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## Morphological and Physiological Bases for *Laminaria* Selection Protocols in Long Island Sound Aquaculture

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### Abstract

Considerable progress has been made over the last five years toward development of genetic selection procedures for the kelp, *Laminaria*, in a collaborative research program between the State University of New York and the University of Connecticut. We review here the current status of taxonomy and our investigations into genetics and breeding of *Laminaria*. Growth and reproduction characteristics of *L. saccharina* from Long Island and *L. longicruris* from eastern Connecticut are compared. We emphasize application of gradient plate studies to development and growth characteristics from *L. saccharina* and *L. longicruris* populations in Long Island Sound. Such studies have yielded important insights into the possibility of selecting strains that are superior for given combinations of light and temperature. Preliminary crossing experiments between these local entities indicate a sex-linkage for certain morphological characters.

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## Introduction

Geographic variation among seaweed populations has resulted in considerable taxonomic confusion where morphological or physiological characters have been used to delineate species (Mathieson *et al.*, 1981; Rice and Chapman, 1985). Certainly, the definition of what constitutes a species lies at the heart of taxonomic disputes. The classically accepted definition states that true biological species are reproductively isolated. Where "species" cannot be demonstrated due to a lack of sterility barriers, ecotypic status is frequently assigned to the taxon. By definition, an ecotype is the product of a genotypic response of a species to a particular environmental condition of a habitat, and it implies inter-fertility with other members of the species (Turesson, 1922). Both physiological and morphological ecotypes have been described for various algae (e.g., Gerard and Mann, 1979; Yarish *et al.*, 1979; Mathieson *et al.*, 1981; Russell and Fielding, 1981; Espinoza and Chapman, 1983; Bolton, 1983; Innes, 1984; Gerard, 1988; Gerard and Du Bois, 1988). The occurrence of ecotypic variation in seaweeds has been taken for evidence of genetic differentiation among populations, whose members are perhaps in the process of speciation (Innes, 1984). It is this premise that facilitates efforts directed at selection of strains with both morphologically and physiologically desirable qualities.

Taxonomic delineation in brown seaweeds has been conducted mainly on the basis of phenotypic characters observed in the field and in culture (Russell, 1978). The developmental state of plants and their responses to environmental conditions have caused the greatest consternation among brown algal taxonomists using phenotypic characters to delineate species. With the advent of computers, hierarchical analysis in numerical taxonomy has been attempted as a means of simplifying taxonomic criteria and identification of species (e.g., Widdowson, 1971; Russell and Fletcher, 1975; Prud'homme van Reine, 1978; Pankhurst and Tittley, 1978; Marsden *et al.*, 1983; Rice and Chapman, 1985). These methods have had limited success in natural groups, but have failed where

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phenotypic variability is poorly understood. Many of the criteria used are based on gut feeling or intuitive weighting. Russell (1978) cited numerous instances where the role of genotype has been inadequately separated from phenotype in dictating morphological form. The influence of common environmental factors on morphological characters of seaweeds has recently been reviewed by Norton *et al.*, (1981, 1982). Frequently, attempts to culture representatives compound the problem since responses in culture are not analogous to responses to variable environmental conditions in the field. The lack of appreciation of phenotypic vs. genotypic variability makes attempts to describe phytogeographic distribution difficult. It also hampers selection of new strains for use in mariculture. To date, there has been only one attempt at using numerical taxonomic methods in the study of laminarian populations, namely *Alaria* (Widdowson, 1971).

The genetic basis of population differentiation in the Laminariales has been inferred from observations after one or more generations reared under similar laboratory conditions, reciprocal transplants between field sites, outplants of germlings to a common "garden", and reciprocal crosses between geographically separated populations (Lüning, 1975; Lüning *et al.*, 1978; Bolton *et al.*, 1983; Espinoza and Chapman, 1983). The most extensive kelp genetics experiments have been conducted by Chinese workers (Fang *et al.*, 1962a/b, 1963, 1965, 1966, 1978, 1979; Fang and Li 1963, 1965; Fang and Dai, 1980; Fang, 1984) in attempts to generate new strains with higher temperature tolerance and increased iodine content. Only attempts at the latter were successful (see Brinkhuis *et al.*, 1987 for review).

Crossing experiments offer a means of assessing differentiation when correlated to specific environmental differences. However, interpretation of such experiments is not straightforward. Genetic differentiation may evolve without affecting compatibility, and intersterility does not necessarily indicate accumulation of a large number of genetic differences (Innes, 1984). Recent studies have found that greater incompatibility is associated with greater geographical separation (Rueness, 1973; Müller, 1979; West *et al.*, 1978; Guiry and West, 1983), but there are numerous examples

that have demonstrated genetic differentiation among populations separated by only short distances (e.g., Russell and Morris, 1970; DeSilva and Burrows, 1973; Espinoza and Chapman, 1983; Innes, 1983).

In this paper, we review aspects of morphological variation in certain *Laminaria* species, variation that has complicated the species concept in this genus. This variation also permits a basis for selection protocols, as certain morphological attributes are considered desirable for particular mariculture objectives. For example, plants producing wider or longer blades might be required if the objective is to maximize biomass production. Similarly, plants with longer stipes might be desirable if the objective is to maximize biomass of stipe material that generally has higher alginic content. Selection criteria also apply to determining the most appropriate conditions for obtaining the best growing materials. Our review, then, is followed by experiments we have conducted following these guidelines.

### **Taxonomic characteristics of North Atlantic *Laminaria* species**

The genus *Laminaria* inhabits temperate and polar waters in the northern and temperate waters in the southern hemispheres. It is presently believed that the genus originated in the northern Pacific (Lüning, 1985). The Pacific is characterized by greater numbers of genera and species of Laminariales than is the Atlantic. This is probably due to repeated displacements of the marine flora towards the south during the cold periods of the Pleistocene (Hoek, 1984; Yarish *et al.*, 1984; Lüning, 1985). Development of cold water-resistant algae probably occurred during the Miocene, 21 million years ago. Cooling of the earth in the late Tertiary forced the newly-formed cold water species in a circumpolar route along the still ice-free coasts of the Arctic into the North Atlantic (Simmons, 1906; Lüning, 1985). This paleo-history has been linked to plate tectonic patterns occurring during the Tertiary (Lüning, 1985).

The laminarian sporophyte is in three distinct parts: holdfast,

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stipe and lamina. The lamina, or blade, of *Laminaria* may be simple and undivided (Section Simplicis), or digitate (Section Digitatae). The primary growth is intercalary, occurring in the transition zone between stipe and lamina. Some morphological characteristics used to distinguish species within the genus (mucilage duct anatomy, stipe anatomy and bullations in lamina) are now known, or suspected to be highly variable and subject to change in response to environmental differences (see Kain, 1979 for review). In the Section Digitatae from the North Atlantic, Sundene (1959, 1964) found that the taxa *Laminaria stenophylla*, *L. intermedia*, *L. platymeris*, and *L. cucullata* were merely environmentally induced forms of the highly variable *L. digitata*. Similarly, Wilce (1959) found *L. cuneifolia* and *L. groenlandica* in the Section Simplicis were identical. Our detailed analysis of pertinent *Laminaria* literature is described below.

#### Mucilage ducts as a taxonomic character

The presence or absence of mucilage ducts was proposed by Fritsch (1945) as a character to delineate *Laminaria groenlandica* Rosenv. (ducts in laminae and stipes), *L. saccharina* (L.) Lamour. (ducts only in laminae) and *L. agardhii* Kjellm. (no ducts). Wilce (1965) doubted the validity of mucilage ducts as a taxonomic character, particularly because of the tendency for duct occurrence and size to increase with latitude (decreasing temperature). In contrast, Burrows (1964) found that duct occurrence and size increased with increasing temperature (implying decreasing latitude) after a comparative culture study of *L. saccharina* and *L. agardhii* from Europe at 5 and 10°C. However, Wilce (1965) argued that the ductless plants (*L. agardhii*) Burrows found at 5°C were, in fact, a ductless form of *L. saccharina*, because Burrows' use of 5°C did not approach the cold temperatures of Arctic waters, and because the west and northwest coasts of Norway (Burrows obtained plants from Spitzbergen) are still somewhat under the influence Gulf Stream water, an environment no more severe than that of some areas of North America where *L. saccharina* (= *L. agardhii*) is dominant.

Thus, *Laminaria saccharina* has three ecotypes (Wilce, 1965) based on mucilage duct anatomy. Wilce (1965) concluded that there were only three species in the Section *Simplices* from the North Atlantic. These are *L. solidungula* J. Ag. (with a distinct discoid holdfast, whereas all other species have haptera), *L. saccharina* and *L. longicuris* de la Pylaie. According to Wilce (1965), *Laminaria* at its southern distribution should not have ducts. We have recently determined that plants in Long Island Sound may exhibit ducts at various times, but there is no apparent relationship to taxonomic affinity (Levine, Collantes and Brinkhuis, unpublished data).

*Laminaria longicuris* is characterized by being the only species in the genus having a long and hollow stipe (Wilce, 1965). This species was also described as having three ecotypes based on duct anatomy: *L. longicuris* with ducts in laminae and stipes from the Northwestern Atlantic, *L. faeroensis* Børgesen from the Northeastern Atlantic with ducts only in laminae, and an unnamed ecotype without ducts described from the Western Atlantic. Based on the invalidity of duct anatomy as a taxonomic character, Kain (1976) suggested that *L. faeroensis* be placed within *L. longicuris*. Wilce (1965) proposed that all hollow-stiped plants be referred to as *L. longicuris* and all solid-stiped as *L. saccharina* in his revision of the northern Atlantic *Simplices* section, since mucilage ducts could be found in either species.

Chapman (1975) conducted crossing experiments with three "species" and examined the mucilage duct heritability component using materials from Nova Scotia (no mucilage ducts present) and Newfoundland (both with and without ducts in blade or stipes). Various combinations of ducts were present in stipes and blades of Newfoundland populations. There were no discontinuities in the series of biotypes. There was a large environmental component in the expression of phenotypic variance, and there were no internal reproductive barriers between any of the anatomical types. Thus, he concluded that this character does not conform to the biological species concept. Nova Scotian plants never exhibit mucilage ducts, and this character breeds true. These breed freely with plants from Newfoundland showing canals, but the

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heritability component of the phenotypic variance was low. The regression of offspring measurements on parental mean measurements gives an estimate of heritability. Heritability is the ratio of additive gene variance to total phenotypic variance- a low heritability indicates high environmental component in phenotypic variance observed. Chapman suggests that the two "species" be given ecotypic status. An ecotype is the product arising as the result of genotypic response of a species to its particular habitat (Turesson, 1922) and this status implies interfertility. Recently, Müller *et al.*, (1985) have found that pheromones in the Laminariaceae are identical, suggesting a possible mechanism for interfertility in *Laminaria*. Chapman concluded that *L. longicruris*, and *L. saccharina* (= *L. agardhii*) are synonymous and should be placed within the taxon *L. saccharina*. Interestingly, some workers from Nova Scotia still refer to their local form as *L. longicruris*.

In crosses between European (with ducts) and Nova Scotian (ductless) strains, Lüning *et al.* (1978) found that hybrids all lacked ducts. However, Bolton *et al.* (1983) reported that hybrids produced from crosses of ductless Nova Scotian and ducted Brittany (France) plants exhibited ducts on two separate occasions. They also reported that hybrids from crosses of Helgoland (Germany) and Nova Scotia material exhibited ducts in 1980 experiments, but not in 1981. They suggested that these latter inconsistencies may have been due to differences in maturity of the plants, but came to the same conclusion as Chapman (1975) that the presence or absence of mucilage ducts is largely environmentally induced. Which environmental variables effect exhibition of ducts and their functional role is unknown (Lüning *et al.*, 1978).

#### Stipe anatomy as a taxonomic character

Stipe anatomy and morphology in kelps are important characters, not only for taxonomic criteria, but for commercial applications. For example, Chinese mariculturists have bred lines of *Laminaria japonica* with shorter stipes to minimize stipe biomass and increase blade production (they eat blade tissues, not the stipe). On the other hand, the algininate content of stipes is roughly twice



that of laminae on a dry weight basis (Brinkhuis and Pabst, unpublished data) and use of *Laminaria* for the alginate industry could exploit strains or species with longer or more solid stipes. The increasing emphasis of Chinese kelp cultivation for the production of alginates (1.6 million wet tons of kelp and 7,000 tons of alginate were produced in 1986- Tseng, personal communication) may redirect efforts to producing varieties with longer, more valuable stipes.

The published distribution of hollow-stiped plants (in Kain, 1976) is from Cape Cod to Ellesmere Island (Taylor, 1957), west Greenland (Lund, 1959), Iceland (Jonsson, 1912), the Faeroes (Børgesen, 1903-1908; Irvine, 1982; Price and Farnham, 1982; Tittley *et al.*, 1982) and the Shetland Isles (Irvine *et al.*, 1975). However, Parke (1948) encountered plants with hollow stipes in Argyll, Scotland. Kain (1976) noted Parke's observation, but Parke (1948) attributes the finding to the species *Laminaria saccharina*. Kain did not compare any of the features between populations at Devon (short, solid stipe) and Argyll (long hollow stipe). Was Parke's record *L. longicuris*? It appears so. Parke (1948) concluded that the hollow stipe is produced in summer- or autumn-developed plants because of rapid growth in length and thickness during the first growth period and, as a result, the medullary tissue does not keep pace with that of the cortical tissue so that air pockets develop in the central portion of the stipe. If this is the case, then why don't *L. saccharina* plants produce long hollow stipes? What other environmental conditions could induce this phenomenon?

The use of the hollow stipe as a taxonomic character was first questioned by Mann (1971), who had difficulty separating *Laminaria longicuris* from *L. agardhii*. Chapman (1973) shared similar doubts when he found a clinal relationship of stipe length and hollow condition with environmental conditions. According to Chapman (1974), these two taxa are conspecific by the following reasoning:

1. no discontinuities in the variation of phenotypic characters previously used to separate the taxa;

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2. the two species are fully interfertile and produced fertile hybrids; and

3. parents of each species produced at least some offspring resembling the other.

However, our analysis of Chapman's (1974) results found the following causes for concern regarding his interpretations:

1. both stipe length and hollow diameter exhibit considerable variation at both exposed and sheltered sites that would obscure statistically significant differences. Some of the data also suggest seasonal and substratum effects on stipe length;

2. there is a strong genetic component controlling stipe length and hollowness, explaining the lack of change in specimens transplanted from exposed (normally short, solid stipes) to sheltered (normally long, hollow stipes) locations;

3. no transplants or outplants of materials were conducted before the critical stipe length increase period (spring);

4. six parents were selected from an exposed and seven from a sheltered site resulting in production of 13 full-sibling families. There is no indication as to how crosses were made (i.e., random matings, self- crosses, or reciprocal male / female crosses);

5. pooling all 13 families showed that there was significant among-family variation for the stipe length character. However, there was also significant variation among families from the sheltered and exposed sites. The latter means one can not determine the genetic component of variability;

6. stipe morphology and measurements were not presented.

Further, there is apparent confusion concerning short solid, short hollow, and long hollow stipes in Chapman (1973, 1974).

No short, hollow-stiped mature forms occur in the *L. saccharina* or *L. longicuris*. Børgesen's materials from the Faeroes did include short (10-15 cm), hollow stipes in *L. faeroensis*. Kain (1976) stated "inflation of the stipe is not solely the result of continued growth in length and thus diameter, but a particular event which occurs after the stipe is about 0.4 m long". She also presents three hypotheses with regard to stipe morphology:

1. *L. saccharina* and *L. longicuris* are distinct species;
2. hollow stipes are produced by sheltered conditions and low temperatures, but similar conditions exist in the fjords of Norway where the species has not been recorded; and
3. one species is involved as in (2) above, but there has been an inflow of genes into the area resulting in long hollow stipes under fairly sheltered conditions.

A number of studies have reported crossing *Laminaria saccharina* with *L. longicuris* (Lüning *et al.*, 1978; Bolton *et al.*, 1983). These crosses have been made between European and Pacific representatives of *L. saccharina* and Canadian specimens of *L. longicuris* using both male and female gametophytes of each species for reciprocal crosses (Table 1). Lüning *et al.* (1978) produced hybrids from *L. saccharina* (Helgoland, Isle of Man) X *L. longicuris* (Nova Scotia) crosses, with the exception of a female *L. longicuris* X male *L. saccharina* (Isle of Man) cross. Maximum stipe lengths of all crosses conducted in the above experiments were 10 cm. Bolton *et al.* (1983) produced successful hybrids from *L. longicuris* X *L. saccharina* (Brittany and Helgoland) crosses with stipe lengths similar to those reported by Lüning *et al.* (1978). *L. longicuris* X *L. longicuris* also produced short solid stipes. All of these experiments were conducted in holding tanks or in the sea at Helgoland, Germany. Are conditions there not conducive to stipe elongation and hollow development? Lüning (pers. comm.) suggested that perhaps the outplants were too young to exhibit hollow or long stipes. Interestingly, no

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crosses between *L. saccharina* and *L. longicuris* from the western Atlantic Ocean have been reported by Lüning and Bolton.

Table 1. Origin of parent *Laminaria saccharina* (L.s.) and *L. longicuris* (L.l.) sporophytes.

Locality	Species	Morphology
Nova Scotia	L.l.	Bullate wide blade, long hollow stipe, no mucilage ducts
Helgoland	L.s.	Smooth narrow blade, short solid stipe, mucilage ducts in blade
Isle of Man	L.s.	Bullate narrow blade, solid short stipe, mucilage ducts not examined
Brittany	L.s.	same as for Isle of Man
Vancouver	L.s.	same as for Isle of Man

Chapman (1974) indicates he made crosses between 3 hollow-stiped and 3 solid-stiped plants, but states "plants with long, hollow stipes and those with short, hollow stipes belong to the same biological species". No data from these crosses are presented. Furthermore, all of the crosses reported thus far have been made with materials collected from near the middle of the latitudinal distribution ranges for the genus. Lüning (pers. comm.) has urged that crosses between *Laminaria longicuris* and *L. saccharina* from the northwest Atlantic be performed to clear up the picture for the eastern North America coast.

Chapman (1978) summarized a variety of hybridization studies with kelps and suggested that crossability tests are an effective way to evaluate genetic and taxonomic affinities of seaweeds. The primary conclusion from these studies is that where species are easily distinguished morphologically, there is usually reproductive isolation while morphologically confused species are interfertile (Mathieson *et al.*, 1981). However, Bolton *et al.* (1983) suggested

that great care should be exercised in assessing the value of hybridization experiments in the taxonomy of the Phaeophyta. The experiments of Lüning *et al.* (1978) and Bolton *et al.* (1983) have shown that isolates of *Laminaria* from different geographical regions and different oceans hybridize both within and between species, whereas a sterility barrier has been demonstrated between some trans-Atlantic members of the Simplicies (as noted above). The fact that Laminariaceae share a common sex pheromone (Müller *et al.*, 1985) is further reason to expect interfertility. Sanbonsuga and Neushul (1978) demonstrated interfertility in float-bearing kelps between genera, resulting in intermediate morphological forms. Stace (1980) remarks "in a great many groups of plants morphologically distinct species capable of hybridizing with others are the usual situation, and cannot be considered in any way abnormal".

While Chapman (1978) suggests that crossability tests are effective, one must have some reservations about results reported in Chapman (1974), Lüning *et al.* (1978) and Bolton *et al.* (1983) due to the failure of some crossability experiments, some of which were not complete designs. Percent fertility of the offspring was not assessed, F<sub>2</sub> generation crosses were not conducted, and no backcrosses with parents were carried out.

While phenetic variation in stipe morphology has been documented in *Laminaria longicruris* by Chapman (1973), Bolton *et al.* (1983) found no evidence that *L. saccharina* from the Isle of Man, Brittany, Helgoland, or the northeast Pacific can be environmentally induced to produce long hollow stipes. Thus, they concluded that the ability to produce these characters under particular conditions appears to be genetically determined. This is in contrast to data in Gerard and Mann (1979) suggesting that stipe length is inversely related to exposure and water movement. However, the relationship of stipe length to exposure is not discussed and is far from clear. Druehl (1967) noted that *L. groenlandica* stipe length was shorter in more exposed sites, and distinguishes this species from *L. saccharina* in the Pacific. However, Wilce (1965) placed the British Columbian *L. groenlandica* in synonymy with *L. saccharina*. No one has reported crossing *L. saccharina* with this

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"*L. groenlandica*", but Bolton *et al.* (1983) did use material from the Pacific where the latter is presumed to occur, according to Druehl (1967). Bolton *et al.* (1983) consider this species as synonymous with *L. saccharina*, citing Wilce (1965). Wilce (pers. comm.) doubts that the Vancouver *L. groenlandica* has any relationship to the material from the West Greenland area described by Rosenvinge. The Vancouver material reportedly can produce a digitate blade (not caused by physical ripping of the blade, Druehl 1967) and its taxonomic position still needs to be established (Wilce, pers. comm.). Setchell and Gardner (1925), unlike Druehl, recognized that their *L. cuneifolia* were different from the Greenland type-material. They state that *L. cuneifolia* from Greenland seems to be a different species and is closely related to *L. groenlandica* described by Rosenvinge. Recall that Wilce (1959) placed *L. groenlandica* and *L. cuneifolia* from the Atlantic in synonymy, and subsequently combined *L. groenlandica* and *L. agardhii* into *L. saccharina* (Wilce, 1965).

#### Bullations as a taxonomic character

Bullations are indentations that appear seasonally in some species of *Laminaria*. Their physiological significance has been suggested to be related to increasing lamina surface area for absorption of nutrients, aiding in the disruption of boundary layers to enhance nutrient uptake under conditions of low water flow over lamina. From a maricultural standpoint, production of increased blade area through bullation formation means more biomass for harvesting.

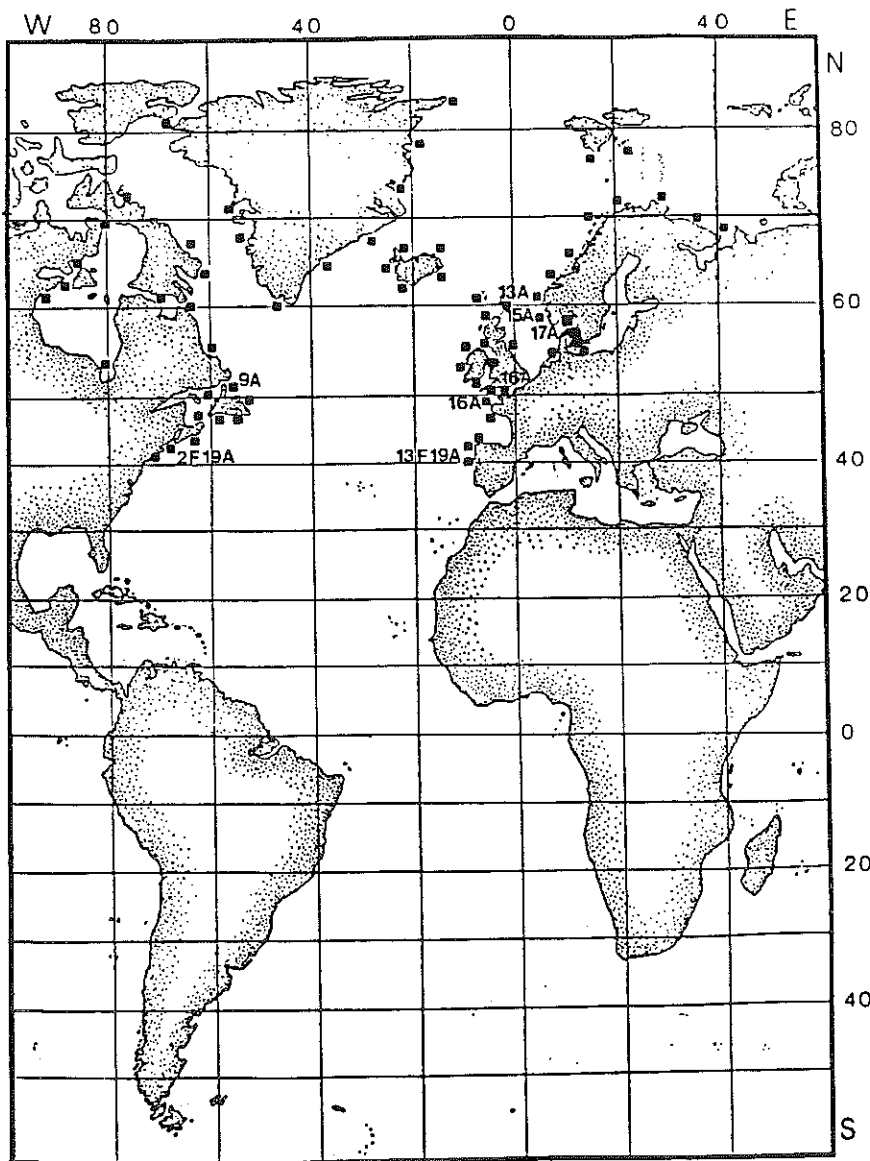
What conditions induce the development of bullations on the laminae of some Simplicies laminarians? Setchell (1900) wrote, "In *Laminaria agardhii* and *L. saccharina* of the New England coast, the writer has found that the summer form is usually ample, with ruffles and rows of indentations fully developed; but in August, a change takes place and this summer blade is replaced by a winter blade which is perfectly plane and devoid of both these features. Again, in the spring, this plane blade is replaced by the ruffled and indented form".

This same phenomenon was noted by Lüning *et al.* (1978) with crosses involving *Laminaria saccharina* from Helgoland and *L. longicuris* from Nova Scotia, and in hybrids (Bolton *et al.*, 1983) produced by crosses between *L. saccharina* from Vancouver and Helgoland and between *L. longicuris* (Nova Scotia) and *L. saccharina* (Helgoland). In the latter studies, pure strains from Vancouver and Nova Scotia produced bullations year-round. In European *L. saccharina*, the presence or absence of bullations appears to be a fixed genetic trait with the occurrence of this character being dominant (Lüning, 1975; Lüning *et al.*, 1978). Bolton *et al.* (1983) point out that in other species of non-digitate *Laminaria* the inheritance of this trait is more complicated than that found in Europe. These authors all suggest the ability to produce bullae seasonally is controlled by some environmental aspect. Our own work (Brinkhuis and Yarish, unpublished data) further supports that contention. Bullae are initiated in December and initiation ceases in late May.

### **Biogeography of *Laminaria***

To characterize potential genetic morphological differentiation in *Laminaria*, we can first examine its biogeography over a large scale (Egan and Yarish, 1988). We have synthesized the stipe morphology observations and plotted the biogeographic distribution of *L. saccharina* (Fig. 1) and *L. longicuris* (Fig. 2) in the North Atlantic and Arctic Oceans. The figures also include mean sea surface temperature (°C) in February (F) and August (A). The distribution data is based on the following sources: Batters (1889), Børgesen (1903-08), Christensen and Thomsen (1974), Guiry (1978), Hoek (1982a,b), Hylander (1928), Irvine (1974), Jonsson (1912), Kain (1976), Kylin (1947), Lee (1980), Lund (1959), Lüning (1975, 1985), Lüning *et al.* (1978), Parke (1948), Parke and Dixon (1976), Taylor (1957), and Turner (1802). Ocean isotherms were derived from Sverdrup *et al.* (1942). Wilce (1965) indicated that the southern limit of *Laminaria* distribution in the western Atlantic is Long Island, New York. However, Egan and Yarish (1988) have recently reported discovery of a deep-water population of *L. saccharina* off the coast of New Jersey.

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*Figure 1. The reported distribution of Laminaria saccharina in the North Atlantic. Sources are those listed in Egan and Yarish (1988). Additional sources are referenced in the text.*



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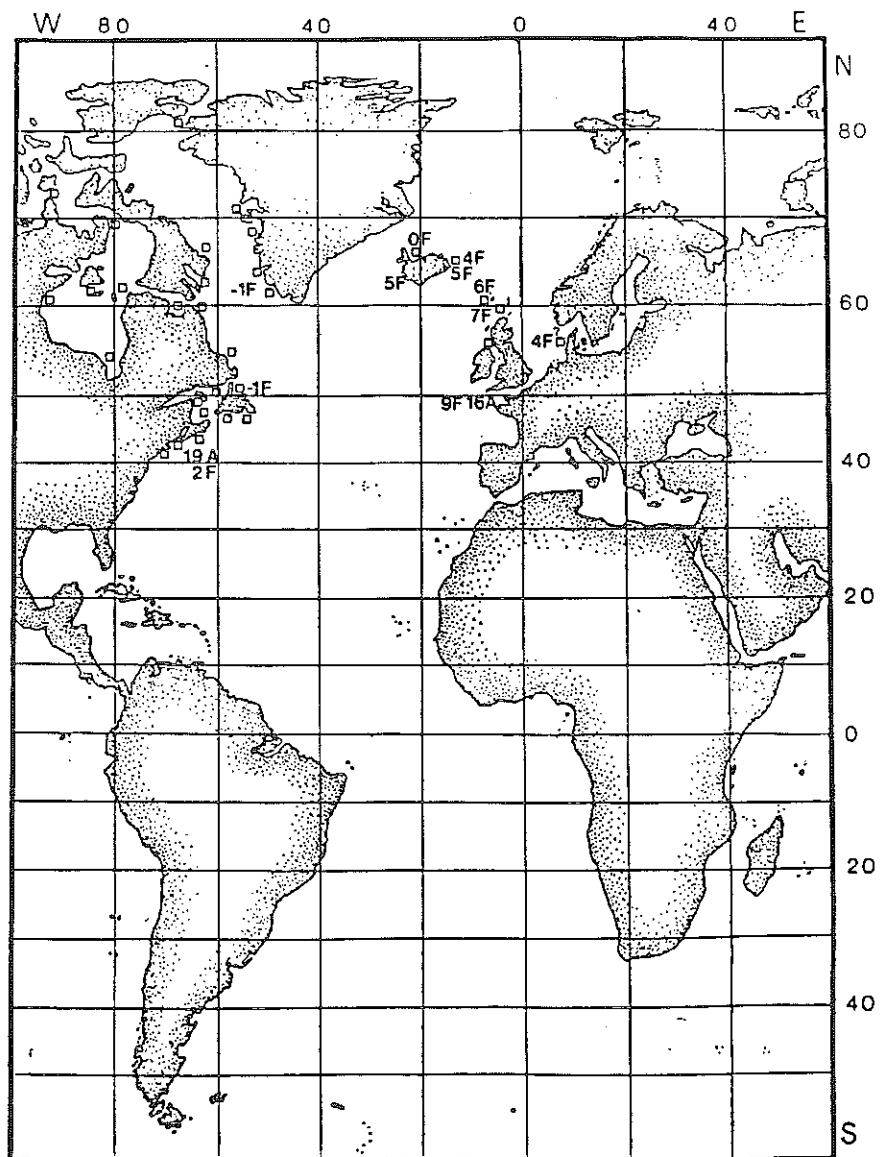


Figure 2. The reported distribution of *Laminaria longicuris* in the North Atlantic. Sources are those listed in Egan and Yarish (1988). Additional sources are referenced in the text.

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On a small scale, we can examine the distribution of *Laminaria* in Long Island Sound. The importance of Long Island Sound to an analysis of taxonomic variability is that it is the only documented location where clearly identifiable and apparently segregated populations exist near each other. Our observations on distribution of these two entities in Long Island Sound, using stipe morphology, are shown in Fig. 3. Two species of *Laminaria* are found on Long Island, *L. saccharina* and *L. digitata*. *L. digitata* is found at Montauk Point only (see Fig. 3). *L. saccharina* is found primarily along the north shore of the Island wherever cobble or rock deposited during the last glaciation occur; it also occurs at Montauk Point. Plants were found in 1969 by Yarish as far west on the south shore as the jetty at Shinnecock Inlet (unpublished data); Liddle (pers. comm.) reported its continued presence there in the winter of 1985. Populations are rarely found at depths greater than 5 m along the north shore. All of the plants have stipe lengths and morphology typical of *L. saccharina*. The period of maximum stipe elongation is spring and stipes reach a mean length of 4.5 cm by July (Lee and Brinkhuis, 1986). Occasionally, longer-stiped plants can be found at Montauk Point, a more exposed environment than other north shore locations. Some plants with stipes up to 60 cm long have been collected, but these have not been observed to be hollow.

Figure 3 shows that *Laminaria longicruris*-type plants have been observed as far west as the Thimble Islands (Branford, Connecticut) in water 5 m deep. *L. digitata* only penetrates as far west as New Haven, CT, or, in depths of 7 m. Significant stands of *L. saccharina* type plants occur as far west as Stamford, Connecticut, in water depths rarely exceeding 4 m.

#### Physiological differentiation

Several studies have pointed out that physiological ecotypes of *Laminaria* exist along the Atlantic coast of North America. Gagné *et al.* (1982) reported that there are seasonal differences between some kelp populations, i.e. ones from nutrient-poor and others from nutrient-rich environments. If nitrate was available in high

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concentrations during winter and spring, maximum growth occurred at that time of year. Findings of these workers suggested ecotypic differentiation in nutrient/growth interactions for *L. longicruris*. These authors reported that accumulation of large tissue nitrate reserves was unnecessary in nitrate-rich environments.

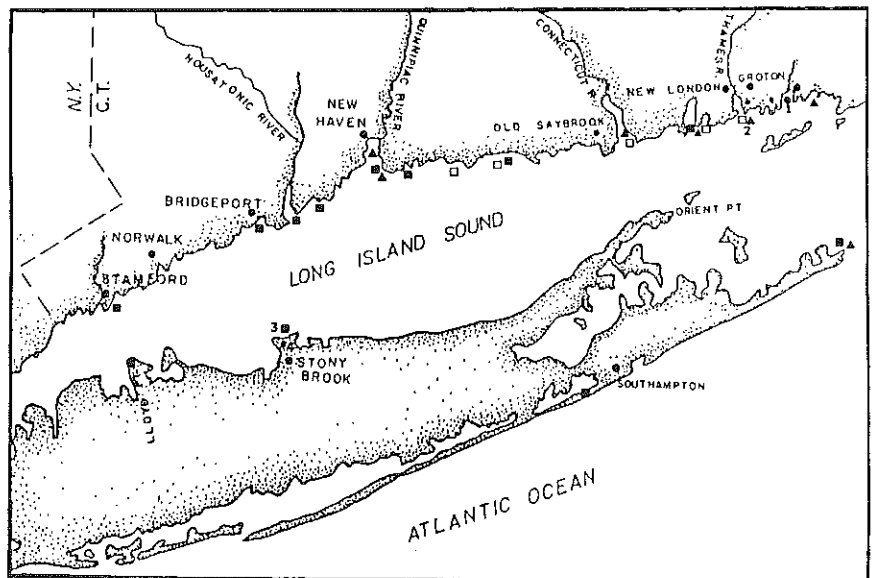


Figure 3. The reported distribution of *Laminaria saccharina* (solid squares), *L. longicruris* (open squares) and *L. digitata* (solid triangles) in Long Island Sound. Sources are those listed in Egan and Yarish (1988).

Other types of differentiation in *Laminaria* have been reported as well. Gerard and co-workers have described ecotypic differentiation in light/photosynthesis interactions (Gerard, 1988) and photosynthesis/temperature interactions (Gerard and Du Bois, 1988) of sporophytes. Yarish and Egan (1987) compared growth of nine microsporophytic strains at 15°C and noticed significant differences in growth rate after 43 days. Subsequently, Yarish and Egan (1989) demonstrated that self-crosses from 15 additional gametophytic isolates produced microsporophytes with significantly different thermal tolerances. A thermal gradient was created by utilizing temperature gradient plates (Yarish *et al.*, 1979; Yarish and Edwards, 1982; Lee and Brinkhuis, 1988) at an irradiance

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optimal for microsporophyte production. Sporophyte growth was optimal at 17°C for 12 strains and at 19°C for the remaining three strains after 38 days. Lüning *et al.* (1978) reported that there are thermal differences among populations of *L. saccharina*.

#### Materials and Methods

A unique combination of culture facilities at the University of Connecticut at Stamford (UCONN) and the State University of New York at Stony Brook (SUSB) exists. At UCONN, several environmental growth chambers were used to conduct culture studies of gametophytic and juvenile sporophytic plants. SUSB also has growth chambers for gametophyte cultivation and a flow-through marine greenhouse for maintaining large sporophytes (see Brinkhuis and Hanisak, 1982).

Field observations on *Laminaria* populations have been conducted for several years on the Connecticut and Long Island sides of Long Island Sound. For the sake of brevity, the reader is referred to several recent publications that describe the approaches taken to studying growth and reproduction in these populations (Brinkhuis *et al.*, 1983, 1984; Lee and Brinkhuis, 1986; Yarish and Egan, 1987; Egan and Yarish 1988; Yarish and Egan, 1989).

Gradient plate studies have been conducted on *Laminaria saccharina* (Lee and Brinkhuis, 1986, 1988) and on *L. longicuris* (Yarish and Egan, 1988; Egan *et al.*, 1989). For a review of methods, see Lee and Brinkhuis (1988) and Egan *et al.* (1989).

We also conducted reciprocal crossing experiments between *Laminaria saccharina* from Long Island and *L. longicuris* from Connecticut. Meiospores from a single isolate of each species were raised to the immature gametophytic stage, at which time cultures were placed under red light to inhibit sexual development and reproduction. Gametophytes were then sexed and separated for continued vegetative growth under red light, producing masses of male and female gametophytes. In February (1988), these masses were gently ground in a mortar and pestle, and crosses between males and females from each species were placed under white light, which stimulated reproductive development. When

sporophytes became evident, cultures were transferred to 4-liter glass jars and maintained in an incubator at 15°C until mid-March, 1988. At that time, sporophytes were transferred to the greenhouse at SUSB. We recorded growth rates by measuring blade length changes over two week intervals, as well as using the hole-punch technique (Parke, 1948). Measurements of stipe length and blade width were also recorded bi-weekly.

## Results and Discussion

### *Field cultivation observations*

Growth and reproduction of *Laminaria saccharina* has been extensively studied at one site, Crane Neck, NY, over a several-year period (Fig. 4a). The period of maximum blade elongation occurs in April-May when water temperatures range from 10 - 15°C. Meristematic growth virtually ceases during July as water temperatures reach 18 - 20°C. Severe distal erosion follows, and most of the adult population disappears during August (Brinkhuis *et al.*, 1983, 1984; Lee and Brinkhuis, 1986). Warm summer seawater temperatures result in growth reduction before the plants exhaust internal nitrogen reserves (Brinkhuis and Charnon, unpublished data), unlike further north where either limiting irradiance or nitrogen supply limits growth (e.g., Chapman and Craigie, 1977; 1978; Chapman and Lindley, 1980).

*Laminaria saccharina* on Long Island primarily behaves as an annual plant. Reproductive activity in sporophytes is maximal in autumn and April-July, when the greatest number of plants are fertile (Fig. 5a). However, fertile plants may be found throughout the year, except August and September when few adults are present. There is some year-to-year variability in the proportion of the population that becomes reproductive, but the pattern from one year to another is similar. Meiospore release and reproductive success are maximum in the spring (Lee and Brinkhuis, 1986). During late September, small sporophytes may be found at Crane Neck. Thus, Lee and Brinkhuis (1986) believed that the superior reproductive activity period in April-May was responsible for the major recruitment in the population. During the April-May period,

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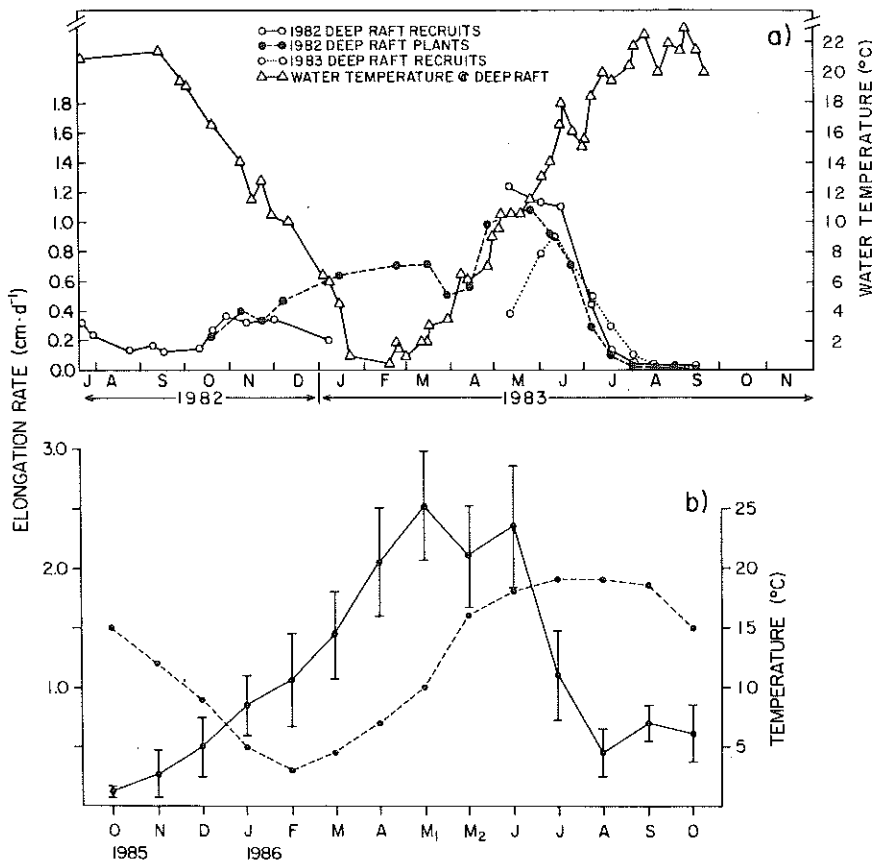


Figure 4. Seasonal variations in meristematic growth rates (means  $\pm$  S.D.,  $\text{cm d}^{-1}$ ) and water temperatures in Long Island Sound for *Laminaria saccharina* (a) and *L. longicuris* (b).

juvenile sporophytes resulting from earlier reproduction may be found, but these don't survive summer conditions. Thus, it was believed that the population "over summers" in the gametophytic stage. Other workers have found that kelp gametophytes have higher temperature survival limits than sporophytes (e.g., Bolton *et al.*, 1983).

Recent studies (Lee and Brinkhuis, 1988) have shown, however, that the annual recruitment pattern does not involve an over-summering phenomenon. The autumn sporulation results in the

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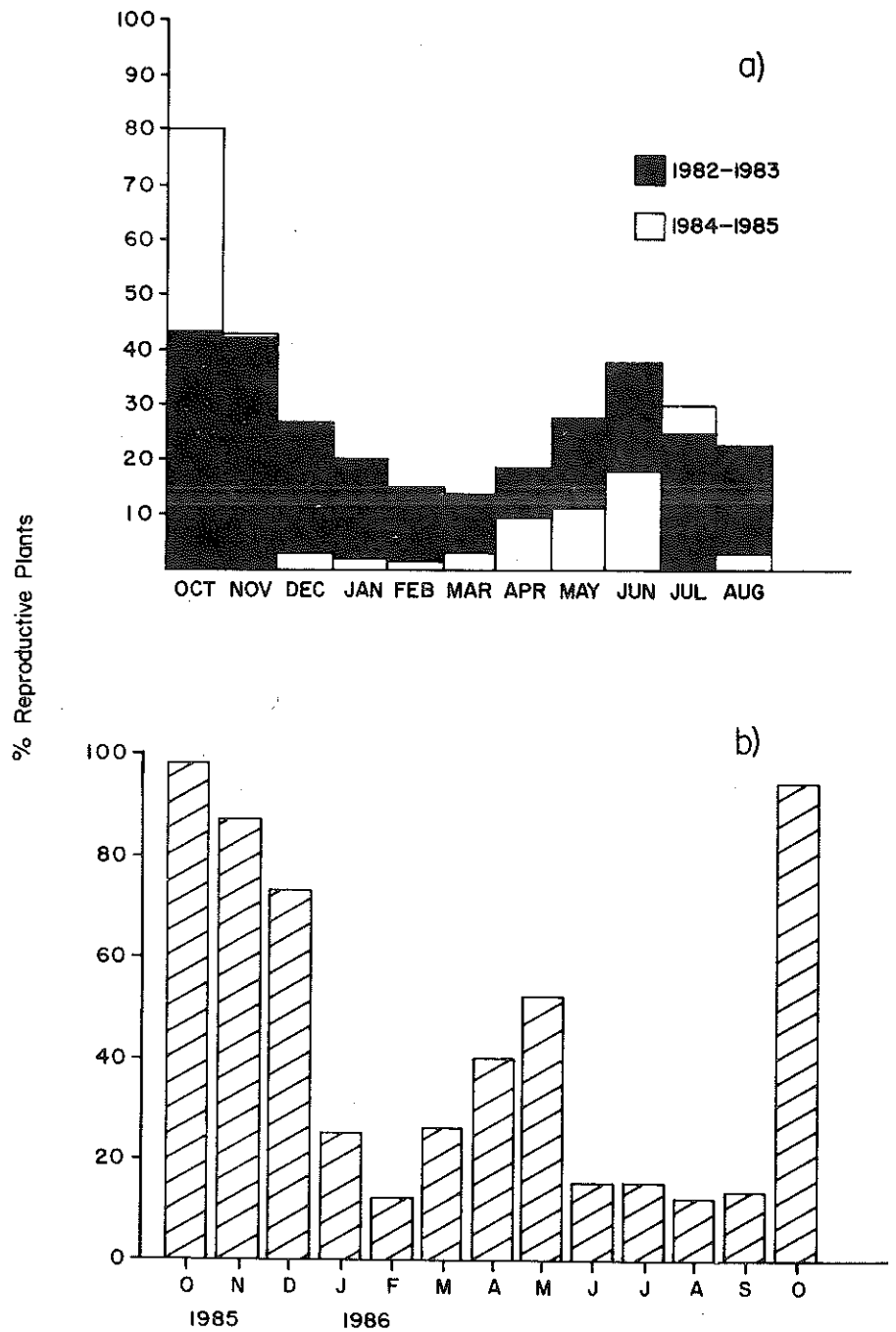


Figure 5. Per cent reproductive sporophytes with blades > 60 g possessing sorus tissue for *Laminaria saccharina* (a), *L. longicuris* (b). Data derived from tagged populations in Long Island Sound.

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only offspring that survive the summer conditions as mature sporophytes. While tissue erosion is significant and the majority of the mature plants succumb to high water temperatures, some sporophytes survive. These now small sporophytes (due to blade erosion) have a small meristematic region that begins to grow again in September when water temperatures fall. The blades that form when growth initiates have a wide, short segment of new tissue, to which are attached remnants of the old blades. These older tissues rapidly become reproductive in early-October, perpetuating the annual pattern. Interestingly, the superior characteristics of the spring sporulation (fecundity, growth, etc.) are of little consequence to the survival of the species in Long Island populations.

Growth and reproduction of *Laminaria longicruris* has been intensively studied at one site, Black Ledge (Groton, CT) over the last two years (Fig. 4b). The period of maximum stipe elongation is spring and stipes reach a mean length of 120 cm by June (Egan and Yarish, 1988). These plants all exhibit hollow stipes by spring, in an area of moderate exposure. The period of maximum blade elongation is April-May when water temperatures range from 8 to 12°C. Meristematic growth decreases during July when water temperatures reach 16 - 17°C (Yarish and Egan, 1987). Sporophyte reproductive activity is maximum in October, when the greatest number of fertile plants are found; another peak occurs in April-May (Fig. 5b). Meiospore release and subsequent reproductive success following gametogenesis also is maximum at this time. *Laminaria longicruris* in eastern Connecticut (Black Ledge) behaves as a perennial plant, whereas *L. saccharina* in western Connecticut (Stamford) behaves as an annual in a manner similar to that on Long Island (New York).

The annual patterns of growth and reproduction are very similar for both *Laminaria saccharina* in New York and *L. longicruris* in Connecticut. Seawater temperatures at the eastern Connecticut site appear to be cooler, and this probably accounts for the perennial life history of *L. longicruris*. Here, greater numbers of adult sporophytes survive during summer (Yarish and Egan, 1989).



### *Tank cultivation observations*

At Stony Brook, we conducted experiments aimed at identifying fast-growing individuals that could be used to establish new strains. An extensive data base exists for measurements of *Laminaria* plants from many areas of the world, and this could be used to make comparisons. However, size-dependent growth rates complicate such comparisons. It is, therefore, essential that plants which are growing fast relative to other members of their size class be identified. Attempts to describe size-dependent growth rates have resulted in several biomass-growth models for the Laminariales (e.g. Mann and Mann, 1981; Gendron, 1985). A major assumption of these models is that size-dependent growth remains the same throughout the year. In other words, the size-growth relationship for a given size class remains constant.

We maintained a population of 150 plants in a greenhouse and monitored growth and morphology between December, 1984 and April, 1985. The plants were harvested from a natural population at Crane Neck, NY. Figure 6 depicts a time-series of growth rate plotted against total blade length. During December, there is a strong linearity of size-dependent growth rates. In January, the relationship is still linear, but the slope has decreased dramatically. Growth rate decreased uniformly across all sizes. At this time, water temperature is near 0°C, while for December it was 6 - 10°C. Irradiance also decreases to its yearly minimum in January. By early February, the slope of the relationship had increased again. Growth rate had reached a maximum at the end of April. These data show that the size-dependent relationship is not constant over time and the previous models are not applicable to Long Island Sound populations. The examples shown provide some indication of non-linear relationships between blade length and growth rate; a point is reached beyond which increased size is not accompanied by an increase in growth rate. Gendron's (1985) data also exhibit non-linear relationships, but her treatment ignored this.

The relationship between blade length and width also is non-linear. Figure 7 shows this relationship in December for blade width 10 cm above the stipe and widest blade dimension. Note the

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BLADE LENGTH vs MERISTEMATIC GROWTH

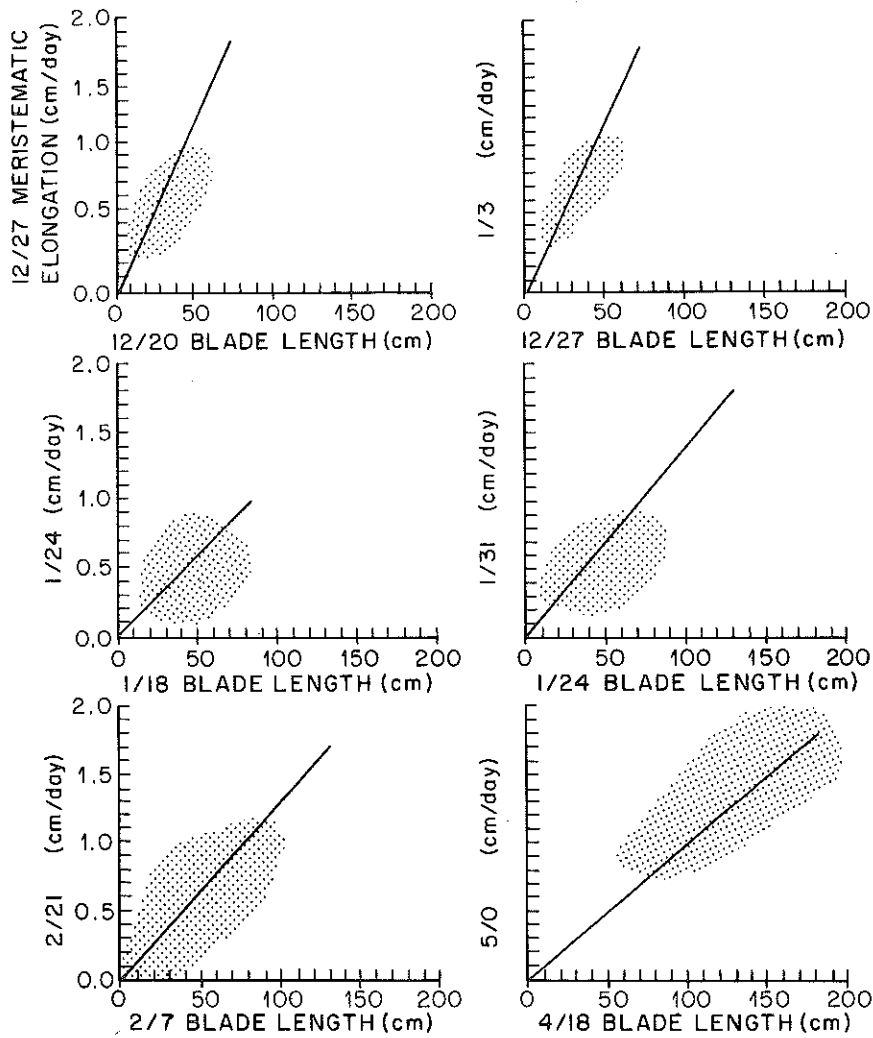
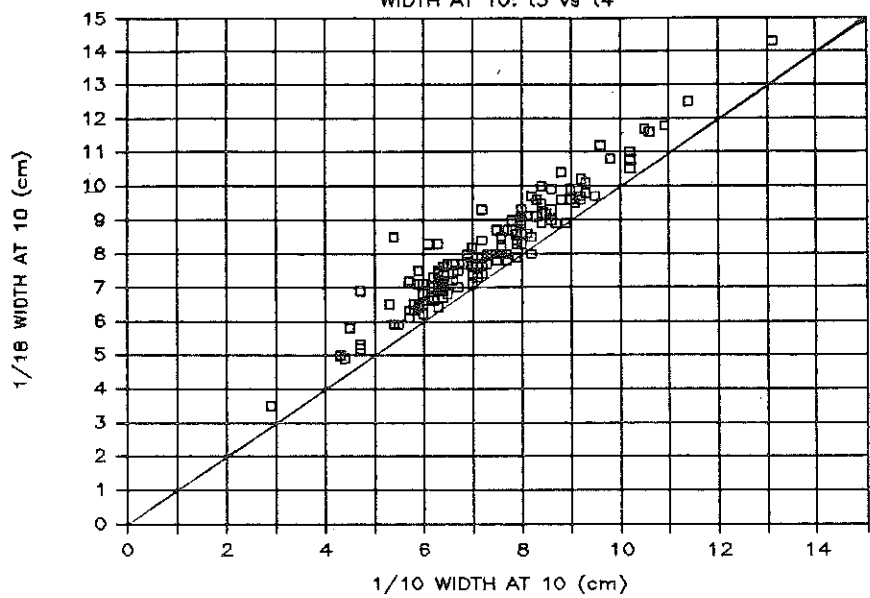


Figure 6. Time series of plots of meristematic growth rates of *Laminaria saccharina* versus total lamina length from a population of 150 plants maintained in the greenhouse culture. Plants were harvested from a natural population at Crane Neck, New York. Note the size-dependent relationship is not constant over time.

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### ESL TANK POPULATION

WIDTH AT 10: t3 vs t4



### ESL TANK POPULATION

WIDTH AT 10: t11 vs t12

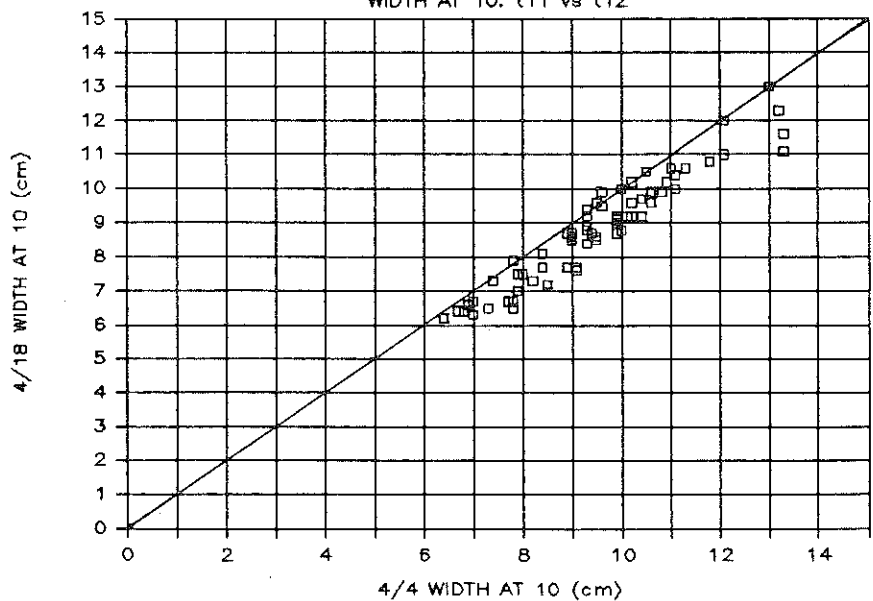


Figure 7. Plot of blade length (cm) versus lamina width (cm) of *Laminaria saccharina* from January and April greenhouse reared plants. Note the line transecting the plot and that the x-axis is blade width at the beginning of a growth interval and the y-axis is width at the end of the interval.

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line transecting the plot and that the x-axis is blade width at the beginning of a growth interval and the y-axis is width at the end of the interval. Here, the width at 10 cm provides an indication of what happened during growth in the most recently laid down tissue. This "unity" line indicates that in early January the population was expanding in width in a uniformly linear fashion, i.e., as a function of original blade width. During April, widths at 10 cm seem to be decreasing.

In summary, the previous growth models overestimate production because they measured the relationship only during the period of maximum growth rate and/or size and extrapolated this relationship over the year. The types of plots depicted provide a tool for selecting the consistently best-growing individuals whose spore crop can be harvested for subsequent breeding experiments. Careful record keeping is essential in assessing inconsistencies. For example, we have noted the appearance of blade damage can explain subsequent decreases in growth rate.

#### *Gradient plate observations*

The interaction of irradiance and temperature on meiospore germination, gametophyte development and growth, and juvenile sporophyte growth in *Laminaria saccharina* from New York was recently reported by Lee and Brinkhuis (1988). That study utilized crossed light:temperature gradient plates to examine seasonal differences during 1985. Similar studies on *L. longicuris* were conducted by the UCONN group (Egan *et al.*, 1989). For comparison, we illustrate juvenile sporophyte growth in the two species (Figs. 8 and 9).

*Laminaria saccharina* embryonic sporophyte growth was a function of irradiance and temperature throughout the year (Fig. 8). However, temperature was the single most important determining factor. Most often, low irradiances were not conducive to juvenile sporophyte growth. Sporophytes exhibited a much narrower range of survival temperature than gametophytic stages (Lee and Brinkhuis, 1988). Growth exhibited seasonal differences. From November to March, the optimal temperature for growth was 11°C.

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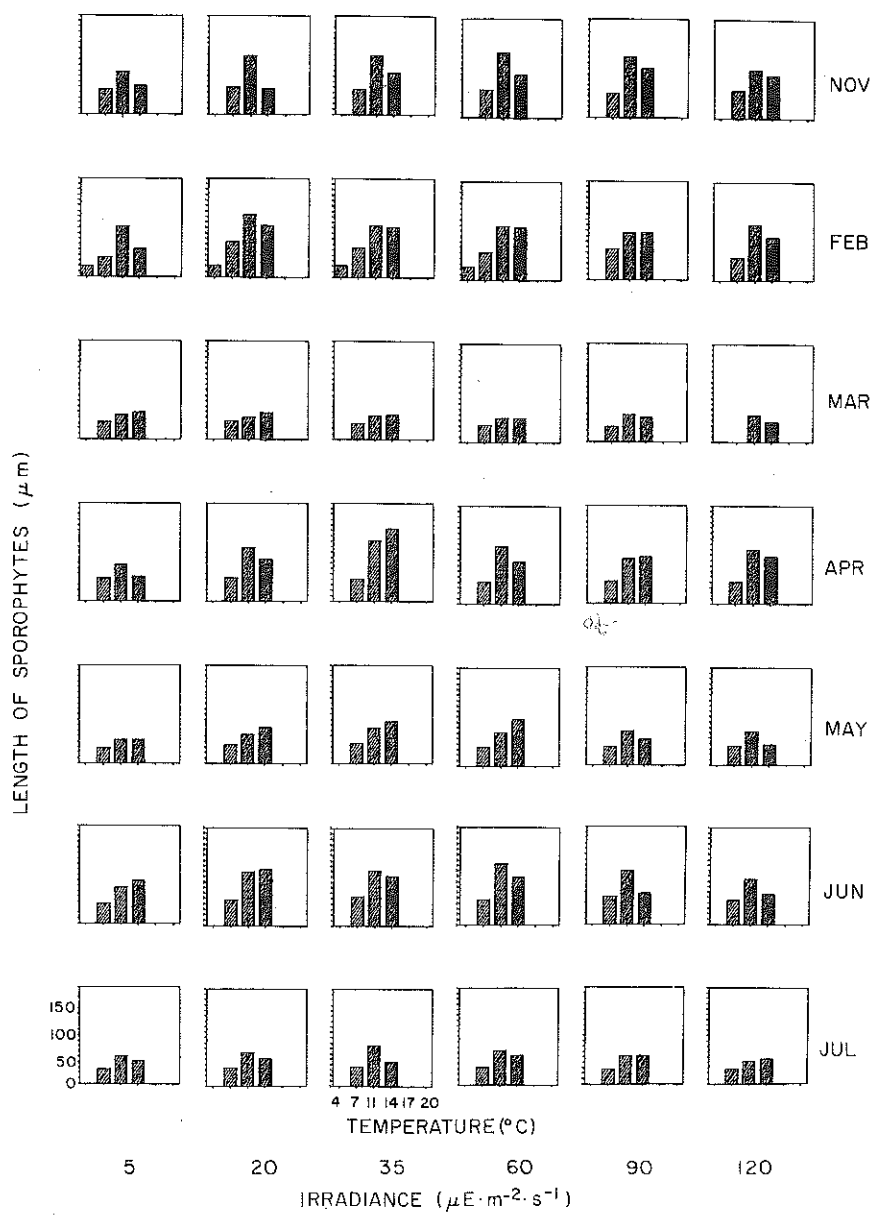


Figure 8. Growth (length  $\mu\text{m}$ ) of 23-day-old *Laminaria saccharina* sporophytes from gradient plate studies.

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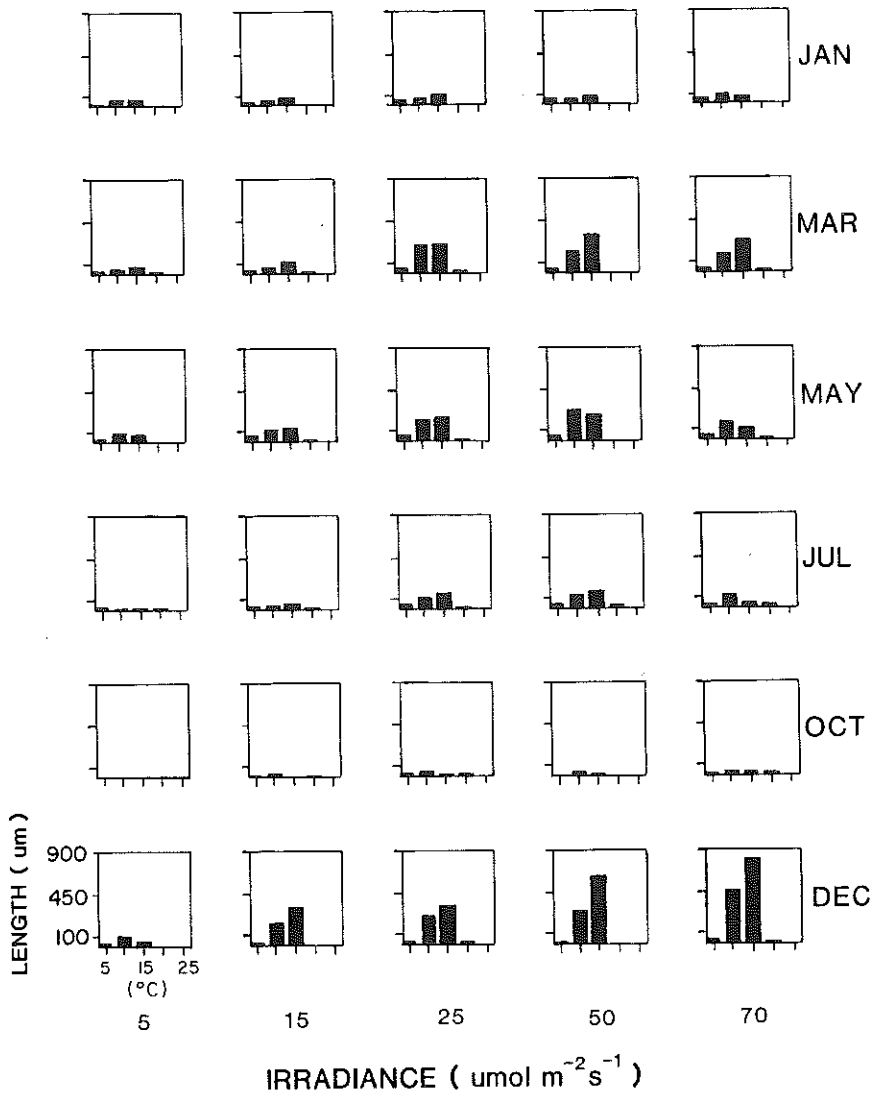


Figure 9. Growth (length  $\mu\text{m}$ ) of 23-day-old *Laminaria longicuris* sporophytes from gradient plate studies. Courtesy of Elsevier Science Publishers B.V.

From April to July, 14°C was the optimum growing temperature. The best growth was observed in April at 14°C and 35  $\mu\text{E m}^{-2} \text{s}^{-1}$ , resulting in sporophytes 133.4  $\mu\text{m}$  long two weeks after meiospores were seeded. This possibly is an adaptation response to seasonally increasing ambient temperatures. Temperatures of 17 - 20°C always totally suppressed sporophyte development and growth. There appeared to be a case of adaptation to cold temperatures in February, as this was the only month in which sporophyte development and growth was seen at 4°C.

Seasonal growth responses of *Laminaria longicuris* to light and temperature (Fig. 9) exhibit differences in comparison to *L. saccharina*. The most rapid development and growth of *L. longicuris* sporophytes occurred during December. At the time of meiospore production, developing sporophytes exhibited a clear response to light, as well as to temperature. Optimal growth was seen at 15°C and 70  $\mu\text{E m}^{-2} \text{s}^{-1}$ . Poorest development and growth in *L. longicuris* was seen in October and January.

To better illustrate differences between the two species, the months of March, May and July can be compared directly. Growth of *Laminaria saccharina* juvenile sporophytes was independent of light, and temperatures between 7 and 14°C supported growth equally well (except at 120  $\mu\text{E m}^{-2} \text{s}^{-1}$  and 7°C). However, growth in March was the poorest of all months. In contrast, growth of *L. longicuris* sporophytes was quite good in March. Above 15  $\mu\text{E m}^{-2} \text{s}^{-1}$ , growth was independent of light, and there is a clear relationship to temperature. Also, *L. longicuris* sporophytes grew at a temperature of 20°C; this was never observed in *L. saccharina*. Development and growth of *L. longicuris* in May was comparable to that of *L. saccharina*, except that the former's sporophytes grew to a larger size, i.e. more quickly. Responses to light and temperature are quite similar. However, some growth at 5°C was seen in *L. longicuris* sporophytes and growth was not observed in *L. saccharina* at 4°C. In July, *L. longicuris* sporophytes grew best at irradiances above 15  $\mu\text{E m}^{-2} \text{s}^{-1}$  and the best growth was observed at 15°C (except at 70  $\mu\text{E m}^{-2} \text{s}^{-1}$ ). In the other hand, *L. saccharina* sporophytes grew equally well at all irradiances and best at a temperature of 11°C. Sporophytes in both species reached

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approximately the same lengths under their respective optimum growth conditions.

We also examined differences between the two species in the sex ratio of gametophytes with respect to incubation temperature on the gradient plate. The ratio of female:male gametophytes in *L. saccharina* was the same at temperatures between 4 and 14° C (Fig. 10a). At higher temperatures, males were more prevalent. In contrast, male gametophytes in *L. longicruris* became more prevalent as temperature increased from 5 to 15° C (Fig. 10b). There were significantly more female gametophytes at 5° C. At 20° C, the number of males and females was similar.

In summary, these data illustrate species differences in when to obtain meiospore material for culture of gametophytic and sporophytic material for seeding in mariculture. These differences are probably due to ecotypic differentiation, as are other physiological traits. It appears anomalous that the species that experiences a warmer summer (*Laminaria saccharina*) does not exhibit survival at warmer temperatures, i.e. 20° C, and that *L. longicruris* living in cooler waters does. The gradient plate approach has not only provided a means of selecting the best seed harvest time and the optimal growth conditions, but also is a tool that can be used to screen for ecotypic differentiation and selection of superior strains.

#### Crossing experiments and taxonomic resolutions

During the spring of 1985, we conducted preliminary experiments in which juvenile sporophytes from Black Ledge, CT and New York populations were grown side by side in the same greenhouse culture tank. The range in blade lengths of measured plants on June 24, 1985 was 17-74 cm for *Laminaria saccharina* and 18-99 cm for *L. longicruris*. Thus, many size classes were sampled. Stipe elongation was significantly greater in *L. longicruris*, but blade elongation rates were statistically similar (Egan and Yarish, 1988).

Crossing experiments provided further insight into differences in growth rates (Fig. 11), blade width (Fig. 12), and stipe length (Fig. 13). Mean growth rates in March (n=54 for each cross) were



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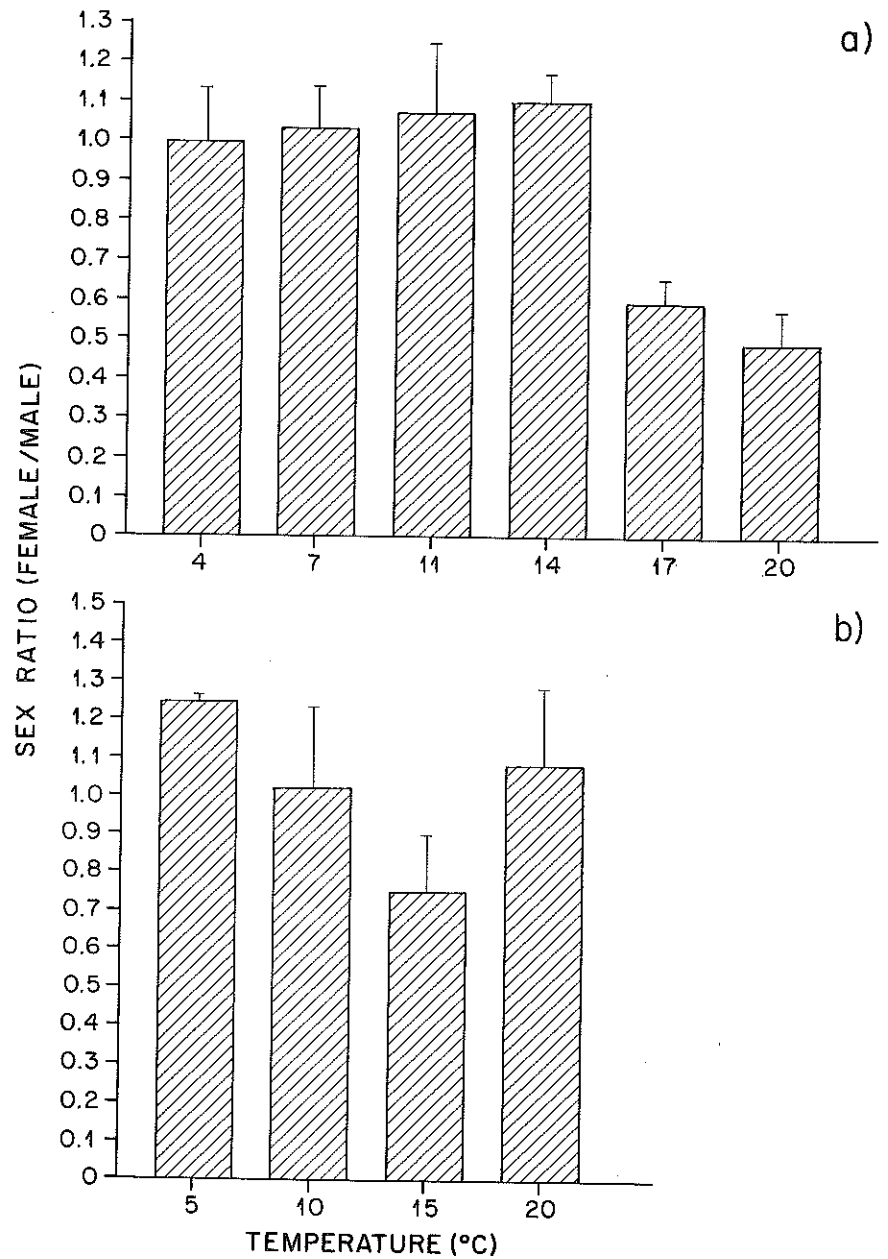


Figure 10. The ratio of females:male gametophytes versus temperature for *Laminaria saccharina* (a) and *L. longicuris* (b) from May, 1985 gradient plate studies.

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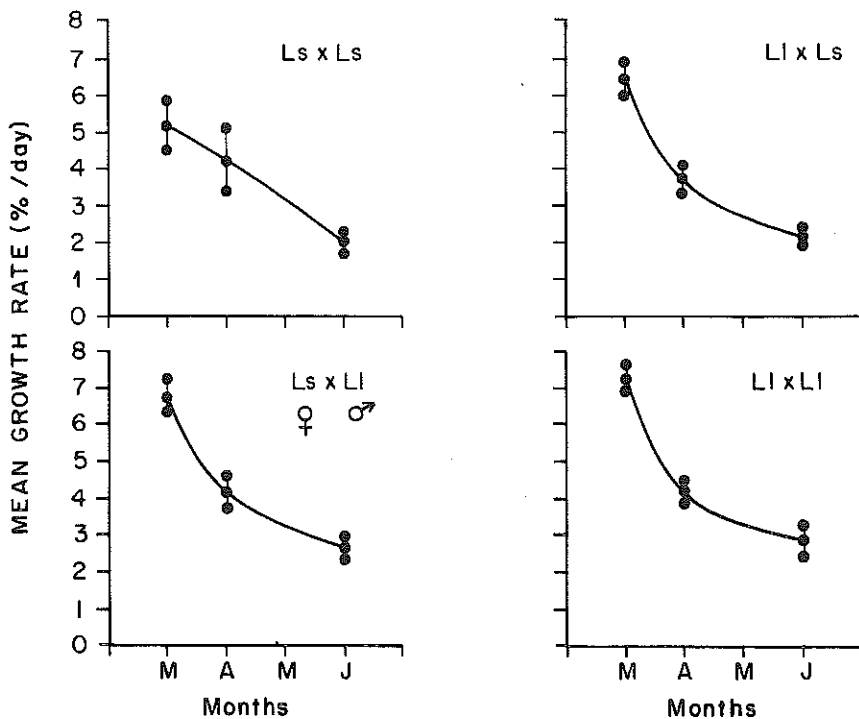


Figure 11. Mean growth rate (% day) of F<sub>1</sub> progenies from crosses of *Laminaria saccharina* and *L. longicuris* in greenhouse culture. First species code listed for each cross represents the female.

highest for the *Laminaria longicuris* self-cross and lowest for the *L. saccharina* self-cross; this difference was significant. Growth rates for interspecific crosses were intermediate, and the difference between the male *L. longicuris*: female *L. saccharina* and the *L. longicuris* self-cross was not significant. On the other hand, growth rates of the alternate inter-cross were significantly different from both self-crosses. Generally, these patterns were observed in April and June measurement intervals as well. The data suggests growth rate inheritance is linked to the *L. longicuris* plants. Further, these data contradict the finding of Egan and Yarish (1988) that growth rates of *L. saccharina* and *L. longicuris* are similar.

Mean maximum blade widths recorded on 1 July, 1988 for each of the crosses (Fig. 12) also indicate differences. Blade

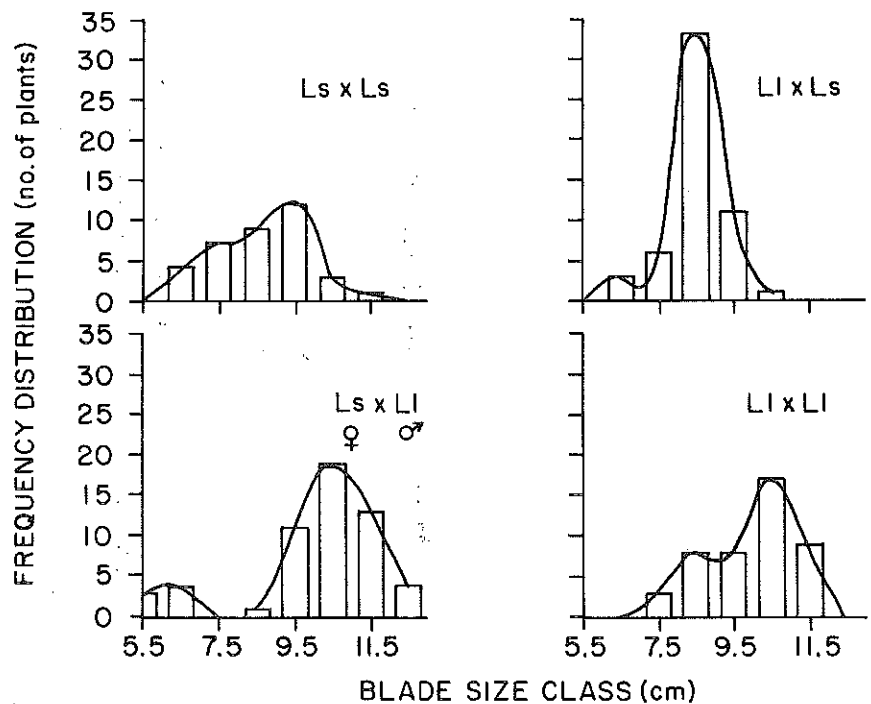


Figure 12. Frequency distributions for maximum blade width (cm) of  $F_1$  progenies from crosses of *Laminaria saccharina* and *L. longicuris* in greenhouse cultured plants. Data from 1 July, 1988. First species code listed for each cross represents the female.

widths for self-crossed *Laminaria saccharina* were narrower than those of the *L. longicuris* self-cross. The male *L. longicuris*: female *L. saccharina* inter-cross exhibited blade widths similar to those of the *L. longicuris* self-cross, and the alternate inter-cross blade widths were most similar to the *L. saccharina* self-cross. The data suggest sex-linkage to the male gametophyte.

Mean stipe lengths shown for 1 July, 1988 (Fig. 13) indicate self-crosses of *Laminaria saccharina* and *L. longicuris* were significantly different; the range of stipe lengths for *L. saccharina* is smaller. On the other hand, stipe lengths of reciprocal crosses between male and female gametophytes of each species were intermediate, with both exhibiting a wider range of lengths than either self-cross. The data suggest stipe length is linked to the female gametophyte.

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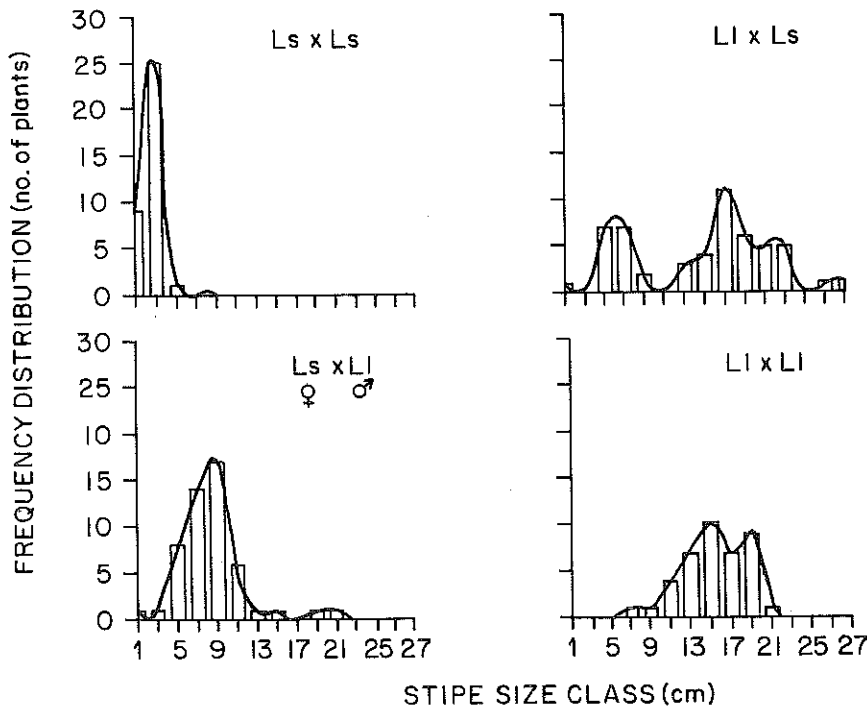


Figure 13. Frequency distributions for stipe length (cm) of  $F_1$  progenies from crosses of *Laminaria saccharina* and *L. longicruris* in greenhouse cultures plants. Data from 1 July, 1988. First species code listed for each cross represents the female.

## Conclusions

*Laminaria longicruris* and *L. saccharina* are dominant members of productive subtidal communities in Long Island Sound and throughout the western North Atlantic basin. Long Island Sound is a unique area in which to study morphological and growth variability in these two entities. This communication has reviewed the taxonomic problems separating these species. Through an integrated, experimental field and laboratory culture approach, our preliminary crossing and morphometric studies of *L. longicruris* and *L. saccharina* have enabled us to determine some degree of genetic differentiation with respect to genotypic and phenotypic characters. This study has illustrated how protocols should be developed to determine which morphological characters have a

genetic basis and, therefore, hold promise for selection and use in mariculture applications.

### Acknowledgments

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### References

- Batters, E. A. L. 1889. *A List of the Marine Algae of Berwick-on-Tweed*. Henry H. Blair, Alnwick. 177 pp.
- Bolton, J. J. 1983. Ecoclinal variation in *Ectocarpus siliculosus* (Phaeophyceae) with respect to temperature growth optima and survival limits. *Mar. Biol.* 73:131-138.
- Bolton, J. J., I. Germann, and K. Lüning, 1983. Hybridization between Atlantic and Pacific representatives of the section *Simplices* of *Laminaria* (Phaeophyta). *Phycologia* 22:133-140.
- Børgeson, F. 1903. II. Marine algae of the Faeroes (1903): In: *Botany of the Faeroes* II:339-532; Det. Nordiske Forlag
- Børgeson, F. 1908. III. The algae vegetation of the Faeroese coasts (1908). In: *Botany of the Faeroes*. III:683-834., Det. Nordiske Forlag
- Brinkhuis, B. H., V. Breda, S. Tobin, and B.A. Macler. 1983. New York Marine Biomass Program- culture of *Laminaria saccharina*. *J. World Maricult. Soc.* 14:360-379.
- Brinkhuis, B.H. and M. D. Hanisak. 1982. Development of a marine biomass program in New York. pp. 682-692. In: *Proc. Int. Gas Research Conf. 1981*. Govt. Institutes, Inc., Rockville, MD.
- Brinkhuis, B. H., H.G. Levine, C.G. Schlenk, and S. Tobin. 1987. Cultivation of *Laminaria* in the Far East and North America. pp. 107-146. In: *Marine Macroalgal Farming for Energy*. K.T. Bird and P. Benson, Eds. Elsevier Sci. Publ.
- Brinkhuis, B. H., E.C. Mariani, V.A. Breda, and M.M. Brady-Campbell. 1984.

ECONOMICALLY IMPORTANT MARINE PLANTS OF THE ATLANTIC

- Cultivation of *Laminaria saccharina* in the New York Marine Biomass Program. *Hydrobiologia* 116/117:266-71.
- Burrows, E. M. 1964. An experimental assessment of some of the characters used for specific delimitation in the genus *Laminaria*. *J. Mar. Biol. Assoc. U. K.* 44:137-143.
- Chapman, A. R. O. 1973. Phenetic variability of stipe morphology in relation to season, exposure, and depth in the non-digitate complex of *Laminaria* Lamour. (Phaeophyta, Laminariales) in Nova Scotia. *Phycologia* 12:53-7.
- Chapman, A. R. O. 1974. The genetic basis of morphological differentiation in some *Laminaria* populations. *Mar. Biol.* 24:85-91.
- Chapman, A. R. O. 1975. Inheritance of mucilage canals in *Laminaria* (Section Simplicis) in eastern Canada. *Br. Phycol. J.* 10:219-223.
- Chapman, A. R. O. 1978. Experimental and numerical taxonomy of the Laminariales. pp. 423-432. In: *Modern Approaches to the Taxonomy of Red and Brown Algae*. D.E.G. Irvine and J. H. Price, Eds. Academic Press, London.
- Chapman, A. R. O. and J.S. Craigie. 1977. Seasonal growth in *Laminaria longicuris*: Relations with dissolved inorganic nutrients and internal reserves of nitrogen. *Mar. Biol.* 40:197-205.
- Chapman, A. R. O. and J.S. Craigie. 1978. Seasonal growth in *Laminaria longicuris*: Relations with reserve carbohydrate storage and production. *Mar. Biol.* 46:209-13.
- Chapman, A. R. O. and J.E. Lindley. 1980. Seasonal growth of *Laminaria solidungula* in the Canadian high arctic in relation to irradiance and dissolved nutrient concentrations. *Mar. Biol.* 57:1-5.
- Christensen, T. and H.A. Thomsen. 1974. *Algefertegnelse*. Universitets Bogladen Naturfagsbogladen der Kobenhavn. 35 pp.
- DeSilva, M. W. R. N. and E.M. Burrows. 1973. An experimental assessment of the status of the species *Enteromorpha intestinalis* (L.) Link and *Enteromorpha compressa* (L.) Grev. *J. Mar. Biol. Assoc. U. K.* 53:895-904.
- Druehl, L. D. 1967. Distribution of two species of *Laminaria* as related to some environmental factors. *J. Phycol.* 3:103-108.
- Egan, B., A. Vlasto and C. Yarish. 1989. Seasonal acclimation to temperature and light in *Laminaria longicuris* de la Pyl. (Phaeophyta). *J. Exp. Mar. Biol. Ecol.* 129:1-16.
- Egan, B. and C. Yarish. 1988. The distribution of the genus *Laminaria* (Phaeophyta) at its southern limit in the western Atlantic Ocean. *Bot. Mar.* 31:155-161.
- Espinoza, J. and A. R. O. Chapman. 1983. Ecotypic differentiation of *Laminaria longicuris* in relation to seawater nitrate concentration. *Mar. Biol.* 74:213-218.
- Fang, T. C. 1984. Some genetic features revealed from culturing the haploid cells of kelps. *Hydrobiologia* 116/117:317-318.
- Fang, T. C. and J.X. Dai. 1980. The use of haploid phases in the genetic study of *Laminaria japonica*. *Acta Genet. Sin.* 7:19-25.

- Fang, T. C., J.X. Dai, and T.C. Chen. 1979. Parthenogenesis and the genetic properties of parthenosporophytes of *Undaria pinnatifida*. *Acta Oceanol. Sin.* 1:112-119.
- Fang, T. C., J.X. Dai, Y.L. Ou, C.C. Tseui, and T.C. Chen. 1978. Some genetic observations on the monoploid breeding of *Laminaria japonica*. *Scientia Sin.* 21:401-408.
- Fang, T. C., B. Y. Jiang and J.J. Li. 1965. Further studies of the genetics of blade length of *Laminaria japonica*. *Oceanol. Limnol. Sin.* 7:59-66.
- Fang, T. C., B.Y. Jiang, and J.J. Li. 1966. The breeding of a long-frond variety of *Laminaria japonica* Aresch. *Oceanol. Limnol. Sin.* 8:43-50.
- Fang, T. C. and J.J. Li. 1963. Effects of inbreeding on female gametophytes and young sporophytes of *Laminaria japonica*. *Oceanol. Limnol. Sin.* 5:333-345.
- Fang, T. C. and J.J. Li. 1965. The effects of temperature and heredity on cell number and maturity rate of female Haidai (*Laminaria japonica*) gametophytes. *Oceanol. Limnol. Sin.* 7:385-395.
- Fang, T. C., C.Y. Wu and J.J. Li. 1962a. Increased adaptability to high temperature of gametophytes and sporelings of the Haiqing No. 1 breed of *Laminaria japonica* Aresch. *Oceanol. Limnol. Sin.* 4:29-37.
- Fang, T. C., C.Y. Wu, J.J. Li, and K.Z. Ren. 1962b. The breeding of a new breed of Haidai (*Laminaria japonica* Aresch.) and its preliminary genetic analysis. *Acta Bot. Sin.* 4:197-209.
- Fang, T. C., C.Y. Wu, B.Y. Jiang, and K.Z. Ren. 1963. The breeding of a new breed of Haidai (*Laminaria japonica* Aresch.). *Scientia Sin.* 12:1011-1018.
- Fritsch, F. E. 1945. *The Structure and Reproduction of the Algae: Phaeophyceae, Rhodophyceae, Myxophyceae and a Foreward*. Cambridge University Press, London. 396 pp.
- Gagné, J. A., K.H. Mann, and A.R.O. Chapman. 1982. Seasonal patterns of growth and storage in *Laminaria longicruris* in relation to differing patterns of availability of nitrogen in the water. *Mar. Biol.* 21:91-101.
- Gendron, L. 1985. Conversion of blade length increments to biomass production estimates in *Laminaria longicruris*. *Can. J. Fish. Aquat. Sci.* 42:33-37.
- Gerard, V. A. 1988. Ecotypic differentiation in light-related traits of the kelp *Laminaria saccharina*. *Mar. Biol.* 97:25-36.
- Gerard, V. A. and K.R. DuBois. 1988. Temperature ecotypes near the southern boundary of the kelp *Laminaria saccharina*. *Mar. Biol.* 97:575-580.
- Gerard, V. A. and K.H. Mann. 1979. Growth and production of *Laminaria longicruris* (Phaeophyta) populations exposed to different intensities of water movement. *J. Phycol.* 15:33-41.
- Guiry, M. D. 1978. *A Consensus and Bibliography of Irish Seaweeds, Bibliotheca Phycologia vol. 44...* Cramer, Valduz. 278 pp.
- Guiry, M. D. and J.A. West. 1983. Life history and hybridization studies on *Gigartina stellata* and *Petrocelis cruenta* (Rhodophyta) in the North Atlantic. *J. Phycol.* 19:474-494.
- Hoek, C. van den. 1982a. Phytogeographic distribution groups of benthic marine

#### ECONOMICALLY IMPORTANT MARINE PLANTS OF THE ATLANTIC

- algae in the North Atlantic Ocean. A review of experimental evidence from life history studies. *Helgoländer Meeresunters.* 35:153-214.
- Hoek, C. van den. 1982b. The distribution of benthic marine algae in relation to the temperature regulation of their life histories. *Biol. J. Linn. Soc.* 18:81-144.
- Hoek, C. van den. 1984. World-wide longitudinal seaweed distribution patterns and their possible causes, as illustrated by distribution of Rhodophyten genera. *Helgoländer Meeresunters.* 37:227-57.
- Hylander, C. J. 1928. The algae of Connecticut. *Bull. Geol. Nat. Hist. Surv. Conn.* 42:1-245.
- Innes, D. J. 1983. Genetic Variation and Adaptation in the Asexually Reproducing Alga *Enteromorpha linza*. State University of New York, Ph. D. Diss. 203 pp.
- Innes, D. J. 1984. Genetic differentiation among populations of marine algae. *Helgoländer Meeresunters.* 38:401-417.
- Irvine, D. E. G. 1974. The marine vegetation of the Shetland Isles. pp. 107-113, In: *The Natural Environment of the Shetland Isles*, R. Goodier, Ed., Edinburgh.
- Irvine, D. E. G. 1982. Seaweeds of the Faeroes. 1. The flora. *Bull. Br. Mus. Nat. Hist. (Bot.)* 10:109-131.
- Irvine, D. E. G., M.D. Guiry, I. Tittley, and G. Russell. 1975. New and interesting marine algae from the Shetland Isles. *Br. Phycol. J.* 10:57-71.
- Jonsson, H. 1912. *The Botany of Iceland. I. Marine Algal Vegetation*. Frimodt, Copenhagen. 186 pp.
- Kain, J. M. 1976. New and interesting algae from the Shetland Isles. II. Hollow and solid stiped *Laminaria* (Simplices). *Br. Phycol. J.* 11:1-11.
- Kain, J. M. 1979. A view of the genus *Laminaria*. *Oceanogr. Mar. Biol. Ann. Rev.* 17:101-161.
- Kylin, H. 1947. Die Phaeophyceen der schwedischen Westküste. *Lunds Univ. Arssk., N.F., Adv.* 2, 43:1-99.
- Lee, R. K. S. 1980. A Catalogue of the Marine Algae of the Canadian Arctic. *Publications in Botany* 9, Nat. Mus. Nat. Sci. Can. 82 pp.
- Lee, J. A. and B.H. Brinkhuis. 1986. Reproductive phenology of *Laminaria saccharina* (L.) Lamour. (Phaeophyta) at the southern limit of its distribution in the Northwestern Atlantic Ocean. *J. Phycol.* 22:276-285.
- Lee, J. A. and B.H. Brinkhuis. 1988. Seasonal light and temperature interaction effects on development of *Laminaria saccharina* gametophytes and juvenile sporophytes. *J. Phycol.* 24:181-191.
- Lund, S. 1959. The marine algae of east Greenland. I. Taxonomical part. *Meddr. Grønland.* 156:1-247.
- Lüning, K. 1975. Kreuzungsexperimente an *Laminaria saccharina* von Helgoland und von der Isle of Man. *Helgoländer Meeresunters.* 27:108-14.
- Lüning, K. 1985. *Meeresbotanik: Verbreitung, Ökophysiologie und Nutzung der Marinen Makroalgen*. Thieme Verlag, Stuttgart. 341 pp.



- Lüning, K., A.R.O. Chapman and K. H. Mann. 1978. Crossing experiments in the non-digitate complex of *Laminaria* from both sides of the Atlantic. *Phycologia* 17:293-298.
- Mann, K. H. 1971. Relation between stipe length, environment and the taxonomic characters of *Laminaria*. *J. Fish. Res. Bd. Can.* 28:778-780.
- Mann, K. H. and C. Mann. 1981. Problems of converting linear growth increments of kelps to estimates of biomass production. *Proc. Int. Seaweed Symp.* 10:699-704.
- Marsden, W. J. N., L.V. Evans and J.A. Callow. 1983. Analysis of character variation in *Fucus* L. I. Discriminant analysis of morphometric estimates. *Bot. Mar.* 26:383-392.
- Mathieson, A. C., T.A. Norton and M. Neushul. 1981. The taxonomic implications of genetic and environmentally induced variations in seaweed morphology. *Bot. Rev.* 47:313-347.
- Müller, D.G. 1979. Genetic affinity of *Ectocarpus siliculosus* (Dillw.) Lyngb. from the Mediterranean, North Atlantic, and Australia. *Phycologia* 18:312-318.
- Müller, D. G., I. Maier, and G. Gassmann. 1985. Survey on sexual pheromone specificity in Laminariales (Phaeophyceae). *Phycologia* 24:475-477.
- Norton, T. A., A.C. Mathieson and M. Neushul. 1981. Morphology and environment. pp. 421-451. In: *The Biology of Seaweeds.*, C.S. Lobban and M.J. Wynne, Eds., Blackwell, Oxford.
- Norton, T. A., A.C. Mathieson. and M. Neushul 1982. A review of some aspects of form and function in seaweeds. *Bot. Mar.* 25:501-510.
- Pankhurst, R. J. and I. Tittley 1978. The application of computers to the identification of the Phaeophyta. pp. 325-337. In: *Modern Approaches to the Taxonomy of Red and Brown Algae.* D.E.G. Irvine and J.H. Price, Eds. Academic Press, London.
- Parke, M. 1948. Studies on British Laminariaceae. I. Growth in *Laminaria saccharina* (L.) Lamour. *J. Mar. Biol. Assoc. U. K.* 27:651-709.
- Parke, M. and P.S. Dixon. 1976. Checklist of British marine algae- third revision. *J. Mar. Biol. Assoc. U.K.* 56:527-594.
- Price, J. H. and W.F. Farnham. 1982. Seaweeds of the Faeroes. 3. Open shores. *Bull. Br. Mus. Nat. Hist. (Bot.)* 10:153-225.
- Prud'homme van Reine, W. F. 1978. Criteria used in systematic studies of Sphacelariales. pp. 301-323. In: *Modern Approaches to the Taxonomy of Red and Brown Algae.* D.E.G. Irvine and J.H. Price, Eds. Academic Press, London.
- Rice, E. L. and A.R.O. Chapman. 1985. A numerical taxonomic study of *Fucus distichus* (Phaeophyta). *J. Mar. Biol. Assoc. U.K.* 65:433-459.
- Rueneß, J. 1973. Speciation in *Polysiphonia* (Rhodophyceae, Ceramiales) in view of hybridization experiments: *P. hemisphaerica* and *P. boldii*. *Phycologia* 12:107-109.
- Russell, G. 1978. Environment and form in the discrimination of taxa in brown

ECONOMICALLY IMPORTANT MARINE PLANTS OF THE ATLANTIC

- algae. pp. 339-369. In: *Modern Approaches to the Taxonomy of Red and Brown Algae*. D.E.G. Irvine and J.H. Price, Eds. Academic Press, London.
- Russell, G. and A.H. Fielding. 1981. Individuals, populations and communities. pp. 394-411. In: *The Biology of Seaweeds*. C.S. Lobban and M.J. Wynne, Eds. Blackwell, Oxford.
- Russell, G. and R.L. Fletcher. 1975. A numerical taxonomic study of the British Phaeophyta. *J. Mar. Biol. Assoc. U. K.* 55:763-783.
- Russell, G. and O.P. Morris. 1970. Copper tolerance in the marine fouling alga *Ectocarpus siliculosus*. *Nature (London)* 228:288-289.
- Sanbonsuga, Y. and M. Neushul. 1978. Hybridization of *Macrocystis* (Phaeophyta) with other float-bearing kelps. *J. Phycol.* 14:214-224.
- Setchell, W. A. 1900. Critical notes on the New England species of *Laminaria*. *Rhodora* 2:115-119.
- Setchell, W.A. and N. Gardner. 1925. *The Marine Algae of the Pacific Coast of North America. Part III. Melanophyceae*. Univ. of California Press, Berkeley. 898 pp.
- Simmons, H. G. 1906. Remarks about the relations of the floras of the Northern Atlantic, the Polar Sea, and the Northern Pacific. *Bot. Zentralbl.* 19:149-194.
- Stace, C. A. 1980. *Plant Taxonomy and Biosystematics*. Edward Arnold, London. 279 pp.
- Sundene, O. 1959. Form variation in *Antithamnion plumula*. Experiments on Plymouth and Oslofjord strains in culture. *Nytt Mag. Bot.* 7:181-187.
- Sundene, O. 1964. The ecology of *Laminaria digitata* in Norway in view of transplant experiments. *Nytt Mag. Bot.* 11:83-107.
- Sverdrup, H. U., M.W. Johnson and R.H. Fleming. 1942. *The Oceans*. Prentice-Hall, Englewood Cliffs. 1060 pp.
- Taylor, W. R. 1957. *Marine Algae of the Northeastern Coast of North America*. University of Michigan Press, Ann Arbor. 870 pp.
- Tittley, I., W.F. Farnham and P.W.G. Gray. 1982. Seaweeds of the Faeroes. 2. Sheltered fjords and sounds. *Bull. Br. Mus. Nat. Hist. (Bot.)* 10:133-151.
- Turesson, G. 1922. The species and the variety as ecological units. *Hereditas* 3:100-113.
- Turner, D. 1802. *A Synopsis of the British Fuci*. Vol. 1. F. Bush, Yarmouth. 400 pp.
- West, J. A., A.R. Polanshek and D.E. Shevlin. 1978. Field and culture studies on *Gigartina agardhii* (Rhodophyta). *J. Phycol.* 14:416-426.
- Widdowson, T. B. 1971. A statistical analysis of variation in the brown algae *Alaria*. *Syesis* 4:125-143.
- Wilce, R. T. 1959. The marine algae of the Labrador Peninsula and Northwest Newfoundland (ecology and distribution). *Nat. Mus. Can. Bull.* 158:103.
- Wilce, R. T. 1965. Studies in the genus *Laminaria*. III. A revision of the North Atlantic species of the Simplices section of *Laminaria*. *Bot. Gothoburg.* 3:247-256.

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- Yarish, C., A.M. Breeman and C. van den Hoek. 1984. Temperature, light and photoperiod responses of some Northeast American and West European endemic rhodophytes in relation to their geographic distribution. *Helgoländer Meeresunters.* 38:273-304.
- Yarish, C., and P. Edwards. 1982. Field and cultural studies of the seasonal and horizontal distribution of estuarine red algae of New Jersey. *Phycologia* 21:112-124.
- Yarish, C., P. Edwards and P. Casey. 1979a. A culture study of salinity responses in ecotypes of two estuarine red algae. *J. Phycol.* 15:341-346.
- Yarish, C. and B. Egan. 1989. The biology of *Laminaria longicruris* and its potential for mariculture in Long Island Sound. pp. 55-89. In: *The Second Conference on the Aquatic Environment: Problems and Perspectives*. K. Kanungo, D. Brousseau, R. Singletary, and L. Liscek, Eds. Fairfield Univ. Press, Fairfield.
- Yarish, C. and P.F. Egan. 1987. Biological studies on *Laminaria longicruris* and its aquaculture potential in Long Island Sound. pp. 189-215. In: *Columbia University Seminars on Pollution and Water Resources* 20 G. J. Halasi-Kun, Ed. Columbia University Press.
- Yarish, C., K.W. Lee and P. Edwards. 1979b. An improved apparatus for the culture of algae under varying regimes of temperature and light intensity. *Bot. Mar.* 22:395-397.