Allocation of Blade Surface to Reproduction in Laminaria longicruris de la Pylaie in the Northwestern Atlantic Ocean

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THE ALLOCATION OF BLADE SURFACE TO REPRODUCTION
OF *LAMINARIA LONGICRURIS* DE LA PYLAIE
IN THE NORTHWESTERN ATLANTIC OCEAN

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A. A., Mohegan Community College, 1984
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THE ALLOCATION OF BLADE SURFACE TO REPRODUCTION OF LAMINARIA LONGICRURIS DE LA PYLAIE IN THE NORTHWESTERN ATLANTIC OCEAN

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CHAPTER 1.
GENERAL INTRODUCTION

Laminariales, or brown kelp, have the greatest biomass and structural complexity of all the algae (Bold and Wynne, 1985), and are thus one of the most important benthic genera in the rocky subtidal euphotic zone (Kain, 1979; Mann, 1982). They occur in temperate and polar latitudes, and include both semelparous and iteroparous species. Kelp are important both economically and ecologically (Mann, 1972; Tseng, 1987; Yarish et al., 1990). While the Laminariales have been studied extensively, much remains to be learned about their reproduction, particularly in regards to the formation of sori.

The objectives of this study are twofold: to quantify the allocation of resources to reproduction (reproductive effort) in *Laminaria longicruris* de la Pyl. (Phaeophyta), with emphasis on a population from Black Ledge in Long Island Sound, a site near the southern biogeographical limit of its range, and to examine the effects of temperature on sorus formation. Interseasonal comparisons of the Long Island Sound population are presented in Chapter 2, and comparisons of this population with populations at three other locations in the Northwestern Atlantic Ocean are made in Chapter 3.

An organism's reproductive strategy is an important part of its ecology. It may be advantageous for an organism to devote more or less effort to reproduction, depending on the prevailing environmental conditions and resources available. The organism must assimilate and
partition the available resources among the necessary functions of maintenance, growth, defense, and reproduction (Harper, 1977; Bloom, et al. 1985; Willson, 1990; Kozlowski, 1992). The specific allocation of resources to each function often varies. For example, reproductive effort can shift with environmental conditions (Barbour, et al., 1980; Bloom, et al. 1985; Mathieson and Guo, 1992). The process of natural selection operates in the choice of the reproductive strategy and an optimal resource allocation pattern, which partly defines the organism’s ecological niche (Slobodkin and Rapoport, 1974; Harper, 1977; Willson, 1983).

Several workers have noticed that growth generally ceases before the formation of sori, and have suggested a possible “trade-off” between these functions, involving a switch in the allocation of resources (i.e., Kain, 1972; Dieckmann, 1980; DeWreede and Klinger, 1988). An examination of the seasonal variation in the amount and timing allocation of resources to reproduction, in relation to the occurrence of growth may help to clarify this question.

Various methods have been used to quantify the allocation of resources to reproduction, and there is disagreement on the meaning of the term “reproductive effort”, even for higher plants (Thompson and Stewart, 1981; Bazzaz and Reekie, 1985; Reekie and Bazzaz, 1987).

Investigators have measured reproductive effort in the macroalgae as a) the number of propagules (Chapman, 1984), b) the proportion of thallus incorporated into gametes (Vernet and Harper, 1980), c) the proportion of thallus incorporated into gametes plus
associated reproductive structures (i.e., Cousens, 1981, 1986; Ang, 1991; Mathieson and Guo, 1992), or d) as the ratio of reproductive tissue to vegetative tissue measured by area (Klinger, 1985; DeWreede and Klinger, 1988). (For review and discussion, see DeWreede and Klinger, 1988; Santelices, 1990; Mathieson and Guo, 1992). Because of the variety and diversity of macroalgal thallus morphologies, there is no one generally accepted method that applies to all macroalgae.

Cousens (1986) points out that reproductive effort is especially difficult to define for some macroalgae because reproductive structures are embedded in the vegetative tissue. In addition, Santelices (1990) observes that there may be a lack of ancillary reproductive structures, and that due to the plastic morphology of the macroalgae, many structures have multiple functions and are difficult to classify. All of these concerns apply to Laminaria longicurris.

Because this study concerns a species with a relatively two-dimensional, sheet-like morphology, the concept of reproductive effort used by Klinger (1985) was selected; namely, the ratio of sorus tissue area to total blade (lamina) area. Because of the confusion surrounding the term reproductive effort, it is avoided in this study, using instead "the allocation of blade surface to reproduction", as measured by the ratio of sorus area to blade area, or "reproductive output".

While some early work which estimated reproductive output in the macroalgae only examined the percent of fertile adults, Cosson (1976) observed that the reproductive output of Laminaria populations depends not only on the number of reproductive thalli, but also on the
relative extent of the sori, the quantity of spores released by sporangia, and the frequency of reproduction. Therefore, this study will consider the density of the sporangia and number of spores within each, the areal extent of the sori, and the percent of reproductive individuals.

The number of times that reproduction occurs over the lifespan defines classification of a plant as semelparous or iteroparous (Harper, 1977; Willson, 1990). Semelparous species reproduce only once during their lifespan, often produce large numbers of propagules, and become senescent during or following reproduction. Iteroparous species may reproduce repeatedly, although not necessarily continuously, and not always with equal abundance. Reproductive output in iteroparous individuals can vary over the life span, influenced by available resources and environmental conditions. Laminaria longicruris populations are potentially perennial, or iteroparous, since a new blade may be generated as long as the holdfast and stipe persist. Mostly, they behave as biennials, however, since the typical lifespan is 24 months (Kain, 1979). Whether a population behaves as an annual, biennial, or perennial depends on the time of recruitment as well as tolerance to environmental factors such as temperature. Both annual and biennial populations of L. longicruris have been observed growing concurrently in Long Island Sound (Egan & Yarish, 1990).

While extensive data has been collected and analyzed for Laminaria longicruris in Long Island Sound, the allocation of resources to reproduction remains to be quantified, and the conditions under which sori form or fail to form need clarification.
This study addresses the following questions:

1) What is the allocation of resources to reproduction for *Laminaria longicruris* in Long Island Sound, as measured by the ratio of sorus area to blade area?

2) What is the seasonal variation in reproductive output for *L. longicruris* at Black Ledge in Long Island Sound?

3) What is the meiospore yield for *L. longicruris* at Black Ledge in Long Island Sound?

4) Is there a trade-off of resources allocated between growth and reproduction in this population?

5) How does the meiospore yield for *L. longicruris* at Black Ledge compare to that of other populations in the Northwestern Atlantic Ocean?

6) How does temperature affect sorus formation at sites with different temperatures but similar light regimes?

7) Is the allocation of blade surface to reproduction (as a measure of reproductive output) relatively low for *L. longicruris* in Long Island Sound, the southern limit of its distribution, compared to other populations?
Background

Sporophyte Morphology

The kelp sporophyte consists of three distinctly differentiated parts: holdfast (attachment organ), stipe, and blade, or lamina (Figure 1). The holdfast, or attachment organ, may be a collection of haptera or, less commonly, a disc. The stipe is cylindrical, and may be relatively short or long. The blade may be undivided or divided into segments. Construction is parenchymatous. As with many other macroalgae, much phenetic plasticity occurs in the genus. The lamina edges may or may not be bullate (Kain, 1979; Yarish et al., 1990). The blade may be narrow and straplike or relatively wide, according to environmental parameters such as wave action (Gerard and Mann, 1979). Interestingly, both narrow forms without bullations and wide forms with bullations representing different generations were observed simultaneously at the same location in this study.

Life History

Like many of the Phaeophyceae, the life history of the order Laminariales includes heteromorphic alternation between a macroscopic diploid phase and a microscopic haploid phase (Figure 2). This life history pattern is classified as a D_h, h+d strategy (Bold and Wynne, 1985). Meiosis occurs in unilocular sporangia borne by the sporophyte
Figure 1. Thallus morphology of *Laminaria longicurris* sporophyte, showing blade, stipe, holdfast, and sorus.
Figure 2. Life history of *Laminaria longicuris*, showing the alternation of haploid and diploid generations. Redrawn from Bold and Wynne (1985) and Yarish and Egan (1989).
in distinct, irregular patches of sorus tissue. Flagellated, motile meiospores are released from the mature sporangia, disperse through the water column, and settle on the bottom. The meiospores germinate into dioecious gametophytes, then gametogenesis occurs, triggered by light from the blue part of the spectrum (Lüning and Dring (1972). Haploid, motile antherozoids develop in gametangia, and are released at maturity, with some fraction subsequently fertilizing eggs in oogonia (Kain, 1979). Syngamy gives rise to the diploid sporophyte. Under certain conditions, maturation may be delayed, resulting in the vegetative growth of filamentous gametophytes. These multicellular filamentous female gametophytes may become reproductive at a later date, with every cell potentially producing oogonia (Kain, 1990; South and Whittick, 1987; Bold and Wynne, 1985).

Sori appear in the median distal portion of the blade as dark, linear bands (Figure 2). They may develop only after the lamina tissue has stopped expanding, so the plant is generally at least five months old before reproduction (Parke, 1948). Variations in the size, shape, and position of sori are related to variation in growth rate with changes in season, habitat, and geographical position (Parke, 1948), but do not appear to be related to age (Klinger, 1985; Ang and De Wreede, 1990). Sori in kelp may appear at all months of the year (Parke, 1948; Keats and South, 1985; Egan and Yarish, 1989; and this study), but show definite seasonal trends.
Mature meiospores have been described as pear-shaped, 8-9 µm long and 4-5 µm wide (Kain, 1979) with one chromatophore and two laterally inserted flagella. The number of spores produced per sporangium for Laminaria is always 32 (Schreiber, 1930; Kain, 1979). Gametophyte sex is genotypically controlled, with a 1:1 sex ratio, or 16 male and 16 female gametes from each single sporangium (Kain, 1979).

Taxonomy

The genus Laminaria was first designated in 1813, when Lamouroux separated it from Fucus because of the distinctive holdfast with haptera (Kain, 1979). This characteristic became obsolete as a basis for generic distinction, however, when it was found that some Laminaria, i.e. L. solidungula, have discoid holdfasts. The genus is divided into two sections, the Simplices section (undivided lamina) and the Digitate section (lamina split into segments).

Two similar species, possibly ecotypes, from the Simplices section dominate the North Atlantic: Laminaria longicurris and L. saccharina Lamour. Both are at their southern limit of distribution in the western Atlantic in Long Island Sound and are sometimes confused with each other. Several characteristics that were formerly used as a basis for taxonomic distinction have been found to be a response to environment (Wilce, 1965; Lüning et al. 1978), including the presence or absence of blade bullations and mucilage ducts. The main difference in morphology is the presence of a long, hollow stipe in L. longicurris and
a short, solid stipe in *L. saccharina* (Chapman, 1973; Kain, 1979; Egan and Yarish, 1989). Mann (1971) suggested that the stipe length and hollowness may not be a valid genetic basis for species distinction. Some authors consider the two to be conspecific (Chapman, 1974; Garcia-Esquivel, 1990) and successful crosses with fertile offspring have been reported (Chapman, 1974; Lüning et al., 1978; Bolton et al., 1983; Egan et al., 1990; Yarish et al., 1990).

**Growth**

Light, temperature, and nutrient supply, particularly nitrogen, are considered to be the principal factors affecting growth and survival of *Laminaria* species (Kain, 1979). Population dynamics are therefore seasonally controlled. Temperature in extreme environments, e.g. an estuary such as Long Island Sound, influences aspects of reproduction, including meiospore germination in *Laminaria longicurris* (Egan et al., 1989). Predation by grazers and substrate suitability may also control survival (Lee, 1987). Primary growth is linear, occurring within an intercalary meristem located in the proximal portion of the blade. The blade also increases in girth by means of a superficial meristoderm (Bold and Wynne, 1985).

*Laminaria longicurris* in Long Island Sound grows most rapidly in the winter and early spring, reaching a maximum rate of 2.5 cm per day in May (Egan and Yarish 1989). Growth is minimal in the late summer due to high water temperatures and nutrient depletion, particularly
nitrogen limitation (Egan and Yarish, 1989), even though photosynthetic ability is at a maximum. Kelp store internally excess carbohydrates produced in late summer for use in the winter, and nitrates acquired in the winter for use in the spring (Chapman and Craigie, 1977, 1978). Where nutrients are abundant year-round, light level, temperature, or some other parameter may be limiting factors (Anderson et al., 1981). Maximum growth rates were observed in the laboratory at 10° C, decreasing at higher temperatures, with 100% mortality occurring at 23° C (Bolton and Lüning, 1982). Summer temperatures south of Long Island may limit the southward expansion of Laminaria species in the western Atlantic (Lee and Brinkhuis, 1986; Egan and Yarish, 1988).

Productivity

Estimates of Laminaria sporophyte productivity in the North Atlantic Ocean vary from 120 gCm⁻² yr⁻¹ in Scotland (Johnston et al., 1977) to 2366 gCm⁻² yr⁻¹ in Narragansett Bay, RI (Brady-Campbell et al., 1984). Most values are in excess of 1000 gCm⁻² yr⁻¹ (Mann, 1982). Recently Egan and Yarish (1990) reported high productivity values for L. longicurris in Long Island Sound (100.53 gCm⁻² d⁻¹ in May of 1986, and 413.32 gCm⁻² d⁻¹ in May of 1987) and concluded that L. longicurris in Long Island Sound is as productive, or more productive, than other kelp species worldwide.
Kelp can play an important role in secondary productivity in a host of marine organisms. For example, Sieburth (1969) estimated from laboratory experiments that *Laminaria* may exude about 40% of the carbon fixed into the water column as dissolved organic matter. Using stable carbon isotope analysis, Dugginset al., (1989) found that the growth rates of a variety of benthic suspension feeders greatly increased in the presence of organic detritus (both dissolved organic matter and particulate organic matter) originating from kelp.

**Economic Importance**

Kelp is an important source of iodine, and is consumed directly by humans in the Orient as a vegetable, kombu. It has been sold in Chinese markets for more than 1000 years (Tseng, 1987) and is also commonly used as a soup base for many Japanese dishes. Kelp has been used historically in Europe and in the Orient as fertilizer and as food for sea urchins and abalone in aquaculture operations (Yarish, personal communication). Kelp may also be used in seaweed biomass-to-energy conversion (Brinkhuis, 1986; Chapman, 1987; Lüning, 1990). Kelp mariculture in China using floating rafts has been practiced since 1952 (Tseng, 1987). In addition, it is harvested and commercially processed by the phycocolloid industry for the alginate present in the stipe walls. Alginate is used as a gelling agent and stabilizer in food products, pharmaceuticals, and paper and textile finishes (Yarish and Egan, 1987).
In the United States, most commercial harvesting is done on the West Coast using *Macrocystis* spp. Although no commercial kelp farms exist in North America (Yarish, 1987), some East Coast *Laminaria* harvesting has begun on a small-scale, for use as fertilizer (Yarish, personal communication).

**Ecological Importance**

Kelp are highly productive, and can be an important part of nearshore food webs (Mann, 1973; 1982). Kelp sporophytes are grazed by gastropod mollusks, notably *Lacuna vincta* Montagu, sea urchins, crustaceans and fish ((Fralick *et al.*, 1974; Brady-Campbell *et al.*, 1984; Foster and Schiel, 1985; Johnson and Mann, 1986 and personal observations). Kelp also provide substrate for epiphytes and shelter for lobsters and other benthic organisms (Foster and Schiel, 1985).

While the ultimate fate of organic material derived from kelp produced in nearshore waters is still under investigation, we know that drifting fragments of blade tissue are directly consumed by pelagic detritivores, or decomposed by bacteria and fungi (Dayton, 1985). The dissolved organic components of kelp mucilage support large populations of microheterotrophs as well (Newell *et al.*, 1980; Linley *et al.*, 1981; Lucas *et al.*, 1981; Stuart *et al.*, 1981).

While we do have knowledge about food-web interactions of the kelp sporophyte, we know much less about the fate of the brown-pigmented meiospores or "swarmers" that are released into the water
column from the mature sporangia, however. In a review of macroalgal propagules and microclimate, Amsler et al. (1992) notes that the characteristics of macroalgal propagules are related to both the reproductive strategies of sporophytes and the successful development of gametophytes. Water movement is important as a dispersal mechanism for the liberated propagules, so the timing of sorus formation and release must coincide with favorable hydrodynamic conditions if dispersal, settlement, and recruitment are to be successful. After release from sporangia, sinking meiospores may settle, become suspended in the slow-moving boundary layer near the sea bottom, or be resuspended in the surge or current zones as meroplankton. Recently settled spores and germlings are grazed by protozoans, amphipods, and larger benthic animals (Amsler et al., 1992).

Unlike most terrestrial spores, kelp meiospores do not have a hard outer covering. They are naked cells bounded by a plasma membrane (Clayton, 1992), thus easily consumed by predators.

Meiospores are brown-pigmented, thus capable of photosynthesis, yet have not routinely been considered in estimates of primary production. Brawley and Johnson (1992) emphasize the need for ecological studies in the macroalgae that examine external cues from interacting environmental factors such as temperature and photoperiod, in order to define the conditions required for reproduction. In the kelp, sexual reproduction can only occur if the asexual phase has produced enough meiospores to successfully settle, germinate, and survive to recruitment.
CHAPTER 2.
SEASONAL COMPARISONS OF ALLOCATION
OF BLADE SURFACE TO REPRODUCTION OF
LAMINARIA LONGICRURIS IN LONG ISLAND SOUND

Long Island Sound represents the southernmost boundary of the distribution of *Laminaria longicruris* in the Western Atlantic Ocean (Egan & Yarish, 1988). This southern limit of geographical distribution corresponds to the lethal temperature limit for this species (van den Hoek, 1982). Although *L. longicruris* has been studied extensively, much remains to be learned about the microscopic stages and the factors that influence the timing and process of sorus formation. The morphology and life history of benthic macroalgae are strongly influenced by abiotic factors, and two key abiotic factors known to affect the reproductive processes of the brown algae are temperature and the quantity and quality of light (Lobban et al. 1985; Lüning, 1980; 1990).

While light is an important consideration to any photosynthetic organism, temperature affects all of the aspects of an organism’s metabolism (Lobban et al., 1984). Macroalgae are poikilotherms, unable to regulate their own temperature; thus thalli have internal cellular temperatures very near that of the surrounding water column. Temperature is also known to have quantitative effects on macroalgal reproduction (Dring, 1974; Lüning 1980). Indeed, different temperature optima may be required for various steps in the reproductive processes (Lobban et al., 1984). The role of temperature in
the gametogenesis of *Laminaria longicurris* has been investigated in culture and found to be of critical importance for gametophyte fertility and egg release (Egan *et al.*, 1989) but has not to my knowledge been related to the timing of and allocation of blade surface to sorus formation in this species.

The objectives of this portion of the study are: 1) to quantify the amount of blade tissue allocated to reproduction; 2) to estimate meiospore yield in *Laminaria longicurris*, at a site in Long Island Sound, near the southern limit of its geographical distribution; 3) to examine the seasonal effects of temperature on sporulation; and 4) to compare the timing and rate of growth with the monthly allocation of resources to reproduction. Interseasonal variations in sorus extent and sporangial density are quantified, and the relationships between sporogenesis, sporophyte growth and mean temperature of surface water are examined.

**Methods**

*Site description.*

The Black Ledge study site is a rocky shoal area off Groton, Connecticut (Figure 3), situated on the eastern end of Long Island Sound (41° 17' N; 72° 04' W). Long Island Sound is connected on the western end to New York Harbor and is open to the Atlantic Ocean on the eastern end. The Black Ledge site was chosen because it has one of the most extensive *Laminaria* populations in Long Island Sound (Egan and Yarish, 1990), with an area of ~1 km². It is located 1 km offshore, east of the mouth of the Thames River, at ~4m below MLW. The location is moderately exposed, with currents of 50 cm s⁻¹ at times of peak ebb and flood tides (Egan & Yarish,
Figure 3. Chart showing the location of the Black ledge study site, a rocky shoal in Long Island Sound, about 1 kilometer off Groton, Connecticut (41°17'N, 72°04'W).
1988). The rocky substrate consists of heaped angular boulders with many crevices between them, probably man-made rip-rap (Taxon, Inc. and Marine Surveys Inc., 1982), which provides microhabitats at various levels of vertical stratification.

**Morphometric analysis.**

Specimens at the Black Ledge study site were tagged randomly, using SCUBA, observed *in situ* and harvested monthly for twenty-two months, from January 1985 to October 1986. Harvested individuals were weighed, and lengths and widths of both blade and sorus tissue were measured. The percentage of plants that were reproductive (bearing sori) and plant density in quadrats was noted. These data were previously analyzed for biomass and growth rates (Egan and Yarish, 1990).

The allocation to reproduction was measured by determining the ratio of sorus (reproductive) tissue area to total area of the vegetative blade, *sensu* Klinger (1985). The more darkly pigmented sorus tissue was easily distinguished visually from blade tissue. Area was determined by tracing the perimeters of sporophytes and sorus tissue onto paper, cutting the tracings out, and weighing, an established technique (e.g., Monahan, 1969) whose application to macroalgal blade surface was suggested by Brinkhuis (1985). A Mettler PM 300 balance was used for weighing. Area was calculated by dividing the weight of the tracings by the areal density of the paper. The precision of this method was tested by having three individuals do independent trials using two replicates. Results varied by only 0.5%. The correlation of length times width, i.e., the area of the rectangle encompassing the region of sorus or entire blade, to the calculated area using this method
was very high (Figure 4). In order to estimate actual blade or sorus area from the determinations of the area of the encompassing rectangles, conversion factors were determined by finding the average ratio of blade area or sorus area to its encompassing rectangle. The conversion factors were 71% for sporophyte blades, and 85% for the more rectangular sorus region. This conversion facilitated the use of earlier data for 1985-1986 that recorded only maximum length and maximum width for blades and patches of sori.

The present study uses the lengths and widths of blades and sorus tissue from that data set, with the addition of four more recent samples taken from the site in 1991 and 1992. The population was sampled in mid-April, the period of maximum growth, in 1991 and 1992, mid-July in 1991, and mid-November, the period of maximum reproduction, in 1991. The percentage of fertile individuals was recorded.

*Statistical Analysis.*

Data were analyzed for monthly variation, then grouped into seasons: winter (Dec., Jan., and Feb., n=79), spring (Mar., Apr., May, n=115), summer (June, July, Aug., n=54), and fall (Sept., Oct., Nov., n=168), and compared for interseasonal variation. The three coldest months of the Northern hemisphere year were chosen for winter, the three warmest for summer, and the months between winter and summer were designated as spring and fall, in accord with standard meteorological seasonal definitions (McGraw-Hill, 1974). Nonparametric statistics were chosen for the statistical analysis, because sample sizes were unequal and sometimes small, variances were unequal, and all data were highly skewed to the right.
Figure 4. Regression line showing the relationship of calculated blade area to a rectangle encompassing the entire blade, i.e. length times width ($r^2=0.98$).
Comparisons of Reproductive Output to Growth Rates and Temperatures

Monthly temperature data for the study site for twenty-two months were plotted with allocation to reproduction during the same period. Temperatures were taken at a depth of 4m, corresponding to the sampling depth, using a Yellow Springs model 43TD Tele-thermometer.

Existing data on growth rates (Egan and Yarish, 1990) were plotted against the allocation to reproduction, as estimated by the mean ratios of sorus area to blade area of reproductive blades only. The growth rates were recorded by monitoring tagged individuals in situ over two-week intervals, using the hole-punch technique of Parke (1948). For further details see Egan and Yarish (1990).

Sporangia Density.

Densities of mature sporangia per linear unit were counted microscopically using sorus tissue excised from Black Ledge samples. Transverse and longitudinal sections were prepared from fresh sorus tissue, using a freezing microtome. The following stains were tested for staining spores and sporangia: hematoxylin, aniline blue, and fuchsin-acetic acid stain. Aniline blue and hematoxylin gave especially good visual clarity. Sporangia were then counted at a magnification of 230x and 430x, and converted to density per square centimeter. Results were combined with average seasonal soral area and an estimate of the size and density of the Laminaria longicruris population at Black Ledge to give an estimate of meiospore production for the study area. Photographs were taken for additional documentation of sporangia, using a Wild M20 microscope with
an Olympus camera attachment and Kodak TMAX 35mm black and white film, ASA 100 (Figure 5).

Results

Interseasonal Comparison of Ratio of Sorus Area to Blade Area

Statistical analysis using the Kruskal-Wallis test (Conover, 1971) showed very significant interseasonal differences ($T=193.4$, $df=3$, $p<0.000001$) in the allocation of blade surface to reproduction for Black Ledge samples taken monthly over the two-years period (Figure 6). Pairwise comparisons indicated highly significant differences between all samples, except spring and summer (Table 1). In 1985, the mean ratio of sorus area to blade area ranged from a low of 1% in May to a high of 37% in November (Figure 7a). In 1986, the ratio ranged from a low of 1% in May to a high of 14% in October (Figure 7b). (November and December 1986 were omitted because funding ran out.) One individual in this sample had 99% of its blade covered by sorus tissue.

In 1991, the mean reproductive output of a Spring sample of 34 fertile individuals was 5% in April with a range of <1% to 27% (Figure 7c). In July, 5 individuals had a mean reproductive output of 9%, ranging from 8% to 11%. In November, mean reproductive output of 50 fertile individuals was 20%, with a range of <1% to 69%. In April, 1992, the mean reproductive effort was 4%. 
Figure 5. Photomicrograph showing sporangia of *L. longicuruis* in Long Island Sound at a) 230X and b) 430X. Scale: Bar = 50μ.
Figure 6. Box-and-whisker plot of interseasonal allocation of blade surface to reproduction of *Laminaria longicurulis* in Long Island Sound. Circles within boxes indicate means; horizontal lines are medians.
Table 1. Kruskal-Wallis test for interseasonal variation in reproductive output of *Laminaria longicurris* at Black Ledge, Long Island Sound. Test statistic $T=193.4$, D.F. = 3, $p < 0.0000001$.
Codes: 1 = Winter; 2 = Spring; 3 = Summer; 4 = Fall. ns=* 

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</table>

Pairwise comparisons between seasons:

| Seasons | $\left| \frac{R_i - R_j}{\sqrt{n_i/n_j}} \right|$ | z     | p-value     |
|---------|---------------------------------------------|-------|-------------|
| 1 & 2   | 97.5                                        | 7.57  | 0.0000001   |
| 1 & 3   | 93.8                                        | 6.01  | 0.0000001   |
| 1 & 4   | 85.8                                        | 7.15  | 0.0000001   |
| 2 & 3   | 3.70                                         | 0.25  | 0.7992590*  |
| 2 & 4   | 83.3                                        | 7.81  | 0.0000001   |
| 3 & 4   | 79.6                                        | 5.79  | 0.0000001   |
Figure 7. Comparison of monthly allocation of blade surface to reproduction of *Laminaria longicruris* in Long Island Sound for a) 1985, b) 1986, and c) 1991-92 samples. Vertical bars represent ± standard deviation from the mean.
Overall, allocation of blade surface to reproduction was highest in the fall (October and November), slightly less in winter, and low in the spring and summer months. The percentage of reproductive individuals was also highest in the autumn (> 90%) (Figure 8). In spring samples, 20 - 30% of the individuals had sori in early spring, increasing to 40 - 50% by May. Reproduction was always minimal in the extent of soral tissue and number of fertile sporophytes from June to early September.

*Relationship of water temperature to reproduction.*

Mean surface water temperatures were in 1985 and 1986 were highest in July and August when the allocation of blade area to sorus tissue was minimal (Figure 9). Sample sizes, however, were very small at this time due to high mortality, blade erosion, and sporophyte deterioration at high temperatures. A small drop in temperature subsequent to the August peak preceded the major burst of sporogenesis in the fall.

*Relationship of Growth Rates to Reproduction.*

Growth rates for the Long Island Sound *L. longicruris* population plotted with the ratio of sorus area to blade area in 1985-86 (Figure 10) show that maximum growth occurred in the spring (March—May), while the extent of sori was minimal. Growth slowed during the summer and was minimal during July and August. Growth rates continued to decline through the fall, while soral area increased to maximum values.
Figure 8. Percent of sporogenous (reproductive) adults in *Laminaria longicruris* samples from Black Ledge, Long Island Sound.
Figure 9. Plot of mean monthly sea surface temperature at Black Ledge study site with ratio of sorus area to blade area (reproductive output) for *Laminaria longicruris*, 1985-1986. Vertical bars represent ± standard error of the mean.
Figure 10. Plot of mean monthly growth rates with ratio of sorus area to blade area (reproductive output) for *L. longicruris*, 1985-1986. Vertical bars indicate ± standard error of the mean.
Sporangia Density.

Fall 1991, samples of sporangia showed a mean value of 19.1 sporangia per 250 μm (n=11, S.D. = ± 1.99), a value equivalent to an areal density of 5.84 x 10⁵ sporangia per cm². Spring 1992 samples had a mean value of 18.2 sporangia per 250 μm (n=10, S.D. ± 2.62), an areal density of 5.30 x 10⁵ sporangia per cm². Assuming a value of 32 spores per sporangium (Schreiber, 1930) this yields 1.70 x 10⁷ spores per cm² sorus tissue for spring, and 1.87 x 10⁷ spores per cm² of soral tissue for fall 1991. A student’s t-test shows no significant differences between these two samples.

Discussion

Although the quantification of reproductive output has been documented for Laminaria longicruris in Nova Scotia (Chapman, 1974, 1984), these data represent the first time that meiospore production has been quantified for L. longicruris at the southern limit of its geographical range of the species. Results indicate marked seasonal variation in meiospore production in eastern Long Island Sound, with a large spurt of sporogenesis occurring in late fall and winter.

In a review of parameters affecting seaweed propagules, Hoffman (1987) suggested that in temperate species, there are often two peaks of spore production, one in the spring and one in the fall. Hoffman’s review further suggests that at the limits of a species’ distribution, the abundance of spores produced may show marked seasonal reduction, or a switch to forms of vegetative reproduction. Examination of the percentage of fertile plants
alone would suggest that peak reproduction occurs in the eastern Long Island Sound population in the fall and spring, as Hoffman predicts. As Cosson (1976) observed, however, any attempt to quantify reproduction in kelp must take into account not only the percentage of fertile adults in the population, but also the extent of the sorus tissue and the density of the sporangia. Although there are many fertile individuals in the spring, the mean extent of the soral area on these individuals is quite small. The highly significant variation in the ratio of blade area covered by sorus between the seasons shows that maximum reproduction of *Laminaria longicruris* sporophytes occurs in the fall, with a secondary peak in the winter months.

The values for mean reproductive output are all quite low compared to the reproductive potential of the individual, as evidenced by one individual in an October sample with 99% of its lamina area covered with sori. The low allocation of blade surface to sorus production at times of temperature increase appear to indicate that temperature stress at the southernmost border of the biogeographical limit of the species results in less allocation of resources to reproduction (and presumably more expended for survival). However, it may be that a relatively low allocation to reproduction is typical of the species. The values obtained are comparable to those reported by Klinger (1985) in British Columbia (1-37% for *Laminaria setchelli* Silva, an iteroparous species, and 13-32% for *L. ephemera* Setchell, a semelparous species), and to that reported for the giant kelp *Macrocystis pyriforma* L. (4 %) in the Pacific Ocean (Neushul, 1963).

While temperature and light are probably the most important factors limiting reproduction in a non-nutrient limited environment, other factors, such as high energy environments with strong currents and high wave
action, and the density of epiphyte coverage, may decrease reproductive output (Reed, 1987; Mathieson & Guo, 1992) to some extent. At Black Ledge, however, the site is in a semi-enclosed estuary, and epiphyte coverage was observed to be dense only in late summer. The much higher values reported in previous studies for reproductive effort in fucoid species (i.e. Cousens, 1986; Ang, 1991; Mathieson & Guo, 1992) reflects the fact that reproductive effort was measured as biomass in fucoids and included receptacles, for which there are no analogous structures in kelp.

The comparison of growth rates with allocation of blade surface to reproduction clearly shows a strong inverse relationship, with the onset of sorus formation occurring subsequent to a decline or cessation in blade growth. However, it would be premature to conclude that there is a trade-off of resources from growth to reproduction, as suggested by DeWreede & Klinger (1988). Because meiospores are autotrophic, very small, and formed within pre-existing cells rather than ancillary structures, they require little investment of resources. There may be other explanations besides a resource trade-off for the fall switch from growth to reproduction. It may be that a decline in growth occurs simultaneously with the initiation of reproduction because both processes are triggered by the same environmental cue, i.e., daylength signal, as suggested by Lüning (1988) and tom Dieck (1991).

Blue light has been found to play a regulatory role in many physiological functions of the macroalgae (Dring, 1984), including both egg formation and release in *L. saccharina*. Lüning (1988) found that a short-day photoperiod regime initiated sorus production in *Laminaria saccharina* sporophytes from Helgoland at an optimal temperature of 10-15°C. This does not appear to be the case in eastern Long Island Sound, however, since the
major peak of reproduction for *L. longicurris* occurs in the fall. It is possible that Long Island Sound sporophytes induced to sorus formation by photoperiod in early spring may be inhibited by a temperature block. The summer temperature rise is very rapid, and at this southern boundary location, is very close to the lethal limit of 23°C (Bolton & Lüning, 1982) for the species. More resources would be devoted to maintenance and survival at this time, with a hiatus in reproduction, until the slight temperature decrease in late August or early September.

Seasonal acclimation to temperature tolerances have been observed for the germination of *Laminaria longicurris* meiospores at this site (Egan et al., 1989). However, these workers found that while young sporophytes may survive heat stress and blade erosion during the summer, there is no evidence for "oversummering" of meiospores or gametophytes. They suggest that only young sporophytes acclimated to highest temperatures survive to fall recruitment. Therefore, the fall sporulation is of much greater importance to recruitment of this population.

The conditions under which the formation of sori can be initiated in the laboratory have puzzled workers for some time. Early workers who attempted to initiate sorus formation in *Laminaria* by manipulating temperature were largely unsuccessful (Hasegawa and Sanbonsuga, 1972). Some later experiments carried out in the hopes of producing sori in *L. japonica* for commercial purposes (Xuankui et al., 1989) concluded that temperature must play a key role in triggering sporogenesis, and that very high temperatures inhibited sori, but were unable to clarify the necessary temperature conditions. Yoneshigue-Valentin (1990), on the other hand, was successful in achieving the formation of sori on *Laminaria abyssalis*
sporophytes in culture when sporophytes were transferred from culture at 18-20°C. to tanks kept at the lethal limit of the species, 23°C.

The plotting of a temperature curve for this portion of Long Island Sound and a curve of allocation of blade surface to reproduction for Laminaria longicruris for the two-year sampling period support suggestions by earlier workers that small-scale fluctuations in temperature may have a role in triggering sporogenesis (Lee, 1987; Costa, 1989). In another laboratory experiment, Lee (1987) found no effect of temperature, including small rapid decreases, on sporogenesis for L. saccharina from Long Island Sound. Culture tanks were maintained at 20°C, 17°C, and 15°C and temperature was decreased in one tank from 17°C to 15°C. However, when sporophytes collected at 17°C in the field were inadvertently placed in the 20°C tank, followed by a reduction in temperature of 3°C, sporogenesis occurred in most most individuals.

Costa (1989) also tested the effects of small-scale temperature change on the induction of sorus formation in Laminaria saccharina from Long Island Sound, finding that spring sporophytes formed sori when subjected to temperatures 2°C and 4°C higher than control temperatures. Sporophytes subjected to decreases from control temperatures did not display sorus formation. The sample sizes were very small (n=3 individuals per treatment), however, and there were problems with disintegration of blades after the first week. Neither Lee or Costa subjected sporophytes to a temperature increase above 20°C followed by a slight decrease in temperature. However, these laboratory findings, when put together with the field results in Figure 10, suggest that the combination of temperature increase to some maximum value near the seasonal temperature maximum, followed by a small, rapid
decrease of ~3°C, may trigger an onset of sporogenesis in the fall for eastern Long Island Sound kelp populations.

It is interesting to compare a similar response to temperature observed in a field study by Haroun et al. (1989) in Shimoda, Japan (35°N). The onset of peak seasonal sorus formation of another kelp, Ecklonia cava, Kjellman was subsequent to a temperature increase to a maximum of 25°C in August (when there were no sori) followed by a drop of ~3°C in September. The curve of seasonal surface seawater temperature in Shimoda (Haroun et al., Figure 3) is very similar to that for the Black Ledge study site.

Future laboratory experiments might test the effects on kelp sorus formation of a temperature increase to a level near the lethal limit for the species, followed by a small, rapid decrease over a time frame of one month or less. While temperature fluctuation is not the only means of initiating sporogenesis, since some individuals are found to be reproductive at any time of year, it is a key factor.

Estimation of Meiospore Yield for Long Island Sound

Both sporangial density and the seasonal extent of sorus tissue must be taken into account when estimating reproductive output. For a eastern Long Island Sound sporophyte in the spring, with 130 cm² of sorus, 2.2 x 10⁹ spores are produced. A typical sporophyte in the fall, with a soral area of 400 cm² yields 7.5 x 10⁹ spores, a figure comparable with Chapman's (1985) estimate of 8 x 10⁹ spores for a single Laminaria longicuris individual in a Nova Scotia population. For comparison, Neushul (1959) found that an individual giant kelp (Macrocystis pyrifera L.) on the Pacific coast of North America may produce 3 x 10¹¹ meiospores in one reproductive event, and
Joska and Bolton (1987) calculated a yield of $3.07 \times 10^{10}$ spores per year for *Ecklonia maxima* (Osbeck) Papenf. If we assume an adult sporophyte density of 7 m$^{-2}$ for the Black Ledge *L. longicruris* population, the lowest density reported by Egan and Yarish (1990) for this site in the fall, we arrive at a figure of $5.25 \times 10^{10}$ spores m$^{-2}$ of substrate, if all individuals were reproductive. By contrast, Chapman (1984) found $9 \times 10^9$ spores m$^{-2}$ of substrate. The difference in these figures is due to the much lower density of plants at the Abbott Harbor, Nova Scotia site (estimated at 1.24 m$^{-2}$) and the fact that I have not considered blade erosion rates here. Sporophytes were unusually dense at the Black Ledge site because of the many niches created by the vertical stratification of the heaped rocks, with individuals established in crevices and at several elevations on heterogeneous substrate, with the holdfasts of several stipes intertwined.

Although little work has been attempted to determine the exact fate of the meiospores, the fact that only 1 in 9 million of the microscopic *Laminaria longicruris* individuals survives to adulthood (Chapman, 1984) would suggest that meiospore production of this magnitude produces large dispersal shadows. This supports the suggestion by Niesenbaum (1988) that "swarmers", macroalgal spores and gametes, make a considerable contribution to the phytoplankton, for a brief period of time, and thus are important to grazing food webs in addition to their traditional role in detrital food webs. This contribution is of particular importance because it peaks in the late fall and winter, a time when planktonic microalgae in Long Island Sound are low in abundance (Riley, 1941; Conover, 1956).

In summary, sporogenesis for *Laminaria longicruris* is related to season in Long Island Sound and is strongly influenced by temperature. Only
in the fall months do temperature and light conditions prevail in Long Island Sound to allow the process of sporogenesis to proceed to an extent that is important for the major recruitment of the population. It is probable that the major sporogenesis process, induced by blue light-mediated photomorphogenesis during the short days of winter and early spring, is delayed until fall when optimal temperature conditions prevail.
CHAPTER 3.

VARIATION IN SORUS PRODUCTION IN LAMINARIA LONGICRURIS IN WESTERN ATLANTIC POPULATIONS ALONG A TEMPERATURE GRADIENT

Long Island Sound (Connecticut and New York, USA) represents the southernmost boundary of the distribution of Laminaria longicruris in the western Atlantic Ocean (Egan and Yarish, 1988). The two abiotic factors that most influence the physiological processes of the brown algae are temperature and light, specifically photoperiod (Lobban et al. 1985). Production of sorus tissue in L. saccharina, was initiated by blue light in a short-day regime in Helgoland samples (Luning, 1988), but this cue is probably less important in L. longicruris in Long Island Sound, since there are reproductive individuals year-round (Chapter 2; Egan and Yarish, 1990). The role of temperature in the timing and allocation of resources to reproduction has not been investigated in L. longicruris, but a temperature increase to 23°C causes blade disintegration resulting in 100% mortality in culture (Egan et al., 1989). High temperatures in Long Island Sound in late summer cause blade erosion and loss of sporophytes.

While Chapter 1 presented evidence that temperature plays a major role in initiating sporogenesis in Laminaria longicruris in the Northwestern Atlantic Ocean, the effects of temperature and light were not separate. The objective of this chapter is to examine the effects of temperature on the allocation of blade surface to reproduction, separating the effects of light and
temperature to a marked extent. Comparisons of reproductive output of the Long Island Sound samples are made to that of samples from other latitudes in the geographical range, to suggest whether the low reproductive ratios observed for the Long Island Sound samples are indeed lower because of temperature stress at the southern most limit of distribution, or whether such low ratios are typical of *L. longicurris* in general.

**Methods**

Fertile *Laminaria longicurris* sporophytes were collected by stratified random sampling during Spring, 1992 from three field locations at different latitudes, within a two-week time frame. Adult sporophytes were collected in Long Island Sound (Connecticut and New York, U.S.A.) at 41° 17' N, 72° 04'W, in the Gulf of Maine (Portsmouth, New Hampshire) at 43° 03'N, 70° 45' W, and in Halifax Harbor, Nova Scotia, at 44° 38' N, 63° 34' W (Figure 11). The sites were selected at latitudes chosen to separate the effects of light from those of temperature. The effects of photoperiod and insolation can be very difficult to separate from the effects of temperature because the two interact. For this experiment, sites were selected along a temperature gradient but within a small change in latitude, so that the quantity and duration of light would be nearly the same for all.

The temperature range at the sampling time was ~6° C. Insolation is virtually the same for all three sites, as indicated in Figure 2-6 of Critchfield (1966), annual total insolation at the earth's surface. Although the angle of incident light entering the water would vary somewhat, it can be shown by a
Figure 11. Locations of three coastal collection sites for *Laminaria longicurulis* off the Northwestern Atlantic Ocean, selected along a temperature gradient. From North to South: Halifax Harbor, Nova Scotia; Portsmouth, New Hampshire, Gulf of Maine; and Black Ledge, Long Island Sound.
simple linear interpolation of the data in Figure 3-12 of Miller and Thompson (1990), undepleted insolation as a function of latitude and date, that photoperiod at these three latitudes does not differ by more than 15 minutes per day in any season. Thus, light intensity and duration are equivalent at these three sites, while temperatures are cooler at the more northerly sites.

The southernmost site, Black Ledge, Long Island Sound, has been studied extensively and is described in Chapter 2 and elsewhere (Egan and Yarish 1990). Mean temperature for mid-April 1992 was 6.7°C. The Gulf of Maine samples were collected from three sites in close proximity in Portsmouth, New Hampshire: the Port Authority, Fish Pier, and Prescott Pier (Figure 12). Individuals were harvested from beneath floating docks. Mean temperature was 5.0°C. Samples were collected at the Nova Scotia site in Halifax Harbor (Figure 13) at a depth of 3 - 5 m. Mean temperature at collection depth was 2.3°C.

*Laminaria longicruris* was distinguished from its ecotype, *L. saccharina*, on the basis of three parameters: stipe length, stipe hollowness, and blade width at 10 centimeters. Sporophytes were taken to the laboratory and kept in coolers while the morphometric analysis was conducted. Maximum lengths and widths of both blade and sorus tissue of individuals were measured, then converted to area by the same method described for the Long Island Sound samples. The allocation of blade surface to reproduction was determined by finding the ratio of sorus area to blade area, as described in the Methods section of Chapter 2.
Figure 12. Chart showing location of Portsmouth, New Hampshire collection sites in the Great Bay Estuary system, Gulf of Maine (43° 03' N, 70°45'W).
Figure 13. Chart showing location of Halifax Harbor, Nova Scotia collection site (44°38'N, 63°34'W).
Results

Significant variations in reproductive output, or ratio of sorus area to blade area, were found for Spring 1992 populations collected at the three different sites along a temperature gradient. The Kruskal-Wallis test \( (T=16.06, \text{df}=2, p = 0.0003) \) showed differences between all three populations (Table 2). Pairwise comparison showed less variation between the Gulf of Maine and Halifax, Nova Scotia populations than between either the Gulf of Maine and Long Island Sound populations or the Nova Scotia and Long Island Sound populations.

Reproductive output increased slightly with latitude (Figure 14). A regression line fit to the data for the three latitudes (Figure 15) had an equation of \( Y = -0.4603 + 0.01287x \). The 90% confidence interval lower bound is defined by a line with a slope of 0.0035, and the 90% confidence interval upper bound is given by a line with a slope of 0.0174. The p-value for the regression is 0.00012, indicating there are less than 2 chances in 10,000 that the actual relationship between reproductive output and latitude is given by a line of zero slope, i.e. that reproductive output is independent of latitude. We may therefore conclude that there is a positive correlation between reproductive effort and latitude. Given the relatively large standard error for the slope (±0.00346), it is not appropriate to attach much significance to the intercept of the x-axis, but it is nonetheless interesting to note that the x-intercept shows zero reproductive effort occurring at a latitude of \( \sim 37.8^\circ \text{N} \).
Table 2. Kruskal-Wallis test for inter-location variation between Spring, 1992 samples at different latitudes. Test statistic $T = 16.06$, D.F. = 2, $p = 0.0003$. Codes: 1 = Long Island Sound, 2 = New Hampshire, 3 = Nova Scotia.

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Pairwise comparisons:

| Locations | $\frac{|R_i - R_j|}{\sqrt{\frac{n_i}{n_i} + \frac{n_j}{n_j}}}$ | z    | p-value |
|-----------|-------------------------------------------------|------|---------|
| 1&2       | 24.8                                            | 2.66 | 0.008   |
| 1&3       | 39.7                                            | 4.19 | 0.000   |
| 2&3       | 14.9                                            | 2.12 | 0.034   |
Figure 14. Box-and-whisker plots showing comparison of allocation of blade surface to reproduction in *Laminaria longicur ris* for spring 1992 samples at three latitudes in the northwestern Atlantic Ocean. Circles within boxes represent means; horizontal lines are medians.
Figure 15. Regression of latitudes vs. ratio of sorus area to blade area for samples of *Laminaria longicruris* from three locations along a temperature gradient in the northwestern Atlantic Ocean.
The mean ratios of sorus area to blade area for Spring 1992 samples for the Gulf of Maine sites in Portsmouth, New Hampshire were 9% for Prescott Pier, 5% for Fish Pier, and 6% for the Port Authority, giving a combined mean of ~ 6.7% (n= 61). At Prescott Pier, individual values for reproductive output ranged from 1% to 29%. An average sporophyte was 222 cm long and 31 cm wide. Mean blade area was 5083 cm², and mean sorus area 457 cm². At Fish Pier, individual values for reproductive output ranged from 1% to 14%. An average sporophyte was 172 cm long and 37 cm wide. Mean blade area was 4681 cm², and mean sorus area 221 cm². At the Port Authority, individual values for reproductive output varied from 1% to 13%. Mean blade length was 153 cm, mean width was 32 cm, mean blade area 3516 cm², and mean sorus area 221 cm². Data from the three sites were pooled for the interlocation test for reproductive output, since individual samples were small, all were in close proximity, and the standard deviations from the means of the data overlapped (Xsp = 0.0639 ± 0.0389, n=17; Xfp = 0.05084 ± 0.03762, n=16; Xpp = 0.0926 ± 0.0639, n=28).

Mean ratio of sorus area to total blade area of fertile Spring, 1992 sporophytes in Halifax Harbor, Nova Scotia, was ~ 9% (n= 54). Individual values for reproductive effort ranged from a low value of 2% to a high of 21%. An average sporophyte was 172 cm long and 70 cm wide. Mean blade area was 8744 cm², and mean sorus area 828 cm².

A regression of the mean water temperatures at collection depth for the three study areas and the reproductive output is shown in Figure 16. Reproductive output decreases slightly with increasing water temperature.
Figure 16. Regression of temperatures vs. reproductive output for *Laminaria longicruris* samples from three locations along a temperature gradient in the northwestern Atlantic Ocean.
$Y = 0.11409 + -0.0091096 \times X$
The 90% confidence level lower bound is given by -0.0093, and the complementary 90% confidence level higher bound is represented by -0.0007. This regression yielded a p-value of 0.00024; i.e., there is less than 3 chances in 10,000 that reproductive output is independent of water temperature. The slope of the line has, as did the reproductive output vs. latitude regression line, a large standard error (in this instance ±0.00242), but note that the temperature at which the x-intercept occurs is approximately 12.5°C.

Discussion

There is highly significant variation in allocation of resources to reproduction with temperature, with the greatest reproduction of typical sporophytes occurring at the northernmost latitude and the least reproduction occurring at the southernmost latitude, the values are all quite low compared to the reproductive potential of the individual, as discussed in Chapter 2. The data support the original hypothesis that temperature stress at the southernmost border of the biogeographical range of the species results in less allocation of resources to reproduction.

A regression of the reproductive ratio with latitudes at the three latitudes indicates that theoretically, no reproduction should occur below a latitude of 38° N. While Long Island Sound is generally considered to be the southernmost boundary for the species, an isolated population of Laminaria saccharina was found at a latitude of 39° N, on a wreck off New Jersey (Egan & Yarish, 1988). The reason that Laminaria populations are not endemic to latitudes down to 38° in the western Atlantic Ocean is probably because of
the lack of rocky substrate. *L. longicurris* is not known to be found west of New Haven Harbor in Long Island Sound, and this may be due to the warm summer temperatures or possibly some other factor.

A regression of the reproductive ratios of spring samples with temperatures shows that, theoretically, 13° is the maximum temperature tolerance for *Laminaria longicurris*. At first glance, this may seem far-fetched, since we know that growth and reproduction occur at much higher temperatures. The southern limits of *L. longicurris* are known to be determined by the 19°C August isotherm (Egan & Yarish 1988). However, it must be remembered that these are spring samples. Examination of the geographical distribution of kelp with global isotherms shows that 13° does appear to be the upper temperature limit for spring samples (Lüning, 1990).

In summary, it is apparent that temperature variation significantly affects the reproductive effort of *L. longicurris*, as measured by the allocation of blade surface to reproduction. The ratio of sorus area to blade surface area increases with latitude, and is decreased by temperature stress. It appears that a relatively low reproductive allocation compared to the macroalgae as a whole is typical of the kelp (Table 3). While comparable to those reported for two congeneric species by Klinger (1985), and slightly higher than those reported for giant kelp, *Macrocystis pyrifera*, (4%) in the Pacific Ocean (Neushul, 1963) the reproductive output is generally lower than that of the fucoids, as discussed in Chapter 2, as well as representatives of the red and green algae. Nevertheless, kelp sporulation is vital to the recruitment process and should be examined further to determine its significance to food webs.
Table 3. Comparisons of macroalgal reproductive output, reported as percent reproductive tissue to thallus.

(* measured as ratio of reproductive area to entire blade area; all others as ratio of reproductive biomass to thallus biomass)

<table>
<thead>
<tr>
<th>Kelp Species</th>
<th>Reproductive Output</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Laminaria longicuris, LIS* (annual)</td>
<td>1-37%</td>
<td>This paper</td>
</tr>
<tr>
<td>Laminaria longicuris, LIS* (Spring)</td>
<td>5%</td>
<td>&quot;</td>
</tr>
<tr>
<td>L. longicuris, Gulf of Maine*</td>
<td>7%</td>
<td>&quot;</td>
</tr>
<tr>
<td>L. longicuris, Nova Scotia*</td>
<td>9%</td>
<td>&quot;</td>
</tr>
<tr>
<td>L. saccharina*</td>
<td>2.4-18%</td>
<td>Lee &amp; Brinkhuis (1986)</td>
</tr>
<tr>
<td>L. ephemera*</td>
<td>32%</td>
<td>Klinger (1985)</td>
</tr>
<tr>
<td>L. setchelli*</td>
<td>30%</td>
<td>Klinger (1985)</td>
</tr>
<tr>
<td>Ecklonia cava</td>
<td>19 - 29%</td>
<td>Novaczek (1984)</td>
</tr>
<tr>
<td>E. cava</td>
<td>18.9 - 28.9%</td>
<td>Aruga et al. (1990)</td>
</tr>
<tr>
<td>Macrocystis pyrifera</td>
<td>4%</td>
<td>Neushul (1963)</td>
</tr>
</tbody>
</table>

Other Phaeophyta Species

| Ascophyllum nodosum (estuarine)      | 67%                 | Mathieson and Guo (1992)       |
| A. nodosum (coastal)                | 33 - 84%            | "                              |
| A. nodosum                          | 29 - 70%            | Cousens (1981)                  |
| Fucus spiralis                      | 28 - 72%            | Mathieson and Guo (1992)       |
| F. vesiculosus                      | 23 - 62%            | "                              |

Other Macroalgae

| Ulva lactuca (Chlorophyta)           | 20 - 60%            | Niesenbaum (1988)              |
| Lithophyllum incrustans (Rhodophyta) | 10 - 55%           | Edyvean and Ford (1984)        |
| Chondrus crispus (Rhodophyta)       | 0.6 - 2.4%          | Chopin et al. (1988)           |
REFERENCES


