

A demographic study of the sublittoral brown alga *Ecklonia cava* KJELLMAN in coastal water of Shima Peninsula, Japan

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The demography of *Ecklonia cava* was studied in 2 quadrats (1 m × 3 m) from 1982 to 1986 in the sublittoral zone off Hamajima, Shima Peninsula, central Japan. A total of 874 plants were marked in 2 quadrats for five years. The Weibull frequency distribution was used to analyze the factors controlling the mortality from the survivor curve. At the young stage during the first 24 months, intraspecific competition for getting the required light was the main factor. 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 mean life span of *Ec. cava* was 16.5 months and the maximum life expectancy of 21.1 months was obtained at 6th month after recruiting. The maximum life span was more than 5 years but less than 6 years.

Key Index Words: demography—*Ecklonia cava*—life table—mortality—survivor rate.

The brown alga *Ecklonia cava* KJELLMAN has a wide distribution along the Pacific coast of central Japan, and is an important alga both ecologically and economically. Wherever water condition and substratum are suitable in a coastal region facing open sea, it forms a dense and expansive marine forest in the sublittoral zone as does *Eisenia bicyclis* SETCHELL, the latter occupying shallower water than the former. *Ec. cava* is perennial and has potential to live at least 5 years (HAYASHIDA 1977), and therefore population density of this species depends to some extent on the number of recruitments and loss in a growing site. It is commercially and ecologically interesting to study the population dynamics of reproduction, recruitment and mortality of the algae, as CHAPMAN (1979) has stressed the need for such works in his review of seaweed biology. Demographic studies lead to a greater

understanding of population biology and production ecology. Recently, several demographic studies for algae, including life table analysis, were reported from an ecological point of view, e.g., GUNNILL (1980) for *Pelvetia fastigiata*, CHAPMAN and GOUDEY (1983) for *Leathesia difformis*, COYER and ZAUGG-HAGLUND (1982) for *Pelagophycus porra*, and CHAPMAN (1986) for *Laminaria longicruris*.

In a previous paper (KIDA and MAEGAWA 1985) we found the characteristic annual changes in the population density and the age distribution of *Ec. cava*. The density of canopy fronds controls the light condition in the community. Particularly, the light condition on the community floor is the most important factor for young plants to survive and grow to the adult stage (HAYASHIDA 1986, MAEGAWA and KIDA 1987, MAEGAWA *et al.* 1987, 1988).

The present study was undertaken to

determine the regeneration process of the population utilizing demographic method. We investigated the changes in the population density, size frequency distribution, mortality rate and loss in the permanent quadrats for five years. By analyzing these data, it was possible to know the factors controlling recruitment and mortality of *Ec. cava*.

Materials and Methods

The study site was located off Hamajima, Shima Peninsula, central Japan, where the sublittoral substratum mainly consists of rocks suitable for kelp communities. *Ecklonia cava* and *Eisenia bicyclis* are the major components of sublittoral vegetation comprising the dense, expansive marine forest (KIDA and MAEGAWA 1982, 1983). *Ec. cava* usually grows in water deeper than 3–5 m through 25 m, and *Ei. bicyclis* occupies shallow water down to 5 m in the sublittoral zone. In May 1982, 2 quadrats of 1 m × 3 m constructed with ropes were set on the flat rock within the population at a depth of 8 m. All individuals of *Ec. cava* in the quadrats were marked by tagging sequentially numbered plastic plates (1 cm × 2 cm) around the holdfasts of adult plants, or by 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 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 fifteen times at two- or three-month intervals from 1982 to 1984, and at six-month intervals from 1984 to 1986. A total of 874 plants were marked in 2 quadrats for 5 years. Such numerous data enabled us to conduct a comprehensive study of demography.

Survival data of the recruits were ana-

lyzed by the method of "survivorship directly observed" as described in DEEVEY (1947) in which the survivor rate can be computed directly from the survivor 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 last seen and the date when its disappearance was confirmed. At the beginning of the observation in June 1982, the kelp population was composed of plants of various ages. Each age group was separated according to the range of stipe length by the allometric relationship (MAEGAWA and KIDA 1984). Since almost all of the recruits of *Ec. cava* could be visible in Morch, 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 (1980) employed.

For analyzing factors on recruitment success and mortality of *Ec. cava*, the "Weibull frequency distribution" was employed as a model of survivor curve (PINDER *et al.* 1978). The Weibull equation represents extremely flexible distribution which can possess either positive or negative skewness usually observed in various types of survivor curves for animals (PINDER *et al.* 1978). COUSENS (1985) used the Weibull frequency distribution to analyze survivorship in *Ascophyllum nodosum*. A similar concept could be applied to the demography of *Ec. cava* in the present study

Results

Fig. 1 shows the changes in frequency distribution of the stipe length of *Ec. cava* in two quadrats obtained in June each year from 1982 to 1986. In 1982 large fronds with stipe length longer than 20 cm occupied greater parts, but in 1983 most of the large fronds in canopy disappeared and many recruits were produced. In

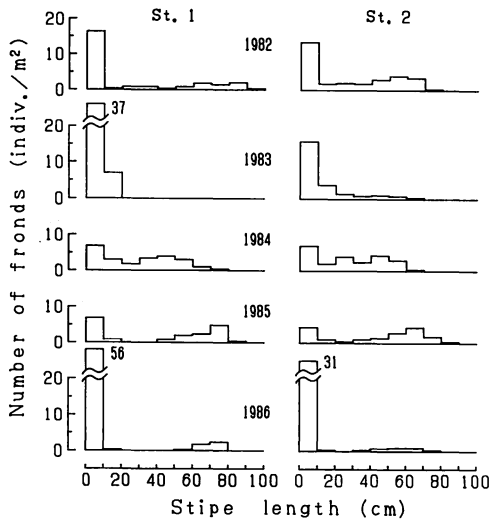


Fig. 1. Changes in frequency distribution of the stipe length of *Ecklonia cava* in 2 quadrats obtained in June of each year from 1982 to 1986.

1984 and 1985 large fronds which were developed from the recruits of 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 and showed a similar frequency distribution as in 1983. Thus, the number of recruits was controlled by the density of large fronds. After most of the large canopy fronds disappeared or drifted out, many recruits were produced and grew to form a canopy one and two years later.

Since the changes in frequency distribution of stipe length and density at St. 1 and St. 2 showed a similar tendency, the average survivor rates were computed in both quadrats as shown in Fig. 2. The survivor data for 1000 recruits were expressed both on a linear scale and on a logarithmic scale. The number of recruits greatly decreased during the first year, early in the lifetime, and then 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 5 to 6 years. The mortality rate, expressed by the inclination of the line on a logarithmic

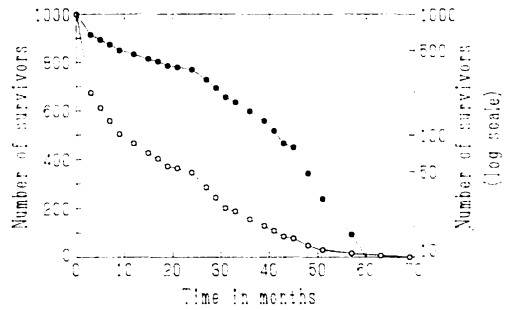


Fig. 2. Survivor curves of *Ecklonia cava* for 1000 individuals. Data were expressed both on a linear scale (open circles) and on logarithmic scale (solid circles).

mic scale, was low during the first two years except the rate during 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*, and it was not possible to extrapolate the rate to the exponential equation as done by CHAPMAN (1986), the log-log equation as done by GUNNILL (1980) or the Gompertz equation as done by CHAPMAN and GOUDEY (1983). Therefore, in the present study the Weibull equation was employed 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 time, n is the scale parameter and m is the shape parameter. The degree of skewness in the survivor curve is determined by m , and the mean life span is determined by both m and n . When $m > 1$, the mortality rate increases with age. When $m = 1$, this equation shows that the mortality rate is constant, and it conforms to the exponential distribution. When $m < 1$, the mortality rate decreases with age. These three cases correspond to Type I, Type II and Type III survivor curves of DEEVEY (1947), respectively. For calculating the regression line the Weibull equation was transformed as follows:

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

The relation between $\ln \ln(I/l_x)$ and $\ln(t)$ is linear, as the result the survivor data could be fitted to the Weibull frequency distribution by the least squares method.

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

Life table of *Ec. cava* is shown in Table 1. The number of survivors (l_x) for a 3-month interval was calculated from 3

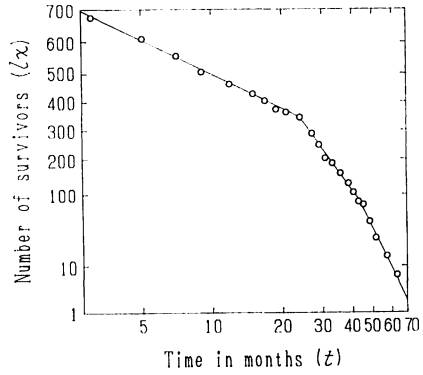


Fig. 3. The Weibull frequency distribution fitted to the survivor data of *Ecklonia cava*.

0-24 months; $l_x = 1000 \exp-(t/20.3)^{0.488}$

24-42 months; $l_x = 1000 \exp-(t/22.7)^{1.376}$

42-69 months; $l_x = 1000 \exp-(t/27.5)^{1.976}$

Table 1. Life table of *Ecklonia cava*. Abbreviations are as follows; t , age in months; l_x , the number of survivors at age t ; d_x , the number of individuals disappeared during each interval; $1000q_x$, the number of individuals disappeared for 1000 individuals alive at age t ; L_x , the number of individuals alive between age t and age $t+3$; T_x , sum of months of the remaining life of the individuals at age t ; e_x , the mean life expectancy (months) for those at age t . Data of l_x from 0-66 months were calculated by the 3 Weibull equations in Fig. 3.

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

Weibull equations as shown in Fig. 3. No individuals could have been alive for 69 months in the surveyed quadrats, consequently l_x at the 69th month was 0. The mean life span of the cohort or the mean life expectancy (e_x), when $t=0$, was 16.5 months, and the maximum value of the mean life expectancy (e_x) was 21.1 months when $t=6$ months. The maximum life span of *Ec. cava* was 5 years or more, but did not reach 6 years. The value of relative mortality rate for 1000 individuals ($1000 q_x$) decreased during the first 2 years, then it increased gradually, as expected in the Weibull frequency distribution in Fig. 3.

Discussion

Within an *Ec. cava* population there was dynamic equilibrium in the density and population structure (KIDA and MAEGAWA 1985), which changed at intervals of three years (Fig. 1). The density of recruits was controlled through the density of adult fronds forming a kelp canopy (BLACK 1974, HAY and SOUTH 1979, KIRKMAN 1982, SANTELICES *et al.* 1980). The light intensity on the population floor which was determined through the density of adult fronds, was the most important factor for young *Ec. cava* to grow (HAYASHIDA 1986, MAEGAWA *et al.* 1987, 1988). When there were a few or no canopy fronds many recruits occupied the substratum, similar to the report by IWAHASHI (1971). However, only one third of them survived after 2 years. In particular, the first 3 months comprised the most critical period for the juveniles, showing very high mortality (Fig. 2). A similar tendency was also found by COYER and ZAUGG-HAGLUND (1982) in the case of *Pelagophycus porra* and by ROSENTHAL *et al.* (1974) in *Macrocystis pyrifera*.

In the life table analysis of seaweed populations several equations have been used to calculate the number of survivors for the selected time intervals throughout the lifetime, e.g., the exponential equation (CHAPMAN 1986), the log-log equation (GUNNILL

1980) and the Gompertz equation (CHAPMAN and GOUDEY 1983). In the present study the changes of mortality rate exhibited no uniformity within the lifetime of *Ec. cava*, as a result the survivor data were fitted for the 3 Weibull equations for 3 periods, during the first 24 months, from the 24th to the 42nd month and from the 42nd to the 69th month, respectively. This indicates that the main factor controlling the mortality rate of *Ec. cava* varied in different periods in the lifetime. For the demographic study, the parameter m in Weibull frequency distribution is very useful in determining 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 (PINDER *et al.* 1978), i.e., the values of mortality rate decrease gradually as the values of age increase. In the young stage of *Ec. cava* ($m = 0.488$ in the present study), the factor controlling the mortality rate is the intraspecific competition exhibited by the self-shading for getting light. During the period from late winter to spring when juveniles of *Ec. cava* germinated, the blade biomass of canopy fronds showed a lower peak (YOKOHAMA 1984), then the juveniles could receive enough light to grow. Thereafter, the blade biomass increased to maximum in summer. In a fully grown population of *Ec. cava* in summer, the light condition on the population floor decreased to only 1% or less, of light intensity on the water surface, and the critical light condition of young *Ec. cava* fronds was 0.6% (MAEGAWA *et al.* 1987). It is therefore apparent that light was the limiting factor for young *Ec. cava* plants to survive and grow. Another factor might have been the large plants sweeping over the substratum or characteristics of the substratum upon which the young plants were attached (COYER and ZAUGG-HAGLUND 1982).

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 24th to the 42nd

month in the lifetime of *Ec. cava*. It was thought that the loss of adult fronds in this period was caused by wave action. *Ec. cava* fronds grew to adulthood and reached the canopy layer within 2 years. Wave action influenced large canopy fronds more significantly than the young fronds within a population. When $m > 1$, the mortality rate is an increasing function of age (PINDER *et al.* 1979), i.e., the value of mortality rate increases gradually as the value of age increases. During the last period from the 42nd to the 69th month ($m = 1.976$ in this study), loss 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 (1982). Survivor curves of *Pelagophycus 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, the survivor curve does not show a smooth line but shows remarkable changes in skewness (cf. Fig. 2).

In the demographic study of *Laminaria longicuris*, CHAPMAN (1986) 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 (1947). However, paying attention to the figure showing the distribution of survivor data of *L. longicuris*, it appears that the mortality rate varied with age, similar to our studies of *Ec. cava*. In the life table analysis of *L. longicuris* by CHAPMAN (1986), there is underestimation of mean life expectancy (e_x) due to miscalculation of T_x column. The same sort of miscalculation is also found in CHAPMAN (1979) for *Macro-*

cystis pyrifer based on the data of ROSENTHAL *et al.* (1974). In the life table of *Pelvetia fastigiata* in GUNNILL (1980) mean life expectancy (e_x) was represented by the survival of 50% of the individuals existed at the start of each interval. This is another concept of e_x used in demographic studies.

In the present study the census of *Ec. cava* was taken using 1–3 cm long recruits. However, extremely high mortality of this species occurred before plants reached this size as mentioned in other kelp species (KAIN 1975, CHAPMAN 1984). The major determinant of the mortality at this stage has not been identified in the present study. More advanced techniques and equipments usable in water and in laboratory will enable us to do more comprehensive studies in demography of algae.

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前川行幸*・喜田和四郎*・有賀祐勝**：三重県志摩半島沿岸におけるカジメ（褐藻）の生命表解析

漸深帯に大規模な海中林を形成する大型褐藻カジメ (*Ecklonia cava*) の生存曲線及び生命表について研究を行った。三重県志摩半島浜島沖に2つの永久コドラート (1 m×3 m) を設置し、1982年から1986年までの約5年間に出現した874個体の発生及び死亡のデータを用いて解析を行なった。生存曲線から死亡要因を推定するため、ワイブル関数を用いた。発芽後24ヶ月目までの幼体期の主な死亡要因は、種内競争によるものであった。24ヶ月目から42ヶ月目までの大型個体が林冠を形成する時期は、波浪などの物理的要因が主な死亡要因であった。42ヶ月以降は、寿命が主な死亡要因であった。カジメの生命表から、平均寿命（発芽直後の平均余命）は16.5ヶ月であり、発芽6ヶ月後に最大の平均余命21.1ヶ月を示した。また、カジメの最大寿命は約5年であり、6年に達する個体はみられなかった。（*514 三重県津市江戸橋2-80 三重大学生物資源学部藻類増殖学研究室，**108 東京都港区港南4-5-7 東京水産大学藻類学研究室）