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Colonization and growth dynamics of three species of *Fucus*

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ABSTRACT: Colonization, growth and mortality of *Fucus vesiculosus* L., *F. vesiculosus* L. var. *spiralis* Farl. and *F. distichus* L. subsp. *edentatus* (Pyl.) Powell were investigated from August 1973 to April 1976. Grazing by *Littorina littorea* L. retarded but did not prevent colonization of *Fucus*. Growth of *Fucus* spp. was characterized by high variability both within and among sites. The general growth pattern consisted of slow to moderate growth during winter and early spring and rapid growth throughout summer and autumn. Growth was inversely proportional to intertidal height. Removing *Ascophyllum nodosum* (L.) Le Jol., and *Chondrus crispus* Stackh., from protected rocky shores permitted colonization and development of *F. vesiculosus* throughout the intertidal region. Following colonization, the mortality of *F. vesiculosus* germlings was high. Such losses were not reflected in areal cover measurements, however, because of the continued growth of surviving thalli. Mortality of large plants occurred mainly during winter, owing to ice and storm damage. This mortality, as well as a reduced growth rate, was responsible for the slow increase in algal cover during winter.

INTRODUCTION

Several *Fucus* species and *Ascophyllum nodosum* (L.) Le Jol. are the dominant intertidal algae along Maine's rocky coastline (Kemp, 1862; Johnson and Skutch, 1928a, b; Taylor, 1957; Vadas et al., 1976; Topinka et al., 1981). *A. nodosum* dominates sheltered areas of the open coast but is gradually replaced by *Fucus* spp. as exposure increases. In Maine estuaries, *F. vesiculosus* L. and *F. vesiculosus* L. var. *spiralis* Farl. are limited to small patches within the broad cover of *A. nodosum* and to the upper and lower fringes of the *A. nodosum* zone (Vadas et al., 1976). *F. vesiculosus* becomes more dominant as exposure increases to moderate levels (Keser et al., 1981; Topinka et al., 1981); but *F. vesiculosus* var. *spiralis* is restricted to the estuaries. Similar fucoid distribution and abundance patterns have been observed in New England (Lamb and Zimmermann, 1964; Mathieson et al., 1981; Mathieson and Hehre, 1982), Canada (MacFarlane, 1953; Berard-Therriault and Cardinal, 1973), Norway (Baardseth, 1955, 1958), Sweden (Aleem, 1969), Iceland (Munda, 1964), and in the British Isles (David, 1943; Walker, 1947; Knight and Parke, 1950; Schonbeck and Norton, 1978). More exposed habitats in Maine are dominated by *F. distichus* L. subsp. *edentatus* (Pyl.) Powell (Keser, 1978). The studies of Powell (1963) represent the best taxonomic review of the systematics and world wide distribution of the genus.

The present study examines the colonization, growth and mortality of *Fucus vesiculosus, F. vesiculosus* var. *spiralis,* and *F. distichus* subsp. *edentatus* in Maine. It also includes data from a large number of plants from a population of known age structure. The extended period of the study (1973–1976) allows assessment of seasonal and yearly variability.

MATERIAL AND METHODS

Five study sites were designated in August 1973 (Fig. 1). *Fucus vesiculosus* was studied at 2 estuarine sites (Ferry Site and Foxbird Island in Montsweag Bay), and at a moderately exposed site (Pemaquid Point-Sheltered). Another sheltered estuarine site (Bennett Neck in Damariscotta River) was used to study a form of *F. vesiculosus* which has been attributed by previous authors (e.g. Taylor, 1957; Mathieson et al., 1981) to var. *spiralis* Farlow. The

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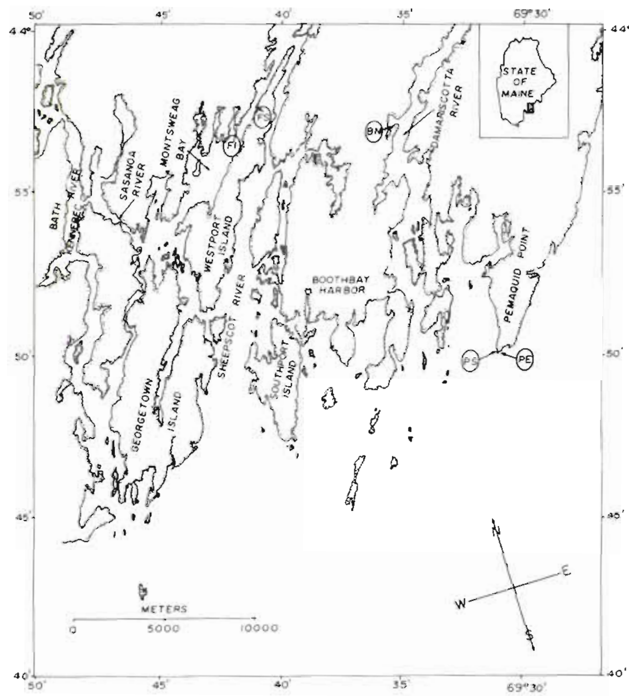

Fig. 1. Location of sampling stations. FI Foxbird Island; FS Ferry Site; BN Bennett Neck; PE Pemaquid Point-Exposed; PS Pemaquid Point-Sheltered

taxonomic status of this form needs investigation, but our data indicate a degree of distinctness, whether genotypic or phenotypic. *F. distichus* subsp. *edentatus* was studied at Pemaquid Point-Exposed, an exposed site 400 m south-southeast from Pemaquid Point-Sheltered.

Prior to the experiment, substrata at Ferry Site, Foxbird Island, and Bennett Neck were dominated by *Ascophyllum nodosum* (78 to 92% of wet weight biomass). At Pemaquid Point-Sheltered, *Ascophyllum* accounted for 47% of the algal biomass, *Fucus vesiculosus* 33%, *Chondrus crispus* Stackh. 14%, and *Polysiphonia lanosa* (L.) Tandy 6%; barnacles were also common. *Ascophyllum* was absent from Pemaquid Point-Exposed; there, *Fucus* spp. accounted for almost 100% of the algal biomass, but only 20% of the substratum coverage (50% was barnacles, 15% mussels, the remainder bare rock and ephemeral algae).

Three permanently marked strips of rocky shore (granitic and basaltic ledges), perpendicular to the waterline, were scraped clean and burned with a propane torch at each of the 5 sites in August 1973. Each strip was 0.5 m wide and extended from mean high water (MHW) to mean low water (MLW) levels. Three additional strips were cleared and burned at each site in winter (December 1973 or January 1974) and in spring (June 1974) to study seasonal effects on colonization. To assess yearly variability and to replicate the previous summer's denudings, 3 additional strips were denuded at each site in August 1974.

The denuded strips were divided into 3 zones representing upper (Zone I), middle (Zone II), and low intertidal (Zone III) regions; the vertical tidal range averaged 2.7 m. Depending upon substratum slope at each site, the designated intertidal zones contained 3 to 9 quadrats (replicates), each measuring 0.5 × 1.0 m. The percentage of substratum coverage was estimated for each species in each quadrat. Owing to their phenotypic plasticity (Powell, 1957, 1963), specific identification of *Fucus* germlings was impossible; they were recorded as *Fucus* sp. Length measurements of the germlings were made monthly until subsequent development enabled specific identification; further growth was measured seasonally.

Plant lengths were determined from holdfast to tip of the longest branch. Length increases were expressed as mean increase in mm mo^{-1}, obtained by dividing the length increase by time between consecutive sampling dates. Twenty *Fucus* plants $quadrat^{-1}$ were measured at each site during each census (therefore, because of differences in slope noted above, each zone was represented by 60 to 180 plants).

Grazer exclusion cages were placed at Bennett Neck in one of the strips denuded in June 1974 to determine the influence of grazing by *Littorina littorea* L. on the colonization and subsequent growth of *Fucus vesiculosus* var. *spiralis*. A single cage and control area were located in each intertidal zone and a cover (cage with open sides) was placed in Zone III. Exclusion cages measured 20 × 20 × 5 cm, and were constructed of stainless steel (mesh size 3 × 3 mm); each cage was fastened to the substratum with 4 stainless steel screws.

Plant density of *Fucus vesiculosus* at Ferry Site was determined by counting germlings that colonized Zone III of the strips denuded in August 1974. Plants were counted in 10 randomly placed subquadrats (each 5 × 5 cm); counts were averaged and converted to number of plants m^{-2}. Detailed descriptions of the sites and environment (salinity, temperature, light, and extinction coefficients) have been given by Vadas et al. (1976, 1978), Keser (1978), and Keser et al. (1981).

RESULTS

Fucus vesiculosus at Ferry Site, Foxbird Island, and Pemaquid Point-Sheltered

Fucus vesiculosus was the only species of *Fucus* to recover at these sites, and the time needed to colonize most denuded substrata ranged from 3 to 21 mo at Ferry Site, 4 to 9 mo at Foxbird Island, and 4 to 12 mo at

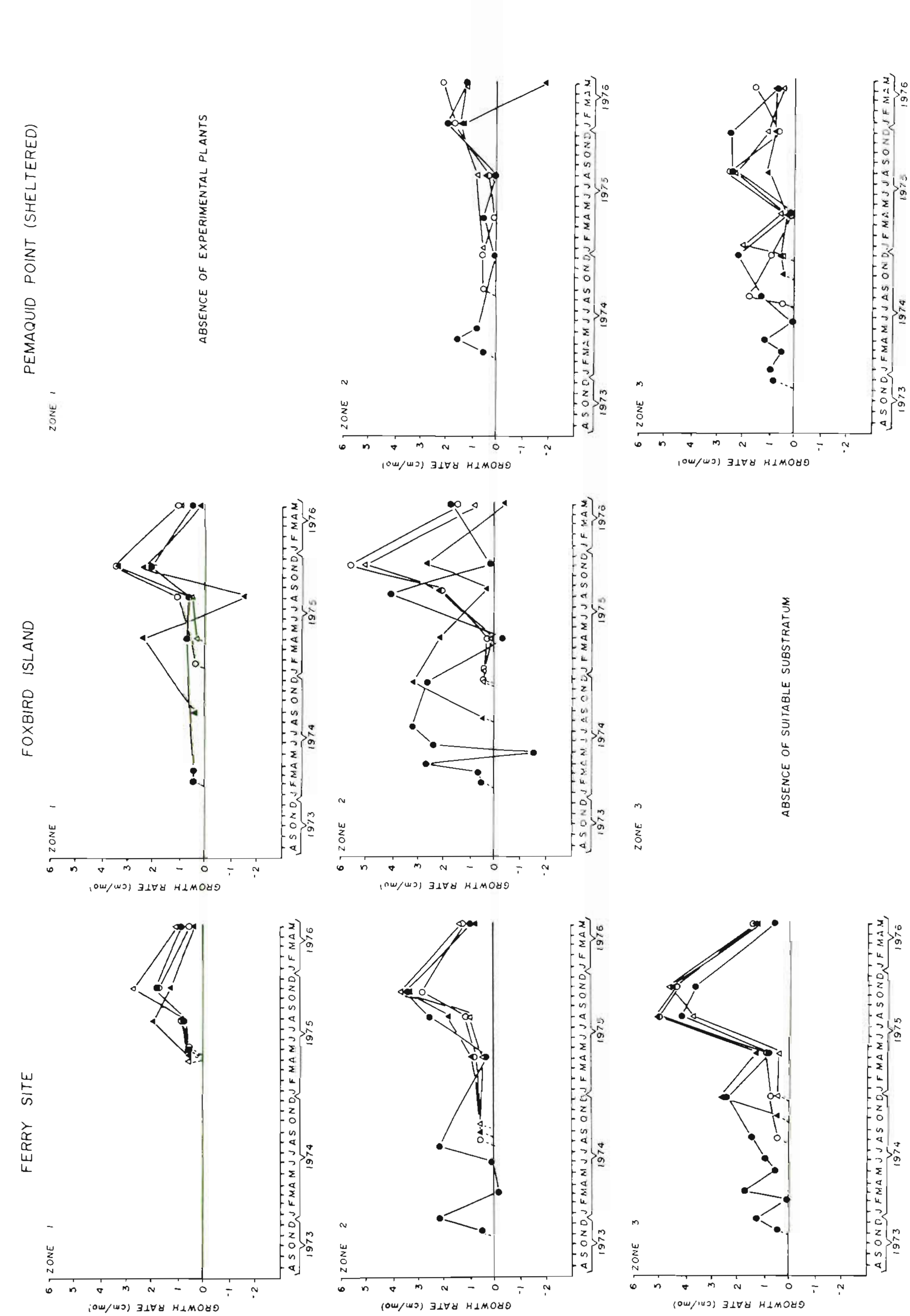

Fig. 2. *Fucus vesiculosus*. Average growth (cm mo^{-1}) at Ferry Site, Foxbird Island and Pemaquid Point-Sheltered. Dates of denuding: ● August 1973; ○ December 1973; ▲ June 1974; △ August 1974

Table 1. *Fucus vesiculosus*. Variability in length (mm) in Zone III at Ferry Site (based on 6 quadrats denuded in August 1973). Each mean based on measurements of 20 plants

	Quadrat number 1		2		3		4		5		6	
	$\bar{X}$	CV[a]	$\bar{X}$	CV	$\bar{X}$	CV	$\bar{X}$	CV	$\bar{X}$	CV	$\bar{X}$	CV
Dec 73	18	33.3	14	42.9	13	53.8	20	65.0	21	42.9	21	52.4
Feb 74	22	50.0	16	56.2	18	0	22	72.7	20	45.0	20	55.0
Mar 74	23	56.5	48	16.7	49	8.2	b		29	41.4	b	
May 74	b		73	21.9	46	43.5	15	26.7	b		b	
Jun 74	40	30.0	86	22.1	60	46.7	36	33.3	73	43.8	23	13.0
Aug 74	61	22.9	186	21.5	41	29.3	35	28.6	99	30.3	76	31.6
Dec 74	181	11.0	270	22.2	176	24.4	140	28.6	158	24.7	129	35.7
Apr 75	240	13.3	351	16.5	205	15.6	209	12.4	160	30.0	131	17.6
Aug 75	360	5.8	460	18.2	321	15.6	378	17.5	404	15.8	362	19.1
Nov 75	562	17.1	571	9.8	499	16.2	544	8.6	390	6.7	409	24.9
May 76	635	7.6	592	9.1	491	11.0	592	6.4	511	6.1	439	15.0

a = Coefficient of variation
b = Missing data

Pemaquid Point-Sheltered (Fig. 2). Zone I at Pemaquid Point-Sheltered had not been colonized by the end of the experiment (May 1976; 33 mo after the first denuding). Zone III at Foxbird Island was a mudflat, with no substratum suitable for denuding or colonization by *Fucus*. Rates of colonization and subsequent growth were inversely related to intertidal height, i.e. fastest in Zone III and slowest in Zone I. Settlement of *F. vesiculosus* in Zones II and III, at Ferry Site and Foxbird Island, occurred in late summer or autumn regardless of the time of denuding. Colonization at Pemaquid Point-Sheltered appeared to be random, and was not closely related to either time of year or time since denuding. Zone I of most strips denuded at different seasons were colonized by *F. vesiculosus* in late winter–early spring.

Table 2. Growth, as increase in percent cover, of: *Fucus vesiculosus* at Ferry Site, Foxbird Island, and Pemaquid Point-Sheltered; *F. vesiculosus* var. *spiralis* at Bennett Neck; *F. distichus* subsp. *edentatus* at Pemaquid Point-Exposed

	August 73			December 73			June 74			August 74		
	ZI	ZII	ZIII	ZI	ZII	ZIII	ZI	ZII	ZIII	ZI	ZII	ZIII
Ferry Site												
May 74	0	0	1	0	0	0	–	–	–	–	–	–
May 75	1	20	68	2	10	68	1	8	55	2	10	57
May 76	25	95	92	25	85	84	40	95	88	54	95	81
Foxbird Island												
May 74	1	3		0	0		–	–		–	–	
May 75	16	92		7	14		1	11		1	6	
May 76	71	65		38	61		53	79		32	79	
Pemaquid Point – Sheltered												
May 74	0	0	4	0	0	0	–	–	–	–	–	–
May 75	0	2	43	0	2	28	0	0	1	0	1	5
May 76	0	13	49	0	9	49	0	0	17	0	28	43
Bennett Neck												
May 74	0	0	0	0	0	0	–	–	–	–	–	–
May 75	1	5	15	2	6	14	1	2	6	0	1	2
Apr 76	3	27	52	9	30	51	1	28	40	9	21	24
Pemaquid Point – Exposed												
Apr 74	0	0	0	0	0	0	–	–	–	–	–	–
May 75	2	4	29	1	6	24	0	1	5	0	0	0
May 76	8	13	51	6	20	54	12	32	63	1	1	4

Maximum growth ranged from ca. 3.5 cm mo^{-1} at Ferry Site, 4.0 to 6.0 cm mo^{-1} at Foxbird Island, 2.0 to 2.5 cm mo^{-1} at Pemaquid Point-Sheltered. Growth was generally fastest in late summer and autumn, and slowest in winter and spring. Decreases in average length were attributed to plant mortality and breakage, especially during winter and early spring storms.

Growth was variable among quadrats in the same zone, and even among plants within the same quadrat. As a representative example, Table 1 presents average lengths of 20 plants in each of 6 quadrats from Zone III of the August 1973 denuding at Ferry Site. An analysis of variance performed on square-root transformed data from May 1976 showed that differences in length between quadrats were highly significant ($p < 0.01$), even though the plants had colonized at the same time.

The inverse relationship of intertidal height to rates of colonization and growth was also evidenced by percent cover measurements. Table 2 summarizes growth data (increase in percent cover) for up to 3 yr; values for each sampling time are presented in Keser (1978). The percent cover of *Fucus vesiculosus* increased with time, and was generally greatest in Zone III; however, coverage varied both within and among stations, and values at the end of the experiment did not necessarily correspond to the time since initial colonization. Partial or total thallus loss could cause a decrease cover from one sampling period to the next, especially in Zone III.

Density patterns of *Fucus vesiculosus* predictably showed an inverse relationship with time. At Ferry Site, densities following the August 1974 denuding averaged 43,600 plants m^{-2} in April 1975 (Fig. 3). Subsequently, densities declined to 3,880 plants m^{-2} in November 1975, to 2,240 plants m^{-2} in May 1976, and to 480 plants m^{-2} in April 1977. Despite the loss of over 90% of the plants between April and November 1975, percent coverage increased from 32 to 94% over the same period, owing to continued growth of surviving individuals. However, subsequent mortality reduced coverage to 81% by May 1976 and 18% by April 1977; concurrently, the average plant length decreased. By the end of the experiment, only holdfasts and midrib stumps of the original plants remained.

Fucus vesiculosus var. *spiralis* at Bennett Neck

Substrata denuded at Bennett Neck were colonized by *Fucus vesiculosus* var. *spiralis* within 3 to 13 mo after denudation (Fig. 4), and no other form of *Fucus* was found during the experiment. The same general trend of more rapid colonization and growth with decreased intertidal height was evident, but to a lesser degree than noted for *F. vesiculosus*. Regardless of denudation time, the patterns of colonization were similar. Plants first appeared in crevices and later on smooth surfaces. Once germlings were established,

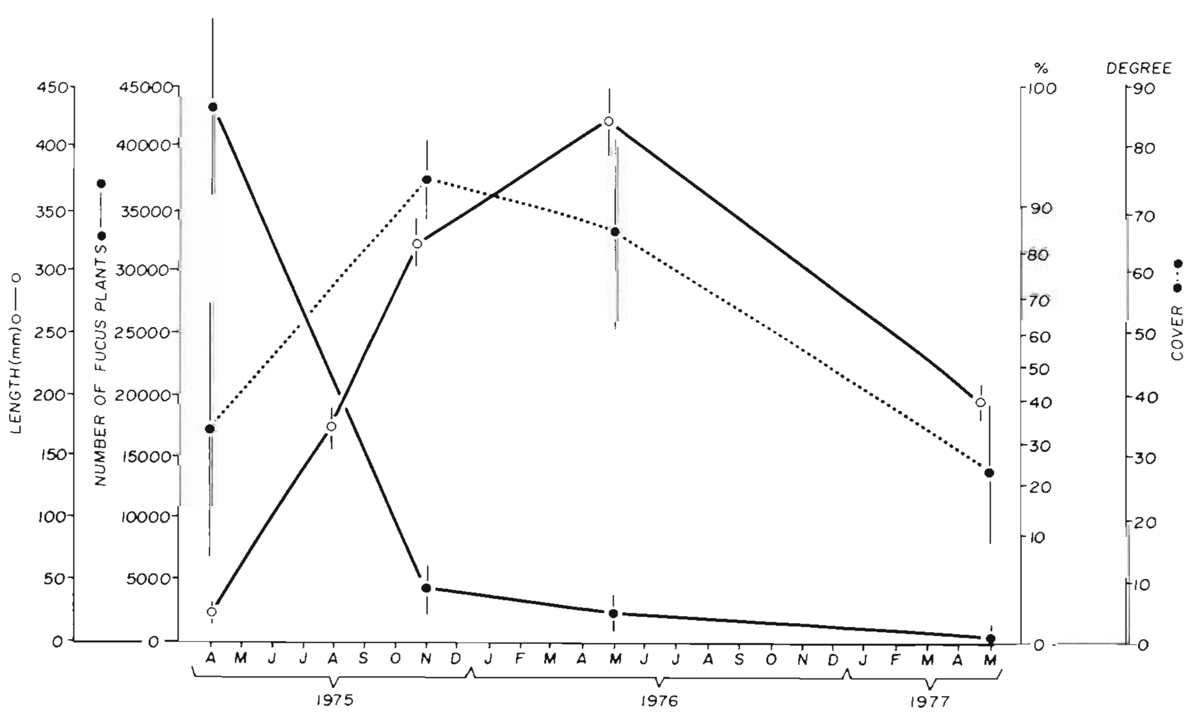

Fig. 3. *Fucus vesiculosus.* Density, length, and percent cover in Zone III at Ferry Site, following August 1974 denuding. Bars: 95% confidence intervals. Percent cover data were transformed with the angular transformation

cover increased continuously in Zones II and III (but not in Zone I). At the conclusion of the study, coverage by *F. vesiculosus* var. *spiralis* ranged from 1 to 52% (Table 2), and was highest in Zone III. Mean growth ranged from 0.3 to 1.0 cm mo^{-1}.

The same trend of rapid growth of established germlings was evident from the grazer exclusion study (Table 3). The cages provided a more effective refuge for *Fucus* germlings than did crevices. In Zone I, neither caged nor control areas were appreciably colonized (≤ 2%). In Zones II and III, *Fucus* covered 70 and 50%, respectively, of the caged area after 7 mo and plants averaged 2.2 cm in length. In the same period, *F. vesiculosus* var. *spiralis* covered less than 2% of the control areas. In order to test effect of cages on *Fucus* growth, cages were removed in March 1975. Coverage increased to 100% within 1 yr, due to continued growth of existing plants. Coverage of the control areas also increased, but more slowly. The percent cover of *Fucus* in the area under the open sided cage in Zone III was virtually the same as in the uncaged control area throughout the study.

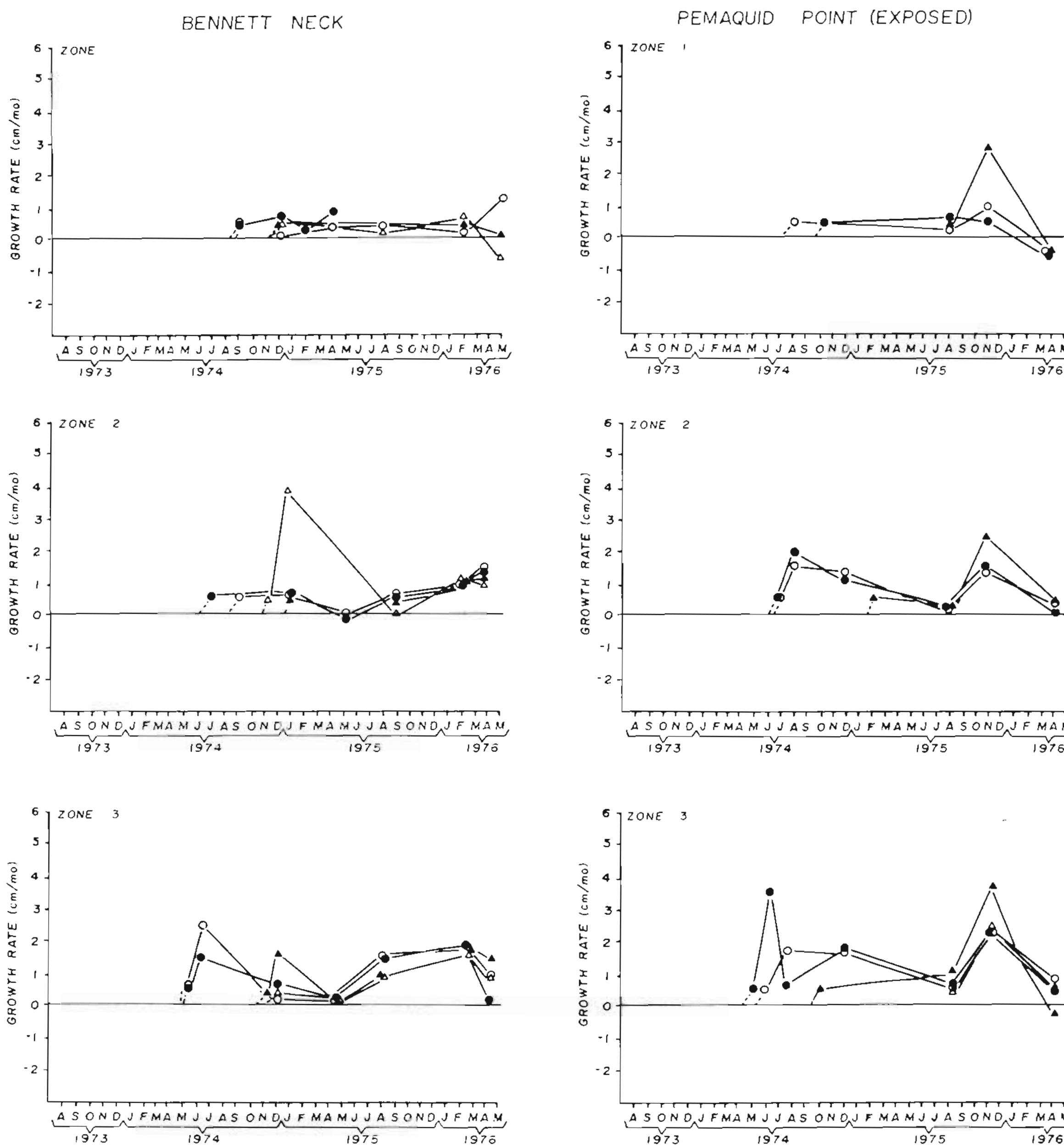

Fig. 4. Average growth (cm mo^{-1}) of *Fucus vesiculosus* var. *spiralis* at Bennett Neck and *F. distichus* ssp. *edentatus* at Pemaquid Point-Exposed. Dates of denuding: ● August 1973; ○ January 1974; ▲ June 1974; △ August 1974

Table 3. *Fucus vesiculosus* var. *spiralis*. Percent cover at Bennett Neck

	Zone I		Zone II		Zone III		
	E	C	E	C	E	C	E(c)
Jun 74	Areas denuded at this time						
Jul 74							
Aug 74							
Sep 74							
Nov 74			55		10		
Dec 74		1	75	1	25	1	1
Jan 75		1	75	1	55	2	2
*Mar 75		1	70	1	50	1	1
Apr 75		1	83	1	18	3	2
May 75		1	92	2	25	6	4
Aug 75			98	8	78	14	10
Feb 76	1	2	96	27	100	37	35
Apr 76	1	2	100	28	100	40	45

E Experimental (complete exclusion cage)
C Control (No cover)
E(c) Experimental (cage without sides)
* Cages removed March 16, 1975

Fucus distichus subsp. *edentatus* at Pemaquid Point-Exposed

Colonization of denuded substrata at Pemaquid Point-Exposed by *Fucus* was accomplished exclusively by *F. distichus* subsp. *edentatus* (hereafter referred to as *F. d. edentatus*). This occurred as soon as 4 mo after denuding, but in some cases had not occurred by the end of the experiment (21 mo after denuding, Fig. 4). In most cases, *F. d. edentatus* first appeared in late summer or autumn. Growth was variable between zones, seasons, and strips denuded at different times. Maximum values ranged from ca. 2.5 to 4.0 cm mo^{-1}, and usually occurred in autumn.

The percent cover of *Fucus d. edentatus* was also inversely related to intertidal height (Tab. 2); values generally increased gradually following colonization, but declined during winter (Keser, 1978). At the conclusion of the study, the percent coverage of the areas denuded in August 1973, January 1974, and June 1974 ranged from 6 to 12% in Zone I, 13 to 32% in Zone II, and 51 to 63% in Zone III (Tab. 2). The lowest coverage by *F. d. edentatus* resulted from the August 1974 denuding (1%, 1%, and 4% in Zones I, II, and III, respectively).

DISCUSSION

Fucus was the first perennial alga to colonize the experimentally denuded transects, even at sites and tidal levels that had been initially dominated by *Ascophyllum* or *Chondrus*. Absence of *Ascophyllum* plants following experimental or natural substratum denudation has been reported (Knight and Parke, 1950; Printz, 1956, 1959; Baardseth, 1970; Sundene, 1973). Lubchenco (1980) showed that removal of *Chondrus* from low intertidal permitted dense settlement of *Fucus*.

In this study *Fucus* colonization was usually preceded by the establishment of populations of ephemeral algae (e.g. *Porphyra umbilicalis*, *Enteromorpha* spp., *Ulothrix flacca*, *Bangia atropurpurea*, or diatoms), or of barnacles (*Balanus balanoides* L.). A similar pattern was observed at rocky shores in West Cornwall following the 'Torrey Canyon' oil spill (Southward and Southward, 1978; Southward, 1979). The presence of barnacles or ephemeral algal was not prerequiste for *Fucus* colonization. Sometimes, *Fucus* initiated colonization on denuded substrata.

On the basis of the present study, we can only infer periodicity of gamete release from the appearance of *Fucus* germlings. Newly settled germlings of *F. vesiculosus* were found in most months, indicating a broad period of reproductivity. European populations of *F. vesiculosus* also show long reproductive periods (Knight and Parke, 1950; Printz, 1959). *F. vesiculosus* var. *spiralis* and *F. d. edentatus* settled over a shorter period (May–December), perhaps reflecting a narrower period of reproductive activity. Maximum reproduction for *F. vesiculosus* var. *spiralis* in New Hampshire (USA) occurred from March–June, but fertile plants were found throughout the year (at least in some years; Mathieson et al., 1976).

Colonization by *Fucus* spp. occurred earliest in the low intertidal zone, and subsequent growth was fastest in this zone (cf. Lubchenco, 1980). Slower colonization and growth in Zone I (and occasional failure to colonize, e.g. at Pemaquid Point-Sheltered) was in part due to grazing by *Littorina littorea*, which has seldom been reported to be important in the high intertidal. Studies in Connecticut, USA, indicate that *L. littorea* may be seasonally abundant in high intertidal areas, and that its feeding activities may exert considerable influence on upper intertidal communities (NUSCo 1981).

The absence of *Fucus* from Pemaquid Point-Exposed following the August 1974 denuding appeared to result from interspecific competition for substratum. *Porphyra umbilicalis* (L.) J. Ag. and *Enteromorpha* spp. appeared in all 3 zones within a month following denudation; *Porphyra* quickly dominated, and accounted for almost 100% of the coverage by the following spring. The alga continued to dominate all 3 strips denuded in August 1974 (but not the 9 strips denuded earlier), although coverage values decreased somewhat. *F. distichus* subsp. *edentatus* appeared in these strips for the first time in November 1975, and at the conclusion of the experiment (April 1976), was still scarce. Southward and Southward (1978) also reported delay in *Fucus* colonization following prolonged 'greening' by ephemeral algae at some of their sites.

The above discussion, as well as the wide discrepancies in colonization times (even when denudings were established in the same month of successive years), illustrates the variability associated with *Fucus* colonization within and among stations, and between years. This implies that colonization in intertidal areas may be determined more by stochastic events, or random selection from possible alternatives, than from specific successional sequences.

The growth of *Fucus* has generally been measured as linear increase (Knight and Parke, 1950), but increases in thickness, lateral growth, and dichotomies are produced concurrently and are also growth indicators (Lund, 1936). Some of these parameters are closely correlated to linear increases. For example, the number of dichotomies is proportional to plant length (Knight and Parke, 1950; Subrahmanyan, 1961). In searching for additional criteria to assess *Fucus* growth, Knight and Parke (1950) recognized the futility of attempting to relate the number of frond apices to growth because of extensive frond mortality in the field.

Similarly, we found the number of dichotomies inadequate to assess *Fucus* growth, and increase in percent cover was a more representative parameter. Biomass measurements were not made, because these samples were part of a long-term, non-destructive successional study. However, other studies of *F. vesiculosus* in Maine have shown biomass to be highly variable among and within sites, and between years at the same site (Keser, 1978; Keser et al., 1981; Topinka et al., 1981).

Growth patterns were similar for all *Fucus* spp. studied, using both linear increase and percent cover increase. Growth was low in winter, increased in spring, stabilized through summer, and reached maxima in autumn (Fig. 2 and 4). During the winter, increased plant mortality (partial or total) resulted in decreased average length and percent cover.

The observation that *Fucus* colonization occurred earliest in the low intertidal may be a simple function of the length of time available for settling. Since submergence time is inversely related to intertidal height, fertilized eggs in the water column have a better chance of settling on suitable substrata in the low intertidal. Baker (1910) found that the greatest development of germlings, including those of *F. vesiculosus,* occurred under a desiccation regime that simulated low intertidal conditions, i.e. 11 h immersed and 1 h emersed. Lubchenco (1980) reported that *F. vesiculosus* and *F. d. edentatus* grew better in low- than in mid-shore zones, although they were excluded from the low intertidal by competition from *Chondrus crispus*.

Comparison of our results to those of other researchers is difficult. Most investigators did not report the number of plants studied or intertidal elevation. Also, growth determinations varied from measuring growth of old plants (Printz, 1959) to growth of newly colonized individuals (Knight and Parke, 1950). Many studies failed to describe degree of exposure to waves and water movement, others were of too short a duration to assess temporal variability (Hariot, 1909; Lemoine, 1913; Gislen, 1930; Hatton, 1932; Burrows, 1956). The few long-term studies (Nienburg, 1930; Moore, 1939), as well as ours, emphasize the variability of seasonal and yearly growth.

Despite the problems of different approaches to the assessment of *Fucus* growth, some comparisons can be made. Converting our growth to yearly averages, our growth for *F. vesiculosus* in Maine (15 to 21 mm mo^{-1}) is slightly less than that reported from Canada (16 to 32 mm mo^{-1}; Breton-Provencher et al., 1979). Our values are approximately midway in the range reported from Europe; 6 to 10 mm mo^{-1} in Norway (Printz, 1959), 10 to 28 mm mo^{-1} in Great Britain (Knight and Parke, 1950), and 25 to 33 mm mo^{-1} in France (Lemoine, 1913).

The growth of *Fucus vesiculosus* var. *spiralis* in Maine ranged from 3 to 20 mm mo^{-1}; these values are lower than reported for New Hampshire (23 mm mo^{-1}; Mathieson et al., 1976) and for Long Island, New York (21 to 32 mm mo^{-1}; Brinkhuis, 1975), but differences in methodology may explain some of the discrepancies. Our values for *F. d. edentatus* (6 to 10 mm mo^{-1}) are also lower than those reported for Canada (16 to 23 mm mo^{-1}, Breton-Provencher et al., 1979).

The longevity of *Fucus vesiculosus* and *F. vesiculosus* var. *spiralis* ranged from 2 to 4 yr at the estuarine site, and slightly less at the more exposed site on Pemaquid Point. The oldest individuals of *F. d. edentatus* in the experimental strips at Pemaquid Point-Exposed were 2 yr old in the spring of 1976, when extensive mortality occurred, associated with heavy growth of epiphytes. Similar age distributions for *Fucus* spp. have been reported by others (Nienburg, 1930; Rees, 1932; Knight and Parke, 1950; Niemeck and Mathieson, 1976).

At some sites, the loss of germlings and young *Fucus* plants was related to grazing activity. For example, *Littorina littorea* was present throughout the year at Pemaquid Point-Sheltered and Bennett Neck. Seasonally, snails were most abundant in spring and autumn, at times exceeding 200 snails m^{-2}. When snails were excluded by cages following denuding, as at Bennett Neck, *Fucus* colonization occurred sooner and subsequent growth was more rapid (Tab. 3). Similar results were obtained in Connecticut (NUSCo, 1981) and, similarly, the removal of limpets from the shore in England increased the density of fucoids (Jones, 1948; Lodge, 1948; Southward, 1953, 1956, 1964; Boney, 1965).

Snails could also be excluded from the study areas by unfavorable environmental conditions. *Littorina littorea* was rare at Foxbird Island and Ferry Site, most likely a result of large fluctuations in salinity (10 to 20‰), and at Pemaquid Point-Exposed, due to high wave exposure. Therefore, the observed mortality of young *Fucus* germlings at these sites could not be attributed to grazing. At Ferry Site, for instance, the loss of *F. vesiculosus* germlings was most likely caused by competition for light and space (Fig. 3). There simply was not enough substratum available to support the extremely high initial densities of germlings (> 43,000 m^{-2}). Large germling mortality due to intraspecific competition was also noted by Knight and Parke (1950) and by Subrahmanyan (1961).

Grazing was not considered to be a major source of mortality for mature plants at any site (cf. Lubchenco, 1978; Keser, 1978); rather, loss was due to extrinsic physical factors (e.g. winter storms and ice scouring).

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