

Annual growth cycle of the brown alga *Ecklonia cava* in central Japan

R. HAROUN^{1,3}, Y. YOKOHAMA² & Y. ARUGA¹

¹Laboratory of Phycology, Tokyo Univ. of Fisheries, Konan 4-5-7, Minato-ku, Tokyo, 108, Japan.

²Shimoda Marine Research Center, Univ. of Tsukuba, Shimoda, Shizuoka, 415, Japan.

³Present address: Department of Plant Biology, University of La Laguna, Tenerife, Canary Is. Spain.

SUMMARY: *Ecklonia cava* Kjellman (Laminariales, Phaeophyta), a perennial seaweed, is one of the main components of the marine forests along the Pacific coasts of Japan. Its standing crop attains a maximum in summer and a minimum in winter. This is due primarily to seasonal variation of pinnate blade biomass. The present investigation was conducted on an *E. cava* community in Nabeta Bay, Shimoda (central Japan), with monthly samplings at 5 m depth, in order to quantify the growth process of this species. In the laboratory several biometrical parameters were measured. Although there were individual variations among the samples, it was possible to define several trends in the growth cycle of *E. cava* on the basis of the monthly averages. The number of young bladelets was 0-7; they increased from autumn to the beginning of winter, remaining constant for a short period until spring when they began to decrease, reaching a minimum in late summer. The longest bladelet appeared in spring and early summer, while the shortest one was found in early winter. The dry weight per unit area of bladelets increased with growth, and was low ($6-9 \text{ mg cm}^{-2}$) during winter-spring and high ($18-21 \text{ mg cm}^{-2}$) during the reproductive season. Based on the results, 4 periods can be distinguished in the annual growth cycle of the *E. cava* blade: 1) period of active formation of new primary blade and bladelets; 2) period of active growth of bladelets; 3) period of thickening of bladelets and development of sori, and 4) period of decay of old bladelets.

Key words: brown algae, growth cycle, *Ecklonia*, Laminariales.

INTRODUCTION

In the shallow sublittoral waters of temperate regions the kelps are major components for the marine primary production (MANN, 1973) and their large biomass is being used in both the Pacific rim (California, Japan, Korea, China) and Europe (France, Norway) for commercial purposes (MICHANEK, 1975; LEVRING, 1977; TSENG, 1981). Recently, their ecological role (MANN, 1982) and importance to fisheries as nursery areas or habitats are being enhanced (WHEELER, 1980; KIKUCHI & UKI, 1981; WARNER, 1984; OHNO, 1985).

Some members of the Laminariales have received a lot of attention, especially *Laminaria* and *Macrocystis*, with many published papers about diverse aspects of their biology (NORTH, 1971; KAIN, 1979; SCHMITZ, 1981). In Japanese waters, sporophytes of *Ecklonia cava* Kjellman form extensive kelp beds on rocky shores along the Pacific coasts from central

Honshu to Kyūshu, and their ecological role in the shallow marine ecosystems is starting to be understood. In recent years the work of several Japanese investigators has shed some light on the structural aspects of community (IWAHASHI, 1968a, 1968b; IWAHASHI *et al.*, 1979; HAYASHIDA, 1977, 1984, 1986; KIDA & MAEGAWA, 1982, 1983; OHNO & ISHIKAWA, 1982; KASAHARA & OHNO, 1983; MAEGAWA & KIDA, 1984), on culture (MIGITA, 1984) and productivity (YOKOHAMA, 1977; YOKOHAMA *et al.*, 1987; MAEGAWA *et al.*, 1987) of *E. cava*. In previous papers (ARUGA, 1981; YOKOHAMA *et al.*, 1987) it was reported that the standing crop of *E. cava* communities attains a maximum in summer and a minimum in winter; this is mainly related to the seasonal variation of the pinnate blade biomass.

The present investigation was conducted to quantify the growth process of this species during a one-year period and to relate the growth pattern to some possible factors.

MATERIAL AND METHODS

Morphologically, the *E. cava* sporophyte can be divided into three parts: a conical holdfast with many rhizoids, a long stipe (length > 50 cm in adult plant) and a pinnate blade (HAYASHIDA, 1977) (Fig. 1). The general morphology of *E. cava* is very similar to that of *E. radiata* (C. Ag.) J. Ag. of southern Australia (KIRKMAN, 1984), but the former has a longer stipe and the margins of the primary blade have many digitations from which the bladelets appear. As in other Laminariales primary growth is intercalary, located in the transitional zone between stipe and blade (some also in the proximal portion of the blade). When growth is initiated the primary blade moves upward, developing several bladelets (usually with lateral protuberances), and erodes from the distal ends of both primary blade and bladelets (Fig. 1).

The research was conducted on an *E. cava* forest located at Nabeta Bay (Izu Peninsula), near the Shimoda Marine Research Center of the University of Tsukuba, from April 1986 to March 1987. Every month 10 adult plants (3 or more years old) were randomly sampled from a homogeneous population of *E. cava* at 5 m depth (Fig. 2). In the laboratory the following dimensions were measured: total length, stipe length and diameter, primary blade and bladelets length, total number of bladelets, number of young bladelets (length < 10 cm), number of bladelets with sori (if present) and the dry weight (80 °C, 24 hours) of a 3.2 cm² disc taken from the central part of each bladelet and primary blade (Fig. 1). The bladelet position number was assigned from the proximal to the distal part, i.e. number 1 was assigned to the smallest primordia, number 2 to the next one and so on. Later, the different biometrical parameters of each month were averaged.

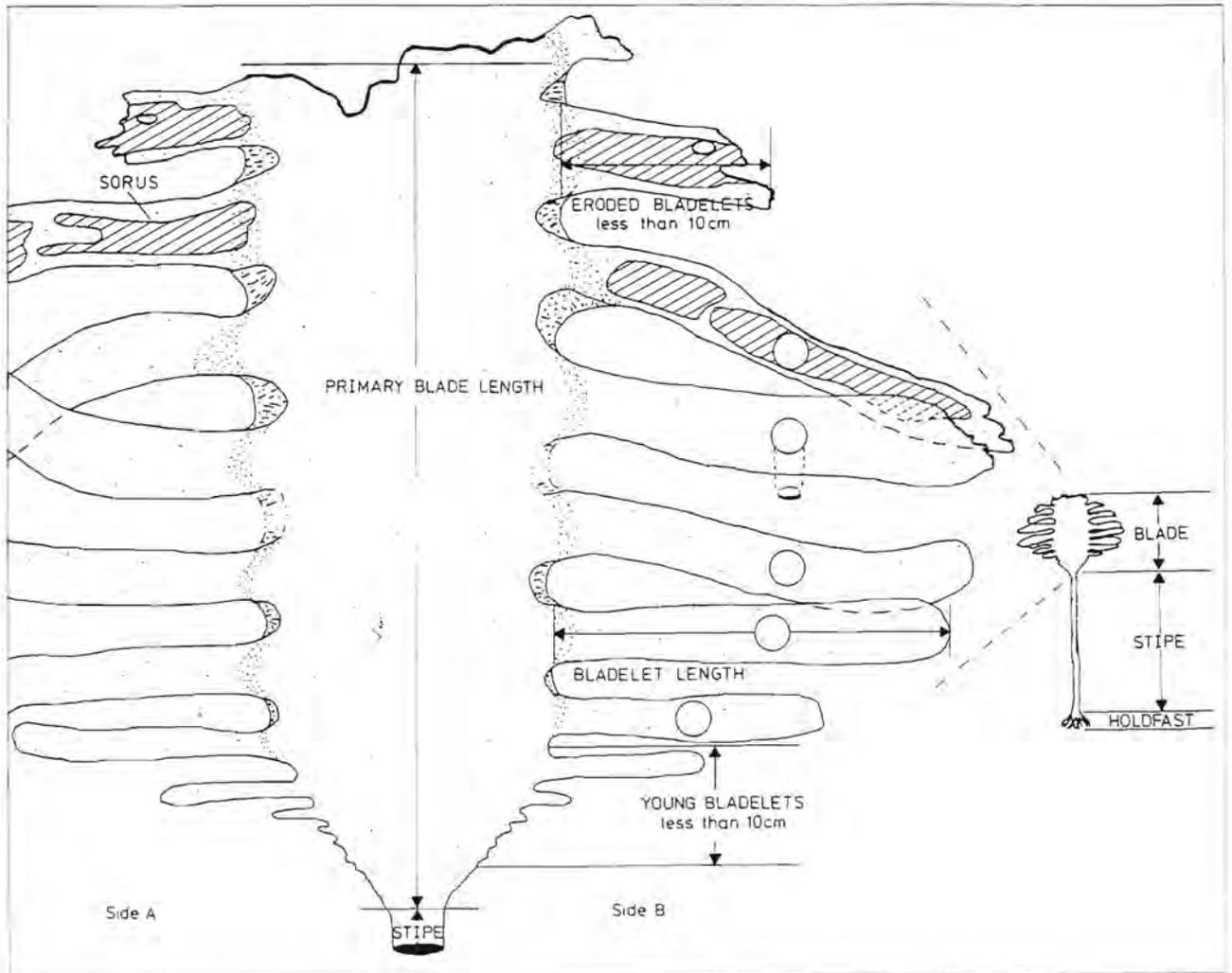


FIG. 1. — Simplified drawings of the *Ecklonia cava* sporophyte showing different parts of a frond measured. Central discs of bladelets were used to obtain the dry weight.

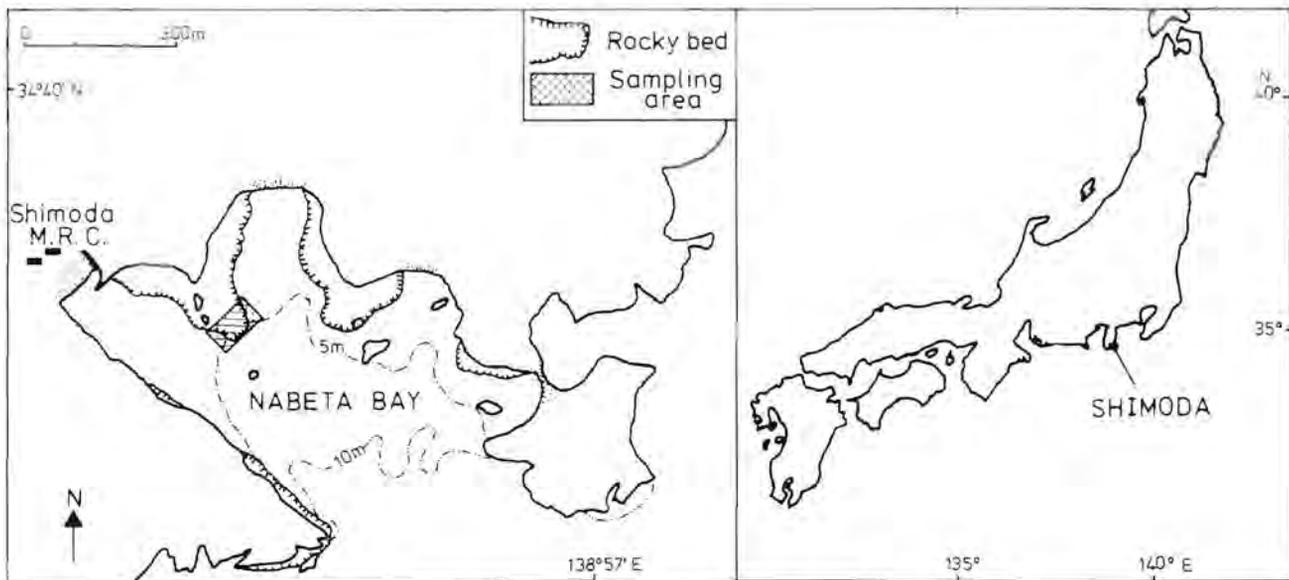


FIG. 2. — Maps showing the location of sampling area in Nabeta Bay, Shimoda, central Japan.

RESULTS

In figure 3 is represented the seasonal variation of seawater temperature (average of 6 years, ANON., 1981-'86). It has a minimum in mid-winter (February, 12.8 °C), and a maximum in late summer (August, 25 °C).

Figure 4 shows the results of measurements of the bladelet length and dry weight and their averages in April, June, August, October, December and February. From early spring to summer the total number of bladelets increased, but the meristematic tissue activity gradually slowed down and finally stopped in late summer. There was no young bladelet formation in August (Fig. 5). During the summer only upper bladelets had sori, but in early autumn almost all the bladelets had sori and the transitional zone started again to divide at a high rate, producing numerous primordial bladelets for the next growing season (Figs. 4 and 5).

In December, the upper parts of the blades still held bladelets with sori, however, these bladelets as well as the sori were very eroded and in a progressive process of degradation. Moreover, in the proximal part of the blade the next season's primary blade was in active growth with many bladelets in formation (Fig. 4). Between December and January the remnants of the old blades finally broke from a weak area, leaving the fresh blade alone. In winter (Fig. 4), the *E. cava* sporophyte was at the peak of the growing season producing many long bladelets which through the spring will start to thicken and subsequently produce sori.

The longest bladelets were usually located at bladelet position 7-17, with the smallest position

number in September and the largest position number in November after the onset of bladelet primordia formation. The length of bladelets increased quickly during late winter and early spring and the erosion process dominated in late summer and autumn; the shortest bladelet appeared in early winter (Fig. 6).

The dry weight per unit area of each bladelet, represented by circles in the histograms in figure 4, also showed clear seasonal variations (Fig. 6), increasing with growth through the spring and reaching maximum values of 18-21 mg cm⁻² during the reproductive season; the minimum values of 6-7 mg cm⁻² were found in winter (Fig. 6). Another interesting trend is that in winter and early spring (Fig.

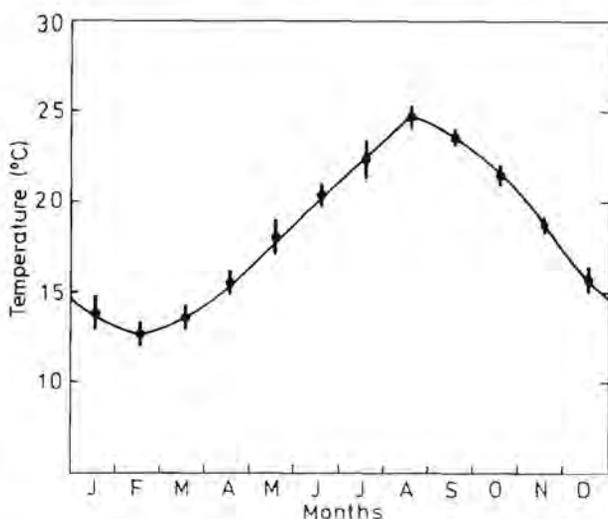


FIG. 3. — Seasonal change of the surface seawater temperature in Nabeta Bay. Average of 6 years from 1981 to 1986.

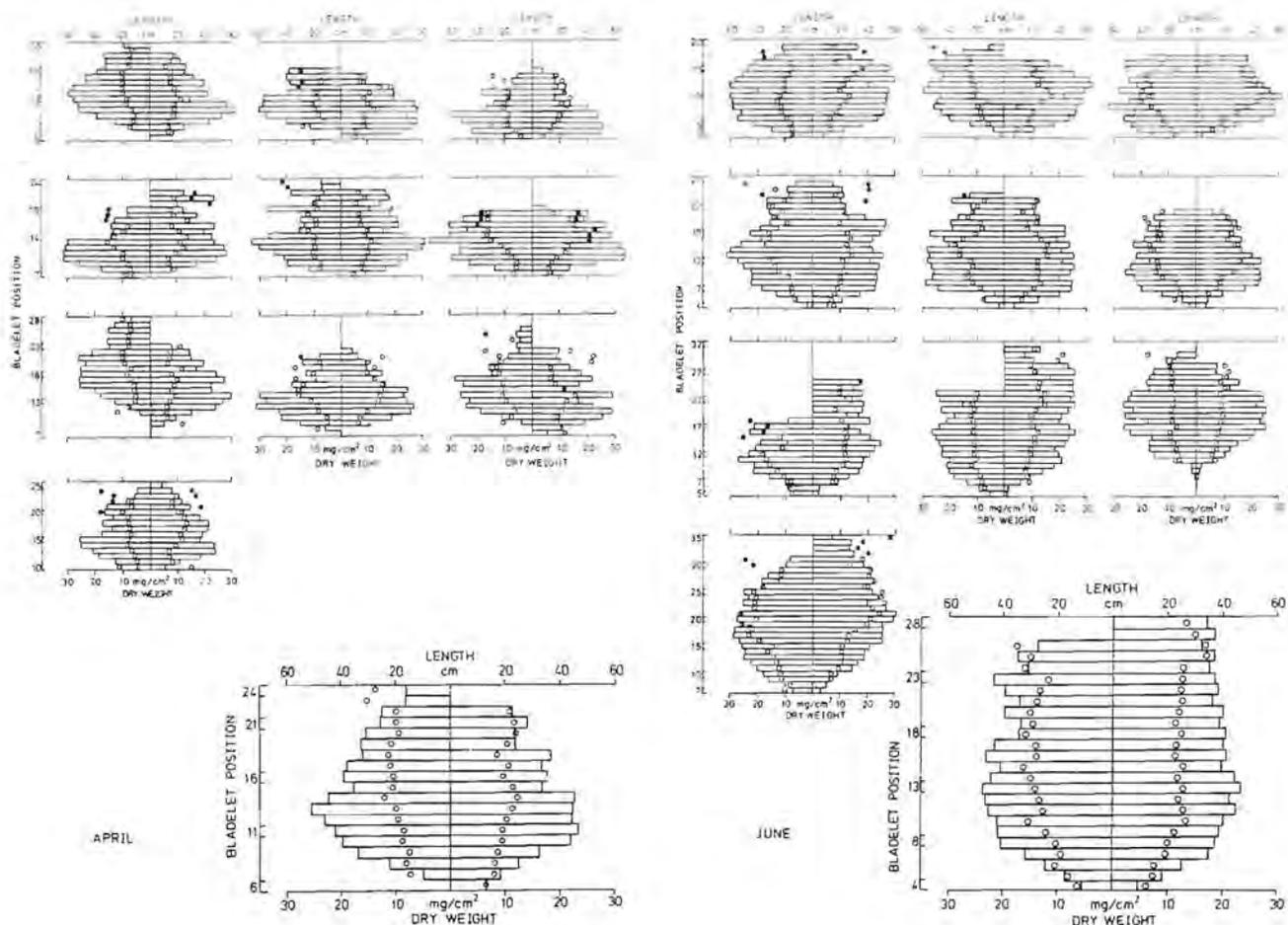


FIG. 4a.

FIG. 4. — Diagrams showing the bladelet length (histograms) and dry weight (open circles, without sori; solid circles, with sori) of individuals samples of *Ecklonia cava* in Nabeta Bay. The lowermost diagram shows the average of 10 samples in each month. April 1986 – February 1987.

4) the dry weight per unit area of each bladelet was more or less similar all along the blade, but in the reproductive season the values of the upper bladelets were 2-3 times higher than those of the lower ones (Fig. 4).

There were only a few bladelets with mature sori in spring. The number of bladelet with mature sori gradually increased during summer until it reached a peak in October. In December a greater part of the sori sloughed off, discolored and degraded. During January and February not one sorus was encountered (Figs. 4 and 5).

The formation of sori in one particular blade started from the upper bladelets and subsequently the process moved downward (Fig. 4). The sori first appeared at the basal portion of bladelets and then they extended to the apical portion. The shape of the early spring sori were irregular and of small area coverage, while the sori formed in summer occupied most of the bladelet areas and fit the general morphology of the bladelets. There was an increase of

sorus coverage from spring (20 %) to late summer (80-90 %). In late summer many bladelets were covered by epizoon, especially bryozoans, so that in some way they may have inhibited the normal development of the sori.

From the above-mentioned results it is possible to define the growth process of the *E. cava* blade on an annual basis with 4 successive periods (Fig. 7):

1) Period of active formation of new primary blade and bladelets. In early autumn the transitional zone between stipe and blade started to produce the next year's primary blade and numerous bladelet primordia appeared. The activity of the meristematic tissues increased until winter, then remained constant for a short time, and in late spring the production of young bladelets decreased; in summer not one young bladelet appeared. Thus, the formation of the primary blade is mainly concentrated in winter and early spring.

2) Period of active growth of bladelets. The bladelets produced in winter elongated very quickly

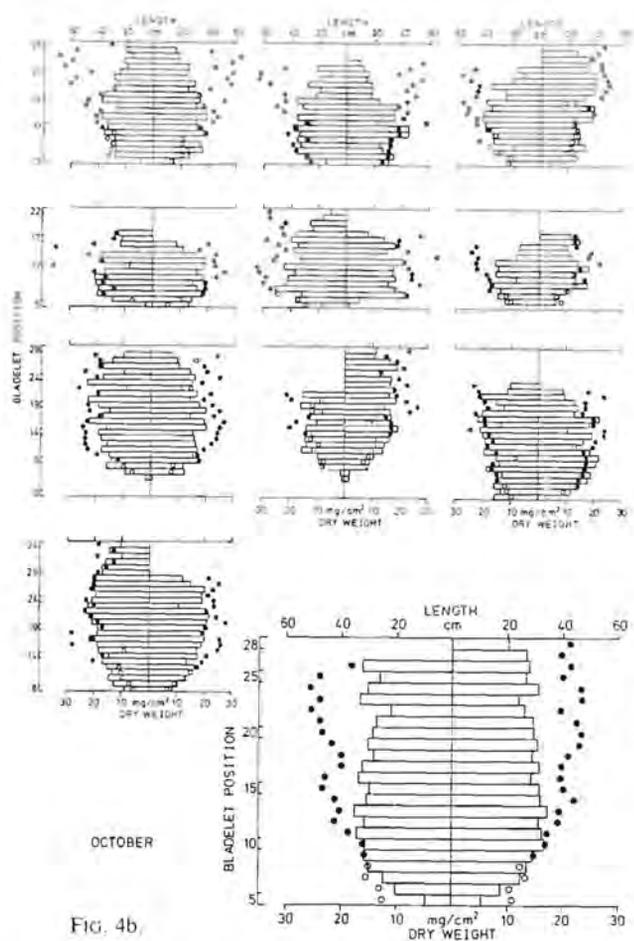
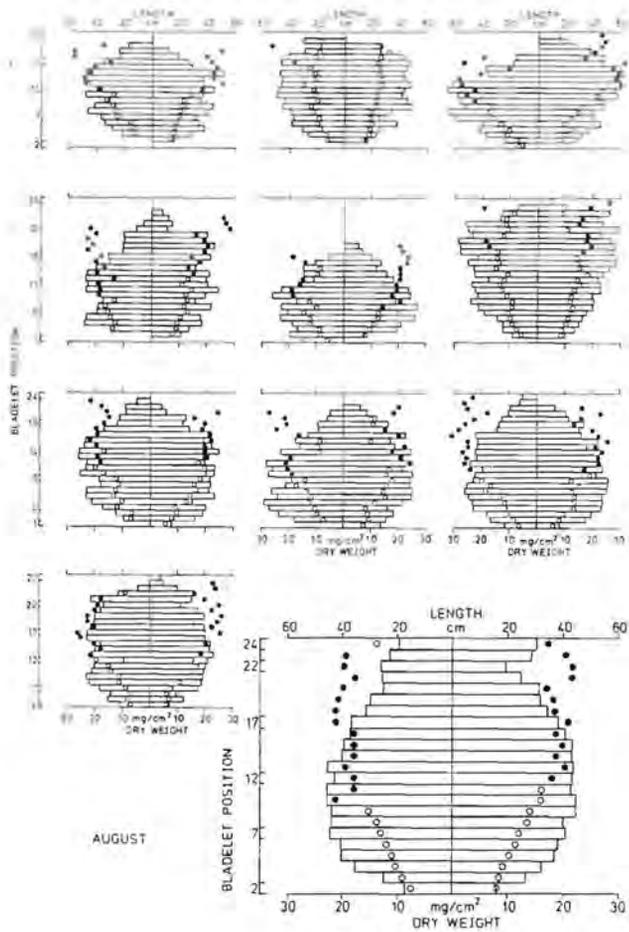


FIG. 4b.

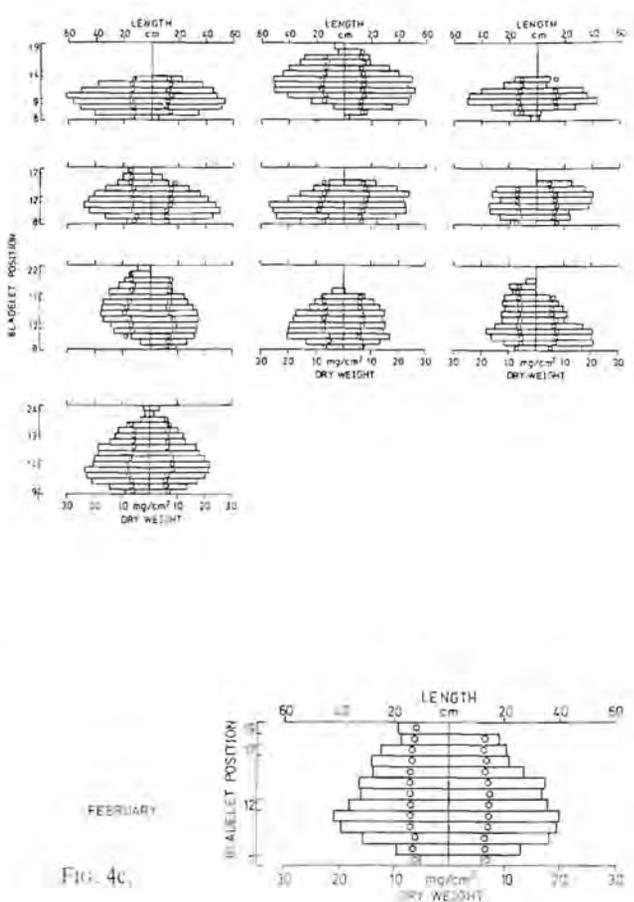
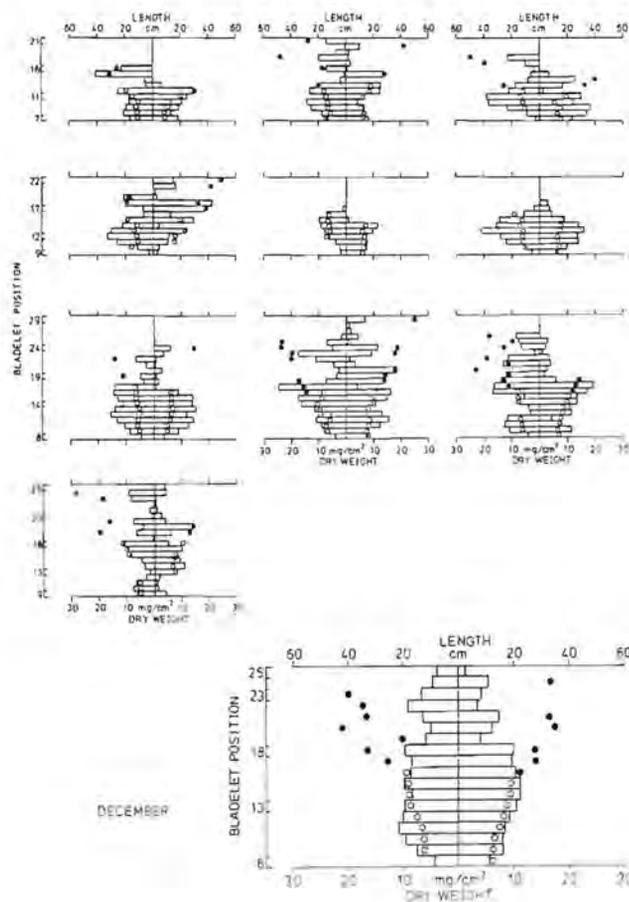


FIG. 4c.

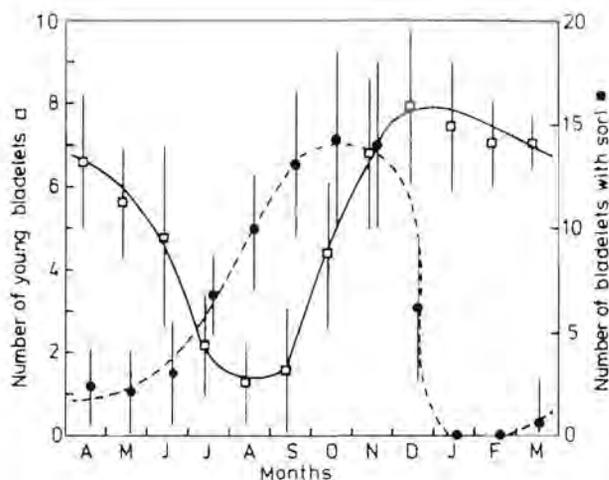


FIG. 5. — Seasonal changes of the number of young bladelets less than 10 cm and the number of bladelets with sori of *Ecklonia cava* in Nabeta Bay. Average of 10 samples and SD. April 1986 – March 1987.

and attained 50-60 cm long in spring. The elongation rate of the primary blade was very high, and it was possible to observe many thin and long primary blades moving by the surge force during the period.

3) Period of thickening of bladelets and development of sori. From late spring the bladelets gradually started to thicken and many of them, especially the distal ones, began to develop sori. At the same time, the primary blade became heavier. Although we encountered bladelets with sori as early as in March, the reproductive season of *E. cava* can be delineated from early summer to autumn. Before the general development of sori preceded some of them started to release zoospores as early as in June, and in August all the blades sampled were in a reproductive stage. Later, during the peak of the reproductive season sori on the upper bladelets were almost ex-

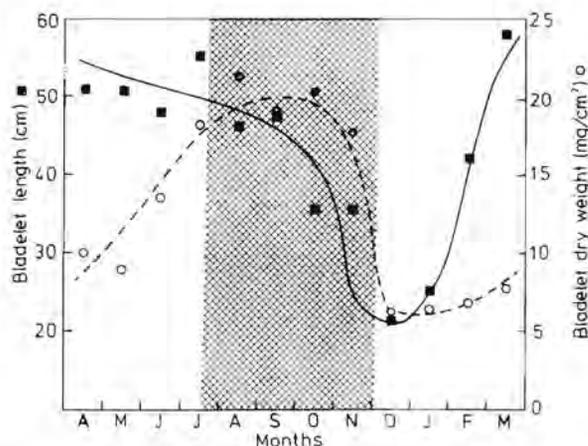
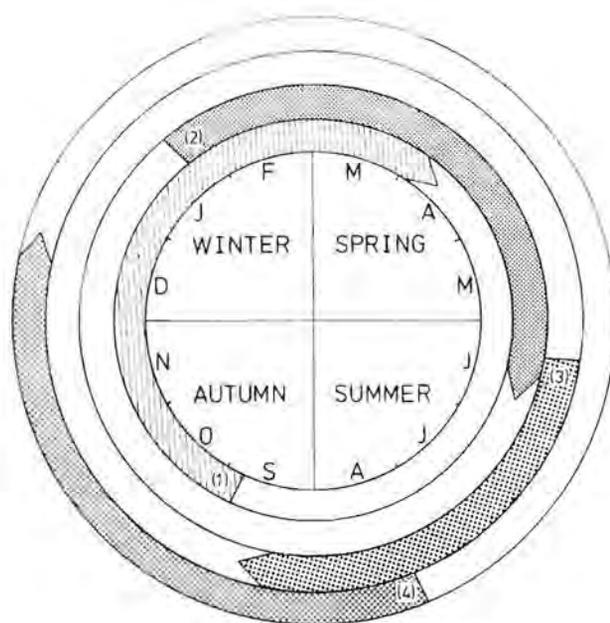


FIG. 6. — Seasonal changes of the bladelet length and dry weight for the longest bladelet in the average diagram (Fig. 4) of *Ecklonia cava* in Nabeta Bay. The shaded area represents the reproductive season. April 1986-March 1987.



- (1) Formation of new primary blade and bladelets
- (2) Growth of bladelets
- (3) Thickening of bladelets and development of sori
- (4) Decay of old bladelets

FIG. 7. — The annual growth cycle of a blade of the adult *Ecklonia cava* sporophyte in Nabeta Bay.

hausted, but those on the median and lower ones started to release zoospores.

4) Period of decay of old bladelets. When the reproductive season was over, the old bladelets with empty and bleached sori eroded and their length slowly decreased during the autumn months; the fate of these bladelets would have been to enter into the detrital food chains of the surrounding coastal areas. In the meantime the next season's primary blade was developing in the proximal part of the blade.

DISCUSSION

As in other Laminariales, the *Ecklonia cava* sporophyte exhibits a distinct seasonal growth cycle, with a reproductive period in late summer and a rapid growth phase in mid-winter. The same pattern of growth was observed by IWAHASHI (1968b) and HAYASHIDA (1984) in a deeper community of *E. cava*, with a little delay in the onset of vegetative growth. Moreover, the results of standing crop measurements by KIRKMAN (1984) suggest that the *E. radiata* sporophyte may well have the same type of blade growth process.

In *E. cava* the sporophyte stopped to grow in July, the number of young bladelets decreased to a

low value, and at that time the seawater temperature surpassed 22 °C, and then the reproductive activity reached a peak. The slowdown of the growth rate was inversely correlated with the reproductive activity, and this feature could be explained by diversion of the supply of photoassimilates from the growth processes to the development of sori as was pointed out by DIECKMANN (1980) and YOKOHAMA *et al.* (1987).

During the period of formation of new primary blade and bladelets it was possible to distinguish two different phases in *E. cava*: one is the phase of slow growth (October-December) and the other is that of rapid growth (January-April). A similar pattern was observed in *Laminaria saccharina* (L.) Lamour. (PARKE, 1948) and in *L. digitata* (Huds.) Lamour. (MANN, 1972). The shape of the bladelets in *E. cava* at each phase was different, with few lateral protuberances in the short autumn bladelets (maximum length, 22 cm) in contrast with the profusely branched, long winter bladelets (maximum length, 60 cm). Furthermore, in *E. cava* the sori never appeared in the autumn bladelets; there was a gap of 5-6 months between the onset of vegetative growth and that of the development of sori.

The slowdown of the growth rate during the summer months may well correlate with seawater temperature increase and/or nutrient supply. The triggering mechanism is still speculative and several hypotheses are being proposed. In *L. pallida* (Grev.) J. Ag. (DIECKMAN, 1980) it was found that the light factor played an important role in regulating growth rate, but in the literature other factors have been pointed out, such as temperature (SUNDENE, 1964; LÜNING, 1982; KIRKMAN, 1984), nutrient concentration (HATCHER *et al.*, 1977; CHAPMAN & CRAIGIE, 1977; GAGNE *et al.*, 1982), or canopy density (YOKOHAMA *et al.*, 1987). Probably the seasonal cycle of kelp is regulated by more than one factor (endogenous or environmental), each one affecting different phases of the growth cycle. CHAPMAN *et al.*, (1978) suggested that light conditions and nutrient supply may control the growth process of *Laminaria*.

Although we found some sori from March to December, the peak of reproduction activity was reached during August-October in *E. cava*. Both the sorus development and the frond weight of *E. cava* followed the same trends as KAIN (1975) reported for *L. hyperborea*. Another interesting feature is that the first sori appeared in the upper bladelets and then the maturation process moved downward, suggesting a possible meristematic inhibition or age-related control (PARKE, 1948; LÜNING, 1982). In mid-summer, when no young bladelets were growing, almost all the bladelets were in some reproductive stage.

As the life span of the *E. cava* sporophyte is of 5-7 years (HAYASHIDA, 1977) and the fronds become

adult in the 2nd or 3rd year, the above-described annual growth cycle of the blade of *E. cava* is probably repeated 2-4 times without any external disturbance. The blade growth of the *E. cava* sporophyte looks like the «conveyer belt» as mentioned by MANN (1973) with new tissues formed in the junction between blade and stipe which are lost by erosion or grazing in the distal ends. In late autumn large pieces of the blade broken off and the resulted organic matter would play an important role in the detrital food chain of the surrounding coastal waters. The blade of *E. cava* can be treated like a storage deposit of organic matter that is slowly liberated from the tips when grazed and in large quantities after the breakdown of old blades in late autumn.

REFERENCES

- ANONYMOUS, 1981-'86. Report of Coastal Observations. *Shimoda Mar. Res. Center Univ. Tsukuba*, 31-36: 1-7.
- ARUGA, Y. 1981. Physiological characteristics of *Eisenia bicyclis* and *Ecklonia cava*. *Report Marine Ranching Program 1980*: 29-34.
- CHAPMAN, A. R. O. & CRAIGIE, J. S. 1977. Seasonal growth in *Laminaria longicruris*: relations with dissolved inorganic nutrients and internal reserves of nitrogen. *Mar. Biol.*, 40: 197-205.
- CHAPMAN, A. R. O., MARKHAM, J. W. & LÜNING, K. 1978. Effects of nitrate concentration on the growth and physiology of *Laminaria saccharina* (Phaeophyta) in culture. *J. Phycol.*, 14: 195-198.
- DIECKMANN, G. S. 1980. Aspects of the ecology of *Laminaria pallida* (Grev.) J. Ag. off the Cape Peninsula (South Africa) I. Seasonal growth. *Bot. Mar.*, 23: 579-585.
- GAGNE, J. A., MANN, K. H. & CHAPMAN, A. R. O. 1982. Seasonal patterns of growth and storage in *Laminaria longicruris* in relation to different patterns of availability of nitrogen in the water. *Mar. Biol.*, 69: 91-101.
- HATCHER, B. G., CHAPMAN, A. R. O. & MANN, K. H. 1977. An annual carbon budget for the kelp *Laminaria longicruris*. *Mar. Biol.*, 44: 85-96.
- HAYASHIDA, F. 1977. On age and growth of a brown alga, *Ecklonia cava* Kjellman, forming aquatic forest. *Bull. Jap. Soc. Sci. Fish.*, 43: 1043-1051 (in Japanese with English summary).
- HAYASHIDA, F. 1984. Synecological studies of a brown alga, *Ecklonia cava* Kjellman, forming aquatic forest — II. On growth of *Ecklonia cava*. *J. Fac. Mar. Sci. Technol., Tokai Univ.*, 18: 275-280 (in Japanese with English summary).
- HAYASHIDA, F. 1986. Synecological studies of a brown alga, *Ecklonia cava* Kjellman, forming aquatic forest — III. Structure of *Ecklonia cava* population. *J. Fac. Mar. Sci. Technol., Tokai Univ.*, 22: 159-169 (in Japanese with English summary).
- IWAHASHI, Y. 1968a. Ecological studies on *Eisenia* and *Ecklonia* in the coast of Izu Peninsula — I. On the growth of *Ecklonia cava* Kjellman. *Bull. Shizuoka Pref. Fish. Exp. Sta.*, 1: 27-31 (in Japanese).
- IWAHASHI, Y. 1968b. Ecological studies on *Eisenia* and *Ecklonia* in the coast of Izu Peninsula — II. Seasonal variation of weight of *Ecklonia cava* Kjellman. *Bull. Shizuoka Pref. Fish. Exp. Sta.*, 1: 33-36 (in Japanese).
- IWAHASHI, Y., INABA, S., FUSHIMI, H., SASAKI, T. & OHSUGA, H. 1979. Ecological studies on *Eisenia* and *Ecklonia* in the coast of Izu Peninsula — IV. The distribution and characteristics of kelp stand. *Bull. Shizuoka Pref. Fish. Exp. Sta.*, 13: 75-82 (in Japanese).
- KAIN, J. M. 1975. The biology of *Laminaria hyperborea* VII. Reproduction of the sporophyte. *J. mar. biol. Ass. U. K.*, 55: 567-582.
- KAIN, J. M. 1979. A view of the genus *Laminaria*. *Oceanogr. Mar. Biol. Ann. Rev.*, 17: 101-161.
- KASAHARA, H. & OHNO, M. 1983. Physiological ecology of brown

- algae, *Ecklonia* on the coast of Tosa Bay, southern Japan. III. Growth and morphological change. *Rep. mar. biol. Inst. Kochi Univ.*, 5: 77-84 (in Japanese with English summary).
- KIDA, W. & MAEGAWA, M. 1982. Ecological studies on *Eisenia bicyclis* and *Ecklonia cava* communities. I. Distribution and composition of the community around the coast of Cape Goza, Shima Peninsula. *Rep. Fish. Res. Lab. Mie Univ.*, 3: 41-54 (in Japanese with English Summary).
- KIDA, W. & MAEGAWA, M. 1983. Ecological studies on *Eisenia bicyclis* and *Ecklonia cava* communities. II. Distribution and composition of the community in the coastal areas of Kumano-nada. *Bull. Fac. Fish. Mie Univ.*, 10: 57-69 (in Japanese with English summary).
- KIKUCHI, S. & UKI, N. 1981. Productivity of benthic grazers, abalone and sea urchin in *Laminaria* beds. In: *Seaweed Beds* (Jap. Soc. Sci. Fish., ed.): 9-23. Koseishakoseikaku, Tokyo (in Japanese).
- KIRKMAN, H. 1984. Standing stock and production of *Ecklonia radiata* (C. Ag.) J. Agardh. *J. Exp. Mar. Biol. Ecol.*, 76: 119-130.
- LEVING, T. 1977. Potential yields of marine algae — with emphasis on European species. In: *The Marine Plant Biomass of the Pacific Northwest Coast* (R. W. Krauss, ed.): 251-270. Oregon State Univ. Press, Oregon.
- LUNING, K. 1982. Seasonality in large brown algae and its possible regulation by the environment. In: *Synthetic and Degradative Processes in Marine Macrophytes*, (L. M. Srivastava, ed.): 47-67. De Gruyter, Berlin.
- MAEGAWA, M. & KIDA, W. 1984. Ecological studies on *Eisenia bicyclis* and *Ecklonia cava* communities. IV. Seasonal change in allometric relation of *Ecklonia* frond. *Bull. Fac. Fish. Mie Univ.*, 11: 199-206 (in Japanese with English summary).
- MAEGAWA, M., YOKOHAMA, Y. & ARUGA, Y. 1987. Critical light conditions for young *Ecklonia cava* and *Eisenia bicyclis* with reference to photosynthesis. *Hydrobiologia*, 151-152: 447-455.
- MANN, K. H. 1972. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. II. Productivity of the seaweeds. *Mar. Biol.*, 14: 199-209.
- MANN, K. H. 1973. Seaweeds: their productivity and strategy for growth. *Science*, 182: 975-981.
- MANN, K. H. 1982. *Ecology of Coastal Waters: A Systems Approach*. Blackwell, Oxford.
- MICHANEK, G. 1975. Seaweed Resources of the Ocean. *FAO Fish. Techn. Paper*, 138. FAO, Rome.
- MIGITA, S. 1984. Intergeneric and interspecific hybridization between four species of *Eisenia* and *Ecklonia*. *Bull. Fac. Fish. Nagasaki Univ.*, 56: 15-20.
- NORTH, W. J. 1971. The Biology of Giant Kelp (*Macrocystis*) in California. *Beth. Nova Hedwigia*, 32: 1-600.
- OHNO, M. 1985. Marine forests — ecology and technological construction. *Marine Science Monthly*, 17: 706-713 (in Japanese).
- OHNO, M. & ISHIIKAWA, M. 1982. Physiological ecology of brown alga, *Ecklonia* on coast of Tosa Bay, southern Japan. I. Seasonal variation of *Ecklonia* bed. *Rep. Usa mar. biol. Inst.*, (4): 59-73 (in Japanese with English summary).
- PARKE, M. 1948. Studies on British Laminariaceae. I. Growth in *Laminaria saccharina* (L.) Lamour. *J. mar. biol. Assoc. U. K.*, 27: 651-709.
- SCHMITZ, K. 1981. Translocation. In: *The Biology of Seaweeds* (C. S. Lobban & M. J. Wynne, eds.): 534-558. Blackwell, Oxford.
- SUNDENE, O. 1964. The ecology of *Laminaria digitata* in Norway in view of transplant experiments. *Nytt Mag. Bot.*, 11: 83-107.
- TSENG, C. K. 1981. Commercial cultivation. In: *The Biology of Seaweeds*, (C. S. Lobban & M. J. Wynne, eds.): 680-725. Blackwell, Oxford.
- WARNER, G. F. 1984. *Diving and Marine Biology. The Ecology of Sublittoral*. Cambridge Univ. Press, Cambridge.
- WHEELER, A. 1980. Fish-algal relations in temperate waters. In: *The Shore Environment. 2: Ecosystems* (J. H. Price, D. E. G. Farnham, & W. F. Irvine, eds.): 677-698. Academic Press, London.
- YOKOHAMA, Y. 1977. Productivity of seaweeds. In: *Productivity of Biocenoses in Coastal Regions of Japan* (K. Hogetsu et al., eds.): 119-127. Univ. Tokyo Press, Tokyo.
- YOKOHAMA, Y., TANAKA, J. & CHIHARA, M. 1987. Productivity of the *Ecklonia cava* community in a bay of Izu Peninsula on the Pacific coast of Japan. *Bot. Mag. Tokyo*, 100: 129-141.