

Productivity and life history of *Laminaria longicruris* at its southern limit in the Western Atlantic Ocean

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ABSTRACT: The seasonal population dynamics of *Laminaria longicruris* de la Pyl. were studied in Long Island Sound (Connecticut, USA). Linear growth rates were minimal during August and September, subsequently increased through the remainder of the year and reached a maximum (2.5 cm d^{-1}) in May. Productivity per plant (fresh weight) was maximal January to May (11.4 to $15.7 \text{ mg g}^{-1} \text{ d}^{-1}$); productivity m^{-2} was maximum in May ($110.53 \text{ g m}^{-2} \text{ d}^{-1}$ in 1986 and $413.32 \text{ g m}^{-2} \text{ d}^{-1}$ in 1987). Production was 10.6 kg m^{-2} in 1986 and was estimated to have been 46 to 50 kg m^{-2} in 1987. Maximum standing crop was observed in May (1986: 24 kg m^{-2} ; 1987: 47 kg m^{-2}). Maximum densities of new recruits were 1000 ind. m^{-2} . Densities of plants with blades $> 50 \text{ g}$ were 92 and $167 \text{ plants m}^{-2}$ in January and May, respectively. Carbon and nitrogen contents were minimal and maximal, respectively, in winter; the reverse was true for summer measurements. Highest percentages of fertile plants were observed during October to December. Succession in generations of plants behaving as either annuals or biennials is also noted and discussed.

INTRODUCTION

Members of the genus *Laminaria* comprise an important group of benthic marine macrophytes, both ecologically (Mann 1972b, Chapman & Craigie 1977, Chapman 1987) and economically (Okazaki 1971, Chapman & Chapman 1980, Pringle & Sharp 1980, Tseng 1981, Brinkhuis et al. 1987). These kelps possess a fairly low maximum temperature tolerance and consequently, are limited to temperate and polar regions in the northern, and temperate regions in the southern, hemispheres (Kain 1979, Hoek 1982, Lüning 1985, Egan & Yarish 1988).

Laminaria longicruris de la Pyl. only occurs in the North Atlantic Ocean (Egan & Yarish 1988). It is most commonly found in the northwestern regions of this ocean and is at its southern geographical limit proximal to the northern shores of eastern Long Island Sound, USA (Egan & Yarish 1988).

Laminaria longicruris shares certain morphological characteristics with *Laminaria saccharina* (L.) Lamour. Both species possess a simple or undivided blade

(lamina) and their morphological development is similar. However, differences exist in the stipe morphologies of the 2 species (Wilce 1965). The stipes of *L. longicruris* elongate considerably and become hollow at their distal regions, at the end of the first year or during the second year of growth (Egan & Yarish 1988). The solid stipes of *L. saccharina* are usually much shorter (Yarish et al. 1990). *L. longicruris* has been considered to be conspecific with *L. saccharina* (Chapman 1974, Lüning et al. 1978). However, data presented by Egan & Yarish (1988), Egan et al. (1990) and Yarish et al. (1990) show that there are very distinctive characters separating the 2 forms, especially with regards to stipe morphology.

Sub-tidal areas inhabited by *Laminaria* spp. are characterized by high primary productivity and large biomass (see review by Kain 1979). The most extensive data on kelp productivity have been presented for the mid-range of their latitudinal distribution (Mann 1972a, b, Chapman 1984, 1987, Gendron 1985). Information on populations at or near their southern distributional ranges is limited. Brady-Campbell et al. (1984) found that seasonal primary productivity patterns of *L. saccharina* near its southern limit in Rhode Island, USA,

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paralleled those presented for more northerly locations. Previously, no information on seasonal primary production of *L. longicuris* at its southern boundary has been presented despite extensive kelps beds along the Connecticut coast (Yarish & Egan 1989).

In the following study we report seasonal measurements and observations on growth rates, standing crop and productivity, sorus formation, nutrient status and morphological development of *Laminaria longicuris* at its southern limit in the Western Atlantic Ocean. We subsequently compare these data with those presented for both *L. saccharina* and *L. longicuris* from the North Atlantic, as well as kelp species from other regions.

Mann & Kirkman (1981) proposed that the calculation of production on plants brought back to the laboratory offered a much less cumbersome approach to measuring productivity in kelp beds than field measurements. Although their new technique was initially tested on *Ecklonia radiata* (C. Ag.) J. Agardh from the southwest coast of Western Australia, the authors expressed little doubt about its applicability to *Laminaria* spp. Mann & Mann (1981) compared this biomass model with exponential and chordal models. In a later study, Gendron (1985) examined the differences between these models during 3 consecutive 3 wk periods for *L. longicuris* from the Baie des Chaleurs, Quebec, Canada. We adopted Mann & Kirkman's (1981) technique during our study, and to our knowledge it is the first time it has been applied to an annual study of *Laminaria*.

MATERIAL AND METHODS

Site description. Long Island Sound (LIS) is situated (41° 10' 85"N, 72° 04' W) in a densely populated and

highly industrialized region of southern New England, USA (Fig. 1). The ca 200 × 39 (widest) km embayment is connected on the west to New York Harbour via the East River and opens to the Atlantic Ocean on the east. Depths range from 100 m in the eastern end to 35 m in the central and western basins (Riley 1959, 1961). Black Ledge, Groton, Connecticut was selected as study site because it has one of the most extensive *Laminaria* populations in LIS. The ledge is located in a moderately exposed area 1 km offshore and to the east of the mouth of the Thames River Estuary (Fig. 1). The subtidal study site, which is at 4 m below MLW and has an area of ca 1 km², is exposed to currents of 50 cm s⁻¹ during peak ebb and flood tides (Egan & Yarish 1988). The *L. longicuris* meadow was sampled by a stratified random sampling technique.

Morphometric data. One hundred plants were tagged in the subtidal using either forester's plastic tape or potted plant plastic identification stakes tied to the bases of their stipes. All tagged plants were selected for approximate uniform size and with stipe lengths at least 30 cm long. Monthly morphometric measurements (blade length and width, stipe length and linear meristematic growth) were made in situ, using SCUBA, from December 1984 to August 1985. Meristematic growth rates were determined by using the hole-punch technique of Parke (1948). Holes (0.5 cm diam.) were punched 10.0 cm above the stipe-blade juncture at each site visit.

The sampling procedures of Mann & Kirkman (1981) were employed from August 1985 to October 1986, and in January 1987 and May 1987. Sixty plants of approximate uniform size were selected and tagged each month. Different coloured tags were used each month. Holes were punched in the blades 10.0 cm above the stipe-blade junctures. On each subsequent visit, all

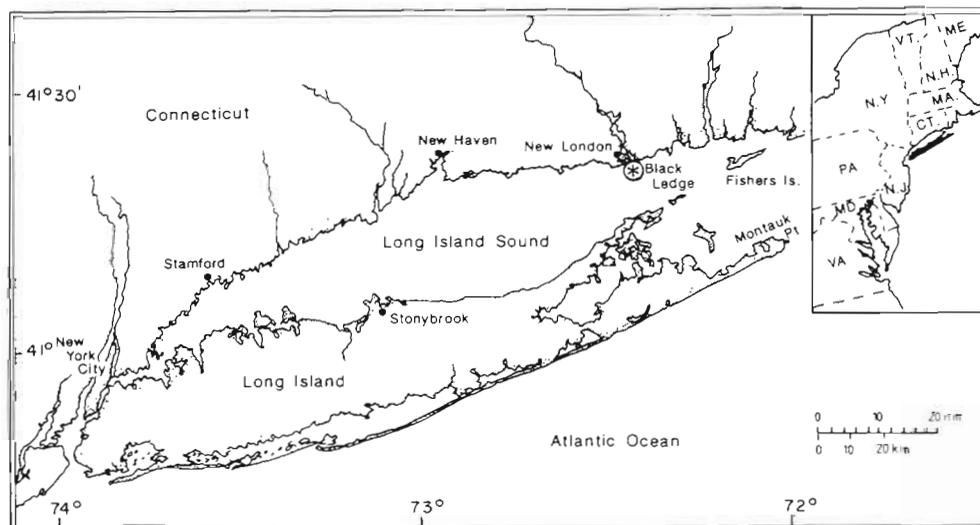


Fig. 1 Location of Black Ledge study site in eastern Long Island Sound, USA

Table 1. *Laminaria longicruris*. Seasonal variability of wet/dry weight ratios (slope of linear regression model) for blades, stipes, holdfasts, and total weight of plants from Long Island Sound. There were no significant differences ($p \geq 0.05$; t-test) between wet/dry wt ratio of plants sampled in April and July

Month	Blade	Stipe	Holdfast	Total
Jan	11.8	11.0	23.0	11.9
Apr	9.6	8.5	17.7	9.7
Jul	17.7	14.3	33.9	17.5

plants previously tagged were harvested and returned to the laboratory for measurements. Observations on blade and stipe morphology as well as sorus production were also documented.

Water temperatures were measured during each site visit with a YSI (Yellow Springs Instruments, Yellow Springs, OH, USA) Model 43TD Tele-thermometer. Light measurements at the site have been reported elsewhere (Yarish & Egan 1987).

Discs (0.5 cm diameter) were punched from the centre of 10 blades 12 cm above the blade-stipe juncture for each month. The use of tissue from this particular plant region reduces plant-to-plant variability (Lee & Brinkhuis 1986). The discs were washed thoroughly with de-ionized, distilled water. They were then oven-dried at 60 °C for 48 h and analyzed in either a Carlo Erba Model 1106 or 1500 Elemental Analyzer to determine the percentages of carbon and nitrogen present.

Dry weight to wet weight ratios were determined for plants harvested in January, April, and July 1986 by a linear regression model. Holdfasts, stipes and blades were sectioned and weighed. They were then wrapped in aluminium foil and oven-dried for 5 d at 60 °C. Ratios are presented in Table 1.

Biomass and density data. Six 0.25 m² quadrats of *Laminaria longicruris* (> 1 cm) were harvested during each monthly site visit. The following data were col-

lected in the laboratory for each quadrat: plant density (regardless of age class), holdfast, stipe and blade weights (fresh weights with excess water having been shaken from each plant section prior to weighing).

Productivity data. Productivity data were collected for the tagged plants returned to the laboratory each month after August 1985. Only plants with blades ≥ 50 g were used for productivity assessments. (Approximate blade dimensions of a plant [ca 1 yr old] with a blade = 50 g were 120 × 17 cm in January 1987). The protocols used in productivity determinations were those presented by Mann & Kirkman (1981) and Kirkman (1984).

RESULTS

Growth of *Laminaria longicruris*

The seasonal patterns in meristematic growth rates of *Laminaria longicruris* in LIS were similar during both years (Fig. 2). Highest linear growth rates occurred during spring (2.5 cm d⁻¹). Water temperatures during the rapid-growth periods were 10 °C (May 1985) and 14 °C (May 1986) (Fig. 2). Growth decreased from June to September as water temperatures reached 20 to 23 °C. The lowest linear growth rate (0.1 cm d⁻¹) occurred during September 1985; the lowest linear growth rate of 1986 (0.5 cm d⁻¹) occurred during August. Faster growth resumed during the autumn.

In contrast, maximum growth as mg g⁻¹ d⁻¹ (15.5 to 15.9) occurred during winter (Fig. 3) when water temperatures (2 to 3 °C) were lowest (Fig. 2). Relatively high growth values were maintained into spring, with lowest values (0.7 to 3.6 mg g⁻¹ d⁻¹) occurring during August to November (Fig. 3).

Seasonal changes in blade dimensions (length and greatest width; Fig. 4) were similar to seasonal patterns of meristematic growth (Fig. 2). Maximum blade dimensions (ca 320 × 25 cm) occurred during June;

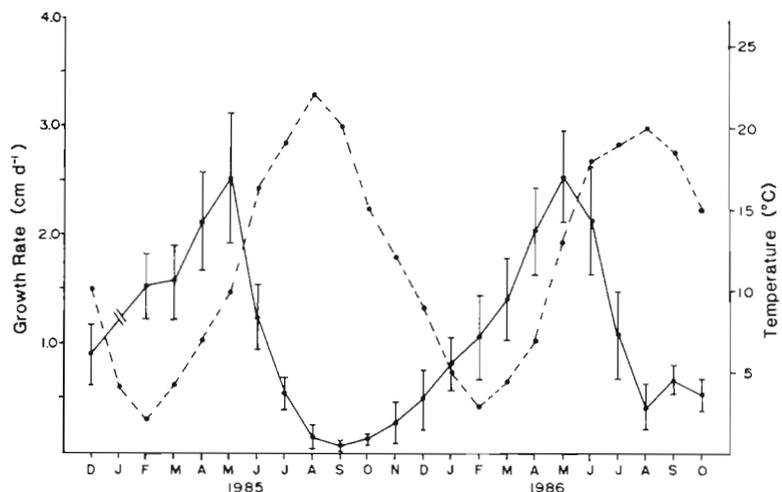


Fig. 2. *Laminaria longicruris*. Seasonal variations in meristematic growth rates (means \pm SD, cm d⁻¹) (continuous line), and water temperatures (dashed line) at Black Ledge, Long Island Sound

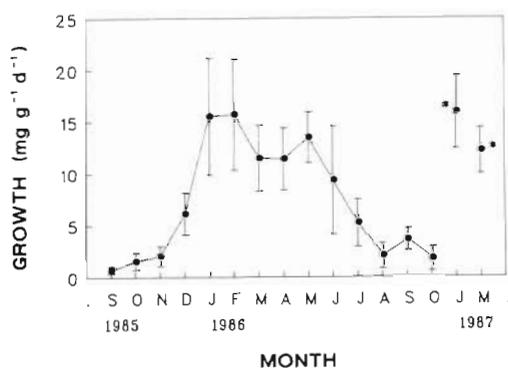


Fig. 3. *Laminaria longicruris*. Seasonal variations in growth rates ($\text{mg g}^{-1} \text{d}^{-1}$, fresh weight) of plants from Long Island Sound. Asterisks: 2 non-continuous samples for January and May 1987. Data points are means \pm SD

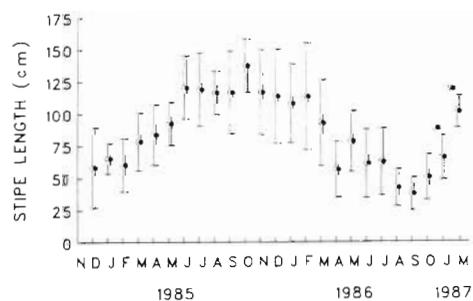
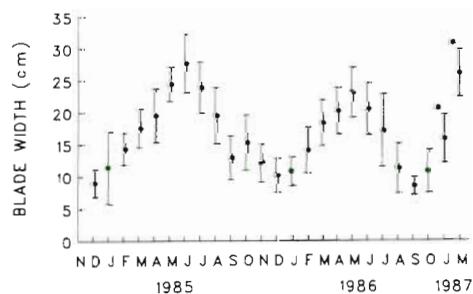
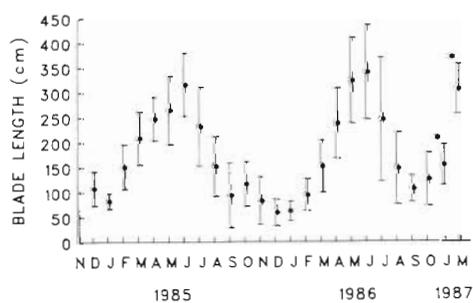


Fig. 4. *Laminaria longicruris*. Seasonal variations in blade length, blade width, and stipe length of plants from Long Island Sound. Asterisks: 2 non-continuous samples for January and May 1987. Data points are means \pm SD

lowest values were observed during September to December (Fig. 4). Erosion of the tips and edges of blades occurred from July to September, which corresponded with periods of maximum temperatures and lowest growth rates (Fig. 2).

Seasonal variations also occurred in blade morphology. Ruffling of the outer edges of the blades commenced during December. Bullations (indentations or corrugations) were formed immediately above the meristematic zone in late December and January. Bullation and ruffle production terminated in April/May and May/June, respectively. Smooth plane blades, darker brown in colour, were initiated in the meristematic region during this period. These smooth plane blades persisted until December.

Blades were seriously weakened during June to August 1986 due to grazing activity by the prosobranch gastropod *Lacuna vincta* (Montagu). The density of *L. vincta* was 22 ind. m^{-2} of blade area in quadrats sampled in July 1986.

Carbon content of the blades was maximal during late summer and minimal during winter (Table 2). By contrast, nitrogen content was maximal during winter and minimal during summer (Table 2).

Stipe length increased from 60 cm in December 1984

Table 2. *Laminaria longicruris*. Carbon and nitrogen contents (mean [\pm SD] percent dry weights) of plants from Long Island Sound. Data are for median portions of 10 blades, 12 cm above blade/stipe juncture for each month

Month	Carbon	Nitrogen
Jan	27.53 (3.96)	2.61 (0.17)
Feb	30.78 (4.25)	2.55 (0.26)
Mar	31.03 (2.32)	1.92 (0.19)
Apr	33.29 (3.13)	2.07 (0.20)
May	30.28 (1.79)	2.06 (0.36)
Jun	30.63 (2.62)	1.80 (0.15)
Jul	33.67 (2.62)	1.60 (0.28)
Aug	ND	ND
Sep	37.77 (1.54)	1.80 (0.15)
Oct	34.78 (3.53)	2.07 (0.27)
Nov	34.46 (1.45)	2.18 (0.18)
Dec	28.61 (2.31)	2.06 (0.33)
Jan	29.22 (2.89)	2.69 (0.27)
Feb	34.90 (2.96)	2.15 (0.32)
Mar	35.23 (0.50)	2.79 (0.25)
Apr	ND	ND
May	33.92 (1.97)	1.74 (0.23)
Jun	33.34 (1.97)	1.62 (0.19)
Jul	35.64 (1.29)	1.48 (0.19)
Aug	34.76 (1.01)	1.68 (0.13)
Sep	37.22 (1.01)	1.68 (0.13)
Oct	29.99 (1.52)	1.77 (0.16)

ND: not determined

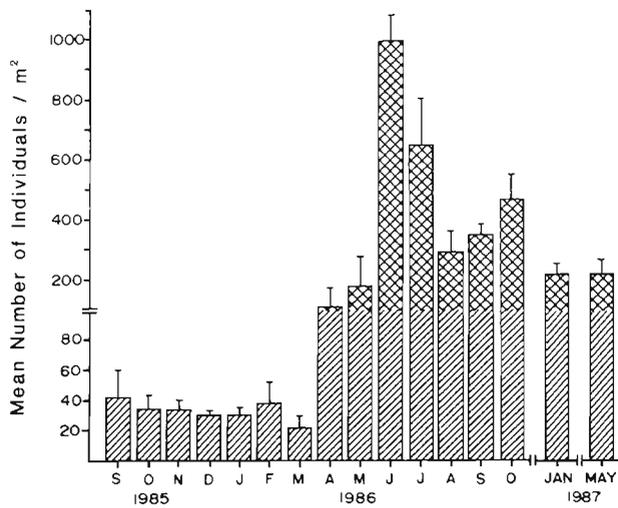


Fig. 5. *Laminaria longicruris*. Total density (mean \pm SD) at Black Ledge, Long Island Sound. Cross hatching on upper portions of some bars corresponds with scale change on y-axis

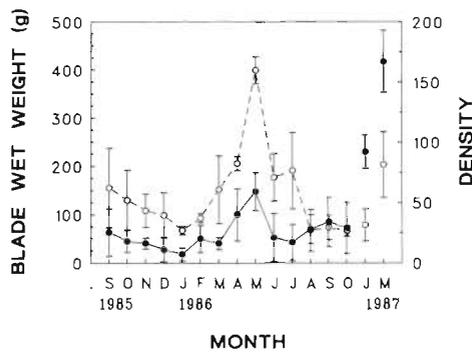


Fig. 6. *Laminaria longicruris*. Mean (\pm SD) blade weight (g fresh weight) of individuals with blades \geq 50 g sampled from quadrats (\circ), and density m^{-2} with blades \geq 50 g (\bullet) at Black Ledge, Long Island Sound. (J, M 1987 = January and May 1987)

to a maximum of 140 cm in October 1985 (Fig. 4). The highest rate of stipe growth occurred during May and June 1985.

Density and biomass

Lowest total plant density (25 to 44 m^{-2}) occurred from September 1985 to March 1986 (Fig. 5). Blade weights and the density of individuals with blade weights $>$ 50 g decreased from 25 to 7 m^{-2} during September to January (Fig. 6). Wet weights of these blades (Fig. 6) followed similar seasonal patterns to linear growth (Fig. 2) and blade dimensions (Fig. 4). Individual blade weights m^{-2} and plant density increased through May (Fig. 6). Increasing total

densities of individuals occurred in April and June (Fig. 5). The density of plants with blades \geq 50 g (Fig. 6) accounted for less than 2 % of the almost 1000 plants m^{-2} in June (Fig. 5). The density of plants (Fig. 6) increased to 92 m^{-2} in January and 167 m^{-2} in May, comprising 46 and 84 %, respectively, of total plant densities.

Maximum biomass occurred during late spring/early summer (Fig. 7). The standing crop in May 1986 was 24 $kg m^{-2}$ while it was only 2.5 $kg m^{-2}$ in January 1986. Stipes contributed more biomass than blades during September 1985 to February 1986 (Fig. 8). Total biomass values of 8 to 12 $kg m^{-2}$ were maintained throughout summer 1986 (Fig. 7). Standing crop values for winter and late spring 1987 were much higher than those for 1986 (Figs. 7 and 8). The standing crop during May 1987 was 47 $kg m^{-2}$.

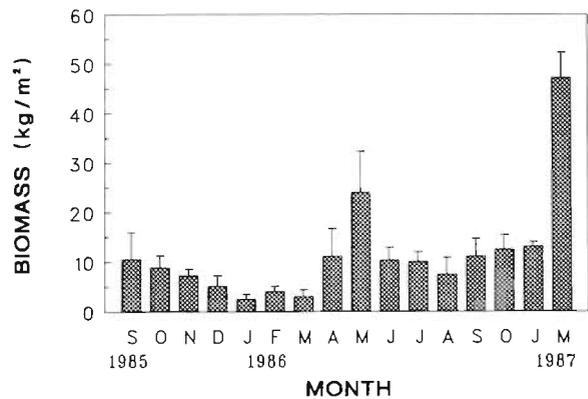


Fig. 7. *Laminaria longicruris*. Standing crop (biomass fresh weight, $kg m^{-2}$) at Black Ledge, Long Island Sound. (J, M 1987 = January and May 1987). Values are means \pm SD

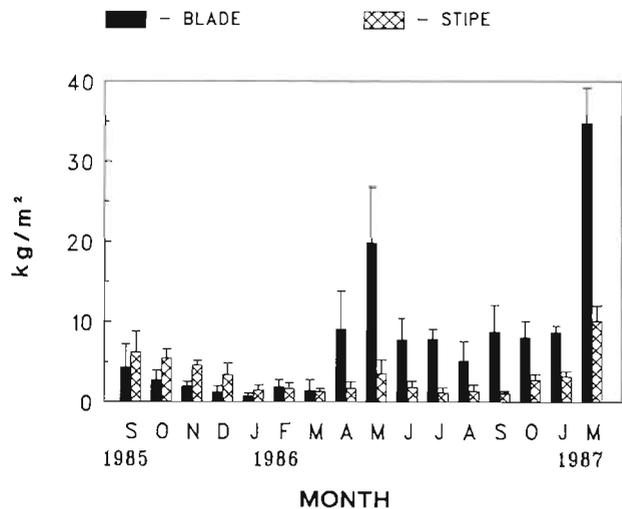


Fig. 8. *Laminaria longicruris*. Relative contributions ($kg m^{-2}$, fresh weight) of blades and stipes to overall standing crop (Fig. 7) at Black Ledge, Long Island Sound. (J, M 1987 = January and May 1987). Values are means \pm SD

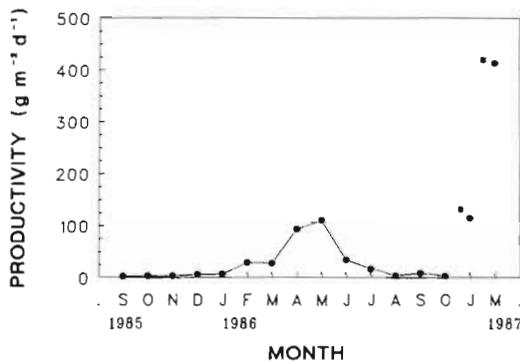


Fig. 9. *Laminaria longicuris*. Productivity ($\text{g m}^{-2} \text{d}^{-1}$) of blades at Black Ledge, Long Island Sound. Asterisks: 2 non-continuous samples for January and May 1987. Values are means; standard deviations (SD) were too small to be included

Productivity

Seasonal patterns in productivity (Fig. 9) were similar to those for linear growth (Fig. 2), blade dimensions (Fig. 4) and standing crop (Fig. 7). Highest productivity values were observed in spring ($110.53 \text{ g m}^{-2} \text{d}^{-1}$, May 1986; $413.32 \text{ g m}^{-2} \text{d}^{-1}$, May 1987). Although there was little difference between the individual blade weights of January 1986 (66.7 g) and January 1987 (78.6 g) (Fig. 6), and between growth values (15.5 , January 1986; $15.89 \text{ mg g}^{-1} \text{d}^{-1}$, January 1987; Fig. 3) the relatively higher productivity in January 1987 ($115 \text{ g m}^{-2} \text{d}^{-1}$) was due to a higher population density during the latter month (Fig. 6). Similarly, productivity during May 1987 was influenced by high densities.

Seasonal trends in the production of sorus (reproductive) tissue on blades were also apparent (Fig. 10). Maximum production (75 to 90%) occurred from October to December. The presence of sorus was relatively constant (40 to 55%) during January to May 1985. In contrast, only 20 to 30% of plants were observed bearing sorus during January to April 1986, increasing to 52% in May. Sorus production was always minimal during June to September (Fig. 10).

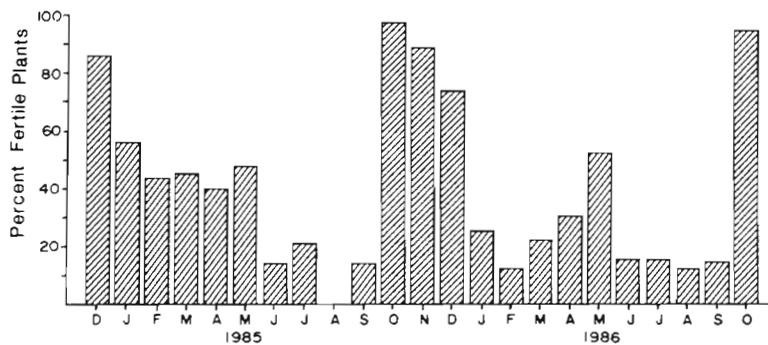


Fig. 10. *Laminaria longicuris*. Percent sporophytes with blades $\geq 50 \text{ g}$ possessing sorus tissue. Data are derived from the tagged population (December 1984 to September 1985) and standing crop quadrat samples (October 1985 to October 1986)

No conspicuous seasonal variations in seawater salinity and pH were observed; salinity and pH ranges were 30 to 33 ‰ and 7.9 to 8.3, respectively.

DISCUSSION

Laminaria sporophytes are potentially perennial due to the survival of adult plants through successive years. Although Parke (1948) and Reynolds (1974) have reported life-spans of up to 3 yr in individuals, Parke (1948) demonstrated that the average life expectancy for *L. saccharina* in Great Britain was 2 yr. Chapman (1984) and Smith (1985) reported that the longevity of *L. longicuris* in Nova Scotia, Canada, was 25 and 20 mo, respectively. Populations of *L. saccharina* from LIS (Brinkhuis et al. 1983) and intertidal populations of the same species from British Columbia, Canada, (Druehl & Hsiao 1977) were described as being annuals. Brinkhuis et al. (1983) attributed the annual behaviour of LIS populations to the loss of most sporophytes in summer because of high water temperatures. During our study we observed 2 new cohorts of plants populate the area, plants which attained and subsequently exceeded the minimum plant size class for sampling ($> 1 \text{ cm}$). The stipe data (Fig. 4) support these field observations that there were 3 successive macrosporophytic generations of *L. longicuris* at Black Ledge from December 1984 to May 1987. We will arbitrarily designate these as Generations # 1, 2, and 3. We observed a decline in the density of large plants comprising the initial macrosporophytic generation from October 1985 to March 1986 (supported also by data in Fig. 6). The decrease in stipe lengths observed February to April 1986 (Fig. 4) would have been due to a replacement of one macrosporophytic generation (# 1) with another developing macrosporophytic generation (# 2) having shorter stipes. The decrease in stipe lengths was not due to erosion. Stipes do not undergo periods of erosion and subsequent re-growth. Therefore, the overall annual stipe patterns do not

resemble those of blades. Based on the data on stipe growth and development presented by Egan & Yarish (1988), the macrosporophytic generation studied in 1984/85 (Generation # 1) appears to have been from an autumn 1983 recruitment. The stipe data (April to August 1986, ≤ 75 cm) are highly similar to the stipe data of 13 to 16 mo-old early spring recruits (Egan & Yarish 1988). This would mean that Generation # 2 was recruited in March to May 1985 when 40 to 50 % of Generation # 1 was reproductive (Fig. 10) and the macrosporophytic generation studied in May 1987 (Generation # 3; 1.5 yr old) was an autumn 1985 recruitment. Plants of Generation # 3 reached the minimum size class for sampling and succeeded Generation # 2 during August and September 1986. The field observations are once again supported by the stipe data in Fig. 4. Plants with shorter stipes than those in the previous 3 mo were sampled in September 1986 (Fig. 4). This implies that the plants of Generations # 1 and # 3 are biennials, and those of Generation # 2 are annuals. We are not aware of any other areas that possess fluctuating annual-biennial generations of kelp.

The seasonal trends in growth and production of *Laminaria longicuris* at its southern limit in the Western Atlantic Ocean are similar to those already presented for other populations of *L. longicuris* and *L. saccharina* in the North Atlantic (e.g. Parke 1948, Mann 1972a, b, Chapman & Craigie 1977, Lüning 1979, Brady-Campbell et al. 1984, Brinkhuis et al. 1984, Gendron 1985). Maximum linear growth rates compared favourably with those presented previously (Table 3).

Optimum growth of *Laminaria* occurs at 10 to 15 °C (Bolton & Lüning 1982). In the present study, the growth of *L. longicuris* decreased prior to ambient water temperatures reaching 15 °C (Fig. 2). Growth of *L. longicuris* in St. Margaret's Bay, Nova Scotia, was correlated with ambient nitrogen availability (Gagné et al. 1982). Seasonal patterns of tissue nitrogen (Table 2) are similar to those of Gagné et al. (1982) with the lowest values in July presumably being unable to support growth. Seasonal trends in tissue nitrogen and carbon contents (Table 2) are similar to those presented for *L. saccharina* from LIS by Lee & Brinkhuis (1986). However, winter nitrogen content was slightly higher in *L. saccharina*.

High growth rates can be maintained through summer if there is a sufficient nitrogen supply (Chapman & Craigie 1977, Anderson et al. 1981, Gagné et al. 1982). However, growth was found to be a function of light and/or temperature in such a situation e.g. at Pubnico, Nova Scotia (Anderson et al. 1981, Gagné et al. 1982). High summer temperatures would probably restrict growth in LIS in a similar case. Genetic differentiation in temperature tolerance between New York and Maine (USA) populations of *Laminaria saccharina* have been reported by Gerard & Du Bois (1988). Seasonal acclimation to high summer temperatures has been observed for meiospore germination, growth (Lee & Brinkhuis 1988, Egan et al. 1989) and survival (Egan et al. 1989) of *Laminaria* gametophytes. Similar responses were noted for young sporophytes (Egan et al. 1989). In addition, Yarish & Egan (1989) have observed that some individual strains of young sporophytes have

Table 3. *Laminaria* spp. Growth rates for 2 species with non-digitate blades from the North Atlantic Ocean

Species	Location	Month	Growth rate (cm d ⁻¹)	Source
<i>L. longicuris</i>	Nova Scotia	May/Jun	1.0	Chapman & Craigie (1977)
<i>L. longicuris</i>	Nova Scotia	May/Jun	1.0	Gerard & Mann (1979)
<i>L. longicuris</i>	Quebec	Jun	2.3	Gendron (1985)
<i>L. longicuris</i>	Quebec	Jun/Jul	3.4	Anderson et al. (1981)
<i>L. longicuris</i>	LIS	May	2.5	This study
<i>L. saccharina</i> ^a	Scotland	Apr	1.7	Parke (1948)
<i>L. saccharina</i>	LIS	May/Jun	1.5	Brinkhuis et al. (1984)
<i>L. saccharina</i>	LIS	May	1.1	Lee & Brinkhuis (1986)
<i>L. saccharina</i>	Rhode Island	May/Jun	2.0	Brady-Campbell et al. (1984)
<i>L. saccharina</i> ^b	Maine	Jul	1.2	Boden (1979)
<i>L. saccharina</i>	Helgoland, North Sea	Jun	1.5	Lüning (1979)
<i>L. saccharina</i>	England	May	1.1	Burrows & Pybus (1971)
<i>L. saccharina</i>	England	Mar/Apr	1.5	Parke (1948)
<i>L. saccharina</i> ^c	Scotland	May	1.7	Parke (1948)

^a Probably *L. longicuris*. Plants possessed long, hollow stipes
^b 7 to 75 % of plants possessed long, hollow stipes
^c Intertidal population

higher optimal growth temperatures than others. Two of these isolates were from the vicinity of a nuclear power plant thermal outflow in LIS.

Growth of *Laminaria longicuris* (as $\text{mg g}^{-1} \text{d}^{-1}$) followed similar seasonal patterns to those presented for *Ecklonia radiata* (Kirkman 1984). Direct comparisons can be made in this case because we employed identical methods to his. Overall, the growth of *L. longicuris* was slightly better (Fig. 3) than that of *E. radiata* (Fig. 7 of Kirkman 1984). During peak growth, values for *L. longicuris* exceeded those for *E. radiata* by ca. $6.5 \text{ mg g}^{-1} \text{d}^{-1}$. However, individual plant weights were higher for *E. radiata*.

The data presented here indicate an annual blade production of 10.6 kg m^{-2} during October 1985 to October 1986. Production during May 1987 alone was 12.8 kg m^{-2} . It is clear that higher densities were attributable for the higher productivity in 1987 (January 1987 = $16 \times$ January 1986; May 1987 = $3.75 \times$ May 1986). We estimate an approximate annual production of 46 to 50 kg m^{-2} between October 1986 and October 1987 based upon trends from the previous year and 2 productivity values during 1987. Gerard & Mann (1979) found an annual production of 10.6 kg m^{-2} for *Laminaria longicuris* in Nova Scotia while Kain (1977) reported a production value of $6.5 \text{ kg m}^{-2} \text{yr}^{-1}$ for *Laminaria hyperborea* (Gunn.) Fosl. off the Isle of Man, UK. The annual production of *Ecklonia radiata* in SW Australia was 27 kg m^{-2} (Kirkman 1984).

The mean standing crop of *Laminaria longicuris* (Fig. 7) varied with generation, season, and plant density. Highest values were 24 kg m^{-2} for Generation # 2 in May 1986 and 46.8 kg m^{-2} for Generation # 3 in May 1987. The standing crop in May 1985 (Generation # 1) was 27.8 kg m^{-2} (Yarish & Egan 1987). The standing crop of 1-yr-old plants of Generation # 3 in January 1987 was 13 kg m^{-2} . Reported standing crop values for other localities are: 6.5 kg m^{-2} (Smith 1985) and 11 kg m^{-2} (Mann 1972a) for *L. longicuris* in Nova Scotia; 7.0 kg m^{-2} (Lüning 1969) and 10 to 20 kg m^{-2} (Kain 1977) for European populations of *L. saccharina* and *L. hyperborea*, respectively; 6 to 18 kg m^{-2} for *Ecklonia radiata* in SW Australia (Kirkman 1984); and 3 to 22 kg m^{-2} for *Macrocystis pyrifera* (L.) C. Agardh in Southern and Baja California (North 1957). Grua (1964) obtained an average 140 kg m^{-2} for *M. pyrifera* in the Kerguelen Archipelago. However, this value was influenced by high densities of fronds.

Although the density of young recruits was 1000 m^{-2} in June 1986 (Fig. 5), the number of plants with blades $\geq 50 \text{ g}$ stabilized between 92 and 167 m^{-2} during the third quarter of the life-span of Generation # 3 (Fig. 6). Up to 800 ind. m^{-2} of *Laminaria saccharina* have been reported for Rhode Island (Brady-Campbell et al. 1984). The highest density of *Ecklonia radiata* in Kirkman's

(1984) study was 60 m^{-2} . The density of *L. longicuris* in SW Nova Scotia, which was constant through 1 yr, was 1.2 m^{-2} (Chapman 1984). On the other hand, Gerard & Mann (1979) reported densities of 8 and 24 ind. m^{-2} for sheltered and exposed sites, respectively, in Nova Scotia.

Grazing of *Laminaria* populations by *Lacuna vincta* has been reported previously (Fralick et al. 1974, Brady-Campbell et al. 1984, Johnson & Mann 1986). Although present throughout the study period, the snail reached its highest densities during the summer of 1986. Johnson & Mann (1986) found that elevated levels of polyphenols in *L. longicuris* inhibited grazing by *L. vincta*. Perhaps annual *L. longicuris* plants have different overall polyphenol concentrations than perennial plants (Yarish & Egan 1987) which would imply that the population dynamics of *L. longicuris* and *L. vincta* are closely interconnected.

Seasonal changes in blade morphology, observed during the present study, have also been reported elsewhere. Setchell (1900) wrote 'In *L. agardhii* and *L. saccharina* of the New England coast (North America), the writer has found that the summer form is usually ample, with ruffles and rows of indentations fully developed; but in August a change takes place and this summer blade is replaced by a winter blade which is perfectly plane and devoid of both these features. Again, in the spring, this plane blade is replaced by the ruffled and indented form'. In contrast to Setchell's (1900) observations, the bullate (indented) form was produced in winter (January) being replaced by the plane blade form in summer (June), during the present study.

Lüning (1975) and Lüning et al. (1978) reported genetic differentiation between European populations of *Laminaria saccharina* with regard to blade morphology. A smooth plane blade form appears restricted to the Baltic Sea, the west coast of Sweden, and Helgoland, North Sea (see Lüning 1975, Lüning et al. 1978), while the bullate form is found throughout the remainder of the range for the species. In crosses between the plane and bullate forms the offspring always possessed bullations; nonbullate plants always bred true (Lüning 1975, Lüning et al. 1978, Bolton et al. 1983). However, Lüning (pers. comm.) has produced offspring from crosses of *L. saccharina* from Espeyrend, Norway, exhibiting seasonal dimorphism of blade morphology.

We hypothesize that the seasonal changes in blade morphology are temperature/temperature-photoperiod related responses and are survival adaptations for temperature extremes such as those found in the LIS region. A smooth plane blade form would have less surface area exposed to its adverse surroundings. McMillan & Bridges (1982) reported variable leaf morphologies in the Pacific seagrass *Halophila ovalis*

(R.Br.) Hook. f. var. *bullosa* Setchell due to temperature. Exposure to high temperatures resulted in more leaf damage to plants with bullate leaves. In addition, plants with bullate leaves produced smooth leaves after exposure to high temperatures. Bullate leaf production was resumed after the temperature was lowered (McMillan & Bridges 1982). Lüning et al. (1978) reported that the bullate form of *Laminaria saccharina* died at temperatures above 16 °C, whereas the plane form from Helgoland tolerated 18 °C. Ardré (1971) reported morphological variations of *L. saccharina* blades at Montedor, Portugal, where summer water temperatures exceed 16 °C. The absence of, or lack of production of, the bullate form in Helgoland and parts of the Baltic may also in some way be light-related. 'Arctic conditions' (in relation to light availability) occur from October to February in these areas (see Lüning 1985).

Sorus formation most commonly occurs during autumn and winter in both *Laminaria longicuris* (Chapman 1973) and *L. saccharina* (Parke 1948, Kain 1979). The sudden appearance of sorus and high percentages of plants bearing sorus in October (Fig. 10) is somewhat similar to the sudden and synchronous sorus formation in *Saccorhiza dermatodea* (Pyl.) J. Ag. in Newfoundland (Keats & South 1985). The latter authors suspected the phenomenon was under photoperiodic control. Lüning (1988) has shown that sorus formation in *L. saccharina* from Helgoland is indeed a short-day response. However, *L. saccharina* in LIS undergoes 2 peak periods (spring and autumn) of sorus formation (Lee & Brinkhuis 1986). Although some tagged individuals in the present study, and monitored through 1985, also behaved in a similar manner to *L. saccharina*, this was not the case for the different generations in general. The reproductive peaks observed in late autumn (1984 and 1985; Fig. 10) would have been produced by Generation # 1. The peak observed during October to December 1985 was also at the end of the 2 yr cycle for Generation # 1. Then the low percentages of fertile sporophytes observed during January to March 1986 (Fig. 10) would not have been due to a hiatus in sorus formation but rather reflected succession by plants of Generation # 2. Generation # 2 became reproductive near the end of its 1 yr cycle in May 1986 before being succeeded by Generation # 3.

Lüning (1988) contends that LIS populations may be comprised of day-neutral plants or that short-day conditions are not essential for, but may promote sorus formation. We propose that sorus formation in LIS plants is probably a short-day response. However, low winter temperatures may block the effects of the initial stimulus (hence the winter hiatus in sorus production) until water temperatures increase again in spring. The above would not explain the continued sorus produc-

tion from autumn 1984 through May 1985 by Generation # 1 (Fig. 10). Perhaps the physiologies of the annual and perennial plants are fundamentally different.

In conclusion, *Laminaria longicuris* at its southern limit in the western Atlantic Ocean is as productive as, or even more productive than other kelp species worldwide. Furthermore, the productivity measurement methodology of Mann & Kirkman (1981) is easily used for studies on *Laminaria* species with non-digitate blades.

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