

JEM 235

## STANDING STOCK AND PRODUCTION OF *ECKLONIA RADIATA* (C.Ag.)

J. Agardh

HUGH KIRKMAN

*CSIRO Division of Fisheries Research, P.O. Box 20, North Beach, W.A. 6020, Australia*

**Abstract:** The monthly productivity, standing stock, plant size and density of *Ecklonia radiata* (C.Ag.) J. Agardh is presented for a 2-yr period. Annual production was  $20.7 \text{ kg wet wt} \cdot \text{m}^{-2}$  with maximum growth of 0.9% per day in spring (October–December) and minimum growth of 0.2% per day in late summer (March–April). A close negative correlation was found between spring and summer growth and water temperature. Maximum biomass ( $18 \text{ kg wet wt} \cdot \text{m}^{-2}$ ) did not coincide with maximum growth but occurred in late summer. Minimum biomass ( $6 \text{ kg wet wt} \cdot \text{m}^{-2}$ ) occurred in winter. An estimate of erosion of plant material from the kelp bed was made from these data and a hypothesis concerning the ultimate destination of eroded and removed kelp plants was formulated.

### INTRODUCTION

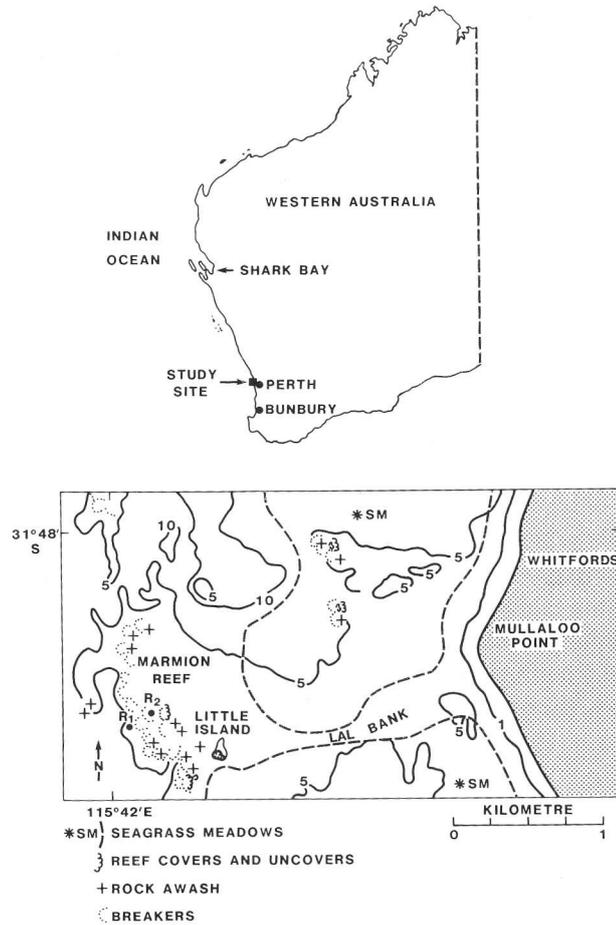
Even though *Ecklonia radiata* (C.Ag.) J. Agardh is the dominant algal species (cover and biomass) in the subtidal reefs of most of southern Australia (Kirkman, 1981; Womersley, 1981) little is known of its seasonal changes in biomass or productivity. The first year in the life history of *E. radiata* has been described by Kirkman (1981) who also mentioned some of the physical conditions which are prevalent on these limestone reefs. *Ecklonia* is an important component of the detrital food web (Edmonds & Francesconi, 1981a; Robertson & Lucas, 1983).

In other parts of the world kelps (Laminariales) have received considerable attention because of their large biomass (North, 1957; Kain, 1977; Levring, 1977), their commercial use, and their importance to fisheries as nursery areas or habitats for lobsters or abalone. Apart from ecological research considerations, it is necessary to know biomass and productivity for potential use in mariculture.

To understand what happens to kelp plants as they grow, die and decompose it is necessary to know the plant's biology, seasonal biomass, and productivity. Generally the plant erodes from the distal ends of secondary lateral blades. Direct grazing is rarely seen in *E. radiata* on Western Australian reefs. In large storms plants may be torn and large pieces broken off. Particulate matter from *E. radiata* may be used as a food source for bacteria (Edmonds & Francesconi, 1981b), small crustaceans, fish, and molluscs or it may be broken down physically (Robertson & Hansen, 1982). Some of this organic matter may be carried along by waves and currents to wash up eventually on the shore or be carried westward to the deep sea where it settles in troughs or trenches. In other parts of the world, Wolff (1976) has found some sea grasses in abyssal depths. Evidence

of kelp and other brown and green algae in the deep sea has been recorded; Mortensen (1938), Okutani (1969), Schoener & Rowe (1970), and Wolff (1962) found pieces of seaweed in deep-sea animals. The particulate matter which is carried onshore is broken down by wave and sand action. Large pieces of plant material may remain in the surf zone for some days (pers. obs.) or they may be thrown to dry further up the beach. The ultimate fate of these pieces of *E. radiata* depends on whether they are covered by sand and detritus and broken down anaerobically or left to rot slowly in air. After break down the organic matter is remineralized into nutrients available to plants.

The objectives of the present study were to determine monthly productivity, density, and biomass of *E. radiata*.



## MATERIAL AND METHODS

## AREA STUDIED

This study was carried out at Marmion Reef, Whitfords on the southwestern coast of Western Australia  $\approx 20$  km north of Perth (Fig. 1). *E. radiata* grows on the limestone reefs of Western Australia from a depth of 1.5 to 30 m. At Whitfords, *E. radiata* grows at depths of 1.5 to 21 m. The sites studied at Whitfords were chosen to represent the most common topographical features and physical conditions of the reef at 2 to 7 m depth. Site R<sub>1</sub> (Fig. 1) is on the outer reef and receives direct swell and waves; Site R<sub>2</sub>, 50 m inshore, is protected from direct impact of waves and swell by the reef. Site R<sub>1</sub> has a rugged topography with many caves, crevices, and rocky outcrops, whereas Site R<sub>2</sub> has a relatively smooth surface and less vertical relief. At both sites *E. radiata* forms continuous beds which in summer completely cover the substratum (Fig. 2).



Fig. 2. *Ecklonia radiata* bed at site studied.

*E. RADIATA* STANDING STOCK MEASUREMENTS

Standing stock is the biomass of plant material per square metre at any time. Simplified drawings of the three developmental stages of *E. radiata* plants are given in Fig. 3 and the approximate size ranges of the three stages in Table I. Stage 1 represents early sporophyte plants; their blades are entire and of oblong to linear shape. Stage 2

TABLE I

Length of primary blade and biomass per unit length, in each of the three growth stages of *Ecklonia radiata*: growth stages are defined in the text and in Fig. 2.

Stage of development	<i>n</i>	Length range (cm)	Biomass per unit length (g/cm), mean $\pm$ SD
1	21	6.5-27	0.3 $\pm$ 0.15
2	23	19-34	0.8 $\pm$ 0.47
3	38	30-90	14.9 $\pm$ 5.4

plants show protuberances on the blade just above the stipe and secondary blades are simple and entire. Stage 3 plants have compound lateral blades emanating from the central lamina. The most usual form is the Stage 3 plant. The stipe is short, usually < 10 cm long, and there is a central lamina with secondary laterals of complex shapes. The plant is attached to the reef by a holdfast consisting of many haptera.

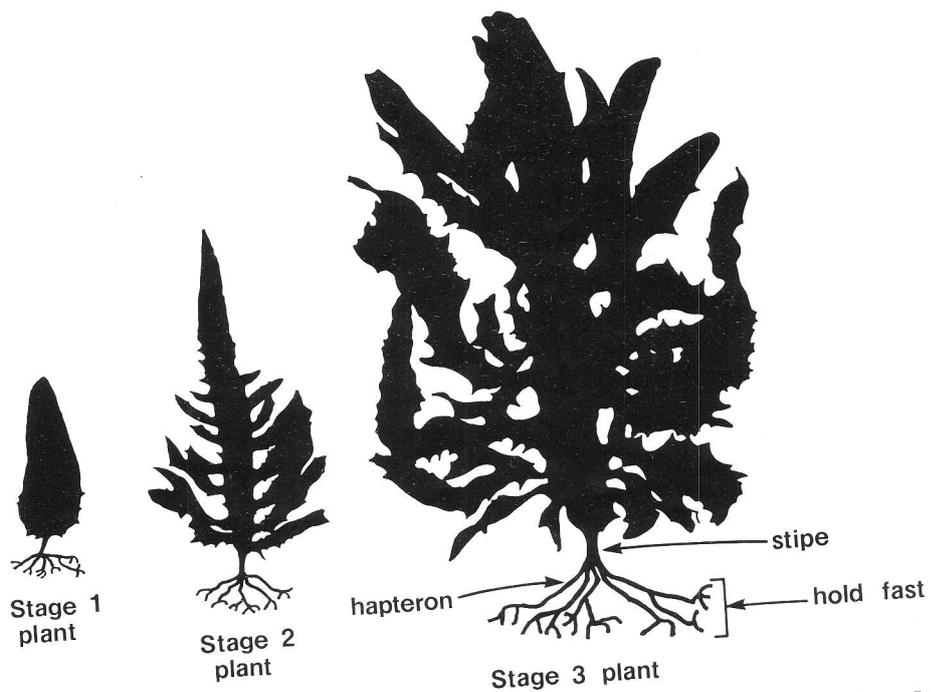


Fig. 3. Diagram of three stages of *E. radiata*, not to scale: Stage 1, 6.5-27 cm; Stage 2, 19-34 cm; Stage 3, 30-90 cm in length.

Sampling was carried out in *E. radiata* beds. Uncovered patches of sand or areas where the shape of the reef excluded large plants were avoided when sampling, so no

measurement of patchiness was made. Samples of *E. radiata* were taken once every 2 months from March 1979 until November 1979 and then monthly until April 1981. Sampling frequency from November 1979 was increased because significant differences in biomass were seen between each 2-month interval, and the standard errors of the mean were small enough to detect monthly differences (Fig. 4). Sixteen randomly

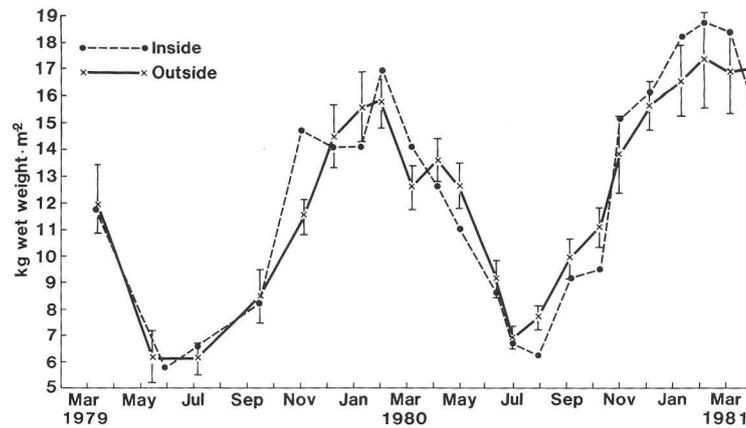


Fig. 4. Biomass at R<sub>1</sub> (×) and R<sub>2</sub> (●), separately: bars are 1 SE about the mean and have been included only for R<sub>1</sub>; R<sub>2</sub> error bars are similar.

located 0.25-m<sup>2</sup> quadrats were sampled each time at each of the sites. The square quadrats of 0.5-m sides consisted of three sides made from 10-mm diameter steel rod and an open side which allowed the quadrat to be pushed in amongst the stipes. To ensure that the quadrats were placed at random each diver carried a card on which eight directions and numbers up to 20, were recorded. For each of the directions the diver swam the corresponding number of strokes and dropped the quadrat. If a quadrat landed on a bare patch or on the edge of the *E. radiata* bed it was moved to the nearest continuous *E. radiata* cover. Each month the boat was anchored in a different place so that the same random number card could be used. Once the quadrat was in place each plant in the quadrat was cut just above the holdfast and the plant bagged. The 32 samples were returned to the laboratory, weighed and plants sorted into one of the three developmental stages.

#### PRODUCTIVITY MEASUREMENT

Productivity is defined here as the rate at which new organic matter is created by photosynthesis. The method described by Mann & Kirkman (1981) was used to measure monthly production for 2 yr.

Each month the laminae of 60 *E. radiata* plants had a hole punched 10 cm above the top of the stipe and were labelled. After  $\approx$  1 month the labelled plants were harvested

and returned to the laboratory. The distance that the punched hole had moved in the lamina during the month was measured and converted to a biomass (Mann & Kirkman, 1981). Only Stage 3 plants heavier than 150 g wet wt were used in productivity calculations because the method of Mann & Kirkman (1981) was suitable only for these. Recovery rate was always better than 80% but plants that were badly torn or in growth Stages 1 and 2 were not used in productivity measurements. Individual stipe length, plant weight and total length were recorded for each plant.

#### TEMPERATURE MEASUREMENTS

From June 1979, temperature readings were taken at the reef study site using a Hamon temperature-salinity bridge (Autolab). After July 1980 temperature readings were made with a thermometer at least once a week. In the initial stages both bottom and surface waters were sampled, but since results showed complete vertical mixing, bottom sampling was discontinued.

### RESULTS

#### *E. RADIATA* STANDING STOCK MEASUREMENT

The standing stock of *E. radiata* at different times of year showed little difference between the protected area of reef ( $R_2$ ) and the outside area ( $R_1$ ) open to ocean swells (Fig. 4). Biomass was greatest in January and February for the two years of the study and least from June to September. Seasonal changes of individual plant weight and total biomass showed similar patterns (Figs. 4 and 5). Early winter storms broke off ends of the blades and reduced individual plant weight.

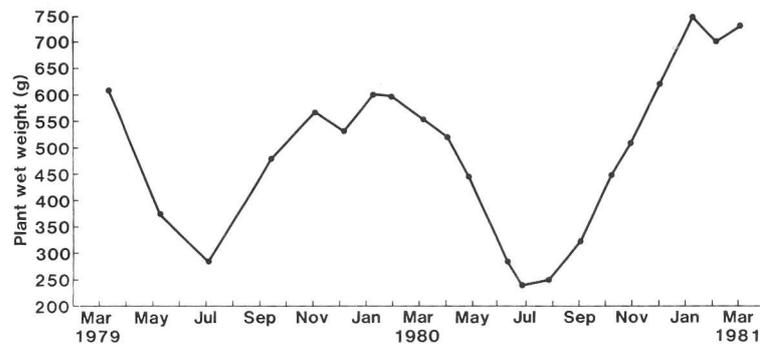


Fig. 5. Mean individual plant weight calculated from biomass collection at  $R_1$  and  $R_2$ .

## POPULATION DENSITY

Mean population density of Stage 3 plants showed a slight but significant increase during the first year of the study but remained relatively constant during the next year (Fig. 6). There may be a slight seasonal decline to autumn (March–May) each year but the sampling method was not precise enough to define this clearly. The small increase in plant numbers in the first year was reflected in an increase in standing stock between the summer (November–March) of 1979–1980 and the summer of 1980–1981 (Fig. 4).

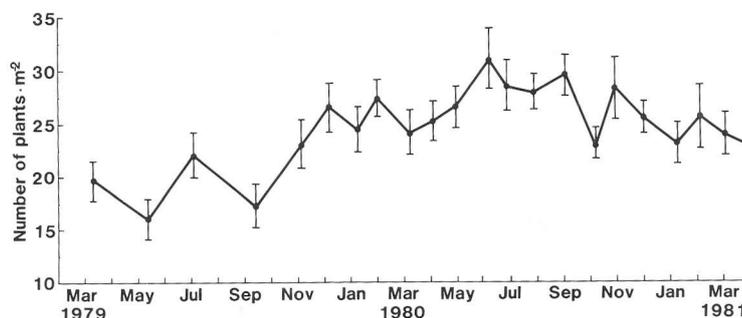


Fig. 6. Mean number of plants · m<sup>-2</sup> for Stage 3 plants: bars are 1 SE about the mean.

Schiel & Choat (1980) found a positive correlation between the biomass per square metre and plant density and between dry weight and plant density. In this paper I have used the term "per cent variation accounted for". It is defined as  $100(\text{total MS} - \text{residual MS})/(\text{total MS})$ , where MS is the mean sum of squares of deviations from the model. It is thus a similar measure to  $r^2$  (the coefficient of determination or squared correlation coefficient) which uses sum of squares instead of MS in the above formula. The per cent variation of density accounted for by total yield (wet wt per m<sup>2</sup>) and the per cent variation of density accounted for by mean plant weight varied between months (Table II).

Yoda *et al.* (1963) demonstrated, in an almost monospecific natural population, that self-thinning takes place when the log plant weight/log density approximates a slope of  $-1.5$ , this is called the  $-3/2$  thinning law and has been demonstrated in seaweeds by Cousens & Hutchings (1983). The *E. radiata* stands at Whitfords did not show this relationship and the per cent variation of log density accounted for by log plant weight varied each month (Table II).

TABLE II

Percentage accounted for by density and yield ( $\text{wet wt} \cdot \text{m}^{-2}$ ), density and plant weight, and for log plant weight and log density for plants harvested each month.

Date	Wet wt $\cdot \text{m}^{-2}$ vs. density (%)	Weight of plant vs. density (%)	Log weight of plant vs. log density (%)
9 Mar. 1979	66.7	9.6	12.8
11 May 1979	26.5	6.4	1.0
2 July 1979	35.0	19.6	21.7
13 Sept. 1979	62.6	3.2	1.7
2 Nov. 1979	45.6	34.0	38.9
5 Dec. 1979	46.6	15.0	10.0
7 Jan. 1980	51.4	4.6	2.8
31 Jan. 1980	48.4	None	None
5 Mar. 1980	57.3	23.6	22.0
2 April 1980	26.8	10.9	9.9
29 April 1980	32.0	31.1	34.7
9 June 1980	56.1	25.7	28.4
28 June 1980	48.3	65.2	65.1
29 July 1980	30.4	9.6	8.7
7 Oct. 1980	48.1	15.8	15.7
30 Oct. 1980	61.2	34.0	33.9
2 Dec. 1980	43.8	15.4	14.6
10 Jan. 1981	53.4	24.3	20.7
5 Feb. 1981	76.0	7.3	6.6
4 Mar. 1981	79.2	None	None
28 Mar. 1981	50.1	19.0	22.5

#### E. *RADIATA* PRODUCTIVITY

Growth of *E. radiata* showed distinct seasonal variation with a maximum in spring (October–December) then declining rapidly to a minimum during January through March. Summer growth was inversely related to water temperature ( $r = -0.971$ ). Growth slowed rapidly as temperature rose above  $18.5^\circ\text{C}$ . For the whole year, however,

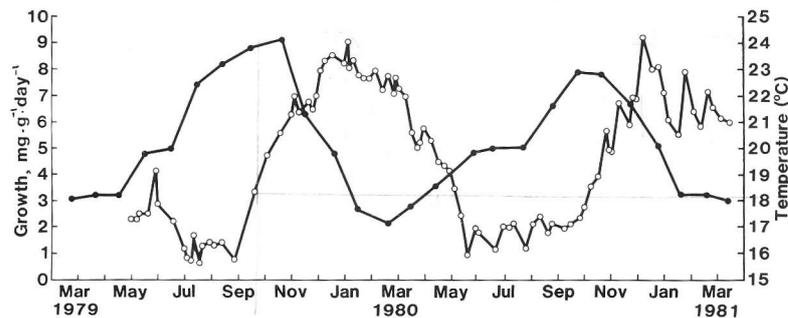


Fig. 7. Growth of Stage 3 plants (●) and water temperature (○) at Marmion Reef.

growth and temperature were not significantly correlated ( $r = -0.55$ ) (Fig. 7). Productivity also showed marked seasonal variation with more than a five-fold increase in summer compared with winter (Fig. 8).

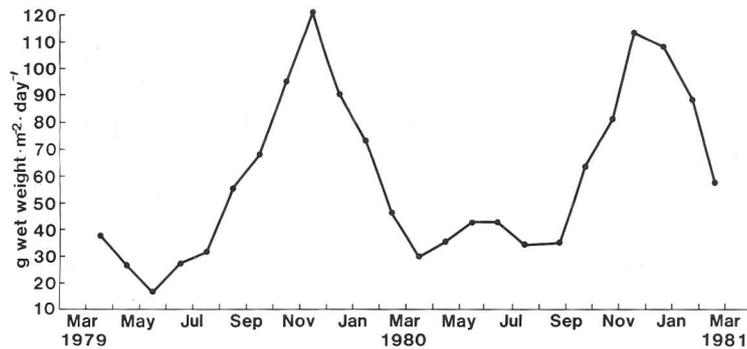


Fig. 8. Productivity · m<sup>-2</sup> · day<sup>-1</sup> of *E. radiata* plants at Marmion Reef: SE bars are too small to show.

#### ESTIMATED DETRITUS PRODUCTION

Biomass present in a particular month was predicted using the following algebraic expression:

$$M_p = \text{antilog}_e (nP_{E-1} + \log_e M_{E-1}),$$

where  $M_p$  = predicted biomass for month  $t$  (g · m<sup>-2</sup>),  $M_{E-1}$  = estimated biomass for month  $t - 1$  (g · m<sup>-2</sup>),  $n$  = number of days between estimation date (d) and required prediction date,  $P_{E-1}$  = productivity per day for month  $t - 1$  (g · g<sup>-1</sup> · d<sup>-1</sup>).

Tissue lost by erosion of kelp blades was then taken as the difference between the predicted standing crop and the standing stock measurement for that month. Estimated detritus production was greatest from April to July (Fig. 9). Approximately 20 wet kg · m<sup>-2</sup> of fresh *E. radiata* plant material was lost from the standing crop each year.

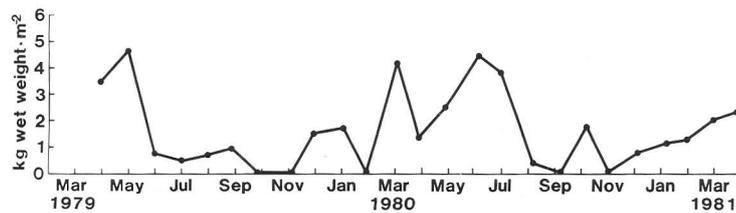


Fig. 9. Monthly erosion of *E. radiata* from Marmion reef calculated from monthly productivity and biomass measurements: see text.

## DISCUSSION

The results reported here show a yearly production of  $20.7 \text{ kg} \cdot \text{m}^{-2}$  in *E. radiata* beds. *E. radiata* at Whitfords has a large biomass per unit area and is highly productive compared with laminarians in other parts of the world. Levring (1977) recorded productivity of *Laminaria hyperborea* at  $1.2$  to  $2.4 \text{ kg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ; Gerard & Mann (1979) found a yearly production of  $10.6 \text{ kg} \cdot \text{m}^{-2}$  wet wt for *L. longicruris* in Nova Scotia, and Kain (1977) found annual production of  $6.5 \text{ kg wet wt} \cdot \text{m}^{-2}$  off the Isle of Man for *L. hyperborea*. Field *et al.* (1977) estimated a net production using a hole punching method of  $10.3 \text{ kg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  for *L. pallida*.

Factors affecting productivity per square metre in *Ecklonia radiata* at Whitfords are winter storms and lower productivity per gram plant material in late summer and winter. Counteracting the production of increased biomass as summer progresses is the reduced growth of plants. The mean standing stock of kelp varied seasonally between  $6 \text{ kg} \cdot \text{m}^{-2}$  and  $18 \text{ kg} \cdot \text{m}^{-2}$  wet wt (Fig. 5). The figures again are higher than indicated for *Laminaria hyperborea* in Europe which had a mean value of  $7.2 \text{ kg} \cdot \text{m}^{-2}$  (Levring, 1977). Kain (1977) estimated wet weights between  $10$  and  $20 \text{ kg} \cdot \text{m}^{-2}$  for the same species. For southern and Baja California North (1957) measured *Macrocystis pyrifera* at between  $3$  and  $22 \text{ kg} \cdot \text{m}^{-2}$  fresh wt while Aleem (1956) gave figures for La Jolla, California at  $5$  to  $9 \text{ kg} \cdot \text{m}^{-2}$ . For 24 stations in the Kerguelen Archipelago, Grua (1964) obtained a range of  $95$  to  $606 \text{ kg} \cdot \text{m}^{-2}$  with an average of  $140 \text{ kg} \cdot \text{m}^{-2}$  for *Macrocystis*. These large standing crops resulted mainly from high densities of fronds ( $20$  to  $290 \cdot \text{m}^{-2}$  at Kerguelen compared with  $2$  to  $15 \cdot \text{m}^{-2}$  for California).

The meristematic region of *Ecklonia radiata* lies between the top of the stipe and  $10 \text{ cm}$  up the lamina. The lamina expands horizontally and vertically and the laterals develop in this region. At the distal end of the plant senescence of plant tissue and erosion occurs. Thus, as Mann (1973) described this process, the plant is like a moving conveyor belt, with new material being added at the base and old material being broken off at the ends. The reduction in plant biomass from April onwards coincided with an increase in beach drift of *E. radiata* after storms. Because plant density did not change with season but plant size did, beach drift should have contained few entire plants with holdfasts attached. This has indeed been confirmed (W. Wood, pers. comm.).

This high productivity and standing stock of *E. radiata* may be because it is a small plant and not as complex as *Macrocystis*. The 2- to 7-m contour at which these studies were made may be the ideal depth for growth of *Ecklonia radiata*. Sunlight and water motion may be at an optimum while density appears to be restricted only by area of substratum.

Schiel & Choat (1980) found densities of up to  $40 \cdot \text{m}^{-2}$  in New Zealand and concluded that the  $-3/2$  thinning law did not hold for *E. radiata* in New Zealand. The plant density of *E. radiata* at Whitfords did not follow the  $-3/2$  thinning law (Table II, fourth column) but neither did it conform to the data and model proposed by Schiel & Choat (1980). The total yield did not reach a constant value up to the highest plant

densities found which were almost  $60 \text{ plants} \cdot \text{m}^{-2}$  compared to  $\approx 45 \text{ plants} \cdot \text{m}^{-2}$  reported by Schiel & Choat (1980). Plant density at Whitfords may have been limited by an external factor not important in other areas. The slight increase in plant density shown in Fig. 5 may indicate that the reef had been gradually recovering from a catastrophic event in some previous year, but that equilibrium had been achieved in the summer of 1980–1981. The 2-yr term of this study was, however, too short to allow one to judge adequately whether or not the small increase in plant density was significant over longer periods. If the bed is in dynamic equilibrium yearly erosion of plant material should equal the net productivity, and yearly production and seasonal biomass for each year should be equal.

The close negative correlation between growth and temperature from October to January suggested that growth was controlled by temperature at least during that period. Temperatures below  $18.5^\circ\text{C}$  favoured high growth rates. Fortes & Lüning (1980) found that *Laminaria saccharina* from Helgoland had a maximum specific growth rate at  $\approx 15^\circ\text{C}$ , above which the growth rate fell rapidly and  $25^\circ\text{C}$  was lethal. In *L. saccharina*, tolerance to high temperature was found to vary between blades of differing morphology (Lüning, 1975; Lüning *et al.*, 1978). North (1971) found a variety of *Macrocystis pyrifera* in which frond elongation was reduced in cold water. This strain also possessed unusual tolerance to warm water compared with other *Macrocystis* varieties.

During other times of the year light intensity and nutrient regime may be limiting to plant growth. The nitrate concentration of the water is higher in winter and autumn (May–September) while light intensity is lower (Kirkman, pers. obs.). Water movement is also greater thus reducing the boundary layer around the plants and making more nutrient available (Jackson, 1977).

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