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Seasonal growth and composition of fronds of *Macrocystis pyrifera* in the Falkland Islands

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Abstract

Frond growth of *Macrocystis pyrifera* in the Falkland Islands was monitored in shallow coastal water from December 1985 to March 1987, and at a different site in deeper water from December 1985 to June 1986. Growth rates in the deeper bed were generally higher than those recorded in the coastal zone. At both sites, node initiation and elongation rate fluctuated according to the seasonal pattern of light or water temperature. In the shallow coastal area, nitrate was abundant in the winter and below detection levels during late spring and summer. Correlation analysis suggests that the production of the fronds of the giant kelp in this area was probably inhibited during the summer months by extremely low concentrations of nutrients. Internal nitrogen was exhausted approximately one month after a sharp decline in ambient nitrate concentration, and carbon reserves were formed. In the deeper bed of *M. pyrifera*, nitrogen was abundant all year round and the production of the fronds reflected the seasonal pattern of light or water temperature. The nitrogen content of the tissue probably did not drop below a level that limited production, and no internal carbon reserves were accumulated.

Introduction

Macrocystis pyrifera is the most abundant species of kelp around the Falkland Islands and forms extensive beds along the coastlines (Fig. 1). Few studies have been made of the giant kelp at these islands, although the beds are amongst the largest in the world. Skottsberg (1908, 1921) gave a detailed description of *M. pyrifera* he found during his expedition in subantarctic and Antarctic regions. Powell (1981) visited the islands to observe the distribution and general ecology of the kelp beds by means of a boat and areal survey. His conclusions were very general and merely mentioned that *M. pyrifera* was abundant along the south and east coasts of East Falkland and that it can be found from the intertidal to a depth of ca. 25 m.

In the Falkland Islands, the giant kelp occurs in shallow coastal zones and in deeper beds further offshore. In the present study, seasonal frond growth was studied for *Macrocystis pyrifera* in a shallow coastal zone and in a bed in deeper water. The differences found between these two populations were related to environmental factors and carbon and nitrogen content of the fronds.

Frond growth of *Macrocystis pyrifera* in relation to environmental factors has been studied extensively in deep offshore beds in California (Wheeler and North 1980, 1981, Gerard 1982a, Dean and Jacobsen 1984, Zimmerman and Kremer 1986). California, at 32°N to 38°N, is situated closer to the equator than the Falkland Islands (Fig. 1) and environmental factors related to solar radiation could result in differences in frond growth of the giant kelp from these two areas.

Asensi et al. (1981) studied frond growth of *Macrocystis pyrifera* over 9 mo in a deep field in the Kerguelen Islands. Although the subantarctic Falkland Islands and the Antarctic Kerguelen Islands are roughly positioned at the same latitude, surface-water temperatures are lower at Kerguelen.

Lobban (1978) studied the frond growth of *Macrocystis integrifolia* in a coastal zone at British Columbia, Canada; however, no measurements of environmental factors were carried out. The Falkland Islands and British Columbia are climatologically similar, although water temperatures are slightly higher at the latter location (Druehl 1978). These environmental similarities could result in comparable frond growth of giant kelp in the shallow coastal zones, even though the giant kelp from the two areas are different species.

No studies have been carried out to compare the seasonal fluctuations in frond growth of *Macrocystis* spp. in shallow and nearby deeper water. Neither has the growth of this genus in temperate regions been related to environmental factors. The environmental conditions in the shallow

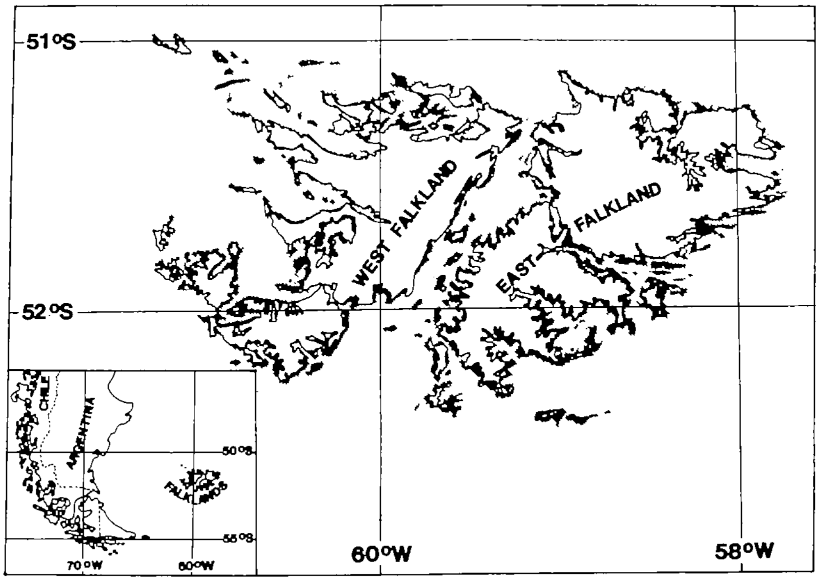

Fig. 1. Falkland Islands. Hatching outlines larger beds of *Macrocystis pyrifera* (drawn from charts and maps)

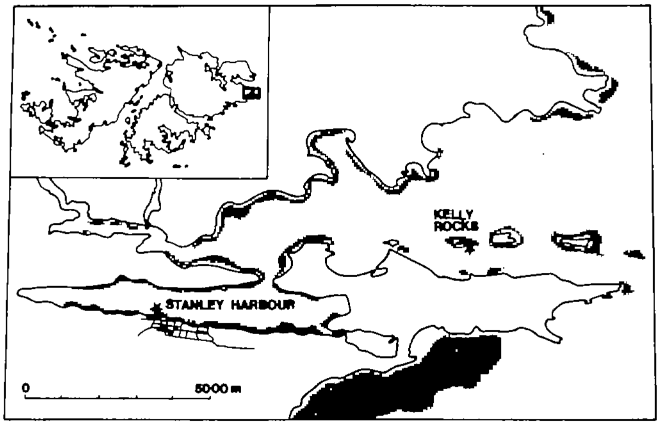

Fig. 2. Study areas, Stanley Harbour and Kelly Rocks, Falkland Islands. Stippling represents beds of *Macrocystis pyrifera;* stars indicate areas where studies were carried out

water of Stanley Harbour, Falkland Islands, is unique for *Macrocystis* spp. growth studies: in late spring and summer the water temperature is relatively low and the ambient nitrate concentration below detection level. Investigations in this area will add to the understanding of the influence of nutrients and temperature of *Macrocystis* spp. growth.

Materials and methods

Study areas

In Stanley Harbour, *Macrocystis pyrifera* forms a coastal zone (Fig. 2) from the intertidal to a depth of 3 to 4 m. At extreme low tides the kelp nearest to the coast is exposed to the air and dries out. The width of the zone varies between 10 and 60 m, generally being ca. 40 m. Holdfasts are attached to small rocks scattered on the sandy substratum, and the outer border of the zone is probably determined by the lack of available hard substratum. The kelp in the area studied is exposed to strong winds blowing from west to north which are fairly constant throughout the year; south-western gales do not affect this area. Although relatively exposed to strong winds, waves never reach a great height. In periods of heavy rain or wind the turbidity of the water is high due to a large amount of suspended matter in the water. Tidal differences are not very large; the average level of the high tides during the present study was 1.5 m and the mean low tide level was 0.6 m.

The giant kelp studied at Kelly Rocks (Fig. 2) occurs at a depth of ca. 5 m. Sporophytes are attached to large rocks and to a wooden wreck. The site is relatively sheltered against winds from most directions, only a northerly or a south-westerly wind directly affecting the area. However, heavy swells, caused by storms, occur at this site. The water is generally fairly clear for temperate waters (ca. 5 to 10 m visibility).

Frond growth

Growth was measured as the increase in number of nodes on the fronds. Bright orange, nylon ribbons were used to tag the fronds. A canopy frond was tagged 20 nodes away from the first slit in the apical scimitar, whilst a submersed frond received a tag 10 nodes from the first slit. These fronds were collected 4 to 6 wk later; they were taken to the laboratory and the number of nodes from the tags of the first slit was recorded. Additionally, a number of untagged fronds of different sizes was collected. At the same time, a new set of fronds of different plants in the same area was tagged, and recording was continued as above.

The number of nodes (including those of the apical scimitar), length and wet weight were determined for each frond sampled. No corrections were made for encrustations as these were restricted to very limited areas on the oldest basal part of mature fronds and their weight was negligible. No compensations were made for missing blades. Regression curves of the length or wet weights vs the number of nodes were constructed. With the aid of these curves, the corresponding length and weight of a frond with a certain number of nodes at tagging and at harvesting time was calculated to obtain a value for the increment in length or weight of a tagged frond. The number of nodes of a frond at time of tagging was determined by substracting the number of initiated nodes (i.e., number of new blades formed during the observation period) from the number of nodes of the harvested frond. Node-initiation rate (nodes per day), elongation rate (cm d^{-1}) and production (g wet wt d^{-1}) of the fronds were obtained by dividing the increment in number of nodes, length and wet weight, respectively, by the number of days of observation.

As large sporophylls can affect the total wet weight of the fronds, all sporophylls were excluded from measurements to improve standardization. Fronds with a damaged apical scimitar or a terminal bulb were discarded.

The giant kelp in Stanley Habour was reached by wading during low spring tides. Plants at a depth of 1 to 1.5 m below the low-water line were used for measurements. Growth was recorded every 4 or 6 wk from December 1985 to March 1987. On each occasion, a different set of 40 plants was tagged; markers on the shore were used to relocate tagged plants. Generally, 25 to 50% of these fronds were lost due to frond damage, frond detachment or plant loss. At the end of each sampling period a total number of ca. 50 tagged and untagged fronds was collected for measurement in the laboratory.

At Kelly Rocks, the kelp was measured by means of SCUBA diving. The area was marked at the surface by a small buoy, whilst underwater a wreck was used for navigation. Growth was measured every 4 to 6 wk from November 1985 until the end of June 1986. On each occasion, two or three different plants were used for growth measurements and 20 fronds were tagged. A total number of ca. 25 tagged and untagged fronds was collected at the end of each sampling period. Although losses were generally not very large, it was at times difficult to relocate the tagged canopy fronds in the dense canopy and usually only half of these was sampled.

In order to compare the calculated elongation rates with the actual length increment of the fronds, direct measurements of frond elongation were carried out in Stanley Harbour, once in the winter, from May to June 1986, and once in the summer, from January to February 1987. Thirty fronds of different sizes received a ribbon with a numbered tag 2 to 3 m from the apical scimitar. If the length of the frond were less than several metres it was tagged at the base. The exact distance from the node at the basal side of the tag to the first slit of the apical scimitar was recorded. The same fronds were tagged as decribed for measurement of the node initiation rate. After one month the fronds were collected and the number of nodes and length of each frond were measured.

Environmental factors

Sea-water shoreline temperatures at Stanley Harbour were measured at least once every two weeks at midday. Every month two 50 ml water samples were taken and stored in a deep-freeze for later determination of nitrate concentration. Nitrate was determined by the method of Strickland and Parsons (1968) after filtration to remove silt particles. At Kelly Rocks, temperature was recorded and water samples were taken each time the site was visited.

Carbon and nitrogen content

The top 2 m of several well-developed canopy fronds were dried at 60 °C for of ca. 18 h and percentage dry weight was determined. A fine meal was made of the dried kelp by grinding it in a IKA A10 analytical mill; two or three subsamples were taken, and total carbon and nitrogen content of a 0.9 to 1.1 mg sample were measured with a Carlo Erba Srumentazione Elemental Analyser (Model 1106).

Computation and statistics

Regressions were computed with the aid of the General Linear Interactive Modelling (GLIM) package of the Royal Statistical Society, London. Unlike many statistical packages, GLIM fits the regression by the method of maximum log likelihood instead of least-squares. As the data were normally distributed, the identity-link function was used. Box-Cox transformations were applied to a test if transformation of the Y-variable was necessary (Sokal and Rohlf 1981).

The weight of a frond bearing the same number of nodes varied with time of year. The following equation was used to calculate the corresponding wet weight of a frond with a certain number of nodes at different times of the year.

$$\ln(\text{weight}) = \ln(\text{nodes}) + \sin(\text{time} + p) + I,$$

where p = phaseshift (in radians), I = interactive term, and time = time of the year (in radians). The equation is nonlinear in p, and the value of p was determined by the direct approach technique.

An analysis of paired comparisons was made to test whether there was a difference in node initiation rate between submersed and canopy fronds (Sokal and Rohlf 1981). The analysis was carried out separately for Stanley Harbour and Kelly Rocks for grouped data collected at different times of the year.

A single-factor analysis of variance (ANOVA) was used to test for differences between elongation calculated with the aid of regressions and elongation measured in the field (Sokal and Rohlf 1981).

A product-moment correlation coefficient was used to determine possible correlations between environmental factors and growth or carbon and nitrogen content of the kelp. A Student's t-test was used to test the statistical significance of these coefficients (Zar 1974).

Results

Computed regressions

Regression curves of frond length vs number of nodes were calculated separately for submersed and canopy fronds of

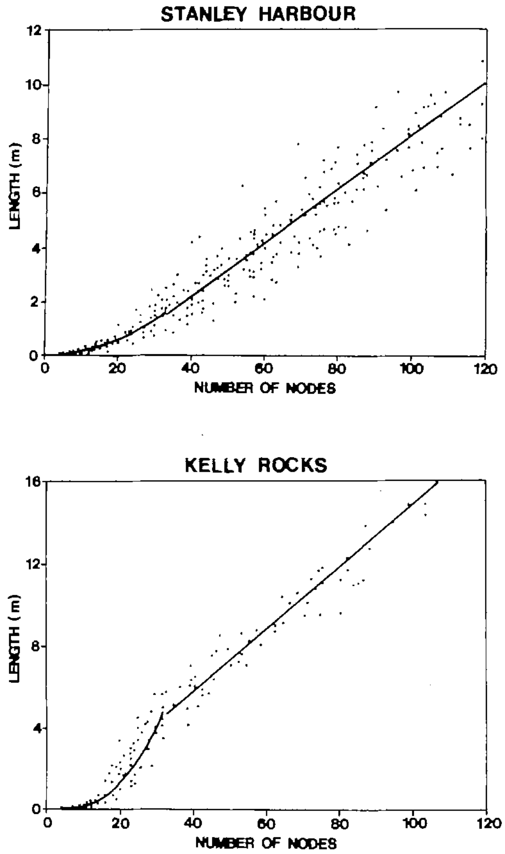

Fig. 3. *Macrocystis pyrifera*. Regressions of length vs number of nodes on fronds. For submersed fronds (i.e., those with <34 nodes), double-log curves were fitted; relation was linear for canopy fronds (i.e., those with >33 nodes). 40% of data points fitted are plotted for Stanley Harbour, 70% for Kelly Rocks. Note differing ordinate scales. See Table 1 for regression equations

Table 1. *Macrocystis pyrifera*. Regression equations for length (L, cm) or wet weight (W, g) vs number of nodes (N) on fronds from Stanley Harbour (SH) and Kelly Rocks (KR). S: submersed frond, C: canopy frond. T: time of year (radians)

Area	Frond	Equation	R^2
SH	S	$L=\exp(-2.32+2.11\ln(N))$	0.93
SH	C	$W=-185.40+9.78N$	0.87
SH	S+C	$W=\exp(-1.48+1.88\ln(N)-0.36\sin(T+2.81)+0.23\ln(N)\sin(T+2.81))$	0.90
KR	S	$L=\exp(-3.28+2.72\ln(N))$	0.91
KR	C	$L=-43.49+15.03N$	0.93
KR	S+C	$W=\exp(-2.42+2.29\ln(N)+0.07\ln(N)\sin(T+0.52))$	0.95

Macrocystis pyrifera. Fronds were considered as being submersed at low water when they were less than 1.5 m long in Stanley Harbour and less than 4.5 to 5 m long at Kelly Rocks, these lengths roughly corresponding to a frond with less than 30 to 40 nodes. For the calculations, fronds with less than 34 nodes were considered as submersed, those with more than 33 nodes as canopy-forming. Transformation of the Y variable was necessary in order to achieve homoscedasticy for submersed fronds; this resulted in a double-log relation between frond length and number of nodes (Fig. 3). The residuals were equally distributed for plots of length vs number of nodes for canopy fronds; thus, the relation between length and number of nodes was linear. The equations of the regression curves are listed in Table 1.

A double logarithmic relation was found between wet weight and number of nodes of fronds, independent of whether they were submersed or canopy-forming. The wet weight of fronds with the same number of nodes displayed seasonal fluctuations. In Stanley Harbour, frond weight was maximum in spring (Fig. 4). Seasonal fluctuations in frond weight at Kelly Rocks were not as large as those in Stanley Harbour, and frond weight was maximum in late summer (Fig. 5). The equations of the regression curves are also listed in Table 1.

Frond growth

Node initiation rate was dependent on frond size, smaller fronds exhibiting a lower rate than larger ones. Fig. 6 illustrates node initiation rates from January through February 1986 for fronds bearing different numbers of nodes. The fronds were divided into two size groups, roughly corresponding to submersed and canopy fronds. An analysis of paired comparisons was used to test whether the node initiation rates of these two groups differed significantly. For Stanley Harbour fronds, the F-value was maximal when a frond bearing between 30 to 34 nodes was considered to be the largest submersed frond ($F=37.05$, $n=353$). At Kelly Rocks, the highest F-value was attained when the maximum number of nodes of a submersed frond was considered to lie between 32 and 34 nodes ($F=21.83$, $n=87$). This corresponded with the number of nodes of submersed and canopy fronds calculated from the regressions of length vs number of nodes. Calculations of average node-initiation rates were made separately for submersed and canopy fronds. The number of nodes expressing the size of submersed and canopy fronds, used for growth measurements, was the median number of nodes during the period measured [no. nodes $=(n0+n1)/2$, where $n0=$ no. nodes at the time of tagging, $n1=$ no. nodes at the time of harvesting].

The average node initiation rate for submersed and canopy fronds at different times of the year is presented in Figs. 7 and 8 for Stanley Harbour and Kelly Rocks, respectively. The node-initiation rate showed a similar pattern at both sites, i.e., the rate was high in the summer, decreasing in autumn and winter. At Kelly Rocks, however, canopy fronds maintained a high node-initiation rate throughout late summer and early autumn, the rate decreasing only in the period May to June.

The calculated frond elongation of the submersed fronds was dependent on frond size. Fig. 9 presents an example of frond elongation as a function of frond size for the period January until February. Once the fronds reached the surface, the elongation rate was the same for all canopy fronds, independent of size. The seasonal growth pattern of frond elongation was similar to that recorded for node initiation

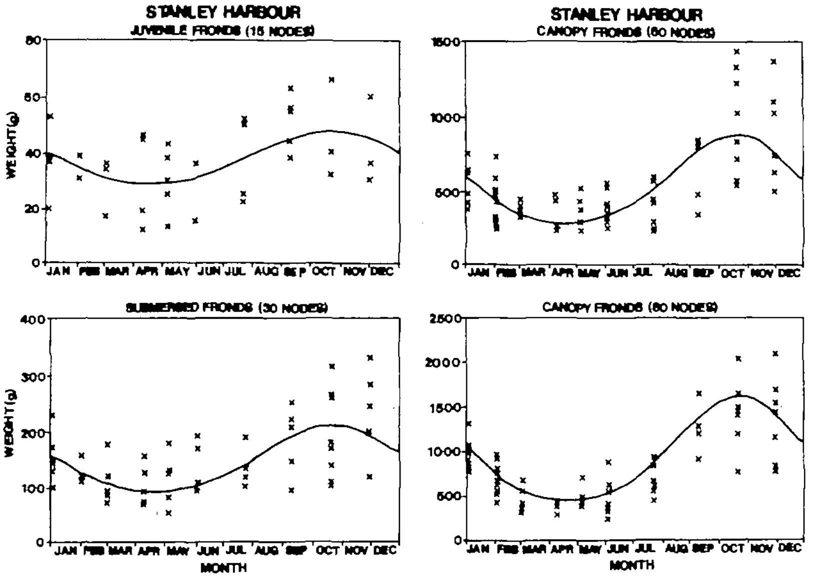

Fig. 4. *Macrocystis pyrifera.* Wet weight vs number of nodes on fronds of giant kelp in Stanley Harbour at different times of the year (1985–1987: combined data). Regression curves were fitted for juvenile fronds (15 nodes), submersed fronds (30 nodes) and canopy fronds with 60 and 80 nodes. Data points indicate weight recorded for fronds bearing between 12 and 17 nodes for juvenile fronds, between 25 and 35 nodes for submersed fronds, between 51 and 69 nodes for smaller canopy fronds, and between 70 and 90 nodes for larger canopy fronds. Note differing ordinate scales. See Table 1 for regression equations

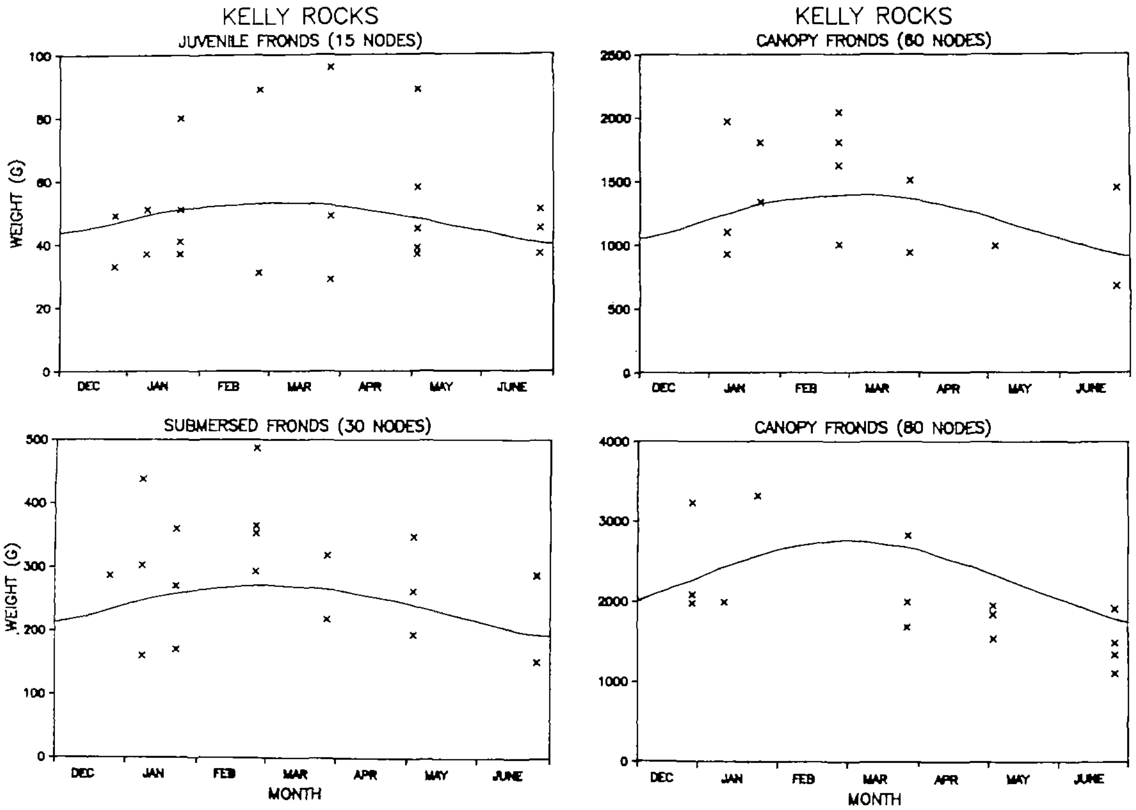

Fig. 5. *Macrocystis pyrifera.* Wet weight vs number of nodes on fronds of giant kelp at Kelly Rocks at different times of the year (1985–1986). Further details as in legend to Fig. 4

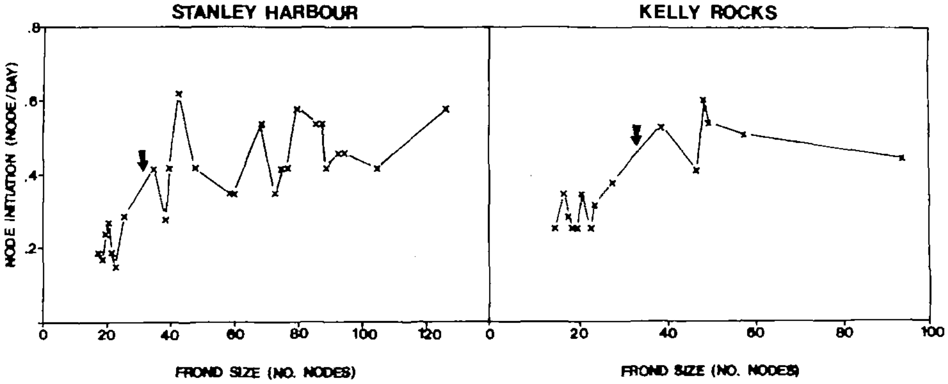

Fig. 6. *Macrocystis pyrifera.* Node initiation rate from January through February 1986 for different sizes of fronds from Stanley Harbour and Kelly Rocks. Frond size is expressed as median number of nodes counted during this period. Arrow indicates frond which has just reached water surface

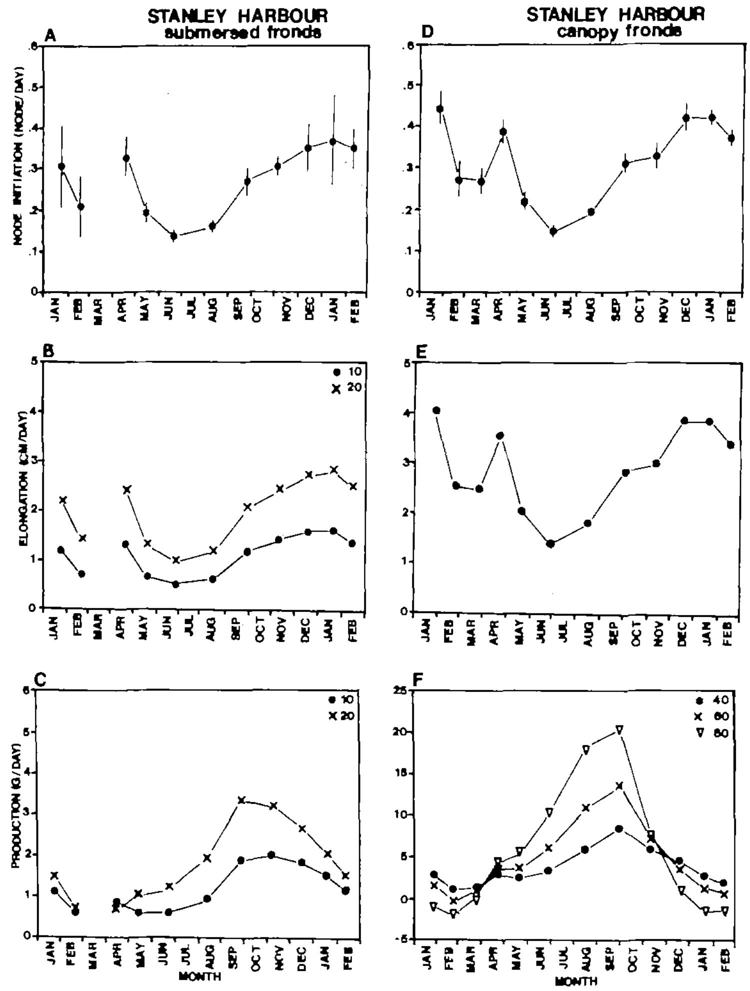

Fig. 7. *Macrocystis pyrifera*. Growth of fronds from December 1985 until March 1987 in Stanley Harbour. Mean node-initiation rate with 95% confidence limits (A, D), calculated frond elongation rate (B, E) and frond production in wet weight (C, F) for submersed fronds and canopy fronds. Sample size varied between 7 and 17 for submersed fronds (< 34 nodes) and between 11 and 29 for canopy fronds (> 33 nodes). Points are drawn at median time during the period measured; thus, first point presented is growth recorded from mid-January until mid-February. No submersed fronds were sampled from March through April 1986. Numbers in symbol key indicate number of nodes borne by fronds at time of tagging. Note differing ordinate scales for (C) and (F)

Table 2. *Macrocytis pyrifera*. Results of single-classification analysis of variance between calculated (E_{cal}) and measured (E_{meas}) frond elongation. Measurements were taken of submersed and canopy fronds in winter (May–June 1986) and summer (January–February 1987). Average calculated and measured elongation of these fronds is also listed. – : insufficient data were available to carry out analysis of variance

Frond sample	*F*-value	*n*	$E_{p=0.05}$	E_{cal}	E_{meas}
Submersed					
winter	0.33	6	10.0	1.52	1.66
summer	–	3	–	2.84	2.77
Canopy					
winter	0.06	14	6.41	2.17	2.13
summer	1.47	19	5.45	4.13	3.84

rate (Figs. 7 and 8 for Stanley Harbour and Kelly Rocks, respectively). Frond elongation was maximal in summer, minimal in winter.

The *F*-values of the analysis of variance of submersed and canopy fronds in Stanley Harbour testing differences between calculated and measured elongation rates, were not statistically important ($p = 0.05$; Table 2), indicating that calculated daily length increment for fronds in Stanley Harbour provide an accurate estimate of frond elongation.

In Stanley Harbour, net production of large canopy fronds was negative during mid-summer, i.e., loss of frond tissue was larger than that gained by production of new tissue (Fig. 7). In autumn production increased, reaching a maximum in October–November, corresponding with austral late spring. At Kelly Rocks, calculated frond production was high in summer, declining during autumn (Fig. 8).

Carbon and nitrogen content of kelp tissue

Fluctuations in percentage dry weight on wet weight basis and percentage carbon on dry weight basis, followed a similar seasonal pattern (Fig. 10). In Stanley Harbour, dry weight varied between 11 and 17% of wet weight, with a maximum in summer and a minimum in mid-winter. Carbon content varied between 25 and 30.5% of dry weight. At Kelly Rocks, percentage dry weight and carbon were generally lower and displayed less variation than those of the kelp from Stanley Harbour. Dry weight was maintained at between 12 and 13% of wet weight, being maximum at the onset of the autumn; carbon fluctuated between 24 and 27% of dry weight during the measurement period.

The total nitrogen content of the giant kelp in Stanley Harbour fluctuated over the year (Fig. 10). In summer it was

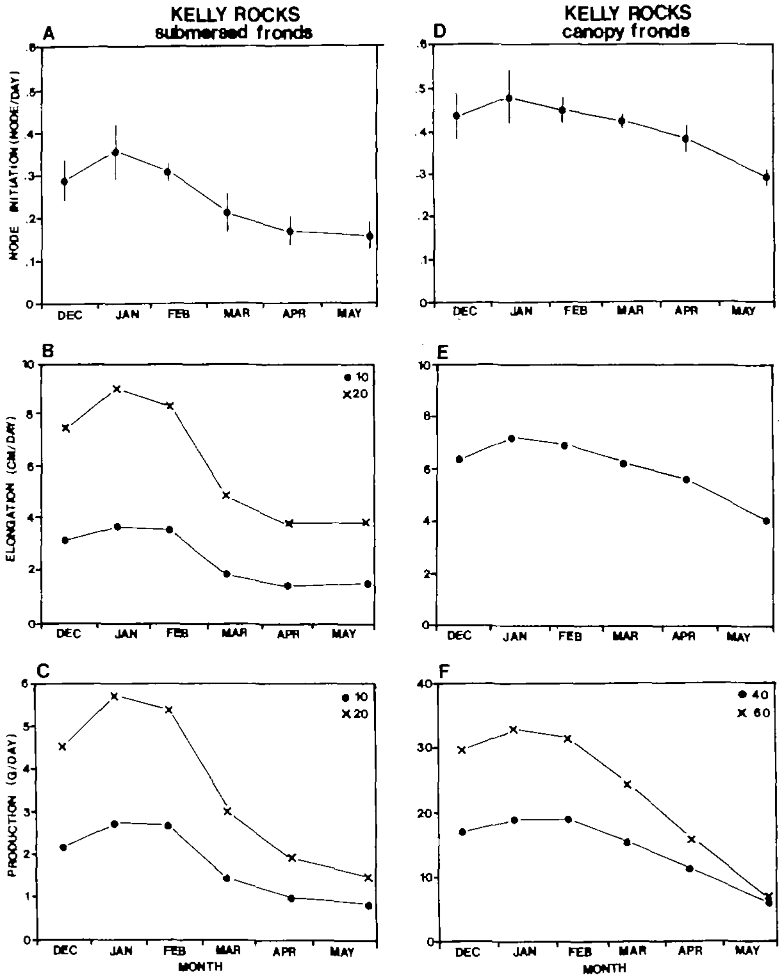

Fig. 8. *Macrocystis pyrifera*. Growth of fronds in deep bed at Kelly Rocks from November 1985 until June 1986. Sample size varied between 7 and 12 for submersed fronds and between 5 and 8 for canopy fronds. Further details as in legend to Fig. 7

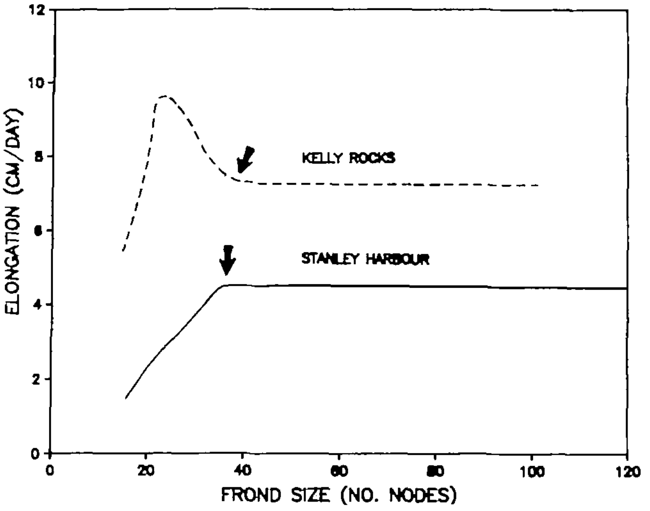

Fig. 9. *Macrocystis pyrifera*. Calculated elongation rates of fronds as a function of size for period January through February 1986. Frond size is expressed as median number of nodes counted during period studied. Arrow indicates frond which has just reached water surface

low (between 0.8 and 1.0% of the dry weight), increased in autumn, reached a maximum in mid-winter, and declined rapidly during late spring. Fluctuations in nitrogen content of fronds at Kelly Rocks were small (between 1.8 and 2.0% of dry weight; Fig. 10).

Correlations between growth, tissue composition and environment

Ambient water temperatures, nitrate concentration and day length are presented in Fig. 11. It was impossible to separate the effects on growth rate of water temperature or day length, since these were closely related to each other ($r = 0.89$, Student's $t = 11.59$, $n = 38$ in Stanley Harbour and $r = 0.85$, $t = 5.89$, $n = 13$ at Kelly Rocks). Table 3 gives the correlation coefficients between some environmental factors and growth and tissue composition of the giant kelp. Negative correlations are not listed, since these were considered to be incidental due to negative correlation between water temperature and ambient nitrate concentration ($r = -0.90$, Student's $t = 6.91$, $n = 13$ in Stanley Harbour and $r = -0.89$, $t = 3.11$, $n = 6$ at Kelly Rocks).

Node initiation rates of kelp at Stanley Harbour and at Kelly Rocks were positively correlated with water temperature. Frond elongation showed the same seasonal pattern as node initiation and their correlation coefficients are similar. In Stanley Harbour, frond production was positively correlated to nitrate concentration of the water, whilst at Kelly Rocks a positive correlation was found between production and water temperature.

The tissue nitrogen of giant kelp in Stanley Harbour was positively correlated with ambient nitrate concentration and

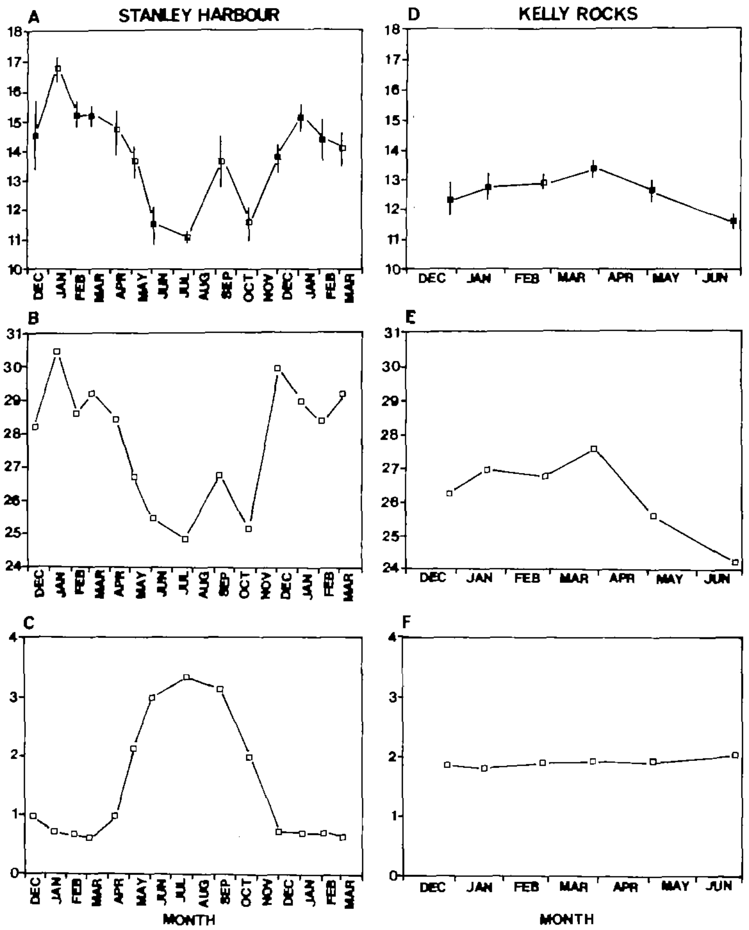

Fig. 10. *Macrocystis pyrifera.* Percentage dry weight on wet weight basis ± standard errors, $n=4$ (A, D) percentage carbon on dry weight basis (B, E) and percentage nitrogen on dry weight basis (C, F) from December 1985 to March 1987 for top 2 m of fronds from Stanley Harbour and from December 1985 to June 1986 for top 2 m of fronds from Kelly Rocks

with frond production; tissue percentage dry weight and carbon content were correlated with water temperature and with node initiation rate. At Kelly Rocks, no correlation was found between tissue nitrogen and nitrate concentration; positive correlations were found between the tissue carbon content and node initiation or production.

Discussion and conclusions

Frond growth

The node initiation rates of submersed fronds of *Macrocystis pyrifera* in the Falkland Islands was lower than those of canopy fronds. A similar increase in node initiation rate with increasing frond size was recorded by Gerard (1976), who found that a frond reached its maximum growth rate at a size when it bore 30 to 40 nodes, maintaining this rate until a size at which it bore ca. 90 nodes. Above this size, node initiation rate again decreased, in contrast to my findings in

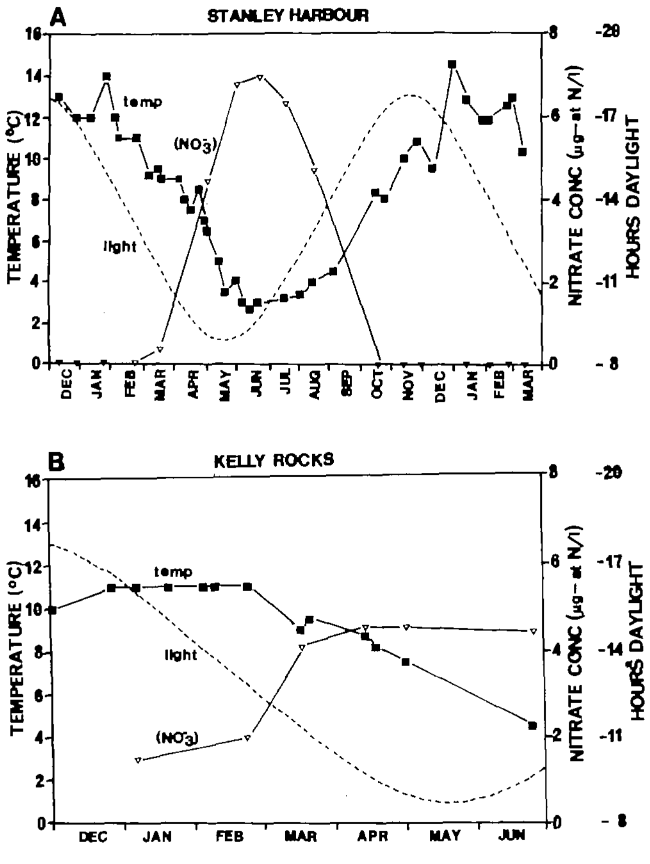

Fig. 11. Temperature and nitrate concentration of water at Stanley Harbour and Kelly Rocks. Zero data points for nitrate concentration in Stanley Harbour graph indicate that concentration was below detection levels. Day length is also shown (provided by Main Meteorological Office, Mount Pleasant, Falkland Islands)

Table 3. *Macrocystis pyrifera.* Correlation coefficients and their Student's *t*-values (in parentheses) between environmental factors, tissue composition and growth of fronds. Number of observations in Stanley Harbour was 13, at Kelly Rocks, 6. *T*: water temperature; [NO_3^-]: nitrate concentration of ambient water; Node-init: average node-initiation rate of canopy fronds; Product: production rate calculated for fronds of 60 nodes; %DM: dry weight of tissue; %C: tissue carbon content; %N: tissue nitrogen content; –: negative correlation found

Comparison growth/composition with environmental factors

	Stanley Harbour		Kelly Rocks	
	T	[NO_3^-]	*T*	[NO_3^-]
Node-init.	0.77 (4.05)	–	0.89 (3.84)	–
Product	–	0.71 (3.40)	0.88 (3.77)	–
% DM	0.78 (4.57)	–	NS	NS
% C	0.80 (4,.69)	–	0.87 (3.51)	NS
% N	–	0.98 (15.59)	NS	NS

Comparison composition of kelp tissue with growth

	Stanley Harbour		Kelly Rocks	
	Node-init	Product	Node-init	Product
% DM	0.61 (2.58)	–	NS	NS
% C	0.72 (3.42)	–	0.73 (2.16)	0.69 (2.08)
% N	–	0.69 (3.15)	–	–

the Falkland Islands, where fronds maintained a high node initiation rate until attaining at least 120 nodes in Stanley Harbour or 100 nodes at Kelly Rocks.

The elongation rate of submersed fronds increased with size until, at the surface, it became constant up to a frond bearing more than 100 nodes. In Stanley Harbour, the elongation rate of canopy fronds was higher than that of submersed fronds. At Kelly Rocks, the elongation rate decreased before the frond reached the surface, as recorded by North (1971, 1972) for *Macrocystis pyrifera* in California and Lobban (1978) for *M. integrifolia* in British Columbia. However, unlike the fronds from the Falkland Islands, those investigated by North (1971, 1972) and Lobban (1978) did not maintain a constant elongation level once they had become canopy-forming, and frond elongation rate declined with increasing size.

The elongation rate of submersed fronds at Kelly Rocks was more than twice that recorded for submersed fronds in Stanley Harbour. The regression of frond length on number of nodes indicates that the internodes of the submersed fronds at Kelly Rocks were substantially longer than those of the fronds in Stanley Habour. A similar increase in internode length with depth for *Macrocystis pyrifera* was recorded by Clendenning (1963), North (1971, 1972) and Kain (1982). North (1972) also recorded a faster elongation rate for fronds at greater depths, postulating that these extended more than those in shallower water in order to form a photosynthetic canopy at the surface where light is strongest.

The slope of the regression of length on number of nodes for the canopy fronds was steeper for Kelly Rocks than for Stanley Harbour, indicating that the internodes of the fronds at Kelly Rocks were longer. Kain (1982) recorded longer internodes for canopy fronds at two of three sites surveyed in New Zealand, and suggested that this difference between sites was probably due to tidal currents. The elongation rates of fronds at Kelly Rocks were at all times higher than those in Stanley Harbour. Pace (1972) found that frond elongation varied directly as a function of water movement, fronds in areas with more water movement growing faster. Unlike Stanley Harbour, large swells occur at Kelly Rocks, and the higher frond elongation rate recorded at the latter site might be due to the larger amount of water movement there.

Production of the fronds at Kelly Rocks was considerably higher than that of fronds with the same number of nodes in Stanley Harbour. As discussed below ("Seasonal growth fluctuations and environmental factors"), nutrient availability is an important contributory factor to this difference in production.

In addition to environmental factors, other differences between the two sites studied could have affected growth rates. The water at Kelly Rocks is generally clearer and water temperatures less extreme than at Stanley Harbour. Additionally, the giant kelp in Stanley Harbour was occasionally exposed during extreme low tides and was more prone to abrasion by stones and small rocks. Further studies are necessary to determine the effect of these and other factors on frond growth.

Growth rates of *Macrocystis pyrifera* fronds in the Falkland Islands were lower than those recorded in California. In Monterey Bay, Gerard (1976) recorded a node initiation rate of ca. 40 blades per month during a low-growth period, while during a high-growth period ca. 60 blades were formed each month, corresponding to an elongation rate of 18 or 25 cm d^{-1} and a production of 30 or 50 g d^{-1} in low and high growth periods, respectively. Similar elongation rates were recorded by North (1971, 1972) for this species at the same site. Kain (1982) recorded a node initiation rate of 1.1 nodes d^{-1} in California, which agreed with the findings of Gerard (1976). In California, *M. pyrifera* forms beds only in deeper waters; thus, growth rates can best be compared with rates recorded at Kelly Rocks in the Falkland Islands. A canopy frond of the giant kelp at this site formed 9 to 15 new blades per month, dependent on time of year. Maximum elongation rate was 7 cm d^{-1} and maximum production of a large canopy found was 30 g wet wt d^{-1}. Zimmerman and Kremer (1986) studied *M. pyrifera* at a different site in California and recorded elongation rates between 4 and 14 cm per day for submersed fronds. This was only slightly higher than the values of 2 to 10 cm per day recorded for submersed fronds at Kelly Rocks.

Macrocystis integrifolia, forming coastal zones in British Columbia, had a maximum node initiation rate of 0.4 nodes d^{-1} and a corresponding elongation rate of 4 cm d^{-1} (Lobban 1978). Similar maximum rates of 0.45 nodes d^{-1} and 4 cm d^{-1} were recorded for *M. pyrifera* in Stanley Harbour in the present study.

In Tasmania, Cribb (1954) recorded an elongation rate of 3.4 cm d^{-1} for *Macrocystis pyrifera* in the summer, which is comparable to the rate found for the canopy fronds in Stanley Harbour at the same time of year. Kain (1982) recorded a growth rate of 1 node every two days in New Zealand in late summer, which is slightly higher than the growth rate recorded for the fronds in the Falkland Islands. Comparison of growth rates between the Falkland Islands and the Kerguelen Islands is of interest since they are positioned at roughly the same latitude and nutrients are generally abundant in both areas (Zentara and Kamikowski 1981); however, the waters of the Kergulen Islands are substantially colder, since they are situated south of the Antarctic Convergence (Knox 1970). The growth rates of giant kelp in the Kerguelen Islands at a depth of 5 m were 0.3 nodes d^{-1} (2 cm d^{-1}) in summer and less than 0.2 nodes d^{-1} (1 cm d^{-1}) in winter (Asensi et al. 1981). These rates were lower than those recorded for a comparable site at Kelly Rocks in the Falkland Islands, perhaps due to the lower water temperatures at the Kerguelen Islands.

Seasonal growth fluctuations and environmental factors

Node initiation and frond elongation of the giant kelp in Stanley Harbour and at Kelly Rocks displayed a similar seasonal pattern. Values were high in the summer, declining in autumn and winter. The lower elongation and node initiation rates in winter were probably due either to lower temperatures or reduced light intensity.

In Stanley Harbour, the fronds of *Macrocystis pyrifera* attained maximum production rate in early spring, i.e., from September to October, probably because of the high nitrate concentration in the water at this time. The decline in production during late spring and summer could have been caused by low nutrient availability (see "Discussion and conclusions – Frond growth"). This is supported by the high correlation between frond production, nitrogen content of the kelp tissue and the ambient nitrate concentration. At Kelly Rocks, production of the fronds reached its maximum in the summer and no positive correlation was found between nutrient concentration and production. Nutrients were abundant throughout the period, in agreement with data of Zentara and Kamykowski (1981), who reported an excess of nitrate in subantarctic open-ocean surface water. Thus, at Kelly Rocks, ambient nitrate concentration probably never dropped below the level limiting for growth, as also indicated by the internal nitrogen content which remained well above the critical level of 1.1% considered as limiting to production (Gerard 1982b). Consequently, at this site, production was maintained at a relatively high level throughout the study, fluctuating as a function of light intensity or water temperature. The low nutrient concentrations during late spring and summer in Stanley Harbour may be caused by solar heating reinforced by poor nutrient exchange with outside water, due to the narrow passage connecting the harbour with the open ocean.

Records by Lobban (1978) of seasonal fluctuations in frond elongation rates of *Macrocystis integrifolia* in a shallow zone in Barkley Sound, Vancouver Island, British Columbia, are similar to those of *M. pyrifera* in Stanley Harbour. Frond elongation of *M. integrifolia* increased in late winter, reached a maximum in the summer, and declined during autumn (Lobban 1978), whereas the nitrate concentration of the ambient waters showed summer minima and winter maxima (Wheeler and Srivastava 1984). This suggests that the frond elongation of *M. integrifolia* in British Columbia reflects the seasonal pattern of either light intensity or temperature, as for *M. pyrifera* in the Falkland Islands. Asensi et al. (1981), who studied *M. pyrifera* at the Kerguelen Islands, also found a periodicity in node initiation and frond elongation rates corresponding to fluctuations in solar radiation.

Neither North (1971), Gerard (1976) nor Wheeler and North (1981) found any seasonal fluctuations in node initiation or elongation rates for *Macrocystis pyrifera* in California. However, erratic fluctuations were recorded and it was found that these were not related to the nutrient content of the water (Gerard 1976, Wheeler and North 1981). Zimmerman and Kremer (1986) studied *M. pyrifera* at a different site in California, and recorded a seasonal fluctuation in frond elongation rate, with a maximum in winter and a minimum in summer. They found a positive correlation between nitrate concentration of the water and elongation rate; however, elongation rates were not related to nitrogen content of mature blades. Wheeler and North (1980) found that the production rate of juvenile fronds in the laboratory was linearily related to ambient nitrogen concentration. Gerard (1982b) constructed a predictive model for NO_3^- uptake and nitrogen-limited production of *M. pyrifera* in which she postulated that production was limited at a NO_3^- concentration below 1 to 2 μM. She also transplanted plants of giant kelp to a low-nutrient environment and examined both elongation rate and productivity of the fronds, which decreased after 3 wk in this environment; they increased again after fertilization (Gerard 1982a). However, Druehl (1984) found that only the elongation rate increased after fertilization, no effect being made on the weight of the plants. Dean and Jacobsen (1984) reported strong stimulatory effects of elevated nitrogen levels on the elongation of juvenile fronds of giant kelp. North and Zimmerman (1984) recorded that deterioration of the canopy was retarded after fertilization in mid-summer.

These results are confusing, and it appears that both the elongation rate and production of the fronds of *Macrocystis pyrifera* in California are, under certain circumstances in different environments, limited by ambient nutrient concentrations. Some of the results found for the giant kelp in California agree with the findings in the Falkland Islands in the present study, whilst others contradict them. Two very important differences in the environmental factors in California and the Falkland Islands are light intensity and water temperature. The light levels in California are high and fairly constant throughout the year, whilst they fluctuate drastically in the Falkland Islands. High temperatures in the summer might possibly have a negative effect on the growth of *M. pyrifera* in California (Dean and Jacobsen 1984, Zimmerman and Kremer 1986), whilst in the Falkland Islands low temperatures in the winter might inhibit growth and summer temperatures probably do not reach a level high enough to be limiting. Additionally, nitrate was abundant throughout the study period at Kelly Rocks, Falkland Islands; a situation which does not occur at any site in California.

Carbon and nitrogen content of kelp tissue

Relations between growth, nutrients and internal nitrogen and carbon reserves have been more extensively studied for species of *Laminaria* than of *Macrocystis*. Chapman and Craigie (1977, 1978) found the onset of winter growth of *L. longicruris* to be correlated with a higher level of dissolved nitrate in the sea. A high growth rate was maintained for two months after nitrate depletion of the water, until the internal nitrogen reserves were exhausted. As the growth rate declined, carbohydrate reserves were formed, a result of the combination of saturating light levels and nutrient depletion.

Similar alternating maxima and minima in internal carbon and nitrogen content have been found for *Macrocystis pyrifera* in Stanley Harbour and in southern California by Wheeler and North (1981) and by Zimmerman and Kremer (1986) and also for *M. integrifolia* in British Columbia by Rosell and Srivastava (1985). All these studies showed that *Macrocystis* spp. stored nitrogen for shorter periods than *Laminaria* spp. In Stanley Harbour, in the present study, *M. pyrifera* stored nitrogen for a period of one month, as indicated by the decline in the internal nitrogen level to below 1% one month after depletion of the nitrate in the ambient water. A similar time lag between decreased internal nitrogen and depletion of ambient nitrate was found by Zimmerman and Kremer (1986) for *M. pyrifera* in California. For the same species, Gerard (1982 a) found that growth decreased two weeks after transplantation to a low-nutrient environment, suggesting that the internal nitrogen pool was exhausted after this period.

Gagné et al. (1982) compared growth of *Laminaria longicruris* from an area where nitrogen was abundant all year round with growth of plants from an area where nitrogen was low during the summer. Their results indicated that in the area where ambient nitrate concentration was low during summer, growth (i.e., blade elongation rate) and tissue nitrogen and carbon content followed a similar pattern in relation to ambient nitrates as that recorded by Chapman and Craigie (1977, 1978). However, when nitrogen was abundant all-year round, growth was correlated with seasonal patterns of light intensity, with high growth rates in the summer, and no internal carbon reserves were formed. Lüning (1979) reported similar results for *L. digitata* in a nutrient-rich environment in Helgoland, Germany. *L. hyberborea* and *L. saccharina*, however, ceased growing in mid-summer and accumulated carbon reserves.

At Kelly Rocks in the present study, *Macrocystis pyrifera* displayed a similar rection to that of *Laminaria longicruris* and *L. digitata*. Growth fluctuated as a function of light intensity or water temperature, and no internal carbon reserves were accumulated. This is illustrated by the stable but low C:N ratio for the kelp at Kelly Rocks, contrasting with the highly fluctuating C:N ratio of the giant kelp in Stanley Harbour (Fig. 12).

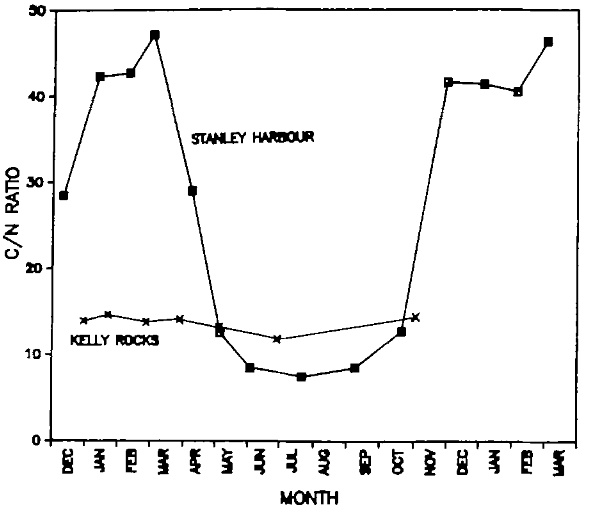

Fig. 12. *Macrocystis pyrifera*. C:N ratios for fronds from Stanley Harbour and Kelly Rocks, December 1985 to March 1987

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