

Age- and size-dependent growth and mortality in a population of *Fucus distichus*

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ABSTRACT: A *Fucus distichus* L. emend. Powell population at False Creek, Vancouver, Canada, showed seasonal variations in plant mean length and growth rates. Mean length was greater in winter (4.2 to 5.3 cm) and lower in summers of 1986 and 1987 (2.7 to 4.3 cm). Absolute growth rates showed a significantly opposite trend, being higher in spring and summer (0.24 to 1.17 cm mo⁻¹) and lower in fall to winter (-0.5 to 0.4 cm mo⁻¹). Spearman rank-order correlation indicated that, with some exceptions, monthly patterns of change in plant mean length for plants of different ages were significantly correlated, but growth rates were not significantly correlated among ages. Patterns of change in length among cohorts were significantly correlated, but those of growth rates were not, suggesting a low dependence of growth rate on age. Growth rate was significantly correlated (Spearman rank-order correlation) with plant length, and the patterns of change in growth rates among plants of different size classes were also significantly correlated (Pearson's correlation), suggesting that growth rate is strongly size-dependent. A seasonal pattern became more obvious only if plants were grouped by size rather than by age. Plants from different cohorts generally had constant rates of mortality. Mortality was generally higher for younger and smaller plants during winter and spring, and for older and larger plants during summer. Older plants also exhibited higher mortality in the fall. Log linear analysis indicated that the effects of both size (length) and age on growth rate, with or without the effect of mortality, and on mortality considered alone, were significant. However, when the contribution of size was known, the effect of age on mortality became insignificant. Size is shown by association analyses to be a better predictor of growth and mortality than age.

INTRODUCTION

The use of an appropriate state variable to describe demographic parameters such as growth, mortality, reproduction, and recruitment, is of fundamental importance in understanding the dynamics of a population (Caswell 1989). Because of the plastic morphology of many clonal organisms, e.g. scleractinian corals and bryozoans, and modular characters of higher plants, demographic theories and concepts developed based on solitary individuals and using age as a state variable are often inadequate when applied to them (e.g. Hughes 1984, Hughes & Jackson 1985). Demographic parameters of these organisms are more often size-related, rather than age-related. Size can therefore more accurately predict the fate of these organisms than age (Harper 1977, Hughes 1984, Hughes & Jackson 1985, Caswell 1989).

Many algae exhibit modular construction similar to that of higher plants. Although the population ecology of many algae has been examined, the question of the appropriateness of any state variable used to describe algal demographic parameters is seldom addressed. Many algal population studies are concerned with seasonal changes in plant size and growth rate. Size has been expressed in terms of length (Sideman & Mathieson 1983, Ang 1985, Klein 1987, Nelson 1989), area of the thallus (Kain 1976a, b), volume (Gunnill 1985), biomass wet weight (Kain 1976a, b, van Tussenbroek 1989), dry weight (Sheppard et al. 1978, Nelson 1989), percent cover (Keser & Larson 1984) or other parameters unique to the species or population [e.g. bushiness in *Gelidiella acerosa* (Forsk.) Feldmann et Hamel (Thomas et al. 1975), number of dichotomies in *Chondrus crispus* Stackhouse (Pringle & Semple 1988), or number of nodes on the fronds of *Macrocystis pyrifera* (L.) C. Ag. (van Tussenbroek 1989)]. Growth is usually expressed in absolute terms as a change in size over a fixed time period. It can also be expressed in relative terms as a change in size with respect to the

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initial size of the individual per unit time (Bird & McLachlan 1976, Kain 1976a, b, 1987).

Studies that deal with survivorship (or mortality) in algae are relatively few. Survivorship has been evaluated with respect to age, i.e. in a depletion curve (e.g. Chapman 1984, Dayton et al. 1984) or in a life table analysis (e.g. Gunnill 1980, Coyer & Zaugg-Haglund 1982, Dayton et al. 1984). More rarely, it has also been assessed with respect to frond size (e.g. Bhattacharya 1985).

The different variables used in algal population studies, such as age, length, wet weight, and dry weight, may all be important parameter descriptors. However, destructive sampling is necessary in order to obtain information about most of them. Individual plants have to be sacrificed in a destructive sampling. This reduces the sample size and changes the structure of the population under study. 'Destructive' variables such as weight and volume are thus limited in their utility as descriptors of demographic parameters. On the other hand, many of these variables are inter-related. For example, Gunnill (1985) found damp weight (fresh weight) of *Pelvetia fastigiata* (J. Ag.) de Toni to be strongly and positively related to dry weight, length and displacement volumes. Cheshire & Hallam (1989), citing Cheshire (1985), mentioned a highly significant allometric relationship between stipe circumference and palm thickness in *Durvillaea potatorum* (La Billardiere) Areschoug. De Wreede (1984) and Hymanson et al. (1990) found stipe length of *Pterygophora californica* Ruprecht to be significantly correlated with age, though the relationship is also site-dependent. Hence, it may be possible to make use of the 'non-destructive' or 'less-destructive' variables like age, length and area to assess population change. Plant age can be assessed by following plants through time (Dayton et al. 1984), although this is a tedious process. Other methods of age determination, such as counting growth rings, are destructive (De Wreede 1984, Hymanson et al. 1990). Area may be a better measure of frond size, e.g. in *Laminaria hyperborea* (Gunn.) Fosl. (Kain 1976a), but accurate measurement of area *in situ* is unlikely to be possible given the morphology of most algae. Thallus length (or width) appears to be logistically the simplest non-destructive way to measure a plant.

Ang (1991a) found plant length to be a better predictor of reproductive events than plant age in a population of *Fucus distichus* L. *emend.* Powell. This was also the conclusion of Chapman (1986) for *Laminaria longicruris* Pyle. Chapman (1984) found survivorship to be significantly affected by initial plant size in *L. longicruris* but not in *L. digitata* (Huds.) Lamour. In a subsequent study on *L. longicruris*, however, Chapman (1986) found that within age classes, size was not

related to survivorship, and only within one size class (301 to 400 cm length) was survivorship significantly affected by age. In another population of *L. longicruris*, Smith (1985) found no relationship between plant size and survivorship among plants > 50 cm long. Black (1974) found a positive relationship between growth rate and initial length in *Egregia laevigata* (Setchell). Sheppard et al. (1978) mentioned the positive relationship between age and growth in *L. hyperborea* and *L. ochroleuca* Pyl., but it is not clear how they estimated plant age or determined the growth-age relationship.

In this paper, seasonal patterns of change in plant age structure and plant length of *Fucus distichus* are presented. Growth rate and mortality (survivorship) are then evaluated with respect to plant age and plant length using correlation and log linear analyses and analysis of simple, multiple and partial association to assess which of the state variables is a better descriptor of these parameters.

MATERIALS AND METHODS

The study area is located along the southern seawall of False Creek, Vancouver, British Columbia, Canada (49° 17' N, 123° 7' W). The wall supports an almost pure stand of *Fucus distichus* L. *emend.* Powell which forms a distinct zone (hereafter referred to as the *Fucus* zone) 1.5 to 2 m in width along the seawall 2.5 m above the Lowest Normal Tides (LNT).

Age, size (length), and absolute growth rates. Three 50 × 50 cm permanent quadrats were randomly set up in the *Fucus* zone. All plants within each quadrat were mapped monthly, and thus aged, from July 1985 to November 1987 (except August 1985 and November 1986) as described in Ang (1991a). A plant was designated as Age 1 at the time when it first appeared in the quadrat. Monthly mean frequency (%) distribution of age classes was calculated based on the number of plants in each monthly age class over the total number of plants of known age in each quadrat. Linear sizes of these plants were measured to the nearest mm from the base of the holdfast to the tip of the longest branch. Mean frequency (%) size class distribution was then calculated based on the number of plants in each size class over the total number of plants in each quadrat. Size classes were designated as follow: Size Class 1 included plants < 1 cm long; Size Class 2, ≥ 1 to < 2.5 cm; Size Class 3, ≥ 2.5 to < 4.5 cm; Size Class 4, ≥ 4.5 to < 9.5 cm; and Size Class 5 included plants ≥ 9.5 cm long. Growth of individuals was monitored by changes in plant length. Detailed length measurements were recorded only for plants ≥ 1 cm. Absolute growth rate (AGR) was calculated as an increase (or decrease) in length over a time period (usually 1 mo) using the equation:

$$\text{AGR} = \frac{(L_{t_2} - L_{t_1})}{(t_2 - t_1)}$$

where L_{t_1} is the length of the plant at Time 1 (t_1), and L_{t_2} is the length of the plant at Time 2 (t_2). For comparative purposes, any decrease in plant length over time due to attrition or degeneration (die-back) is referred to as negative growth, so values of AGR can be positive or negative.

Mortality and survivorship. The fate of each individual was monitored based on monthly mappings. Any individual that disappeared from the permanent quadrats was considered dead. Mortality was measured as a percentage of plants lost over time (usually 1 mo) by the equation:

$$M = \frac{(N_{t_1} - N_{t_2})}{N_{t_1}} \times 100$$

where M = percent mortality; N_{t_1} = number of plants per quadrat at Time 1; and N_{t_2} = the remaining number of plants per quadrat at Time 2, excluding the new recruits. Percent survivorship (S) is given as:

$$S = 100\% - M.$$

All plants, including those < 1 cm in length, were monitored in the mortality study. The minimal detectable size was around 1 mm. Plants that were first detected in each quadrat in each month were considered as new recruits (see Ang 1991a) and each set of new recruits was monitored as a monthly cohort.

When permanent quadrats were first set up in July 1985, a set of plants < 1 cm long were present. This set of plants was included in the analysis as a monthly cohort. It is not known how many of these plants were actually new recruits for July 1985. Thus, this cohort included all plants that recruited on or before July 1985 and were < 1 cm at the time of sampling. Quadrats were not checked in August 1985, so plants that were recorded as new in September 1985 actually represented individuals that recruited in either August or September.

Age vs size as the descriptor (predictor) of growth and mortality. Growth rates were correlated separately with plant age and size from each quadrat at each month of the monitoring period from September 1985 to October 1987. Furthermore, as in Ang (1991a), log linear analyses and simple, multiple and partial associations were used to evaluate age vs size as a predictor of absolute growth rate and of mortality. Log linear analysis evaluates qualitatively, and association analysis quantitatively, the contribution of age vs size to the knowledge of growth rates and mortality. More details about these 2 methods are described in Ang (1991a) and in Caswell (1989).

For purposes of these evaluations, only plants of known age were used. To minimize the number of

sparse cells in the contingency table, plants of different ages were grouped into the following age classes: Age Class 1 for plants 1 to 2 mo old; Age Class 2, 3 to 4 mo old; Age Class 3, 5 to 6 mo old; Age Class 4, 7 to 9 mo old; and Age Class 5 for plants > 9 mo old. Likewise, these plants were grouped into the different size classes designated earlier. Based on absolute growth rates (AGR), plants were also divided into 4 categories: plants that died were given a growth rate of -100 cm mo^{-1} (a rate that no plant could actually attain), and grouped as AGR 1; AGR 2 for plants with a growth rate -100 to $\leq 0 \text{ cm mo}^{-1}$; AGR 3, > 0 to 2 cm mo^{-1} ; and AGR 4 for plants with a growth rate $> 2 \text{ cm mo}^{-1}$. In addition, plants were classified into 2 groups, those that died and those that survived.

The range of categories used to partition plants with different growth rates was obtained based on the distribution of data points in growth vs length and growth vs age scatter plots. Further division of the categories into smaller ranges resulted in more than 20 % of cells in the contingency tables having a value less than 5.

To evaluate the effect of age vs size on growth rates, Size Class 1 and Age Class 1 were not included in the analyses. Plants of Age Class 1 (1 to 2 mo old) were usually < 1 cm long. Their length was not recorded in detail, hence information on their growth rates was not available. Although these plants may have experienced a high mortality rate, because they were mostly < 1 cm long, their exclusion should not affect the analyses on age- or size-dependence. AGR 1 was included in the evaluation of the respective effects of age vs size on mortality.

Statistical analyses. Data were first tested for normality (Lilliefors's test) and homogeneity of variances (Bartlett's test) before application of parametric statistical analyses. If necessary, data were transformed to meet the parametric assumptions. Distribution-free statistics were used if data transformation was unsuccessful. Pearson's linear correlation or Spearman rank-order correlation were used to relate the patterns of change in length, growth rate and mortality among cohorts, time, age and size classes. Analysis of covariance (ANCOVA) was used to evaluate the effect of time on the survivorship of plants of each cohort. All analyses were performed using SYSTAT (Wilkinson 1988).

RESULTS

Overall seasonal trend

Mean length and growth rate of the *Fucus* population at False Creek were negatively correlated (Spearman rank-order correlation, $r_s = -0.453$, $p < 0.001$, $n = 74$). Largest plants were initially recorded in summer 1985.

Mean length subsequently declined from fall-winter 1985–86 to level off in the summer of 1986, then increased through winter 1986 and declined again in the summer of 1987 (Fig. 1). Mean growth rate showed an opposite trend, with higher growth rates in the spring and summer and lower growth rates in the fall and winter (Fig. 1).

Age distribution, length and growth

For all months, mean frequency (%) of age distribution for plants of known age in the permanent quadrats was highly skewed, with most of the plants in the younger age classes (Fig. 2). Age class distributions presented for November 1985 through July 1986 did not represent the true age structure of all the plants within the quadrats. Ages of the plants which were already present at the beginning of sampling in July 1985, and which survived through this period, were not known. Nevertheless, recruits of < 1 cm in size (ca 1 mo old) were usually the most numerous among the total number of plants (see 'Size class distribution, age and growth' below), hence the true age class distributions of all the plants within the quadrats during this period were most likely to be highly skewed as well.

For each monthly cohort, plant length generally increased with plant age (Table 1, Spearman rank-order correlation between age and length) but the

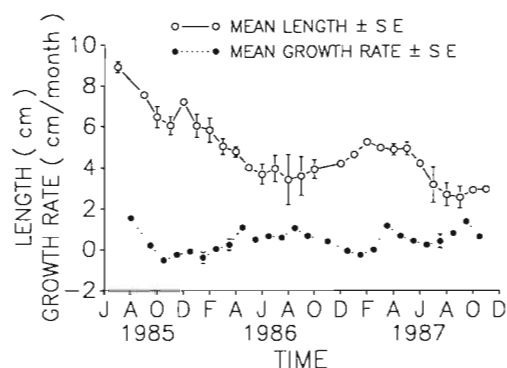


Fig. 1. *Fucus distichus*. Seasonal patterns of change in mean (\pm SE) plant length and absolute growth rates of the population from False Creek. Error bars < 0.4 cm or cm mo^{-1} not shown

increase was not monotonic (Fig. 3). At any one time, the longest plants were not necessarily the oldest ones. The pattern of change in mean growth rate among cohorts was less consistent over time (Fig. 3). Cohorts from April to July 1986 tended to show a negative correlation, and those from other months a positive correlation, between plant age and growth rate (Table 1). This means that compared to older plants, younger plants tended to show higher growth rates between late spring and early summer of 1986 and lower growth rates during other times. It is not known if this pattern held for monthly cohorts initiated beyond May 1987

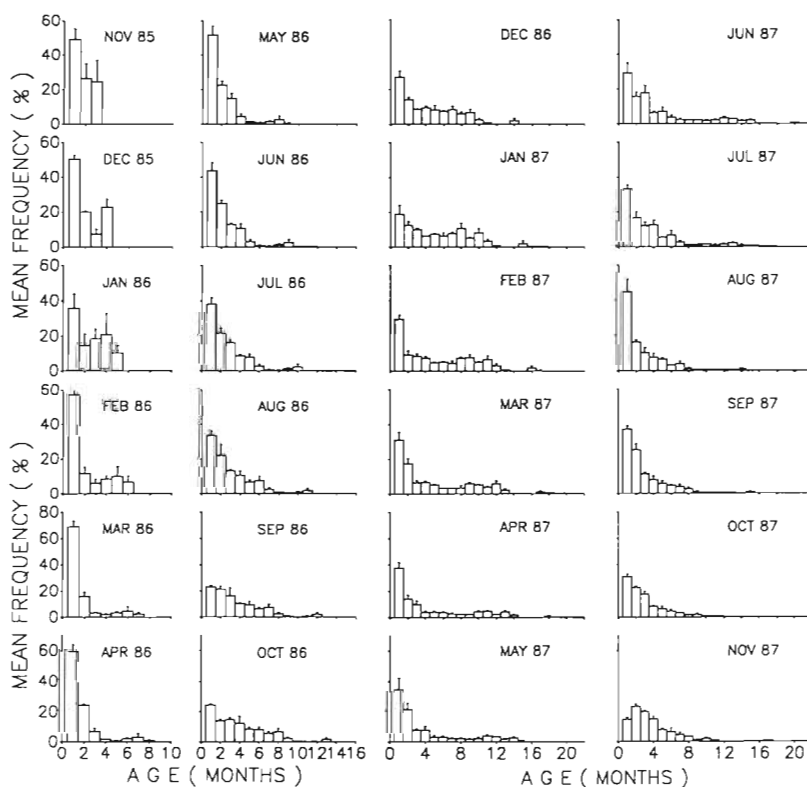


Fig. 2. *Fucus distichus*. Monthly mean (\pm SE) age structure of the population. Data are from means of 3 quadrats

Table 1. *Fucus distichus*. Matrix of Spearman rank-order correlation coefficients between age and growth rate (AGR), and age and length in different cohorts in each quadrat (Q). n: sample size

Cohort	Q	n	AGR	Length	Cohort	Q	n	AGR	Length
Sep 85	1	123	0.357*	0.817*	Jul 86	1	331	0.047	0.406*
	2	71	0.574*	0.762*		2	77	-0.103	0.410*
Oct 85	1	9	0.783*	0.937*		3	21	-0.526*	0.644*
	2	41	-0.267	0.554*	Aug 86	1	108	0.065	0.491*
	3	151	0.020	0.549*		2	65	0.278*	0.419*
Nov 85	1	30	0.496*	0.832*		3	14	0.135	0.768*
	2	62	0.252*	0.761*	Sep 86	1	49	0.504*	0.573*
	3	41	-0.156	0.743*		2	46	0.114	0.543*
Dec 85	1	29	0.412*	0.887*		3	21	0.722*	0.742*
	2	57	0.166	0.757*	Oct 86	1	38	0.646*	0.682*
Jan 86	1	31	0.070	0.966*		2	23	0.516*	0.306
	2	70	0.086	0.684*		3	20	0.684*	0.879*
	3	13	-0.361	0.588*	Dec 86	1	46	0.197	0.406*
Feb 86	1	39	-0.049	0.628*		2	16	-0.099	0.258
	2	239	0.003	0.606*		3	11	0.159	0.348
	3	49	0.172	0.355*	Jan 87	1	69	0.039	0.414*
Mar 86	1	194	0.077	0.703*		2	4	0.316	0.833
	2	349	0.039	0.734*		3	23	0.415*	0.734*
	3	122	0.203*	0.654*	Feb 87	1	118	0.241*	0.551*
Apr 86	1	216	-0.149*	0.631*		2	9	0.375	0.491*
	2	185	-0.049	0.484*		3	42	0.531*	0.704*
	3	62	0.025	0.660*	Mar 87	1	42	0.307*	0.592*
May 86	1	229	-0.159*	0.630*		2	33	0.532*	0.797*
	2	138	-0.053	0.585*		3	24	0.395*	0.564*
	3	106	-0.233*	0.528*	Apr 87	1	95	0.322*	0.552*
Jun 86	1	350	-0.125*	0.728*		2	60	0.468*	0.591*
	2	134	-0.176*	0.466*		3	30	0.229	0.802*
	3	67	0.265*	0.709*	May 87	1	29	0.224	0.515*
						2	44	0.026	0.759*
						3	65	-0.028	0.504*

* $p \leq 0.05$

and through summer 1987. Monitoring of the quadrats was terminated in November 1987, hence insufficient data were available about these cohorts to provide a meaningful analysis of the pattern observed.

Plants of the same age differed in their mean length at different times (Fig. 4). The mean length of 3 to 7 mo old plants was longer between summer and fall of 1986, shorter between winter and spring of 1987, and became longer again in the fall of 1987. Patterns for plants ≥ 8 mo old were more irregular. A decrease in plant length was usually preceded by a decrease in growth rates (Fig. 4). However, most plants did not exhibit any consistent pattern of change in their growth rates over time.

Size class distribution, age and growth

Mean monthly size class distribution of the plants of known age was monitored from the time they were first

detected in the permanent quadrats. Early on, only young and small plants were of known age. This explains the high proportion of plants in Size Class 1 up to July 1986 (Fig. 5). By August 1986, more than 90 % of the plants in the quadrats were of known age. The pattern of distribution from August 1986 onward is therefore a better representation of the actual frequency distribution of the population. Except for the last 2 mo of the monitoring, plants in Size Class 1 were consistently the most numerous, ranging from 40 to 60 % of the total population (Fig. 5).

For plants ≥ 1 cm, monthly data from 61.5 % (40 out of 65) of the quadrats showed a significant positive correlation between plant length and growth rate (Table 2), suggesting that growth rate is largely size-dependent. This is further shown in cohort data, with 63.8 % (37 out of 58) of the cohorts showing a positive correlation between plant length and growth rate (Table 3).

Mean monthly plant length within the different size

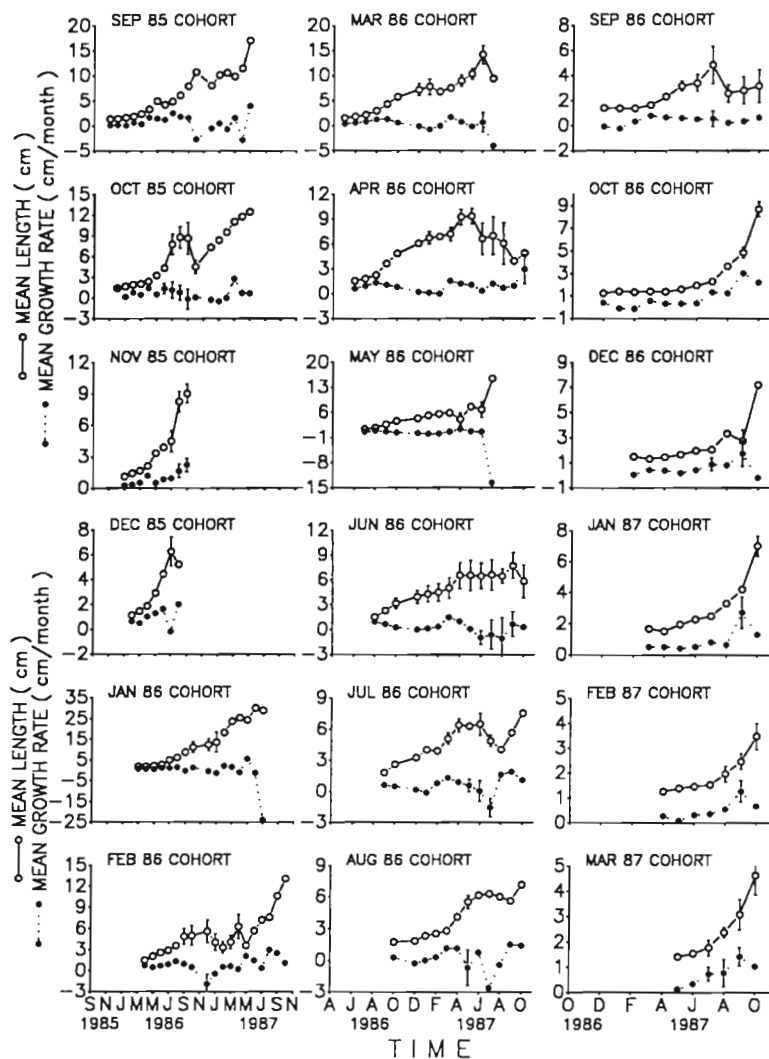


Fig. 3. *Fucus distichus*. Patterns of change in mean (\pm SE) length and growth rates of cohorts from the 3 permanent quadrats over time. Date in each graph indicates the time when the cohort was first detected in the population. Error bars < 2.0 cm or cm mo^{-1} not shown

classes showed considerable variation (Fig. 6). This was especially so in Size Class 5. Given that this size class included plants in a wider range of sizes, a wider range of variation of monthly mean plant length was expected. Within this size class, plants were longer during summer and shorter between fall and winter. This pattern was not consistent in other size classes, although a decrease in plant length was mainly associated with late spring and summer months.

Plants in the larger size classes were generally older than those in the smaller size classes, although there were considerable overlaps of mean plant ages among them (Fig. 6). The presence of younger plants in Size Classes 2 to 4 early on was partly an artifact of sampling, where only the younger plants were of known ages. The increase in the mean plant age in all size classes starting in October 1986 was related to the degeneration (negative growth) of terminal branches among older and larger plants (cf. Figs. 6 & 7). The

subsequent loss of these plants in different size classes at different times caused the decline in the mean plant age (see 'Mortality and survivorship' below).

Mean growth rates were generally lower during winter and higher during summer (Fig. 7). This trend was less distinct in Size Class 4 where lower growth rates were also recorded in the summer months of 1987. Plants in Size Class 5 experienced negative growth rates in summer, and higher positive growth rates in spring and fall. Patterns of change in mean plant length over time were generally not significantly correlated with those of mean age and growth rates within each size class (Spearman rank-order correlation, $r_s > 0.05$).

Mortality and survivorship

The survivorship of different monthly cohorts from July 1985 to October 1986, when expressed in a log

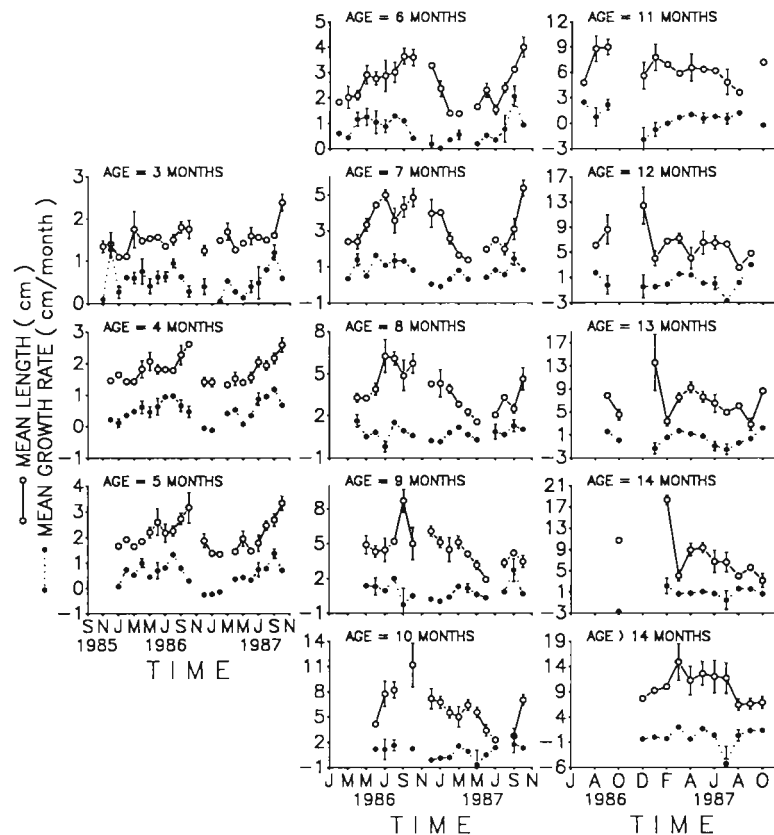


Fig. 4. *Fucus distichus*. Mean (\pm SE) length and growth rates of plants of the same age at different times during the monitoring period from September 1985 to November 1987. Error bars < 2.0 cm or cm mo^{-1} not shown. Due to differences in the longevity of monthly cohorts, plants of all ages are not always present at all times

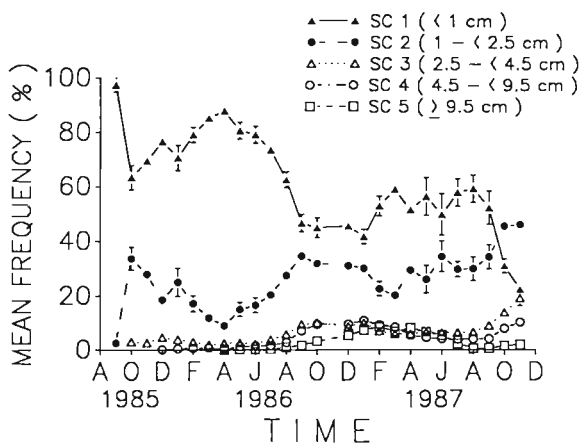


Fig. 5. *Fucus distichus*. Mean frequency ($\% \pm$ SE) size class distribution of plants of known age. Data are from mean values of the 3 permanent quadrats. Error bars < 2.5 % not shown

scale, generally assumes a straight line. This suggests a constant rate of survivorship among these cohorts over time. However, mortality frequently increased when the plants became older (Fig. 8). Results of the ANCOVA (Table 4A) indicate that not all survivorship curves have the same slope, i.e. not all cohorts had the same survival rate over time. Cohorts of July, Sep-

tember, and October 1985, and of January and February 1986, did not differ significantly in their survival rate (Table 4B). Calculated from a regression line on pooled data, these cohorts had a survival rate of 89 % per month (linear regression: $\text{Log } Y = 1.831 - 0.050X$, $r^2 = 0.535$, $p < 0.001$, $n = 218$). Monthly cohorts of March to June 1986 can also be pooled (Table 4C) and showed a survival rate at 81 % per month (linear regression: $\text{Log } Y = 2.654 - 0.092X$, $r^2 = 0.874$, $p < 0.001$, $n = 196$). Cohorts of November and December 1985, which had very short life span (< 12 mo) are grouped with cohorts of June 1986 to May of 1987 (Table 4D). These latter cohorts were not followed to the end of their life span. The resulting regression line from the pooled data indicates a high survival rate of 91.6 % per month (linear regression: $\text{Log } Y = 1.957 - 0.038X$, $r^2 = 0.193$, $p < 0.001$, $n = 367$). However, although the regression is significant, it accounts for only 20 % of the variation within the pooled data.

Ages of plants that either died or survived in each month were significantly different among the 3 quadrats (Kruskal-Wallis 1-way ANOVA by rank, $p \leq 0.05$). Based on mean values for each quadrat (Fig. 9A), results from paired t -tests indicate that the mean age of plants that survived was significantly different from the mean age of those that died ($t = -2.128$, $df = 65$,

Table 2. *Fucus distichus*. Matrix of Spearman rank-order correlation coefficients between plant length and growth rate (AGR) per quadrat (Q) over different time periods. n: sample size

Time	Q	n	AGR	Time	Q	n	AGR
Dec 85	1	14	-0.369	Dec 86	1	143	0.254*
	2	14	0.312		2	112	0.190*
					3	52	0.075
Jan 86	1	19	0.097	Jan 87	1	102	0.392*
	2	18	-0.046		2	79	0.340*
	3	23	-0.383		3	49	0.011
Feb 86	1	20	-0.357	Feb 87	1	90	0.152
	2	30	0.363*		2	63	0.185
	3	23	0.427*		3	40	0.113
Mar 86	1	34	0.160	Mar 87	1	88	0.702*
	2	49	0.025		2	54	0.656*
	3	25	0.525*		3	43	0.512*
Apr 86	1	36	0.134	Apr 87	1	119	0.582*
	2	83	0.478*		2	52	0.688*
	3	27	0.637*		3	44	0.374*
May 86	1	82	0.341*	May 87	1	104	0.290*
	2	166	0.315*		2	45	0.309*
	3	45	0.191		3	40	0.306
Jun 86	1	136	0.306*	Jun 87	1	100	0.477*
	2	196	0.379*		2	32	-0.104
	3	42	0.121		3	35	0.246
Jul 86	1	97	0.405*	Jul 87	1	78	-0.086
	2	113	0.385*		2	37	0.060
	3	50	0.171		3	36	0.310
Aug 86	1	179	0.425*	Aug 87	1	80	0.519*
	2	165	0.524*		2	50	0.205
	3	58	0.388*		3	61	0.192
Sep 86	1	319	0.457*	Sep 87	1	115	0.380*
	2	172	0.505*		2	61	0.459*
	3	63	0.555*		3	94	0.550*
Oct 86	1	197	0.252*	Oct 87	1	176	0.440*
	2	134	0.229*		2	114	0.420*
	3	59	0.326*		3	101	0.420*

* $p \leq 0.05$

$p = 0.037$). This is mainly because plants that died from May to August 1987 were significantly older than those that survived (t -test, $t = 2.842$, $df = 22$, $p = 0.009$).

Lengths of plants that either died or survived in each month were not significantly different among quadrats (Kruskal-Wallis 1-way ANOVA by rank, $p > 0.05$). Monthly data from the 3 quadrats were therefore pooled. Over the whole sampling period (Fig. 9B), the mean length of plants that survived was not significantly different from that of those that died (paired t -test, $t = 0.757$, $df = 22$, $p = 0.457$). However, on a month to month basis, the difference was significant (Mann-Whitney U -test, $p < 0.05$) in February, April, June, and September 1986 to January 1987 where

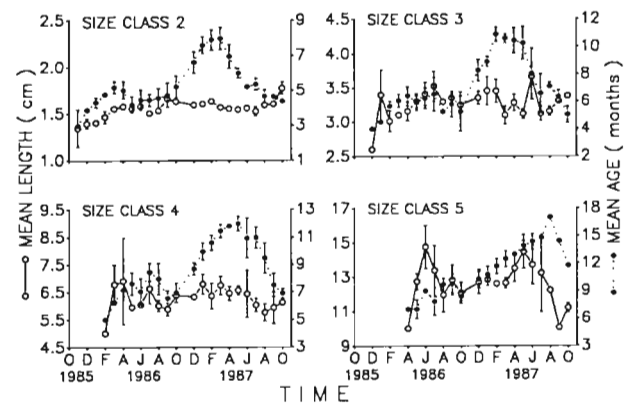


Fig. 6. *Fucus distichus*. Seasonal patterns of change in mean (\pm SE) age and length of plants in different size classes. Data are from mean values of the 3 permanent quadrats. Error bars < 2.5 mo or 0.04 cm not shown

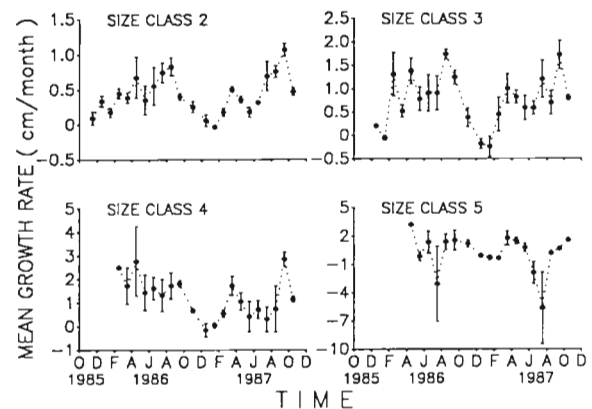


Fig. 7. *Fucus distichus*. Seasonal patterns of change in mean (\pm SE) growth rate of plants in different size classes. Data are from mean values of the 3 permanent quadrats. Error bars < 0.25 cm mo $^{-1}$ not shown

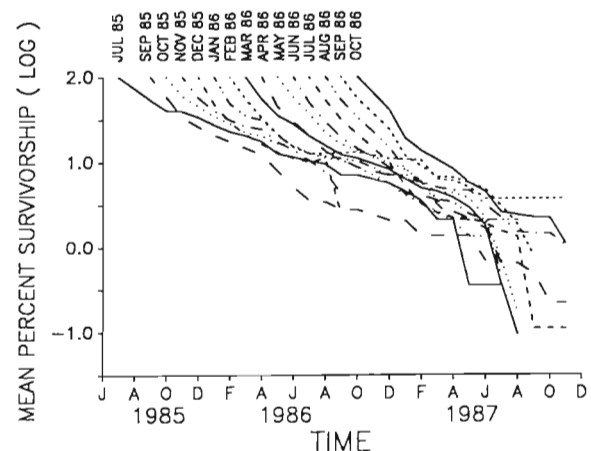


Fig. 8. *Fucus distichus*. Mean survivorship curves (\log_{10}) of different cohorts in the 3 permanent quadrats. Data for July 1985 included all plants < 1 cm which were present in July 1985. Error bars not shown

Table 3. *Fucus distichus*. Matrix of Spearman rank-order correlation coefficients between plant length and growth rate (AGR) in different cohorts in each quadrat (Q). n: sample size

Cohort	Q	n	AGR	Cohort	Q	n	AGR
Sep 85	1	123	0.321*	Jul 86	1	331	0.383*
	2	71	0.518*		2	77	0.116
Oct 85					3	21	-0.136
			Aug 86	1	108	0.225*	
				2	65	0.254*	
3	14	0.416					
Nov 85	1	30	0.344	Sep 86	1	49	0.528*
	2	62	0.496*		2	46	-0.186
	3	41	0.135		3	21	0.618*
Dec 85	1	29	0.430*	Oct 86	1	38	0.485*
	2	57	0.312*		2	23	0.086
Jan 86					3	20	0.576*
			Dec 86	1	46	0.175	
				2	16	-0.130	
3	11	0.828*					
Feb 86	1	39	0.369*	Jan 87	1	69	0.437*
	2	239	0.291*		2	4	0.632
	3	49	0.111		3	23	0.503*
Mar 86	1	194	0.190*	Feb 87	1	118	0.262*
	2	349	0.175*		2	9	0.775*
	3	122	0.264*		3	42	0.465*
Apr 86	1	216	0.089	Mar 87	1	42	0.400*
	2	185	0.400*		2	33	0.420*
	3	62	0.284*		3	24	0.130
May 86	1	229	0.188*	Apr 87	1	95	0.418*
	2	138	0.257*		2	60	0.266*
	3	106	-0.077		3	30	0.254
Jun 86	1	350	0.142*	May 87	1	29	0.247
	2	134	0.121		2	44	0.255
	3	67	0.299*		3	65	0.281*

* p ≤ 0.05

* $p \leq 0.05$

plants that died were smaller than those that survived, and from May to June 1987, where larger plants were the ones that died.

Plants 1 mo old generally suffered greater mortality (ca 40 %) than older plants, although plants ≥ 9 mo old occasionally had mortality exceeding 80 %. There was an increase in mortality among plants 1 to 4 mo old between fall 1986 and winter 1986–87. If examined by seasons (Fig. 10), some of the older plants (≥ 9 mo) suffered very high mortality in summer and fall (up to 100 %), much higher than that experienced by younger plants. In the winter and spring of 1987, younger plants appeared to suffer greater mortality than did the older plants. However, the patterns observed for 1986 were not similar to those observed for 1987, suggesting significant interannual variation in mortality among plants of different ages.

When grouped by size, plants in Size Class 1 (< 1 cm long) generally exhibited a greater mortality (ca 40 %) than those in other size classes (Fig. 11). However, plants in other size classes suffered higher than 40 %

mortality at times. The overall patterns were similar only between plants in Size Classes 2 and 3, and in Size Classes 3 and 5 (Spearman rank-order correlation, $p < 0.05$ for both tests). Mortality was generally higher (40 to 60 %) for Size Class 1 in most seasons except summer when mortality in Size Classes 3 to 5 could be as high as 60 to 70 % (Fig. 12).

Log linear and association analyses on age vs size as descriptor of growth and mortality

Growth and mortality rates were significantly different among plants from different quadrats at different times of the year (Kruskal-Wallis 1-way ANOVA by rank, $p < 0.05$). If all the plants monitored are considered, irrespective of seasonality and their spatial location among quadrats, results of log linear analyses (Table 5) indicate a highly significant effect of age and/or size (as length) on growth, with or without the effect of mortality. The effects of age or size may be taken

Table 4. *Fucus distichus*. Results of ANCOVA on the effect of time on the survivorship of plants of each cohort. The covariates are the cohorts listed in the table

Source of variation	df	MS	F	p
A. All monthly cohorts from July 1985 to May 1987				
Time	1	35.476	696.05	< 0.001
Cohorts	23	1.090	21.38	< 0.001
Time × Cohorts	23	0.560	10.99	< 0.001
Error	811	0.051		
B. Cohorts of July, September, October 1985, January, February 1986				
Time	1	23.415	366.85	< 0.001
Cohorts	4	0.045	0.70	0.592
Time × Cohorts	4	0.151	2.37	0.054
Error	208	0.064		
C. Monthly cohorts of March to June 1986				
Time	1	44.389	1560.14	< 0.001
Cohorts	3	0.092	3.24	0.023
Time × Cohorts	3	0.035	1.24	0.295
Error	188	0.028		
D. Monthly cohorts of November, December 1985, and June 1986 to May 1987				
Time	1	37.914	950.59	< 0.001
Cohorts	11	0.450	11.28	< 0.001
Time × Cohorts	11	0.046	1.15	0.324
Error	343	0.040		

together (Age × Size × Growth) or considered alone (Age × Growth or Size × Growth), or the effect of age on growth may be evaluated given the known contribution of size (Age × Growth/Size) or vice versa

(Size × Growth/Age). Similarly, the effect of age and/or size on mortality is also highly significant except in the case where the effect of age on mortality is evaluated given the known contribution of size (Table 5C). When data were pooled to reflect seasonality and differences among plants in each quadrat, the effect of size on growth with or without the effect of mortality, and on mortality alone, is significant in a greater number of cases than is the effect of age. This is true either when size or age is considered alone, or when the contribution of age or size respectively is known.

Association analyses indicate that on average among the 3 quadrats, size is more important than age by 9.3 % (± 4.1 % SE) as a predictor of growth when the effect of mortality is considered, and by 24.0 % (± 8.9 %) without the effect of mortality (Fig. 13). Size is also a better predictor of mortality than age by 12.7 % (± 4.7 %) (Fig. 13). Based on pooled seasonal data from each quadrat, there are a few cases when age is more important than size as a descriptor of growth or mortality. However, no consistent pattern is present to indicate any seasonal trend.

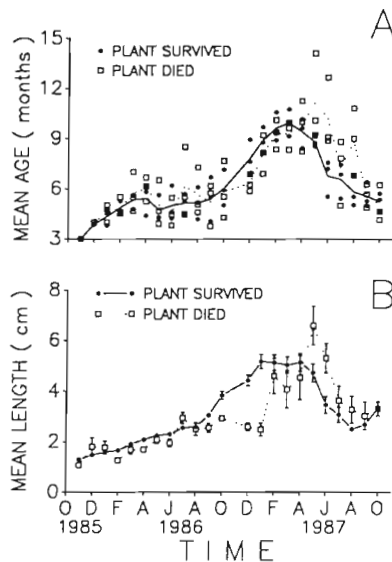


Fig. 9. *Fucus distichus*. (A) Mean age of plants that survived and died during the monitoring period. Data are mean values for each permanent quadrat. Mean ages of plants that survived (—) or died (---) from the 3 quadrats are also given. Error bars not shown. (B) Mean (\pm SE) length of plants that survived and died during the same period. Data are from mean values of the 3 permanent quadrats. Error bars < 0.16 cm not shown

DISCUSSION

For the population of *Fucus distichus* at False Creek, the decrease in plant mean length from fall-winter 1985–86 to summer 1986 suggests either an increase in the number of smaller plants or a greater loss of larger

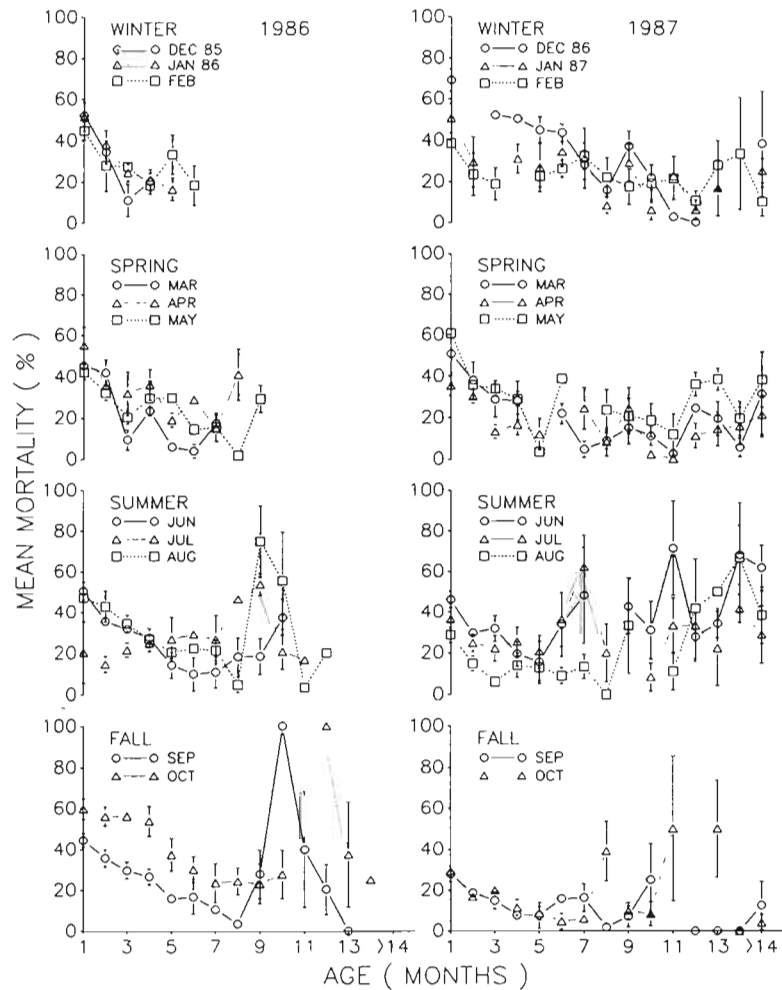


Fig. 10. *Fucus distichus*. Monthly mean probability of mortality ($\% \pm \text{SE}$) of plants of different ages. Data are from mean values of the permanent quadrats. Error bars $< 3.0\%$ not shown

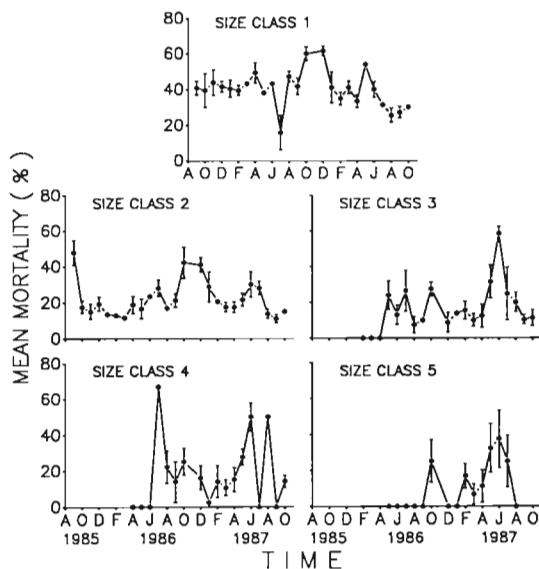


Fig. 11. *Fucus distichus*. Mean probability of mortality ($\% \pm \text{SE}$) of plants from the same size class over time. Data are from mean values of the permanent quadrats. Error bars $< 2.5\%$ not shown

plants or both at this time. The significant increase in the number of recruits in the quadrats between March and July 1986 (see Ang 1991a) may explain the decrease in the mean length of the population during this same period. However, there was no corresponding increase in the number of recruits in the second summer, i.e. between July and September of 1987, but the population still experienced a decrease in mean length. Plants that died between fall and early winter of 1986 were smaller, but between late spring and summer of 1987 were larger, than those that survived (see Figs. 9 & 12). Thus, changes in the mean length of the population from October (1986) to the end of the monitoring period in November (1987) could be explained by the variation in survival of different sizes of plants. While the increase in the number of recruits may account for the decrease in the mean size of the population in the spring and summer of 1986, mortality of the larger plants contributed to this decline as well.

Seasonal patterns of change in the growth rate of the *Fucus* population from False Creek are comparable to those reported for *Fucus distichus* L. *edentatus* (Pyl.)

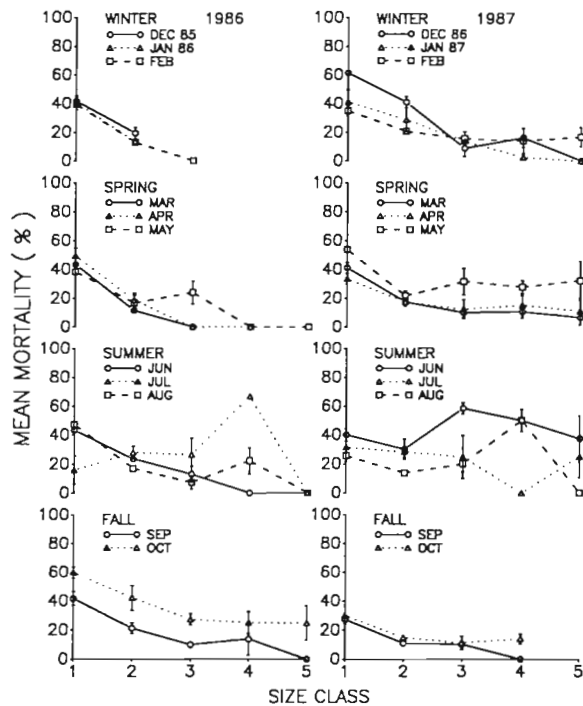


Fig. 12. *Fucus distichus*. Monthly mean probability of mortality (% \pm SE) of plants from different size classes. Data are from mean values of the permanent quadrats. Error bars $< 3.0\%$ not shown

Table 5. *Fucus distichus*. Results of log linear analysis on the effect of age vs size on growth, with or without the effect of mortality, and on mortality alone. See text for explanation of models

Models	df	G	p
A. Age vs size on growth with the effect of mortality			
Age \times Size \times Growth	27	94.04	< 0.0001
Age \times Growth	9	250.28	< 0.0001
Size \times Growth	9	940.06	< 0.0001
Age \times Growth/Size	9	189.30	< 0.0001
Size \times Growth/Age	9	879.08	< 0.0001
B. Age vs size on growth without the effect of mortality			
Age \times Size \times Growth	18	54.04	< 0.0001
Age \times Growth	6	230.20	< 0.0001
Size \times Growth	6	900.48	< 0.0001
Age \times Growth/Size	6	194.50	< 0.0001
Size \times Growth/Age	6	864.78	< 0.0001
C. Effect of age vs size on mortality			
Age \times Size \times Mortality	12	63.80	< 0.0001
Age \times Mortality	3	76.68	< 0.0001
Size \times Mortality	4	307.88	< 0.0001
Age \times Mortality/Size	3	5.62	0.1316
Size \times Mortality/Age	4	236.82	< 0.0001

Powell (Sideman & Mathieson 1983) and *F. vesiculosus* L. var. *spiralis* Farl. (Keser & Larson 1984) from the northeastern coast of the USA. However, the maximum absolute growth rate of 1.4 cm mo^{-1} in September 1987

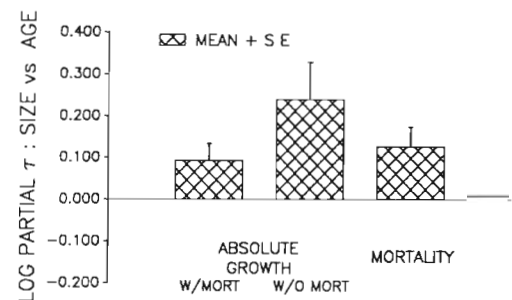


Fig. 13. *Fucus distichus*. Mean (+ SE) ratio of log partial association coefficient (τ) of size vs age as a state variable in describing growth rates with or without the effect of mortality, and in describing mortality. Data are based on mean values for the permanent quadrats. A ratio > 0 indicates that size is more important than age as a predictor of the demographic parameter

is much lower than that reported for other *Fucus* species, e.g. 2.5 to 4.0 cm mo^{-1} for *F. distichus edentatus* from Maine (Keser & Larson 1984), 3.5 cm mo^{-1} for the same species from New England (Sideman & Mathieson 1983), 4 to 6.0 cm mo^{-1} for *F. vesiculosus* var. *spiralis* from Maine (Keser & Larson 1984), 3.5 cm mo^{-1} for *F. vesiculosus* from New Hampshire and Maine (Mathieson et al. 1976), and 1.9 to 2.8 cm mo^{-1} for *F. spiralis* L. from New Hampshire (Niemeck & Mathieson 1976).

The generally lower mean maximum and minimum growth rates recorded for the population that I observed, compared to other published data, may be due to different study techniques. All the plants in my quadrats were mapped and sizes of the plants $\geq 1 \text{ cm}$ were measured in detail. Growth rates were then calculated based on changes in the length of all plants measured. In some other studies, growth rates were calculated based on plants randomly or haphazardly selected and tagged. Changes in the sizes of the tagged plants were then monitored over time. New plants were tagged from time to time depending on the loss rate of the tags. Assuming that the plants randomly tagged truly represent the size variation within the population, monitoring of plants tagged at one or a few times alone would result in missing newly recruited (younger and smaller) plants, unless recruitment is strongly seasonal. If these young plants have significantly different growth rates than those of the older or larger tagged plants, then results from monitoring the tagged plants alone would be very different from results that included the young plants. Comparing my study with that by Sideman & Mathieson (1983) where only plants 1 yr or older (and $> 10 \text{ cm}$) were tagged and monitored, the maximum growth rate of 3.5 cm mo^{-1} that they reported for *Fucus distichus* ssp. *edentatus* is comparable to that of my plants in Size Classes 4 and 5

at 2.9 and 3.2 cm mo⁻¹, respectively. Inclusion of plants from Size Classes 2 and 3, which have lower growth rates, lowers the overall mean growth rate calculated for the population in False Creek. It seems obvious that changes in the size structure of a plant population can be inferred from an understanding of the growth dynamics of the individuals. The failure to include smaller plants in growth rate studies could result in an under- or overestimation of the growth dynamics and hence, the dynamics of the population size structure. How serious this under- or overestimation may be will depend on how dominant these smaller plants are and how different their growth patterns are from the larger plants.

From my observations, some *Fucus* plants may be lost altogether between sampling periods. Among other plants, terminal branches that formed receptacles became necrotic after shedding of eggs. Thus, plants could experience an initial decrease in size due to the decay of the reproductive terminal branches but could eventually increase in size when branches that did not form receptacles continued to grow. This process was also observed by Knight & Parker (1950) for *Fucus vesiculosus*. If receptacles were formed on all terminal branches, then the whole plant eventually decayed. The whole plant may also be torn, leaving a small stump or holdfast which eventually disappeared. Regeneration from the stump or holdfast was not observed in *F. distichus* except in very young plants. Reduction in size due to necrosis of terminal branches was the main reason for the negative growth recorded for plants in all size classes in the fall and winter of 1986. The loss of whole plants, leaving small stumps or holdfasts, explains the negative growth exhibited by plants in Size Class 5 in the summers of 1986 and 1987 (Fig. 7).

Most studies on fucoids did not show any negative mean growth in their populations, except perhaps for Keser & Larson (1984) for *Fucus vesiculosus* and Gunnill (1985) for *Pelvetia fastigiata*. In some of these studies, it is possible that tags on plants with significant tissue erosion were lost, such that these plants were recorded (in error) as dead (or lost) rather than as exhibiting a negative growth. However, it is also possible that most of these fucoid populations may not have experienced extensive erosion or attrition of individual thalli. Because of the modular character of fucoid plants, non-reproductive and reproductive terminal branches within the same plant could have different growth patterns. While the longest terminal branches are usually reproductive, formation of receptacles eventually terminates growth in these branches. Non-reproductive branches could then grow over time to become the longest branch(es) before any die back of the older reproductive branches sets in. In that case,

any decrease in plant length will not be detected. The absence of any negative growth, therefore, could indicate a fast turnover of longest terminal branches and thus, an increase in the reproductive potential of the plant as terminal branches eventually become reproductive.

The few cases of significant correlations between age and growth and variations in growth rate associated especially with older plants strongly suggest that growth rate is only occasionally age-dependent. Such variations also explain the more consistent seasonal pattern of change in growth rate discernable only among plants < 8 mo old. While seasonal patterns of mean plant length and mean growth rate are negatively correlated (Fig. 1), within each month or each cohort, patterns of plant length and absolute growth are mainly positively correlated (Tables 2 & 3). This suggests that while growth rate is very often size-dependent, it is also season-dependent. A seasonal pattern becomes more obvious only when plants are grouped by size rather than by age. Similar results were obtained if growth rate was expressed in relative terms with respect to initial plant length.

The skewed age structure observed in the *Fucus* population from False Creek is similar to that observed for some populations of *Laminaria hyperborea* (Kain 1963), *L. setchellii* Silva (Dayton et al. 1984) and *Ascophyllum nodosum* (L.) Le Jolis (Keser et al. 1981). Other populations of *L. hyperborea* and *A. nodosum*, however, showed a bimodal age structure (Kain 1963, Keser et al. 1981). A unimodal, approximately normal distribution of age structure has been reported for other algal populations, e.g. *Pterygophora californica* (Dayton et al. 1984, De Wreede 1984). Skewed age structure appears to be typical of dense, all-aged population (Cousens 1985) and its maintenance throughout the year in the False Creek population is probably a result of the continuous influx of new recruits. It is also a result of the near constant rate of mortality among the recruited plants (Fig. 8).

The critical stage for survival in many algae is probably the microscopic germling or sporeling stage (Chapman 1984, Reed 1990; see also Ang 1991b). Once recruits become large enough to be visible, the risk of mortality becomes less. This appears to be typical of many perennial populations. Populations of *Pelvetia fastigiata* (Gunnill 1980), *Laminaria digitata* (Chapman 1984), *L. longicuris* (Chapman 1984, 1986), and *Chondrus crispus* (Bhattacharya 1985) all showed such a pattern. Some variations do exist. De Wreede (1986) found age-specific survivorship of *Pterygophora californica* to be variable. One population that he monitored had a relatively constant age-specific survivorship, but in another population there was a greater mortality among younger plants. Annuals such as

Leathesia difformis (L.) Areschoug showed a high survivorship for younger plants and a high mortality for older plants (Chapman & Goudey 1983).

For the False Creek population, the probability of mortality is not uniform for plants of the same age or size at different times of the year. Seasonal effects appear to outweigh the effect of age and/or size such that greater risk of mortality was experienced by older and larger plants in summer but not in winter and spring. Only older, but not necessarily larger, plants suffered greater mortality in the fall.

During summer, long exposure at daytime low tide is likely to be one of the main causes of mortality for the bigger plants. Smaller plants are covered and hence possibly protected by the canopy. *Fucus* plants do not usually die abruptly and disappear from the population. The whole thallus may be torn away but it usually takes 1 to 2 mo for the remaining stump or holdfast to be eroded and lost. In the fall, older and dying plants first became much smaller before being considered as dead (lost). This explains the apparent discrepancy observed, i.e. the greater probability of mortality for older, but not necessarily the larger, plants during this time. If plants which had lost a considerable part of their thallus were considered as dead, then the mortality rate of the larger plants in the fall would have been much higher.

During winter, lower low tide occurs at night. In contrast to what was observed in summer, the retention of moisture under the overlying canopy appeared to cause softening of the tissues of understory plants and their eventual decay. This scenario is analogous to decay of fallen leaves, where those at the bottom tend to be moist and to decay first. This decay may be facilitated by detritus feeders and grazers like amphipods and littorines. In this sense, it may be speculated that herbivory also contributed to the higher mortality of the smaller plants. Crowding (Black 1974) may also affect mortality. Because all the plants monitored in my study were in the same permanent quadrats, density effects experienced by plants of different age or size classes should be comparable. However, there may be a compounding effect of crowding on age- or size-specific mortality, e.g. shading of light as a result of crowding will be experienced more by the smaller plants than by the larger plants, thus will have more effect on the smaller plants than on the larger ones.

Because tips of *Fucus* plants could be eroded and growth of understory plants may be suppressed by the canopy, the relationship between age and length is not always a positive or a direct one. Although in most cases the correlation between these 2 variables is positive and significant, variation in this relationship is indicated by the relatively low correlation coefficients ($r_s < 0.7$). Such variation was also observed by Gunnill

(1985) for the population of *Pelvetia fastigiata*, and Keser & Larson (1984) for *Fucus* spp.

Given that a significant correlation exists between age and length, it is not surprising to find that both these state variables are significant as predictors of growth and mortality, as indicated by the log linear analysis. However, it is interesting to note that age is insignificant as a predictor of mortality when the contribution of size (length) is known. Furthermore, size is consistently shown to be more important than age as a predictor for both parameters in the association analyses. This clearly indicates that both growth and mortality are more size-dependent than age-dependent. Given that plant length is also significantly related to reproduction (Ang 1991a) and plant biomass (Ang 1991b), the use of plant length as a state variable is definitely more desirable than the use of age in demographic analyses of the *Fucus* population from False Creek. However, it is still premature to make a generalization about the importance of plant length in other algal populations. Other size parameters, such as width and biomass, may be used as state variables. Evaluation of the relative significance of these size parameters as well as age vs size as a state variable should be carried out in future algal population ecological studies to ascertain the appropriateness of the state variable employed.

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