including the fronds with non- and one ring, but were slightly low in the groups with more than two rings.

On the other hand, the allometric relations of *Ec. cava* between stipe diameter,  $D^2H$  and frond weight showed non linear relationships as shown in Fig. 11, M-R. These results may suggest that a stipe diameter has a maximum size. A stipe length, which may also have a maximum, reaches it slower than stipe diameter does. Therefore, the growth rate of stipe diameter have no linear correlation to that of other weight parameters. Then, the extended allometry, which had a maximum value for  $Y$  (stipe diameter), was adopted in the relation between stipe length and stipe diameter as shown in Fig. 12,S-T for *Ei. bicyclis* and *Ec. cava*, respectively. The extended allometry is expressed as follows;

$$1/Y = 1/aX^b + 1/MAX,$$



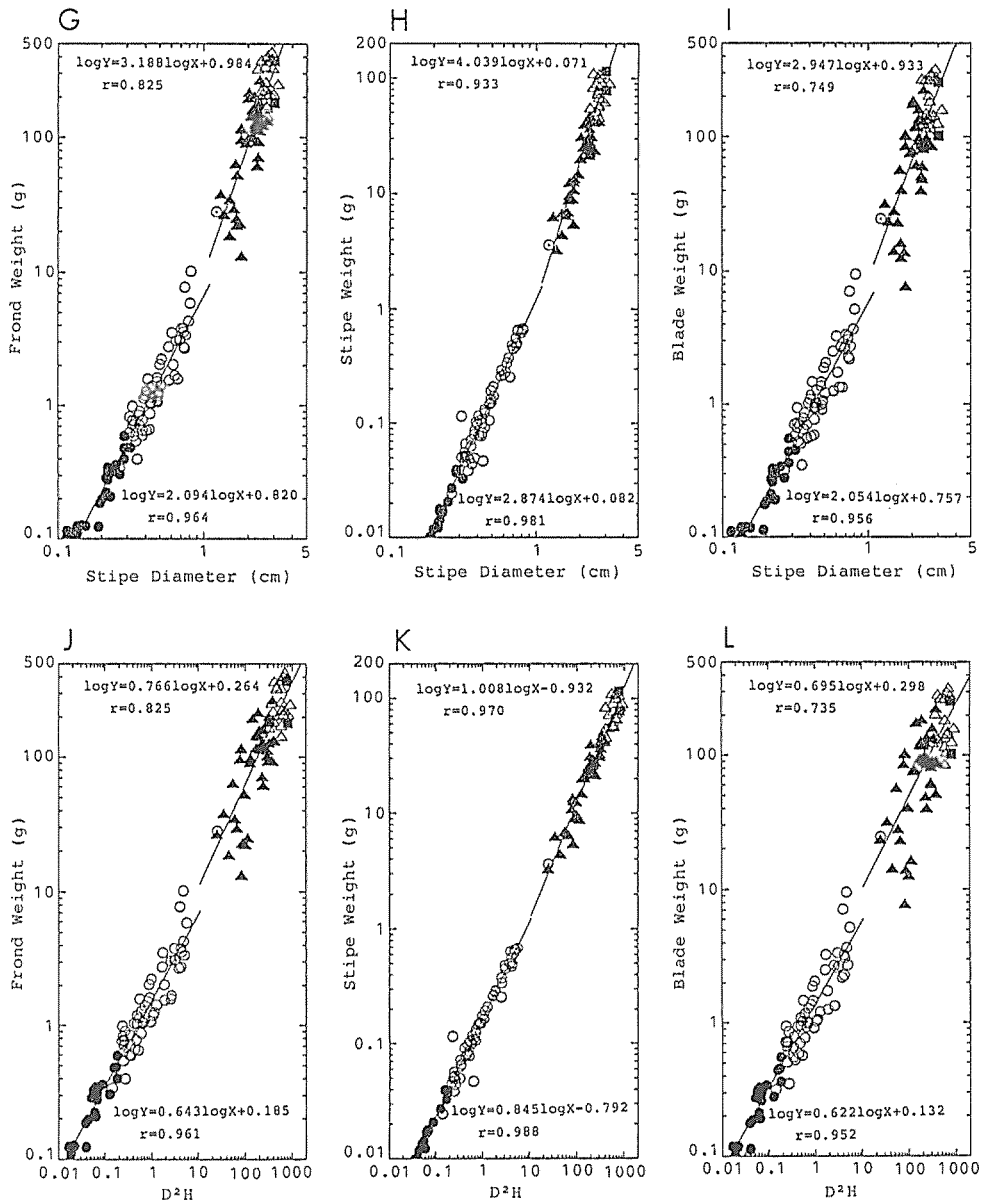


Fig. 10. Allometric relations of *Eisenia bicyclis* in June 1983. Regression equation and correlation coefficients are shown together. Symbols show fronds with no ring (●), one ring (○), one ring with fork stipe (⊙), two rings (▲), three rings (△) and four rings (□).

- G; Stipe Diameter–Frond Weight
- H; Stipe Diameter–Stipe Weight
- I; Stipe Diameter–Blade Weight
- J;  $D^2H$ –Frond Weight
- K;  $D^2H$ –Stipe Weight
- L;  $D^2H$ –Blade Weight

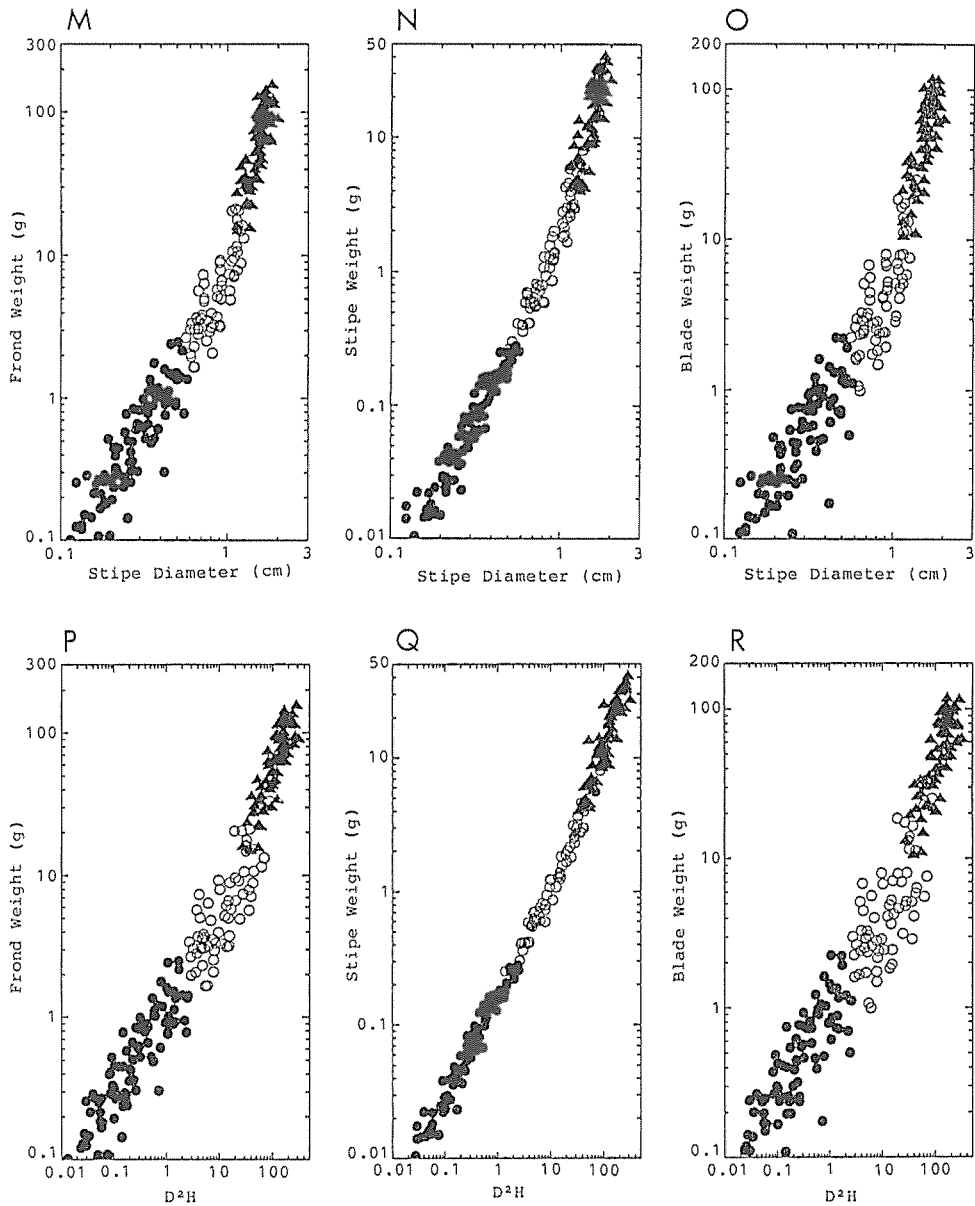


Fig. 11. Allometric relations of *Ecklonia cava* in June 1983. Symbols show fronds with no ring (●), one ring (○), two rings (▲) and three rings (△).

M; Stipe Diameter–Frond Weight  
 N; Stipe Diameter–Stipe Weight  
 O; Stipe Diameter–Blade Weight  
 P;  $D^2H$ –Frond Weight  
 Q;  $D^2H$ –Stipe Weight  
 R;  $D^2H$ –Blade Weight

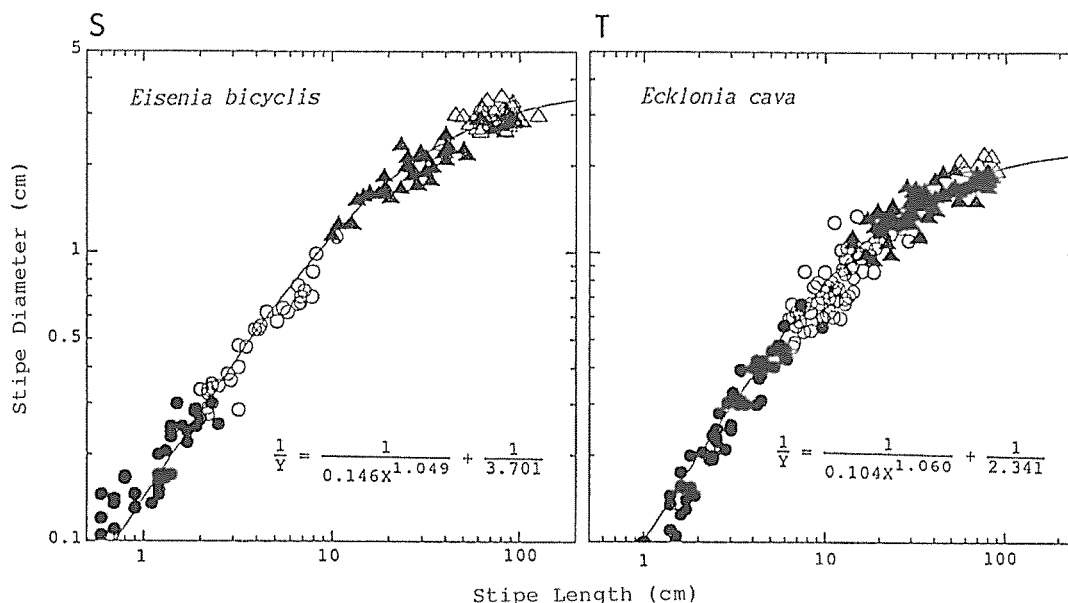


Fig. 12. Extended allometric relation between stipe length and stipe diameter of *Eisenia bicyclis* and *Ecklonia cava* in October 1983. Regression equations are shown together. Symbols show fronds with no ring (●), one ring (○), one ring with fork stipe (⊙), two rings (▲), three rings (△) and four rings (■).

where  $Y$  is the stipe diameter,  $X$  is the stipe length,  $MAX$  is the maximum size of stipe diameter, and  $a$  and  $b$  are the constants. The maximum size of diameter estimated is 3.701 for *Ei. bicyclis* and 2.341 for *Ec. cava*.

Some standard measuring characters used for analyzing structure and age distribution in the population have been reported for *Ei. bicyclis* and *Ec. cava*, i.e. stipe diameter by KOJIMA<sup>10)</sup>, D<sup>2</sup>H by HAYASHIDA<sup>11)</sup> and TAKAMA<sup>11)</sup>, stipe length by MAEGAWA and KIDA<sup>18,19)</sup>. In this study, stipe length was adopted as the standard measuring character for analyzing population structures of both *Ei. bicyclis* and *Ec. cava*. The stipe length had a linear relationship to the weight parameters such as total frond, blade and stipe weight in allometry, and was easy to measure under water. In addition, the frequency distribution of stipe length represented the vertical structure of the population, which was important for taking fundamental data to analyze the regeneration process and estimate the light condition in the population.

As OKAMURA<sup>75)</sup> pointed out in his early observation for *Ei. bicyclis*, stipe length of adult plants varied according to the depth where the plants grow, i.e. fronds growing in shallow water near high tide had shorter stipes than those in deep water. In Tables 1 and 2 the variations of stipe length of *Ei. bicyclis* and *Ec. cava* in relation to the growing depth were indicated in each age group collected in my study area around Shima Peninsula. As the results, there are no significant differences in  $t$  test ( $<0.05$ ) between growing depth and stipe length in each age group of both species. YOSHIDA<sup>9)</sup> also reported that there are no marked differences in stipe length, frond weight and number of bladelet of *Ei. bicyclis* among those collected from 2 and 4 meters in depth. Consequently, it was thought that the adult *Ei. bicyclis* fronds with short stipes only grew in the shallowest limit of its distributional range, such as the lowest band of the intertidal zone. *Ec. cava* had no variations in their stipe length with the growing depth.

**Table 1.** Changes with depth in stipe length (cm) of *Eisenia bicyclis* in each age group. Values are means  $\pm$  95% confidence limits

Age	Depth (m)		
	2	4	8
1	1.47 $\pm$ 0.17	1.75 $\pm$ 0.45	1.33 $\pm$ 0.30
2	5.15 $\pm$ 1.14	6.99 $\pm$ 0.83	6.72 $\pm$ 1.39
3	37.82 $\pm$ 4.99	40.26 $\pm$ 6.34	35.41 $\pm$ 5.46
4	66.09 $\pm$ 6.65	76.58 $\pm$ 7.70	75.21 $\pm$ 4.13

**Table 2.** Changes with depth in stipe length (cm) of *Ecklonia cava* in each age group. Values are means  $\pm$  95% confidence limits

Age	Depth (m)		
	5	7	17
1	2.93 $\pm$ 0.59	3.87 $\pm$ 0.73	2.82 $\pm$ 0.45
2	10.98 $\pm$ 1.41	13.70 $\pm$ 2.89	10.23 $\pm$ 1.56
3	48.21 $\pm$ 4.80	53.77 $\pm$ 4.30	46.46 $\pm$ 4.62
4	53.30 $\pm$ 16.74	77.45 $\pm$ 6.22	82.00 $\pm$ 31.95

### c) Regeneration

The yearly changes of frequency distribution of stipe length in 4 quadrats in June from 1982 to 1987 (to 1988 for *Ei. bicyclis*) are shown in Fig. 13 for *Ei. bicyclis*, and in Fig. 14 for *Ec. cava*. The shaded parts show the number of loss during a period till the following year.

As for the *Ei. bicyclis* populations in Fig. 13 (St. 1 and St. 2), there were no marked changes in frequency distribution of stipe length throughout the period of this study. The adult fronds always dominated to form a dense marine forest. The fronds with stipe lengths more than 20 cm observed in 1982 were usually more than 2 years old, estimated from the allometric relationships in Fig. 8. In 1983 many recruits appeared, but almost all of those drifted out and were lost or died till the following year. The density of adult fronds decreased gradually from 13.3 to 6.7 individuals per m<sup>2</sup> at St. 1, and from 20 to 10.7 individuals per m<sup>2</sup> at St. 2 during 6 years from 1982 to 1987. From 1987 to 1988, nearly half of the large canopy fronds were lost and many recruits appeared again. It is thought that the remarkable change in density of canopy fronds is the key to the beginning of regeneration. The loss of many canopy fronds provide favorable light condition for recruits to germ and grow on the population floor.

As for *Ec. cava* populations in Fig. 14, the yearly changes of frequency distribution of stipe length in both quadrats also showed a similar tendency. In contrast with *Ei. bicyclis* population, *Ec. cava* population showed remarkable yearly changes. In 1982 large fronds with stipe length of more than 20 cm occupied greater parts, but in 1983 most of the 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 a canopy. In 1986 most of the 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 controlled by the density of large fronds. After most of the large fronds forming a canopy were lost or drifted out, many recruits were produced and grew to the canopy one to two years later. Consequently, the turnover time of the canopy layer of the *Ec. cava* 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.

Figs. 15 and 16 show the seasonal and yearly changes in density, standing stock and mean stipe length with advancement of the regeneration process in both populations at Sts. 1–4. Standing stock was calculated from the allometric relation between stipe length and total fronds weight as indicated in previous section. Mean stipe length is the average of total fronds in the quadrat at every census. Therefore, it is a parameter representing

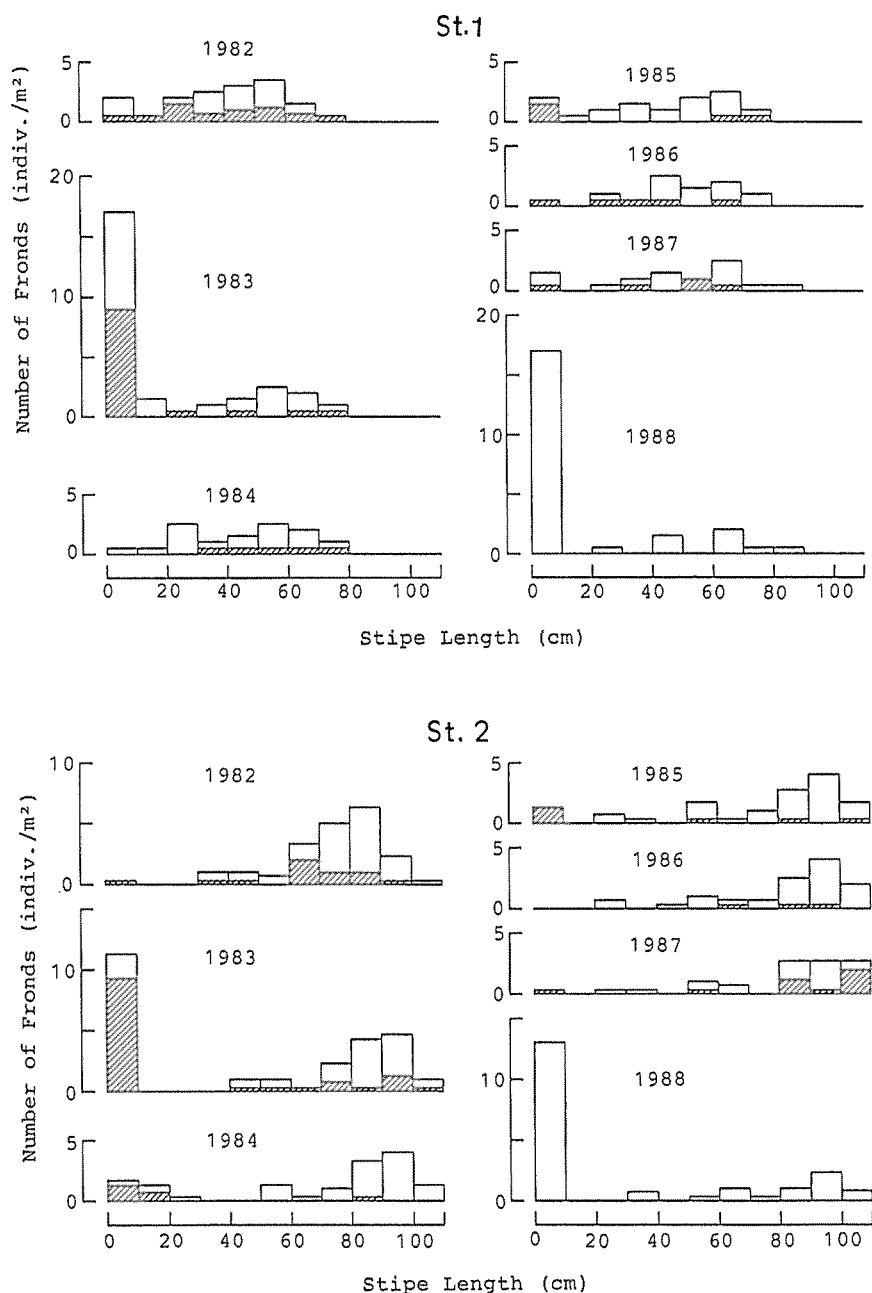


Fig. 13. Yearly changes in frequency distribution of stipe length of *Eisenia bicyclis* population at Sts. 1 and 2 from 1982 to 1988. Shaded portions show the loss by the next year.

the height of the population.

As for the *Ei. bicyclis* population in Fig. 15 at St. 1 and St. 2, the density of adult fronds more than 20 cm in stipe length was high at the beginning of the study in 1982, and thereafter it decreased gradually. The density of young fronds shorter than 20 cm in stipe length was low except for 1983 and 1988. The changes of standing

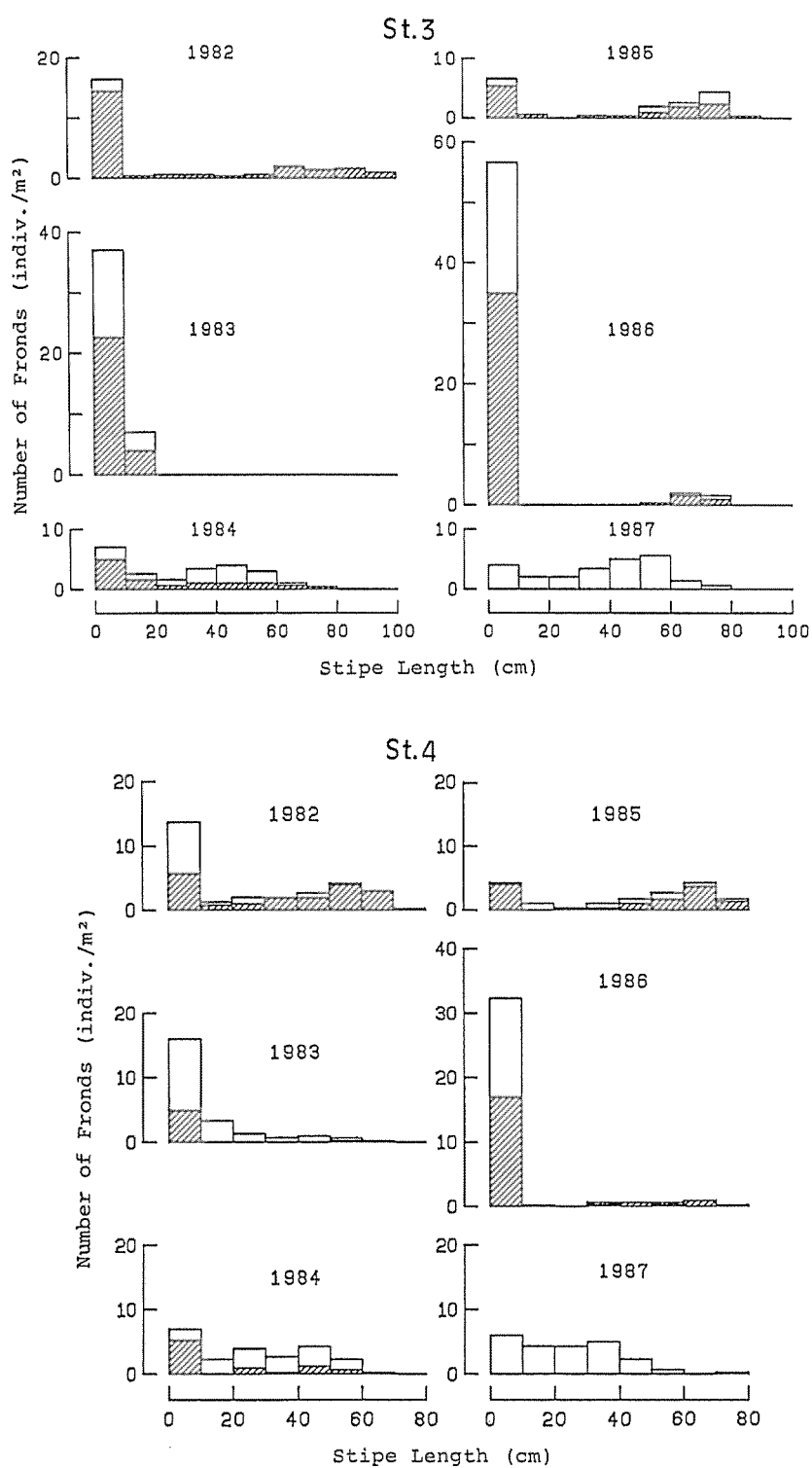


Fig. 14. Yearly changes in frequency distribution of stipe length of *Ecklonia cava* population at Sts. 3 and 4 from 1982 to 1987. Shaded portions show the loss by the next year.

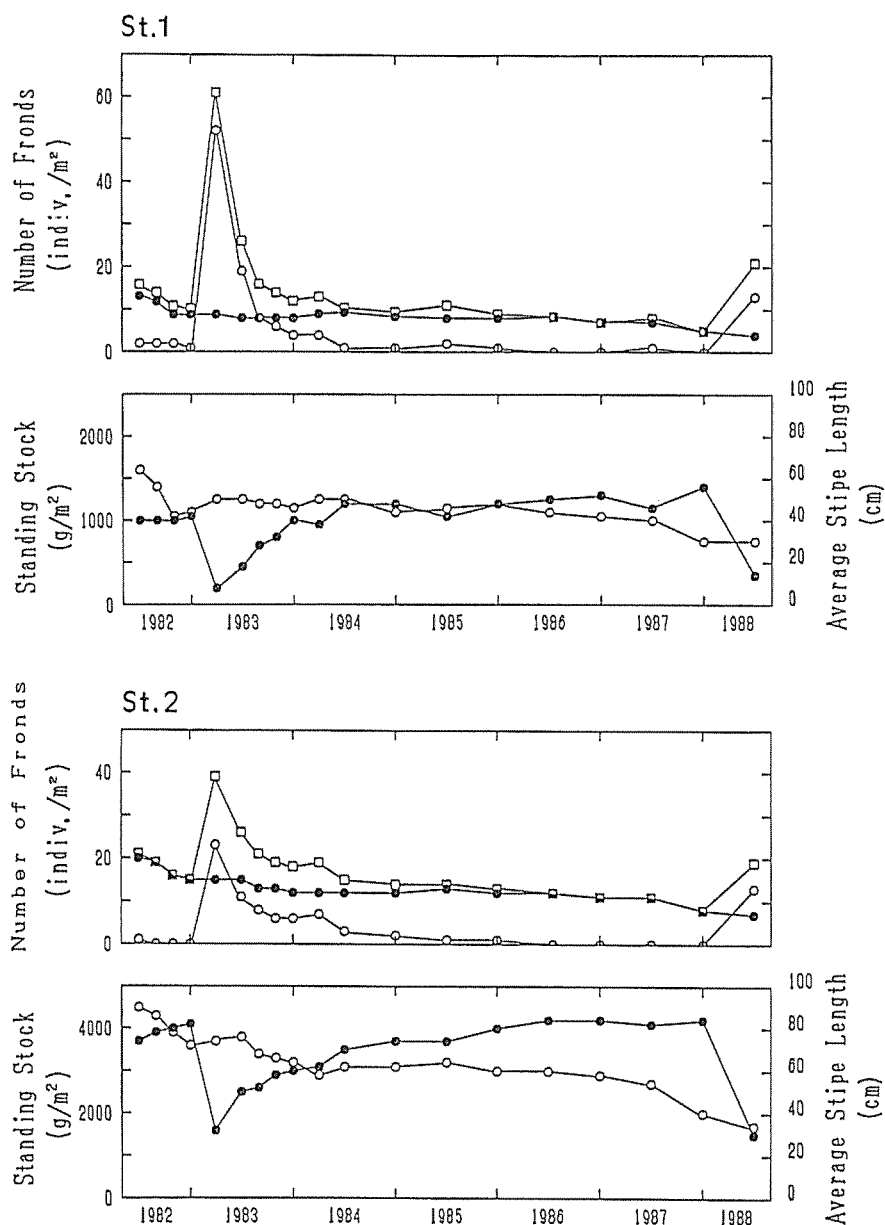


Fig. 15. Changes in the population density total fronds (—□—), young fronds (—○—) and adult fronds (—●—) (upper figure), and in the average stipe length (—●—) and the standing stock (—○—) (lower figure) of *Eisenia bicyclis* at Sts. 1 and 2 from 1982 to 1988. Young fronds are shorter than 20 cm in stipe length, and adult fronds are longer than 20 cm in stipe length.

stock were similar to those in the density of adult fronds, which were high at the start of this study, and thereafter it decreased gradually. The maximum standing stock was 1571 g/m<sup>2</sup> at St. 1 and 4483 g/m<sup>2</sup> at St. 2, which were recorded in June 1982 at the start of this study. The mean stipe length was high in 1982, 1984, 1985, 1986 and 1987, and low in 1983 and 1988 when many recruits developed.

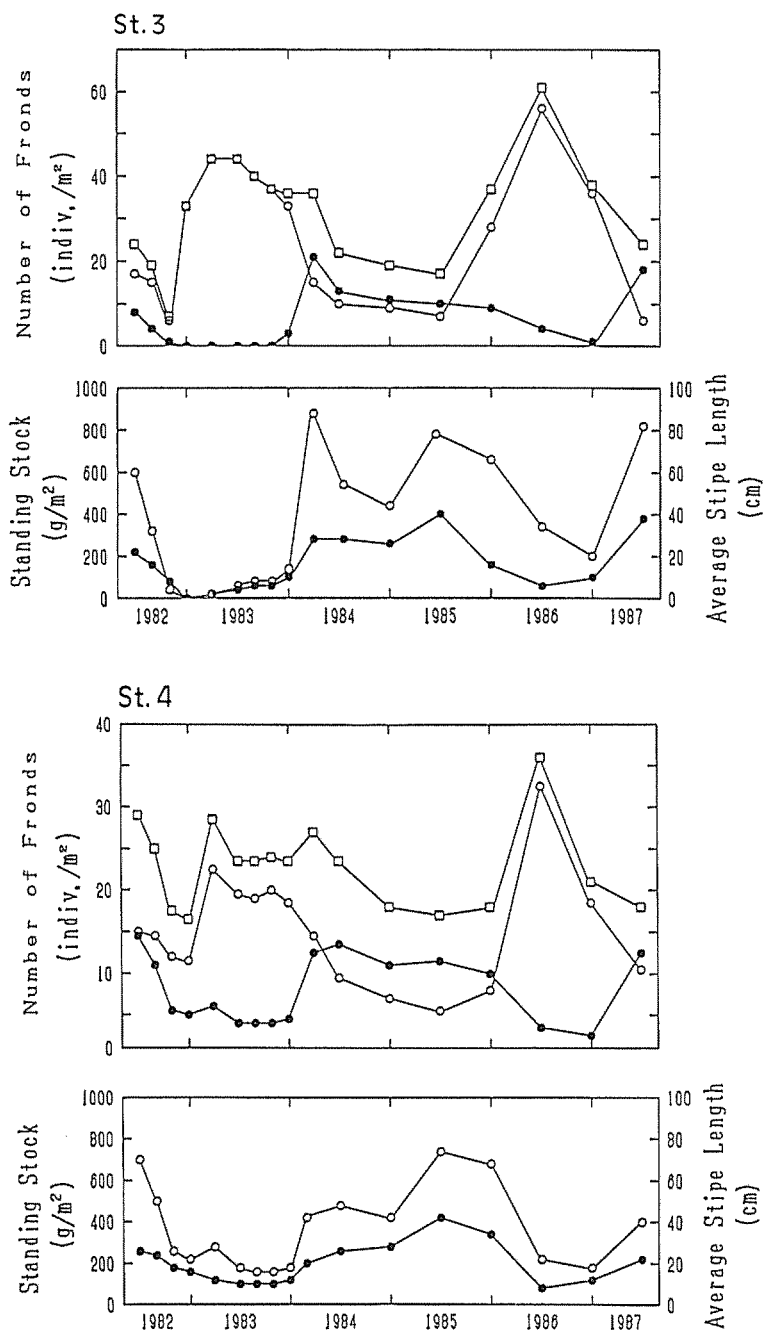


Fig. 16. Changes in the population density total fronds (—□—), young fronds (—○—) and adult fronds (—●—) (upper figure), and in the average stipe length (—●—) and the standing stock (—○—) (lower figure) of *Ecklonia cava* at Sts. 3 and 4 from 1982 to 1987. Young fronds are shorter than 20 cm in stipe length, and adult fronds are longer than 20 cm in stipe length.



On the other hand, in the *Ec. cava* population (Fig. 16) the total number of fronds varied irregularly. However, the number of young fronds exhibited periodic changes at intervals of three 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 the adult fronds formed a dense canopy as shown in Fig. 14. The maximum density of adult fronds was about 14 individuals/m<sup>2</sup> 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. The maximum values of standing stock and mean stipe length were 0.8 kg/m<sup>2</sup> and 30–40 cm, respectively.

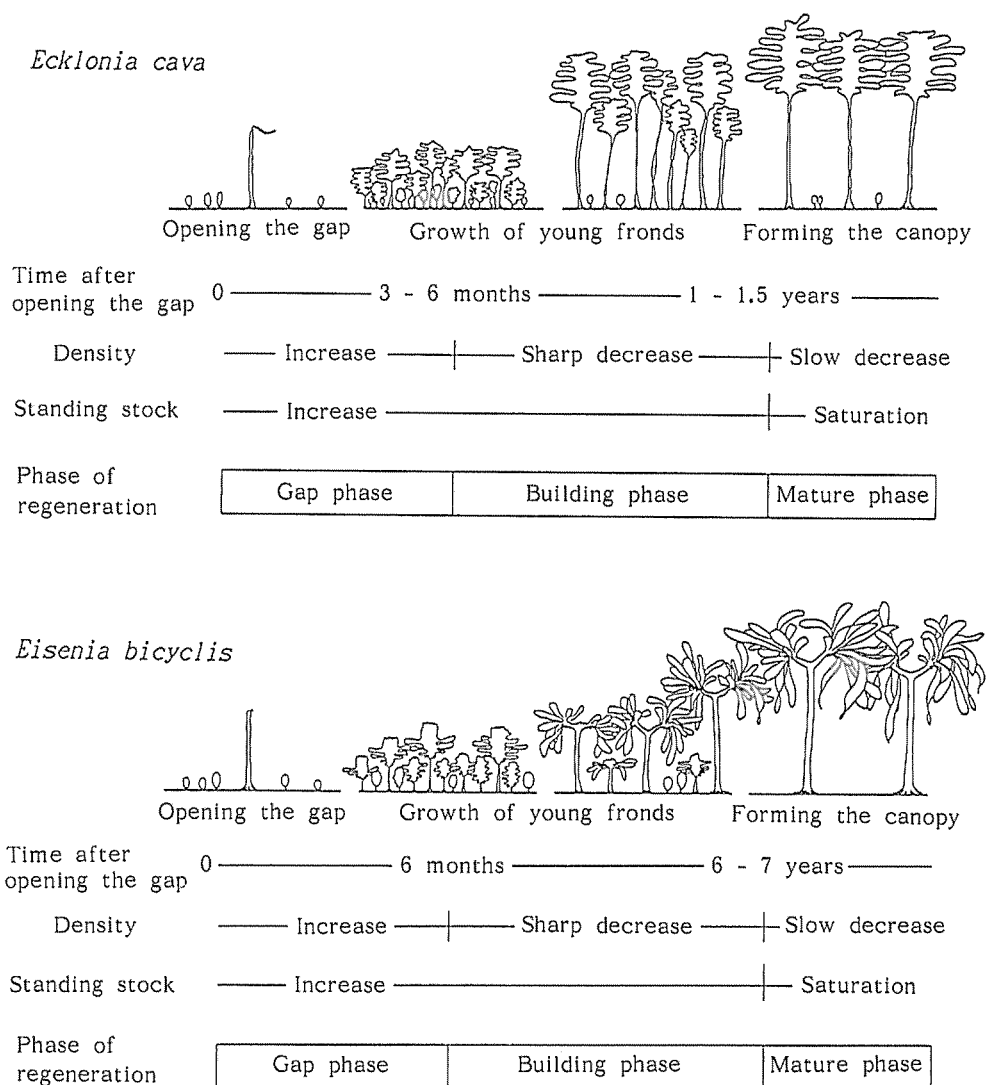


Fig. 17. Schematic diagram of the regeneration process in *Ecklonia cava* and *Eisenia bicyclis* population, and changes in the population density and the standing stock with advancement of the regeneration process.

From the results mentioned above, the schematic diagram was drawn for a *Ec. cava* population as illustrated in Fig. 17 to summarize the changes in density, standing stock and regeneration process. The three phases could be distinguished with reference to the structures and the features of the population through the regeneration process. In the first place, the gap is opened by the loss of many large fronds which form a 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, population density decreases gradually (mature phase). The mature phase is maintained for about one year. The regeneration process of the *Ec. cava* marine forest corresponds well to the typical “gap regeneration” in terrestrial climax forests.

The regeneration process of the *Ei. bicyclis* population in Fig. 17 is almost the same as the *Ec. cava* population, although the turnover time of the former is longer than that of the latter. The period and structure of the gap phase and building phase are similar in both populations. In the mature phase, *Ei. bicyclis* maintains the canopy for a considerable time, 6 or 7 years. As the result, the turnover time of the *Ei. bicyclis* population is more than 8 years. The turnover time of *Ec. cava* is only 3 years. The difference of turnover time is attributed to *Ei. bicyclis* having a longer life span than *Ec. cava*. More details about the life span for both species will be discussed in Chapter III.

Recently, long time 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<sup>33,40,84,85</sup> and/or grazing by herbivores<sup>34,37,38</sup> which act as external factors. So, until now it has been thought 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, I propose another factor which might be the most important one controlling the population structure of marine forests of *Ei. bicyclis* and *Ec. cava*. It is an intraspecific competition like self-thinning which acts as an internal factor with advancement of the regeneration process. Consequently, such structures 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. More details concerning intraspecific competition and light condition as limiting factors will be discussed in the next section and in Chapter II.

In the *Ec. cava* population many recruits, which were 45–60 fronds/m<sup>2</sup> at St. 3 and 25–35 fronds/m<sup>2</sup> at St. 4, 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 available space on the substratum for germination and growth of young fronds. A large number of recruits as mentioned above decreased rapidly to 10–15 fronds/m<sup>2</sup> in one year. This decrease in density supports the evidence of self-thinning which is caused by changes of the light condition in a population. A large number of recruits germed 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 germed earlier or grown rapidly have a possibility to survive to canopy fronds. Recruits which were densely produced 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 subject to high mortality. As the result, the 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<sup>49)</sup>.

Regeneration of climax marine forests such as *Ei. bicyclis* and *Ec. cava* populations is usually initiated by the formation of the gap formed by 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 assemblages of canopy fronds lose 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/m<sup>2</sup>. IWAHASHI<sup>7)</sup> also observed that a lot of recruits of *Ec. cava* occurred when the density of adult plant decreased to 1–2 frond/m<sup>2</sup> in the coastal water of Izu Peninsula.

WATT<sup>60)</sup> suggested that terrestrial forest communities have mosaics of patches in which various phases of the regeneration process 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<sup>55,59,87–92)</sup> and is a valuable concept for understanding terrestrial forest structures and regeneration. WATT<sup>60)</sup> distinguished four phases (gap, building, mature, and degeneration) in the course of regeneration. WHITMORE<sup>93)</sup> recognized three phases (gap, building, and mature) in the regeneration process of many terrestrial forests. In this study, I also verified three phases (gap, building, and mature) in the regeneration process in *Ei. bicyclis* and *Ec. cava* marine forests which are 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 the population and/or community and in biological and physiological characteristics of the component species between the two. Specifically, the most important difference is the turnover time of regeneration, which is 100–200 years or more for terrestrial forests<sup>94,95)</sup>, while only 3 and 8 years for *Ec. cava* and *Ei. bicyclis*.

It has been generally observed that there was considerable skewness of age distribution in *Ei. bicyclis* population<sup>9,11–13,17)</sup> and the *Ec. cava* population<sup>5–7,11–13,15)</sup>. The skewness in *Ei. bicyclis* was not so marked as in *Ec. cava*. Specifically, young fronds can scarcely grow in a fully developed population of *Ei. bicyclis* in the mature phase. A quadrat sampling method has generally been employed for analyzing the age distribution and for estimating the standing stock of the algal population. When the 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 population, and the mean standing stock in the area may be overestimated. It is thought that many and large scale quadrat methods and 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.

#### d) Intraspecific Competition

In this section, the distributional patterns mainly for *Ec. cava* population rather than for *Ei. bicyclis* population will be examined and discussed. I could follow the regeneration process of *Ec. cava* for two cycles, which was enough to yield data to analyze the distributional patterns. However, I could not get sufficient data of *Ei. bicyclis* to analyze the distributional pattern with advancement of the regeneration process to the extent of this study for seven years as described in the previous section. I can, however, discuss to a limited degree on *Ei.*

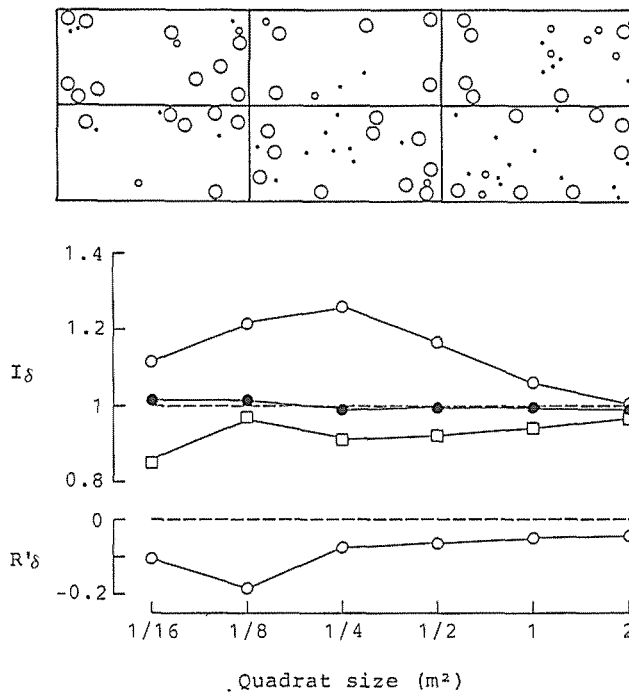


Fig. 18. Analysis of distributional patterns of the *Ecklonia cava* population in June 1982. Upper; Dispersion map of individuals in the permanent quadrat in June 1982 at St. 3. The size of circles indicate the stipe length; large open circles, adult fronds longer than 20 cm; small open circles, young fronds of 10–20 cm; small solid circles, young fronds shorter than 10 cm. Middle;  $I_{\delta}$ -quadrat size relationships for adult fronds (—□—), young fronds (—○—), and total fronds (—●—). Lower; interspecific association,  $R'_{\delta}$ , between young fronds and adult fronds.

*bicyclis* population, which may depend fundamentally on a factor similar to the distributional pattern of *Ec. cava* population.

Fig. 18 shows the dispersion of individuals and the results of analysis of the distributional pattern and the intraspecific correlation of the *Ec. cava* population in June 1982, which was in the typical mature phase. The distributional patterns were calculated in three groups; young individuals less than 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 more than one in  $I_{\delta}$  value. 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<sup>63)</sup>. 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, indicating two groups repulsive with each other.

Fig. 19 shows yearly changes in dispersion of individuals and distributional patterns in June from 1983 to

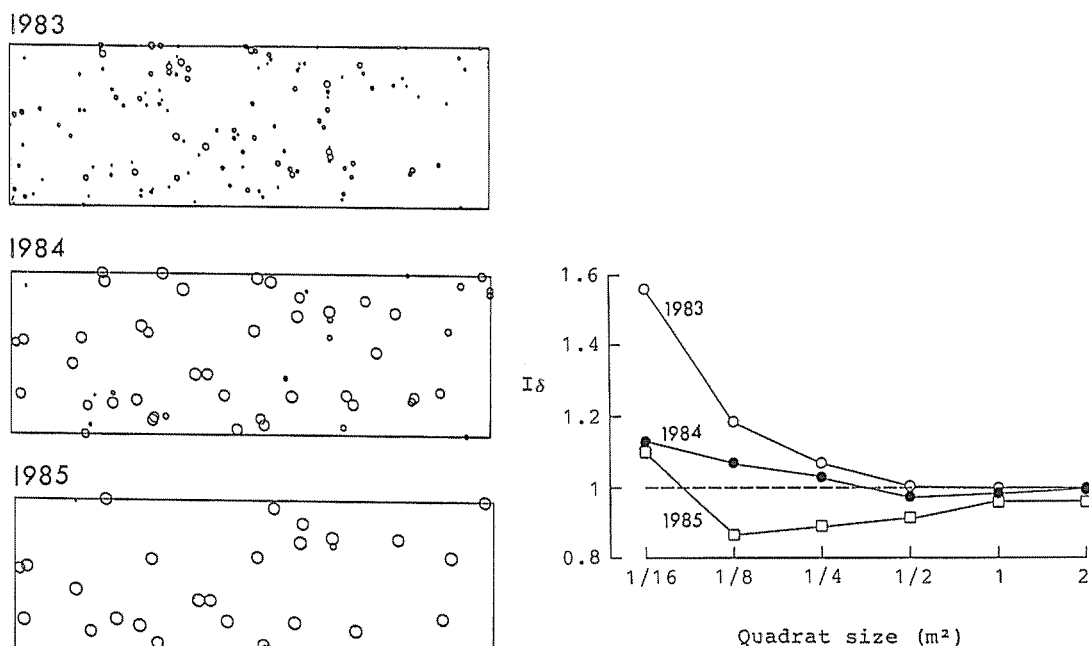


Fig. 19. Changes in the dispersion of individuals and corresponding  $I\delta$  - quadrat size relationships with advancement of the regeneration of *Ecklonia cava* population from 1983 (—○—) through 1984 (—●—) to 1985 (—□—). The size of circles indicate the stipe length; large open circles, longer than 20 cm; small open circles, 10–20 cm; solid circles, shorter than 10 cm.

1985 at St. 3 of the *Ec. 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, population density decreased rapidly as shown in the last section. Adult individuals in the mature phase in 1985 showed regular distribution in the same manner as shown in Fig. 15. From 1984 to 1985, population density decreased gradually. It was apparent that the distributional pattern changed with advancement of the generation process and according to the changes of the population density.

In this study, I found out that the distributional pattern of the *Ec. 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, and recruits is restricted by other sessile organisms or by the conditions of substratum, *i.e.* ups and downs of population floor, and rock boulder, gravel, or sand. One of the most important reasons for the contagious distribution of recruits is to be competition for light between young and adult individuals. Germination and growth of the recruits are suppressed by dim light just beneath the adult canopy fronds. As the result, the recruits can occupy only small openings where the canopy fronds leave some

distance 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. This results in death of many competitively inferior individuals which may be small and/or shaded, so that a few competitively superior individuals survive and can form a canopy. It is a typical model of "self-thinning". Individuals in the dense 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 *Ec. cava*, contagious to regular through random distribution, is quite similar to that of dominant tree species of terrestrial forests of Type III by TAGAWA<sup>67)</sup>, although the period of each phase of the regeneration process of *Ec. cava* is extremely shorter in marine forests than in terrestrial forests. There appears to be fundamental similarity in behavior 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<sup>96)</sup>.

It is concluded that one of the most important factors controlling the structure of algal population is the light condition in it. The distributional pattern is also a result of intraspecific competition for getting light through the growth of individuals, according to such a density-depending function as self-thinning. More discussion about the importance of light condition in the population will be made in the next Chapter.

## Chapter II. Light and Production

### 1. Introduction

Light is, without doubt, the most important factor affecting plants, and it is also one of the most complex. This complexity arises in the first place from the nature of light itself, and secondly from the great number of effects on plants. Seaweeds grow in an exceptionally dynamic and diverse light environment. The continuous ebb and flood of tides and the properties of water column and sea surface like wave action have a great effect on the quantity and quality of solar energy reaching seaweeds.

Solar radiation is an ultimate source of biological production which is initiated in the conversion of its radiant energy into chemical energy in organic matter through photosynthesis of plants, the primary producers. Particularly, photosynthetically active radiation (PAR), which is defined as wavelengths of 400 to 700 nm, is available for photosynthesis. Distribution and diurnal changes of solar radiation, especially of photosynthetically active radiation (PAR), are important for algal photosynthesis in the sea<sup>97,98)</sup>. Primary production in the coastal areas of the sea is carried out mainly by macroalgae. Furthermore, light is the signal for many events throughout the life cycles of algae, including reproduction, growth, distribution, and change of algal community structure.

In spite of its ecological significance, only a little attention has thus far been paid to evaluating the daily photosynthetic production under natural light conditions of aquatic plants<sup>2,99-103)</sup>, probably because of the difficulty of light measurement in the community under natural conditions and accurate photosynthetic measurement under dim light conditions. On the community floor of *Ei. bicyclis* and *Ec. cava*, the light intensity

is critical for their young fronds to survive and to grow to adulthood. Photosynthetic characteristics of young fronds of seaweed species under dim light condition near the daily light compensation level will provide insight into understanding the difference in vertical distributions of the two species.

A plant community has its own peculiar structure, in which physical and biological environments are different largely from outside of the community. Each individual or organ, such as blades, functions in an altered environment in the community. Therefore, it is necessary to grasp the structure forming a community and the changes in environmental factors affecting the community structure exactly. Community structure relating closely to biomass production is characterized by the vertical distribution of blades as photosynthetic organs and by the changes in light condition in the community.

In the previous chapter, I emphasized the importance of the light condition in a population in affecting the regeneration process and controlling the distributional pattern of *Ei. bicyclis* and *Ec. cava*. However, in many aspects of the kelp forest, the light environment remains undefined. The relationship between kelp population density or structure and light penetration has been examined by only a few investigators, although much work has been done on this kind of relationship in terrestrial plant communities<sup>104</sup>. Vertical and horizontal variability in irradiance has also been extensively examined in terrestrial forests<sup>105-107</sup>, but few such measurements exist for marine forests<sup>2,30,45,108</sup>.

Relatively extensive and advanced studies for *Macrocystis* marine forests have been carried out from an ecological and physiological point of view since NORTH<sup>109</sup>. In the forest of *Macrocystis pyrifera*, canopy forming plants have a major effect on the underwater light condition. Several studies showed that photosynthetically active radiation (PAR) at near-bottom depths within giant kelp forests was only 0.1 to 5% of the surface irradiance<sup>43,44,108,110</sup> and that shading by *M. pyrifera* reduced light by up to 99 %<sup>45</sup>. The most important effect of such strong shading is a low rate of carbon fixation by kelp tissues located below the surface canopy<sup>111</sup>. An enhanced abundance of recruits following removal of the kelp canopy indicated that shading often limits recruitment and growth of juveniles of *M. pyrifera* and other understory algae<sup>33,43,86,112,113</sup>.

As for *Ei. bicyclis* and *Ec. cava*, considerable knowledge has also been accumulated on their distribution and population structures from an ecological point of view, as shown in Chapter I. There are, however, few studies on their light environments and photosynthesis which are important for estimating the primary production<sup>20,21</sup> and for production ecology<sup>22</sup>. The method of measuring production structure, developed by MONSI and SAEKI<sup>114</sup> is greatly useful to analyze vertical arrangement of plant biomass and vertical distribution of light. There are, however, few studies of the production structure of marine algae as compared to numerous studies of terrestrial plant communities. TANIGUCHI and YAMADA<sup>29</sup> and TANIGUCHI and KITO<sup>24</sup> estimated annual net production of *Sargassum patens*, *Sargassum serratifolium* and *Sargassum hornerii* by measuring seasonal variations of the production structure. HAYASHIDA<sup>30</sup> reported seasonal changes in production structure and light distribution in an *Ec. cava* population. It is thought that the studies in production ecology of aquatic plants is far behind those of terrestrial plants.

A large part of biomass and production of *Ei. bicyclis* and *Ec. cava* populations is accounted for by adult fronds forming the canopy<sup>23,25,30</sup>. However, young fronds on the community floor play an important role as major constituents of the coming generation. In this chapter, I intend to take a serious view of the young fronds of both species. Knowing how the young fronds respond and behave to various light environments may lead us to the key in comprehending a population structure more accurately.

The main external factor influencing the productivity of algal communities is, of course, incident solar

radiation. On the community floor of *Ec. cava* and *Ei. bicyclis*, however, the light intensity is very low<sup>25),30)</sup>, because the light is absorbed by blades in the canopy and also by the water column. It is necessary for young fronds of these species to receive enough light, at least more than daily light compensation point, for their growth. Thus, the light condition in the communities is the most important factor allowing young fronds to survive and grow to adulthood. In addition, it is important to accurately know the photosynthetic activity at low light levels near the compensation point for estimating daily light requirements. Furthermore, the distribution and diurnal changes in solar radiation are important for determining the daily net production and the daily compensation point.

In this chapter studies were undertaken, first, to know the light condition in both populations by using the method of production structure, second, to know changes in the natural light conditions in the populations, and third, to determine the critical light conditions for young fronds of both species with reference to the characteristics of photosynthesis. This kind of information is also useful to determine factors governing the difference in vertical distribution between the two species.

## 2. Materials and Methods

### a) Radiant Energy and Measurement

Radiant energy from the sun, propagated through space in the form of waves, ranges across the electromagnetic spectrum from the long-wave, low-energy quanta of the radio region to the short-wave, high-energy cosmic rays. "Light" refers to the narrow region of the spectrum that is visible to the human eyes, plus ultraviolet and infrared wavelengths. There are important differences between the spectral sensitivities of the human eye and plant photosynthetic pigments. Rodopsin, the visual pigment, has one major peak at 556 nm with absorption decreasing on either side (see Fig. 20), whereas the chlorophylls and other photosynthetic pigments have many absorption peaks across a broad region<sup>115-117)</sup>. The term "photosynthetically active

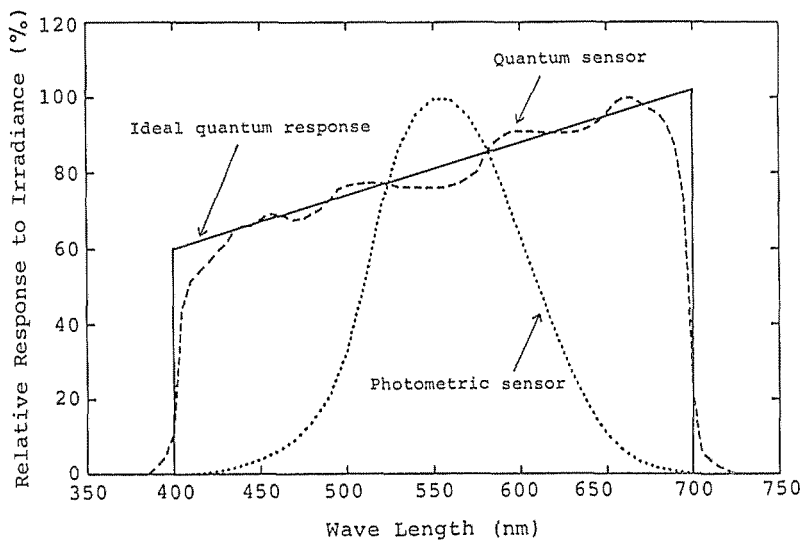


Fig. 20. Energy sensitivity of an ideal quanta meter (straight line) compared with quantum sensor (broken line) used in this study and photometric sensor (dotted line). (From LI-192SB under water quantum sensor instruction manual with permission of LI-COR Inc.)



radiation" (PAR) has come into more descriptive use of the spectral properties for photosynthetic pigment. PAR is defined as wavelengths from 400 to 700 nm.

Specific terms are used to distinguish between energy emitting from a source, whether it is the sun or lamp, and energy being intercepted by an object such as a seaweed. "Radiance" is the flux (rate of flow) radiated by a source: "Irradiance" is the flux intercepted per unit area. Typically, plant physiologists are concerned with irradiance. Often the term "light intensity" is used loosely and incorrectly instead of irradiance.

All the terms mentioned above apply to energy. The energy of a photon is inversely proportional to the wavelength. Thus as the wavelength increases from the blue region (400 nm) to the red region (700 nm), the amount of energy per photon decrease. Pigments absorbing photons at different wavelengths are receiving different amounts of energy, but the energy available for photosynthesis is the same in all cases<sup>118</sup>; thus the number of photons received (photon flux density) is a useful measure of irradiance.

The unit most commonly used to measure photon flux density is the einstein (E) or microeinstein ( $\mu$ E), which refers to a mole of photons (1 mole = 1 einstein =  $6.022 \times 10^{23}$  photons). Some authors would simply use mole or micromole because the einstein is not an SI unit. The appropriate SI units for measuring energy are joules (J) and watts (W). The joule is used to measure the total quantity of energy transferred in the quanta. The watt is used to measure radiant flux<sup>119</sup>. Thus,  $1 \text{ W/m}^2 = 1 \text{ J/m}^2/\text{s}$ .

Perhaps the most common in older biological literature, and unfortunately is still in use, are the illuminance units for photometry, such as foot-candle and lux. Photometry refers to the measurement of visible radiation with a sensor having a spectral responsibility curve equal, not to the photosynthetic plant pigments, but to the average human eye or rodopsin. Illuminance units cannot be precisely converted into irradiance units except for specified light sources, but some approximate values for conversion are given by Lüning<sup>120</sup>. The reason why much of the biological light data are given in lux or foot-candles is that photometers or light meters are easy to use and inexpensive; they had been the only instruments available for a long period of time.

An important part of the light measuring instrument, especially one used underwater, is the collector. This is the window through which the light beams pass on their way to the detector. The window may be a flat surface of translucent diffusing material, such as opal glass, known as a  $2\pi$  or cosine collector, which measures all rays coming from the hemisphere above it. Alternatively, it may be a  $4\pi$  collector, *i.e.* a sphere collecting rays from all directions. Both types are useful for biological measurements. Phytoplankton are more or less spherical, as are their plastids, so they are essentially  $4\pi$  collectors. Many seaweeds have a more or less horizontal surface to collect radiant energy, and might be better represented by a  $2\pi$  collector.

In this study, I used the quantum sensor with a  $2\pi$  collector (LI-COR 190SB, 192SB) for measuring the radiant energy in photon flux density in water and in the laboratory. The unit is expressed in einstein (E) or microeinstein ( $\mu$ E), although they are not SI units. The ideal instrument for plant physiology would measure the exact number of quanta absorbed by plant pigments. Such an ideal is unattainable, but it is possible to measure the energy or quanta relatively uniformly across the spectrum, and thus obtain a better measure of the light available to plants than is obtained from an illuminance meter. Instruments are presently available that can measure total irradiance and/or total quanta across the PAR spectrum (400–700 nm), as shown in Fig. 20.

The distribution and diurnal changes in solar radiation are important for determining daily net production and the daily compensation point. In this study, PAR on the horizontal plane have been continuously monitored since April 1986, at the campus of Mie University about 70 km to the north of the sampling site. Values were integrated every one second and recorded at 10 minutes interval to the data-logger (LI-COR LI-1000).

## b) Stratified Clip Method

The stratified clip method was developed by MONSI und SAEKI<sup>114)</sup>, by which vertical structure of the community was schematized as a particular form named production structure. A profile diagram of production structure represents a vertical arrangement of plant biomass and the light distribution in a community, so that, it is available not only for estimating a production but also for studies of inter-, intraspecific competition or succession.

A study in production structure of *Ei. bicyclis* and *Ec. cava* populations was carried out in the coastal area of Shima Peninsula, Mie Prefecture, from June to July 1984. Study sites were located at a depth of 3 m off Iwaizaki for *Ei. bicyclis* and at a depth of 8 m off Hamajima for *Ec. cava*. Six quadrats (1 m × 1 m) were set in each study site, where I chose a population with a different type of structure and on a similar property of substratum at the same depth. Furthermore, quadrats for both species were set in renewing populations following removal of all the fronds in previous October 1983.

Before cutting down all the fronds for the stratified clip, light condition in the population was measured. Unfortunately quantum sensor was not available in time before the production structure study; therefore, I used the photometric sensor (MINOLTA T-1) only in the production structure study. Light intensity was measured every 20 cm from the bottom to the top of the canopy and on the sea surface. Light data were simultaneously monitored by a recorder (YHP 3057) on a boat, and the relative light intensity was calculated. Light measurement was carried out under diffuse light condition on a cloudy day.

It was very difficult to apply the stratified clip method in practice underwater; therefore I planned the following procedure. All individuals in the quadrat were cut just below the stipe, and then carried to the Fisheries Research Laboratory of Mie University in Ago Bay. After the measurement of stipe length and age, each material was arranged horizontally on a board as natural in the form in water as possible; visible observation and photographs were used for reference. Thereafter, fronds were cut off every 10 cm from just below the stipes to the top of the blades. Samples in each layer were divided into two parts (blades and stipes), rinsed with freshwater, and dried at 85°C overnight to obtain dry weight.

To determine the critical light condition of the young fronds of *Ei. bicyclis* and *Ec. cava*, the light distribution on the community floor was measured. Studies were carried out at 4 m in depth off Iwaizaki, Mie Prefecture, on June 13, 1986, for *Ei. bicyclis* population, and at 5 m in depth in Nabeta Bay near the Shimoda Marine Research Center, University of Tsukuba, on June 21, 1985, for *Ec. cava* population. All of the fronds in the quadrat (1 m × 1 m) were labeled and marked on a dispersion map. The light distribution on the population floor was measured at 121 points 10 cm apart from each other by using a quantum meter system (LI-185B/LI-192SB). Photon flux density on the population floor and the sea surface was simultaneously monitored by a two-pen recorder (YHP 3057) on a boat, and relative irradiance on the population floor was calculated. After the light measurement, production structure of both populations was obtained by the stratified clip technique mentioned above.

## c) Photosynthesis and Respiration

Photosynthesis and respiration of young *Ei. bicyclis* and *Ec. cava* were measured from April to July 1986. Intact young fronds less than one year old<sup>18,19)</sup> with frond area of 15–35 cm<sup>2</sup> and dry weight of 60–250 g were collected from the communities at depths of 3–4 m for *Ei. bicyclis* and 7–10 m for *Ec. cava* around the coast of Shima Peninsula, Mie Prefecture. When samples were collected, photon flux density at the growing site was

measured. Samples were transported to the Fisheries Research Laboratory of Mie University and were rinsed with filtered seawater to be free of obvious epiphytes with careful handling not to wound the fronds and to protect them from direct sunlight.

After keeping the sample fronds in running seawater overnight to avoid abnormal results caused by cutting<sup>20)</sup>, photosynthesis and respiration were measured with a differential gas-volumeter, "Product-meter"<sup>121,122)</sup>, adapting for large seaweeds or pieces<sup>123)</sup>. Twenty-one samples of young *Ei. bicyclis* and thirteen samples of young *Ec. cava* were used for photosynthetic and respiratory measurements. Measurements of photosynthesis and respiration were carried out at 20°C at 8 different photon flux densities from 0 to 400  $\mu\text{E}/\text{m}^2/\text{s}$  by using a projector lamp (Kondo 100V-300W) as a light source. The photon flux density was changed with neutral density filters (Toshiba TND-50, -25, -12.5).

Culture flasks of about 250 ml capacity were used for reaction and reference vessels, and filtered seawater (50 ml) was poured into both vessels with a sample frond in the reaction vessel. After pre-incubation for 30 minutes at 400  $\mu\text{E}/\text{m}^2/\text{s}$ , seawater in both vessels was renewed, and the photosynthetic measurement was started from high to low irradiance with the same frond. Photosynthesis was also measured with the sample frond irradiated from one side or from both sides of the blade. Respiration was measured after the photosynthetic measurements. Each measurement of photosynthesis and respiration took about 25 minutes and the seawater was renewed each time. As the result, it took 5–6 hours from 09:00 h for a series of measurement. After the measurement, sample fronds were rinsed with freshwater and provided for measurements of area and chlorophyll *a*. The chlorophyll *a* content was calculated by the SCOR-UNESCO<sup>124)</sup> formula. They were then dried at 85°C overnight to obtain dry weight.

### 3. Results and Discussion

#### a) Production Structure

Figs. 21 and 22 show production structure diagrams of *Ec. cava* and *Ei. bicyclis* populations, respectively. The frequency distributions of stipe length and age, which was estimated by counting the number of growth rings as mentioned above in Chapter II, were also shown in each production structure diagram.

As for *Ec. cava* in Fig. 21, the production structure at Sts. 5, 6, and 7 corresponded to the herb type reported in terrestrial plant communities. A great part of blade biomass was distributed in the upper layer from 30 to 110 cm, particularly in 70–80 cm layer; maximum values of 251, 178 and 140 g were recorded in each study site, respectively. Stipe biomass was high in the bottom layer less than 10 cm, and decreased gradually toward the top of the canopy. Light was absorbed greatly in the upper layer where the blade biomass concentrated densely. There are important characteristics of the typical herb type of production structure. Relative light intensity decreased rapidly downwards and showed an almost constant level of 10% in the layer under 50 cm. The number of stipes increased gradually from the top to the bottom of the population, and specifically it increased considerably in 80–60 cm and 20–10 cm layers. In the frequency distribution of stipe length, there were two groups; one was adult group longer than 50 cm in stipe length and 3–4 years old, and the other was young group shorter than 20 cm in stipe length and 1–2 years old.

Sts. 8 and 9 were different from previous stations, having a wide distribution of blade biomass from 30 to 80 cm in 20–90 cm layers and no clear maximum. Light was not much absorbed in the upper layer and penetrated to the bottom of population. Relative light intensity on the population floor was 13%; this was higher than that of the herb type production structure. Stipe biomass was scarce in the upper layer and had a maximum value in

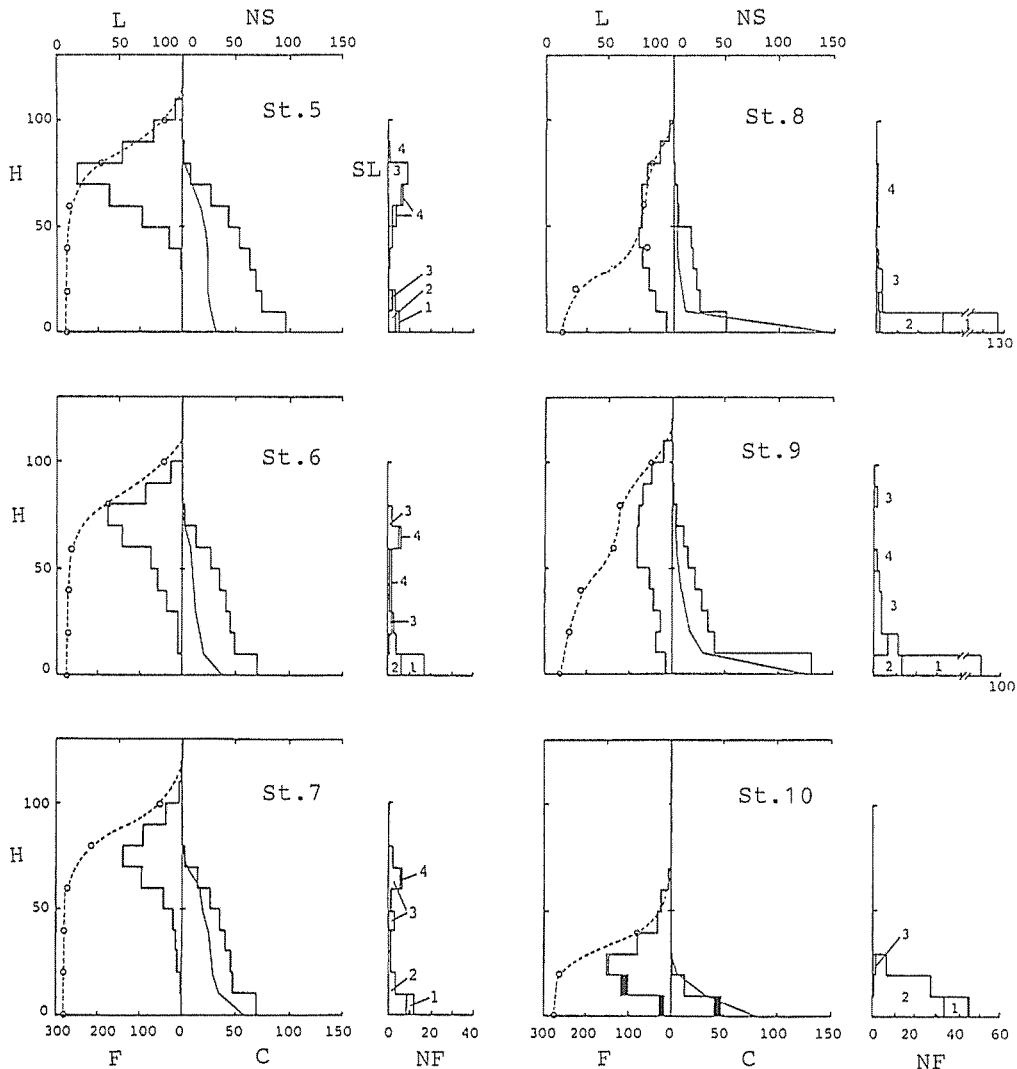


Fig. 21. Production structure diagrams and the frequency distributions of stipe length and age of *Ecklonia cava* communities at St. 5-10. H, height of population (cm); L, relative light intensity (%); NS, number of stipes; F, photosynthetic organs (blades, g dry weight); C, non-photosynthetic organs (stipes, g dry weight); SL, stipe length (cm); NF, number of fronds. Numerals 1-5 in diagrams of the frequency distribution of stipe length show the age (years). Shaded parts are for *Eisenia bicyclis*.

the lowest layer, 48 g at St. 4 and 131 g at St. 5. In the frequency distribution of the stipe length, there were few adult fronds and were numerous young fronds less than 10 cm in the stipe length at the age of 1-2 years old. The density of young fronds at Sts. 8 and 9 was 133 and 121 individuals/m<sup>2</sup>, respectively.

St. 10 was the renewing population after cutting down all fronds about a year before, and was akin to a grass type production structure, which was characterized by the blade biomass mostly distributed in the lower layer. The blade biomass was highest (153 g) in 20-30 cm layer, and the stipe biomass was 49 g in the lowest layer. Relative light intensity decreased greatly in 30-80 cm layer, and reached 10% on the bottom. In this population

one individual of *Ec. cava* was mixed.

The *Ei. bicyclis* population at Sts. 11 and 12 (Fig. 22) showed the typical herb type of production structure. Blade biomass was distributed from the upper to the middle layers; maximum values of 788 g (St. 11) and 517 g (St. 12) occurred in 70–80 cm layer. The stipe biomass increased gradually from the top to 50 cm layer, was almost constant from 50 to 10 cm layer, and showed a maximum value in the bottom layer. Measurement of light distribution was not carried out at St. 12. At St. 11, a greater part of light was absorbed in the upper layer more than 60 cm, as is characteristic of the typical herb type production structure. Relative light intensity

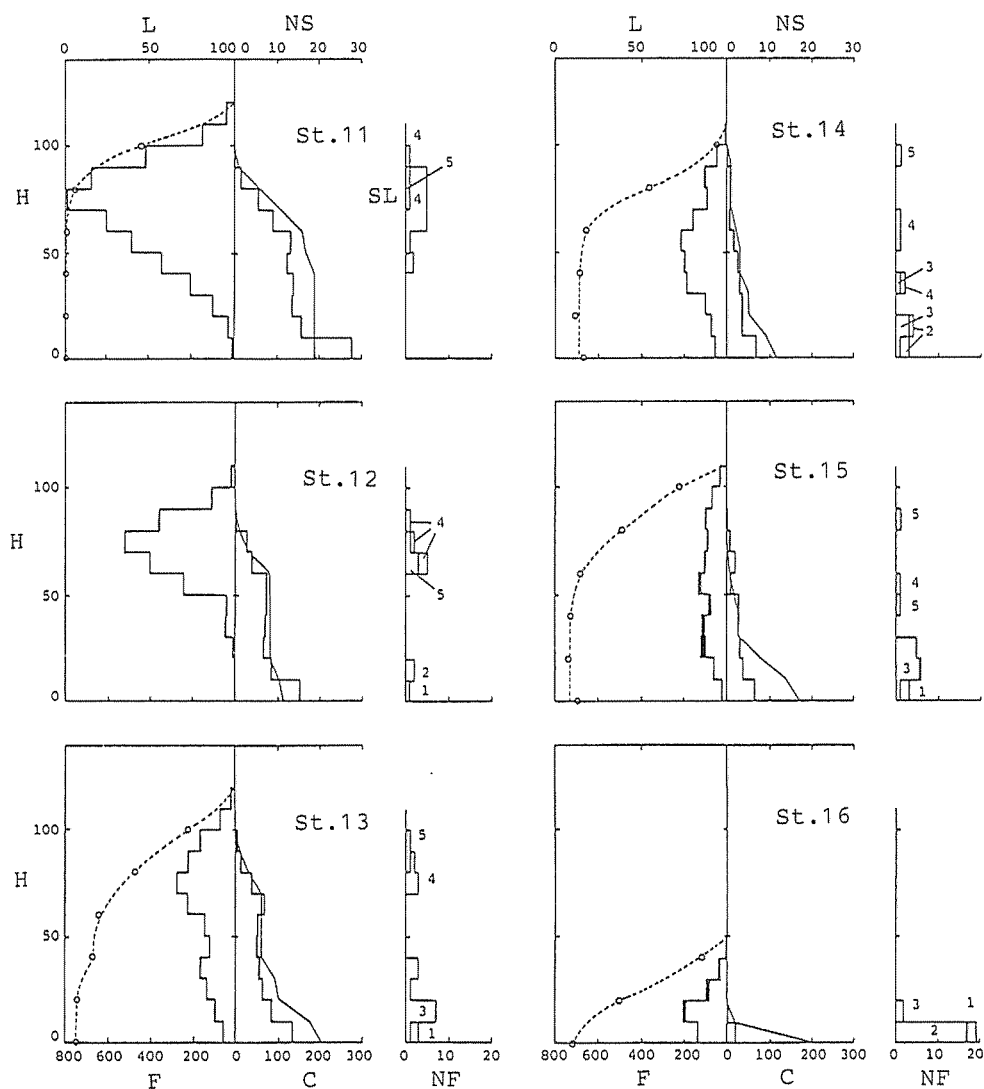


Fig. 22. Production structure diagrams and the frequency distributions of stipe length and age of *Eisenia bicyclis* communities at St. 11–16. H, height of population (cm); L, relative light intensity (%); NS, number of stipes; F, photosynthetic organs (blades, g dry weight); C, nonphotosynthetic organs (stipes, g dry weight); SL, stipe length (cm); NF, number of fronds. Numerals 1–4 in diagrams of the frequency distribution of stipe length show the age (years). Shaded parts are for *Ecklonia cava*.

decreased rapidly in the upper layer, and was very low (about 1%) in the middle and lower layers. There were no young fronds at St. 11 and a few at St. 8. Adult fronds more than 40 cm in stipe length and more than 4 years old dominated in this type of production structure.

At St. 13, the blade biomass distributed in wide ranges of the layers and showed two peaks; 280 g in the 70–80 cm layer and 170 g in the 30–40 cm layer. From the viewpoint of frequency distribution of stipe length, this population was constituted by two groups; one was adult generations more than 70 cm in stipe length and more than 4 years old, and the other was young generations shorter than 40 cm in stipe length and less than 3 years old. Relative light intensity decreased rapidly in the upper layer more than 60 cm, and decreased gradually downwards to 7% on the population floor.

At Sts. 14 and 15 the population showed a wide distribution of blade biomass and showed no conspicuous peak in the same manner as the *Ec. cava* population at Sts. 8 and 9. The blade biomass varied from 50 to 215 g at St. 10 and from 60 to 124 g at St. 15, except for the upper and the lowest layers. Relative light intensity decreased rapidly in the upper layer higher than 60 cm, and it decrease downwards gradually to 10–17% on the bottom layer. In the frequency distribution of stipe length, the adult generation more than 4 years old was scattered in the upper layer and the young generation less than 3 years old dominated in the lower layer.

At St. 16 the population was the renewing one after cutting down all fronds about a year before, and was like the grass type in production structure, in same manner as the *Ec. cava* population at St. 10. The blade biomass was highest (200 g) in 10–20 cm layer, and the stipe biomass was 22 g in the lowest layer. Relative light intensity decreased greatly to 10% on the bottom. At Sts. 15 and 16 the *Ei. bicyclis* population contained one individual of *Ec. cava*.

Table 3 shows standing stock, C/F ratio, and density of *Ei. bicyclis* and *Ec. cava* populations surveyed in this study. The C/F ratio is a relative value of nonphotosynthetic organs to photosynthetic organs. In this study, I calculated it as a ratio of stipe and blade biomass, although a considerable amount of photosynthetic pigment is contained in cortex of the stipe. Standing stock was higher in *Ei. bicyclis* than in *Ec. cava*; the maximum value of the total biomass recorded at St. 11 for the former was four times as much as that at St. 5 for the latter. This

**Table 3.** Standing stock (dry weight), C/F (stipes/blades ratio), and density of the *Eisenia bicyclis* and *Ecklonia cava* populations

	St.	Standing Stock (g/m <sup>2</sup> )			C/F	Density (indiv./m <sup>2</sup> )
		Blade	Stipe	Total		
<i>Ec. cava</i>	5	793	448	1241	0.55	32
	6	612	295	907	0.48	38
	7	431	285	716	0.66	31
	8	532	137	669	0.62	133
	9	544	297	841	0.55	121
	10	438	59	497	0.13	92
<i>Ei. bicyclis</i>	11	3746	1146	4917	0.30	19
	12	1745	573	2318	0.33	11
	13	1735	536	2298	0.32	20
	14	1238	229	1467	0.18	12
	15	889	214	1103	0.24	17
	16	470	26	496	0.06	22

difference of the total biomass was attributed mainly to the difference of the blade biomass between both species. On the other hand, the population density was higher in *Ec. cava* than in *Ei. bicyclis*, particularly, it was considerably high at Sts. 8 and 9. C/F ratio varied from 0.06 to 0.66 in both species, was somewhat higher in *Ec. cava* than in *Ei. bicyclis*.

Three characteristic types of production structure were found in both *Ei. bicyclis* and *Ec. cava* populations. The first one was the herb type observed in fully grown populations in which most of the blade biomass was distributed in upper layer of the population and large fronds dominated (Sts. 4, 5, 6, 11 and 12). The second one was the type in which the blade biomass was distributed widely in every layers of the population and small fronds dominated (Sts. 8, 9, 13, 14 and 15). The third one was the grass type in which most of the blade biomass was distributed in lower layer and the height of the population was low (Sts. 10 and 16).

These three types of the production structure of *Ei. bicyclis* and *Ec. cava* fundamentally resemble those of terrestrial plant communities; however, there are some characteristic differences between them. For examples, C/F ratio of the population of both species was considerably lower than that of terrestrial plant communities. The C/F ratio was 1–10 in grasslands and 20–50 in terrestrial forest<sup>104,114</sup>, in contrast to 0.06–0.66 in *Ei. bicyclis* and *Ec. cava* populations in this study. YOKOHAMA *et al.*<sup>23</sup>) also reported a low C/F ratio of 0.24–0.23 in *Ec. cava* populations around the coast of Shimoda, Izu Peninsula from June to August. This is because the density of water is 750 times as high as that of air at normal temperature, and usually aquatic macrophytes do not need non-photosynthetic organs to support the blade and canopy, being different from terrestrial plants. Some species of filmy algae such as those of Ulvaceae have no non-photosynthetic organs. Such a low C/F ratio is also reported in submerged plants in freshwater<sup>100</sup>. As the result, this is a general characteristic represented by macrophytes growing in water. A little or lack of non-photosynthetic organs allow high net production of algae because of low respiratory loss<sup>102,103</sup>.

As solar radiation penetrates the sea it is altered both qualitatively and quantitatively. The light attenuation results from absorption and scattering by water, which is the main reason for a rapid decrease of solar radiation in water as compared to the decrease in atmosphere. In this study light was reduced to 60% on the top of *Ei. bicyclis* population, and to 30% on the top of *Ec. cava* population.

The density of small and young fronds was controlled by the light condition which was related to the density of large and adult fronds forming a canopy. In the fully grown *Ec. cava* population of the herb type production structure (Sts. 5, 6 and 7), large and adult individuals dominated and small and young fronds were scarce. This type of population is characterized by the rapid absorption of light in the upper layer, and the light intensity in the bottom layer decreases to 10% of the top of canopy (only 3% of water surface). It is thought that such a low light condition suppresses the germination and growth of young fronds. Conversely, at Sts. 8 and 9 young fronds dominated and adult fronds were scarce. In such populations, light intensity on the bottom layer is higher (13–20% of the top of canopy) than that in the herb type production structure. Such a relatively high light intensity enable numerous young fronds to germ and grow. The results obtained in this study corresponded well to those reported by HAYASHIDA<sup>30</sup>) for the *Ec. cava* population in Izu Peninsula, Shizuoka Prefecture. I emphasize that light condition on the population floor is one of the most important limiting factors for growth of young fronds, as HAYASHIDA<sup>30</sup>) observed.

In *Ei. bicyclis* populations there are three types of production structure which are the same as in *Ec. cava* populations. *Ei. bicyclis*, however, has more blade biomass than *Ec. cava*; consequently, light is absorbed greatly in the upper layer and decreases to 10% or less even in the type showing wide distribution of blade

biomass (Sts. 13, 14 and 15). Such a low light intensity may suppress the germination and growth of young fronds, in the same manner as in *Ec. cava*.

In Chapter I, I intended to trace yearly changes of population structure, and I succeeded to find out the gap regeneration in *Ei. bicyclis* and *Ec. cava* populations. Three phases in the regeneration process (gap, building and mature phase) were distinguished by examining the change of the structure and the features of both populations. In other words, structure and feature of both populations change periodically with advancement of the regeneration process. One of the most characteristic changes of the population structure was periodical replacement of the dominant groups, young and adult ones, which were altered after a period of 3 years for *Ec. cava* and 7–8 years for *Ei. bicyclis*. According to WATT's<sup>(60)</sup> mosaic theory, various phases of the regeneration process distribute randomly in mosaic of patches. As the result, I postulated that each type of the population structure in this study corresponded to a step of the regeneration process; for example, the herb type production structure corresponds to the mature phase of the regeneration process.

However, it is well known that population structures or features vary largely depending on the biological and physical disturbances in the growing site<sup>31–35</sup>. Grazing disturbance plays an important role to construct and maintain the algal population and/or community<sup>68–70</sup>. Natural or artificial reductions in herbivore density lead to increasing algal abundance and changing in species composition and structure, and this also alters plant-plant competition<sup>43,70,125,126</sup>. The effect of physical disturbance can be much the same as that of biological disturbance; the disturbance may act directly on plants or indirectly by affecting other organisms which interact with plants. In marine macroalgal assemblages, physical disturbance is often caused by high water motion that may remove vegetation<sup>33,36,40,84</sup>. Furthermore, structures of the community and life forms of algae depend on the stability of substratum<sup>28,40</sup>. In Chapter I, I confirmed that the vertical distributional pattern and population structure varied with the locality, depending on such characters as the degree of wave action, topography of substratum and stability of substratum, although a frequency distribution of stipe length and density was similar within a small area at the same depth on the flat bottom.

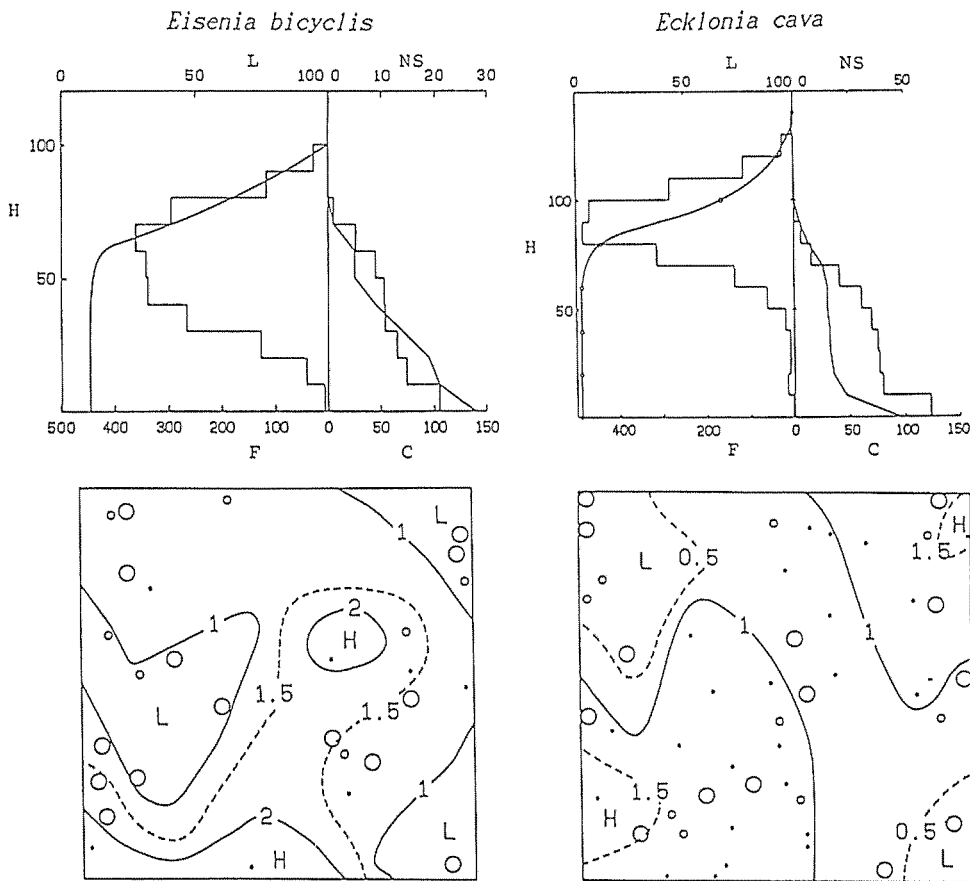
In the study of production structure, I chose areas where both species were fully developed, and set each quadrat on the flat rock within the population at the same depth in a small area. Therefore, it is thought that biological and physical disturbance have an almost equal effect on the population in each quadrat. Accordingly, I conclude that each type of the population structures in this study correspond not to the difference in characteristic of the locality, but to a step in the regeneration process. It is apparent that the herb type production structure in both species (Sts. 5, 6, 11, 12 and 13) is in the mature phase, and the grass type of production structure (Sts. 10 and 16) is in the building phase. Another type of production structure having wide distribution of blade with numerous young individuals of *Ec. cava* was in the gap phase (Sts. 7, 8, 9, 14 and 15).

The *Ei. bicyclis* population, however, have more blade biomass than the *Ec. cava* population, so that in the *Ei. bicyclis* population the light is absorbed greatly in the upper layer by only a few canopy fronds and decreases to 10% or less, even in the type having wide distribution of blade biomass (Sts. 14 and 15). Accordingly, the gap formation in *Ei. bicyclis* will occur when loss of the assemblage of canopy fronds takes place at the same time, and thereafter a relatively large opening is formed.

## b) Critical Light for Young Fronds

Fig. 23 show the production structures of *Ei. bicyclis* and *Ec. cava* population, and the distribution of relative photon flux density on the population floor together with the distribution of individual fronds for the species





**Fig. 23.** Production structure diagram (upper), and distributions of the relative light intensity (% of the water surface intensity) and individuals on the floor (lower) of *Eisenia bicyclis* and *Ecklonia cava* populations at a depth of 5 m. H, height of population (cm); L, relative light intensity (%); NS, number of stipes; F, photosynthetic organs (blades, g dry wt.); C, non-photosynthetic organs (stipes, g dry wt.); NF, number of fronds. The size of circles indicate the stipe length; large open circles, longer than 30 cm; small open circles, 10–20 cm; small solid circles, shorter than 10 cm.

illustrated in the upper figure. Standing stock of the *Ei. bicyclis* population was 2348 g (dry weight)/m<sup>2</sup>: 1921 g of blades and 427 g of stipes, and that of the *Ec. cava* population was 2505 g (dry weight)/m<sup>2</sup>: 1955 g of blades and 550 g of stipes. Density was 28 individuals/m<sup>2</sup> in the *Ei. bicyclis* population and 49 individuals/m<sup>2</sup> in the *Ec. cava* population. The production structure of both species corresponded to the typical herb type. Consequently, the light was absorbed greatly in the upper layers and decreased to only 3% and 2% on the population floor of *Ei. bicyclis* and *Ec. cava*, respectively. The photon flux density on the top of both populations was reduced by water to about 50% of the surface value (4–5 m in depth from the sea surface to the top of the populations). So, the relative photon flux density on the population floor was only about 1.5% of the surface value for *Ei. bicyclis* and 1% for *Ec. cava*.

Relative photon flux density on the population floor varied from 0.6 to 2.2% of the sea surface for *Ei. bicyclis*, and from 0.2 to 1.8% of the sea surface for *Ec. cava*. Most of the young fronds shorter than 10 cm in

stipe length were found growing in the places where relative photon flux density was higher than 1.0% for *Ei. bicyclis* and 0.5% for *Ec. cava*. It should be noted that the critical light condition for survival and growth in between 1.0 and 1.5% for the former and between 0.5 and 1.0% for the latter. Thus it is clear that young fronds of the two species were growing under very dim light condition on the population floor. The relative photon flux density of 1% corresponded to about  $20 \mu\text{E}/\text{m}^2/\text{s}$  at local noon on fine days from April to July in the region investigated.

During the period from late winter to spring when juveniles of *Ei. bicyclis* and *Ec. cava* germinated, the blade biomass of canopy fronds showed a lower peak (see Chapter I). As a result, the juveniles could receive enough light to grow. Thereafter, the blade biomass increased to reach the maximum in summer. In a fully grown population of both species in summer, the light condition on the population floor decreased to 1–2% of the water surface light intensity, and the critical light condition was 1–1.5% for young *Ei. bicyclis* and 0.5–1% for young *Ec. cava*. It is therefore apparent that light is a limiting factor for young *Ei. bicyclis* and *Ec. cava* to survive and grow.

### c) Estimation of Daily Compensation Point

Photosynthesis-light curves on the frond area basis of young *Ei. bicyclis* and *Ec. cava* are shown in Fig. 24. The photosynthetic rate of both species was almost saturated at  $200 \mu\text{E}/\text{m}^2/\text{s}$ , and the light-saturated photosynthetic rate of *Ei. bicyclis* was higher than that of *Ec. cava*. Under dim light condition lower than  $25 \mu\text{E}/\text{m}^2/\text{s}$ , however, the net photosynthetic rate of *Ec. cava* was higher than that of *Ei. bicyclis* and photosynthesis-light relationship was linear in both species. Table 4 shows the linear photosynthesis-light

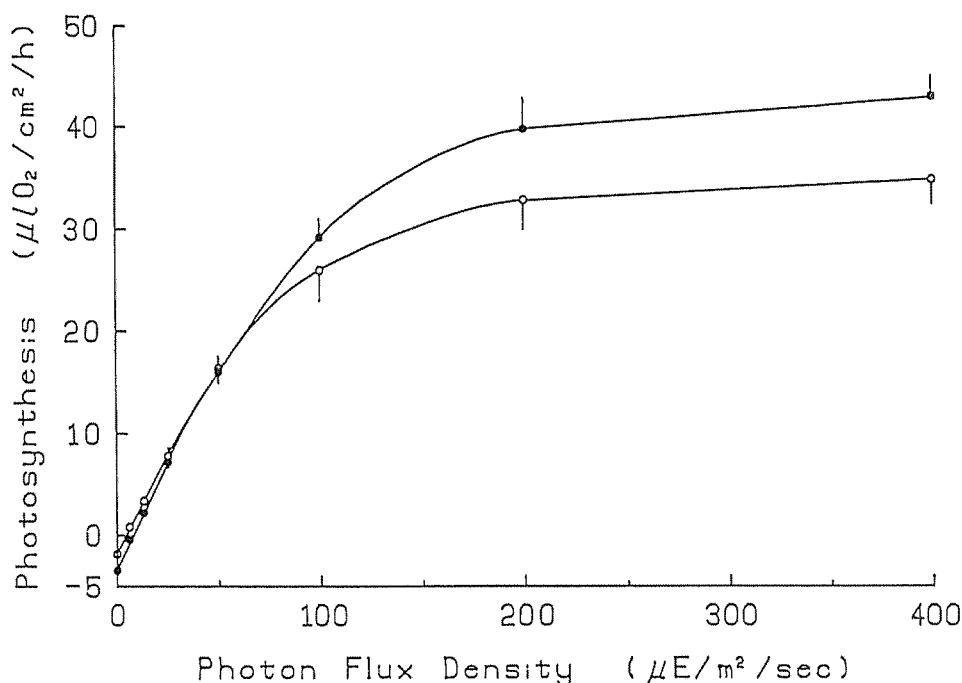
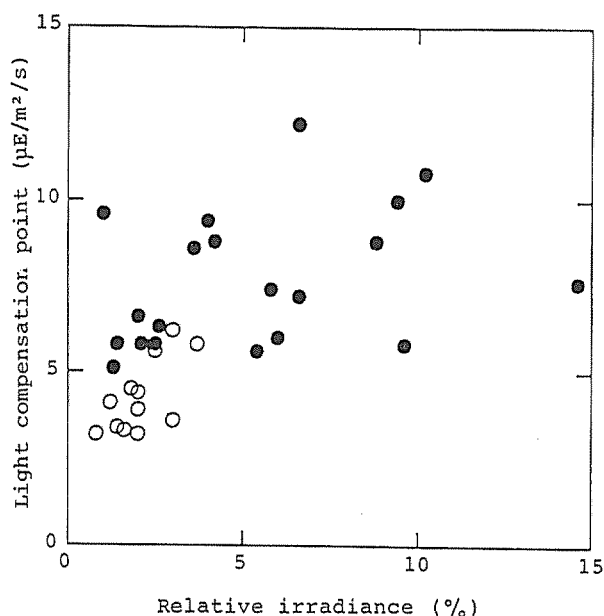


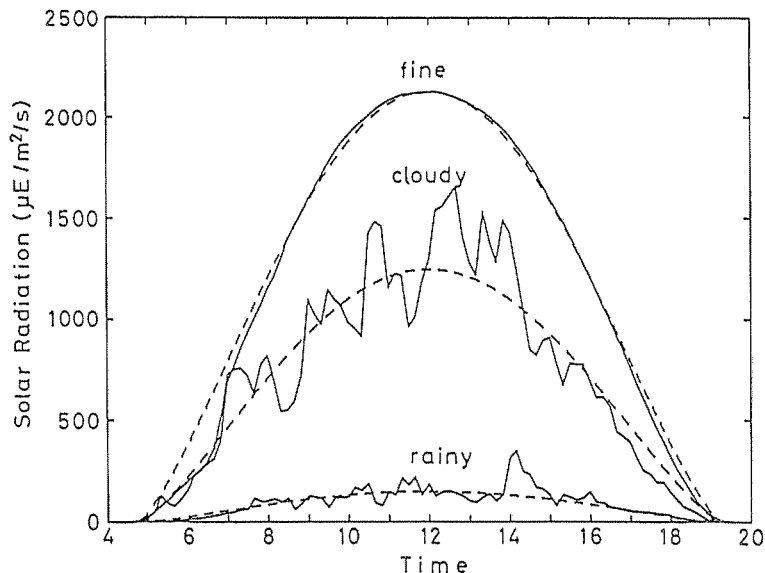
Fig. 24 Photosynthesis light curves at 20°C of young *Eisenia bicyclis* (—●—) and *Ecklonia cava* (—○—). Vertical bars indicate  $\pm 95\%$  confidence limits.

**Table 4.** Photosynthesis light equation on frond area basis, dry weight basis and chl. *a* basis in young *Eisenia bicyclis* and *Ecklonia cava* fronds. *P*, net photosynthetic rate; *I*, photon flux density ( $0 \leq I \leq 25 \mu\text{E}/\text{m}^2/\text{s}$ )

Basis	<i>Ei. bicyclis</i>	<i>Ec. cava</i>
Area	$P=0.41 I-3.38$	$P=1.38 I-1.82$
Dry weight	$P=0.059 I-0.50$	$P=0.063 I-0.29$
Chl. <i>a</i>	$P=0.29 I-2.48$	$P=0.32 I-1.56$



**Fig. 25** Relationship between the relative irradiance on the growing site and the light compensation point of young *Eisenia bicyclis* (●) and *Ecklonia cava* (○).



**Fig. 26.** Diurnal changes in photosynthetically active radiation (PAR) under 3 types of weather conditions. Broken lines show the sine curves fitted.

$$\text{fine, } I_o = 2130 \times \sin^{1.3} (\pi \cdot t/D);$$

$$\text{cloudy, } I_o = 1250 \times \sin^{1.3} (\pi \cdot t/D);$$

$$\text{rainy, } I_o = 150 \times \sin^{1.3} (\pi \cdot t/D).$$

$I_o$ , photon flux density ( $\mu\text{E}/\text{m}^2/\text{h}$ ) at a given time  $t$ ;  $D$ , length of daytime (h).

equations represented on the frond area basis, dry weight basis and chl. *a* basis, which were calculated by the least squares method within photon flux density lower than  $25 \mu\text{E}/\text{m}^2/\text{s}$ . Photosynthesis-light relationships were clearly different between the two species. However, the slope of each line was almost the same (no significant difference at 95% confidence level). On the other hand, the respiratory rate of *Ec. cava* ( $1.82 \mu\text{lO}_2/\text{cm}^2/\text{h}$ ) was almost half that of *Ei. bicyclis* ( $3.38 \mu\text{lO}_2/\text{cm}^2/\text{h}$ ). The compensation light level was  $8.2 \mu\text{E}/\text{m}^2/\text{s}$  for *Ei. bicyclis* and  $4.8 \mu\text{E}/\text{m}^2/\text{s}$  for *Ec. cava*.

Fig. 25 shows the relationships between the light condition (relative irradiance) on growing sites and the light compensation point of young *Ei. bicyclis* and *Ec. cava*. The light compensation point was calculated from each photosynthesis-light equation in the range lower than  $25 \mu\text{E}/\text{m}^2/\text{s}$ . There are no significant correlations between the light condition on growing sites and the light compensation point in both species, although the light compensation point of *Ei. bicyclis* is clearly higher than that of *Ec. cava*.

Fig. 26 shows the diurnal changes in photosynthetically active radiation (PAR) under 3 types of weather conditions, fine, cloudy and rainy day. Solar radiation on the water surface ( $I_o$ ,  $\mu\text{E}/\text{m}^2/\text{s}$ ) at a given time  $t$  hours after sunrise is approximately given by:

$$I_o = I_{\max} \sin^{1.3}(\pi \cdot t/D), \quad \dots\dots(1)$$

where  $I_{\max}$  is the maximum solar radiation during the daytime and  $D$  is the length of daytime from sunrise to sunset. Table 5 summarizes the results of light condition obtained in April, May, June and July during the photosynthetic study. The average  $I_{\max}$  in this period was  $1440 \mu\text{E}/\text{m}^2/\text{s}$ , which was 65.8% of the maximum solar radiation on fine day. The average length of daytime was 13.9 hours.

**Table 5.** Changes in the maximum solar radiation ( $I_{\max}$ ) and the length of daytime from April to July 1986

Month	$I_{\max}$ ( $\mu\text{E}/\text{m}^2/\text{s}$ )		Daytime (h)
	Fine day	Average day	
April	2066	1350	13.1
May	2193	1600	14.0
June	2235	1430	14.4
July	2217	1380	14.2
Mean	2178	1440	13.9

Under natural conditions young fronds receive light from both sides of the blade in the population. However, the photosynthesis-light curves illustrated in Fig. 25 were obtained with fronds irradiated from one side of the blades in the laboratory. Therefore, measurements of the photosynthesis-light relationship were carried out with the same *Ec. cava* frond when irradiated from both sides as well as from one side of the blade. The results are shown in Fig. 27 (upper). The photosynthetic rate saturated at about  $100 \mu\text{E}/\text{m}^2/\text{s}$  when the blade was irradiated from both sides, whereas it saturated at about  $200 \mu\text{E}/\text{m}^2/\text{s}$  when irradiated from one side. The light-saturated photosynthetic rate was nearly the same in both measurements. Under dim light lower than  $25 \mu\text{E}/\text{m}^2/\text{s}$ , the photosynthesis-light relationship was linear in both cases, and the photosynthetic rate when the blade was irradiated from both sides was twice as high as that when irradiated from one side.

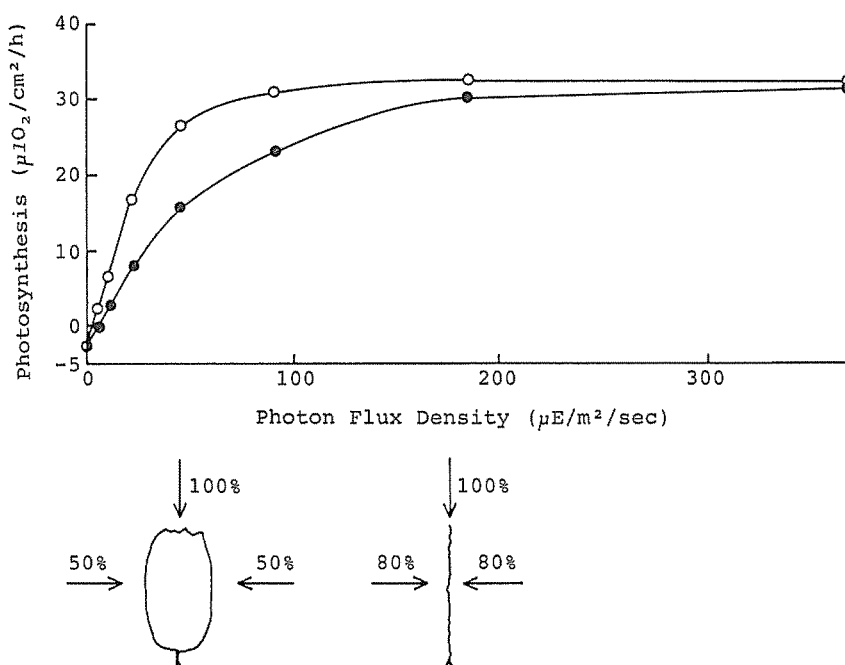


Fig. 27. Photosynthesis light curves of young *Ecklonia cava* when irradiated from both sides (—○—) and from one side (—●—) of the blade (upper). Relative light condition around the young frond near the population floor (lower).

It is considered that photosynthesis in a young frond is more active when the frond is irradiated mainly at a right angle to the blade than when irradiated at other angles. In this study, light data was measured on the horizontal plane. Therefore, the relative photon flux density was measured on the same plane as the blade and reference to the horizontal plane immediately above the blade tip in the population. The results are schematized in Fig. 23. The relative photon flux density on the same plane as the blade was 80% of that of the horizontal plane immediately above the blade which was only 50% of the photon flux density at the sea surface. Thus, the gross photosynthetic rate ( $P_g$ ,  $\mu\text{l O}_2/\text{cm}^2/\text{h}$ ) of both species on a frond area basis can be written as follows:

$$P_g = 2 \times 0.8 \times 0.41 \times I \text{ (for } Ei. bicyclis \text{)} \quad \dots\dots(2)$$

$$P_g = 2 \times 0.8 \times 0.38 \times I \text{ (for } Ec. cava \text{)}, \quad \dots\dots(3)$$

where  $I$  is the photon flux density ( $\mu\text{E}/\text{m}^2/\text{s}$ ) measured on the horizontal plane above the young frond tip in the range lower than  $25 \mu\text{E}/\text{m}^2/\text{s}$ .

Based on the above equations, the daily production and daily compensation light level of young *Ei. bicyclis* fronds were estimated as follows.

The photon flux density on the water surface at a given time  $t$  hours after sunrise can be given by eq. (1). Relative irradiance on the community floor ( $Z$ ) is given by:

$$Z = I/I_0.$$

Hence, the gross photosynthetic rate ( $P_g$ , eq. 2) at a given time  $t$  hours after sunrise is given by:

$$P_g = 0.66 \times Z \times I_{max} \times \sin^{1.3}(\pi \cdot t/D). \quad \text{.....(4)}$$

Thus, the daily gross production ( $Q_g$ ,  $\mu\text{l O}_2/\text{cm}^2/\text{d}$ ) is given by:

$$\begin{aligned} Q_g &= \int_0^D 0.66 \times Z \times I_{max} \times \sin^{1.3}(\pi \cdot t/D) \cdot dt \\ &= 1.21 \times Z \times I_{max} \times D / \pi, \end{aligned} \quad \text{.....(5)}$$

as the function of 3 parameters, the relative irradiance on the community floor ( $Z$ ), maximum photon flux density during the daytime ( $I_{max}$ ) and the length of daytime ( $D$ , 13.9 h in the present case). The daily net production ( $Q_n$ ,  $\mu\text{l O}_2/\text{cm}^2/\text{d}$ ) is also given by:

$$Q_n = 1.21 \times Z \times I_{max} \times D / \pi - 3.38 \times 24. \quad \text{.....(6)}$$

The daily compensation light level ( $Z_{c,d}$ ) is given by:

$$Z_{c,d} = (3.38 \times 24 \times \pi) / (1.21 \times I_{max} \times D). \quad \text{.....(7)}$$

The daily production and daily compensation light levels of young *Ec. cava* were calculated in the same way starting with eq. (1) and eq. (3). The gross photosynthetic rate ( $P_g$ ) at a given time  $t$  hours after sunrise is given by:

$$P_g = 0.61 \times Z \times I_{max} \times \sin^{1.3}(\pi \cdot t/D). \quad \text{.....(8)}$$

The daily gross production ( $Q_g$ ,  $\mu\text{l O}_2/\text{cm}^2/\text{d}$ ) is given by:

$$\begin{aligned} Q_g &= \int_0^D 0.61 \times Z \times I_{max} \times \sin^{1.3}(\pi \cdot t/D) \cdot dt \\ &= 1.12 \times Z \times I_{max} \times D / \pi \end{aligned} \quad \text{.....(9)}$$

The daily net production ( $Q_n$ ,  $\mu\text{l O}_2/\text{cm}^2/\text{d}$ ) is also given by:

$$Q_n = 1.12 \times Z \times I_{max} \times D / \pi - 1.82 \times 24. \quad \text{.....(10)}$$

The daily compensation light level ( $Z_{c,d}$ ) is given by:

$$Z_{c,d} = (1.82 \times 24 \times \pi) / (1.12 \times I_{max} \times D). \quad \text{.....(11)}$$

The relationships between daily net production ( $Q_n$ ) and light condition ( $Z$  and/or  $I_{max}$ ) in both species are examined in Fig. 28. Values of  $I_{max}$  may represent the type of weather conditions; e.g. more than 2000  $\mu\text{E}/\text{m}^2/\text{s}$  on a fine day, lower than 150  $\mu\text{E}/\text{m}^2/\text{s}$  on a rainy day and 1440  $\mu\text{E}/\text{m}^2/\text{s}$  on a day of average solar radiation (cf. Table 5). Plants have a peculiar daily compensation point in which the photosynthetic oxygen production is equivalent to the respiratory loss throughout entire day. The daily compensation point is represented by the broken line in Fig. 28. The compensation points are 1.1% for *Ei. bicyclis* and 0.6% for *Ec. cava* at 1440  $\mu\text{E}/\text{m}^2/\text{s}$  of  $I_{max}$  on an average day in the period of the present study. These values agree well with the observed critical light for both species on the community floor in Fig. 23.

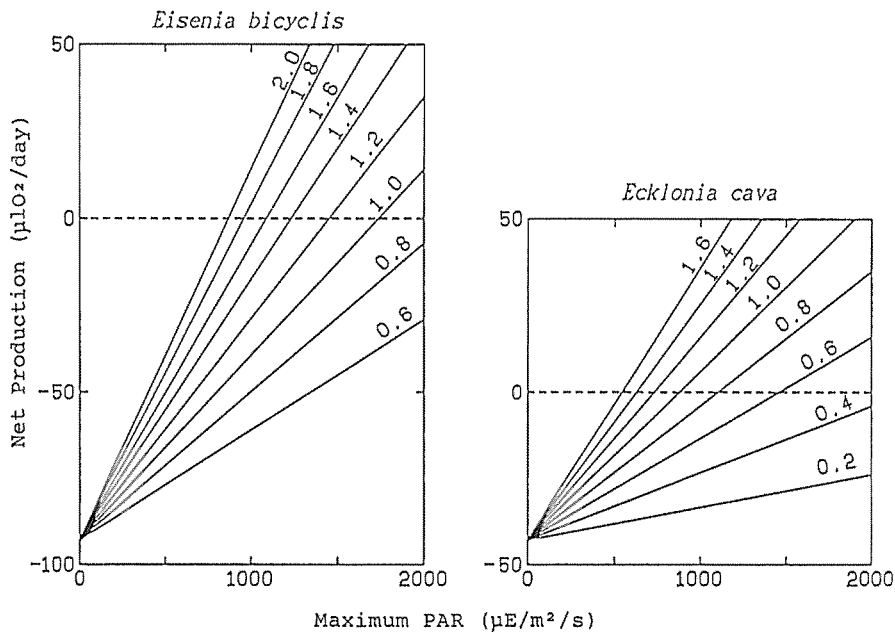


Fig. 28. Relationships of the daily net production to the maximum PAR of daytime for young *Eisenia bicyclis* (left) and *Ecklonia cava* (right) in relation to different relative light intensity (numerals on the line). Broken lines show the daily compensation points.

The light saturated photosynthetic rate, light compensation point and respiratory rate of young *Ei. bicyclis* and *Ec. cava* in the present study were well in agreement with those of adult fronds<sup>20,21</sup>). The light compensation point estimated by the linear photosynthesis-light relationship of young fronds irradiated from one side was  $8.2 \mu\text{E}/\text{m}^2/\text{s}$  for *Ei. bicyclis* and  $4.8 \mu\text{E}/\text{m}^2/\text{s}$  for *Ec. cava*. These values were higher than those of adult or young *Macrocystis pyrifera*<sup>127,128</sup>) and young *Laminaria japonica*<sup>129</sup>), although the saturated light level was almost similar.

It was reported that mature blades of *Macrocystis pyrifera* from different depths exhibited different photosynthetic characteristics; *i.e.* the photosynthetic rate of canopy blades was higher under saturating irradiance and their photosynthetic efficiency was higher at low irradiance than those of deeper blades<sup>130</sup>). These differences in photosynthetic characteristics of blades collected from different depths were primarily attributable to acclimation to light conditions. In young *Ei. bicyclis* and *Ec. cava* of the present study, the compensation light intensity varied with growing sites of various light conditions from where they were collected, even though no significant correlations were found between the light condition at growing sites and the compensation light intensity (Fig. 25). However, the level of compensation light intensity was distinguishable between the two species. The photosynthetic rate under saturating irradiance could also be distinguished clearly between young *Ei. bicyclis* and *Ec. cava* regardless of the light conditions at their growing site in the present study as well as in a previous study<sup>22</sup>).

The difference of photosynthesis-light curve in relation to light quality was reported to be remarkable in green and red algae<sup>115,116</sup>). However, KAGEYAMA and YOKOHAMA<sup>117</sup>) reported that the photosynthesis-light curve was slightly different with the light quality in three species of Phaeophyta, *Ishige sinicola*, *Sargassum*

*ringgoldianum* and *Undaria pinnatifida*, collected from shallow water, but was not different in *Undaria perterseniana* from deeper water. In the present study it was assumed that there was no significant difference in photosynthetic rate between *Ei. bicyclis* and *Ec. cava* in relation to light quality.

It is well known that photosynthesis of marine algae shows a diurnal rhythm. In general, oxygen production is highest in the light period and lowest in the dark period<sup>131,132,133</sup>. In the present investigation the measurements of photosynthesis were carried out during the same period of daytime. Consequently, comparison of the results can be properly made without consideration of the effect of diurnal photosynthetic changes.

According to GERARD<sup>108</sup>, young fronds are exposed to lower and less variable light conditions than canopy blades in the kelp bed, and photosynthetic parameters determined under artificial light in the laboratory may not accurately describe photosynthesis under fluctuating light conditions which characterize a kelp forest. It was, however, very difficult in the present study to measure fluctuating light conditions in *Ec. cava* and *Ei. bicyclis* populations. The problem will be investigated in the future.

In the present study, the improved differential gas-volumeter<sup>123</sup> with large reaction and compensation vessels (250 ml) was used to measure photosynthesis and respiration with intact young fronds of comparatively large area (15–35 cm<sup>2</sup>) of *Ei. bicyclis* and *Ec. cava*, and it was possible to obtain accurate photosynthetic oxygen changes under dim light condition even near the compensation light level.

Estimation of the critical light intensity for young *Ei. bicyclis* and *Ec. cava* was carried out in the present study with special reference to the mathematical model of community photosynthesis for submerged aquatic plants by IKUSIMA<sup>101</sup>. In his report the light intensity on the water surface ( $I$ , klux) at a given time  $t$  hours after sunrise was approximately given by:

$$I = I_{\max} \sin^2(\pi \cdot t/D),$$

where  $I_{\max}$  is the maximum light intensity during daytime and  $D$  is the length of daytime (h). In the present study, however, diurnal change in solar radiation ( $I$ ,  $\mu\text{E}/\text{m}^2/\text{s}$ ) is represented by:

$$I = I_{\max} \sin^{1.3}(\pi \cdot t/D),$$

as shown in Fig. 26. It is thought that the discrepancy between the equations may be due to the difference of measuring methods and units which are illuminance (lux) in the former and photon flux density ( $\mu\text{E}/\text{m}^2/\text{s}$ ) of PAR in the latter.

The estimated critical light level was 1.1% for *Ei. bicyclis* and 0.6% for *Ec. cava* in reference to the light intensity at the water surface (Figs. 27 and 28). These values corresponded to about 0.42  $\text{E}/\text{m}^2/\text{d}$  and 0.24  $\text{E}/\text{m}^2/\text{d}$  respectively, which were almost the same as the daily compensation light level of phytoplankton<sup>134</sup>. Photosynthesis-light relations of *Ei. bicyclis* and *Ec. cava* respectively represented characters of sun and shade types of photosynthesis in terrestrial plant<sup>135</sup>. It is clear that young *Ec. cava* fronds can grow under the lower *in situ* light intensity in deeper water as compared with young *Ei. bicyclis* fronds. This difference in critical light condition is one of the most important factors in determining the differences in their vertical distributions, particularly the lower limit of distribution of both species. The estimated daily compensation light of both species agreed well with the observed critical light conditions on the community floor. This indicates that the present measurements of light conditions in the field and photosynthetic rate in the laboratory were accurately carried out.



### Chapter III. Demography

#### 1. Introduction

*Ei. bicyclis* and *Ec. cava* are both perennial and have a potential to live at least 5 years<sup>14,17)</sup>. Therefore, the population density of both species depends to some extent on the number of recruitment and loss in growing sites. It is of commercial and ecological interest to study the population dynamics of reproduction, recruitment and mortality of these algae as CHAPMAN<sup>136)</sup> has stressed the need for such works in his review of seaweed biology.

Biologists have long been interested in the survivorship of plants and animals in natural populations since the beginning of this century. Three basic survivor patterns, usually summarized as survivor curves, have emerged from earlier studies of DEEVEY<sup>137)</sup>. Survivor curves are graphic expressions of the probability of surviving to a given age (Fig. 29). Type I survivor curve results when the age-specific mortality rate (*i.e.* the probability of dying in a given time interval) decreases with increasing age, and shows the positive skewness on a logarithmic scale. Type II survivor curve results when the age-specific mortality rate is constant and has no relation to the change of age, and shows the linear relationship on a logarithmic scale. Type III survivor curve is produced when the age-specific mortality rate increases with increasing age, and shows the negative skewness on a logarithmic scale. These three types of survivor curves are represented completely by the "Weibull frequency distribution"<sup>138)</sup>. This is an extremely flexible frequency distribution which can possess either positive or negative skewness. It has been widely used in engineering as a time-to-failure model and has previously been considered as a model of human survivorship<sup>139)</sup> and of natural population dynamics of animals<sup>138)</sup>.

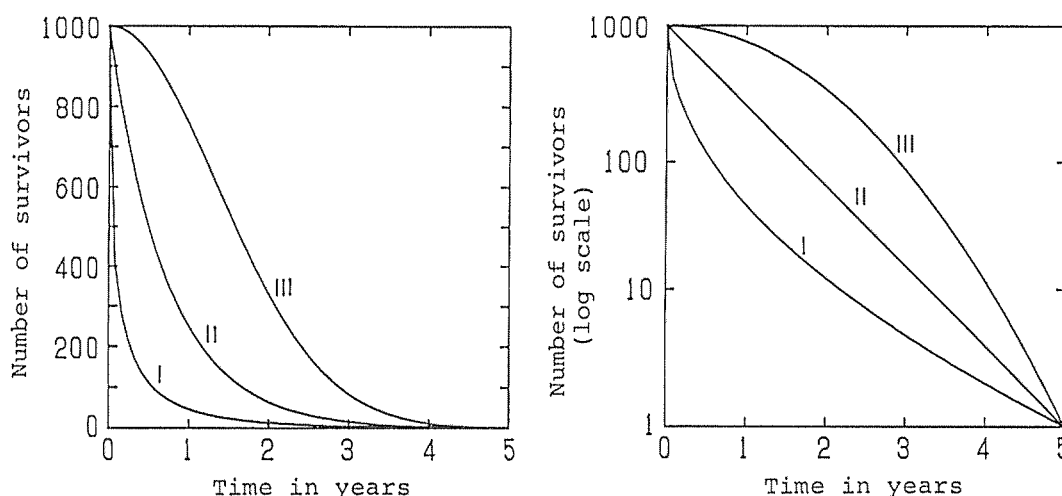


Fig. 29. Survivor curves described by Weibull frequency distributions with various values of the shape parameter  $m$ . Figures are expressed on linear scale and on logarithmic scale. Values of the scale parameter  $n$  have been adjusted so that the surviving proportion approaches zero at age=5 years.

$$\text{I, } R_{00} = 1000 \exp - (t/1.26)^{0.5};$$

$$\text{II, } R_{00} = 1000 \exp - (t/8.70)^1;$$

$$\text{III, } R_{00} = 1000 \exp - (t/22.9)^2.$$

$R_{00}$  number of survivors at a given time  $t$  (years). Each line corresponds to Type I, II, and III survivor curve by DEEVEY<sup>137)</sup>.

Recently, several demographic studies for algae with a life table analysis were reported from an ecological point of view, e.g. GUNNILL<sup>140)</sup> for *Pelvetia fastigiata*, CHAPMAN and GOUDEY<sup>141)</sup> for *Leathesia difformis*, COYER and ZAUGG-HAGLUND<sup>35)</sup> for *Pelagophycus porra*, DAYTON *et al.*<sup>36)</sup> for several macroalgae in their study of patch dynamics and CHAPMAN<sup>142)</sup> for *Laminaria longicururis*. To my knowledge, however, only one study conducted in macroalgae *Ascophyllum nodosum* has experimentally approximated the survivorship data to the Weibull frequency distribution<sup>96)</sup>. There are no studies which examined the survivorship data with reference to the regeneration process or analysis of factors controlling the mortality of algal populations.

In Chapter I and II, I found the characteristic yearly changes of the population density and the age distribution of *Ei. bicyclis* and *Ec. cava* with advancement of the regeneration process. The density of canopy fronds controls the light condition in the community. Particularly, the light condition on the community floor is the most important limiting factor for young plants to survive and grow to the adulthood<sup>2,22,25,30)</sup>. There is strong intra-specific competition for light in the gap and the building phase of regeneration process of *Ei. bicyclis* and *Ec. cava*. Strong algae-algae competition results in the death of inferior individuals. In the mature phase, the most important factor for death is normal senescence. These processes of death can be studied with the method of demography, i.e. survivor curve and life table. Demographic studies lead to a greater understanding of population biology and production ecology.

This chapter is undertaken to determine the regeneration process of both species with the method of demography. I investigated the changes in population density, mortality rate and loss in the permanent quadrats for five years. Analyzing these data with the Weibull frequency distribution, it is possible to determine the factors controlling recruitment and mortality of *Ei. bicyclis* and *Ec. cava*.

## 2. Materials and Methods

### a) Cohort Analysis

Data for demographic study of *Ei. bicyclis* and *Ec. cava* were obtained from four permanent quadrats studied for 5 years from 1982 to 1986 as shown in Chapter I. All individuals in the quadrats were marked by tagging sequentially numbered plastic plates (1 cm × 2 cm) around the holdfasts for adult plants, or plotting the positions of individuals on distribution maps 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 in which the plants were marked through June 1986, presence or absence of individuals and plant size (stipe length) were measured with SCUBA divers. The census in the quadrats was carried out fifteen times at two- or three-month intervals from 1982 to 1984, and at six-month intervals from 1984 to 1986. A total of 514 plants for *Ei. bicyclis* and 874 plants for *Ec. cava* were marked in four quadrats for 5 years. Such numerous data enabled me to conduct a comprehensive study of demography.

Survivorship data of the recruits were analyzed by the method of "survivorship directly observed" as described in DEEVEY<sup>137)</sup> in which the survivor rate could be computed directly from the survivorship data. For a period after the last observation the presence of individuals indicated their survivorship, and their absence implied death or loss during that period. The date of loss for each plant was assumed to be the middle day between the date it was lastly found and the date its disappearance was confirmed. At the beginning of the observation in June 1982, the kelp population was composed of plants with various ages. Each age group was separated according to the range of stipe length by the allometric relationship (cf. Chapter I). Since almost all of the recruits of both species could be visible in March, the survivor curve and life table were calculated by starting

from this month. Thus, the “cohorts” could be created by starting the lifetime simultaneously in the same way as GUNNILL<sup>140)</sup> employed.

#### b) Weibull frequency distribution

For analyzing factors on recruitment success and mortality of *Ei. bicyclis* and *Ec. cava*, the Weibull frequency distribution was employed as a model of survivor curve. If the continuous variable  $t$  has a Weibull distribution, the probability of observing a value equal to or less than a specific  $t$ .  $F(t)$  is given by the cumulative distribution function as follows:

$$F(t) = 1 - \exp - (t/n)^m, \quad \dots\dots(1)$$

where  $n$  is the scale parameter and  $m$  is the shape parameter of the Weibull frequency distribution. Accordingly, the reliability function,  $R(t)$ , is given as follows:

$$\begin{aligned} R(t) &= 1 - F(t) \\ &= \exp - (t/n)^m, \end{aligned} \quad \dots\dots(2)$$

and average of the Weibull distribution,  $E(t)$ , is given by the following equation:

$$\begin{aligned} E(t) &= n\Gamma(1 + 1/m). \\ &(\Gamma: \text{gamma distribution}) \end{aligned} \quad \dots\dots(3)$$

$F(t)$  in equation (1) expresses the ratio of the cumulative number of deaths to total individuals,  $R(t)$  expresses the probability of surviving to a given age  $t$ , and  $E(t)$  expresses the average life span of the cohort in natural population.

Age-specific mortality rate at a given age  $t$ ,  $\lambda(t)$  is given as follows:

$$\lambda(t) = -dR(t)/dt \cdot 1/R(t) \quad \dots\dots(4)$$

$\lambda(t)$  is alternately known as the “force of mortality” in actual work and the “hazard function” in engineering problems involving time-to-failure models. It expresses the conditional probability density of death or failure at a specific  $t$  given that the organism or system survives to time  $t$ . From two equations (2) and (4),  $\lambda(t)$  has the form as follows:

$$\lambda(t) = (m/n)(t/n)^{m-1}. \quad \dots\dots(5)$$

Clearly, when  $m < 1$ ,  $\lambda(t)$  is a monotonously decreasing function of  $t$ . When  $m = 1$ ,  $\lambda(t)$  is constant. When  $m > 1$ ,  $\lambda(t)$  is a monotonously increasing function of  $t$ . In the field of engineering, these three patterns are known as follows: initial failure or decreasing failure; random failure or constant failure; wear out failure or increasing failure, respectively. In demography, these three criteria respectively correspond to Type I, II, and III survivor curves as shown in DEEVEY<sup>137)</sup>. The form of the survivor curve is thus determined entirely by the values of the shape parameter  $m$  and the scale parameter  $n$  as shown in Fig. 29.

Similar values of  $m$  in two populations do not ensure similar average life spans. Although the value of the shape parameter  $m$  may be similar, the value of the scale parameter  $n$  may differ. Because average life span is determined by both  $m$  and  $n$  as shown in equation (3), populations with similar shape parameters can have different average life spans.

PINDER *et al.*<sup>138)</sup> proposed that the Weibull frequency distribution has two potentially important applications in survivorship studies. First, the shape and scale parameters summarize all the survivorship information in a life table. Second, estimates of  $m$  computed from different populations can be compared to determine whether the populations have similarly shaped survivor curves. Furthermore, in this study I propose another important application in the Weibull frequency distribution. If the factors controlling the mortality rate change within a period of lifetime, the value of shape parameter  $m$  also changes. Consequently, it is possible to determine the factors controlling the mortality rate according to the changes in parameter  $m$  within the lifetime.

For approximating the survivorship data to the Weibull frequency distribution and examining the life table, it is required to satisfy a certain condition under which all members in the cohort die out. In the *Ec. cava* population, all members observed at the beginning of the permanent quadrat study died out and were alternated with new members within the period of this study. However, some of *Ei. bicyclis*, which had a longer life span than *Ec. cava*, lived throughout the permanent quadrat study of five years. Therefore, I approximated the survivor data to the Weibull frequency distribution and examined the life table for only the *Ec. cava* population.

### 3. Results and Discussion

#### a) Survivor Curve

As shown in Chapter I, the changes in frequency distribution of stipe length and density showed a similar tendency at Sts. 1 and 2 for *Ei. bicyclis* and Sts. 3 and 4 for *Ec. cava*. Therefore, the average survivorships were computed respectively for both quadrats and the results are shown in Fig. 30. The survivorship data for 1000 recruits are expressed both on a linear scale and on a logarithmic scale.

As for *Ei. bicyclis* in Fig. 30, the number of recruits greatly decreased during the first year early in the lifetime, and thereafter it decreased gradually. The mortality rate, expressed by the inclination of the line on a logarithmic scale, was high during the first 20 months, and thereafter it decreased gradually to the low level. After 69 months from recruiting, 31 out of the initial 1000 individuals survived.

As for *Ec. cava* in Fig. 30, the number of recruits greatly decreased during the first year early in the lifetime as in *Ei. bicyclis*, and thereafter it decreased gradually during the second year. After two years, however, the number of fronds indicated relatively high decrease again. The maximum life span of *Ec. cava* was less than 6 years. The mortality rate, expressed by the inclination of the line on a logarithmic scale, was low during the first two years except relatively high rates in the initial three months. After two years the mortality rate increased gradually.

Thus, the mortality rate did not change uniformly in the lifetime of *Ec. cava*, so that it was not possible to extrapolate the survivor curve to only one specific equation. Therefore, in the present study the Weibull equation was expressed as follows:

$$l_x = I \exp - (t/n)^m,$$

where  $l_x$  is the number of survivors,  $I$  is the initial number of individuals in a population,  $t$  is the time,  $n$ , is the scale parameter and  $m$  is the shape parameter. For calculating the regression line, the Weibull equation is transformed as follows:

$$\ln \ln(I/l_x) = m \ln(t) - m \ln(n). \quad \dots\dots(6)$$

When  $Y = \ln \ln(I/l_x)$ ,  $X = \ln(t)$  and  $B = -m \ln(n)$ , equation (6) is rewritten as follows:

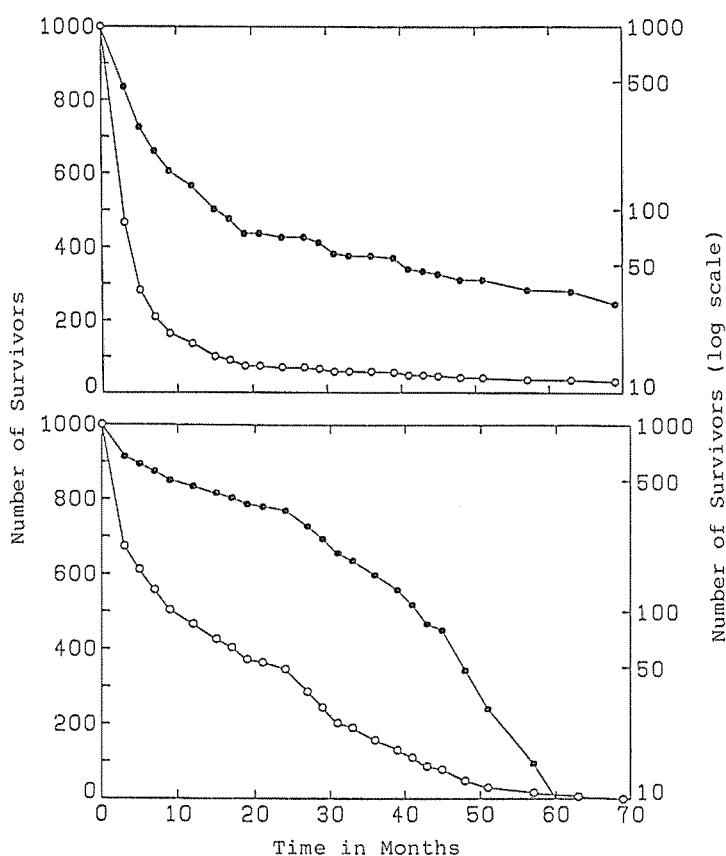


Fig. 30. Survivor curves of *Eisenia bicyclis* and *Ecklonia cava* for 1000 individuals. Data were expressed both on linear scale (—○—) and on logarithmic scale (—●—).

$$Y = mX + B.$$

.....(7)

The relation between  $X$  and  $Y$  is linear, so that the survivor data can be fitted to the Weibull frequency distribution by the least squares method.

Fig. 31 shows a relationship between the number of survivors ( $l_x$ ) for 1000 individuals and time ( $t$ ) in months. The survivor data are approximated on 3 regression lines for 3 periods of the lifetime: during the first 24 months, from the 24 th to the 42 nd month and from the 42 nd to the 69 th month. The shape parameter  $m$  was 0.488, 1.376 and 1.976 for each period, respectively.

In the survivor curve analysis of seaweed populations several equations have been employed to calculate the number of survivors for the selected time intervals throughout the lifetime for life table analysis; e.g. the exponential equation<sup>142)</sup>, the log-log equation<sup>140)</sup> and the Gompertz equation<sup>141)</sup>.

In the present study the changes of mortality rate exhibited no uniformity within the lifetime of *Ec. cava*. Hence the survivorship data fitted for the 3 Weibull equations for the 3 periods as shown previously. These three equations according to the changes of parameters  $m$  and  $n$  indicate that the main factor controlling the mortality rate of *Ec. cava* varies throughout the period in the lifetime. For the demographic study, the

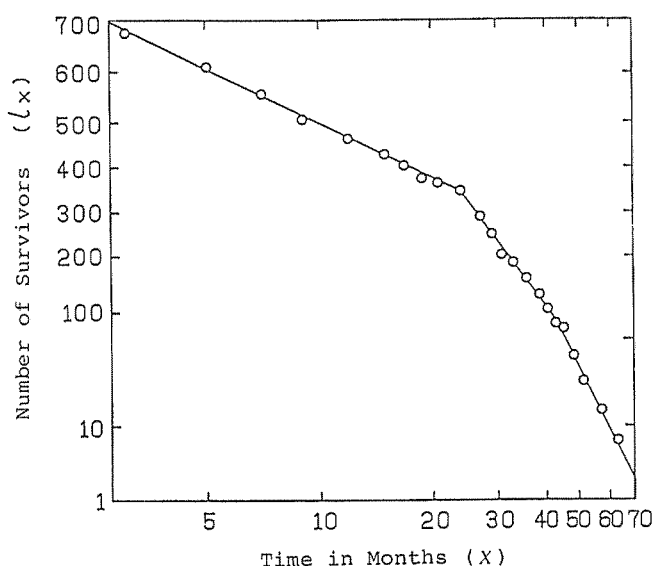


Fig. 31. The Weibull frequency distribution fitted to the survivor date of *Ecklonia cava*.

$$0-24 \text{ months, } l_x = 1000 \exp - (x/20.3)^{0.448},$$

$$24-42 \text{ months, } l_x = 1000 \exp - (x/22.7)^{1.376},$$

$$42-69 \text{ months, } l_x = 1000 \exp - (x/27.5)^{1.976}.$$

$l_x$ , number of survivors at a given time  $t$  (months).

parameter  $m$  in the Weibull equation is more useful to determine the shape of a survivor curve and the factors controlling the mortality rate.

When  $m < 1$ , the mortality rate is a decreasing function of age, *i.e.* the mortality rate decreases gradually as the age increases. In young stage of *Ec. cava* ( $m = 0.488$  in the present study), the factor controlling the mortality rate is the intraspecific competition caused by self-shading, resulting in self-thinning. Competitively inferior recruits, which germ too much later than others or grow under dim light condition beneath a superior neighborhood, are destined to die or lose selectively. With decrease in population density through self-thinning, the mortality rate also decreases from gap to building phase during the first 24 months. Another factor might be sweeping over the substratum by blades of larger plants, or characteristics of substratum upon which young plants were attaching<sup>35</sup>.

When  $m = 1$ , the mortality rate is constant and/or unrelated to age. In the present study, the parameter  $m$  was not far from 1 for the period from the 24 th to the 42 nd month in the lifetime of *Ec. cava*. It was thought that the loss of adult fronds in this period was caused by occasional severe wave action. *Ec. cava* fronds grew to adulthood and reached the canopy surface within 2 years. Wave action influenced large canopy fronds more significantly than young fronds within the population.

When  $m > 1$ , the mortality rate is an increasing function of age, *i.e.* the mortality rate increases gradually as the age increases. During the last period from the 42 nd to the 69 th month ( $m = 1.976$  in this study), loss or drift out of large fronds was clearly the result of normal senescence.

When the population density was high, the survivor curves showed that the mortality of juveniles was much higher than that of older plants. The survivor curve of *Ec. cava* obtained in the present study was similar to that

of *Pelagophycus porra* reported by COYER and ZAUGG-HAGLUND<sup>35)</sup>. Survivor curves of *P. porra* is characterized by a high mortality rate at the younger stage and by a relatively low mortality rate at the adult stage. When the main factor regulating the mortality rate varies in the lifetime of the species, the survivor curve does not show a smooth line but shows remarkable changes in skewness (cf. Fig. 30).

In the demographic study of *Laminaria longicuris*, CHAPMAN<sup>142)</sup> showed that the important demographic parameters in the plant population were more closely related to size (or stage) than to chronological age. He approximated the survivor curve of *L. longicuris* to the exponential distribution, giving constant mortality, which corresponded to Type II model of DEEVEY<sup>137)</sup>. However, paying attention to the figure showing the distribution of survivor data of *L. longicuris*, it appears that the mortality rate varied with age as is similar to my study of *Ec. cava*.

In the present study the census of *Ec. cava* was carried out from recruits 1–3 cm long. However, extremely high mortality of this species occurred before plants reached this size, in a similar manner as mentioned about in other kelp species<sup>143,144)</sup>. The major determinant of the mortality at this stage was not identified in the present study. More advanced techniques and equipments usable in water and in the laboratory will enable us to do more comprehensive studies in demography of algae.

#### b) Life Table

Life table is a convenient format for describing the mortality schedule of a population. Columns of the life table are symbolized by letters, and these symbols are constantly used in demographic study:

$x$  = age,

$l_x$  = number of survivors at the start of age  $x$ ,

$d_x$  = number of individuals dying during the age  $x$  to  $x+a$ ;  $l_x - l_{x+a}$ ,

1000  $q_x$  = rate of mortality during the age  $x$  to  $x+a$  per 1000 individuals; 1000  $q_x/l_x$ ,

$e_x$  = mean life expectancy for organisms alive at the start of age  $x$ ,

( $a$ ; age interval).

To set up a life table, one must decide the age intervals ( $a$ ) to group the data. The age interval may be 1 or 5 years for humans, and it was 3 months for *Ec. cava* in this study. Usually, the age interval takes 1 unit (year, month or day). Additionally,  $L_x$  and  $T_x$  columns, which are necessary to calculate  $e_x$ , may be included in the life table.

The calculation of mean life expectancy ( $e_x$ ) is somewhat complicated. First, age structure or number of individuals alive which are between ages  $x$  and  $x+a$  ( $L_x$ ) is given as follows:

$$L_x = (l_x + l_{x+a})/2.$$

Second, successive values of  $L_x$  obtained in this way are summed from the bottom of the column up to each age  $x$ . This gives  $T_x$ .  $T_x$  is the sum of months of remaining life of the population at age  $x$ . At this time, one should note that values of  $T_x$  are expressed in units of "individuals  $\times$  time units", so that  $T_x$  must be summed as in the following equation:

$$T_x = \sum_{x=0}^{\infty} (L_x \times a).$$

In many cases of life table analyses, time interval is 1 unit (1 year or 1 month). Then,  $T_x$  is obtained only by summing  $L_x$  values from the bottom of the column.

Dividing  $T_x$  by  $l_x$  gives the mean life expectancy ( $e_x$ ) as follows:

$$e_x = T_x / l_x.$$

The value of mean life expectancy at age 0 is the same as the average life span of the cohort. For older individuals, it is the average life span remaining to those attaining a given age.

Life table of *Ec. cava* was shown in Table 6. The number of survivors ( $l_x$ ) for a 3-month interval was calculated from 3 Weibull equations as shown in Fig. 31. No individuals could have been alive for 69 months in the surveyed quadrates; consequently  $l_x$  at 69 th month was 0. When  $x=0$ , the average life span of the cohort or the average life expectancy of each individual ( $e_x$ ) was 16.5 months, and the maximum value of the average life expectancy ( $e_x$ ) was 21.1 months when  $x=6$  months. The maximum life span of *Ec. cava* was 5 years or more, but did not reach 6 years. Relative mortality for 1000 individuals ( $1000 q_x$ ) decreased during the first 2 years; consequently, it increased gradually as expected in the Weibull frequency distribution in Fig. 31.

**Table 6.** Life table of *Ecklonia cava*. Abbreviations are as follows;  $x$ , age in months;  $l_x$ , the number of survivors at age  $x$ ;  $d_x$ , the number of individuals disappeared during each interval;  $1000 q_x$ , the number of individuals disappeared for 1000 individuals alive at age  $x$ ;  $L_x$ , the number of individuals alive between age  $x$  and age  $x+3$ ; ( $T_x$ ), sum of months of the remaining life of the individuals at age  $x$ ;  $e_x$ , the mean life expectancy (months) for those at age  $x$ . Date of  $l_x$  from 0–66 months were calculated by the 3 Weibull equations in Fig. 31

$x$	$l_x$	$d_x$	$1000q_x$	$L_x$	$e_x$	$T_x$	$x$	$l_x$	$d_x$	$1000q_x$	$L_x$	$e_x$	$T_x$
0	1000	326	326	837.0	16.5	16506.0	36	151	30	199	136.0	9.9	1495.5
3	674	99	147	624.5	20.8	13995.0	39	121	24	198	109.0	9.0	1087.5
6	575	65	113	542.5	21.1	12121.5	42	97	27	278	83.5	7.8	760.5
9	510	49	96	485.5	20.6	10494.0	45	70	21	300	59.5	7.3	510.0
12	461	39	85	441.5	19.6	9037.5	48	49	16	327	41.0	6.8	331.5
15	422	33	78	405.5	18.3	7713.0	51	33	11	333	27.5	6.3	208.5
18	389	28	72	375.0	16.7	6496.5	54	22	8	364	18.0	5.7	126.0
21	361	22	61	350.0	14.9	5371.5	57	14	5	357	11.5	5.1	72.0
24	339	59	174	309.5	12.7	4321.5	60	9	4	444	7.0	4.2	37.5
27	280	50	179	255.0	12.1	3393.0	63	5	2	400	4.0	3.3	16.5
30	230	43	187	208.5	11.4	2628.0	66	3	3	1000	1.5	1.5	4.5
33	187	36	193	169.0	10.7	2002.5	69	0					

In the life table analysis of *L. longicruis* by CHAPMAN<sup>142)</sup>, there is an underestimation of mean life expectancy ( $e_x$ ) due to miscalculation of  $T_x$  column. In his table,  $T_x$  is calculated only by summing  $L_x$  values from the bottom of the column, presumably without consideration of age interval of 2 months. The same sort of miscalculation is also found in CHAPMAN<sup>136)</sup> for *Macrocystis pyrifera* based on the data of ROSENTHAL *et al.*<sup>33)</sup>; age interval is 4 months in his case. In the life table of *Pelvetia fastigiata* in GUNNILL<sup>140)</sup>, mean life expectancy ( $e_x$ ) was represented by the survival of 50% of individuals present at the start of each interval. This is another concept of  $e_x$  used in demographic study.



Life table analysis is greatly useful not only for the ecological field to present a concise summary of certain vital statistics of a population but also for fisheries and commercial fields to provide fundamental data for management and conservation of natural bioresources. More comprehensive research about demography of algae accompanied by analyses of survivor curves and life tables is necessary to make clear the population dynamics of algae in nature.

#### Chapter IV. Conclusion

In the course of the present study, I have examined the ecological characteristics of *Ei. bicyclis* and *Ec. cava* marine forests in reference to the following points: distributional pattern, regeneration process, production ecology, and demography. I applied some similar methods used for terrestrial forests to analyze population structure and population dynamics in marine forests of both species. Both marine forests have fundamentally similar structures and functions to terrestrial forests, although there are considerable differences in the scale of population and/or community and in biological and physiological characteristics of the components between the two.

*Eisenia* and *Ecklonia* marine forests offer certain advantages for this type of population study as compared with terrestrial forests. The scale of marine forests is usually small as compared with that of terrestrial forests; this lead me to uncomplicated approach with marine forests for understanding population structure. Furthermore, since *Ei. bicyclis* and *Ec. cava* biologically and physiologically have simpler constitutions than terrestrial plants, it is relatively easy to measure precisely photosynthesis and respiration with the help of "Productmeter". The most important advantage in studying population dynamics of marine forests is an extremely brief turnover time of regeneration as compared with terrestrial forests. These advantages will enhance my study of ecological and physiological aspects of marine algae and marine forests more extensively.

There were allometric relationships between stipe length or diameter and weight of stipe, blade and total frond. Stipe length was the most useful analytic character for understanding the population structure because of its ease in measuring underwater with SCUBA diving.

The regeneration process was studied with the methods of permanent quadrat and mapping for 6 years. The turnover time of the canopy layer (regeneration cycle) was 5–6 years for the *Ei. bicyclis* population and 3 years for the *Ec. cava* population; the regeneration process of both marine forests was so-called "gap regeneration". Three phases of gap, building and mature were distinguished with reference to the structural and dynamic features of the population through the regeneration process.

The analysis of distributional patterns of individuals in *Ei. bicyclis* and *Ec. cava* populations suggested that there was a significant intraspecific competition between the canopy fronds and recruits, and moreover among the same age groups. The distributional patterns appeared as the result of intraspecific competition for light in the mixed assemblage of plants of various ages and sizes.

Production structures of *Ei. bicyclis* and *Ec. cava* populations were studied with special reference to the light conditions in populations. Young fronds of these species were growing under considerably dim light conditions on the population floor. Critical light conditions for young *Ei. bicyclis* and *Ec. cava* observed on the population floor were respectively 1.0–1.5% and 0.5–1.0% of the light intensity at the water surface. The density of small, young fronds was dependent on the light condition which was related to the density of large canopy fronds.

Daily net production was calculated with the mathematical models based on photosynthesis-light equations and natural light conditions. The estimated daily compensation light of young *Ei. bicyclis* was 1.1% and young *Ec. cava* was 0.6% of the water surface light intensity on the day of average solar radiation. The estimated daily compensation light intensity agreed well with the observed critical light intensity for both species. It is clear that young *Ec. cava* fronds can grow under lower *in situ* light intensity in deep water than young *Ei. bicyclis* fronds in shallow water.

Demography was studied mainly for the *Ec. cava* population. The Weibull frequency distribution based on the survivor curve was used to analyze the factors regulating mortality of the population. At the young stage within the first 24 months, intraspecific competition for light was thought to be the main factor in death or loss. At the adult stage from the 24th to the 42nd month when plants formed a canopy, loss was caused mainly by wave action. During the last period from the 42nd to the 69th month, loss of large fronds resulted from normal senescence. The average life span of *Ec. cava* was 16.5 months and the maximum life expectancy of 21.1 months was obtained at the 6th month after recruiting. The longevity of *Ec. cava* was calculated to be 5 years or more, but less than 6 years.

From these results, I concluded that the regeneration process of *Ei. bicyclis* and *Ec. cava* populations was controlled by intraspecific competition for getting light. The difference in regeneration cycle of the two species resulted from the difference in their life span. In addition, the difference in critical light conditions between young fronds of the two species is one of the most important factors in determining the difference in their vertical distributions.

These studies of population structure and dynamics accompanied by production research such as light and photosynthetic measurements will be a useful and essential approach to the ecology of algae.

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## アラメおよびカジメの生態学的研究

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褐藻類コンブ科に属するアラメおよびカジメは本邦暖海域に分布し、1-3 m の高さになる大形海藻である。一般にアラメは潮間帯直下から水深 10 m 付近まで、カジメは水深 4 m 付近から 25 m もしくはそれ以深にまで分布する。本研究は、群落の構造やその変動を解析することにより、アラメおよびカジメの種の特性を生態学的な見地から解明することを目的としたものである。

両種の群落構造を解析するための基準形質を得るため、多くの個体について茎長、茎径、年齢、乾重量等を測定し、各形質間の相対生長関係を検討した。その結果、相関係数、測定の難易度を考慮して茎長を基準形質として採用した。

群落の更新課程を把握するため、アラメおよびカジメ群落内に永久コドラートを設置し、個体の発生、死亡状況および茎長の伸長状況等を6年間にわたり連続的に測定した。カジメ群落では3年周期で成体群と幼体群の交代が行われるのに対し、アラメ群落では成体群が5-6年以上にわたって林冠を形成し続ける。また、分布様式の解析から、小形群の消長は、大形群の密度によって強く支配されることも明かとなった。

群落内の光環境と立体構造を明らかにするため、層別刈取り法により生産構造を求め、解析の基準資料とした。両種とも群落床部の光環境は林冠を形成する大形群の密度に強く支配され、大形個体の少ない群落では、床部の相対光強度は比較的高く、多数の小形個体が生育する。また、アラメ群落はカジメ群落に比べ葉重量が3-4倍多く、光は群落上層で急激に吸収され、小形群の出現や生長が著しく制御される。

光条件がアラメおよびカジメの分布や生長に及ぼす直接的な影響を明らかにするため、両種の幼体について生育場所の光環境、光合成特性、日射の日変化等を測定し、日補償点を推定するためのモデル式を作り、両種幼体の光環境からみた生育限界を解析した。推定された日補償光強度を海面に対する相対光強度で表すと、アラメ幼体では1.1%、カジメ幼体では0.6%であった。これらの値は幼体の生育する群落床部の相対光分布の実測値とよく一致した。

カジメ群落について生存曲線や生命表を作成し、若齢時の死亡要因を検討した結果、幼体の生長に伴う個体群密度の増加が原因となる種内競争が主な死亡要因と考えられ、また、アラメは寿命が7-8年と、カジメの5年に比べ明らかに長く、長期にわたり大形個体が優占する群落を形成し続けることが明かとなった。

以上の結果から、カジメはアラメに比べより弱光に適応しており、両種の光に対する適応の特性や寿命の相違が、両種群落の構造やその更新課程の違いに反映しているものと結論される。