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Ecological Studies of *Codium fragile* in New England, USA*

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Abstract

The seasonal growth and reproduction of *Codium fragile* were studied at Boothbay Harbor, Maine, and at Woods Hole and Wings Neck, Massachusetts (USA), in relation to several environmental parameters. Maximum growth and reproduction occur during periods of highest water temperatures and insolation. The effects of various light intensities and temperatures on the photosynthesis rates of *C. fragile* were determined and correlated with the field results. Optimal conditions for net photosynthesis are 21° to 24 °C and 900 to 1100 foot-candles. It is suggested that *C. fragile* is a warm-temperate plant that is growing near its northern limits in New England, but one that has not extended to its potential southern limits.

Introduction

The siphonous, marine, green alga *Codium fragile* is a recent introduction to the benthic algal community of the northeastern coast of North America. Moeller (1969) speculates that it was introduced from Holland and/or the state of Washington (USA) during transplantation of oysters. The first published record of *C. fragile* on the northeast coast was given by Bouck and Morgan in 1957. Five years later it was introduced to Cape Cod waters with oysters brought from Peconic Bay, Long Island, New York (Galstoff, 1962). Numerous authors (Wood, 1962; Schumacher and Fiore, 1963; Coffin and Stickney, 1966; Taylor, 1967) have subsequently noted the introduction and movement of *Codium* in the northeast, and it is now recorded from Barnegat Bay, New Jersey to Boothbay Harbor, Maine. As suggested by Ramus (1971), *C. fragile* has reached epidemic proportions in southern New England and Long Island Sound, and it threatens the already waning shellfish industry of these areas.

At present little is known regarding the ecology of *Codium fragile* particularly on the northeastern coast of North America. Moeller (1969) investigated the growth and reproduction of *in situ* plants at several locations in Shinnecock Bay, Long Island, New York. Churchill and Moeller (1972) discussed seasonal patterns of reproduction in New York populations of *C. fragile*. Ramus (1972) described the early development of the plant. The abundance of *C. fragile* in New England and its economic importance to scallop and oyster industries motivated us to make a detailed study of the factors responsible for its local growth and distribution. A combination of field and laboratory studies was conducted.

Materials and Methods

Monthly field studies were conducted at Woods Hole, Massachusetts, Wings Neck, Massachusetts, and Boothbay Harbor, Maine, during 1969. Systematic collections and observations of *Codium fragile* populations were made with SCUBA equipment in the sublittoral zones at each site. A variety of growth studies were initiated. Plants (20 to 100) were tagged *in situ* at Boothbay Harbor and Woods Hole; length and number of dichotomies per plant were recorded each month. Random collections of 50 to 75 plants were made monthly at Woods Hole; their length and reproductive state was enumerated. The presence of "gametangia" was determined after a microscopic examination of each plant[1]. Seasonal variations of standing crop (damp-dried weight) and numbers of *C. fragile* plants were recorded every 3 months at Wings Neck, by harvesting random quadrats (m^2).

Surface-water temperature and salinities were recorded during each visit to a station. In addition, daily surface-water temperature and salinity data were obtained from the Woods Hole Oceanographic Institute, Falmouth, Massachusetts (personal communication, D. Bumpus and J. Chase) and the Bureau of Commercial Fisheries Laboratory at Boothbay Harbor, Maine (personal communication, Mr. R. Welch). The hydrographic data were correlated with the growth and reproductive studies.

The effects of various light intensities and temperatures on the assimilation of *Codium fragile* were

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[1] Borden and Stein (1969) describe anisogamous gametes and zygote development for *Codium fragile* populations on the Pacific coast of North America. To date no one has observed zygotic fusion of swarmers for *C. fragile* on the Atlantic Coast of North America; we have designated the reproductive organs "gametangia".

evaluated with a model GRP 14 Gilson differential respirometer. Apparent or net photosynthesis is the excess of photosynthesis over respiration. The respirometer was equipped with 14 Champion incandescent bulbs (50 watt). The light intensity was varied with a rheostat. Healthy fronds of *Codium fragile* were collected (March, 1972) from the sublittoral zone at Wings Neck, returned to the laboratory in an ice chest, dissected into half-inch terminal segments, placed in artificial seawater (Chapman, 1962), and incubated at 15 °C and 400 foot-candles prior to initiation of the experiments. The studies were completed within 48 h after the collection of specimens. Ten replicates were used for each experiment. The manometric techniques employed were similar to those of Mathieson and Burns (1971).

Description of Study Areas and Environmental Factors

Boothbay Harbor is located approximately 40 miles northeast of Portland, Maine (43°51′ N; 69°38′ W). It is a sheltered site, with limited exposure to wave action. The study area was adjacent to the boat ramp of the Bureau of Commercial Fisheries Marine Laboratory. The substrate ranged from small ledges and disarranged boulders in the upper sublittoral zone to silt and mud below 5 m. *Codium fragile* occurred most abundantly between 1 to 3 m below mean low water level (MLW). The harbor often freezes over during the winter. The mean monthly surface-water temperatures ranged from 1.7 °C in February to 15.6 °C in August, while the salinities ranged from 29.9‰ in April and May to 31‰ in January and August (Table 1). Boothbay Harbor was selected as a research site because it is the northernmost location from which *C. fragile* is reported on the northeast coast of North America.

Woods Hole is located in Falmouth, Massachusetts (41°31′ N; 70°40′ W) on the southwest side of the Cape Cod Peninsula. It is sheltered from extreme wave action. A quarried granite jetty was used as the study area, as it supported a prominent *Codium fragile* population in the upper sublittoral zone (1 to 4 m below MLW). Scattered plants extended to 11 m depth. The mean monthly surface-water temperatures and salinities ranged from −1.5 °C (January) to 23.0 °C (August) and 31.1‰ (December) to 32.0‰ (June and July), respectively (Table 1). Wings Neck is located in Bourne, Massachusetts (41°31′ N; 70°40.5′ W); it is adjacent to Woods Hole. The site has moderate exposure to southwest winds, which predominate throughout the year. The shore grades gently from mixed cobbles in the upper sublittoral (0 to 4 m) to sand below 5 m. The temperature and salinity regimes at Wings Neck are similar to those at Woods Hole. There is an almost pure stand of *C. fragile* in the upper sublittoral zone at Wings Neck, and the plants are easily accessible throughout the year.

Table 1 also shows the seasonal changes in day length at Boston, Massachusetts (Latitude 42°22′ N), which is the closest recording station between Cape Cod and Boothbay Harbor (Anonymous, 1969). No other consistent records were available, and the values are probably representative for the two study areas. Day length ranged from 9 h in January and December to 15 h during June and July.

Table 1. *Mean monthly surface-water temperatures and salinities at Woods Hole and Boothbay Harbor and hours of day length at Boston*

Month	Water temperature (°C)		Salinity (‰)		Day length (h)
	Woods Hole	Boothbay Harbor	Woods Hole	Boothbay Harbor	Boston
Jan.	−1.5	3.4	31.8	31.9	9
Feb.	2.0	1.7	31.7	30.8	10
Mar.	2.5	2.08	31.6	31.1	11
Apr.	8.0	5.0	31.5	29.9	12.4
May	15.0	8.4	31.8	29.9	14
June	19.0	13.3	32.0	30.1	15
July	22.0	15.0	32.0	30.4	15
Aug.	23.0	15.6	31.8	31.9	14
Sept.	21.0	14.5	31.8	31.2	13
Oct.	16.0	11.6	31.8	31.5	11.5
Nov.	12.0	9.3	31.4	31.5	10.1
Dec.	8.0	6.0	31.1	30.9	9

Results

Growth and Standing Crop

Fig. 1 shows the seasonal growth of tagged *Codium fragile* plants at Boothbay Harbor and Woods Hole, expressed as the maximum, minimum, and average monthly increase in length. Limited growth was evident at both sites from January through March. Spring growth was initiated earlier (April) at Woods Hole than at Boothbay Harbor (May). Peak growth (10 cm/month) occurred from July to September at Woods Hole; the highest average rate of growth (9.2 cm/month) occurred in August. The maximum growth (5.5 cm/month) at Boothbay Harbor occurred during August. Growth at both sites declined rapidly in the late fall and winter.

Fig. 2 illustrates the seasonal growth of two *Codium fragile* plants at Woods Hole, expressed as the number of dichotomies per plant. Extensive fragmentation of the larger frond occurred during March and April. Thereafter, the plant increased in stature until September. The smaller plant showed no growth or fragmentation from January to March. Subsequently,

it surpassed the other plant in stature during the spring-summer period. The irregular growth pattern and greater age of *C. fragile* plants at Boothbay Harbor, as well as the scarcity of plants for counting, made it difficult to enumerate growth by dichotomy numbers.

Mixed populations of large and small plants were evident throughout the year at Woods Hole. The plants usually ranged from 5 to 40 cm in length. Only limited numbers of healthy, large fronds (20 cm or larger) were evident from January to March, because of severe winter fragmentation (Fralick and Mathieson, 1972). In contrast, the shorter plants did not fragment. New fronds were initiated as small bumps from the prostrate, perennial bases during May; these fronds grew extensively during the subsequent summer and early fall. The largest fronds (45 to 50 cm) were found during July.

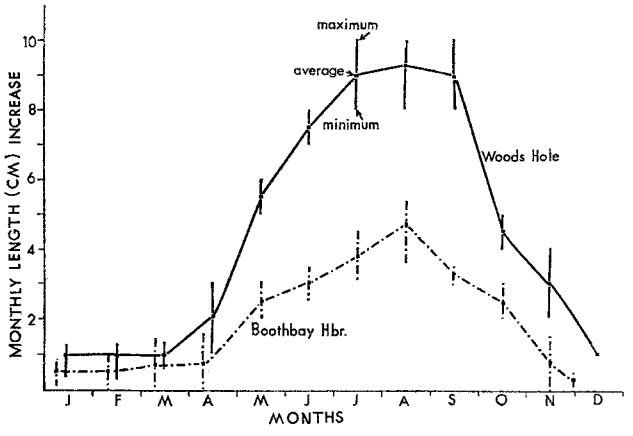

Fig. 1. *Codium fragile.* Seasonal growth expressed as monthly average increase in length

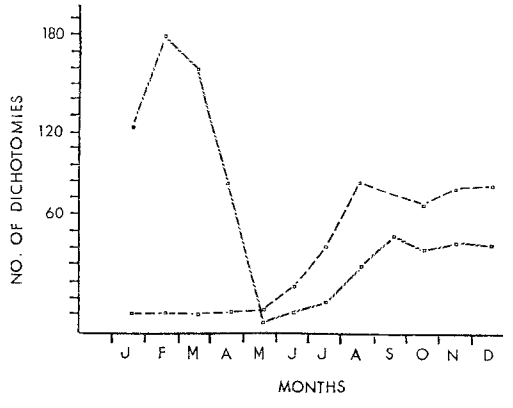

Fig. 2. *Codium fragile.* Seasonal growth of 2 tagged individuals expressed as monthly number of dichotomies per plant

Fig. 3 shows the seasonal variation in weight and number of *Codium fragile* plants at Wings Neck. The lowest biomass was recorded during January (350 g/m^2), while the maximum value was evident in August (2861 g/m^2). The seasonal increase in biomass was associated with a corresponding increase in the number of new plants. The average weight per plant for the same quadrats is shown in Fig. 4. The plants showed a continual increase in weight from January (29 g) to November (231 g).

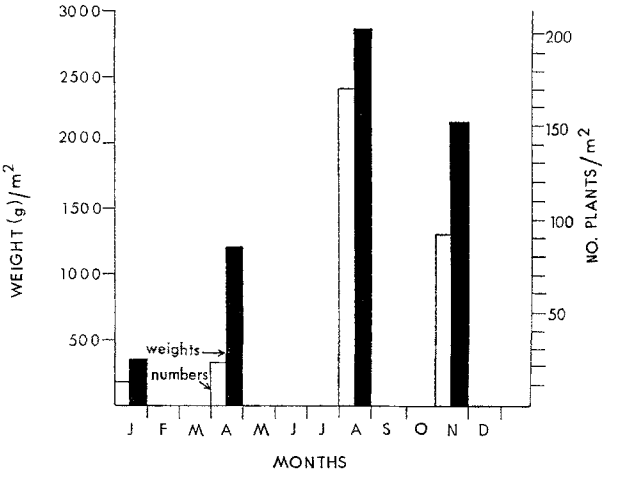

Fig. 3. *Codium fragile.* Seasonal variation of biomass (damp-dried weight) and number of plants at Wings Neck, Massachusetts, USA

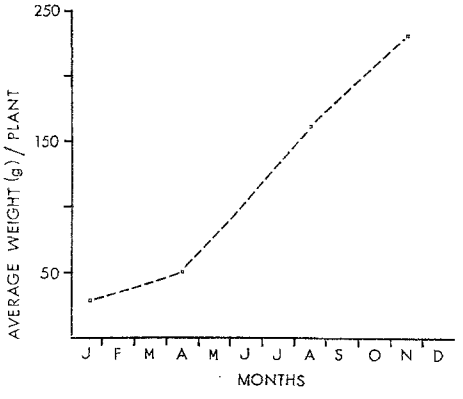

Fig. 4. *Codium fragile.* Seasonal variation of weight per plant (average) at Wings Neck

Reproduction

The liberation of biflagellate swarmers, measuring 5 to 18 μm in diameter and 8 to 27 μm long, was observed in the laboratory on several occasions during the summer and fall of 1969. The swarmers were never observed to fuse; instead they germinated di-

rectly into heterotrichous germlings. We have not followed the maturation of these germlings. However, Ramus (1972) gives a detailed description of the differentiation of *Codium fragile* from both swimming cells and vegetative filaments.

Fig. 5 summarizes the percent occurrence of reproductive plants throughout the year at Woods Hole.

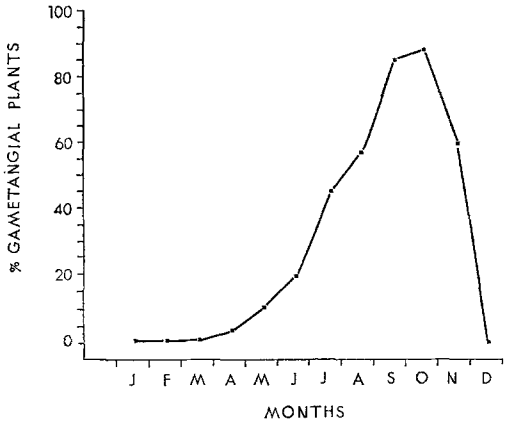

Fig. 5. *Codium fragile.* Seasonal variation of reproductive (gametangial) plants at Woods Hole, Massachusetts

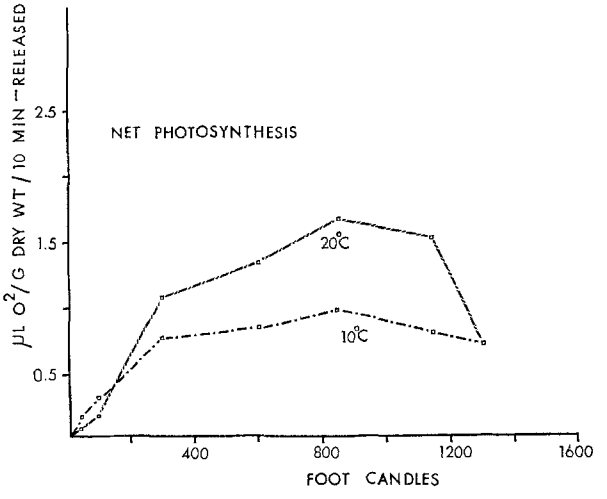

Fig. 6. *Codium fragile.* Apparent photosynthesis at 10° and 20 °C and under various light intensities

No functional reproductive organs ("gametangia") were evident during the winter months of December to March; limited numbers were observed in May and June. During September and October, 85 to 89% of the plants were reproductive. The limited number of plants at Boothbay Harbor did not allow a quantitative evaluation of reproduction. Even so, it was apparent that the reproductive period was initiated later (August) and terminated earlier (November) than at Woods Hole.

Photosynthesis and Respiration

The rate of apparent photosynthesis of *Codium fragile* at 10° and 20 °C and under a variety of different

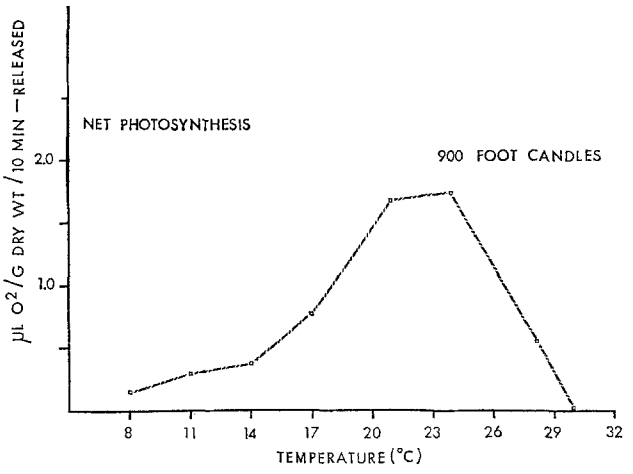

Fig. 7. *Codium fragile.* Apparent photosynthesis at various temperatures and 900 foot-candles

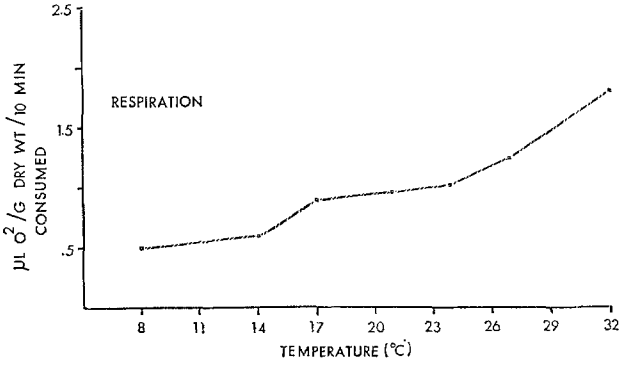

Fig. 8. *Codium fragile.* Respiration at various temperatures

light intensities is given in Fig. 6. The apparent photosynthesis increases with an increase in light intensity up to approximately 900 foot-candles, above which it decreases. Thus, light intensities of less than 900 foot-candles are probably suboptimal, whereas greater intensities are probably saturating. Fig. 7 shows the apparent photosynthesis of *Codium fragile* at various temperatures and 900 foot-candles. The apparent photosynthesis increases with an increase in temperature to approximately 24 °C, above which it decreases. The values at 21 °C were only slightly

less than at 24 °C. A comparison of the respiration rates at different temperatures (Fig. 8) shows a corresponding increase with increasing temperature to 32 °C, at which point thermal injury is probably apparent.

Discussion

Optimal growth of *Codium fragile* occurs during periods of maximum water temperatures and high insolation (c.f. Fig. 1 and Table 1). Thus, maximum growth (10 cm/month) occurred at Woods Hole during July to September, when the surface-water temperatures averaged 21° to 23 °C, while maximum growth (5.5 cm/month) occurred at Boothbay Harbor during August, when the monthly average temperature was 15.6 °C. Minimal growth occurred at both sites when the temperatures were less than 5 °C and the days were short (8 to 11 h sunlight). Cold temperatures (3 °C or less) can also cause fragmentation of the larger fronds (Fralick and Mathieson, 1972), the period of maximum fragmentation corresponds to periods of minimal growth.

There was a good correlation between field studies and laboratory experiments on photosynthesis, as optimal conditions for apparent photosynthesis are 21° to 24 °C. Comparable summer temperatures were found at Woods Hole and Wings Neck. The lower temperatures at Boothbay Harbor were probably responsible for the slower rate of growth and the more restricted period of growth at this site, as compared to Woods Hole. The optimal light requirements of *Codium fragile* are comparable to other sublittoral algae such as *Chondrus crispus* (Mathieson and Burns, 1971). Ramus (1971) states that the vertical distribution of *C. fragile* in Long Island Sound is turbidity limited, for he records deeper vertical distributions in clear water (6 m) than in turbid waters (2 m). Unfortunately, he did not summarize any information on intensities and attenuation.

Codium fragile exhibits maximum reproduction during its period of fastest growth (c.f. Figs. 1 and 5). Thus, 85 to 89% of the plants at Woods Hole were reproductive during September and October. The reproductive period at Boothbay Harbor was initiated later, and terminated sooner than at Woods Hole. The differential hydrographic (temperature) regimes at the two sites are probably responsible for the reduced reproductive period at Boothbay Harbor.

Recent observations by Churchill and Moeller (1972) suggest that New York populations of *Codium fragile* reproduce exclusively by parthenogenetic female gametes, for they found no indication of male gametes or sexual fusion. Our observations confirm their findings. It should be noted that similar parthenogenetic populations have been reported in Europe (Feldmann, 1956; Delépine, 1959; Weber, 1969), where the plant has also become a weed. However, sexual populations are reported for several areas of the world (see Borden and Stein, 1969, for summary). Various types of vegetative propagules have also been reported for *Codium* (Tobler, 1911; Schmidt, 1923; Borden and Stein, 1969), and vegetative propagation is probably widespread in the genus. Borden and Stein (1969) suggest that the regenerative powers of *C. fragile* may account for its recent and rapid dissemination.

According to our findings, *Codium fragile* is a warm temperate plant that is growing near its northern distributional range in New England, but one that has not extended to its potential southern limit. At present, *C. fragile* is reported as far south as Barnegat Bay, New Jersey (Taylor, 1967). Williams (1948) showed that several New England algae occurred at Cape Lookout, North Carolina, during the winter, and that this location was the southern limit of many northern (boreal) species. The warm-water affinities of *C. fragile* suggest that it would grow well within the temperature ranges found between New Jersey and North Carolina (Cape Lookout-Cape Hatteras areas). Thus, *C. fragile* may migrate to the economically important oyster beds of the Chesapeake Bay.

Summary

1. Monthly field studies of *Codium fragile* populations were conducted at Woods Hole, Massachusetts and Boothbay Harbor, Maine, USA during 1969.

2. *C. fragile* exhibits maximum growth during the periods of highest water temperatures and insolation. Peak growth (10 cm/month) occurred from July to September at Woods Hole, while maximum growth at Boothbay Harbor (5.5 cm/month) occurred during August. Minimal growth occurred at both sites when the temperatures were less than 5 °C and the days were short (8 to 11 h sunlight).

3. Biflagellated swarmers were liberated from the macroscopic plant. The swarmers were never observed to fuse; instead they germinated directly into heterotrichous germlings.

4. *C. fragile* exhibits maximum reproduction during its period of fastest growth, i.e., summer and fall. Differential reproductive periods were noted at Woods Hole and Boothbay Harbor, presumably because of varying hydrographic regimes at the two sites.

5. The effects of various light intensities and temperatures on the photosynthesis of *C. fragile* were determined. Optimal conditions for net photosynthesis are 21° to 24 °C and 900 to 1000 foot-candles. The photosynthetic studies are correlated with the field results.

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