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Temperature ecotypes near the southern boundary of the kelp *Laminaria saccharina*

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Abstract

Effects of temperature on survival, growth, and photosynthesis were compared for two USA populations of *Laminaria saccharina* Lamour. One population was located in New York State, near the southern latitudinal boundary of the species in the western North Atlantic. This southern boundary population was exposed to ambient temperatures $\geqq 20\,°C$ for about 6 wk each summer. The second population was located in Maine, toward the center of the latitudinal range of the species, and was rarely exposed to temperatures $> 17\,°C$. Sporophytes from the New York (NY) population exhibited greater tolerance of high temperature than plants from the Maine (ME) site. Juvenile sporophytes from the two sites had similar rates of survivorship and growth at temperatures below 20 °C, but showed different responses at 20 °C in laboratory experiments. NY plants survived and grew for 6 wk at 20 °C. ME plants showed negative growth during wk 2 and 100% mortality during wk 3. NY and ME plants held in situ at the NY site during June to September, 1985, also exhibited differential survivorship when ambient temperatures exceeded 20 °C. Results of photosynthesis and dark respiration measurements on NY and ME plants grown at various temperatures suggested that the high-temperature tolerance of NY plants was attributable to their ability to maintain positive daily net C-fixation at 20 °C. The high-temperature tolerance of the NY plants appeared to be due to genetic adaptation and is probably crucial to the persistence of the species near its southern boundary.

Introduction

Temperature is probably the single most important factor determining the geographic distribution of benthic marine macroalgae (van den Hoek 1975). The effect of temperature on survival, growth, and reproduction is of particular interest in populations near the latitudinal boundaries of a species, because boundary populations are usually subject to the highest or lowest temperatures that the species can withstand. Survival under extreme temperature regimes may depend primarily on phenotypic acclimation, in which case populations from different latitudes exhibit similar temperature responses, such as in the red macroalgae *Dumontia contorta* (Rietema and van den Hoek 1984) and *Chondrus crispus* (Lüning et al. 1987). However, genetic adaptation may also be important to temperature tolerance, especially in species with a wide geographic range. In this case, populations adapted to different temperature regimes exhibit different temperature responses after acclimation to similar conditions. *Ectocarpus siliculosus* populations, for example, showed genetic variation in survival and growth temperatures which correlated with differences in ambient temperature regimes (Bolton 1983). Gametophytes of *Ecklonia radiata* from two sites with different temperature ranges had different temperature requirements for growth and reproduction (Novaczek 1984). *Enteromorpha linza* from high and low intertidal sites exhibited genetic differences in optimum growth temperature (Innes 1984).

The kelp *Laminaria saccharina* Lamour. might be expected to exhibit genetic variation in temperature responses, because this species has a large latitudinal range (Bolton et al. 1983), with populations exposed to very different temperature regimes. Genetic adaptation to high temperature is particularly likely, because the southern limit of this species corresponds to the southern lethal boundary (the highest summer temperature survived for 2 to 4 wk) in both the North Atlantic and North Pacific (van den Hoek 1982). However, Bolton and Lüning (1982) compared the temperature responses of four populations of *L. saccharina* from the eastern North Atlantic and found no differences among plants grown from spores under controlled conditions. They concluded that the wide geographic range of this species was attributable to phenotypic plasticity rather than to genetic adaptation. The four popula-

tions were from sites with a 6 C° range in minimum mean monthly temperature, but only a 3 C° range in maximum temperature, which in all cases fell within or close to the optimal range for growth (Fortes and Lüning 1980, Bolton and Lüning 1982). The possibility remained that *L. saccharina* populations exposed to more extreme summer temperatures might exhibit genetic adaptation. We tested this hypothesis by comparing effects of high temperature on survival, growth, and photosynthesis of sporophytes from a southern boundary population in the western North Atlantic with responses of plants from a more central location in the species' range.

Materials and methods

The southern boundary population of *Laminaria saccharina* was located in Long Island Sound, at Crane Neck Point, New York (40°58′N 73°09′30″W). The more centrally located population was located at Cape Neddick, Maine (43°10′N 70°36′30″W), 320 km northeast of Crane Neck Point. Plants were collected from 5 m depth at both sites. The kelp populations from New York (NY) and Maine (ME) correspond respectively to the "turbid" and "shallow" populations described in a previous study of light-related traits (Gerard 1988). Ambient temperature was measured at 3 m depth at Crane Neck Point, weekly from March, 1982, through September, 1983. Temperature was measured at surface and 1.2 m depths at Jaffrey Point, New Hampshire, monthly from September, 1973, to July, 1978 (Daly et al. 1979, Norall et al. 1983). Jaffrey Point is 15 km south of Cape Neddick.

Laminaria saccharina sporophytes with blade lengths of 3 to 5 cm were collected at the NY and ME sites during April, July, and October, 1985. These plants were grown for 6 wk in temperature-controlled rooms at 8, 15, or 18 °C (± 1 C°). Submersible heaters were used in the 18 °C room to maintain plants at 20 and 24 °C. Five plants from each site (~2 to 3 gm total fresh wt) were held in each 15 l batch culture. Cultures were continuously aerated, and cool-white fluorescent lamps provided irradiance at 100 μE m^{-2} s^{-1} (12 h light : 12 h dark, 4 E m^{-2} d^{-1}), measured with a spherical quantum sensor. Ambient seawater, enriched with NO_3^- and PO_4^{-3} at concentrations corresponding to Provasoli's E. S. medium (660 and 40 μM, respectively), was replaced at 3 to 4 d intervals. Salinity was maintained at 30‰ by adding NaCl when ambient salinity was low. This corresponds to the average salinity at the ME site (28 to 32‰) and is slightly higher than the maximum salinity at the NY site (29‰). Site-specific salinity differences probably had little effect on the experimental results, because kelp sporophytes from both sites exhibited similar growth responses to salinities of 21 to 33‰ (Gerard et al. 1987).

Blades of experimental plants were trimmed to 10 cm weekly to maintain constant biomass density in the batch cultures. Growth of individual plants was measured as weekly increase in blotted wet weight. Specific growth rate was calculated as

$$\mu = 100 \times \ln (W_f/W_i)/d$$

where W_i and W_f are initial and final weights, respectively, and d is days between successive measurements. Plant mortality was determined as loss of the basal, meristematic portion of the blade.

In addition to controlled-temperature experiments in the laboratory, growth and survivorship of *Laminaria saccharina* from the NY and ME sites were also compared under summer conditions in Long Island Sound. In early June, 1985, 20 sporophytes with blade lengths of 30 to 50 cm were transplanted from each site to a common-garden site at 5 m depth at Crane Neck Point. A hole 4 mm in diameter was punched in the blade of each plant, 10 cm from the blade-stipe junction. Rates of meristematic blade elongation were determined for 1 to 2 wk periods from July through September by the hole-punch method of Parke (1948). Total blade length of each plant was also measured during the final month of the study. Survivorship during each growth period was determined as the percentage of plants with the basal, meristematic portion of the blade intact. Ambient minimum and maximum temperatures were determined for each interval using a min/max thermometer.

Rates of photosynthesis and dark respiration were determined for plants from the NY and ME sites after 3 wk of acclimation at 8, 15, 18, or 20 °C in the laboratory. Rate measurements for each plant were made at the temperature at which the plant was grown (± 0.1 C°). A 2.27 cm^2 blade disc (~0.1 g wet wt), cut from the distal 5 cm of the blade, was used for each determination. O_2-consumption and production rates were measured at various quantum irradiances (0, 39, 71, 101, 139, 1130, 1580, 2260 μE m^{-2} s^{-1}) using a Rank Bros. O_2-electrode. Equipment and procedures are described in detail by Gerard (1988). Photosynthesis vs irradiance (PI) parameters were calculated from O_2-exchange rates. Photosynthetic capacity (P_{max}) was determined by averaging O_2-production rates at saturating quantum irradiances (1130 to 2260 μE m^{-2} s^{-1}). Photosynthetic efficiency, defined as the initial slope (α) of the PI curve, was calculated by linear regression analysis of O_2-exchange rates at subsaturating irradiances (0 to 139 μE m^{-2} s^{-1}). Rates of dark respiration and net photosynthesis were added to give gross photosynthesis. Photosynthetic pigment concentrations were determined for blade discs adjacent to the disc used for photosynthesis determinations. Chlorophyll *a* and *c* were extracted with DMSO and methanol, and concentrations were determined according to the method of Duncan and Harrison (1982).

Daily net C-fixation was estimated for NY and ME plants growing at each experimental temperature in the laboratory. Gross C-fixation was calculated as the rate of gross photosynthesis at 100 μE m^{-2} s^{-1} summed over 12 h of light. Net C-fixation was determined by subtracting dark respiration over 24 h. Photosynthetic and respiratory quotients were assumed to be 1. Mean density (mg wet wt cm^{-2}) determined for blade discs used in photosynthesis

measurements was used to express C-fixation on a weight basis for comparison with growth rates.

The statistical significance of differences between mean growth rates or photosynthetic parameters of plants from the same site grown at different temperatures were compared using the GT2-method, when an F_{max}-test indicated homogeneous variances (Sokal and Rohlf 1981). When variances were heterogeneous, means were compared using the Games and Howell (G and H) method. Means were compared for plants from NY and ME, grown at the same temperature, using Student's t-test or, where an F-test showed unequal variances, the t-test (Sokal and Rohlf 1981). In all cases, the null hypothesis was rejected at the 95% confidence level. Results from different collection periods were combined for each population, because plants collected during April, July, and October showed no significant differences in growth rates and photosynthetic parameters after 3 wk of acclimation at 8° or 18 °C (Du Bois 1986).

Results

Laminaria saccharina is exposed to higher temperatures for longer periods at the NY site than at the ME site. Ambient temperature showed a higher summer peak (23 to 24 °C) at the NY site and exceeded 20 °C from late July through mid September (Fig. 1), a period of approximately 6 to 7 wk. The highest summer temperature recorded at the ME site was 19 °C, but temperature generally ranged from 12° to 17 °C during July to September. Temperatures were similar at the two sites during the rest of the year.

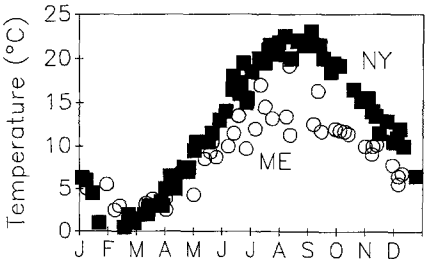

Fig. 1. *Laminaria saccharina.* Ambient temperature regimes of New York (■) and Maine (○) populations. Measurements were made during 1982 to 1983 at Crane Neck Point, New York, and during 1973 to 1978 at Jaffrey Point, New Hampshire, 15 km south of Maine site

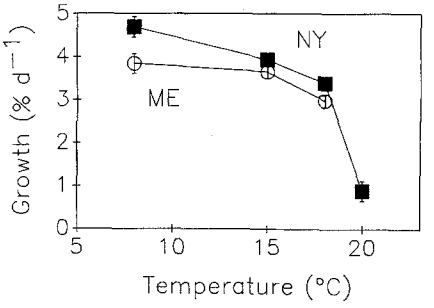

Fig. 2. *Laminaria saccharina.* Specific growth rate (wet wt) vs temperature for juvenile sporophytes from New York (■) and Maine (○). Each point is mean rate for 12 to 25 plants, measured during Wk 3 of growth at experimental temperature; vertical bars represent ±1 SE. All ME plants died during Wk 3 at 20 °C

Population differences in survival and growth at high temperature

Laminaria saccharina from the NY site exhibited higher survivorship at high temperatures than plants from the ME site. In laboratory experiments at 20 °C, 90% of the NY plants survived for 6 wk, while the ME plants suffered 100% mortality during Wk 3. The two groups of plants showed similar survivorship during 6 wk at other experimental temperatures. Both NY and ME plants had high survivorship (> 50%) at 8°, 15°, and 18 °C, and 100% mortality after 3 d at 24 °C.

Growth rates under laboratory conditions were similar for NY and ME plants at 8° to 18 °C, but differed at 20 °C (Fig. 2). NY plants exhibited significantly slower growth at 20 °C than at lower temperatures (G and H-test, $p < 0.05$), but maintained a relatively constant growth rate throughout the 6 wk experiment, with weekly means ranging from 0.9 to 2.1% d^{-1} ($n = 13$–15, SE = 0.2 to 0.3). Growth of ME plants was significantly slower (Student's t-test, $p < 0.05$) than growth of NY plants during Wk 1 at 20 °C. ME plants exhibited a rapid decline in growth rate at 20 °C, from 1.2% d^{-1} ($n = 14$, SE = 0.4) during Wk 1 to −8.5% d^{-1} ($n = 13$, SE = 1.5) during Wk 2. Negative growth was due to distal blade erosion and formation of small holes over the entire blade. The meristematic zone had completely disintegrated by the end of Wk 3.

Observations of growth and survivorship in the field corroborated laboratory results. As ambient temperature increased during July and August, with weekly maximum temperatures exceeding 20 °C (Fig. 3A), both NY and ME plants showed declining growth rates (Fig. 3B). Plants from both populations had high survivorship (Fig. 3C) until the weekly minimum temperature exceeded 20 °C in mid August. While > 50% of the NY plants survived 3 wk of temperatures > 20 °C, the ME plants suffered 100% mortality. As observed in the laboratory, ME plants exhibited severe distal blade erosion and hole formation at temperatures > 20 °C. Their mean total blade length was only 15 cm by late August, and only stipe remained by early September. The surviving NY plants exhibited less severe distal erosion and maintained mean blade lengths of 26 to 34 cm during the same period.

Population differences in photosynthesis at high temperature

NY and ME plants had similar photosynthetic capacity (P_{max}) and efficiency (α) after 3 wk of acclimation at 8 or

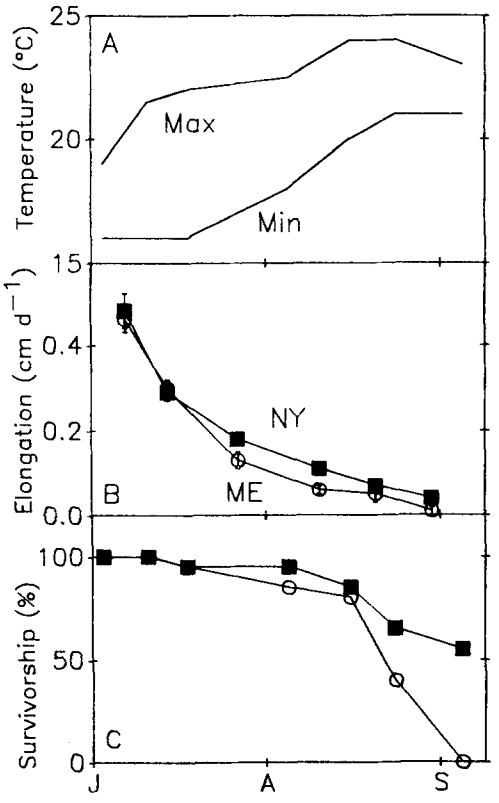

Fig. 3. *Laminaria saccharina.* (A) Weekly minimum and maximum temperatures at New York site during July to September, 1985. (B) Growth rate measured as meristematic blade elongation and (C) survivorship of sporophytes from New York (■) and Maine (○), held at NY site. Each elongation value is the mean for 8 to 20 plants; vertical bars represent ±1 SE

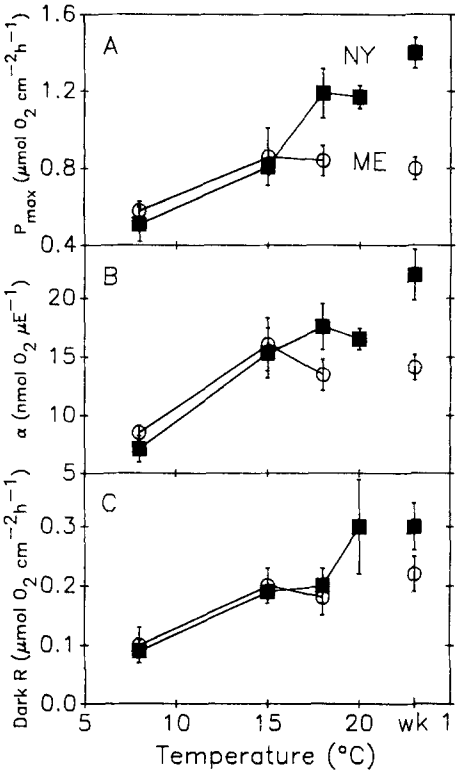

Fig. 4. *Laminaria saccharina.* Photosynthesis vs irradiance (PI) parameters determined for juvenile sporophytes from New York (■) and Maine (○) after 3 wk of growth at 8, 15, 18, or 20 °C. Unconnected points at the right of each graph represent rates determined after 1 wk at 20 °C. (A) Gross photosynthetic capacity, P_{max}, (B) photosynthetic efficiency, α, and (C) dark respiration. Each point is mean for 4 to 9 plants; vertical bars represent ±1 SE

Table 1. *Laminaria saccharina.* Chlorophyll *a* concentration in blade tissue of juvenile sporophytes from New York and Maine after 1 or 3 wk of acclimation to various temperatures. $\bar{X} \pm 1$ SE, (*n*)

Growth temperature	Chlorophyll *a* (μg cm^{-2})	
	New York	Maine
8 °C	8.2±0.9 (4)	10.9±0.5 (5)
18 °C	17.5±1.7 (8)	17.7±3.1 (7)
20 °C (Wk 1)	24.5±7.0 (3)	9.4±0.8 (10)
20 °C (Wk 3)	19.2±1.8 (4)	–

15 °C (Fig. 4A, B). NY plants showed a significant increase in those parameters after acclimation at 18° to 20 °C (*G* and *H*-test, $p < 0.05$), but ME plants showed no significant change in either P_{max} or α between 15 and 18 °C (*G* and *H*-test, $p > 0.05$). At 18 °C, P_{max} was significantly higher for NY plants than for ME plants (Student's *t*-test, $p < 0.05$). ME plants acclimated at 20 °C for only 1 wk also showed significantly lower (Student's *t*-test, $p < 0.01$) values of P_{max} and α than NY plants (Fig. 4A, B). Dark respiration rates were similar for NY and ME plants (Fig. 4C) and generally increased with increasing acclimation temperature, although differences between temperature treatments were not statistically significant (*G* and *H*-test, $p > 0.05$).

Much of the variation in P_{max} and α was attributable to temperature effects on photosynthetic pigment concentrations. Both NY and ME plants had higher chlorophyll *a* concentrations after acclimation at 18 °C than at 8 °C (Table 1). Chlorophyll *a* content was also high in NY plants after 1 and 3 wk of growth at 20 °C. ME plants, however, showed significantly lower chlorophyll than NY plants after 1 wk at 20 °C (Student's *t*-test, $p < 0.05$). Both P_{max} and α were significantly correlated with chlorophyll *a* concentration for all treatment groups ($n = 7$, $r = 0.96$ and 0.87, respectively, $p < 0.05$). The ratio of Chl *c* to Chl *a* ranged from 0.27 to 0.35, did not differ between populations, and was not significantly affected by temperature (*G* and *H*-test, $p > 0.05$).

Estimated daily net C-fixation for NY and ME plants during Wk 3 of growth at 8°, 15°, or 18 °C ranged from 34 to 50 μmol C gm^{-1} wet wt d^{-1}. In contrast, NY plants growing at 20 °C were estimated to have a net daily C-fixation of −1 μmol C gm^{-1} d^{-1}, which is in agreement with the low specific growth rate at that temperature (Fig. 2). Daily net C-fixation during Wk 1 of growth at 20 °C was about twice as high for NY plants (43 μmol C gm^{-1} d^{-1}) as for ME plants (22 μmol C gm^{-1} d^{-1}). Estimated C-fixation was significantly correlated with mean specific growth rate for all treatment groups ($n = 9$, $r = 0.86$, $p < 0.01$).

Discussion

These results support the hypothesis that genetic adaptation has occurred in relation to high-temperature tolerance in a southern boundary population of *Laminaria saccharina*. Plants from the New York site survived 6 wk at 20 °C in the laboratory and 3 wk of temperatures ≧20 °C in the field. In contrast, plants from the Maine site suffered 100% mortality under the same temperature regimes in both laboratory and field experiments. Different responses of plants from NY and ME were evident only at temperatures ≧20 °C; the two populations showed similar temperature effects on survival and growth at lower temperatures. The threshold for the differential response, thus, corresponds to ambient summer temperatures experienced regularly by the NY plants and rarely by the ME plants.

Differential temperature responses of the NY and ME plants appeared to have a genetic basis. Population differences were consistent for plants collected at three different times, and for both small and large sporophytes (3 to 5 and 30 to 50 cm blade lengths) used in laboratory and field experiments. Although responses were not compared for plants grown from spores under controlled conditions, juvenile plants collected during April probably developed under similar temperature regimes at the two sites prior to collection. These plants were used in growth experiments at 8°, 18°, and 20 °C. The NY and ME populations, therefore, appear to represent different temperature ecotypes of *Laminaria saccharina*. However, genetic variability in temperature responses exists within the NY population, as only half of the NY plants survived during the field experiment. Summer mortality is typically high at the NY site (Gerard 1988), and selection for high-temperature tolerant plants probably occurs annually.

The differential response of the NY and ME plants was influenced by both the duration and constancy of high temperature. ME plants survived and grew during Wk 1 at 20 °C in the laboratory, and in the field for 5 wk during which maximum weekly temperatures were ≧20° and minimum temperatures were <20 °C. Brief exposure (≦1 wk) or intermittent periods of lower temperatures moderated the deleterious effects of high temperature. A large proportion of NY plants, on the other hand, survived constant exposure to temperatures ≧20 °C for periods of 6 wk or more. The duration of high-temperature tolerance is an important aspect of adaptation in the NY plants, because summer temperatures exceed 20 °C at this site for about 6 wk each year (Fig. 1). The high-temperature tolerance of the NY population, therefore, effectively extends the southern lethal boundary of *Laminaria saccharina* to ≧20 °C.

The ability of the NY plants to maintain high photosynthetic rates appears to be important to their tolerance of high temperature. The highest photosynthetic capacity and efficiency of this population occurred at 18° to 20 °C. Nevertheless, estimated daily net C-fixation at 20 °C was close to 0 μmol C gm^{-1} d^{-1}, because dark respiration was also highest at this temperature. The low rate of C-fixation probably accounted for the low growth rate of NY plants at 20 °C. In contrast, ME plants showed no increase in photosynthetic capacity or efficiency above 15 °C and, after only 1 wk at 20 °C, their rates of photosynthesis, net C-fixation, and growth were about half that of NY plants. It seems probable that low rates of photosynthesis by the ME plants during Wk 2 and 3 at 20 °C resulted in negative daily net C-fixation and, ultimately, in negative growth rates and mortality. Phenotypic acclimation of *Laminaria saccharina* to extreme temperatures also involves photosynthetic mechanisms. Uniform rates of growth by sporophytes from Helgoland acclimated to a wide range of temperatures were attributed to maintenance of uniform photosynthetic rates through temperature compensation of enzyme activities (Davison 1987, Davison and Davison 1987). However, reduction of net photosynthesis and C-fixation does not appear to be the mechanism of high-temperature effects in all macroalgae. Yarish et al. (1986) found that three species of red algae survived long-term exposure to 25 °C at irradiances of 10 and 20 μE m^{-2} s^{-1}, but not at 40 μE m^{-2} s^{-1}.

Based on the results of the present study, *Laminaria saccharina* populations that are not regularly exposed to ambient summer temperatures ≧20 °C would not be expected to exhibit the high-temperature tolerance of the NY population. Most *L. saccharina* populations, like the ME population, should be unable to withstand extended exposure to temperatures ≧20 °C. This prediction appears to contradict results of several previous studies. Four populations of *L. saccharina* examined by Bolton and Lüning (1982) came from sites with maximum monthly mean temperatures of 14 to 17 °C, but plants from all four sites survived and grew at 20 °C. However, those plants were held at experimental temperatures for only 1 wk. In the present study, deleterious effects of high-temperature on the ME plants became evident only during Wk 2, and mortality occurred during Wk 3. More recently, *L. saccharina* from one of the same sites (Helgoland) survived and grew for 1 mo at 20 °C (Davison 1987, Davison and Davison 1987). In that study, plants were held under continuous light. If, as results of the present study suggest, the deleterious effects of high temperature occur through reduction of daily net C-fixation, continuous light should negate those effects. If the predictions of the present study are correct, plants from the populations examined in those previous studies are not likely to survive through the summer at the NY site. Indeed, three of the four populations exhibited negative growth and mortality at 16° to 18 °C during 2 mo in the sea at Helgoland (Lüning et al. 1978).

The ability of *Laminaria saccharina* sporophytes from the NY site to withstand ambient summer temperatures appears to be important in the life history of this population. Maturation of sporophytes in a single growth season is unlikely. Most of the fertile plants in the natural population are large, with blades 1 to 2 m long. More than 8 mo is required for production of plants this size from spores under optimal conditions in the laboratory (Gerard unpubl.), and development at low ambient light levels is probably

slower. Thus, even plants originating from spores released during early fall are unlikely to become fertile prior to the onset of high summer temperatures. Oversummering of microscopic stages is possible, as gametophytes and microscopic sporophytes of this population survived more than 1 mo at 20 °C (Gerard, unpubl.) and for 3 wk at 23 °C (J.-A. Lee, personal communication). However, spores released during March to July did not result in successful recruitment in situ (Lee 1987), indicating that oversummering of microscopic stages is not a common occurrence. Overall, the high-temperature tolerance exhibited by the NY plants appears to be crucial to the persistence of this southern boundary population.

Responses of *Laminaria saccharina* populations to site-specific variation in temperature provide an example of the complementary roles of phenotypic acclimation and genetic adaptation. The ability to acclimate to a wide range of temperatures (Davison 1987, Davison and Davison 1987) at least partially accounts for the success of this species over a large geographic range (Bolton and Lüning 1982), and genetic adaptation appears to be important to southern boundary populations exposed to extreme summer temperatures. Finally, populations subject to both high summer temperatures and large seasonal variation in temperature, such as the New York population (Fig. 1), must depend on both phenotypic acclimation and genetic adaptation for perennial survival of individual plants and long-term persistence of the population.

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