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AN ECOLOGICAL STUDY OF FUCUS SPIRALIS LINNAEUS

RICHARD ALBERT NIEMECK

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AN ECOLOGICAL STUDY

OF

FUCUS SPIRALIS LINNAEUS.

by

RICHARD A. NIEMECK

B.S., Valparaiso University, 1963
M.A., Valparaiso University, 1965

A THESIS

Submitted to the University of New Hampshire
In Partial Fulfillment of
The Requirements for the Degree of

Doctor of Philosophy

Graduate School
Department of Botany
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This thesis has been examined and approved.

Arthur C. Mathieson, Prof. of Botany

Alan L. Baker, Asst. Prof. of Botany

Robert Blanchard, Asst. Prof. of Botany

A. Linn Bogle, Asso. Prof. of Botany

Robert A. Croker, Asso. Prof. of Zoology

11/11/75

Date
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ABSTRACT

An autecological study of *Fucus spiralis* was conducted at Jaffrey Point, New Castle, New Hampshire and the adjacent Great Bay Estuary System from 1972-1975. The distribution, growth, reproductive periodicity, attrition and longevity of the plants are described in relation to a variety of environmental factors. *Fucus spiralis* exhibits a broad, discontinuous estuarine distribution within the Great Bay Estuary System. The presence or absence of substratum is considered to be a factor determining its discontinuous distribution, as it is usually associated with metasedimentary or metavolcanic rock outcrops. The maximum growth and reproduction of *F. spiralis* occur during the summer, with a maximum in August. A growth rate of 1.9 to 2.8 cm/month was recorded during the summer period, while the average monthly growth rate throughout the year was 1.1 cm/month. Two major attritions of *F. spiralis* populations occur during the winter and summer. The average longevity of *F. spiralis* plants is approximately two years. The *F. spiralis* zone occurs in the uppermost intertidal area between +2.12 and +2.39 meters, above mean low water. A microstratification of biomass, stature and reproduction of *F. spiralis* plants occurs within this zone. Average plant weight, length and fertility tend to decrease with increasing elevation. *Fucus spiralis* loses
water at approximately one-half the rate of the associated fucoid algae *Fucus vesiculosus*, *F. vesiculosus* var. *spiralis* and *Ascophyllum nodosum*. Manometric studies show that *F. spiralis* has a broad tolerance to light, temperature and salinity, in agreement with its natural distribution in coastal and estuarine locales.
INTRODUCTION

The marine brown alga *Fucus spiralis* L. (Fucaceae; Fucales) is one of seven *Fucus* species recorded (Taylor, 1957) from the northeastern coast of North America (Fig.1). It extends from New York to the Lower Saint Lawrence, and Newfoundland to the North Atlantic shore of Europe and the northeast Pacific (Norris and Conway, 1974). *Fucus spiralis* is a common species of the high intertidal area where it is exposed to extreme variations of atmospheric conditions.

Relatively little is known about the autecology of New England seaweeds (Webber, 1975), particularly *F. spiralis*. In contrast, many European workers have conducted extensive autecological studies on other *Fucus* species such as *F. vesiculosus* and *F. serratus* in the British Isles (Knight and Parke, 1950; Burrows and Lodge, 1951) and *F. versoides* in the Adriatic Sea (Linardic, 1940, 1949). As far as I am aware, only one account has been published on the autecology of *F. spiralis* (Subrahmanyan, 1961), and no autecological investigations have been conducted on the species in North America. Subrahmanyan (1961) studied the growth, reproduction and longevity of *F. spiralis* on the Isle of Man. Other than his account, only general descriptions of *F. spiralis* populations are given (Lewis, 1972), as well as occasional references to its physiology and desiccation tolerances.
(Stocker and Holdheide, 1938; Baker, 1910; Zaneveld, 1937; Kristensen, 1968; and Kremer and Schmitz, 1973).

The study was undertaken to elucidate the autecology of *F. spiralis* in New England. The specific objectives of the study were to: (1) establish the plant's seasonal pattern of growth and reproduction; (2) determine the major environmental factors influencing its growth and local distribution; (3) understand the population dynamics of the species and; (4) contrast the autecologies of *Fucus spiralis* with *F. vesiculosus* and its variety *spiralis*. In order to accomplish these objectives, a series of field and laboratory investigations were conducted from 1971-1975.
MATERIALS AND METHODS

Monthly values of surface water temperature and salinity were recorded during high tide at Jaffrey Point, New Hampshire, U.S.A. (Fig. 2 and Table I) from July, 1972 to September, 1973. A laboratory grade mercury thermometer and a set of hydrometers (G.M. Manufacturing Co., New York) were used for the determination of temperature and salinity, respectively. Salinity values were corrected to 15°C.

Random samples of 50 \textit{F. spiralis} plants were collected monthly during the period of the study at Jaffrey Point, New Hampshire, to evaluate the plant's growth and reproduction. Random collections were employed, rather than quadrats, because of the narrowness of the plant's zone and the sparseness of the population during the winter. After collection, the plants were transported to the laboratory in plastic bags and examined within 24 hours. The percentage of fertile receptacles/plant, as well as the damp dried weight and maximum length of each plant were recorded. The following criteria were employed to designate a fertile receptacle (Fig. 1) after sectioning many conceptacles and observing their reproductive development: (1) the tips were two cm or more in length, (2) the tips were swollen and filled with mucilage, (3) exodites or mucilaginous substances were extruded from the conceptacles in large
quantities.

The growth rate (average elongation/month) of tagged in situ plants of *F. spiralis* was also determined at Jaffrey Point. One hundred plants were tagged during July, 1972, by placing plastic tags around their stipes, and their maximum lengths were recorded monthly until October, 1973. Since a large loss of tagged plants occurred, 25 additional plants were tagged on December 18, 1972, and another 20 on April 21, 1973. An attrition rate was calculated from the monthly losses of plants. A statistical analysis of growth rates versus the initial size of the tagged plants was evaluated after the correlation coefficient analysis described by Bishop (1966).

The zonation and biomass distribution of *F. spiralis* and associated fucoids at Jaffrey Point, New Hampshire, were determined during July, 1973. A metered transect line was pulled through the fucoid belts and a 0.25 m$^2$ area was denuded at 0.5 m intervals from the top to the bottom of the belt. The elevation of each quadrat was recorded by a stadia rod and transit, using mean low water mark (MLW) as a reference point (Anon. 1972). All of the plants within the quadrats were harvested with a putty knife. Subsequently the different fucoid species were sorted and then dried for 48 hours at 100 C. The micro-stratification of
F. spiralis within its belt at Jaffrey Point was also studied. Thus, the size, weight, biomass (g dry weight/.03m^2) and frequency of reproduction of F. spiralis were determined during June, 1974.

A general survey of the horizontal and vertical distribution of F. spiralis was conducted from the open coast at Jaffrey Point to Ft. Constitution (Fig. 2), because of the apparent transition from F. spiralis to F. vesiculosus var. spiralis between the two sites. Line transect-quadrat studies were conducted at Fort Constitution in order to evaluate the relative abundance of the intertidal fucoids at this site. A survey of the estuarine distribution of F. spiralis was also undertaken within the Great Bay Estuarine System to correlate the species distribution with one or more environmental factors. Observations and collections of F. spiralis were made at six sites from Jaffrey Point to the headwaters of Great Bay (Fig. 2): (1) Jaffrey Point; (2) a Piscataqua River site opposite the Schiller Power Plant; (3) Dover Point; (4) Fox Point; (5) Adams Point; and (6) Nannie Island. Samples of Fucus plants were collected and habitat notes were recorded. A complete set of herbarium voucher specimens documenting the presence of F. spiralis plants at the six study sites is deposited in the algal herbarium of the University of New
Hampshire (NHA).

Two comparative studies of the in situ rates of water loss in F. spiralis, F. vesiculosus, F. vesiculosus var. spiralis and A. nodosum were conducted. Fucus vesiculosus and F. spiralis were evaluated at Jaffrey Point. Two specimens of F. spiralis were studied from the top, middle, and bottom of its zone (+2.12 to +2.36 m) while four plants of F. vesiculosus were studied, two from the top and two from the bottom of the F. vesiculosus-A. nodosum zone. The specimens of each species were approximately the same size and length. Each of the plants was individually tagged and retained at its original location on the shore. The plants were weighed every 30 minutes from the time of their emersion until they were submerged again. The water loss for each plant was expressed as a percentage of the initial water content. A second desiccation study was conducted on August 23, 1973, at Fort Constitution with four plants each of F. vesiculosus var. spiralis and A. nodosum. Two plants of each species were from the top, and two others were from the bottom of their respective zones.

Comparative manometric studies were conducted on F. spiralis, F. vesiculosus and F. vesiculosus var. spiralis, with the net or apparent photosynthesis being evaluated under a variety of different temperature, light and salinity
conditions. *Fucus spiralis* and *F. vesiculosus* were collected at Jaffrey Point, while *F. vesiculosus* var. *spiralis* was collected at Adams Point. The plants were transported to the laboratory within an hour. Vegetative tips, approximately 1-2 cm long, were employed for all experiments, and were selected randomly from different plants. The tips were immersed in 100 ml of artificial sea water (Chapman, 1962), and then incubated in the dark for 24 to 48 hours. The incubation period was employed to avoid wound respiration and to acclimatize the plants to different temperature and salinity regimes. The rates of apparent or net photosynthesis were measured with a Gilson Differential Respirometer (Model GPR 14), equipped with fourteen 50-watt (Champion) reflector lamps. The intensity of the light reaching the bottom of the flasks was varied with a rheostat. A single tip was used per flask in all of the photosynthetic experiments to avoid shading. Five ml of buffered, artificial sea water (Chapman, 1962) was used in each flask. The tips were equilibrated for 30 minutes in the dark and then another 15 minutes in the light, prior to the beginning of each net photosynthetic run. Each run was 30-60 minutes in length with readings taken at 10-minute intervals. The values for oxygen exchange are expressed as ul O₂/g dry weight/0.5 minutes. Five replicates were used in the light experiments, while 7 and
14 replicates were used in the salinity and temperature experiments, respectively. The number of replicates employed was determined after multiple experiments in which the range of variations was evaluated; the constraints of prolonged time also dictated the number of replicates. The manometric techniques employed were after Mathieson and Burns (1971).

In the salinity experiments, concentrations were made by diluting concentrated (2x) artificial sea water with distilled water, according to the summary in Table II. A uniform buffer solution of NaHCO₃ and Na₂CO₃ (Chapman, 1962) was added after the appropriate dilutions of salt. Thus, the concentration of carbonate buffers in the sea water was the same for all salinities. The pH ranged from 8.1-8.2. Salinity tolerances of *F. spiralis* and *F. vesiculosus* var. *spiralis* were recorded at 5 and 25°C. In the salinity tolerance experiments, 3 replicates were used. The plants were incubated at their respective temperatures and salinities for 48 hours prior to their measurement.
DESCRIPTION OF STUDY AREAS
AND ENVIRONMENTAL CONDITIONS

As stated previously, Jaffrey Point, or Fort Stark as it is commonly called, was the primary study site. It is a semi-exposed, open coastal site located approximately two miles southeast of Portsmouth, New Hampshire, on the southeast corner of Newcastle Island, latitude 43°03'33"N, longitude 70°42'42"W (Fig. 2). The shore consists primarily of large metasedimentary rock outcroppings with several intermittent small sand and gravel beaches. The metasedimentary outcroppings have a rough texture with many large cracks and fissures. A detailed geological description of the area is given by Novotny (1969). A large biomass of fucoid algae occurs throughout the intertidal zone at Jaffrey Point which consists primarily of Fucus vesiculosus, Ascophyllum nodosum and Fucus spiralis.

The seasonal variations in the temperatures and salinities of the surface water at high tide at Jaffrey Point, New Hampshire are shown in Figure 3. A minimum of 3 °C was recorded in December, while maximum temperatures of 18.5-19.5 °C were recorded in July and August. The salinity was relatively stable from July to May, ranging from 30 o/oo to 25 o/oo; the salinities then increased again to 30-31.5 o/oo. The tidal range at spring tide varies from -0.66 to
3.42 m with the average tidal amplitude being +2.64 m (Anon. 1972). Further descriptions of Jaffrey Point are summarized by Mathieson, et al., (in press, a).

The Great Bay Estuary System contains over 11,000 acres of tidewater (Anon. 1960) and it is one of the largest estuary systems on the East Coast of the United States (Fig. 2). The tidal waters enter and leave via the Piscataqua River. The Estuary System consists of Great Bay, Little Bay, Portsmouth Harbor and its tributaries, the Piscataqua River, and seven freshwater rivers, which drain into the basin. These latter rivers are the Salmon Falls, Cocheco, Bellamy, Oyster, Lamprey, Squamscott, and Winnicut. The total drainage area of the System is approximately 930 square miles; the estuary itself contains about 100 miles of shoreline (Mulligan, et al., 1974). The intertidal shoreline primarily consists of scattered, metasedimentary and metavolcanic outcrops, as well as scattered shingle, boulders and pebbles among muddy tidal flats. The intertidal flora is dominated by fucoid (Ascophyllum nodosum and Fucus vesiculosus var. spiralis) and crustose algae (Hildenbrandia prototypus and Protoderma marinum) in association with the marine invertebrates Balanus balanoides, Mytilus edulis and Littorina littorea.

Wide fluctuations of surface water temperature and
salinity occur within the Great Bay Estuary System (Table I). A description of the estuarine stations where *F. spiralis* populations are found is summarized in the appendix. Further descriptions of the Great Bay Estuary System are given by Mathieson, et al., (in press, b).
REPRODUCTION AND GROWTH OF FUCUS SPIRALIS

Figure 4 summarizes the seasonal reproduction of F. spiralis at Jaffrey Point, expressed as the percentage of reproductive plants in the population and the percentage of fertile tips per plant. The period of maximum reproduction occurs from June to September; prior to this period only immature receptacles of vegetative tips were visible (Fig. 1). Thus, the number of reproductive plants increased sharply from May to July and the numbers remained relatively constant until September (approximately 60%); thereafter, it decreased drastically. The number of fertile tips/plant followed a similar pattern, reaching a maximum of 15% in August and declining sharply thereafter. As shown in Figure 5, reproductive plants were 9.5 cm or longer in length during July to September. A maturation sequence is also suggested as the largest plants showed the highest percentage of reproductive plants. Figure 5 also shows a sequential increase in reproductive plants from July to August and a decrease in September. Most (85-90%) of the samples were 9.5 to 24.5 cm in length.

Figure 6 illustrates the seasonal growth of tagged in situ plants of F. spiralis at Jaffrey Point, expressed as the average increase in length per month. A maximum growth rate of 1.9-2.8 cm/month occurred during the summer
(June through August), while a minimal growth rate of 0.6 to 0.8 cm/month occurred from November through March. A comparison of Figures 4 and 6 shows that a fall (October) maximum of growth occurred after the termination of maximum reproduction.

Table III illustrates the annual growth of twelve in situ plants during 1972 and 1973, while Table IV shows the growth of forty plants during July to November, 1972. The annual growth rates of the twelve tagged plants ranged from 0.9 to 1.4 cm/month, and the yearly length increase varied from 9.9 to 15.9 cm. The growth rate from July-November for the forty tagged plants ranged from 1.1 to 2.9 cm/month, while the total length increase for the same period varied from 4.3 to 11.5 cm. Statistical analysis showed no correlation between the rates of growth and the initial size of the twelve and forty tagged plants ($r = 0.22$ and 0.06).

Figure 7 shows the seasonal survival of tagged in situ plants/months at Jaffrey Point. Three separate sets of tagged plants were employed: that is, 100 were tagged in July, 25 were tagged in December and a third set of 20 were tagged in April. There was continual loss of tagged plants after each of the three periods. Even so, the highest attrition occurred from July through September and from February to
March. Figure 8 illustrates the sizes at which the plants of \textit{F. spiralis} were lost. The greatest attrition occurred with plants between 15 to 30 cm long. Very few plants attain a length greater than 35 cm. It should be noted that the smaller plants (0-10 cm) are inadequately represented, because they were difficult to tag.

The seasonal growth of \textit{F. spiralis} expressed as the average weight/plant and the average weight/cm/plant is illustrated in Figure 9. Both of the plots show the same basic pattern, with the largest plants occurring in July and August and the smallest in January. Thus, the average weight/plant varied from 37.8 to 43.9 g during July and August to 7.0 g in January. The average weight/cm/plant ranged from 2.3 g/cm/plant in July and August to 0.5 g/cm/plant in January. The average weight of summer plants was approximately five times that of winter specimens.
VERTICAL DISTRIBUTION AND BIOMASS
OF F. SPIRALIS AND ASSOCIATED FUCOIDS

Figure 10 illustrates the vertical distribution and biomass of the fucoid algae at Jaffrey Point. The F. spiralis belt is the highest within the intertidal zone ranging from +2.12 to +2.36 m above mean low water (M.L.W.). There is a transition area between F. spiralis and the F. vesiculosus-A. nodosum belts at approximately +2.12 m. Even so, all three fucoids were present at this elevation, as well as Fucus plants (hybrids) that were difficult to identify because they were morphologically intermediate between F. spiralis and F. vesiculosus. There was a mixture of A. nodosum and F. vesiculosus between +1.21 to +2.12 m. No fucoid algae were present below +1.21 m, presumably because of a lack of stable substrate. The biomass of F. spiralis varied from 250-270 g/0.25 m² at the top and bottom of the zone to 545 g/0.25 m² in the middle of the zone. The greatest biomass of A. nodosum (660 g/0.25 m²) also occurred in the middle of its zone, with lower values occurring at the lower and higher elevations. The biomass of F. vesiculosus ranged from 36 to 258 g/0.25 m², with no conspicuous stratification between +1.21 and +2.12 m.

The stature and reproductive status of F. spiralis plants at Jaffrey Point also showed a vertical stratification (Fig. 11). Thus, the average weight, length, and fertility
tended to decrease with an increase in elevations. The highest average length and reproductive frequency of *F. spiralis* occurred between +2.09 and +2.18 m. In contrast, the largest average weight tended to occur between +2.15 and +2.27 m. Figure 12 illustrates the size frequency distribution of *F. spiralis* plants at Jaffrey Point. The largest plants (40-50 cm) occurred between +2.12 and +2.15 m. Above and below these elevations the plants were smaller. The highest frequency of small plants (0-20 cm) was recorded between +2.30 and +2.39 m. Thus, a change in size and stature was evident within the *F. spiralis* belt.

Figure 13 illustrates the vertical distribution and standing crop of fucoid algae at Fort Constitution, near the mouth of Portsmouth Harbor (Fig. 2). *Fucus vesiculosus* var. *spiralis* and *A. nodosum* are present, but *F. vesiculosus* and *F. spiralis* are absent. *Fucus vesiculosus* var. *spiralis* occupies the highest part of the shore between +1.82 to +2.12 m with largest biomass (503 g/0.25 m²) occurring towards the lower end of its belt. *Ascophyllum nodosum* is most abundant towards the lower elevations, even though *F. vesiculosus* var. *spiralis* is still present. As at Jaffrey Point, the greatest biomass (1040 g/0.25 m²) of *A. nodosum* occurred in the central portion of the bent (+1.42 to +1.64 m).
HORIZONTAL DISTRIBUTION OF FUCUS SPIRALIS

Although F. spiralis is not evident at Fort Constitution, it extends sporadically throughout the Great Bay Estuary System (Fig. 14). Table I summarizes the maximum, minimum and average values for temperature and salinity within the distributional range of F. spiralis. It is evident that F. spiralis is both eurythermal and euryhaline, occurring within a temperature and salinity range of -0.5 C to 23.1 C and 3.0 o/oo to 31.0 o/oo, respectively.

Figure 14 summarizes the vertical distribution (i.e. the range) of F. spiralis at Jaffrey Point and at five inland estuarine sites. The plant's vertical distribution was higher and broader (+2.12 to +2.36 m) at Jaffrey Point than most of the estuarine sites except Nannie Island. Estuarine populations of F. spiralis tend to form a compressed and often reduced belt above F. vesiculosus var. spiralis. In addition, F. spiralis was always restricted to metasedimentary or metavolcanic outcrops, similar to those at Jaffrey Point.
WATER LOSS OF FUCUS SPIRALIS AND ASSOCIATED FUCOIDS

Figure 15 summarizes the rate of water loss of in situ populations of F. spiralis, F. vesiculosus, F. vesiculosus var. spiralis, and A. nodosum. The highest growing fucoid, F. spiralis, loses water more slowly than the other lower growing species. Thus, F. vesiculosus, F. vesiculosus var. spiralis and A. nodosum lose water at a similar rate of approximately 30%/hour for the first two hours, while F. spiralis showed a lower rate of approximately 15%/hour during the same period. After five hours, the first three fucoids lost approximately 90% of their water content. Fucus spiralis still had 40% of its original water content after five hours and 30% after nine hours. Individual plants of F. spiralis from top, middle and lower elevations lose water at different rates (Fig. 16). For example, a 10% difference in water loss was evident between individuals from the top and bottom of the zone.
MANOMETRIC STUDIES

Light

Figure 17 illustrates the rates of net photosynthesis of Fucus spiralis, Fucus vesiculosus and Fucus vesiculosus var. spiralis at 15 C, 31 o/oo and under varying light intensities. The net photosynthesis of F. spiralis increased with an increase in light intensity to about 1000 foot-candles; beyond this intensity the rates remained relatively constant through 3000 foot-candles. Thus, light intensities of less than 1000 foot-candles are probably suboptimal, while those in excess are probably saturating for net photosynthesis. Fucus vesiculosus and F. vesiculosus var. spiralis showed a similar increase in net photosynthesis with an increase in light intensity up to about 1200 foot-candles; thus, optimal light requirements for the latter species are about 1200 foot-candles but they show a broad tolerance to high light intensities.

Temperature

Figure 18 illustrates the rates of net photosynthesis of summer and winter specimens of F. spiralis at various temperatures, 1000 foot-candles and 31 o/oo. During the summer, the rates of net photosynthesis increased with increasing temperatures from 10 to 25 C, decreased substantially from 25 to 32 C, and then ceased at 37 C. Winter
plants showed the following differences from summer plants:
(1) a higher rate of net photosynthesis between 5-30 C;
(2) a broader "plateau" between 20 and 25 C and; (3) a reduced tolerance to high temperatures. Figures 19 and 20 illustrate seasonal temperature responses of *F. vesiculosus* and *F. vesiculosus* var. *spiralis* at 1000 foot-candles and 31 o/oo. Summer specimens of both species showed a similar temperature optimum of about 25 C, decreasing photosynthesis above 35 C, and no photosynthesis at 37 and 40 C. Winter specimens of *F. vesiculosus* showed a higher rate of net photosynthesis between 5-30 C, temperature optima of 15-20 C, and a reduced temperature tolerance as compared to summer plants. Winter specimens of *F. vesiculosus* var. *spiralis* showed temperature response similar to that of *F. vesiculosus*, except for a somewhat broader plateau between 15-25 C.

A comparison of Figures 18-20 shows a variety of similarities and differences between three fucoid species. Summer specimens of *F. vesiculosus* var. *spiralis* showed the highest temperature tolerance, with net photosynthesis still occurring at 38 C. In contrast, summer specimens of *F. vesiculosus* and *F. spiralis* showed no net photosynthesis at 37 C. Each of the three species exhibited the same maximum temperature tolerance of 35 C during the winter. It should also be noted that *F. vesiculosus* and *F. vesiculosus* var.
spiralis showed a greater increase in their rate of net photosynthesis per degree centigrade during the winter than during the summer.

Salinity

The rates of net photosynthesis for F. spiralis and F. vesiculosus in various salinities, 1000 foot-candles and 15 C are illustrated in Figure 21. Fucus vesiculosus showed a broad tolerance to salinity, with lowest net photosynthesis at 0 and 10 o/oo and a relatively constant response between 20-35 o/oo. Fucus spiralis showed a relatively constant rate of net photosynthesis between 15-30 o/oo, with a slight increase between 30-40 o/oo. The greatest fluctuations of net photosynthesis in both species were evident at 0-15 o/oo. Fucus vesiculosus var. spiralis showed its highest rates of net photosynthesis at 5-15 o/oo, relatively constant rates between 20-40 o/oo, and its lowest net photosynthesis at 50 o/oo (Fig. 22).

Salinity and Temperature

Figure 23 illustrates the rate of net photosynthesis of F. spiralis and F. vesiculosus var. spiralis at 5 and 25 C, 1000 foot-candles and after 48 hours of immersion in solutions of various salinities. Fucus spiralis showed differential tolerances to low salinities at 5 and 25 C. Thus, it showed no marked decrease in net photosynthesis with decreasing
salinity at 5 °C, but a conspicuous decrease in net photosynthesis with decreasing salinities at 25 °C. This same differential salinity tolerance was not evident with *F. vesiculosus* var. *spiralis*; indeed, at 25 °C the net photosynthesis was greater at 0 than at 10 o/oo. The higher rate of net photosynthesis at 5 °C, than at 25 °C was particularly striking, as it was the reverse of that shown in Figure 18.
DISCUSSION

_Fucus spiralis_ shows a pronounced reproductive periodicity similar to other species of fucoid algae, as _Ascophyllum nodosum_ (Baardseth, 1970), _Fucus serratus_ (Lemoine, 1913; Knight and Parke, 1950) and _Fucus vesiculosus_ (Lemoine, 1913; Knight and Parke, 1950; Hamel, 1931). Thus, local populations of _F. spiralis_ from New Hampshire exhibit maximum reproduction during July to September, with a peak in August. Subrahmanyan (1961), Williams, et al. (1965), and Bird and McLachlan (1974) recorded a similar reproductive phenology for British and Canadian populations of _F. spiralis_.

The initiation, maturation and shedding of the receptacles in New Hampshire populations of _F. spiralis_ usually occurs over a ten month period. The receptacles appear during late January-February, gametes are discharged during July or August, and the receptacles are subsequently shed by November. As shown in Figure 5, young plants of _F. spiralis_ usually reach a length of 10 cm or more before they form receptacles; in addition, the number of receptacles/plant increases with the size of the plant. Subrahmanyan (1961) recorded similar observations on _F. spiralis_ populations on the Isle of Man, where the smallest reproductive plants were 8 to 10 cm long. My study also confirms Subrahmanyan's findings that reproduction normally begins during
or at the end of the second year's growth. Thus, there are many similarities between reproductive phenologies of the *F. spiralis* populations on the Isle of Man and in New Hampshire.

The reproductive period of *F. spiralis* occurs later in the year than with *Ascophyllum nodosum* and *Fucus vesiculosus*. For example, the period of maximum reproduction for *A. nodosum* occurs during April-May (David, 1943; Moss, 1970, Baardseth, 1970). Knight and Parke (1950) record a similar period of maximum reproduction in *F. vesiculosus*, as well as the continued release of gametes in small amounts until September. The estuarine variety *spiralis* of *F. vesiculosus* shows a reproductive periodicity in New England similar to that of *F. vesiculosus* on the Isle of Man (A. Mathieson, unpublished data). A comparison of the reproductive phenology of *F. spiralis* and *F. vesiculosus* also shows that there is some overlap between the two lasting into September. Burrows and Lodge (1951) have also noted an overlapping of reproductive periods in these two species.

Munda (1964, 1967) suggested that reduced salinities influence the reproductive phenologies of fucoid algae, and noted that the rate of fructification in *A. nodosum* and *F. vesiculosus* was accelerated in diluted sea water. Burrows (1964) also indicated that the initiation of reproduction
in _F. serratus_ and _F. ceranoides_ occurred in a wide range of salinities. The initiation and maturation of fertile receptacles in _F. spiralis_ populations in New Hampshire also occur during the spring runoff from the Great Bay Estuary System. Unfortunately a detailed, comparative study has not been conducted on New England estuarine populations of _F. spiralis_.

If salinity plays a major role in determining the ripening process of _F. spiralis_ receptacles, as suggested by Munda for related fucoid species, then the period of maximum reproduction and the length of the fertile period might vary according to the hydrographic regimes of the habitat. The lengthening of the reproductive period of _F. spiralis_ could have considerable biological significance as it would increase the reproductive overlap with _F. vesiculosus_ and increase the potential for their hybridization.

Burrows and Lodge (1951) emphasized that the fruiting periods of _F. spiralis_ and _F. vesiculosus_ overlapped extensively near the Mersey River in England; in addition, they noted that the area contained extensive hybrid populations between the two species. Stomps (1911) also found a similar situation on the Belgian Coast where the Chenal de l'Yser River flows into the sea at Nieuport. A variety of field and laboratory studies should be conducted to evaluate the effects of overlapping reproductive periods, salinity effects and
hybridization in the genus *Fucus*.

Several other environmental factors might also play a role in the reproductive phenology of *F. spiralis*, such as nutrients, temperature and photoperiod. David (1943) speculated that a critical balance of carbohydrates and nitrogenous substances is necessary before the initiation of reproduction. Knight and Parke (1950) seem to support David's hypothesis regarding nutrients, for they found that the earliest maturation of *F. vesiculosus* populations occurred near river discharges (e.g., Langness on the Isle of Man), presumably because of the extra organic matter added to the sea water. My study also showed an interrelationship between receptacles initiation and high nutrient concentrations, since the highest concentration of nitrogenous and phosphorous nutrients occurred at Jaffrey Point during January and February (Norall, unpublished data). David (1943) states that cold temperatures may also induce receptacle formation in *F. spiralis*, since they are initiated during the winter. *Fucus spiralis* populations in New England and on the Isle of Man (Subrahmanyan, 1961) also show the same winter initiation of receptacles. Naylor (in Printz, 1956) suggested that photoperiodism might be a major factor determining reproductive phenology of *Ascophyllum* and other fucoid algae because of conspicuous latitudinal variations.
In contrast, McLachlan (1971) suggested that reproduction in *Fucus* may be an intrinsic characteristic. The findings of Burrows (1964) and Moss (1967, 1968) also tend to support McLachlan's findings. Critical laboratory and field studies are needed to evaluate the role of environmental and/or genetic control of reproduction in *F. spiralis*.

A comparison of Figures 4 and 6 shows that the reproduction and growth of *Fucus spiralis* are synchronized, except during the early fall when there is an "enhancement" of growth following reproduction. Thus, the period of maximum growth and reproduction in *F. spiralis* occurs during the late summer, while both are at minimal levels during the winter. In contrast to my findings, Subrahmanyan (1961) reported an alternating periodicity of growth and reproduction with *F. spiralis* populations on the Isle of Man. The cooler temperature regimes in New England versus England may explain the differential growth potential of the two populations: that is, more extensive growth may occur during the fall and winter in England because of the milder temperature conditions. It is of interest to note that both David (1943) and Mathieson (unpublished data) have also noted a similar "enhancement" of growth following reproduction with the fucoid brown algae *Ascophyllum nodosum* and *Fucus vesiculosus var. spiralis*. Such enhancement may be a
As noted previously, the seasonal growth of *Fucus spiralis* in New Hampshire varies from 1.9 to 2.8 cm/month in the summer to 0.7 cm/month in the winter, with an overall monthly average of 1.2 cm/month. Subrahmanyan (1961), working with *F. spiralis* populations on the Isle of Man, found rates varying from 7.9 to 18.7 cm per year; this would average 13.3 cm/year or 1.1 cm/month, comparing favorably with the local growth rates. Hariot (1909) recorded lower growth rates for French populations of *F. spiralis* than those recorded in England or New England - e.g., Hariot observed an average growth rate of 4.5 cm during an eight month period or approximately 0.6 cm/month.

A comparison of the growth rates of *Fucus spiralis* at Jaffrey Point and *Fucus vesiculosus* on the Isle of Man (Knight and Parke, 1950; Subrahmanyan, 1961) indicates that the latter species grows faster than the former. That is, the average growth rate of the mid intertidal fucoid, *F. vesiculosus*, was 1.8 cm/month versus 1.2 cm/month for the high intertidal fucoid, *F. spiralis*. The differential growth rates between the two species is consistent with other workers' findings (Baker, 1910; Gislen, 1930) that the rate of growth decreases with an increase in elevation.

The increased growth of *F. spiralis* from April to
August is associated with a corresponding increase in temperature and light (duration and intensity) conditions. Maximum growth occurs when the surface water temperatures are 18-19°C and daylengths are about 15 hours. The latter "optimal" conditions are similar to those recorded by McLachlan, et al., (1971) and Sheader and Moss (1975) for other fucoid algae.

Longevity of the *Fucus spiralis* plants at Jaffrey Point, New Hampshire usually ranged from 2-2.5 years; however, some plants exceeded four years. If an average growth rate of approximately 1.2 cm/month is assumed, a one year old plant would be approximately 14.4 cm long; a two year old plant would be approximately 28.8 cm long. Most of the *F. spiralis* plants at Jaffrey Point varied from 0.1 to 30 cm long (Fig. 11 and 12). Similar results were also observed with the plants tagged *in situ* since the largest percentage (74%) of these plants attained a length of 15 to 30 cm before they were lost (Fig. 8); very few plants attained a length of 30 to 45 cm (15%). The longest plants observed at Jaffrey Point were approximately 42 cm long. The longevity of *F. spiralis* populations at Jaffrey Point is comparable to that found in Europe. For example, Rees (1932) and Chapman (1968) stated that the average longevity of *F. spiralis* is approximately 1.5 years. Subrahmanyan (1961)
recorded a maximum longevity of 4 to 5 years. According to Rees (1932), *F. spiralis* has a greater longevity than *F. vesiculosus* or *A. nodosum*. In contrast, Boney (1966) stated that the maximum life span of *A. nodosum* is 13-19 years in the British Isles, with an average of 12-13 years.

As shown in Figure 7, *Fucus spiralis* shows two periods of major attrition: (i) during the late summer period of maximum reproduction, and (ii) during the winter period of severe storms and ice scouring. The largest losses of plants occurred during the late summer because of the heavy weight of the mature receptacles and the rapid decay of the stipe by bacterial and fungal action. It should be noted that young plants of *F. spiralis* can quickly replace the older, denuded plants, because of the coincidence of maximum attrition and reproduction. Subrahmanyan (1961) also recorded a high attrition in *F. spiralis* populations on the Isle of Man, while Knight and Parke (1950) recorded the same phenomenon in the other fucoids. Thus, there is a correlation between the attrition, longevity, and time of reproduction in a variety of fucoids.

*Fucus spiralis* forms the uppermost fucoid zone at Jaffrey Point and adjoining sites, occurring between +2.12 and +2.36 m. As a result of its extreme vertical distribution, *F. spiralis* is exposed to the air most of the time.
(60 to 80%), and it must resist a variety of atmospheric extremes, such as high light intensities, temperatures and water loss. A comparison of the photosynthesis-light responses of *F. spiralis* indicates that it is a sun plant, i.e., it is able to withstand a wide range of light intensities and it has a relatively high light optimum (approximately 1000 to 1200 foot-candles). *Fucus vesiculosus, F. vesiculosus* var. *spiralis* and a variety of other seaweeds (Stocker and Holdeheide, 1938; and Kanwisher, 1966) also show the same physiological characteristics.

The broad temperature and light tolerances of *Fucus spiralis*, as well as its slow rate of water loss, also substantiate its tolerances and adaptations to the high intertidal zone. *Fucus spiralis* loses water at approximately one-half the rate of *F. vesiculosus, F. vesiculosus* var. *spiralis*, and *A. nodosum*. Zaneveld (1937), Priou (1963) and Berard-Therriault and Cardinal (1973) also recorded a differential water loss of fucoid algae in relation to their vertical distributions. However, other workers (e.g., Kristensen, 1968) have shown contrary results, relating desiccation and vertical distribution. Even so, Zaneveld (1969) emphasizes that "all measurements thus far taken point toward desiccation and its influence on photosynthesis as the main causal factor determining the upper limits of
vertical distribution of various eulittoral algae". The recent studies of Johnson, et al. (1974) and the earlier studies of Stocker and Holdheide (1938) substantiate Zanen- 
veld's suggestion, for they observed that the photosynthetic rate of *Fucus* sp., as well as other high intertidal seaweeds, were higher under exposed than submerged conditions. It should be emphasized that the "enhancement" phenomenon described by Johnson, et al. (1974) only occurs up to a critical water content, beyond which photosynthesis decreases. Unfortunately comparable desiccation-photosynthesis studies have not been conducted on *F. spiralis*.

A stratification of biomass, stature and reproduction was observed within the *Fucus spiralis* zone at Jaffrey Point. A differential water loss was also evident from the top and bottom; that is, small plants at the top of the zone lost water faster than larger ones from the middle and lower areas. Typically the smaller and less reproductive plants were recorded in the upper belt; the opposite was evident in the lowermost portion of the belt. Thus, there seems to be a relationship between growth (stature) and water loss, with a critical water content ultimately suppressing growth and probably net photosynthesis as well. The same relationships may also exist for reproduction, as Baker (1910) has shown a differential zygote survival under
different exposure periods. Subrahmanyan (1961) and Anand (1937) also documented a morphological stratification of *F. spiralis* plants in Great Britain. In addition, Subrahmanyan noted a differential growth rate at the top (about 8 cm/year) and bottom (13-14 cm/year) of the *F. spiralis* belt.

A mixture of heterogenous *Fucus* species ("hybrids") were recorded from Jaffrey Point at about +2.12 m. The "hybrid"-like plants were difficult to identify as either *F. spiralis* or *F. vesiculosus*. Kneip (1925), Sauvageau (1908) and Burrows and Lodge (1951) also recorded "hybrid" fucoid populations at the transitional zone between *F. spiralis* and *F. vesiculosus*. Burrows and Lodge (1951) emphasized that "hybrids" occur between these two species and that they would be most competitive in the transition areas between the sharply defined zones of the parents. A more detailed investigation will be required on these plants to verify that they are indeed interspecific hybrids.

*Fucus spiralis* is most abundant locally on semi-exposed and sheltered open coastal shores (Mathieson, et al., in press, a). Even so, it exhibits a broad estuarine distribution within the Great Bay Estuary System, extending inland to areas where the temperature and salinity range from -0.5-23 C and 3-32 o/oo, respectively. Nienhuis (1975) also observed a broad estuarine distribution of *F. spiralis*
populations in the Netherlands, where plants extended to the 10 o/oo isohaline. My manometric studies also substantiate the plant's broad tolerance to salinity, as well as temperature. Even so, it should be emphasized that *F. spiralis* is represented by localized and discontinuous populations within the Great Bay Estuary System. Thus, local factors other than temperature and salinity seem to determine its sporadic estuarine distribution. The presence or absence of substratum is probably one of the most important factors determining the local distribution of *F. spiralis*. Specifically the plant was only found on coarse metasedimentary and metavolcanic rocks with an abundance of cracks and fissures. These rocks are sporadically distributed within the Great Bay Estuary System (Novotony, 1969). Several other workers (Chapman, 1968; Doty and Newhouse, 1954; Gibb, 1950) have also emphasized the importance of substratum in determining the horizontal and discontinuous distributions of seaweeds. Lewis (1972) states that *F. spiralis* favors a sheltered rather than an exposed habitat. The rock outcrops described above, with their many cracks and fissures, probably provide some degree of protection for developing zygotes and adult plants of *F. spiralis*.

My manometric experiments with *Fucus spiralis* described above show a close correlation between the summer
rates of the plant and its temperature-net photosynthesis responses. That is, the optimal temperature for net photosynthesis during the summer occurs at approximately 25 °C. Locally the highest surface water temperatures occur during July and August, with a maximum of 17.5 to 19 °C at Jaffrey Point and approximately 23 °C within Great Bay proper (Table I). The latter results are in accord with Ehrke's (1931) findings that there is a correlation between the temperature of maximum photosynthesis and the average temperature of maximum development.

A comparison of the winter net photosynthesis-temperature experiments shows that there is a decrease in the optimal temperature to approximately 20 °C. Winter plants of F. spiralis also show higher rates of net photosynthesis than the summer plants. Yokohama (1972) noted a similar response for several seaweeds collected in the winter. Zanodnik (1973) also recorded a higher rate of photosynthetic activity for winter than summer plant populations of Fucus virsoides that were maintained in the laboratory. He also pointed out that there is a seasonal variation in the chlorophyll (a and c) and carotenoid concentrations, with the highest concentrations occurring during the winter. A variety of other seaweeds, such as Codium (Sevane-Coriba, 1964; Fox, 1971) and Chondrus (Brinkhuris and Jones, 1974)
also show a seasonal variation in chlorophyll pigments; this and other physiological changes could explain the differences between winter and summer net photosynthetic results. *Fucus vesiculosus* and *F. vesiculosus* var. *spiralis* show an even greater difference between their winter and summer rates of net photosynthesis. The different photosynthetic rates among the three plants may be due to the varying reproductive phenologies and ensuing pigment degradation rates. The differences might also suggest a greater tolerance by *F. spiralis* to high light and temperature regimes during the summer months than as shown by the other two fucoids.

The winter net photosynthesis-temperature response of *F. spiralis* follows the same pattern as *Fucus* sp. from the Arctic (Healey, 1972); that is, the maximum net photosynthesis occurs at 20 to 25 C, with the photosynthetic rate at 10 C being two-thirds of the maximum. In comparing the winter and summer photosynthetic responses of *F. spiralis* at 10 C, it is apparent that the winter rate is almost twice the summer rate. This phenomenon could be an indication of low temperature adaptation, as it would result in higher net photosynthesis during the winter.
SUMMARY

1. The autecology of *F. spiralis* in New Hampshire, U.S.A. was investigated from 1972-1975.

2. The fertile receptacles of *F. spiralis* first appear during late January and early February and they are reproductively mature during July to September.

3. The periods of maximum growth and reproduction coincide, i.e., both occur during the late summer. A limited enhancement of growth follows the reproductive period.

4. The average longevity of *F. spiralis* populations is approximately two years in New Hampshire, with a maximum of about four years. Two periods of major attrition occur, i.e., during the late summer period of maximum reproduction and during the winter period of severe storms and ice scouring.

5. The growth rate, longevity and reproductive periodicity of New England populations of *F. spiralis* are comparable with those previously recorded in Europe.

6. A microstratification of biomass, stature and reproduction was observed within the *F. spiralis* zone at Jaffrey Point, New Hampshire.

7. The desiccation rates of *F. spiralis* and associated fucoid algae was evaluated. *Fucus spiralis* shows a very slow rate of water loss, in comparison to the
other fucoid algae.

8. A summary of the vertical and horizontal distribution of *F. spiralis* within the Great Bay Estuary System is given. The presence or absence of substratum is suggested as a causal factor for the sporadic estuarine distribution of *F. spiralis*.

9. Manometric studies on *F. spiralis* were undertaken in relation to varying light intensities, temperatures and salinities. *Fucus spiralis* has a broad tolerance to all three of these parameters, corresponding to its estuarine and vertical distribution.

10. Comparative manometric studies were also made on *F. vesiculosus* and *F. vesiculosus* var. *spiralis*. Both of these species also showed a broad tolerance to temperature, salinity and light regimes.

11. *Fucus spiralis*, *F. vesiculosus* and *F. vesiculosus* var. *spiralis* showed pronounced differences in their net photosynthesis-temperature responses during the winter and summer. Several reasons for this seasonal difference are discussed.
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APPENDIX

STATION DESCRIPTIONS

Jaffrey Point (Station #1): A semi-exposed, open coastal area located on the southeast corner of Newcastle Island approximately two miles from Portsmouth, New Hampshire. The intertidal area primarily consists of massive metasedimentary rock outcrops and scattered boulders; small coarse gravel occurs in a few localized areas.

Schiller Power Plant (Station #2): An estuarine site on the Maine side of the Piscataqua River across from the old Schiller Power Station. The substrate consists of rock outcropings similar to those at Jaffrey Point, as well as boulders, cobbles and mud.

Dover Point (Station #3): An estuarine tidal rapid site at the junction of the Piscataqua River and Little Bay. The intertidal area consists of massive rock pilings, boulders, cobbles and mud.

Fox Point (Station #4): An estuarine site in Little Bay opposite the mouth of the Oyster River. The substrate consists of residual pileage from an old bridge, boulders, cobbles and mud.

Adams Point (Station #5): An estuarine area approximately 4.5 miles southeast of Durham, located at the
junction of Great Bay and Little Bay, and the site of the Jackson Estuarine Laboratory. The substrate consists of small rock outcrops as well as scattered boulders and mud.

Nannie Island (Station #6): A small island located in the southeast corner of Great Bay, opposite Woodman Point. The intertidal area consists of small rock outcrops, scattered boulders, shingle and mud.
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<th>Miles (Nautical)</th>
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TABLE IV

GROWTH OF FORTY TAGGED PLANTS OF FUCUS SPIRALIS
JULY 1972–NOVEMBER 1972

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Figure 2 Map of the New Hampshire Seacoast and Study Sites.
Figure 3  Variations in Surface Water Temperatures and Salinities at Jaffrey Point, New Hampshire, July 1972 to September 1973.
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% of water loss

Hours of exposure
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Figure 19 Net Photosynthesis of Winter and Summer Plants of *Fucus vesiculosus* at Various Temperatures, 1000 foot-candles.
Figure 20 Net Photosynthesis of Winter and Summer Plants of *Fucus vesiculosus* var. *spiralis* at Various Temperatures, 1000 foot-candles.
Figure 21 Net Photosynthesis of *Fucus spiralis* and *Fucus vesiculosis* in Various Salinities and 15 C.
For F. spiralis:

- The graph shows the variation of $pO_2$/g dry wt./0.5min with salinity.
- There is a peak around 10% salinity, with a decrease and then an increase towards higher salinities.

For F. vesiculosus:

- The graph also shows the variation of $pO_2$/g dry wt./0.5min with salinity.
- There is a peak around 5% salinity, with fluctuations and then a general decrease towards higher salinities.

Salinity %

0 5 10 15 20 25 30 35 40 45 50

$pO_2$/g dry wt./0.5min

40 60 80 100
Figure 22 Net Photosynthesis of *Fucus vesiculosus* var. *spiralis* in Various Salinities and 15°C.
Figure 23 Net Photosynthesis of *Fucus spiralis* in Various Salinities, 5 and 25 C.