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ERIC JOSEPH SIDEMAN

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Ecology and Genecology of Fucus distichus (L.) Powell.

BY

Eric Joseph Sideman
B.A. Cornell University
M.S. Northeastern University

A DISSERTATION

Submitted to the University of New Hampshire
in Partial Fulfilment of
the Requirements for the Degree of

Doctor of Philosophy
in
Botany

September, 1982
This dissertation has been examined and approved.

A. C. Mathieson

Dissertation director, Arthur C. Mathieson
Professor of Botany

Garret Crow, Associate Professor of Botany

Thomas D. Lee, Assistant Professor of Botany

Donald P. Cheney, Assistant Professor of Biology,
Northeastern University

Larry G. Harris, Associate Professor of Zoology

6/24/82

Date
ACKNOWLEDGEMENTS

I wish to express my sincere gratitude to Dr. Arthur C. Mathieson for the guidance and encouragement he has provided during my Doctoral Program. His insight and enthusiasm has made this dissertation possible and his assurance and friendship has been peerless. I also wish to thank Dr. Garrett Crow, Dr. Thomas Lee, Dr. Donald Cheney, and Dr. Larry Harris for their assistance throughout the project and for their careful review and criticism of the dissertation.

I am grateful to Clayton Penniman for his ineluctable criticism and his unvarying appreciation of phycology. I am also indebted to Chris Neefus for use of his computer programs. Numerous other friends, especially Michael Wisniewski, have made the duration of my work at the University of New Hampshire most enjoyable.

I would also like to thank the University of New Hampshire Marine Program for providing use of the Jere Chase Research Vessel and Captains Ned McIntoush and Paul Pelletier for their guidance to the Isles of Shoals through varying seas. Financial assistance for the many miles of land traveled during this study was provided by the Central University research Fund, Sigma Xi, and the University of New Hampshire Graduate School. In addition I am grateful to
the Graduate School for providing two Summer Fellowships and a Dissertation Fellowship, and the Department of Botany and Plant Pathology for employment as a Teaching Assistant.
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ABSTRACT

ECOLOGY AND GENEKOLOGY OF

FUCUS DISTICHUS (L.) POWELL

BY

ERIC JOSEPH SIDEMAN

University of New Hampshire, September, 1982

Growth rates, reproductive phenology, and longevity of Fucus distichus ssp. edentatus and F. distichus ssp. evanescens were evaluated in natural populations in New England. Both subspecies exhibited maximum growth during early summer, a slight decline in late summer, and a brief resurgence in the early fall. The maximum growth rates (in terms of elongation) for ssp. edentatus and ssp. evanescens was 3.5 cm/mo and 3.7 cm/mo, respectively. Populations of both subspecies showed a distinct bimodal reproductive periodicity, with maxima in the spring and fall. Individuals within natural populations were reproductive in either the spring or fall but never both seasons. After the reproductive period receptacles dehisced and plants were vegetative or died. Increased rates of plant attrition were observed during periods of reproduction.

The sources of morphological variation of Fucus distichus ssp. edentatus and F. distichus ssp. evanescens
were evaluated in natural populations in New England. Variation of characters (width and length of receptacles, width of fronds, etc.) were shown to be of a continuous nature by frequency distribution plots. On the other hand, individuals from different populations were morphologically distinct as judged by population means and analysis of variance. A correlation between the plant's form and its habitat has been established by field observation. The broadest material grows in calm estuarine habitats, while the narrowest plants occur in exposed, open coastal areas. Major differences in morphology also appear seasonally. In addition, microhabitat factors such as exposure to wave action and elevation explain some morphological variation. Cultured germlings from distinct populations of "evanescens-type" and "edentatus-type" plants have been outplanted to experimental gardens in order to ascertain whether the variation is heritable or environmentally induced. Results of the garden experiments indicate that major differences in morphology are genetically based.

Morphological, ecological, and genetic distinctions of a dwarf, non-tide pool member of the Fucus distichus complex were assessed at an exposed site in southern Maine. Variation in plant stature from typical F. distichus ssp. edentatus to the dwarf form is continuous. On the other hand, measurements of reproductively mature plants collected throughout the eulittoral showed a bimodal pattern, i.e., there was a high frequency of dwarf forms
(4-8 cm) and "edentatus-like" plants (13-28 cm). The two forms can also be distinguished by their differences in reproductive phenology. While the dwarf form exhibits a single reproductive maximum in the fall, ssp. edentatus has a pronounced bimodal reproductive periodicity with maxima in the spring and fall. Differences in stature between the dwarf form and ssp. edentatus were maintained when their respective progeny were grown under common environmental conditions, thus the differences are heritable rather than environmentally induced.
ECOLOGY AND GENCOLOGY OF
FUCUS DISTICHUS (L.) POWELL

PART I.

GROWTH RATES, REPRODUCTIVE PHENOLOGY, AND LONGEVITY
INTRODUCTION

The brown algal genus *Fucus* is common on rocky shores within the north Atlantic and Pacific Oceans. Three of the seven *Fucus* species recorded by Taylor (1962) from the northeastern coast of North America (*F. edentatus*, *F. evanescens*, and *F. filiformis*) are treated by Powell (1957a) as subspecies of *F. distichus*. Each of these subspecies occurs in a relatively unique habitat (Taylor, 1962; South and Hooper, 1981; Mathieson and Hehre, 1982). For example, *Fucus distichus* ssp. *edentatus* grows within the mid-eulittoral to upper sublittoral zones at moderately to very exposed sites, while ssp. *evanescens* exhibits similar zonation but grows at sheltered estuarine and open coastal habitats. *F. distichus* ssp. *distichus* (=*F. filiformis*) is restricted to tide pools at moderate to very exposed open coastal sites. Powell (1957a) recognizes a fourth subspecies (ssp. *anceps*) from the upper eulittoral zone of very exposed open coastal sites; he suggests that it is restricted to the eastern north Atlantic.

In New England, *Fucus distichus* ssp. *edentatus* and ssp. *evanescens* are dominant plants between the lower limits of *Ascophyllum nodosum* and the upper limits of sublittoral kelps. Within this zone competition for space and light between *Fucus distichus* and *Chondrus crispus* plays a
significant role in community structure and development (Menge, 1976; Lubchenco and Menge, 1978; Lubchenco, 1980). Although the ecology of *C. crispus* (Irish moss) is well known in the western north Atlantic (Mathieson, 1982), little is known about the ecology of *F. distichus* within the same geographical region. To date, growth rates and phenological data have only been reported for the tide pool ssp. *distichus* (Edelstein and McLachlan, 1975). In the present account, which is the first in a series dealing with the ecology and genecology of the non-tide pool members of the *Fucus distichus* complex in New England, the seasonal growth, reproduction, and longevity of ssp. *edentatus* and ssp. *evanescens* are summarized and compared with associated fucoid algae and *Chondrus crispus*. 
MATERIALS AND METHODS

Growth studies of *Fucus distichus* ssp. *edentatus* were conducted at an open coastal site in southern Maine (Cape Neddick, Me.). Similar studies with ssp. *evanescens* were made at another open coastal site (Gosport Harbor, Isles of Shoals, Me.) as well as an estuarine site (Durham Point, New Hampshire). See Figure 1 for locations. Approximately 20-30 in situ plants were tagged at each site with individually coded "TY RAPS" (Thomas and Betts Co., Elizabeth, N.J.). Additional plants were tagged each subsequent month because of high attrition. The plants were initially marked when they were approximately 10 cm long and one year old. Subsequently tagged plants were chosen from the same age class as the initial plants in order to compare similar developmental stages. At the end of one year, a second set of one year-old plants was tagged a Cape Neddick and Gosport Harbor. Monthly measurements of maximum length were made from February, 1980 to February, 1982 at Cape Neddick, from February, 1980 to September, 1981 at Gosport Harbor, and from February, 1978 to June, 1979 at Durham Point. Growth rates were calculated as the average elongation (cm) per 28 days, in order to have uniform monthly periods.

Growth rates were also assessed on outplanted cultured
germlings at two experimental garden sites (Jaffrey Point and Durham Point, Fig. 1). The cultures were established from parents of *F. distichus* ssp. *edentatus* and ssp. *evanescens*. After being collected, the fertile receptacles were excised and kept overnight at 10 C on damp (sea water) paper towels under photoperiods simulating natural conditions. After a 10 minute cold treatment (4 C) and washing in cold tap water, the receptacles were placed on ceramic tiles in crystalizing dishes with filtered sea water (30-32 °C) and incubated at 10-14 C. Gametes were shed within a few hours, and were evenly distributed over the tiles. The germlings were grown at 10-14 C under an 8/16 to 12/12 hr light/dark cycle, depending on the date of collection. After 1-2 months, the tiles were transferred to the experimental gardens and attached to bolts cemented into natural substrata. Offspring of *F. distichus* ssp. *evanescens* from Durham Point were grown at Durham Point from March, 1978 to March, 1980. Similarly, progeny of *F. distichus* ssp. *edentatus* collected from Jaffrey Point were grown at Jaffrey Point from January, 1979 to May, 1982. In addition, *F. distichus* ssp. *edentatus* from Cape Neddick and Wallis Sands as well as *F. distichus* ssp. *evanescens* from Gosport Harbor and Dover Point were grown at Jaffrey Point from May, 1980 to May 1982. The maximum length, as well as number of vegetative and fertile tips (receptacles) were recorded seasonally.

Reproductive phenology studies were conducted on random
samples of *F. distichus* ssp. *edentatus* from Cape Neddick, Me, Wallis Sands, N.H., Jaffrey Point, N.H., and Smuttynose Island, Isle of Shoals, Me. and *F. distichus* ssp. *evanescens* populations from Gosport Harbor, Isle of Shoals, Me., Dover Point, N.H., Durham Point, N.H., and Great Neck, Mass. (Fig. 1). The reproductive studies were conducted seasonally during 1978-1980 and monthly (at most sites) from August, 1980 to December, 1981. Four criteria were employed to designate a reproductive plant: 1) most apices possessed fertile receptacles, 2) after sectioning, both antheridia and oogonia with clear septa were visible, 3) the conceptacles were raised above the receptacular surface, and 4) mucilage was extruded from the conceptacles. Reproductive patterns were enumerated in the field by categorizing five types of individuals along a randomly thrown 5 m transect line as follows: 1) vegetative, 2) forming new conceptacles, 3) reproductively mature, 4) possessing degenerating receptacles, or 5) young plants with a small number of precocious receptacles. The percentage occurrence of each type was estimated.

Attrition rates and longevity patterns were estimated by enumerating losses of tagged plants from the *in situ* growth studies and the outplanted germlings. A depletion curve (Harper, 1977) was calculated for the ssp. *edentatus* populations at Cape Neddick and ssp. *evanescens* populations at Gosport Harbor. The number of tagged plants was
initially adjusted to 1,000. Due to high rates of loss, a single cohort could not be followed. Rather, the proportion of the sample surviving from time zero was estimated from the adjusted number of plants surviving each month.
DESCRIPTION OF STUDY SITES

Jaffrey Point is a semi-exposed site in Newcastle, N.H., an island at the mouth of Piscataqua River [Great Bay Estuary System.] The substratum at Jaffrey Point consists of large outcrops of granite and scattered boulders. In contrast, the adjacent Estuary possesses enhanced mud and only scattered rocky substrata. Fucus distichus only grows on boulders or small outcrops within the Estuary. The hydrographic conditions at Jaffrey Point and Durham Point are summarized in Figure 2. The average monthly temperature and salinities at Jaffrey Point range from -1.0°C to 15.0°C and 24.7 to 33.1, versus -1.1°C to 23.4°C and 10.6 to 30.7 at Durham Point (Fig. 2). The water temperatures at both sites were lowest in early winter and highest in August. Seasonal changes of solar irradiance at Durham, N.H. are summarized in Figure 3. A typical seasonal cycle with minimum winter and maximum summer illumination was evident. The spring increase in solar irradiance began in February and peaked in July (539.7 cal/cm).

Due to their close proximity, the seasonal pattern of water temperature at Jaffrey Point and solar irradiance at Durham, N.H. are probably representative of conditions found at Cape Neddick and Gosport Harbor. However, the low spring salinity minima (Fig. 2) found at Jaffrey Point is
probably not present at the other two open coastal sites as they are not adjacent to an estuary (Fig. 1). Cape Neddick is an exposed site with extensive granitic outcropping, while Gosport Harbor is a sheltered area adjacent to a man-made breakwater.
RESULTS

SEASONAL GROWTH of IN SITU PLANTS

_Fucus distichus_ ssp. _edentatus_ and ssp. _evanescens_ exhibited similar seasonal growth patterns (Fig. 4-6). Plants from all three sites showed minimal growth during late fall-early winter followed by enhanced and maximum growth during late spring-early summer. Thereafter, growth declined until the next winter, except for a modest resurgence in early fall. Overall, estuarine populations of ssp. _evanescens_ exhibited the sharpest decrease in summer growth (Fig. 6), while open coastal populations of the same subspecies showed the most gradual curtailment (Fig. 5). The average growth rate of ssp. _edentatus_ during the second year of its life at Cape Neddick (1980) was 2.5 cm/mo (Fig. 4), with maximum and minimum rates in early July (3.5 cm/mo) and late December-January (0.5 cm/mo), respectively. The growth rates for a second set of tagged 1 year old plants in 1981 closely resembled those recorded in 1980 (Fig. 4). The average growth rate of 1 year old ssp. _evanescens_ plants at Gosport Harbor was 1.8 cm/mo (Fig. 5), with the periods of maximum and minimum growth occurring in early July (2.4 cm/mo) and December (0.4 cm/mo), respectively. Although the seasonal growth patterns for ssp. _evanescens_
during 1981 resembled those of 1980, the maximum spring growth rate was much higher (3.7 cm/mo).

Estuarine populations of *F. distichus* ssp. *evanescens* exhibited an average growth rate of 1.3 cm/mo with a July maximum and a January minimum (Fig. 6). No statistical comparison of growth rates of the estuarine and open coastal populations was made because of the different time periods involved. Even so, reproductively mature plants of ssp. *evanescens* growing at Durham point were significantly shorter (*p* < 0.05, ANOVA) than ssp. *edentatus* at Cape Neddick. On the other hand, plants at Cape Neddick had significantly (*p* < 0.01, ANOVA) fewer apicules than those at Durham Point or Gosport Harbor (Table I).

GROWTH OF CULTURED AND OUTPLANTED GERMLINGS

The early germling development of both subspecies was very similar to the description given by McLachlan et al. (1971). For example, the first zygote division occurred in less than 24 hours, and by 5 days a primary rhizoid was distinct from the upper multicellular axis of the plant. Apical hairs were first visible after 1 week. Three weeks later the germlings were 0.58 mm long and had developed a distinct rhizoidal holdfast. By two months, most apical
hairs had degenerated and the cylindrical thalli in both subspecies had flattened. After 3 months the two subspecies could be easily distinguished, as the 1-2 cm long thalli of ssp. *evanescens* were conspicuously wider than the germings of ssp. *edentatus*.

The growth of outplanted germings of *Fucus distichus* ssp. *edentatus* at Jaffrey Point as well as ssp. *evanescens* at Durham Point is illustrated in Figure 7. The maximum rate of elongation occurred in the second spring and summer of the plant's life. At two years of age, most progeny of both subspecies were reproductively mature. Since growth of reproductive fronds ceased as their receptacles were dehisced, only those plants that maintained some vegetative branches grew beyond the reproductive period. The mean maximum length and number of apices of two year old progeny of both subspecies are illustrated in Table II. The progeny of ssp. *evanescens* had a significantly greater number of apices (*p* = 0.01, ANOVA).
SEASONAL REPRODUCTION OF IN SITU PLANTS

Although the formation and maturation of receptacles in *Fucus distichus* ssp. *edentatus* and ssp. *evanescens* is a continuous process, a series of stages can be distinguished between immature and fertile receptacles. For example, individuals that were reproductively mature in March or April bear immature conceptacles and no gametangia during the previous November. With the same plants, uncleaved oogonia were seen in December and January, while distinct eggs were apparent in February. After the spring period of gamete release, the receptacles are spent and they degenerate.

As shown in Figures 8-10, it is possible to find reproductive individuals during most months of the year. However, the proportion of plants at a particular stage within a single population varies from month to month. Some plants bear a few receptacles when they are 1 year old. However, most plants become reproductively mature at 2 years of age, at which time the majority of their apices are fertile. For example, 91.3% of the apices on tagged *F. distichus* ssp. *edentatus* at Cape Neddick were fertile at two years, while 89.2% of the apices of ssp. *evanescens* growing at Gosport Harbor produced fertile receptacles at the same age.

Most populations of *Fucus distichus* ssp. *edentatus* and
ssp. *evanescens* exhibited a bimodal reproductive periodicity, with March-May and August-October maxima (Fig. 8-10). In contrast to open coastal ssp. *edentatus* and ssp. *evanescens*, estuarine plants of ssp. *evanescens* exhibited a reduced fall reproductive period (Fig. 10).

Individuals of the two reproductive periods are distinct from one another. Thus, spring reproductive plants were vegetative in the fall and reproduced the following spring, if they survived. Similarly, individuals reproducing in the fall, were vegetative the following spring and reproductive the following fall, if they survived.

REPRODUCTIVE PATTERNS OF OUTPLANTED GERMLINGS

Most of the progeny grown in the experimental gardens at Jaffrey and Durham Points became reproductive at the same season as their parents. Although some progeny produced a number of receptacles after one year, most did not become reproductively mature until two years of age. For example, 21 of the 44 surviving progeny of *F. distichus* ssp. *evanescens* outplanted to Durham Point in the spring of 1978, became partially reproductive the following spring (1979). At two years (spring, 1980), all
16 surviving ssp. *evanescens* plants, including those that were partially reproductive at one year, became reproductively mature. Similarly, 10 of 13 surviving progeny of ssp. *edentatus* outplanted to Jaffrey Point in the fall of 1979 became reproductively mature in the fall of 1981, at 2 years of age. In addition, most of the progeny of Cape Neddick, Wallis Sands, and Dover Point parents became reproductively mature after 2 years at Jaffrey Point. In contrast, progeny of ssp. *evanescens* from two Gosport Harbor parents became partially reproductive at 1.5 years and were vegetative at two years. Of all the progeny from 15 different parents, only those from the two Gosport Harbor parents did not correspond to their parents.

**LONGEVITY**

As noted earlier, the rate of plant attrition was estimated by recording the monthly loss of tagged plants. Due to the difficulty of tagging young plants, only those one year or older were considered. Indirect observations of seedlings growing in situ and within the experimental gardens indicated that there is a much greater loss during the first than subsequent years of growth. After the plants reach one year of age, the population loss is relatively
constant, except during periods of maximum reproduction (Fig. 11 and 12). The average percent survival per month at Cape Neddick and Gosport Harbor was 77.7% and 77.4%, respectively. During the final month of each reproductive period, the survival rate of reproductively mature plants at Cape Neddick dropped to 28% (October) and 53.8% (late May) versus 25.0% and 44.0% for the same fall and spring periods at Gosport Harbor (Fig. 11 and 12). Furthermore, of all reproductively mature plants tagged in the growth studies only 31% were alive 5 months after gamete release. Similar results were evident in the experimental gardens. For example, of the 13 plants of ssp. edentatus that survived two years, only 3 lived beyond that age.

The seasonal loss of F. distichus ssp. evanescens in the Estuary was similar to that of the open coast, however no tagged plants lived beyond two years of age. Similarly, all of the plants grown in the estuarine experimental garden degenerated after reproducing at 2 years of age.
DISCUSSION

The rate of growth of *Fucus distichus* ssp. *edentatus* and *F. distichus* ssp. *evanescens* is similar to that reported for other fucoid algae. For example, Knight and Parke (1951) report average elongation rates for *F. serratus* and *F. vesiculosus* in Great Britain of 4.9 and 4.8 mm/wk respectively, but they did not outline seasonal variations and thus further comparisons are impossible. Niemeck and Mathieson (1976) record maximum growth of *F. spiralis* populations in New Hampshire from June-August (1.9-2.8 cm/mo); these values are somewhat less than those reported here for both subspecies of *F. distichus*. However, the basic pattern of rapid growth in the early summer and minimal elongation during the winter is similar. Mathieson et al. (1976) examined the seasonal growth of *F. vesiculosus* var. *spiralis* and *Ascophyllum nodosum* in New Hampshire. The former plant, which is common in New England estuarine habitats, exhibited maximum growth during April (3.5 cm/mo) and intermediate growth (2.6-2.9 cm/mo) from June to September in 1973. In 1974, the highest growth rates were recorded in June, similar to *F. distichus* subspecies. *Ascophyllum nodosum* populations showed two distinct periods of maximum growth in 1973, April (3.6 cm/mo) and July (3.4 cm/mo), however no comparable periods
were recorded in 1974. Thus, the growth rate of *Ascophyllum nodosum* is similar to that of *Fucus*, at least for older stages. On the other hand, Sundene (1973) reports that *Ascophyllum nodosum* is only 1.5 cm tall after 1 year's growth, while plants of *Fucus distichus* ssp. *edentatus* and ssp. *evanescens* would be substantially larger at the same age (Fig. 7).

*Fucus distichus* ssp. *edentatus* and ssp. *evanescens*, as well as *Ascophyllum nodosum* (Mathieson et al., 1976), *F. vesiculosus var. spiralis* (Mathieson et al., 1976), and *F. spiralis* (Niemeck and Mathieson, 1976) show maximum growth in the spring and early summer, followed by a late summer decline and a moderate increase in the early fall (Fig. 4-6). As noted by Mathieson and associates (1976) this fall increase suggests that several fucoids have maximum growth during periods of intermediate light levels and water temperatures (Fig. 2 and 3). In contrast, *F. distichus* ssp. *distichus* seems to show its maximum growth in the winter and spring (Edelstein and McLachlan, 1975).

Fucoid algae commonly exhibit a single annual period of reproduction. For example, *Ascophyllum nodosum* is fertile during April and May (Baardseth, 1970; Mathieson et al., 1976); *Fucus spiralis* in July-September (Niemeck and Mathieson, 1976), *F. vesiculosus* in spring-summer (Knight and Parke, 1951), *F. serratus* in fall-winter (Knight and Parke, 1951), and *F. distichus* ssp. *distichus* in November-May (Edelstein and McLachlan, 1975). In contrast,
New England populations of *F. distichus* ssp. *edentatus* and ssp. *evanescens* exhibit a pronounced bimodal reproductive periodicity, with maximum reproduction in the spring and fall. South and Hooper (1981) report a similar bimodal pattern for Newfoundland populations of *F. distichus* ssp. *edentatus*, although they do not characterize it in any detail. Bimodal patterns of reproduction are rare but known in some seaweeds. For example, *Sargassum camouilii* has been shown to express two separate reproductive periods each year (McCourt, 1981). In *Fucus distichus*, the fact that the spring reproductive plants are distinct from fall reproductive plants raises the possibility that the two groups are reproductively isolated. Although experimental garden studies indicate that some reproductive patterns are heritable, the results are inconclusive as reproductive initiation may simply be the result of the season of zygote development. For example, zygotes developing in the spring produce individuals that are reproductive two years hence in the spring.

nodosum takes 5 years to develop into a fertile plant (Sundene, 1973).

Similar to Fucus distichus ssp. edentatus and ssp. evanescens, F. serratus, F. vesiculosus, and F. distichus ssp. ancens (in Great Britain) produce receptacles on a small number of their branches at the end of the first year's growth (Powell, 1957b; Knight and Parke, 1951). In most cases the branches that remain vegetative become reproductive the second year. After the first major reproductive period most fucoids loose vast amounts of tissue as their receptacles are sloughed off and lost. This seasonal loss of tissue adds considerably to detrital pools, particularly in estuarine habitats (Josselyn and Mathieson, 1980). In addition to dehisced receptacles, entire plants of both subspecies may be torn loose due to the weight and drag of their massive receptacles. An increased attrition of individuals during the reproductive period is also reported for F. spiralis (Niemeck and Mathieson, 1976). A life span of 2-3 years has been reported for most species of Fucus, including F. distichus ssp. edentatus and ssp. evanescens (Fig. 11 and 12), F. vesiculosus (Knight and Parke, 1951; Welch, 1960), F. spiralis (Niemeck and Mathieson, 1976), and F. serratus (Knight and Parke, 1951). Only a small percentage of plants from these four species lives to 3 or 4 years.

Since Fucus distichus and Chondrus crispus often grow
in the same vertical zone of the intertidal, growth rates and survivorship may play a major role in competition between the two species. Typically, _F. distichus_ occurs in patches within the lower intertidal beds of _Chondrus_. Lubchenco (1980) has shown that the relative abundance of _C. crispus_ and _F. distichus_ results from a balance of physical factors, grazing (primarily by _Littorina littorea_) and interactions between the two algae. Lubchenco (1980) stresses that _Chondrus_ is the superior competitor in the low littoral primarily due to its strong perennial holdfast. Even so, the present study suggests why _Fucus_ persists as an important member of that community. Most important is the differences in growth rates between the two species. After one year, _Fucus distichus_ ssp. _edentatus_ and ssp. _evanescens_ are approximately 9-12 cm long (Fig. 7) and easily overtop _C. crispus_ that grows to a maximum length of 5-6 cm (Mathieson and Burns, 1975). As a result of differences in growth rates and mature size, _F. distichus_ is more likely to colonize and outcompete _C. crispus_ in newly opened space. On the other hand, _C. crispus_ will form an understory and can persist in the shade (Lubchenco, 1980). The holdfast of _Chondrus crispus_ is a spreading crust that increases in area over many years and becomes a stable, resilient and long-lived source of new fronds (Taylor et al., 1981). Consequently, after a 2 year period, when the majority of the _Fucus distichus_ plants become reproductive and die (Fig. 11 and 12), _Chondrus crispus_ will dominate.
Table I. Mean maximum length and total number of apices of *Fucus distichus* ssp. *edentatus* from Cape Neddick, Me. and *F. distichus* ssp. *evanescens* from Durham Point, New Hampshire, and Gosport Harbor, Isle of Shoals, Me.
<table>
<thead>
<tr>
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<td>73.9</td>
<td>35.6</td>
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<td>3.8</td>
<td>168.6</td>
<td>65.3</td>
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<tr>
<td>Gosport Harbor</td>
<td>25.1</td>
<td>3.2</td>
<td>111.0</td>
<td>56.5</td>
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Table II. Mean maximum length and number of apices on two year old cultured plants of *Fucus distichus* ssp. *evanescens* and *F. distichus* ssp. *edentatus* from parents from populations at Durham Point, New Hampshire and Cape Nedick, Maine, respectively.
<table>
<thead>
<tr>
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<th>S.D.</th>
<th>NUMBER OF APICES</th>
<th>S.D.</th>
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<tbody>
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<td>3.7</td>
<td>150.4</td>
<td>93</td>
</tr>
<tr>
<td>Cape Neddick</td>
<td>24.9</td>
<td>1.7</td>
<td>60.4</td>
<td>25.2</td>
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</table>
Fig. 1. The New England coastline showing the study sites.
Fig. 2. Monthly variations in temperature (°C) and salinity (%) at Durham Point and Jaffrey Point, New Hampshire from February, 1978 to June, 1979 and February, 1978 to October, 1981, respectively (personal communication, C. Penniman).
The graph illustrates the variations in salinity and temperature at two different locations: Durham Pt. and Jaffrey Pt., over the months from January (J) to October (O). The salinity is represented by solid lines, while the temperature is shown by dashed lines. The y-axis on the left measures temperature in °C, ranging from 2 to 24, and the y-axis on the right measures salinity in parts per thousand (%), ranging from 0 to 35. The graph shows significant fluctuations in both parameters throughout the year, indicating the dynamic nature of marine environments.
Fig. 3. Monthly variance in irradiance at Durham, New Hampshire from February, 1978 to May, 1979 (personal communication, G. Pregent).
Fig. 4. Growth rates of two groups of tagged *in situ* plants of *Fucus distichus* ssp. *edentatus* at Cape Nedick, Maine from December, 1980 to May, 1981 and February, 1981 to February, 1982, respectively.
Fig. 5. Growth rates of two groups of *Fucus distichus* ssp. *evanescens* at Gosport Harbor, Maine from February, 1980 to March 1981 and January, 1980 to August, 1982, respectively.
GROWTH RATE (cm/28 days)

MONTH


1980

1981
Fig. 6. Growth rates of *Fucus distichus* ssp. *evanescens* at Durham Point, New Hampshire from January, 1978 to May, 1979.
MONTH

GROWTH RATE (cm/28 days)

J F M A M J J A S O N D J F M A M J
Fig. 7. Mean maximum length of cultured offspring of *Pucus distichus* ssp. *edentatus* and ssp. *evanescens* grown in experimental garden sites of Jaffrey Point and Durham Point, New Hampshire, respectively.
Fig. 8. Percent of in situ population of *Fucus distichus* ssp. edentatus at Cape Neddick, Maine in different reproductive stages.
Few Receptacles

Old Receptacles

Reproductive

Immature Receptacles

Vegetative

MONTH
Fig. 9. Percent of *in situ* population of *Fucus distichus* ssp. *evanescens* at Gosport Harbor, Maine in different reproductive stages.
Fig. 10. Percent of in situ population of *Fucus distichus* ssp. *evanescens* at Durham Point, New Hampshire in different reproductive stages. Note: absence of data for December, January, and February because of ice.
Fig. 11. Number of surviving plants at Cape Nedick, Maine from January 1980 to December, 1981. Vegetative and reproductive plants with receptacles are distinguished.
Fig. 12. Number of surviving plants at Gosport Harbor, Maine from January, 1980 to June, 1981. Vegetative and reproductive plants bearing receptacles are distinguished.
The graph shows the number of plants from 1980 to 1981, with data distinguished between reproductive and vegetative stages. The number of plants decreases significantly over the months, with a more pronounced decline in the reproductive stage.
LITERATURE CITED


ECOLOGY AND GENECOLOGY OF
FUCUS DISTICHUS (L.) POWELL

PART 2.

MORPHOLOGICAL VARIATION WITHIN AND
BETWEEN NATURAL POPULATIONS.
INTRODUCTION

Many wide ranging plant species show pronounced spatial variations in morphology that are often correlated with habitat differences. As suggested by Heslop-Harrison (1964), such environmentally correlated variation may be attributable to a "plastic" modification of individuals or to the action of natural selection in promoting genetic divergence of locally adapted populations. The question as to whether infraspecific variation is directly induced by the environment or genetically based has important genealogical and taxonomic implications. At present, the extent of environmental versus genetic control of thallus morphology within the seaweeds is largely unknown (Russell, 1978).

Species of the cosmopolitan genus Fucus are extremely variable morphologically. Although infraspecific variation is well documented within the genus (Burrows and Lodge, 1951; Jordan and Vadas, 1972; Russell, 1978), few studies have assessed the role of the genotype in development of thallus morphology. Thus, not only is the taxonomy of the group unsettled but genealogical knowledge of numerous taxa remains incomplete. For example, Taylor (1962) records seven species of Fucus from the northeastern Coast of North America; three of these taxa (Fucus edentatus, F. evanescentes, and F. filiformis) are treated as subspecies of F. distichus by
Powell (1957). However, Powell (1957) presents no statistical analysis of morphological variation nor experimental determination of heritability of form.

Extensive variation in thallus form has been reported within the Fucus distichus complex (sensu Powell, 1957), and several investigators (Borjesen, 1902; Jonsson, 1903; Powell, 1957; Schonbeck and Norton, 1981) have correlated this variation with diverse environmental factors, including growth in tide pools, exposure to wave action, elevation, shading, and crowding. Powell (1957) suggests that plants associated with tide pools (ssp. distichus), sheltered habitats (ssp. evanescens), semi-exposed shores (ssp. edentatus), and the high intertidal on very exposed shores (ssp. anceps) should be recognized as ecotypes. However, the genetic distinction and ecology of these ecotypes, as they occur in North America, has only been reported for the tide-pool form, F. distichus ssp. distichus (McLachlan et al., 1971; Edelstein and McLachlan, 1975).

In the present account, which is the second in a series of three, a statistical evaluation of morphological variation of the non-tide pool forms of Fucus distichus both within and between natural populations is given. Culture and outplanting experiments were also employed, in order to determine if the morphological variations observed are genetically based and deserving taxonomic recognition or simply an environmental modification.
MATERIALS AND METHODS

Extensive sampling of natural populations of *Fucus distichus* was conducted at eight sites from southern Maine to northern Massachusetts (Fig. 1). Reproductively mature plants were collected along randomly thrown 5 m transect lines for later morphological comparisons. As shown in Figure 2, several diagnostic characteristics commonly used to identify *Fucus* (Taylor, 1962; South and Hooper, 1981) were measured. The morphological variations within and between populations were tested by ANOVA and Student-Newman-Keuls (Sokal and Rohlf, 1969, 1981).

Intensive sampling of *Fucus distichus* populations on the eastern most tip of Smuttynose Island, Isles of Shoals, Me. was conducted, in order to correlate morphological variation with micro-habitat characteristics. A stratified random sampling technique (Conor and Kemp, 1978) was employed in order insure adequate collection and comparison of plants from different areas of the shore. The study area was divided into 16 distinct subareas based on factors including elevation, wave action, slope, aspect, and surface topography. Correlations between plant form and shore characteristics were evaluated by multiple regression analysis (Sokal and Rohlf, 1981).

The heritability of the various morphological forms of
Fucus distichus from Dover Point, New Hampshire, Cape Neddick, Me., Gosport Harbor, Me., and Wallis Sands, N.H. was assessed by outplanting cultured germlings to an experimental garden at Jaffrey Point, Newcastle, N.H. Specific details on the culturing and outplanting techniques have been previously outlined in Part I. Table I gives a comparative summary of the study sites, including an assessment of available substrata and exposure to wave action. Jaffrey Point is a semi-exposed open coastal site. Voucher specimens from all of the study sites, as well as cultured plants from the experimental gardens are lodged in the Sumner Pike Herbarium at the University of New Hampshire.
RESULTS

MORPHOLOGICAL VARIATION BETWEEN POPULATIONS

The non-tide pool populations of Fucus distichus from the eight study sites exhibit a gradation in morphology from slender and elongated plants with narrow receptacles to broader forms with short, wide receptacles (Fig. 3). Thus, measurements of a variety of diagnostic characteristics showed patterns of continuous distribution (Fig. 4 and 5). For example, the average width of fronds between the second and third vegetative dichotomy ranged from 2-28 mm (Fig. 4), while the average length of fertile receptacles (see Part I for an explanation of reproductive maturity) ranged from 1.0 to 14.5 cm (Fig. 5). Although the patterns of morphological variation are continuous when the taxa is considered as a whole, discrete populations are evident when mean values of individuals from different sites are compared (Fig. 6-8). Furthermore, some morphological forms can be correlated with wave action, as the narrowest plants occur at exposed sites, while the broadest forms occur in calm estuarine habitats (Fig. 6). Receptacular length was shorter in most calm areas than exposed areas (Fig. 7), however the sheltered populations at Great Neck, Mass. were anomalous, as their receptacles were quite elongate (Fig. 7). On the other hand,
the receptacles on the Great Neck plants were broad. Consequently, a better distinction between calm and exposed water forms is the length to width ratio of receptacles (Fig. 8). A Student-Newman-Keuls comparison of means of receptacular length to width ratios for sheltered populations showed no statistical differences (Fig. 9). Similarly, the ratios and frond widths of open coastal populations were not statistically different from each other, but they were distinct from calm water populations (Fig. 9 and 10). Furthermore, Wallis Sands, a site of intermediate exposure and abrasive sand movement (see Table I), had populations of F. distichus which were distinct from those of both sheltered and exposed sites (Fig. 9 and 10).

MORPHOLOGICAL VARIATION WITHIN POPULATIONS

As outlined in Part I, many populations of Fucus distichus exhibit a bimodal reproductive pattern with spring and fall maxima. Statistical evaluations have shown that individuals of the two reproductive periods are distinct and exhibit statistically different (= .01, ANOVA) morphologies. For example, at Wallis Sands, Cape Neddick, and the northern side of Smuttynose Island, fall reproductive plants have smaller receptacular length to width ratios than spring reproductive plants within the same site (Fig. 11).

Some morphological variation is also apparent along
elevational gradients at exposed open coastal sites (Fig. 12 and 13). The most extreme variation was noted on the easternmost shore of Smuttynose Island where a dwarf form of *Fucus distichus* grows in the upper littoral zone. A variety of specific details regarding this dwarf plant are summarized in Part III. A statistical difference in thallus length between individuals of the high and low littoral was evident only at very exposed sites (Fig. 12). Similarly, no statistically significant differences in frond width were observed between individuals of the high and low littoral, except at the most exposed site on Smuttynose Island where the dwarf form occurs (Fig. 13).

Multiple regression was employed to evaluate the sources of variation within exposed populations at Smuttynose Island. When elevation was included as the last factor in the regression model, it explained 46.4% and 41.9% respectively of the variation in thallus length and width accounted for by the model (Table II). However, if the highest elevations, which were dominated by the dwarf form (see Part III), were excluded, elevation accounted for only 13.8% and 24.7% respectively of the variation in thallus length and width (Table III). If the highest elevations were excluded, then exposure of the microhabitat to wave action accounted for 86.5% and 88.3% respectively of the variation in frond length and width explained by the model (Table III).
Heritability of Thallus Form

The variation in morphology noted in natural populations of *Fucus distichus* was maintained when their progeny were raised in an experimental garden at Jaffrey point (Fig. 14). Thus, the progeny of wide parents (i.e., ssp. *evanescens*) possessed wide fronds while the progeny of narrow parents (i.e., ssp. *edentatus*) possessed narrow fronds. For example, progeny of a parent possessing a frond width of 4.0 mm exhibited a mean frond width of 3.3 mm, while progeny of a parent possessing a width of 16.5 mm exhibited a mean width of 20.0 mm (Fig. 15). Progeny of intermediate parents likewise exhibited intermediate frond widths. A similar correspondence between parent morphology and mean offspring morphology was evident when evaluating the length to width ratios of fertile receptacles (Fig. 16). For example, progeny of a parent possessing a receptacle ratio of 2.7 (i.e., ssp. *evanescens*) exhibited receptacles with a mean ratio of 3.0, while progeny of a parent possessing a ratio of 10.9 (i.e., ssp. *edentatus*) exhibited receptacles with a mean ratio of 8.9 (Fig. 16).
DISCUSSION

On the northeastern coast of North America two different types of non-tide pool *Fucus distichus* plants can be distinguished morphologically and ecologically. Previously the two plants were treated as *Fucus edentatus* and *Fucus evanescens* (Taylor, 1962). Powell (1957), as well as Rosenvinge (1893), Børgesen (1902), and Jonsson (1903), observed a morphological continuum between the two plants, as well as a tide pool form (ssp. *distichus*) and a high littoral form (ssp. *anceps*). Consequently, they interpreted all four extreme types as ecological variants of a single species, and Powell (1957) treated them taxonomically as subspecies of *F. distichus* (see Part IV). Although Powell's interpretation is generally accepted in North America (South, 1976; South and Hooper, 1981), his work included few North American collections and he incorporated no statistical or experimental studies. The present investigation emphasizes that morphological variation of several characteristics viewed as diagnostic within *Fucus distichus* is continuous (Fig. 4 and 5), and thus supports Powell's recognition of but a single species.

The present studies also emphasize that morphological variation within the *F. distichus* complex is habitat related and that extreme as well as intermediate growth forms occur in
discrete populations (Fig. 6-10). Pollock (1969) and Schonbeck and Norton (1981) have also noted a correlation between habitat and morphological differences with Pacific Coast populations of F. distichus. As outlined by Russell (1978) and Mathieson et al. (1981), such habitat-linked variation in brown algae is very common, and the question arises as to whether it is phenotypically or genetically based. Both Pollock's and Schonbeck and Norton's studies were inconclusive as their transplants were lost prior to reproductive maturity. In this study, large numbers of F. distichus plants were successfully grown from germlings to reproductive maturity at an experimental garden site. Since the progeny of the various growth forms maintained their differences when grown together under common conditions, the differences are believed to be genetically based and environmentally stable. Thus, the experimental garden results, as well as the statistical evaluations of morphological features, support Powell's contention that the growth forms of F. distichus are ecotypes.

The present study also corroborates an earlier study by McLachlan et al. (1971) which suggests that phenotypic plasticity is not as important in determining morphological variability in Fucus as generally thought. In contrast, phenotypic variation of F. distichus is likely to be the result of natural selection promoting the genetic divergence of locally adapted populations. Although the present study supports the genetic distinction of several forms of
F. distichus, further work is necessary to demonstrate adaptive features of these different phenotypes.
Table I. Assessments of study sites.
<table>
<thead>
<tr>
<th>STATION</th>
<th>DESCRIPTION</th>
</tr>
</thead>
<tbody>
<tr>
<td>Durham Point, N.H. (DP)</td>
<td>Very sheltered estuarine site; substratum of mud, shingle, and scattered boulders; <em>Fucus distichus</em> grows on scattered boulders within the lower littoral zone.</td>
</tr>
<tr>
<td>Dover Point, N.H. (DOV)</td>
<td>Estuarine site exposed to strong tidal currents; substratum of small rock outcrops, boulders, and cobbles; <em>Fucus distichus</em> occurs in lower littoral zone.</td>
</tr>
<tr>
<td>Great Neck, Mass. (GN)</td>
<td>Very sheltered site located at mouth of Ipswich River; substratum of sand covered by extensive beds of blue mussel (<em>Mytilus edulis</em>); <em>Fucus distichus</em> grows tangled amongst the mussel byssus and on boulders.</td>
</tr>
<tr>
<td>Gosport Harbor, Me. (GOS)</td>
<td>Sheltered open coastal site protected by Islands and man-made breaker; substratum of boulders and coarse sand; <em>Fucus distichus</em> occurs within the lower littoral and upper sub-littoral.</td>
</tr>
<tr>
<td>Wallis Sands, N.H. (WS)</td>
<td>Semi-exposed site; substratum of rock outcroppings on sandy beach; <em>Fucus distichus</em> occurs in low littoral.</td>
</tr>
<tr>
<td>North side of Smuttynose I. (SMN)</td>
<td>Semi-exposed open coastal site; substratum of rock outcroppings; <em>Fucus distichus</em> occurs in mid-low littoral.</td>
</tr>
<tr>
<td>Cape Neddick, Me. (CN)</td>
<td>Exposed open coastal site; substratum of granite outcroppings; <em>Fucus distichus</em> occurs in mid-low littoral.</td>
</tr>
<tr>
<td>Eastern side of Smuttynose I. (SME)</td>
<td>Very exposed site which receives continuous swell from the open Atlantic; substratum of granite outcroppings and numerous gullies which offer various degrees of exposure; <em>Fucus distichus</em> occurs in the upper to lower littoral, it is found in greatest abundance on gradually sloping ledges within the mid-littoral.</td>
</tr>
</tbody>
</table>
Table II. ANOVA table illustrating the percent of the variation in frond width and thallus length explained by the regression model (ss factor/ss regression) and total variation (ss factor/ss total) by microhabitat characteristics (elevation, exposure to wave action, and surface configuration (convex, concave, or flat)). All elevations considered.
<table>
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**LOG THALLUS LENGTH**

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<tr>
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<td>7.7</td>
<td>.5</td>
<td>.4</td>
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</table>
Table III. ANOVA table illustrating the percent of the variation in frond width and thallus length explained by the regression model (ss factor/ss regression) and total variation (ss factor/ss total) by microhabitat characteristics, elevation, exposure to wave action, and surface configuration (convex, concave, or flat). Samples at elevations above 1.5 m are not considered.
### FROND WIDTH

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<td>1.4</td>
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<td>0.3</td>
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### LOG THALLUS LENGTH

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<th>MS</th>
<th>F</th>
<th>PERCENT OF REGRESSION</th>
<th>PERCENT OF TOTAL</th>
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<tr>
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<td>.13</td>
<td>27.3</td>
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<td>170.5</td>
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<td>Surface</td>
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<td>5.0</td>
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</table>
Fig. 1. Map of northern New England coastline showing study sites.
Fig. 2. *Fucus distichus* illustrating various points of measurement: 1- length of receptacle, 2- width of receptacle, 3- width of frond at second dichotomy, 4- width of frond half way between second and third dichotomy, and 5- maximum length of thallus.
Fig. 3. Various growth forms of Fucus distichus in New England grading from sheltered plants with short, broad receptacles and wide fronds to plants characteristic of exposed, open coastal sites with narrow receptacles and fronds.
Fig. 4. Frequency distribution of frond width measurements between the second and third dichotomy on *Fucus distichus* based upon randomly collected specimens from various sites between Maine and Massachusetts.
Fig. 5. Frequency distribution of receptacle length measurements on reproductively mature *Fucus distichus* plants collected randomly at sites from Maine to Massachusetts.
Fig. 6. Mean width of frond measurements between the second and third dichotomy for *Fucus distichus* populations from eight study sites between Maine and Massachusetts. The inner error bars indicate the 95% C.I. and the outer bars indicate plus and minus one standard deviation.
WIDTH OF FROND (mm)
Fig. 7. Mean lengths of receptacles on reproducitively mature *Fucus distichus* plants from populations at eight study sites between Maine and Massachusetts. The inner error bars indicate the 95% C.I. while the outer bars indicate plus and minus one standard deviation.
Fig. 8. Mean length/width ratio of fertile receptacles on *Fucus distichus* plants from populations at eight study sites between Maine and Massachusetts. The inner error bars indicate the 95% C.I. while the outer bars indicate plus and minus one standard deviation.
Fig. 9. A Student-Newman-Keuls comparison of fertile receptacles on *Fucus distichus* populations at eight sites between Maine and Massachusetts.
Fig. 10. A Student-Newman-Keuls comparison of mean values of frond width measured between the second and third dichotomy for populations of reproducitively mature *Fucus distichus* from eight study sites between Maine and Massachusetts.
Fig. 11. A comparison of mean length/width of fertile receptacles on spring and fall reproducitively mature *Fucus distichus* at three study sites. Inner error bars indicate 95% C.I. and outer bars indicate plus and minus one standard deviation.
Wallis Sands
spring
fall

Cape Neddick
spring
fall

Smuttynose I.
spring
fall

RATIO OF LENGTH: WIDTH OF RECEPTACLE
Fig. 12. Comparison of mean thallus length for reproducitively mature *Fucus distichus* from the upper and lower littoral zone of four study sites. Error bars indicate 95% C.I.
Fig. 13. Comparison of mean frond width for reproductively mature *Fucus distichus* from the upper and lower littoral zones at four study sites. Error bars indicate 95% C.I.
Fig. 14. Silhouettes of parents and their respective progeny grown at experimental garden sites at Durham Point and Jaffrey Point. A- parent from Cape Meddick, A' progeny; B- parent from Wallis Sands, B' progeny; C- parent from Gosport Harbor, C' progeny.
Fig. 15. Mean frond width (plus and minus one standard deviation) of progeny grown in the experimental garden sites of Durham Point and Jaffrey Point versus their respective parent frond width (mm).
Fig. 16. Mean length/width ratios of fertile receptacles on progeny grown in the experimental garden sites of Durham Point and Jaffrey Point versus their respective parent ratio. Error bars indicate plus and minus one standard deviation.
LITERATURE CITED


ECOLOGY AND GENECOLOGY OF
FUCUS DISTICHUS (L.) POWELL

PART 3.

ECOLOGICAL AND GENECOLOGICAL DISTINCTIONS
OF A DWARF FORM.
INTRODUCTION

The discovery of extensive populations of a dwarf non-tide pool form of *Fucus distichus* (Fig. 1) at Smuttynose Island, Maine (Fig. 2) during the study of morphological variation within the *F. distichus* complex (sensu, Powell, 1957a) stimulated the present investigation of its genecology and biology. The dwarf plant has previously been referred to as *Fucus inflatus* f. *disticha* (Borgesen, 1902) or *F. inflatus* f. *expansa* (Jonsson, 1903), and most recently included in *Fucus distichus* ssp. *aniceps* by Powell (1957a). To date, the dwarf, non-tide pool plant has been reported at only two sites in the northwest Atlantic, and at that time, with expressed uncertainty, it was included in *F. distichus* ssp. *aniceps* (Wilce, 1959). Herein, the plant will be referred to as the dwarf from, pending future taxonomic clarification.

The three major objectives of the present study are: 1) to reassess the plant's distribution in the northwest Atlantic, 2) to ascertain whether the morphology is genetically based or a "plastic response", and 3) to compare the biology and ecology of the dwarf form and other members of the *F. distichus* complex, particularly ssp. *edentatus* (sensu Powell, 1957a).
MATERIALS AND METHODS

Extensive sampling of the dwarf form and associated biota was conducted on the exposed easternmost shore of Smuttynose Island, Me. during the fall of 1981 (Fig. 2), in order to determine their vertical distribution and abundance. Four transect lines 20 m in length and divided into one meter intervals were established perpendicular to the shore and 5 m apart. A 0.25 m Lexan plastic sheet (General Electric) with 100 random dots was used to estimate percent cover (Hardwick-Witman and Mathieson, in press). The quadrats were positioned every 2.0 m along each transect from the top of the eulittoral zone to the upper sublittoral (sensu Lewis, 1964). The elevation of each quadrat was determined with a transit and stadia rod, using mean low water (M.L.W.) as a zero point (Anon., 1980, 1981).

A stratified random sampling technique (Gonor and Kemp, 1978) was employed in order to insure adequate collection and stature measurements of all members of the Fucus distichus complex. The study area was divided into 16 distinct subareas, based on factors including exposure to waves, elevation, slope, aspect, and surface topography. Plants of F. distichus were randomly sampled from each sub-area during February, May, June, September, and October. Only the October collections were analyzed statistically in
order to restrict the morphological comparisons to reproductively mature plants, i.e., plants with most of the frond apices possessing fertile receptacles. The maximum length of each thallus was measured and the variation between the subareas was tested for statistical significance by ANOVA and Student-Newman-Keuls test (Sokal and Rohlf, 1969, 1981).

The heritability of the various morphological forms of Fucus distichus from the Smuttynose Island study site was assessed by outplanting cultured germlings to an experimental garden in the low eulittoral at Jaffrey Point (Fig. 2), which is a semi-exposed, open coastal site near Portsmouth, N.H. (see Mathieson et al., 1982 for a detailed description of this site, and Part I for details of culturing and outplanting techniques).

The reproductive status of natural populations of the dwarf form and Fucus distichus ssp. edentatus was assessed each month from March, 1981 to February, 1982. Three criteria were employed to recognize fertile receptacles; 1) after sectioning, both antheridia and oogonia with distinct septa were visible, 2) the conceptacles were raised above the receptacular surface, and 3) mucilage was extruded from the conceptacles.
RESULTS

HABITAT DESCRIPTION

The study site on the easternmost shore of Smuttynose Island, Maine is a very exposed open coastal habitat, and it is representative of several other areas where the dwarf form has been found (see Fig. 2 and Table I for known distribution). Basically, the Smuttynose site is a promontory-like area with a large degree of fetch to the open Atlantic. Most storms develop winds with a strong easterly component which gives rise to large waves breaking against the coast. The site is also characterized biologically as an exposed habitat because of the presence of large quantities of the cumatophytes Alaria esculenta and Devalorea ramentacea (sensu Guiry, 1982), as well as the abundance of Mytilus edulis (Ballantine, 1961; Lewis, 1964; Dalby et al., 1978). In addition, Alaria shows a substantial uplifting of its maximum vertical distribution to nearly + 1.0 m (Fig. 3). The wave-sensitive species Ascophyllum nodosum is present but it is either restricted to protected microhabitats or extremely stunted in stature.

The easternmost shore of Smuttynose Island consists of irregular granitic platforms bounded by gullies and peaks. The largest platforms, which gently slope towards the sea,
possess extensive patches of the dwarf form. Although the plant may also grow on some vertical faces, it does not occur as abundantly. Overall, the dwarf form grows in areas that are frequently disturbed, as they are often bare and denuded in the winter. Later in the spring these disturbed areas are often colonized by ephemeral green algae like Entomorpha spp. and the barnacle Semibalanus balanoides. The dwarf form is present year-round and is usually found attached to persistent barnacles.

STATURE AND REPRODUCTION

The populations of Fucus distichus on the easternmost shore of Smuttynose Island range in morphology from F. distichus ssp. edentatus plants (sensu South and Hooper, 1981) to the dwarf form (Fig. 4). Although there is a continuous gradation in stature (2 - 35 cm), measurements of over 500 reproductively mature plants from the upper sublittoral to the upper eulittoral show a bimodal distribution pattern (Fig. 5). In other words, there is a high frequency of dwarf forms (4-8 cm) and "edentatus-like" plants (13-28 cm), with relatively few intermediate-length plants (9-12 cm).

The mean length of plants collected from each of the 16 subareas from the upper sublittoral to the upper eulittoral
illustrates a significant distinction between plant stature at elevations above and below +1.5 m (Fig. 6). The mean length of plants between +0.6 and +1.5 m (subareas 1-9) was 16.3-26.8 cm, while those from +1.6 to +1.9 m (subareas 10-16) were 5.0-11.0 cm. A Student-Newman-Keuls evaluation of the stature equivalencies is shown in Figure 7. No significant differences (α = .05) were evident between the nine subareas above +1.5 m (1-9), nor among the seven lower ones (numbers 10-16). However, a significant distinction exists between the higher and lower sets of subareas. Thus, the two forms occur in distinct subareas, and a discontinuity in their zonation exists.

Further support for the distinction between Fucus distichus ssp. edentatus and the dwarf form is provided by the small number of intermediate-length plants at mid-shore elevations. For example, within subarea 10, which was near the transition of the two stature subsets at +1.58 m, the two distinct forms occurred side by side (Fig. 8).

The reproductive phenology of Fucus distichus ssp. edentatus and the dwarf form are conspicuously different (Fig. 9). Fucus distichus ssp. edentatus exhibits a pronounced bimodal reproductive periodicity (Fig. 9), with maximum reproduction in the spring and early fall, while the dwarf form exhibits a single reproductive maximum during September and October (Fig. 9). Similar phenological data were collected during 1978-1980.
PATTERNS OF ABUNDANCE

A knowledge of the varying stature and reproductive characteristics of *Fucus distichus* ssp. *edentatus* and the dwarf form was utilized to describe the differential abundance and zonation patterns of the two plants on the easternmost shore of the island (Fig. 3). The dwarf form occurs throughout most of the eulittoral zone at such exposed sites, even so it is most abundant in the upper eulittoral and it decreases sharply at higher and lower elevations (Fig. 3). *Semibalanus balanoides* shows a similar pattern. In contrast, *F. distichus* ssp. *edentatus* exhibits its maximum abundance in the mid-lower eulittoral, in association with *Mytilus edulis* (Fig. 3). Similar patterns of abundance of the dwarf form have been observed at several sites in Maine and New Hampshire (Fig. 2; also see Table I). In all cases, the dwarf form was most abundant on exposed gently sloping shores. In less exposed micro-habitats at the same sites *Fucus spiralis* often replaces the dwarf form.

EXPERIMENTAL GARDEN

The conspicuous differences in stature between the dwarf form and *Fucus distichus* ssp. *edentatus* were
maintained when their respective progeny were grown under common environmental conditions in an experimental garden at Jaffrey Point (Fig. 10). The mean stature of the progeny of three dwarf form parents ranged from 6.2 to 8.5 cm at reproductive maturity, while progeny of _F. distichus_ ssp. edentatus had a mean length of 24.4 cm (Table II). The garden experiments also revealed a major disparity in age of reproductive maturation between the two forms. Although 76 of the 80 dwarf progeny became reproductively mature at one year or less, none of the 58 offspring of _F. distichus_ ssp. edentatus became reproductive at that age, even though they were considerably larger (Table III). Typically, _Fucus distichus_ ssp. edentatus becomes reproductively mature at two years of age and at approximately 25 cm in length (see Part I).
DISCUSSION

As noted earlier, the only previous records of the dwarf, non-tide pool plant of *Fucus distichus* on the northeast coast of North America is that of Wilce (1959) from Quebec and Maine. The present study has extended this distribution from central Maine to Massachusetts, and has demonstrated its local abundance at a variety of sites in the Gulf of Maine (Fig. 2). In contrast to North America, the dwarf form of *F. distichus* has been more widely recorded in Europe (Borgesen, 1902; Jonsson, 1903; Powell, 1957a, b; Jorde and Klavestad, 1966; Russell, 1974; Munda, 1977). For example, Borgesen (1902) and Jonsson (1903) gave detailed accounts of the dwarf plant and suggested that it represents a part of a continuum involving *F. distichus* ssp. *edentatus* from the lower littoral. On the other hand, Powell (1957b) and Russell (1974) only record the dwarf form at a few very exposed sites in Great Britain, and maintain that *F. distichus* ssp. *edentatus* is restricted to sheltered habitats. In contrast, on the northeast coast of North America, *F. distichus* ssp. *edentatus* is common at exposed sites (Mathieson and Mehre, 1982; South and Hoooper, 1981; also see part II), and the present studies indicate that both ssp. *edentatus* and the dwarf form occur at very exposed sites.
A lack of knowledge regarding the growth and reproductive patterns within the *Fucus distichus* complex probably contributed to a misunderstanding of the dwarf form, particularly in North America. Perhaps, the latter plant has been confused with immature stages of other members of the *F. distichus* complex or been misidentified as other stunted fucoids which often occur within the upper shoreline (Norton *et al.*, 1981). In contrast to Jonsson's (1903) and Borgesen's (1902) description of a morphological continuum between the dwarf form and the "edentatus-like" plants, the present study emphasizes that morphological and ecological differences exist between the two plants as well as a discontinuity of zonation. The fact that both plants can be found growing side by side, although they have zones of maximum abundance (Fig. 3), also substantiates their differences. Lastly, the maintenance of morphological features by progeny of both plants under identical conditions in an experimental garden suggests that the morphological variation between the two plants has a large genetic component and that the populations are genetically different.

Several investigators have described varying reproductive phenologies of individual seaweed species in different habitats (Dixon, 1965; Nienhuis, 1974; Norall *et al.*, 1991). For example, Nienhuis (1981) emphasizes that reduced sexual reproduction exists for some populations of *Phizoclonium riparium* growing in stressful habitats, e.g.,
high versus low shorelines, while Dixon (1965) notes the inhibition of sexual reproduction at the northern distributional limits of several red algae. The present study demonstrates that pronounced differences in reproductive phenologies exist between the high intertidal dwarf form and *Fucus distichus* ssp. *edentatus* (Fig. 9). For example, the dwarf form only exhibits a single reproductive period annually in contrast to the bimodal periodicity of *F. distichus* ssp. *edentatus*. In addition, the dwarf form undergoes an earlier maturation. With these insights, one might question if the varying reproductive patterns of the two fucoid plants are genetically based. The experimental garden studies indicate that the age of reproductive maturity is genetically controlled, and is not affected by either exposure or elevational factors.

In evaluating the varying reproductive patterns of the two fucoid plants (Fig. 9) several speculations can be made. Foremost, the absence of a spring reproductive period for the dwarf form may reflect an adaptation to avoid high desiccation and other environmental extremes within the upper shoreline (see Baker, 1910; Gail, 1918; Zaneveld, 1937; Schonbeck and Norton, 1978, 1980). Thus, if the dwarf form evolved from a lower shore form of *Fucus distichus* having a bimodal reproductive strategy, e.g., an "*edentatus*-like" plant, it is conceivable that there would be a strong selective pressure against a spring reproduction, since it would expose sensitive juvenile
plants to more extreme summer desiccation than a fall reproductive periodicity.

Among others, Suchanek (1981) has emphasized the adaptive significance of the length of initial reproductive maturation. Nevertheless, the earlier age of reproduction expressed by the dwarf form is difficult to explain by a single theory of life history strategies. For example, early reproductive maturation is often attributable to a high degree of habitat disturbance (Harper, 1977; Grime, 1979; Suchanek, 1981). A possible source of disturbance arises due to the settlement of the dwarf form on the barnacle *Semibalanus*, where the plants are susceptible to early dislodgement. Previously, Barnes and Topinka (1969) showed that *Fucus* is more easily removed from animal shells than from rock surfaces. Similarly, Burrows and Lodge (1950) demonstrated that *Fucus vesiculosus* growing on barnacles had an annual cycle, while 2-3 year old plants of the same species are found on rocky surfaces. Although, as emphasized above, the upper littoral is often exposed to disturbance, preliminary observations at the easternmost shore of Smuttynose have shown a large amount of physical disturbance within the lower shoreline, i.e., where *Fucus distichus* ssp. *edentatus* dominates. Thus, both the upper and lower shorelines are often disturbed by winter storms, which tear out clumps of organisms and open up large areas of substrata. The spring reproductive periodicity of *Fucus distichus* ssp. *edentatus* would obviously facilitate the
colonization of such open space (also compare with Bohn and Lein, 1978). Although the dwarf form lacks a spring reproductive periodicity, the opportunity to colonize these winter-denuded sites within the upper shoreline arises again the next fall, as these patches are primarily colonized by short-lived ephemerals, e.g., *Enteromorpha* spp., that die back during the late spring-summer. Since both the dwarf form and *Fucus distichus* ssp. *edentatus* utilize open space caused by disturbance, additional selective forces may have led to their varying reproductive strategies.

One possible source of differential selective pressure on the fucoid populations at the two elevations is interspecific competition. Within the lower littoral zone, *Fucus distichus* ssp. *edentatus* competes for space with *Chondrus crispus*, *Gigartina stellata* and *Mytilus edulis*, and for available light with these and other seaweeds. In contrast, the dwarf form does not compete as strongly for light within the upper shoreline, as *Semibalanus balanoides* is its tallest competitor in a habitat dominated by dwarf forms (Norton et al., 1981). Thus, there is no advantage to height within the upper shoreline. On the other hand, in the lower shoreline where there is major competition for light, faster growth rates and a larger stature may offer a competitive advantage to *Fucus distichus* over *Chondrus crispus* and *Gigartina stellata* (Lubchenco, 1980; also see part I). The growth rates and large stature of *Fucus distichus* ssp. *edentatus* may have led to delayed
reproduction, in that it necessitates an early diversion of energy to vegetative growth. Although early reproduction brings clear advantages in the potential rapid growth of populations (Harper, 1977), the strong selective pressure for a rapid increase in stature overcomes these benefits. Perhaps when the selective advantage of height is removed, as in the upper littoral zone, the benefits from early reproductive maturity may prevail.

Population differentiation has important ecological and evolutionary implications that have received considerable attention (Jain and Bradshaw, 1966; Ehrlich and Raven, 1969; Bradshaw, 1972). Recently it has been shown that genetic divergence of locally adapted populations may occur over very short distances, even in the presence of gene flow (Antonovics and Bradshaw, 1970; Snaydon, 1970; De Silva and Burrows, 1973; Cheney and Mathieson, 1979). For example, Antonovics and Bradshaw (1970) report a significant morphological differentiation between populations of the grass *Anthoxanthum odoratum* growing at a lead/zinc mine and an adjacent pasture. Snaydon (1970) showed that population differences may evolve in less than 40 years in response to soil fertility. De Silva and Burrows (1973), suggest that unbranched and branched plants of the *Enteromorpha intestinalis-compressa* complex, which occur on the upper and lower shore respectively, represent two taxa evolving from a single species. In such cases of pronounced localized population differentiation, the disruptive effects of
contrasting selective pressures must have overcome the integrative effects of gene flow. Since gene flow is likely to occur, at least to a certain extent, between the dwarf form and *Fucus distichus* ssp. *edentatus* (Burrows and Lodge, 1951; Bolwell et al., 1977), the genetic distinction of the adjacent populations is most likely maintained by natural selection of plants better adapted to contrasting intertidal habitats.

In summary, several researchers have not recognized the genetic distinction of the dwarf form (Borgesen, 1902; Jonsson, 1903, Jaasund, 1965). However, the present study demonstrates that the dwarf stature of the high intertidal *Fucus distichus* plant is genetically controlled and suggests that it is an adaptation to a particular set of habitat characteristics. Thus, the ecotypic designation of the dwarf non-tide pool plant of *F. distichus* is appropriate and taxonomic recognition at the subspecific rank, as ssp. *anceps*, by Powell (1957a) is accepted.
Table I. Previous records and new collections of the dwarf, non-tide pool form of *Fucus distichus*. 
Norway

Trondhjemsfjords
Hardangerfjord
Tromso

Great Britain

Scotland
Shetland Islands

Faeroes

Iceland

Ondveroarnes
Gamla-Hrvan
Grimsey
Dyrafjordur

Ireland

Kilkee
Donegal

Greenland

Canada

Ungava Bay, Quebec

United States

Mt. Desert Island, Maine
Mt. Desert Island, Maine
Smuttynose Island, Isles of Shoals, Maine
Star Island, Isles of Shoals, New Hampshire
White Island, Isles of Shoals, Maine
Bald Head Cliff, Maine
Nahant, Massachusetts

Printz, 1926
Jorde, 1963
Jaasund, 1965
Powell, 1952
Russell, 1974
Borgesen, 1903
Jonsson, 1903
Munda, 1976
Munda, 1977
Munda, 1977
Carruthers, 1863
Powell, 1957
Lund, 1959
Wilce, 1959
Wilce, 1959
Present study
Present study
Present study
Present study
Present study
Present study
Table II. Lengths (cm) of sample parents of *F. distichus* ssp. *edentatus* and the mean lengths of the 15 largest progeny of the dwarf form grown in the experimental garden.
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<th>dwarf form</th>
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<tr>
<td>Parent</td>
<td>29.0</td>
<td>6.2</td>
</tr>
<tr>
<td>Progeny</td>
<td>24.4 ± 1.1</td>
<td>6.9 ± .8</td>
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</table>
Table III. Number of *F. distichus* ssp. *edentatus* and the dwarf form progeny that survived to one year of age in the experimental garden (N), plus the number of the surviving plants that became reproductively mature at that age, and the mean length of the surviving plants (cm).
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<th>dwarf form</th>
</tr>
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<tbody>
<tr>
<td>N</td>
<td>58</td>
<td>80</td>
</tr>
<tr>
<td>fertile at one year</td>
<td>0</td>
<td>76</td>
</tr>
<tr>
<td>length</td>
<td>11.8 ± 1.5</td>
<td>6.7 ± 1.5</td>
</tr>
</tbody>
</table>
Fig. 1. Dwarf form of Fucus distichus, reproductively mature (actual size).
Fig. 2. Map illustrating known distribution of the dwarf, non-tide pool form of *Fucus distichus* within the North Atlantic, based upon previous records and the present study.
Fig. 3. Vertical distribution and abundance of macro organisms on the eastern end of Smuttynose Island, Maine.
Fig. 4. Range of morphological variation from the dwarf form (A) to a typical *F. distichus* ssp. *edentatus* (F).
Fig. 5. Frequency distribution of stature of plants from Smuttynose Island, Maine.
Fig. 6. Mean length of plants from 16 subareas at different elevations on the eastern end of Smuttynose Island, Maine. Bars indicate 95% confidence interval.
Fig. 7. Student-Newman-Keuls test of equivalencies of subareas 1-16. The subarea number is positioned opposite its mean plant length (cm) on the scale.
Fig. 8. Frequency distribution of stature of plants from subarea 10 on the eastern end of Smuttynose Island, Maine.
Fig. 9. Percent of populations of the dwarf form and *Fucus distichus* ssp. *edentatus* that is reproductively mature. Based on monthly observations between March, 1981 and February, 1982.
dwarf form

F. distichus  ssp. edentatus

% Reproductive

Month
Fig. 10. Parents and typical progeny of *P. distichus* ssp. *edentatus* and the dwarf form: A, *P. distichus* ssp. *edentatus*; B, progeny of "A" grown in experimental garden; C, dwarf form; D, progeny of "C" grown in experimental garden.


ECOLOGY AND GENEOLOGY OF
FUCUS DISTICHUS (L.) POWELL

PART 4-

TAXONOMIC CONCLUSIONS
Until recently, the *Fucus distichus* complex (sensu Powell, 1957) has been interpreted as distinct species in North America (Taylor, 1962). In contrast, several European authors, including Rosenvinge (1893), Borgesen (1902), and Jonsson (1903) have regarded these hermaphroditic members of the genus *Fucus* as expressions of a single extremely variable species (*F. inflatus* (L.) M. Vahl. Table I summarizes the equivalencies of numerous specific and subspecific designations of the taxa by several authors for the North Atlantic. Powell (1957a) also emphasized that the various forms do not warrant specific status, however, he rejected the name *Fucus inflatus* on the grounds that Linnaeus's original description and fragmentary specimens were inadequate to delimit a particular species of *Fucus*. Likewise, Taylor (1962) examined the same specimens and rejected the name *F. inflatus*.

On the other hand, after an examination of two sheets of specimens labeled *Fucus distichus* in the Linnaean Herbarium (Linn) (numbers 1274.56 and 1274.57 in Savage, 1945) Powell concluded that the name *Fucus distichus* L. referred to the tide-pool form of the same complex. The name *F. distichus* was first used by Linnaeus in 1767 (Linnaeus, 1767). Even though the name *F. linearis* (Oed.) Rosenv. was used earlier (Hudson, 1762), Powell has shown that it referred to a specimen of *F. vesiculosus* L. that lacked vesicles. Thus, the name *F. linearis* was inappropriate for the hermaphroditic forms discussed above.
Further, Powell pointed out that the name *F. filiformis* De la Pylaie, which also predates *F. distichus*, was used with different meanings and cannot be associated with any particular type. Consequently, he chose the name *Fucus distichus* as having priority over any other names for the various hermaphroditic fucoids, other than *F. spiralis*. Furthermore, he considered the four most distinctive growth forms ecotypes and treated them taxonomically as subspecies.

In the present study, statistical comparisons of morphological variation both within and between *Fucus distichus* populations (see Parts II and III) showed the following patterns: 1) that variation lacked discontinuity, 2) discrete populations of various growth forms were present, and 3) some forms similar to those described by Borgesen (1902) and Jonsson (1903) were correlated with habitat characteristics. Consequently, the present study supports Powell's emendation of *F. distichus*. Furthermore, results of transplant studies (see Part II and III), indicate that the form of a particular individual is primarily genetically controlled rather than environmentally induced. Thus, the distinct forms are best treated as ecotypes and taxonomic recognition at the subspecific rank is appropriate.

The subspecies recognized by Powell are essentially equivalent to the taxa recorded by Taylor (1962) from the northeastern coast of North America: *Fucus edentatus*, *F. evanescens*, and *F. filiformis* (the tide-pool form). Some
differences should be noted. *Fucus distichus* ssp. *edentatus* is recognized as a plant of sheltered to semi-exposed sites in Great Britain (Powell, 1957b; Russell, 1974), while in the northwest Atlantic it primarily occurs at semi-exposed to very exposed sites (Edelstein et al., 1971-1973; South and Hooper, 1981; Mathieson and Hehre, 1982). A second difference reflects the recognition and description of a dwarf, non-tide pool form (Table I). Powell (1957a) considers the latter plant as *F. distichus* ssp. *anceps*, but he gives no record of the plant for North America. Similarly, most North American phycologists have not recognized the ssp. *anceps* on northeastern coasts (Taylor, 1962; South, 1976; Edelstein et al., 1971-73; South and Hooper, 1981). On the other hand, Wilce (1959) records a dwarf form in northern Canada (Ungava Bay) and on Mount Desert Island, Me. that resembles *F. distichus* ssp. *anceps*. As a result of the present study, numerous populations of this dwarf plant are now known from central Maine to northern Massachusetts (See part III).

Both Kjellman (1893) and Jonsson (1903) believed that the dwarf form was environmentally induced. They reported a gradual transition in stature from short, dwarf to *edentatus*-like plants along an elevational gradient. In contrast, the present study has shown that although intermediate individuals are present, they are less abundant than either the dwarf form or ssp. *edentatus*. Furthermore, the stature of the dwarf, non-tide pool plant was shown to
be genetically controlled and distinct from _F. distichus_ ssp. _edentatus_ (see Part III).

In New England, the dwarf form grows abundantly within the upper eulittoral zone on very exposed shores, while _F. distichus_ ssp. _edentatus_ occurs in the mid-lower eulittoral (see Part III). Similar situations have been described for the Faeroes (Borqesen, 1902) and Iceland (Jonsson, 1903). However, Powell (1957b) and Russell (1974) only report _F. distichus_ ssp. _anceps_ and not ssp. _edentatus_ at exposed sites in Great Britain and Ireland. The differences may be due to interpretations of ssp. _anceps_ and ssp. _edentatus_. Results of the present study suggest that _F. distichus_ ssp. _anceps_ should be limited to the dwarf, non-tide pool form found on the upper shore, as described by Carruthers (1863), Borqesen (1902), and Jonsson (1903). Nevertheless, I have seen relatively large (18 cm long) British specimens which were identified by E. Conway as _F. distichus_ ssp. _anceps_. These specimens appear to be narrow forms of _F. distichus_ ssp. _edentatus_ as found on northwestern Atlantic shores (referred to as _F. edentatus_ f. _angustior_ by Taylor, 1962). Obviously, further comparative work is necessary on European and American shores in order to clarify the situation.
Table I. Equivalencies of specific and subspecific designations of the forms of the *Fucus distichus* complex (*sensu* Powell).
<table>
<thead>
<tr>
<th>Author</th>
<th>Tide Pool Form</th>
<th>Dwarf Non-Tide Pool Form</th>
<th>Narrow Form</th>
<th>Broad Form</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rosenvinge</td>
<td><em>F. inflatus</em> var. <em>linearis</em></td>
<td></td>
<td><em>F. inflatus</em> var. <em>edentatus</em></td>
<td><em>F. inflatus</em> var. <em>edentatus</em></td>
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<tr>
<td>(Greenland, 1893)</td>
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<tr>
<td>Kjellman</td>
<td><em>F. miclonensis</em></td>
<td><em>F. edentatus</em> f. <em>contracta</em></td>
<td><em>F. edentatus</em> f. <em>typica</em></td>
<td><em>F. evanescens</em></td>
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<tr>
<td>(Arctic Sea, 1883)</td>
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<td></td>
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<tr>
<td>Borgesen</td>
<td><em>F. inflatus</em> f. <em>linearia</em></td>
<td><em>F. inflatus</em> f. <em>disticha</em></td>
<td><em>F. inflatus</em> f. <em>edentata</em></td>
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<tr>
<td>(Faeroes, 1902)</td>
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<tr>
<td>Jonsson</td>
<td><em>F. inflatus</em> f. <em>linearia</em></td>
<td><em>F. inflatus</em> f. <em>exposita</em></td>
<td><em>F. inflatus</em> f. <em>typica</em></td>
<td><em>F. inflatus</em> f. <em>evanescens</em></td>
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<td>(Iceland, 1903)</td>
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<td></td>
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<tr>
<td>Powell</td>
<td><em>F. distichus</em> ssp. <em>distichus</em></td>
<td><em>F. distichus</em> ssp. <em>anceps</em></td>
<td><em>F. distichus</em> ssp. <em>edentatus</em></td>
<td><em>F. distichus</em> ssp. <em>evanescens</em></td>
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<td>(1969)</td>
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<tr>
<td>Taylor</td>
<td><em>F. filiformis</em></td>
<td></td>
<td><em>F. edentatus</em></td>
<td><em>F. evanescens</em></td>
</tr>
<tr>
<td>(N.E. Coast N.A., 1959)</td>
<td></td>
<td></td>
<td><em>F. edentatus</em> f. <em>angustior</em></td>
<td></td>
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<tr>
<td>Jaasund</td>
<td><em>F. distichus</em> ssp. <em>distichus</em></td>
<td><em>F. distichus</em> ssp. <em>anceps</em></td>
<td><em>F. distichus</em> ssp. <em>edentatus</em></td>
<td></td>
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<tr>
<td>(Norway, 1965)</td>
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<tr>
<td>Edelstein et al.</td>
<td><em>F. distichus</em> ssp. <em>distichus</em></td>
<td></td>
<td><em>F. edentatus</em></td>
<td><em>F. distichus</em> ssp. <em>evanescens</em></td>
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<td>(Nova Scotia, 1971–73)</td>
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<td>South and Hooper</td>
<td><em>F. distichus</em> ssp. <em>distichus</em></td>
<td></td>
<td><em>F. distichus</em> ssp. <em>edentatus</em></td>
<td><em>F. distichus</em> ssp. <em>evanescens</em></td>
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<tr>
<td>(Newfoundland, 1981)</td>
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</tbody>
</table>
KEY

1) Plants large, usually exceeding 15.0 cm at reproductive maturity ......................................................... 2

1) Plants small, usually less than 10.0 cm at reproductive maturity ......................................................... 3

2) Receptacles more than 8 times as long as broad, acute, 50-100 mm long; frond narrow, less than 12.0 mm; generally found in mid-low littoral zone at semi-exposed to very exposed, open coastal sites ................. ssp. edentatus

2) Receptacles 1-2 times as long as broad, blunt or rounded, less than 50 mm long; frond wide, more than 12 mm; generally found in lower littoral at sheltered sites, most common in quiet bays and estuaries ................. ssp. evanescens

3) Plants sturdy with well developed holdfast; short, thick stipe; generally found in the upper littoral, associated with barnacles at very exposed sites ........ ssp. anceps

3) Plants delicate, filiform with small holdfast; thin stipe; generally found in tide pools ........ ssp. distichus
LITERATURE CITED


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