

ALLOCATION OF BLADE SURFACE AREA
TO MEIOSPORE PRODUCTION
IN ANNUAL AND PERENNIAL REPRESENTATIVES
OF THE GENUS LAMINARIA

By

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ABSTRACT

Allocation of blade surface area to meiospore production was quantified for semelparous and iteroparous representatives of the genus Laminaria (Phaeophyta: Laminariales) at each of two sites in Barkley Sound, Vancouver Island, B.C. The annual semelparous sporophyte Laminaria ephemera produced sori between April and July; a maximum mean percentage of 31.7% of total vegetative blade area was devoted to sorus production, and 100% of the individuals were reproductive within at least one sample. The perennial iteroparous sporophyte Laminaria setchellii produced sori throughout the year; a maximum mean percentage of 30.4% of total blade area was devoted to sorus production, and a maximum of 54% of the individuals were reproductive within any sample. These results are discussed in the context of life history evolution.

Concentric rings are visible in cross-section of the stipes of Laminaria setchellii. These rings were demonstrated to form annually, and thereby permitted estimation of individual age and of age structure among populations of L. setchellii at two sites in Barkley Sound. Age structures were dissimilar between populations, and showed no evidence of stability. The twelve year age class was most abundant at one site (Wizard Rock), and the two and three year age classes were most abundant at a second site (Execution Bay).

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CHAPTER 1

GENERAL INTRODUCTION

Benthic marine algae exhibit life history characteristics which deviate strongly from many of the life history phenomena described for higher plants and animals. Scientific treatment of algal life histories has traditionally been of a taxonomic or phylogenetic nature, rather than quantitative or theoretical (but for exceptions see Clayton, 1982; Searles, 1980). Evaluation of algal life histories in the context of population dynamics and reproductive strategies is timely and germane to the study of life history evolution.

The kelps (order Laminariales) comprise a taxonomically well-defined group distributed throughout the northern and southern Hemispheres. Members of the order exhibit a heteromorphic alternation of generations, in which the macroscopic sporophyte liberates meiospores which germinate to produce microscopic filamentous gametophytes. Gametophytes mature to produce either oogonia or antheridia; fertilization is oogamous, and results in sporophyte initiation (Kain, 1979, and references therein).

Sporophytes typically are large and show varying degrees of morphological complexity (cf. Setchell and Gardner, 1925). Some perennial species (e.g. Laminaria setchellii Silva, Pterygophora californica Rupr., Eisenia arborea Aresch.) maintain a woody stipe; other perennial species (e.g. Macrocystis pyrifera (L.) C. Ag., Laminaria groenlandica Rosenv.), as well as most annual species (e.g. Nereocystis luetkeana (Mert.) Post. et Rupr.) maintain slender, more pliant stipes. Stipes may be elongate, shortened, or absent entirely.

Blades may be single or multiple, and may be entire or variously dissected. Blades produced by annual species are usually maintained for the

duration of the season, while blades produced by many of the perennial species (e.g. Laminaria setchellii, Pleurophycus gardneri) are deciduous; that is, new blades are formed annually and remnants of old blades are not retained. Blade growth is indeterminate in most species.

Meiosporangia are produced in sporangial sori on the terminal blade (Laminariaceae) or on specialized blades or sporophylls (Alariaceae, Lessoniaceae). Paraphyses and ultimately sporangia originate from mitotic divisions of meristodermal cells (Walker, 1980; Kain, 1979). Both paraphyses and sporangia are pigmented (ibid.), as are liberated meiospores (Kain, 1964). From 16 to 64 spores may be produced per sporangium. Members of the genus Laminaria are reported to consistently produce thirty-two spores per sporangium (Kain, 1979).

The ratio of female to male spores produced per sporangium is reportedly 1:1 (Kain, 1979). Spores germinate within about twenty-four hours of liberation (Kain, 1964); there is no evidence that spores remain planktonic for an extended period.

Nutrients are assimilated across the blade surface from the surrounding medium. Photosynthesis occurs along the length of the thallus, though rates of carbon fixation may vary with distance from the transition zone (Kuppers and Kremer, 1978). The capacity for carbohydrate translocation has been reported for a number of species (Lobban, 1978b; Buggeln, 1977; Schmitz and Lobban, 1976; Schmitz and Srivastava, 1975; Luning et.al., 1972); translocation is generally unidirectional, and towards meristematic regions. Translocation towards reproductive regions has not been reported for members of the Laminariaceae, but may occur among some more specialized members of the Lessoniaceae (Lobban, 1978b).

Kelp gametophytes are known primarily from laboratory studies, although they have occasionally been found in the field (Moss et.al., 1981; Klinger and Moe, unpubl.). Gametophytes are dioecious and sexes are normally heteromorphic (Kain, 1979; Cole, 1968; Hollenberg, 1939; Clare and Herbst, 1938; McKay, 1933; Harries, 1932). Female gametophytes may become reproductive at an early, single-celled stage, or may grow to become tufted filaments, each cell of which potentially can be transformed into an oogonium. Oogonium formation is dependent, in the laboratory, upon temperature and light quality (Luning, 1980; Luning and Neushul, 1978; Luning and Dring, 1975; Luning and Dring, 1972; Hsiao and Druehl, 1971). Male gametophytes grow to filamentous tufts of few to many cells before becoming fertile (Luning and Neushul, 1978). In the laboratory, both male and female vegetative filamentous gametophytes may be fragmented, resuspended, and subsequently cultured to produce multiple reproductive individuals.

The persistence and reproductive behavior of gametophytes in the field is largely unknown. In one exceptional study, Hsiao and Druehl (1973) outplanted labeled gametophytes of Laminaria saccharina in order to follow their seasonal development. They reported continual oogenesis and sporophyte initiation for the study period of July 1968, to June 1971, but observed development of sporophytes only in the late winter and in the early fall. The authors concluded that establishment of macroscopic sporophytes is limited by the action of environmental effects on the embryosporophytes, rather than by environmental suppression of gametogenesis.

Kain (1964) recognized that filamentous vegetative growth of female gametophytes potentially allows gametophytes to "become perennial with indefinite gamete production". Luning and Neushul (1978) argue that

"optimal" conditions of temperature and light quality promote oogenesis among single-celled females, but note that such conditions may be lacking in coastal waters. The possible existence of a dynamic trade-off between precocious development of a single oogonium and delayed production of multiple oogonia has implications for fecundity which can be argued analogously to Charnov and Schaffer's (1973) discussion regarding semelparous versus iteroparous strategies; briefly, those authors attribute advantage to early production of fewer offspring, rather than to delayed production of a greater number of offspring, for the case of the expanding population. The capacity for fragmentation among filamentous gametophytes renders such gametophytes functionally equivalent to iteroparous organisms. The apparent plasticity of gametophyte reproductive behavior is important in that facultative expression of either semelparity or iteroparity has not been previously considered in the literature.

The instantaneous rate of population increase (r) describes the rate at which a given population is expanding or declining, and is a measure of fitness in that it reflects the successful production of offspring by members of a population. " r " is a function of the probabilities of survival and reproduction, as defined by the Euler equation:

$$\int_0^d e^{-rx} l(x) m(x) dx = 1 \quad (1)$$

where $l(x)$ =the probability of survival to age x from birth, $m(x)$ =the instantaneous birth rate, and dx =time interval T to $T+1$ (cf. Michod and Anderson, 1980; Stearns, 1976; Lotka, 1956).

Observed values of $l(x)$ and $m(x)$ may be presented as elements of a Leslie-type matrix, in which probabilities of age-specific fecundity comprise the elements of the first row vector, and age-specific probabilities of

survival are listed on the sub-diagonal (Leslie, 1945). All other matrix elements are zero. The matrix may be solved for the dominant eigenvalue, λ ; then:

$$r = \ln \lambda. \quad (2)$$

The Leslie matrix has been widely used in projection of population growth rates, and has been applied, for example, to populations of humans (Leslie, 1945), and trees (Usher, 1966). The assumptions inherent in construction of the matrix for the purposes of population projection may be constraining, however. For calculation of rate of increase, the matrix model demands that the population be at the stable age distribution, and that empirical determination of $l(x)$ and $m(x)$ be possible.

Leslie-type models constructed for the purposes of population projection are suited largely to diplontic organisms without complexity of life history, such as humans. There exist, however, a number of projection models which consider complexity within the diplontic life history. These typically are tailored to insect populations with stage-specific dynamics (Mills, 1981a; 1981b), or to populations of higher plants in which several demographically-dissimilar stages occur within the life history (Hubbell and Werner, 1979). Common to both non-complex and complex life history models is the assumption that a single ploidy level (usually $2n$) is maintained throughout the life history, and that alternate ploidy levels (usually $1n$) are restricted to transient episodes of sexual reproduction in which syngamy closely follows meiosis. Further, fitness (as " r " or λ) is determined by the demographic parameters ($l(x)$, $m(x)$) of the stage of prevailing ploidy. Mortality occurring within the stage of transitional ploidy is incorporated into the fecundity term of the stage of prevailing ploidy. For the diplontic life

history, no fecundity occurs in the stage of transitional ploidy, by definition.

A simple example may be illustrative. For a sexually reproducing human, $m(x)$ describes the number of daughters born to a female aged x during the time period T to $T+1$.

The value taken by $m(x)$ is therefore the product of the following quantities:

1. number of female gametes produced;
2. probability of survival of female gametes to fertilization;
3. probability of fertilization $\times (0.5)$;
4. probability of zygote survival to birth.

The second and third terms above refer to events occurring within the stage of transitional ploidy (in this example, $1n$). "Mortality" in either of these terms (eg. death of female gametes prior to fertilization) has the effect of reducing the observed fecundity.

For diplontic organisms, each of the foregoing terms is absorbed into the complex term $m(x)$ because of the very small temporal window in which they occur, and, more importantly, because at no point during the stage of transitional ploidy can the absolute number of offspring produced exceed the absolute number of meiotic products multiplied by (0.5) . Birth of twins constitutes a special case and will not be considered here.

The elaboration of the haploid stage in the kelp life history renders models such as those cited above intractable in precisely describing kelp population dynamics. The interposition of an indeterminate number of mitoses between meiosis and syngamy allows the absolute number of diploid offspring produced to exceed the number of original meiotic products $\times (0.5)$, if these

haploid mitotic products are ultimately transformed to oogonia. An important consequence of this possibility is the potential for proliferation of a "successful" haploid genotype prior to recombination.

The average fitness of a population tends to be increased by the action of selective pressures on the net reproductive rates of individuals within the population. Relevant changes in the parameters of age-specific fecundity and mortality can be estimated by construction of the appropriate Leslie-type matrices from empirical data. For diplohaplonts such as the kelps it is therefore tenable that changes in fitness may result from the action of selective pressures upon fecundity and mortality in either stage; that is, change in fitness may be effected within either the gametophyte or sporophyte stage. Under varying selective regimes, the haploid gametophyte and diploid sporophyte may contribute differentially to overall (zygote-to-zygote) fitness.

If the potential for population increase exists within the $1n$ stage independently of and in addition to the potential for increase within the $2n$ stage, then the construction of life tables and Leslie matrices should be possible for both stages independently, if the qualifying assumptions of the Leslie formulation are met. The observable rate of population increase should then be some product of the probabilities of the two independently-constructed matrices.

Interspecific variation in the life history of the kelp sporophyte is well documented (Luning, 1980; Kain, 1979). Sporophytes may be ephemeral (Laminaria ephemera Setchell), annual (Cymathere triplicata (Post. et Rupr.) J. Ag.) short-lived perennial (Laminaria groenlandica Rosenv.), or long-lived perennial (Laminaria setchellii Silva). It is reasonable to expect that

gametophytes of different taxa also exhibit variation in life history parameters. Selective pressures should act to maximize the average probability of successful reproduction by members of a population, and for the kelps, such maximization should occur within sporophyte and gametophyte populations independently.

It is tempting to reduce the complexities of kelp population dynamics by combining multiplicatively the independently-constructed Leslie-type matrices of the sporophyte and gametophyte populations. Schmidt and Lawlor (1983) have justified reduction of the "complex" life history of an annual plant with a seedbank: by wisely choosing their sampling time, they have reduced the sporophyte matrix to a column vector, and have multiplied this vector by the age-classified seedbank matrix. The results are then used to test differential sensitivity of λ to changes in life-history parameters.

Such a manipulation may have some limited applicability to the kelp life history, especially in the case of an annual sporophyte alternating with an age-structured gametophyte population. The formulation, however, would require empirical determination of both sporophyte and gametophyte survivorship and fecundity, and these quantities are unidentifiable for the gametophyte stage in the field.

Fischer (1931) introduced the concept of reproductive value in order to express the value of future production of offspring discounted to the present. For an expanding population, N offspring produced at time $T+0$ are more valuable than the same number of offspring produced at time $T+1$. For a declining population the converse may be true.

Schaffer (1974) and Taylor et.al. (1974) have independently argued that, for strictly age-structured populations, maximizing fitness is equivalent to maximizing reproductive value at each age, subject to the constraints that change in reproductive effort with time has no effect on offspring produced in previous reproductive episodes. Caswell (1982) has further shown that, for stage-classified populations with complex life histories of a certain form, maximizing fitness is equivalent to maximizing reproductive value at each stage; Caswell treats the age-classified models of Schaffer and Taylor et.al. as a special case of his more generalized model.

The models of Schaffer, Taylor et.al., and Caswell, when applied to the kelp life history, are forced to accommodate age structure, stage complexity, and vegetative as well as sexual reproduction in at least one stage (gametophyte). Of the three models, Caswell's may be modified most easily in order to accommodate these added parameters, by construction of a life-cycle graph which is descriptive of the diplohaplontic life history and which remains consistent with the stated assumptions of the model.

Models dependent upon stage-classification are applied to the kelps with difficulty. Stage classifications have been developed expressly in order to describe more precisely populations in which strict age classification has little bearing on schedules on fecundity and survivorship. Stage classification is therefore meant to replace age classification. For the kelps, the stage classification which may be invoked in order to describe the sporophyte/gametophyte alternation may have superimposed upon it at least one, and perhaps two, age structures. That is, any age structure expressed by the sporophyte or gametophyte populations exists in addition to stage complexity. The complexity inherent in the kelp life history is therefore not analogous to

the "complexities" of higher plant and insect populations considered by other authors.

Life history theory is predicated on the assumption of resource limitation (Snell and King, 1977; Gadgil and Bossert, 1970; Cody, 1966; Williams, 1966). That is, a finite and limiting amount of resources are available to individuals, and individuals must therefore partition the available resources between the alternative processes of growth and reproduction. Resource partitioning thus implies the existence of a reproduction-associated cost. This cost function is usually estimated as the increased risk of individual mortality resulting from diversion of resources from growth processes to reproductive processes.

The cost hypothesis in turn allows the prediction that adult survival will vary inversely with fecundity (Bell, 1980). The existence of such an inverse relationship between fecundity and survivorship is testable by both interspecific and intraspecific comparisons, though documentation of the inverse relationship is not itself sufficient to prove the existence of reproduction-associated cost (Bell, 1984).

The cost hypothesis can be used to evaluate some parameters of the kelp life history. We can assume, for the time being, that fecundity in kelps is solely a function of meiospore production, and that gametophytes do not contribute to overall fecundity. The kelp sporophyte is thus rendered functionally equivalent to a diplontic organism. We can then go on to predict that sporophyte fecundity and survivorship are inversely related, and can test this prediction at both interspecific and intraspecific levels.

The evolution of delayed maturity has sometimes been attributed to selection for increased fecundity which may accompany a delay in developmental time-to-maturity (Stearns and Crandall, 1981; Bell, 1980; Gadgil and Bossert, 1970; Tinkle, 1969). A postulated increase in fecundity with an associated decrease in developmental time is testable in the context of the kelp life history, if fecundity and developmental time-to-maturity can be estimated.

The hypotheses of reproduction-associated cost and of delayed maturity thus allow two testable predictions to be made for populations of kelp sporophytes:

- 1) that the annual semelparous sporophyte will exhibit a greater fecundity than the perennial iteroparous sporophyte; and
- 2) that developmental time-to-maturity will be shorter for the semelparous sporophyte, provided it exhibits a greater fecundity than the iteroparous sporophyte.

Several authors have argued that reproductive effort should generally increase with age among iteroparous organisms (Pianka and Parker, 1975; Schaffer, 1974; Gadgil and Bossert, 1970). The ratio of reproductive tissue to vegetative tissue per individual can be used as a measure of reproductive effort (Pianka and Parker, 1975). For the kelps, then, one can estimate reproductive effort by measuring sorus production relative to total (vegetative) blade production. This formulation permits a third testable prediction that the ratio of sorus production to total blade production will increase with age among iteroparous sporophytes.

Two congeneric species were chosen for the purposes of a comparative study. Laminaria ephemera Setchell is a short-lived, semelparous sporophyte

found in lower intertidal and subtidal habitats of the eastern Pacific. L. setchellii Silva is a long-lived iteroparous sporophyte of roughly the same habitat and distribution. These species may be found growing adjacent to one another at many sites in Barkley Sound, Vancouver Island, B.C. Sporophyte populations of the two species do not intermix, each being restricted to slightly different substrata.

Laminaria ephemera was originally described from collections made in Monterey County, California prior to 1901. The species is distinguished from its congeners by the presence of a discoid holdfast, and by the absence of mucilage ducts from both the stipe and blade (Druehl, 1968). The species is reportedly distributed from Volga Island, Alaska to Monterey County, California (Abbott and Hollenberg, 1976), but extends at least to San Luis Obispo County in the south (pers. obs.).

Laminaria ephemera sporophytes display rather simple morphology. The discoid holdfast is small and without haptera, the stipe flexible and terete, the blade single (but sometimes dissected). The sorus is reportedly linear in formation (Abbott and Hollenberg, 1976; Druehl, 1968), though soral patches may in fact be as broad as the width of the blade (Setchell, 1901; and pers. obs.). Sori are formed asynchronously on either side of the blade, and the sorus formed on one side is usually much larger than that formed on the other. Sorus formation is initiated proximally to the transition zone and proceeds distally.

Laminaria ephemera sporophytes are a highly seasonal component of the kelp flora of Barkley Sound, B.C. Juvenile sporophytes are first identifiable in March, depending upon the site and prevailing weather conditions. Most sporophytes disappear by late June or early July. Sporophytes may be

intertidal, but are more commonly subtidal, and are often confined to substrata of cobble or small boulders underlain by soft bottoms of pebble or coarse sand. Individuals are only rarely found on the subtidal granitic pavements and outcrops typical of Barkley Sound.

Laminaria setchellii Silva is a woody-stiped perennial species of the eastern Pacific, distributed from Yakutat, Alaska (Druehl, 1968) to Ensenada, Baja California, Mexico (Abbott and Hollenberg, 1976). The species is characterized by a well-developed, erect stipe and large, repeatedly dissected blade, and by the presence of mucilage ducts in both the stipe and blade. The holdfast is hapterous and ramifying.

The nomenclature of Silva (1957) and of Druehl (1968; 1979) will be followed throughout. Laminaria dentigera (Nicholson, 1976) is not considered to be conspecific with L. setchellii, and the former specific epithet is reserved for a species of Alaskan Laminaria, according to Druehl (1979).

Laminaria setchellii commonly inhabits stable and permanent substrata along exposed, wave-swept rocky shores. Mature plants exist in nearly monospecific stands, and may form dense canopies. Juveniles (1 to 2 years old) are found among stands of adults of the species, but may also occur along the peripheries of populations and on newly-available substrata remote from adult populations.

Visible rings formed by seasonal development of a secondary cortex are obvious in basal cross-section of the stipe. Similar rings are common to other woody-stiped species, including Laminaria hyperborea (Gunn.) Foslie (Kain, 1963), Pterygophora californica Ruprecht (Frye, 1918), and Ecklonia radiata (C. Ag.) J. Ag. (Novaczek, 1981).

The blade of Laminaria setchellii is deciduous. A single blade is initiated from the meristematic region at the transition zone, normally in the months of September through December, depending upon the population and upon the site. The blade develops and persists for about twelve months, at which time it may be shed entirely, leaving a bladeless stipe with a latently active meristematic region. Alternatively, the existing blade may be retained until seasonal initiation of new blade tissues from the transition zone. In this latter case, remnants of the older blade are entirely sloughed shortly after initiation of the new blade.

Seasonal retention or loss of the existing blade seems to be independent of population and of site. There is, however, some age-dependent expression of this trait among the populations studied. All first and second year plants shed the existing blade entirely, and 'overwinter' as bare stipes. Most third and fourth year plants also shed the existing blade. Older plants (5 and more years of age) generally retain at least some portion of the existing blade beyond initiation of the new blade. A small percentage of older plants do, however, lose the existing blade entirely, and persist temporarily as bladeless stipes. Luning (1969; 1971) has reported a similar ontogeny for the seasonal renewal of the blade of Laminaria hyperborea. It appears, however, that the existing blade of L. hyperborea is always maintained beyond new blade initiation. The occurrence of bladeless stipes has not been reported for L. hyperborea.

Small soral patches are generally initiated distally on well-developed fronds of Laminaria setchellii, and usually form synchronously and symmetrically on either side of the blade. As sorus development progresses, the sorus extends in a proximal direction and ultimately adjoins the

transition zone. Not all plants, however, produce such extensive sori. Kain (1971) has described similar development of sori for Laminaria hyperborea.

In the fall months, when remnants of the old blade persist and are distal to newly-formed blade tissues, functional sori may be produced concomitantly along proximal regions of the old blade and distal regions of the new blade. The observation of simultaneous sorus formation on new and old blades of Laminaria setchellii indicates that sorus initiation and development are independent of the age of the blade tissues. In the field, sori have been observed on fronds estimated to be less than one month old.

Blade surface area is deemed the most appropriate parameter for interspecific comparisons of meiospore production within the genus Laminaria. Blade anatomy is consistent along the length of the blade, and the entire blade is pigmented, with meristodermal and upper-cortical cells containing chloroplasts. Sorus formation is the product of mitotic transformations of the meristoderm. Vegetative and reproductive (soral) areas along the blade can be easily distinguished and evaluated with little ambiguity. Fecundity can be estimated by quantification of the number of spores produced per unit sorus area.

Comparison of dry weight of the blade tissues is considered inappropriate for the purposes of the present study. Koppers and Kremer (1978) have demonstrated for two species of Laminaria that dry weight per unit area varies along the length of the blade; dry weight per unit area may change seasonally as well. Spatial and seasonal inconsistencies in dry weight per unit area reflect energetic processes and constraints, especially in terms of storage and utilization of carbohydrates. However, use of dry weight as a comparative parameter in the present study potentially confounds the processes of

carbohydrate metabolism with those of meiospore production. Additionally, observations of dry weight necessarily include the extraneous contribution of epiphytes to total weight. Dry weight is therefore not used for the purposes of this study.

CHAPTER 2

SEASONAL PATTERNS OF RECRUITMENT IN LAMINARIA EPHEMERA

INTRODUCTION

The cobble and boulders supporting dense populations of Laminaria ephemera at Cable Beach and at Execution Bay were unstable and subject to seasonal burial. The seasonal recurrence of short-lived sporophytes on such unstable substrata is of interest. Disallowing that recruitment of L. ephemera sporophytes occurs beyond the settling of meiospores, the L. ephemera gametophyte or embryosporophyte must persist for at least 7 months. Success in the following season requires that gametophytes or embryosporophytes are not overgrown by other algae, grazed by herbivores, or scoured away. Kelp gametophytes are generally capable of survival in the dark (Kain, 1964; and pers. obs.). It might be possible, therefore, that gametophytes can survive burial for extended periods of 7 months or more, if the overlying sediment is of a grain size sufficient to permit oxygenation within the sediment. Gametophytes or embryosporophytes could subsequently emerge to produce macroscopic sporophytes upon seasonal uncovering of the substratum.

Such a scenario potentially obviates problems of overgrowth, grazing, and scouring, and conceivably leads to the production of dense, nearly monospecific stands of L. ephemera. Such high densities of L. ephemera have been repeatedly observed in the field (pers. obs.).

Few or no other kelp species in Barkley Sound are reproductive simultaneously with Laminaria ephemera. Species such as Pterygophora californica, Alaria marginata, and Cymathere triplicata tend to be

reproductive later in the season than L. ephemera. This temporal difference in reproduction, when coupled with seasonal burial and emergence of substrata, reduces the probability of overgrowth or exclusion of L. ephemera by other kelp gametophytes, if burial occurs prior to spore production by kelps other than L. ephemera.

In an attempt to document the observed seasonal pattern of Laminaria ephemera sporophyte recruitment, cobbles were tagged in situ and monitored for an 18 month period (June 1981 through November 1982). Three questions were addressed: 1) in which months were cobbles supporting L. ephemera sporophytes buried and subsequently uncovered? 2) when did meiospore production occur relative to cobble burial? and 3) would L. ephemera sporophytes reappear in the following season on cobbles which had been previously buried?

MATERIALS AND METHODS

Thirty-nine cobbles were tagged and numbered in Execution Bay (re: Figure 2.1) on 27 June 1981. Cobbles included in the study were within an area of less than 50 m², on a sandy bottom, at 4-5 m depth. Cobbles chosen for tagging were of minimum dimensions 15 cm³, and supported at least 5 Laminaria ephemera sporophytes at the time of tagging. Other algal species were present on some cobbles, including juvenile Pterygophora californica, Alaria marginata, and Cymathere triplicata. Tags were fixed in situ by application of underwater epoxy putty to the upper surface of each cobble. Five additional epoxy tags were fixed on rock walls bordering the study site; these were to serve as indicators of tag loss.

Forty-eight hours were allowed for curing of the applied epoxy. Thirty-six of the original 39 tags were well-cured after 48 hours, and the experiment was begun with these 36 cobbles.

On 29 June 1981, and at approximately monthly intervals thereafter, recovery of the tagged cobbles was attempted by underwater survey of the study site. During these surveys, the presence or absence of Laminaria ephemera and of other algal species on the tagged cobbles was recorded, and the reproductive condition of Laminaria ephemera was noted.

RESULTS

Laminaria ephemera sporophytes were reproductive upon initiation of the study (29 June 1981). Observations at Execution Bay have indicated that meiospore production may begin as early as April and may continue until July (re: Chapter 3). No Laminaria ephemera sporophytes remained on tagged cobbles, or within the study area, on 05 August 1981, and L. ephemera sporophytes did not reappear on these cobbles at any time during the subsequent surveys. On 05 August 1981, the holdfasts of juvenile Pterygophora californica remaining on some cobbles were buried beneath approximately 1 cm of sand. On 28 August 1981, there was evidence of tumbling of tagged cobbles, judged by position of the tags and by orientation of stipes of P. californica. Evidence of such tumbling persisted through the subsequent surveys of 25 September, 29 October, and 26 November 1981.

Surveys made after 26 November 1981 failed to recover any tagged cobbles. This failure is attributed to burial of the study site beneath 20-30 cm of sand and pebble. Surveys were continued through November 1982; tagged cobbles

were not uncovered during this entire period. The disappearance of tagged cobbles is assumed to reflect burial rather than tag loss; epoxy tags applied to rock walls bordering the study site were observable throughout the 18 month study period.

Burial was estimated as the rate of cobble disappearance, and is expressed as the percentage of tagged cobbles not recovered during surveys. Values are given in Table 2.1. Estimated burial for every survey prior to 26 November 1981 was 11.1% or less; burial was estimated to be 69.4% for the survey of 26 November 1981. No tags were recovered during the survey made 11 December 1981, or at any time thereafter.

DISCUSSION

The burial of cobbles within the study site is a seasonal phenomenon. Most cobbles exposed in the early summer (June) remain exposed until the late fall (November-December), at which time burial occurs. Burial seems to result from sand and pebble transport by water motion associated with winter storms. Summer hydrographic conditions remove the previously-deposited sand and pebble, again exposing cobbles, but removal may not occur in the season immediately following burial. That is, the cycle of burial and emergence may be of duration in excess of one year, as indicated by the results of this study.

Meiospore production by Laminaria ephemera occurs prior to cobble burial, by as much as 4 months, assuming that meiospores are produced in July and cobbles are buried in November. However, tumbling of cobbles and sand deposition may begin as early as August, closely following meiospore

production by Laminaria ephemera. Pterygophora californica, Alaria marginata, and Cymathere triplicata generally reproduce in August or later.

Laminaria ephemera sporophytes in Barkley Sound grow at high densities (re: Chapter 3) and bear sori on single blades which are usually retained on the parent plant through the period of spore release. Sorus-bearing blades have no means of flotation, and no apparent means of long-distance dispersal. Dispersal of kelp spores after liberation from the sporangium is reported to be minimal (Anderson and North, 1967). It is therefore reasonable to assume that most liberated spores of Laminaria ephemera settle and germinate on cobbles nearby the parent sporophyte. Data presented here and repeated personal observations indicate that these gametophyte-bearing cobbles are subject to seasonal burial.

That the cobbles tagged during this study were buried but not subsequently uncovered allows only speculation regarding the fate of Laminaria ephemera gametophytes. It is possible that some proportion of gametophytes buried for 12 months or more remained viable. This is suggested by the observation, at an adjacent site, of Laminaria ephemera sporophyte development upon emergence of cobbles which had been buried for 8-12 months prior to sporophyte initiation. None of these cobbles were tagged, however, and quantitative data are not available.

In culture, Laminaria ephemera gametophytes are long-lived. Gametophytes germinated from sori collected in Barkley Sound have been retained in culture at low light ($<50 \mu\text{E}/\text{cm}^2/\text{sec.}$), or in the dark with intermittent light breaks, for three years (Klinger, unpubl. obs.). There is no reason to assume reduced gametophyte longevity in the field, though the probability of gametophyte mortality in situ may be substantially enhanced.

Other algal species growing in sandy habitats in British Columbia may possess means of non-sexual reproduction, which are presumably of adaptive value in sand-inundated environments. Markham (1968) has demonstrated sporophyte initiation by vegetative propagation of haptera in Laminaria sinclairii. Mathieson (1967) has reported 'direct development' among sporophytes of Phaeostrophion irregulare, in which unispores liberated by sporophytes give rise to new sporophytes directly, thereby eliminating the microscopic sexual gametophyte from the life history. Newroth and Markham (1972) have proposed that carpospores of Gymnogongrus linearis may develop parthenogenetically, and tetrasporophytes have not been reported for this species. Parthenogenesis among liberated carpospores does not avoid the risk of mortality incumbent upon germlings in sandy habitats, but does reduce the risk inherent in reproduction by eliminating the tetrasporophyte stage from the life history. In addition, Markham and Newroth (1972) have noted that branches of G. linearis which bear cystocarps may be abscised from the parent plant prior to carpospore release, and that such branches may aid dispersal, ostensibly to substrata temporarily free from sand and therefore conducive to carpospore settlement and germination.

The capacity for vegetative propagation, non-sexual reproduction, or long-distance dispersal reduces or eliminates the risk of gamete or zygote mortality due to sand scour and burial. Laminaria ephemera differs from other sandy-habitat species such as Laminaria sinclairii, Phaeostrophion irregulare, and Gymnogongrus linearis in that the species maintains an obligatory microscopic sexual stage, has no alternative means of non-sexual reproduction, and has no apparent means of long-distance dispersal.

Availability of hard substratum is critical for successful meiospore settlement. Laminaria ephemera produces sori during the early summer (re: Chapter 3), when sand levels in the subtidal are lowest, and when cobbles are exposed. This confers the greatest probability of meiospore settlement success. Similarly, Markham (1968) has noted that Laminaria sinclairii in British Columbia produces sori during the winter months, when sand levels in the intertidal are lowest.

It is clear that the microscopic gametophyte or embryosporophyte of Laminaria ephemera must persist for at least 7 months in a habitat subject to sand scour and burial. It is conceivable that burial actually enhances gametophyte survivorship in sandy habitats, by reducing scour, and by reducing or eliminating grazing by herbivores and overgrowth by other algae. The seasonal timing of meiospore release and settlement are therefore critical, both in the availability to the meiospores of suitable hard substratum and in the potential for successful germination prior to burial. The success of Laminaria ephemera in sandy habitats may consequently be attributable to its truncated sporophyte generation, precise period of meiospore liberation, and persistent gametophyte generation.

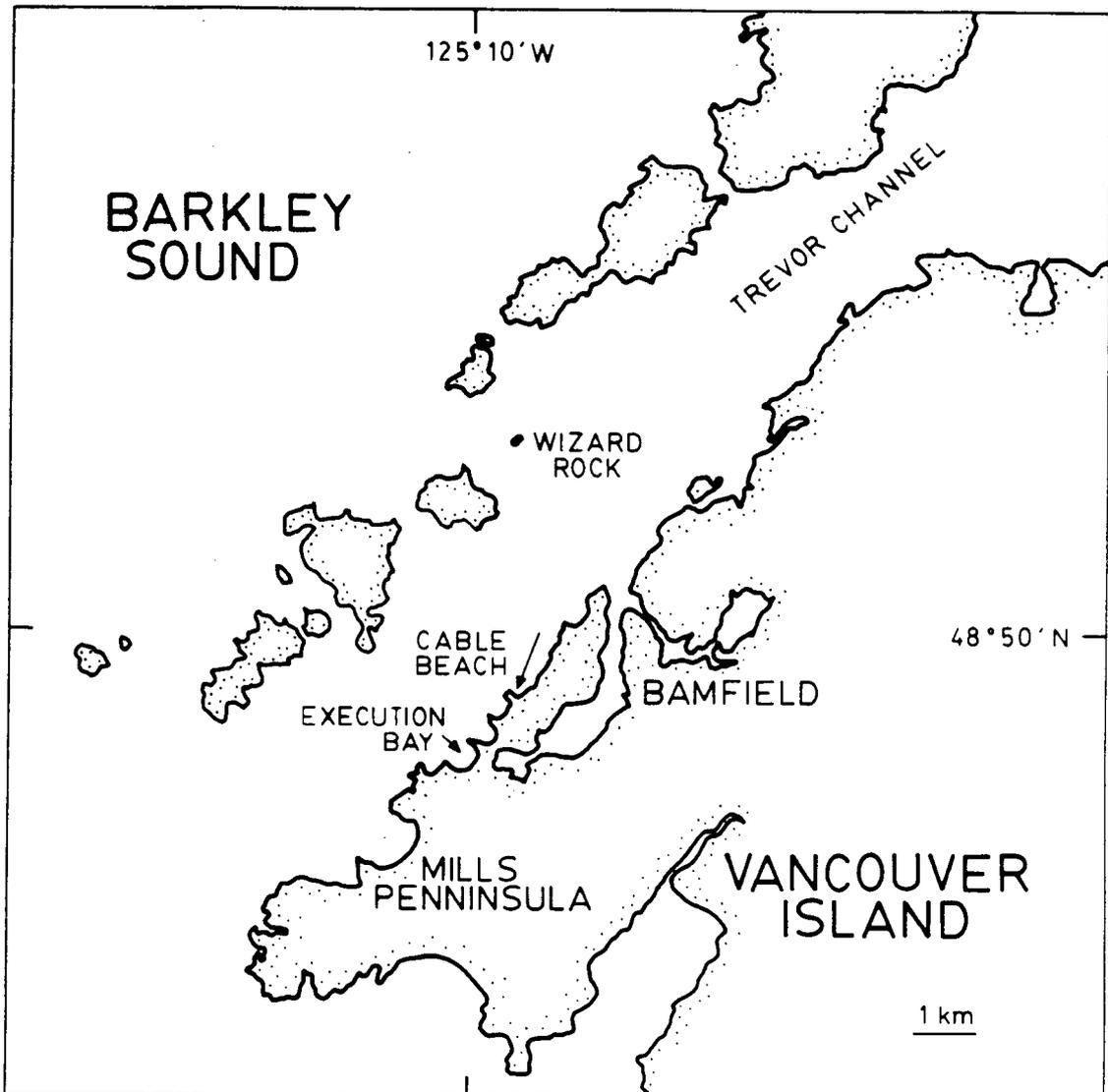


Figure 2.1. Map of Barkley Sound, Vancouver Island, showing 3 study sites: Wizard Rock, Cable Beach, and Execution Bay.

TABLE 2.1.

DATE	PERCENT
29 June 1981	2.77%
05 August 1981	11.11%
28 August 1981	0%
28 September 1981	11.11%
29 October 1981	5.55%
26 November 1981	69.44%

Table 2.1. Number of tagged cobbles not recovered in each of six surveys, expressed as a percentage of the number of cobbles initially tagged (n=36).

CHAPTER 3

ALLOCATION TO MEIOSPORE PRODUCTION IN LAMINARIA EPHEMERA

INTRODUCTION

Sporophytes of Laminaria ephemera are annual and semelparous. The general phenology of the species in Barkley Sound is given in Chapter 1. For the semelparous species, we can predict a relatively high fecundity and a short time-to-maturity, according to arguments presented in Chapter 1. In addition, a comparison of reproductive effort between populations of Laminaria ephemera can be made.

Fecundity among sporophytes can be estimated by determination of the number of spores produced per individual, where the number of spores is proportional to the surface area of the sorus produced. The surface area of the sorus can be measured graphically. Reproductive effort can be estimated as the ratio of vegetative to reproductive (soral) blade surface area.

MATERIALS AND METHODS

Laminaria ephemera was repeatedly harvested from each of two sites along the Mills Peninsula, Barkley Sound, B.C. (Figure 2.1). Dates of sampling are presented in Table 3.1. An east-facing promontory forms the western boundary of Cable Beach. This rock wall extends vertically to a depth of about 5 m, and meets a soft bottom punctuated by rocky outcrops. The site is subject to little wave action, but high surge accompanies winds from the southeast or from the north.

The study site comprised a patch roughly 3 m^2 , at 3 m depth, limited on two sides by rock wall, and characterized by small boulders and large cobble on a shifting, pebbly bottom.

Execution Bay is situated between the promontories of Execution Rock and Nudibranch Point. The back of the bay consists of rocky pavements extending to a bottom of sand and pebble. The study site constituted an area of about 5 m^2 , at 3 m depth, among cobble and boulders.

High initial plant densities (0.98 per cm^2) and small areal extent of each of these two sites allowed the subjective designation of all conspecific individuals within a site as members of a single population. No genetic inferences are made by use of the term "population" here or in the discussion that follows.

Plants were harvested from each site for a twelve week period in April through July, 1982. The sampling period at each site was determined by the developmental status of plants at that site. Sampling was initiated when juvenile sporophytes attained sufficient size for taxonomic identification (about 1 cm blade length), and was continued until fewer than fifty individuals remained within the study area.

The small size of pre-reproductive individuals necessitated use of a compressed air driven airlift sampler. The airlift allowed thorough sampling of the harvested area, without loss of individuals of smaller size classes. Airlift sampling was replaced by hand-collection of plants in samples taken later in the season.

Each sample consisted of all plants removed from an area of about 1 m^2 . Plants were transported to the laboratory in mesh bags, and maintained in

trays of flowing seawater. Blade and sorus perimeter were traced for all individuals within each sample. Larger plants were traced while fresh; smaller plants were pressed and dried prior to tracing. A correction factor of 1.78% was calculated as the mean of 68 replicates, for use in standardizing surface area measurements of pressed and dried plants with those of fresh plants.

Fifty plants were randomly selected from each sample. Total vegetative surface area and total sorus surface area were calculated for each plant by means of integrating the area beneath the traced perimeters, using a digitizing tablet in tandem with an LSI-11 computer. Values were recorded to 0.01 cm². Operator accuracy was estimated to be $\pm 0.19\%$, calculated as the mean of twenty-two trials.

Sorus samples were taken from 5 mature sporophytes from each of 2 study sites (Cable Beach and Execution Bay). One piece of approximately 1 cm² was excised from each plant, from the region immediately distal to the transition zone. Pieces of sorus were preserved in 4% formalin solution in seawater, and later sectioned in both longitudinal and transverse planes; sections from each plane were prepared and viewed independently. Preparations were examined microscopically for determination of number of spores per sporangium, and of number of sporangia per unit blade surface area. Five observations were made per preparation, on replicated sections, for a total of fifty observations per population.

One-way analysis of variance was performed according to Sokal and Rohlf (1969) subsequent to Bartlett's test for homogeneity of variance. Transformation of values prior to analysis was performed when appropriate, and is indicated in the text.

RESULTS

Mean vegetative surface area at Cable Beach decreased from 293.0 cm² (09 April 1982) to 116.6 cm² (13 June 1982; Figure 3.1). Mean soral surface area decreased from 48.4 cm² (09 April 1982) to 22.6 cm² (13 June 1982). Individual values ranged from a vegetative surface area of 0.2 cm² (09 April 1982) to 452.4 cm² (09 April 1982); and from a soral surface area of 0.1 cm² (13 June 1982) to 124.4 cm² (09 April 1982). No plants remained at the study site on the fourth sampling date of 05 July 1982.

Mean vegetative surface area at Execution Bay decreased from 687.6 cm² (19 April 1982) to 115.7 cm² (05 July 1982; Figure 3.2). Mean soral surface area declined from 100.6 cm² (19 April 1982) to 40.6 cm² (05 July 1982). Individual values ranged from a vegetative surface area of 0.3 cm² (19 April 1982) to 999.3 cm² (19 May 1982), and from a soral surface area of 0.7 cm² (13 June 1982) to 245.1 cm² (13 June 1982).

Ninety-two percent of the sample at Cable Beach was reproductive on the final sampling date of 13 June 1982 (Figure 3.3). One-hundred percent of the sample at Execution Bay was reproductive on the final sampling of 05 July 1982 (Figure 3.4). Samples from Cable Beach and from Execution Bay both showed 92% reproductive plants on the common sampling date of 13 June 1982.

The greatest percentage of every sample at Cable Beach fell within the smallest (0.1-100.0 cm²) size class (Figure 3.5). No plants remained within the largest (400.1-500 cm²) size class at the later sampling dates of 04 May and 13 June 1982).

The greatest percentage of each sample at Execution Bay fell within the smallest size class, except for that sample taken on 28 May 1982, in which the greatest percentage fell among the second, third, and fifth size classes (Figure 3.6). Plants were found among the largest size classes (800.1-900.0 and 900.1-1000.0 cm²) only on the sampling dates of 19 May and 28 May 1982. By 05 July 1982, no harvested plants exceeded 400.00 cm².

At Cable Beach, many plants among the larger size classes (up to 100%) were reproductive at all sampling dates (Figure 3.7). Few plants among the smallest size class (0.1-100.0 cm²) were reproductive at early sampling dates; 83.3% of this size class was reproductive at the latest sampling date (13 June 1982).

At Execution Bay, a maximum of 100% of the plants among some larger size classes were reproductive even in the earliest samples (19 April 1982 and 19 May 1982; Figure 3.8). There were no reproductive individuals within the smallest size class (0.1-100.0 cm²) on 19 April 1982, and the percentage of reproductive individuals within this size class remained relatively low until the final sampling date of 05 July 1982, at which time all plants were reproductive.

The mean ratio of sorus surface area to vegetative surface area at Cable Beach increased from 13.2% (09 April 1982) to 19.8% (13 June 1982; Figure 3.11). Individual values for samples from Cable Beach ranged from 0.3% (13 June 1982) to 83.1% (13 June 1982). Mean values for samples from Execution Bay increased from 14.7% (19 April 1982) to 31.7% (05 July 1982; Figure 3.11). Individual values ranged from 1.9% (28 March 1982) to 92.2% (05 July 1982).

All mature sporangia observed contained 32 spores per sporangium. Presumably, 16 of these 32 spores were female, and 16 were male (Kain, 1964). No attempt was made in this study to determine sex ratio of spores.

Microscopic examination of plants from Cable Beach gave a mean value of 7.72 sporangia per 0.012 cm ($n=50$; $S.D.=0.93$). This quantity is equivalent to 4.14×10^5 sporangia per cm^2 . For plants from Execution Bay, a mean value of 8.02 sporangia per 0.012 cm ($n=50$; $S.D.=0.77$) was obtained; this is equivalent to 4.47×10^5 sporangia per cm^2 . Analysis of variance showed no significant difference between the number of sporangia per unit length for plants from these two sites. Estimated mean numbers of spores produced were 1.32×10^7 spores per cm^2 (Cable Beach), and 1.43×10^7 spores per cm^2 (Execution Bay).

A conservative estimate of sporophyte fecundity can be made by combining minimum mean soral surface area with estimates of spores produced per unit area $\times 0.5$. The resulting fecundity estimates are 1.49×10^8 spores (Cable Beach) and 2.90×10^8 spores (Execution Bay).

DISCUSSION

Sporophytes collected from both Cable Beach and from Execution Bay exhibited several characteristics which may be expected of semelparous plants. These include little development of supportive tissues, relatively short time-to-maturity, and high percentage of reproductive plants within the population. At least two characteristics were exhibited which are generally not expected of strongly-semelparous plants; these include a potentially high pre-reproductive mortality and a low reproductive effort, judged by relatively low mean allocation of blade tissue to sorus formation.

The development of little supportive tissue is evident from inspection of the plant thallus, and of blade and stipe cross-sections (cf. Druehl, 1968). Stipes are thin and barely-corticated, and lack mucilage ducts. The holdfast is small and without haptera. Blades are thin, with little cortication and with slight development of medullary tissues.

The occasional formation of sori along the stipe (pers. obs.) indicates that stipe tissues may not be highly differentiated from blade tissues. Sorus formation along the stipe has not been reported for any other kelp species.

Individual time-to-maturity was not measured in this study, but can be estimated from field observation of the populations. Small (less than 10 cm² blade area) sporophytes were first observed at Cable Beach and at Execution Bay on 14 and 15 March, 1982; by 24 March, some plants at Cable Beach had become reproductive. By May, more than 25% of the plants harvested from both sites had produced sori (re: Figures 3.3 and 3.4), and by July, 100% of the harvested plants displayed sori and showed signs of incipient necrosis (Execution Bay), or all plants had disappeared (Cable Beach). Sporophyte life-span is therefore conservatively estimated to be 5 months, and is probably much less than that for an individual within a population. Developmental time-to-maturity may be as short as 1.5 to 2 months.

A very high percentage (Cable Beach: 92%; Execution Bay: 100%) of harvested plants were reproductive at the end of the season. These data do not indicate, however, that 92% or 100% of the initiated sporophytes became reproductive within the season, and there is no estimate available for the number of plants within a population which do not survive to reproductive maturity.

Field observations indicate that pre-reproductive mortality may in fact be high. Densities of very small sporophytes (less than 2 cm² blade surface area) were estimated to be 4.3 per cm² early in the season; such high densities were never observed among reproductive plants later in the season. Further, mortality occurring in the period between zygote formation and growth to identifiable size was not quantified, but is potentially high.

The ratio of soral surface area to vegetative surface area can be used as an estimate of reproductive effort (Pianka and Parker, 1975). This ratio averaged from 13% to 17%, with one outstanding mean value of 32%. Individual values, however, ranged from less than 1% to almost 93%. It appears, therefore, that almost the entire blade is developmentally capable of transformation to sorus tissue; consequently, the relatively low average values of 13% and 17% are unexpected in that they reflect a generally low reproductive effort. Two explanations are immediately apparent: 1) that fitness is not significantly enhanced by increasing the allocation of reproductive tissue to, say, 90%, and therefore no selective pressure favors such an increase; 2) that there exists some cost (sensu Bell, 1980 and 1984; Cody, 1966) associated with sorus production, and that this cost reduces the amount of sorus which can viably and profitably be produced without jeopardizing future survival. However, the existence of such a trade-off between enhanced sorus production and future survival seems untenable for the ephemeral sporophyte, in which survival beyond the end of the present reproductive episode is zero.

There is some evidence of both within- and between-site variation in life history traits. At both Cable Beach and Execution Bay, mean sorus size decreased with time. This trend is due to a small group of plants within each

population which grew very quickly, reached a large size, and produced a large sorus. These large and precocious plants were absent from later samples, which were comprised predominantly of plants of smaller size and smaller sorus area.

Sporophytes at Cable Beach were reproductive earlier in the season, and became senescent earlier in the season, than those at Execution Bay. Mean plant size at Execution Bay was greater, in all samples, than mean plant size for roughly concurrent samples from Cable Beach; a greater percentage of plants among the final sample was reproductive at Execution Bay than at Cable Beach; and reproductive effort (as the mean ratio of soral surface area to vegetative surface area) was, on average, greater at Execution Bay than at Wizard Rock. The population at Cable Beach, then, reproduced earlier, achieved a smaller mean thallus size, exhibited a lower average fecundity and a smaller average reproductive effort, and became senescent earlier in the season than the population at Execution Bay. It is impossible, however, from these data, to discriminate between the contributions of genotypic variation and phenotypic expression in determination of these site-specific traits.

TABLE 3.1.

CABLE BEACH:	09 April 1982	EXECUTION BAY:	19 April 1982
	04 May 1982		19 May 1982
	13 June 1982		28 May 1982
			13 June 1982
			05 July 1982

Table 3.1. Dates of harvests made at each of two sites, Cable Beach and Execution Bay.

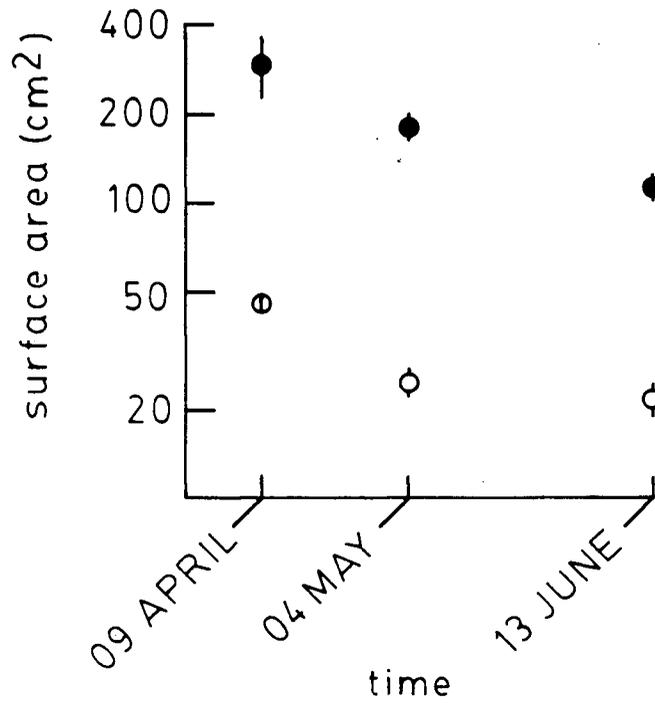


Figure 3.1. Semi-logarithmic plot of mean vegetative surface area (filled circles) and mean soral surface area (open circles), ± 1 S.E., among reproductive plants within samples collected from Cable Beach. (09 April: $n=5$; 04 May: $n=19$; 13 July: $n=46$; variable n results from the variable number of reproductive plants within each sample of 50 individuals).

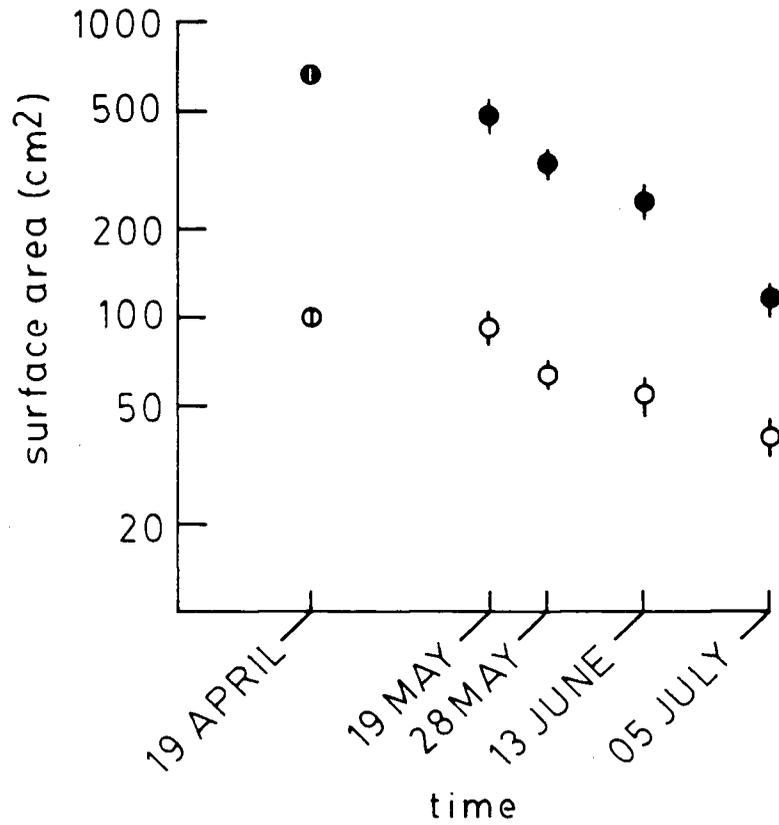


Figure 3.2. Semi-logarithmic plot of mean vegetative surface area (filled circles) and mean soral surface area (open circles), + 1 S.E., among reproductive plants within samples collected from Execution Bay. (19 April: n=2; 19 May: n=28; 28 May: n=44; 13 June: n=46; 05 July: n=50; variable n results from the variable number of reproductive plants within each sample of 50 individuals).

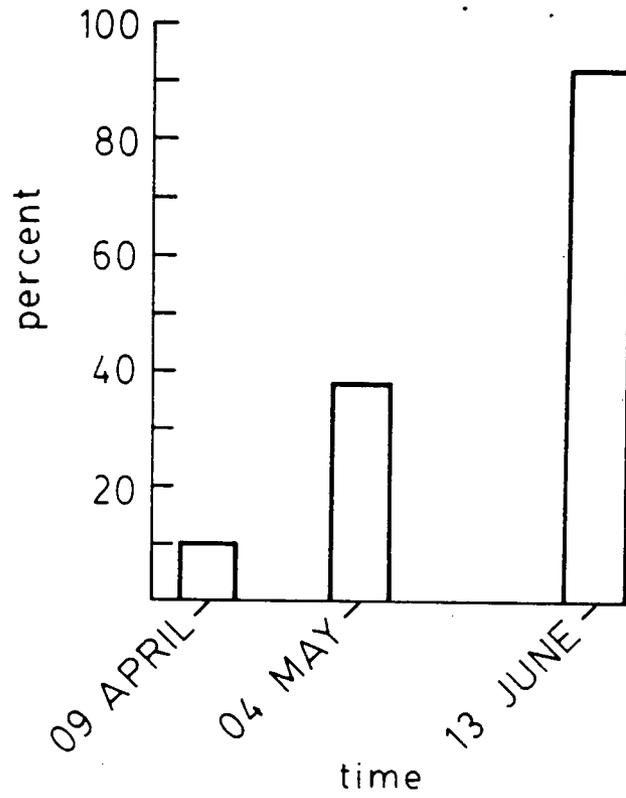


Figure 3.3. Percentage of soral plants among samples from Cable Beach.

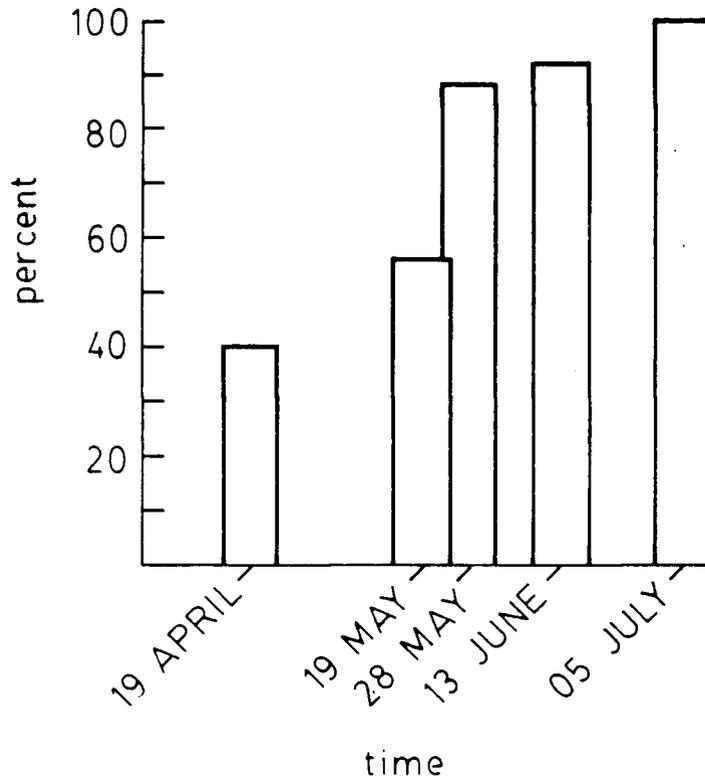


Figure 3.4. Percentage of soral plants among samples from Execution Bay.

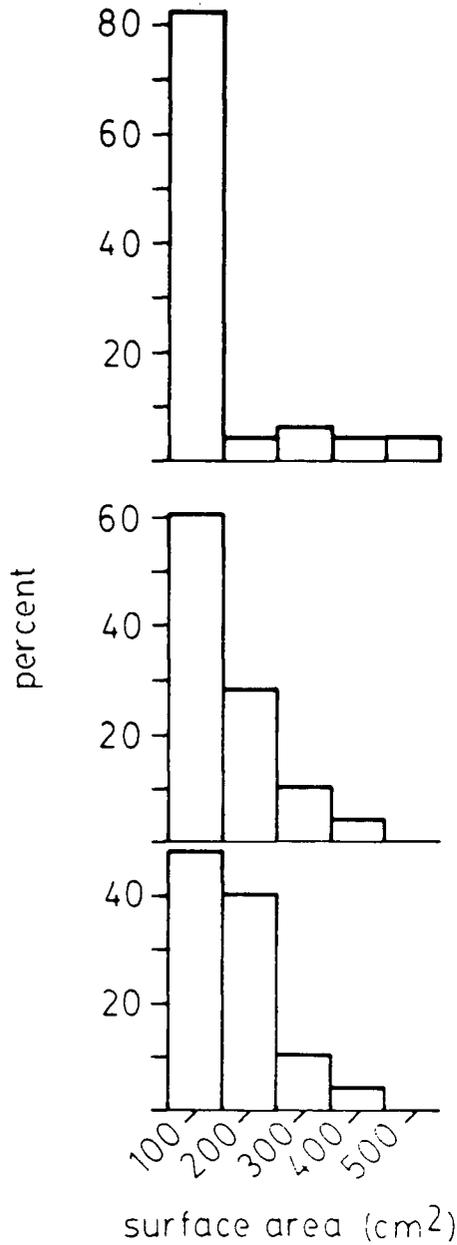


Figure 3.5. Percentage of plants falling within 100 cm² size classes, for three samples from Cable Beach; above: 09 April; middle: 04 May; below: 13 June, 1982.

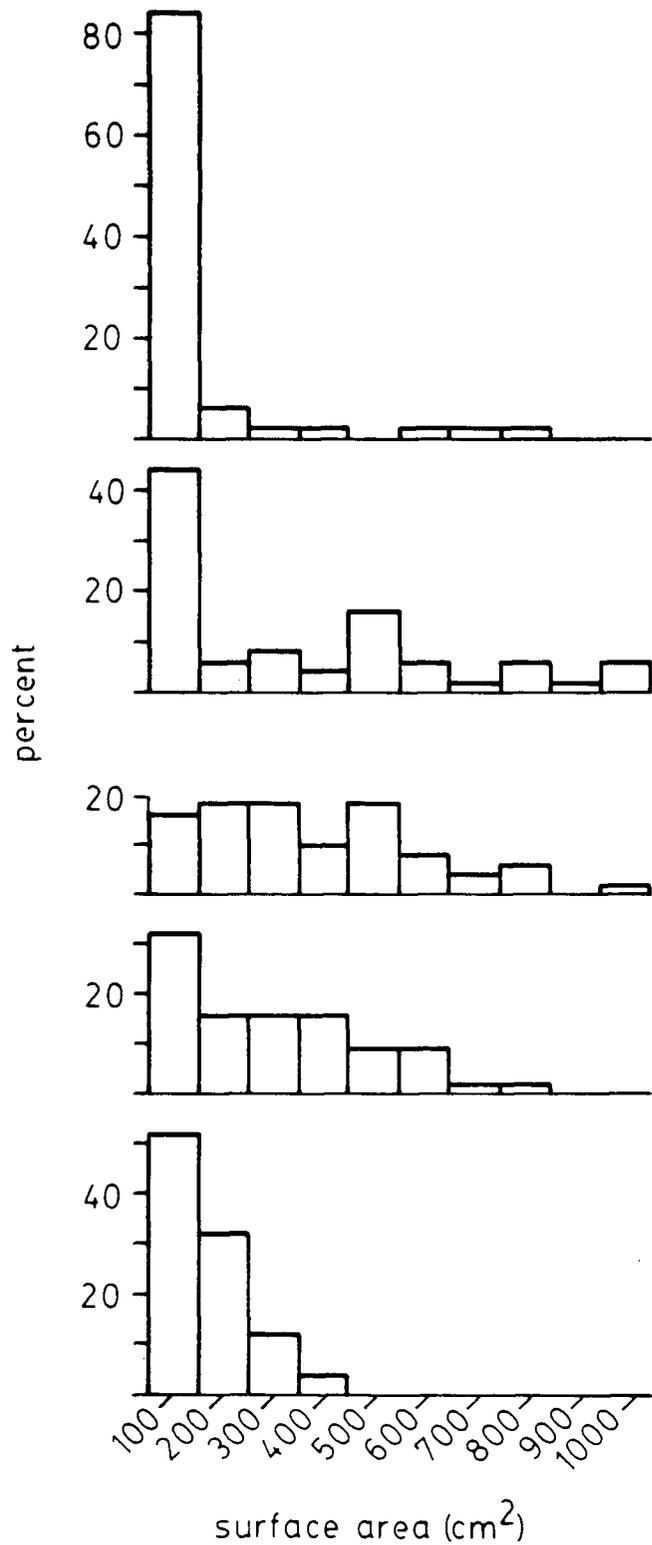
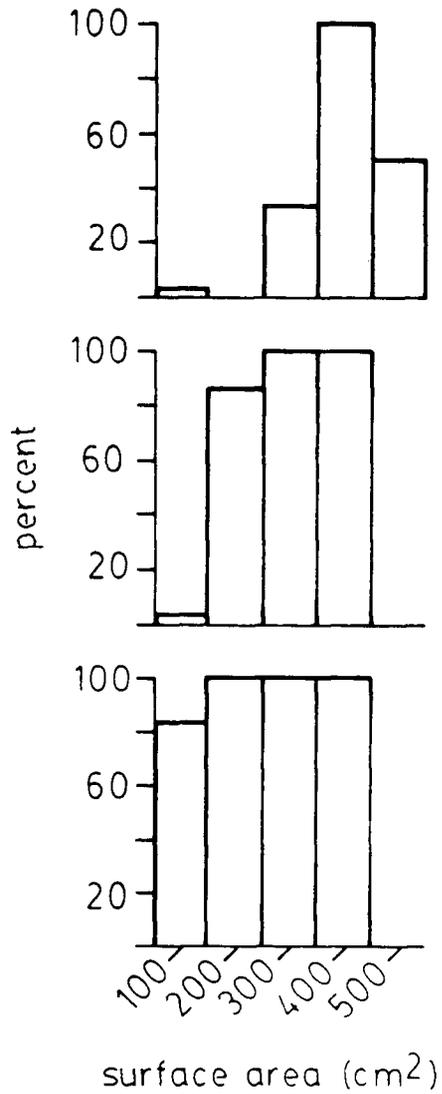


Figure 3.6. Percentage of plants falling within 100 cm² size classes, for five samples from Execution Bay; from top: 19 April; 19 May; 28 May; 13 June; 05 July, 1982.



Figure₂3.7. Percentage of reproductive plants within each 100 cm² (surface area) size class, for samples from Cable Beach. Above: 19 April; middle: 04 May; below: 13 June, 1982.

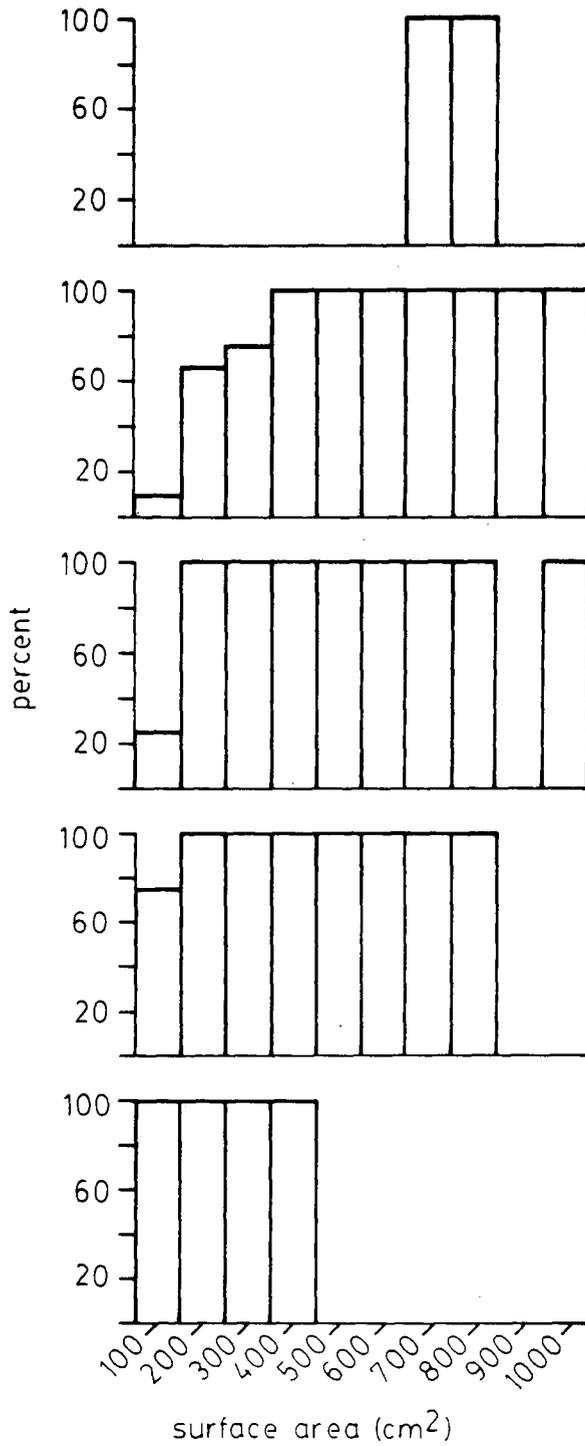


Figure 3.8. Percentage of reproductive plants within each 100 cm² (surface area) size class, for samples from Execution Bay. From top: 19 April; 19 May; 28 May; 13 June; 05 July, 1982.

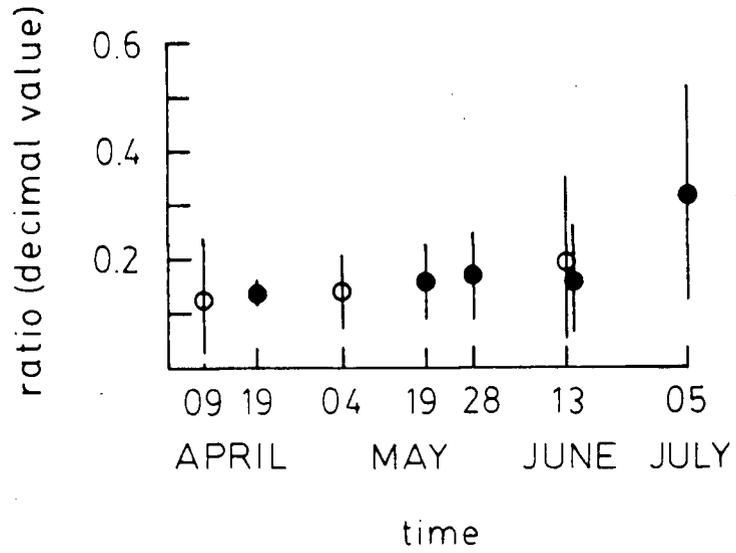


Figure 3.9. Mean ratio (expressed as a decimal value) of soral surface area to vegetative surface area, ± 1 S.D., for samples from Cable Beach (open circles) and from Execution Bay (filled circles).

CHAPTER 4

ALLOCATION TO MEIOSPORE PRODUCTION IN LAMINARIA SETCHELLII

INTRODUCTION

Sporophytes of Laminaria setchellii are perennial and iteroparous. The general phenology of the species in Barkley Sound has been presented in Chapter 1. According to the argument presented in Chapter 1, we can predict that the iteroparous species will exhibit a relatively low annual fecundity, prolonged time-to-maturity, and increasing reproductive effort with age.

Fecundity among sporophytes can be estimated by determination of the number of spores produced per individual, where the number of spores produced is proportional to the surface area of the sorus. Reproductive effort can be estimated as the ratio of vegetative to reproductive (soral) blade surface area.

MATERIALS AND METHODS

Laminaria setchellii was repeatedly harvested in Barkley Sound, B.C., from each of two sites, Wizard Rock and Execution Bay (re: Figure 2.1). Wizard Rock is a small, low island, the long axis of which runs roughly east to west. The northwest shore of the island is subject to little wave action, but high surge and strong currents accompany winds from the southeast or north. The rocky margin of the island extends to about 8 m depth, where it meets a sloping granitic pavement. L. setchellii occupies the sublittoral fringe, from about the 0 m tide level to 4 m depth.

The study population comprised an area of roughly 12 m by 2 m along the upper-subtidal margin. Estimated average density of L. setchellii at this site was 11.2 individuals per 0.25 m² (S.D.=1.55), calculated as the mean of 10 haphazardly placed 0.25 m² quadrats. All conspecific individuals within the study site were subjectively designated as members of a single population. No genetic inferences are made here by use of the term "population" here or in the discussion that follows.

Execution Bay has been previously described in Chapter 2. Laminaria setchellii occurs along the sublittoral margins of Execution Bay, as well as along the margins of wash-rocks and pinnacles in the center of the bay. The study population consisted of plants growing along a 10 m by 2 m length of rocky pavement at the back of the bay. Estimated average plant density for L. setchellii at this site was 13.2 individuals per 0.25 m² (S.D.=1.48), calculated as the mean of 5 haphazardly placed 0.25 m² quadrats. Again, all conspecific individuals within the study area were designated as members of a single population.

Plants were harvested from each study site for a 12 month period beginning in October, 1981 (Wizard Rock) and November, 1981 (Execution Bay). For each harvest, a course perpendicular to shore was chosen. Plants along this course were removed at the holdfast or at the juncture of the holdfast and stipe. No discrimination was made between plants of different size classes during harvesting. All plants encountered along the course were harvested until a total sample of more than 55 individuals had been obtained. An undisturbed area of at least 0.5 m width was allowed between successively harvested courses. Courses were chosen sequentially, in order to avoid sampling of previously harvested areas.

Samples were returned to the laboratory and maintained in flowing sea water prior to processing. For each plant, the blade was removed from the stipe at the transition zone. The perimeter of the entire blade was then traced onto paper. Distinction was made between old or residual blade tissue and newly-generated blade tissue. Blades were examined for the presence of sori; if present, sori were excised and these perimeters were also traced. Blades were discarded after tracing.

Fifty traced plants were randomly chosen from each sample. Total vegetative and total soral surface area was calculated for each plant as described in Chapter 3.

The diameter at the base and the total length of each stipe harvested was measured and recorded. The volume of each stipe was calculated as the volume of a cylinder (volume= πr^2 X height). Basal portions of all stipes were retained and immediately frozen for later sectioning, for purposes of age determination.

Sorus samples were taken from 5 reproductive sporophytes from each study site. One piece of approximately 1 cm² was excised from each individual, from a region midway along the frond. Each excised piece was preserved and later sectioned and examined microscopically as previously described in Chapter 3.

RESULTS

Mean vegetative surface among reproductive plants at Wizard Rock ranged from 299.4 cm² (28 January 1982) to 5254.4 cm² (18 June 1982; Figure 4.1). No discrimination between age or size class was made in calculating these mean values. Individual values among reproductive plants ranged from 55.7 cm² (19

November 1982) to 8136.6 cm² (05 August 1982). Analysis of variance performed on log-transformed values showed significant differences (p<.001 level) in mean vegetative surface area between samples taken on 19 November and 12 December 1981, and 28 January, 29 April, 18 June, and 05 August 1982. Samples taken on 15 October 1981 and 15 March 1982 were excluded from this analysis because of the small number of individuals (n=0 and n=2, respectively) within these samples. Further analysis of between-group differences showed significant difference (p<.001 level) between Group 1 (12 December 1981 and 28 January 1982) and Group 2 (29 April, 18 June, and 05 August 1982). There was no significant difference between samples within Group 2.

Mean soral surface areas at Wizard Rock ranged from 28.1 cm² (28 January 1982) to 109.2 cm² (05 August 1982); Figure 4.1). Individual values ranged from 0.02 cm² (18 June 1982) to 1202.3 cm² (19 November 1981). Analysis of variance performed on log-transformed values showed no significant difference (p<.001 level) between six samples taken 19 November and 12 December 1981, and 28 January, 29 April, 18 June, and 05 August 1982. Samples taken 15 October 1981 and 15 March 1982 were omitted from this analysis, as noted above.

Mean ratios of soral surface area to vegetative surface area at Wizard Rock ranged from 1.25% (18 June 1982) to 18.54% (19 November 1981; Figure 4.2). Individual values ranged from 0.01% (18 June 1982) to 44.80% (19 November 1981). Analysis of variance was performed after arc-sin transformation of decimal values. Results showed a significant difference (p<.001 level) in the ratio of soral surface area to vegetative surface area between samples. Further analysis of between-group variance showed significant difference (p<.001 level) between Group 1 (19 November 1981) and Group 2 (12 December 1981, 28 January, 29 April, 18 June, and 05 August 1982).

There was no significant difference between samples within Group 2.

The percentage of harvested plants bearing sori at Wizard Rock ranged from 0% percent (15 October 1981) to 54% (05 August 1982; Figure 4.3). The greatest number of soral plants was found on 12 December 1981 (34%) and on 05 August 1982 (54%). The smallest number of soral plants was found on 15 October 1982 (0%) and on 15 March 1982 (4%).

Mean vegetative surface areas among reproductive plants at Execution Bay ranged from 341.2 cm² (25 November 1981) to 5026.4 cm² (28 May 1982; Figure 4.4). No discrimination between age or size class was made in calculation of these values. Individual values among reproductive plants ranged from 74.6 cm² (28 January 1982) to 81.9 cm² (28 May 1982). Analysis of variance performed on log-transformed values showed a significant difference (p<.001 level) between samples. Further analysis showed a significant difference (p<.05 level) between Group 1 (15 March and 28 October 1982) and Group 2 (28 May 1982).

Mean soral surface areas at Execution Bay ranged from 40.5 cm² (15 March 1982) to 1116.3 cm² (28 October 1982; Figure 4.4). Individual values ranged from 1.1 cm² (28 May 1982) to 4206.7 cm² (28 October 1982). Analysis of variance performed on log-transformed values showed a significant difference (p<.001 level) between samples. Further analysis of between-group differences showed a significant difference (p<.001 level) between Group 1 (25 November 1981, 28 January, 15 March, and 28 May, 1982) and Group 2 (28 October 1982). There was no significant difference between samples within Group 1.

The mean ratios of soral surface area to vegetative surface area at Execution Bay ranged from 1.74% (28 May 1982) to 30.48% (28 October 1982;

Figure 4.2). Individual values ranged from 0.04% (28 May 1982) to 83.6% (25 November 1981). Analysis of variance performed on arc-sin transformed values showed a significant difference ($p < .001$ level) between samples. Further analysis showed a significant difference ($p < .001$ level) between Group 1 (25 November 1981 and 28 October 1982) and Group 2 (28 January, 15 March, and 28 May 1982). There was no significant difference between samples within either group.

The percentage of plants bearing sori at Execution Bay ranged from 6% (15 March 1982) to 48% (28 October 1982; Figure 4.5). The greatest number of soral plants were found on 28 May 1982 (34%) and on 20 October 1982 (48%), and the smallest number was found on 15 March 1982 (6%).

Correlation analysis (Spain, 1982) of soral surface area versus age showed no significant correlation between these two parameters. Correlation analysis of the percentage of reproductive plants within each sample versus age at Wizard Rock and at Execution Bay showed a significant positive correlation ($p < .001$ level) between these two parameters (Figures 4.6 and 4.7). Differences in the shape of the best-fit curve between these two sites is not considered to be important until confirmed by further sampling and analysis. The results of the analysis indicate that, for sporophytes among the populations samples, the probability of becoming reproductive increases with age.

Correlation analysis of stipe volume versus age showed significant positive correlation ($p < .001$ level) between these two parameters (Figures 4.8-4.11). The coefficient of determination obtained by analysis is not of sufficient magnitude to allow confident prediction of age by observation of stipe volume. These data do indicate, however, that stipe volume increases

with age, and this observation implies the occurrence of energetic processes which may have importance to other energetic aspects of the sporophyte life history.

All mature sporangia observed contained 32 spores per sporangium. A 1:1 sex ratio among spores is assumed (cf. Kain, 1964). A mean value of 7.82 sporangia per linear centimeter ($n=50$; $S.D.=0.87$) was obtained for samples from Wizard Rock. This value is equivalent to 4.25×10^5 sporangia per cm^2 . For samples from Execution Bay, a mean value of 6.36 spores per linear centimeter ($n=50$; $S.D.=1.44$) was obtained; this is equivalent to 2.81×10^5 sporangia per cm^2 . Analysis of variance showed that there exists a significant difference ($p<.001$ level) in number of sporangia per linear centimeter between samples from Wizard Rock and Execution Bay.

A conservative estimate of annual sporophyte fecundity can be made by combining minimum mean soral surface area with estimates of the number of spores produced per unit surface area \times (0.5). The resulting estimates are 1.91×10^8 spores (Wizard Rock) and 1.80×10^8 spores (Execution Bay). This formulation assumes that each plant surviving to reproduce produces a sorus equivalent to the observed minimum mean soral surface area in at least one reproductive period. The lack of age-specificity in the calculation of this estimate precludes assignment of any reproductive value to estimated fecundity.

DISCUSSION

Among the populations studied, there exists a strong seasonality to the processes of blade generation and stipe-holdfast generation, though the

precise timing of these processes may be somewhat site-specific. New blade tissues are generally initiated in October and November (Wizard Rock) or in January (Execution Bay); blade initiation and expansion are followed by stipe elongation and increase in girth, and by production of new haptera, in March and April (both sites). Sorus production may occur throughout the year, but is greatest in summer months (Wizard Rock) and in the fall (Execution Bay). Existing blades deteriorate and are sloughed in the early fall (Wizard Rock) and in the late fall and early winter (Execution Bay).

Populations of Laminaria setchellii at two sites in Barkley Sound show several life history characteristics which are consistent with those expected of iteroparous species. These characteristics include delayed maturity, substantial development of supportive tissues, and an average reproductive effort which is low in comparison with maximum values for individual reproductive effort, where reproductive effort is estimated as the ratio of sorus surface area to vegetative surface area.

Age of first reproduction in Laminaria setchellii is generally delayed until the second or third year, though individuals are capable of reproduction in the first year. Beyond the age of first reproduction, there exists no apparent correlation between age and the magnitude of sorus production in any season. There does exist, however, a positive correlation between age and the probability of sorus production within a season.

The observations of a positive correlation between age and stipe volume, and of no correlation between age and fecundity, suggest differential allocation of resources to these two functions. That is, stipe maintenance and growth may constitute conservative physiological functions which predictably demand a proportion of annual resources, whereas fecundity, with no observable

age-dependent correlation beyond the age of first reproduction, may only occasionally demand resource allocation, this allocation being independent of individual age and perhaps a response to other (unidentified) signals. Implicit in this argument is the existence of within-plant competition for resources; this may not be a justifiable assumption for the kelps, in which stipe, holdfast, blade, and sorus tissues are all pigmented and potentially capable of photosynthesis and nutrient assimilation. Generation of new stipe and holdfast tissues is greatest during March and April; observed sorus production is minimal during these months.

The ratio of sorus surface area to vegetative surface area can be used as a measure of reproductive effort (Pianka and Parker, 1975). The mean ratios (Wizard Rock: 18.54%; Execution Bay: 30.48%) are small when compared with the corresponding maximum individual values (Wizard Rock: 44.80%; Execution Bay: 83.63%). This indicates that reproductive effort is generally low, and that actual allocation to sorus production is less than that which is physiologically possible.

Values obtained for individual and mean sorus production may reflect error inherent in the discrete sampling of a continuous variable. That is, sorus production was not measured through time for any single individual; resulting values reflect an instantaneous measurement and may in fact underestimate sorus production. It should be noted, however, that vegetative surface area also constitutes a continuous variable. Expressing sorus surface area as a fraction of vegetative surface area should therefore reduce this error, and values obtained are considered to be strongly indicative of actual values.

Reproductive individuals were found among populations throughout the year, and only one sample (Wizard Rock: 15 October 1981) contained no reproductive plants. Abundance of reproductive plants varied both seasonally and between populations. At Wizard Rock, soral plants were most abundant in summer months (June and August 1982) and in the winter (December 1981), and were less abundant in the fall and spring. At Execution Bay, reproductive plants were most abundant in the late spring (May 1982) and in the fall (October 1982).

The proportion of reproductive plants was less than 50% in all samples but one (Wizard Rock, 05 August 1982: 54%). This result contrasts sharply with the observed high proportions of reproductive individuals found among populations of a congeneric annual species (re: Chapter 3). It is possible, however, that for Laminaria setchellii, the summed proportion of reproductive individuals for any annual period is greater than the values obtained here. The manner in which these data were collected precludes confident prediction of the total number of individuals reproducing annually.

There is evidence of site-specific differences in expression of life history characteristics among populations of Laminaria setchellii. Timing and magnitude of reproductive events varied between the two populations, as discussed above. It is impossible from these data to distinguish between genotypic differences and phenotypic plasticity in the determination of site-specific traits.

TABLE 4.1.

WIZARD ROCK:	15 October 1981	EXECUTION BAY:	25 November 1981
	19 November 1981		28 January 1982
	28 January 1982		15 March 1982
	29 March 1982		28 May 1982
	18 June 1982		18 October 1982
	05 August 1982		

Table 4.1. Dates of harvests made at each of two sites, Wizard Rock and Execution Bay.

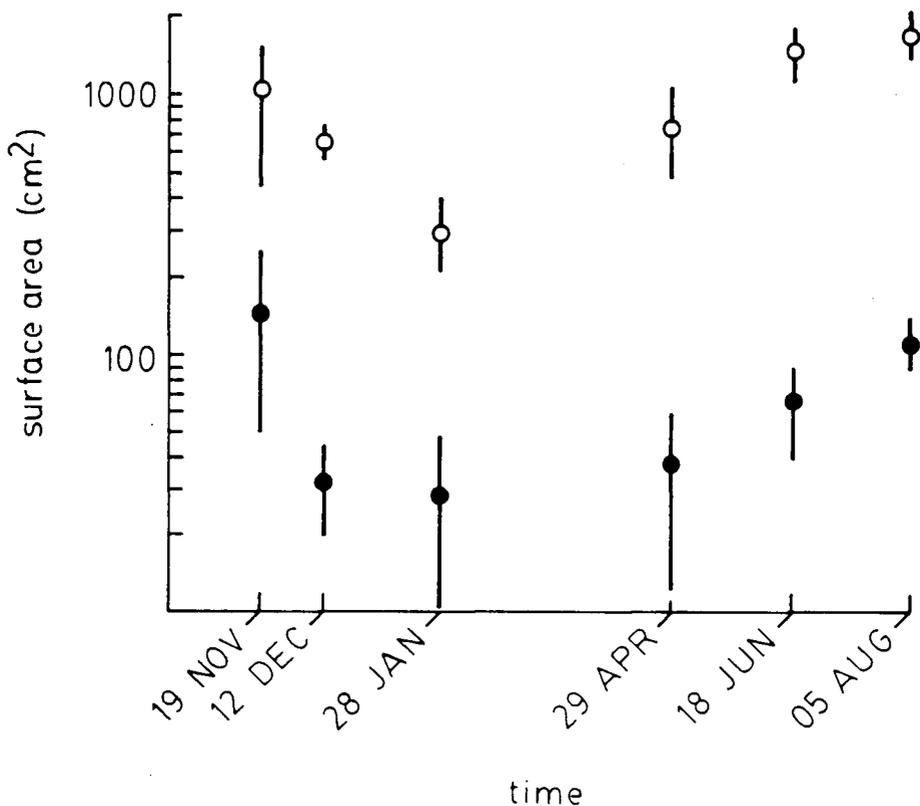


Figure 4.1. Semi-logarithmic plot of mean vegetative surface area (open circles) and mean soral surface area (filled circles), + 1 S.E., among reproductive plants within samples collected from Wizard Rock. (19 Nov.: n=5; 12 Dec.: n=17; 28 Jan.: n=4; 29 April: n=5; 18 June: n=19; 05 Aug.: n=27; variable n results from the variable number of reproductive plants within each sample of 50 individuals).

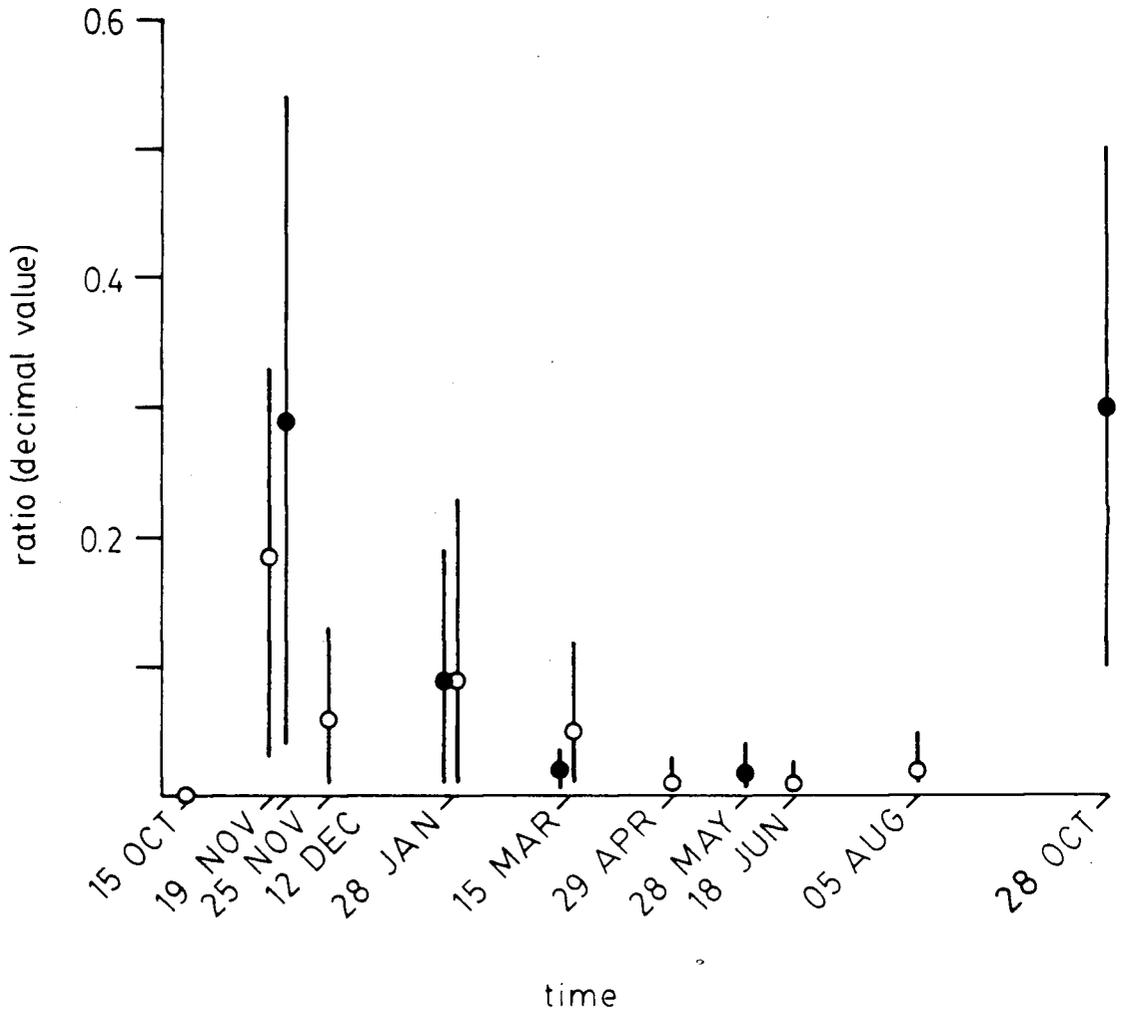


Figure 4.2. Mean ratio (expressed as a decimal value) of soral surface area to vegetative surface area, ± 1 S.D., for samples from Wizard Rock (open circles) and Execution Bay (filled circles).

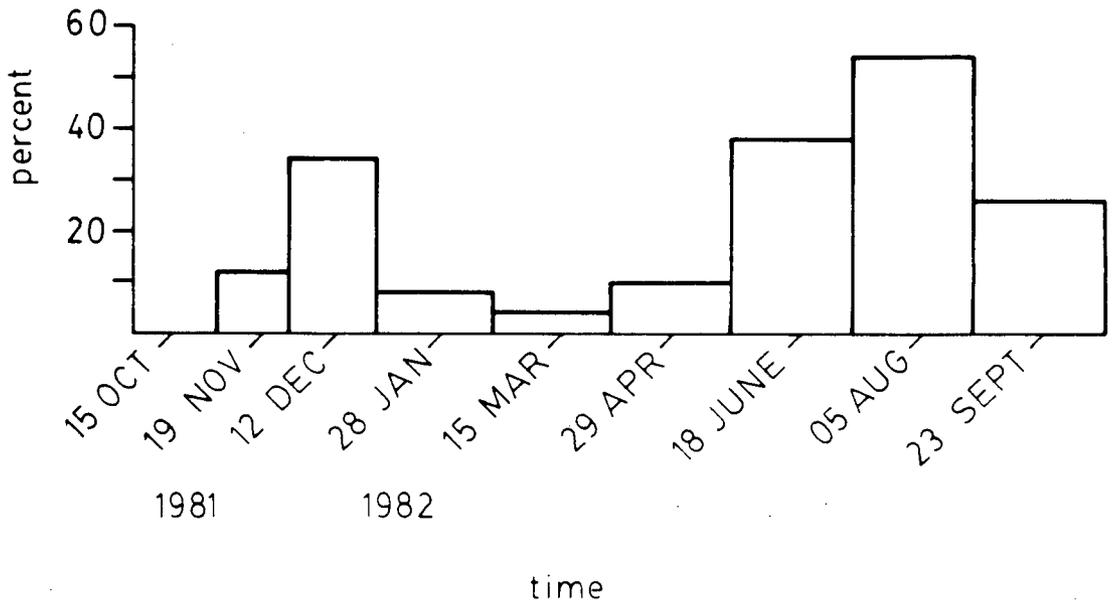


Figure 4.3. Percentage of soral plants among samples at Wizard Rock.

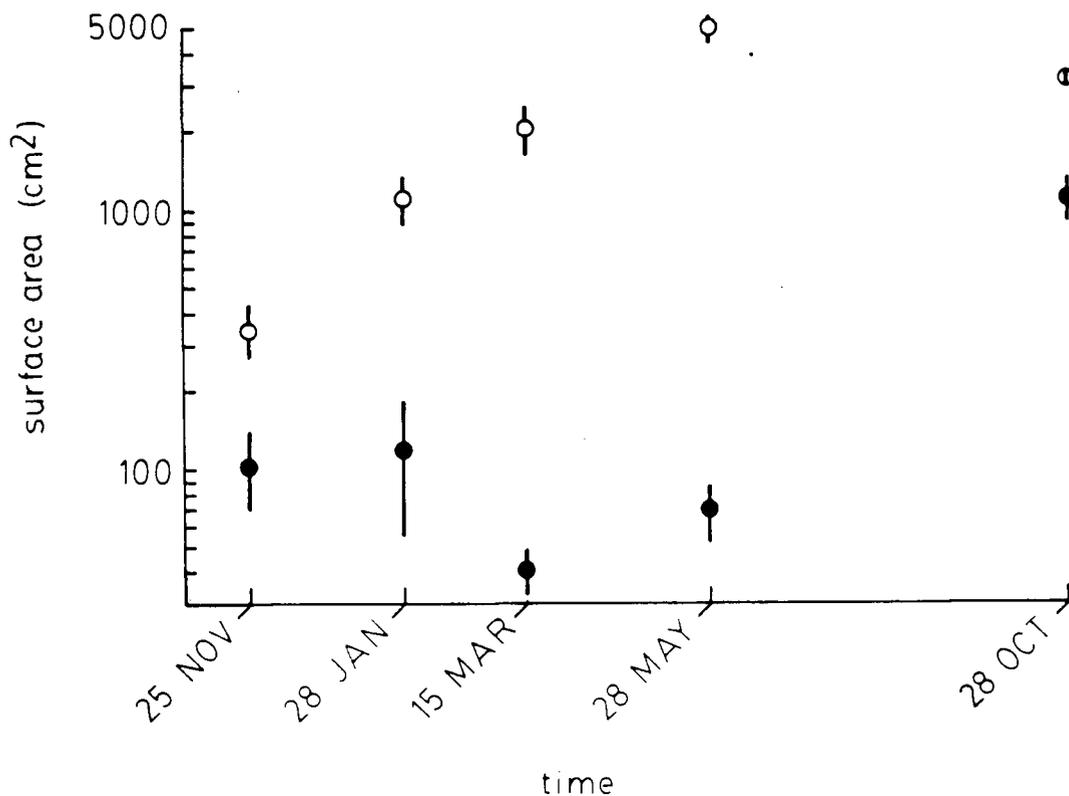


Figure 4.4. Semi-logarithmic plot of mean vegetative surface area (open circles) and mean sororal surface area (filled circles), ± 1 S.E., among reproductive plants within samples collected from Execution Bay. (25 Nov.: n=13; 28 Jan.: n=8; 15 March: n=3; 28 May: n=17; 28 Oct.: n=24).

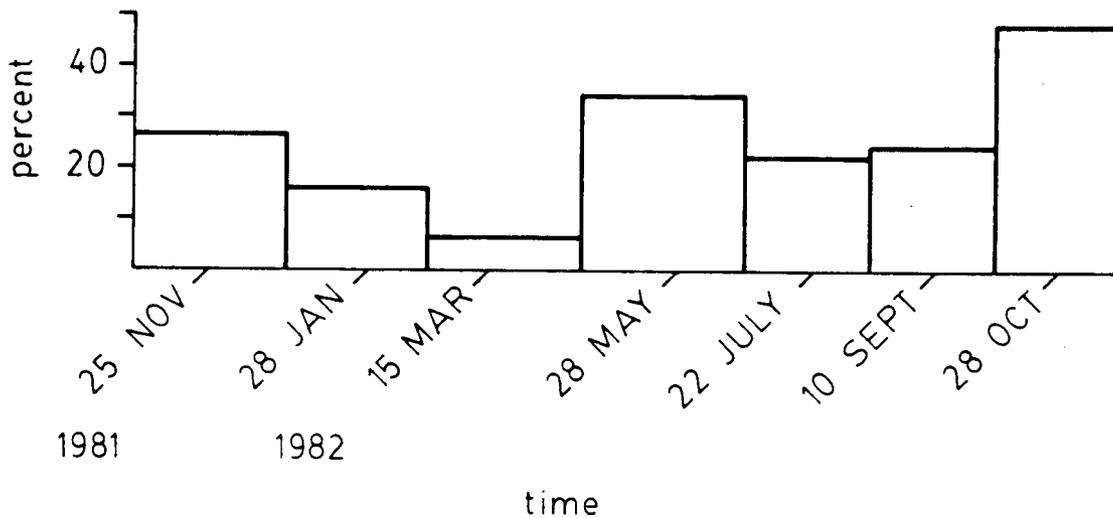


Figure 4.5. Percentage of soral plants among samples from Execution Bay.

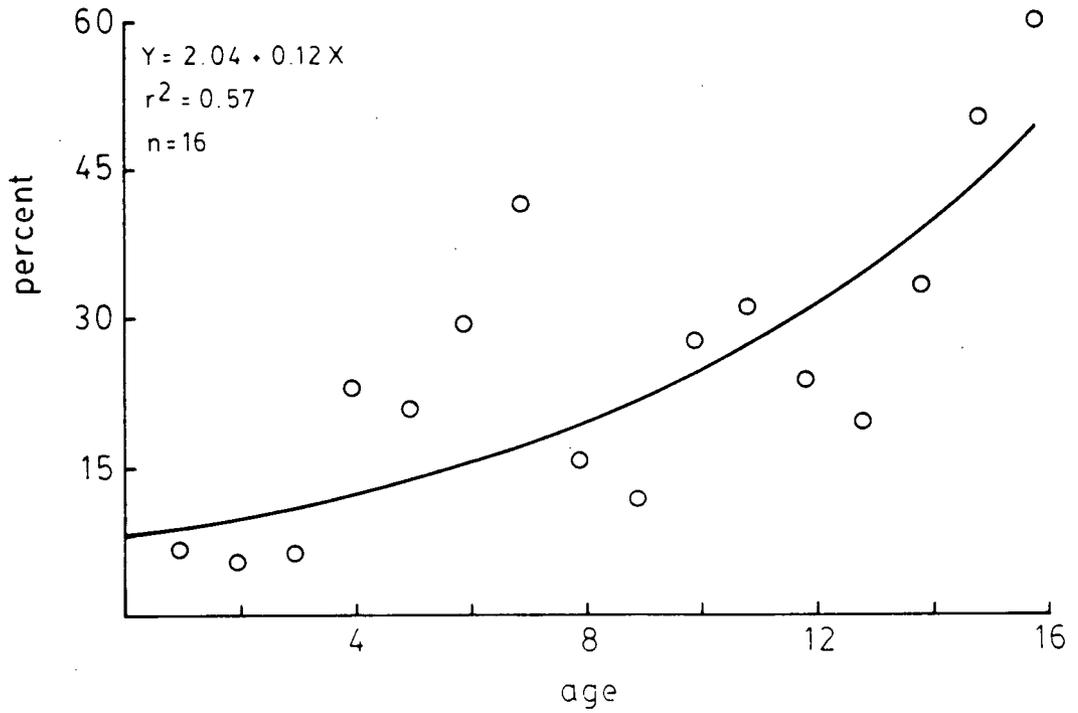


Figure 4.6. Best-fit curve generated by correlation analysis of percentage of reproductive plants versus age, for samples from Wizard Rock.

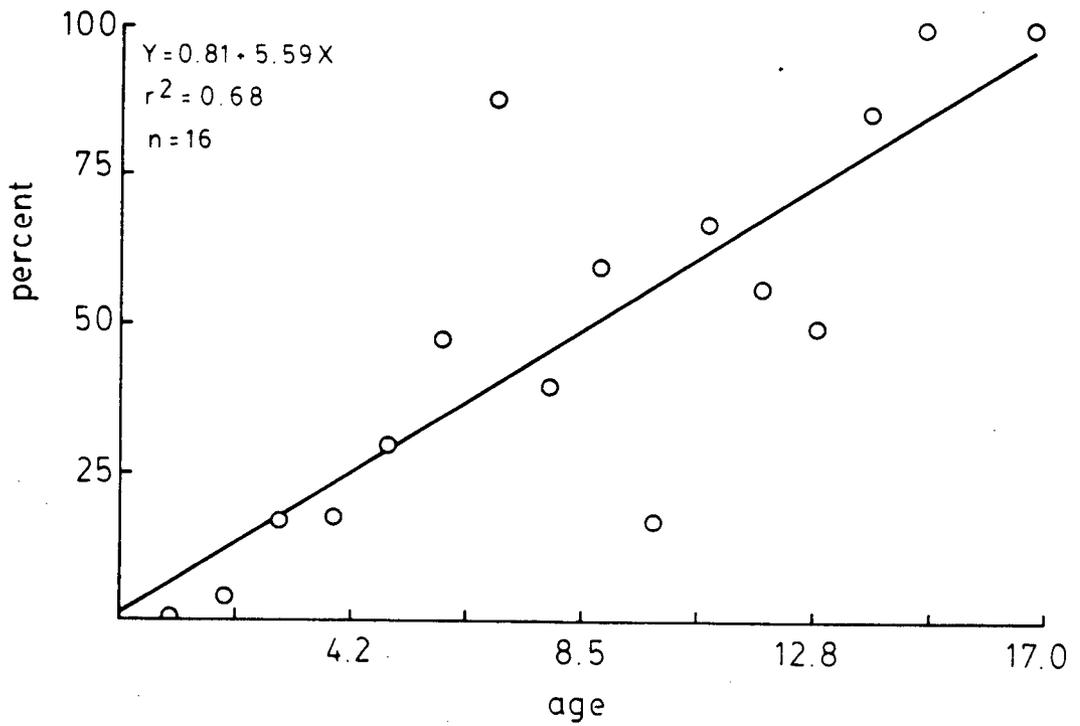


Figure 4.7. Best-fit line generated by correlation analysis of percentage of reproductive plants versus age, for samples from Execution Bay.

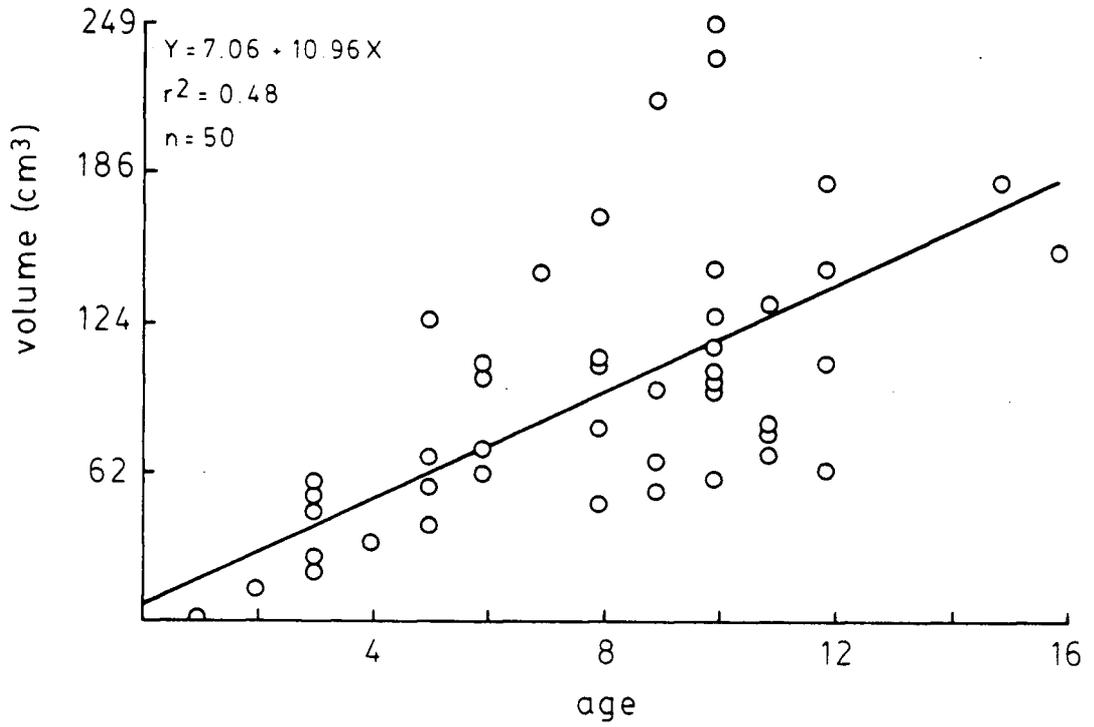


Figure 4.8. Best-fit line generated by correlation analysis of stipe volume versus age at Wizard Rock, 05 Aug. 1982.

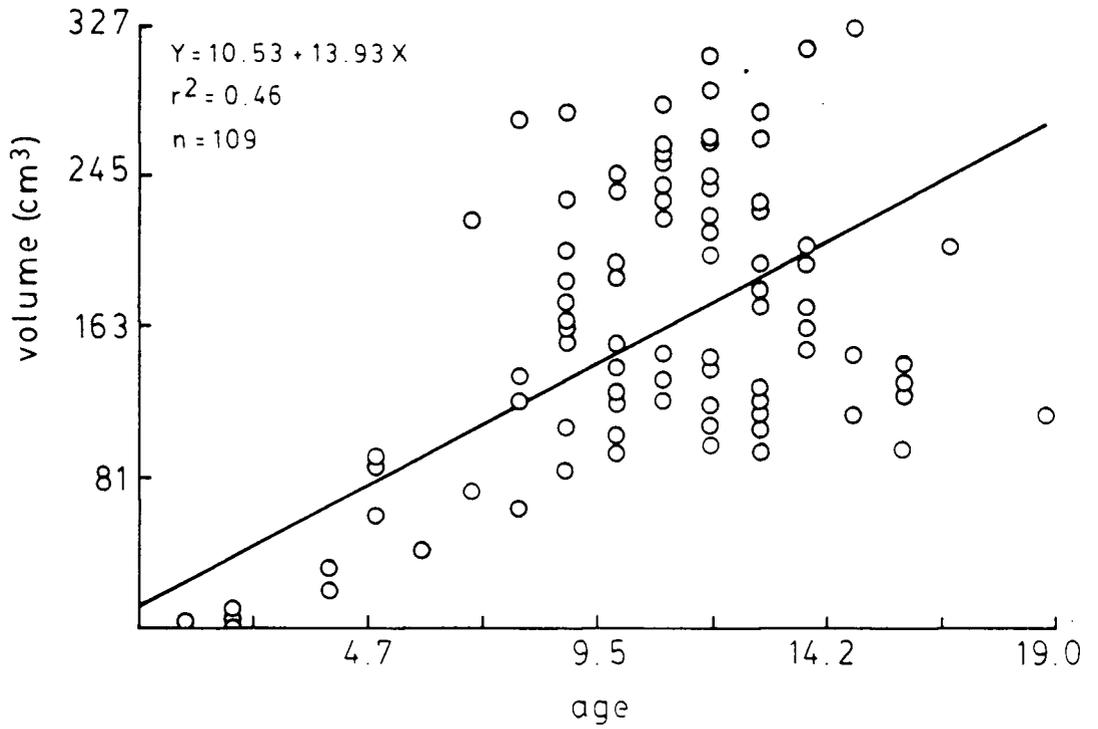


Figure 4.9. Best-fit line generated by correlation analysis of stipe volume versus age at Wizard Rock, 18 Nov. 1982.

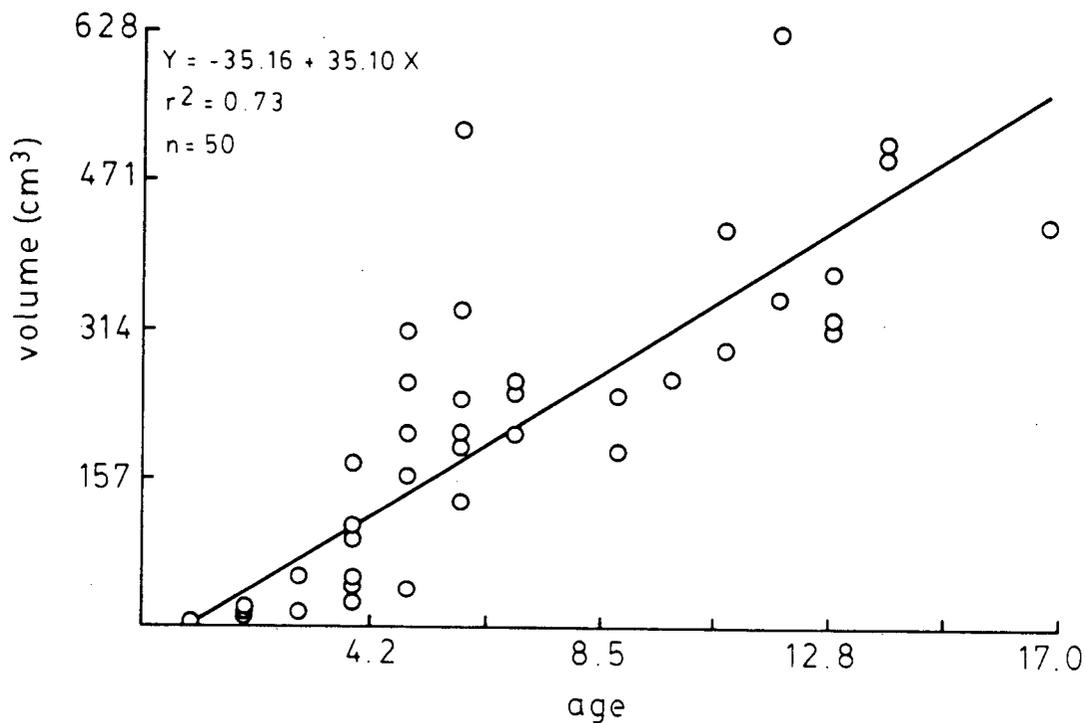


Figure 4.10. Best-fit line generated by correlation analysis of stipe volume versus age at Execution Bay, 28 Oct. 1982.

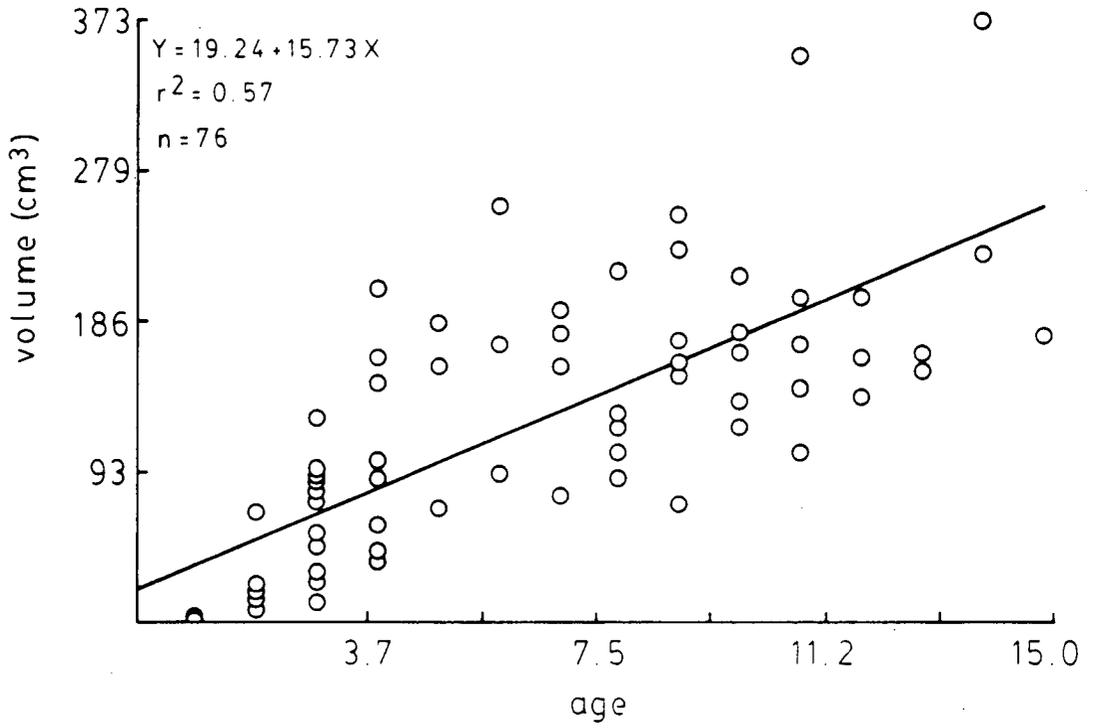


Figure 4.11. Best-fit line generated by correlation analysis of stipe volume versus age at Execution Bay, 10 Nov. 1982.

CHAPTER 5

AGE STRUCTURE AMONG POPULATIONS OF LAMINARIA SETCHELLII

INTRODUCTION

Among populations of perennial organisms, age-specific processes of reproduction and survivorship ultimately determine the population rate of increase. Quantification of the rate of increase consequently demands that these age-specific processes are observable. Identification of individual age is therefore a crucial first step in the determination of population rate of increase.

For the purposes of population projection, 'r', or instantaneous rate of increase, may be calculated as the natural logarithm of the eigenvalue of the age-structured matrix (Leslie, 1945). Such matrix formulations demand that the age distribution of the population be known, and usually require that this age distribution is stable (Michod and Anderson, 1980; Caughley and Birch, 1971; Leslie, 1945).

Age distributions among algal populations are largely unknown, due principally to the lack of an adequate criterion by which to determine individual age. However, Kain (1963), Novaczek (1981), and Dayton et.al. (1984) have used the concentric rings visible in the stipes of some kelps in order to determine age; correlational evidence only has been used to show that such rings are annual in formation. Estimates of individual age and of population age distribution for Laminaria setchellii have not been reported in the literature. The present study describes the age distribution of Laminaria

setchellii at two sites in Barkley Sound, Vancouver Island, B.C.

MATERIALS AND METHODS

Size class frequency by basal diameter was estimated in a series of repeated, non-destructive measurements made on a single population of Laminaria setchellii at each of two study sites, Wizard Rock and Execution Bay. Estimated average density of the population at Wizard Rock was 8.4 plants per $.025 \text{ m}^2$ (calculated as the mean of 5 haphazardly placed 0.25 m^2 quadrats). The population was situated on an outcrop approximately 2.5 m X 2 m, at about 3 m depth. Observed total population size ranged from 99 to 122 individuals for the sampling period of 25 August 1981 to 18 November 1982.

Estimated average density of the population at Execution Bay was 7.4 plants per 0.25 m^2 (calculated as the mean of five haphazardly placed 0.25 m^2 quadrats). The population was situated on an outcrop approximately 2.5 m X 1 m, at a depth of about 2.5 m. Observed total population size ranged from 75 to 92 individuals for the study period of 25 August 1981 to 02 November 1982.

The basal diameter of all identifiable individuals of Laminaria setchellii within each population was measured, in situ, at intervals of about six weeks. Measurements were made using plastic Vernier calipers. Values were recorded to the nearest millimeter. Measurement error was estimated to be not more than 6.77%, calculated as the mean of 20 repeated measurements on tagged (therefore, identifiable) individuals. This error quantity results primarily from the slight eccentricity of the Laminaria setchellii stipe. Success in locating and measuring each plant within the population at a single observation time was 96.1%, calculated as the mean of 4 sequential trials.

All plants remaining among the study populations at both study sites were harvested in November 1982. In the laboratory, the basal diameter of each plant was measured. The basal portion of each stipe was retained and frozen for later sectioning. Age class frequency among the sampled populations was determined by counting basal stipe rings in cross section (re: Appendix A). Each stipe was sectioned at a distance of less than 0.5 cm from the holdfast. Entire cross sections were cut by hand, and these were examined beneath a dissecting microscope using a combination of transmitted and reflected light. The maximum number of annual growth rings were counted and recorded for each harvested plant.

Age class frequencies were determined for one additional population each at Wizard Rock and at Execution Bay. Repeated harvests of 50 plants each were made between 19 November 1981 and 23 September 1982 (Wizard Rock), and between 25 November 1981 and 28 October 1982 (Execution Bay; re: Chapter 4 for harvesting methods). Stipes of all individuals were sectioned and maximum number of rings were counted, as above. Data obtained from repeated harvests at a single site were pooled in groups of 150-200, by date of harvest, for purposes of analysis.

RESULTS

Size class distribution by 2 mm basal diameter increments was determined for a population at Wizard Rock (Figure 5.1). Diameters ranged from 1.0 mm (18 March, 07 July, 18 November 1982) to 28.0 mm (18 March 1982). More than 72% of the plants within within each sample fell among the 12-24 mm size classes. For the first three samples, the greatest percentage of plants fell within the 17-18 mm size classes; this peak shifted to the 19-20 mm size class

for all but one sample taken after 29 October 1981.

The percentage of plants falling within the smallest size class (1-2 mm basal diameter) may be some indication of recruitment during the sampling period. This quantity increased from 0% (29 October 1981) to 11% (11 June and 07 July 1982), and decreased again to 4% (18 November 1982). The age class distribution for this population at Wizard Rock was determined on 18 November 1982 (Fig. 5.2). Seventy percent of the population was of age 8-14 years. Fifteen percent were 1-2 years. The shape of the age class distribution is similar to that of the size class distribution obtained for the same population on 18 November 1982.

The age class distributions for eight harvests from Wizard Rock were pooled in two groups according to date of harvest (Fig. 5.3). No single age class comprised more than 12.5% of the population. The peak of 11.5% at 11 years in the first pooled group (19 November 1981 through 15 March 1982) shifted to 12.5% at 12 years in the second pooled group (29 April through 23 September 1982). Similarly, the minor peak of 8% at five years in the first group shifted to 9% at six years in the second group.

Size class distribution by increments of 2 mm basal diameter was determined for a population at Execution Bay (Fig. 5.4). Stipe diameter ranged from 1.0 mm (11 December 1981, 25 July 1982) to 28.0 mm (02 November 1982). No single size class comprised more than 20% of the population, and no consistent peak size classes were apparent within this population.

The percentage of plants within the 1-2 mm size class increased from 0% (25 August, 26 September, 29 October 1981) to 11% (18 March, 25 July 1982), and decreased again to 1% (16 October 1982). The age class distribution for

this population at Execution Bay was determined on 10 November 1982 (Fig. 5.5). Seventeen percent of the population was three years of age, and 9% were ten years of age.

The age class distributions for seven harvests made at Execution Bay were pooled in two groups according to date of sampling (Fig. 5.6). For the first pooled sample (25 November 1981 through 15 March 1982) 83% of the population was among the 1-5 year age classes, with the remaining seventeen percent distributed between the 6-14 year age classes. For the second pooled samples (28 May through 28 October 1982), 70% of the population was distributed among the 1-6 year age classes; the remaining 30% were distributed among the 7-17 year age classes.

DISCUSSION

Size class distribution of Laminaria setchellii by basal diameter does not necessarily reflect the age class distribution of the population. Size class frequency may, however, reflect populational transitions through time, and the frequencies of the smaller size classes may provide an estimate of recruitment into a population, when repeated measurements are made. The age class distributions presented for 4 populations at 2 sites were neither similar between populations at a single site, nor between sites. The roughly bimodal age class distributions exhibited by these populations indicate that the normal or stable age distribution (sensu Lotka, 1922) has not been achieved. The stable age distribution requires, by definition, that the age distribution is self-perpetuating, and that reversion to such a distribution will occur following disturbance (Lotka, 1922; 1956). The bimodal age distribution is intuitively unstable in that an age class exhibiting a low-frequency at an intermediate age cannot generate an age class of greater

frequency at a later age. For example, at Wizard Rock (Fig. 5.2), a frequency of 0% among the 3 year age class cannot give rise to a frequency of 14% among the 12 year age class, under conditions of stability.

Two processes may account for the observed age distributions. Annual fluctuations in sporophyte or gametophyte fecundity may produce variable numbers of zygotes and, in turn, variable numbers of annual recruits. Comparison of the very high numbers of spores produced (re: Chapter 4) with the small numbers of recruits observed within these populations does not, however, support this argument. Specifically, the high number of spores produced by a population is not likely to limit recruitment into that population.

It is more likely that the observed age distributions are the product of episodic recruitment and variable survivorship among recruits. It has been demonstrated (Kirkman, 1981; Pearse and Hines, 1979; Lobban, 1978a) that recruitment beneath an established canopy is minimal. Successful recruitment may depend upon the creation of newly-available space. Patch size and the temporal window of space availability would therefore determine recruitment success within a canopy; these two factors are sufficient to explain both the observed differences in age structure between the populations studied, and the absence of the normal age distribution among these populations.

Kain (1971; 1963) has reported age distributions for populations of Laminaria hyperborea in the North Atlantic. The reported age distributions exhibit no similarity between populations, and show no evidence of the normal age distribution. Dayton et.al. (1984) have reported a weakly bimodal age distribution for a population Laminaria setchellii in California in which the first and fourth year classes are most abundant. The data of Kain (1971;

1963) and of Dayton et.al. (1984) are consistent with data obtained in this study for Laminaria setchellii in British Columbia; Kain's data support the argument proposed above concerning saltatory recruitment in Laminaria.

Absence of the normal age distribution among the populations studied does not necessarily imply that the populations are declining in size. If the number of embryosporophytes produced within a population each year is sufficient to entirely replace that same population (and estimates of meiospore production indicate that this is plausible), then the population may experience no decrease in size.

One can postulate that the number of embryosporophytes initiated far exceeds the number of recruits surviving to begin the second year. If this is true, then the populations studied may best be described by a Deevey Type III survivorship curve. Williams (1975) has discussed the ramifications of a very high rate of gamete production coupled with a very low rate of offspring survival. Williams' discussion makes the important point that such systems may not, in fact, behave according to Markovian dynamics. Markovian dynamics demand, strictly, that the sum of the elements of each column in the appropriate Leslie-type matrix equals one, and further assume that the state of the system (population) at time $T+1$ is predictable from the observed state at time $T+0$. If a system proves to be non-Markovian in behavior, then conventional matrix formulations are not applicable. An important consequence of non-Markovian behavior to the dynamics of Laminaria setchellii in particular, and to the kelp life history in general, is that if population size at time $T+1$ is not determined by the life history parameters observable at time $T+0$, then the population dynamics may be the result of stochastic processes which cannot be estimated according to existing models.

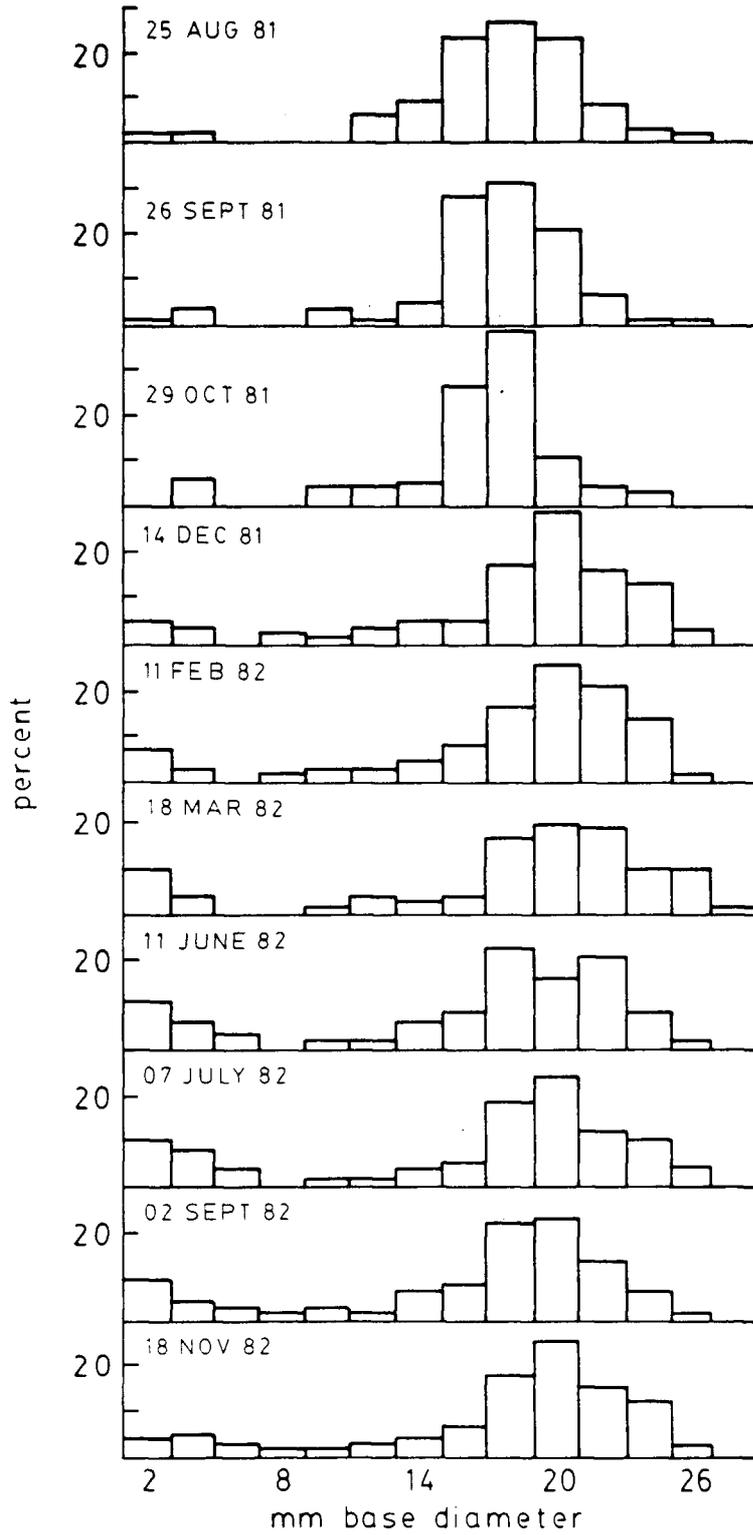


Figure 5.1. Size class distribution by basal diameter for ten repeated samples at Wizard Rock.

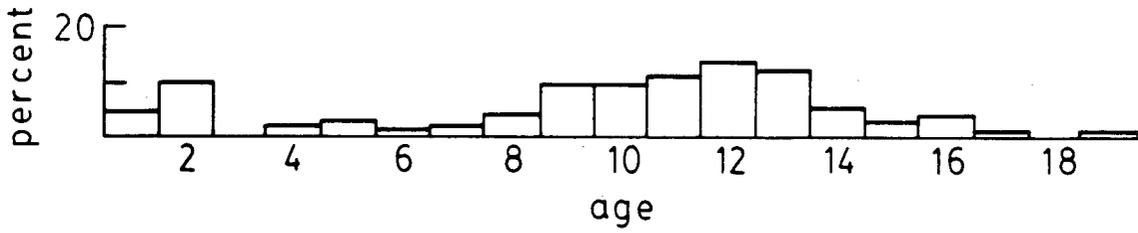


Figure 5.2. Age class distribution at Wizard Rock, 18 Nov. 1982.

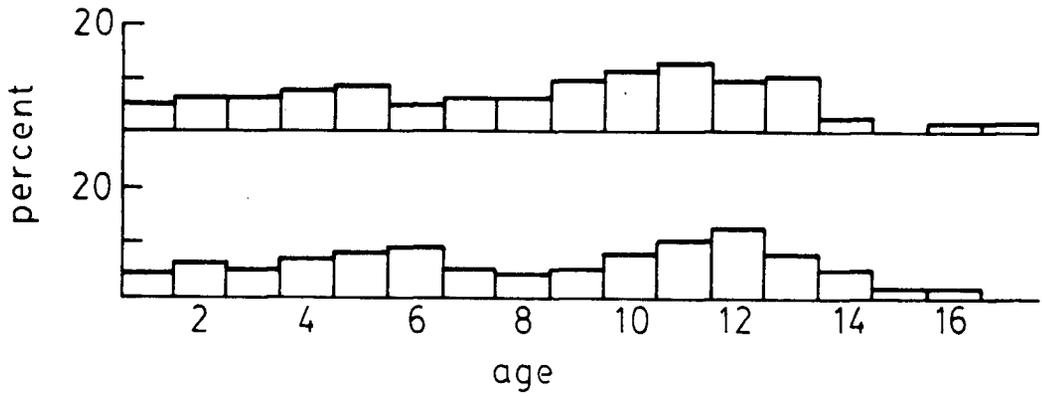


Figure 5.3. Age class distribution among each of two pooled samples from Wizard Rock. Above: November, December, 1981, and January, March, 1982; below: April, June, July, September, 1982.

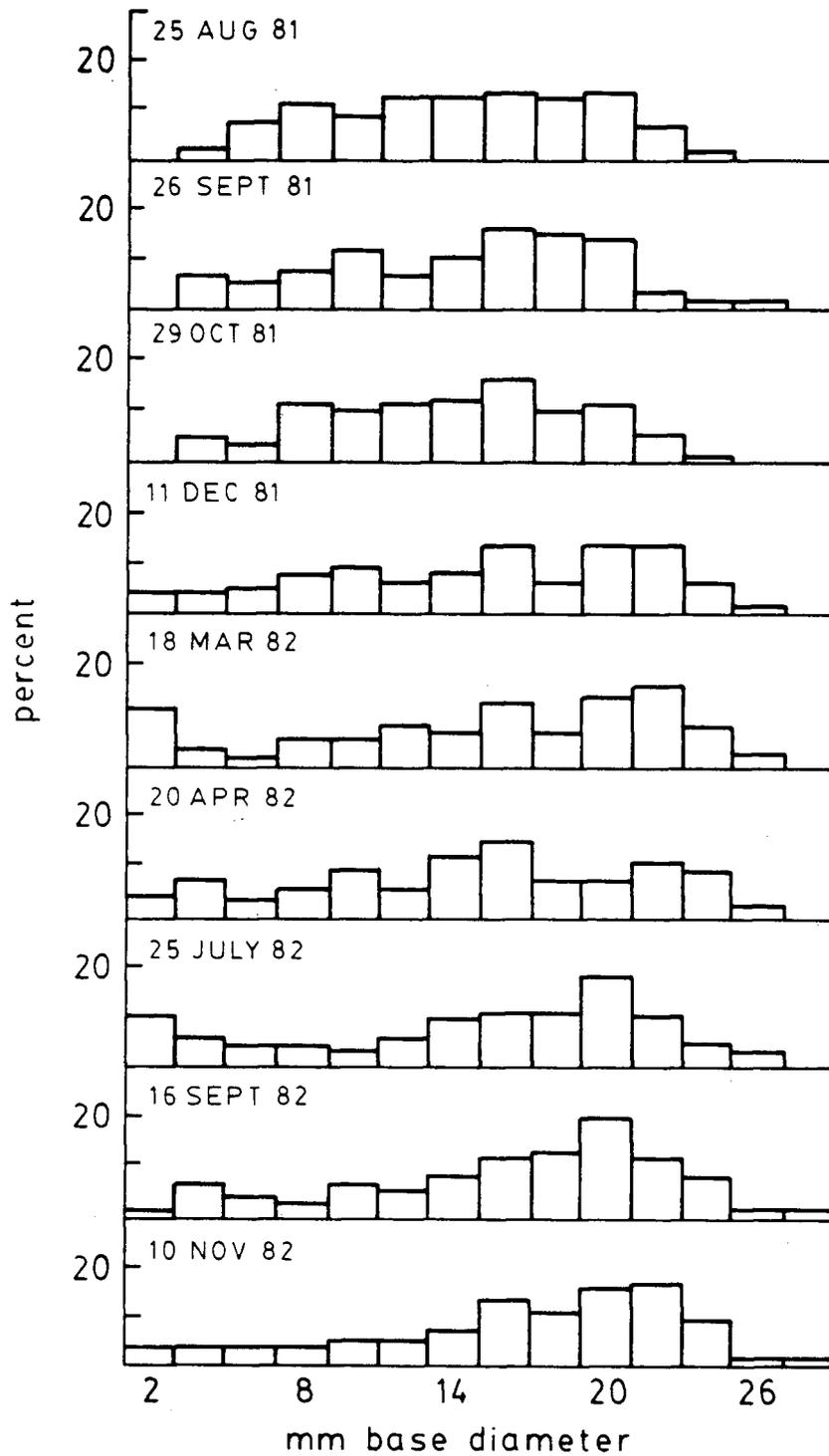


Figure 5.4. Size class distribution by basal diameter for nine repeated samples at Execution Bay.

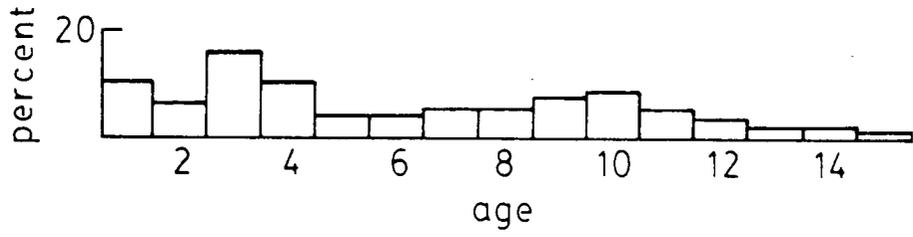


Figure 5.5. Age class distribution at Execution Bay, 10 Nov. 1982.

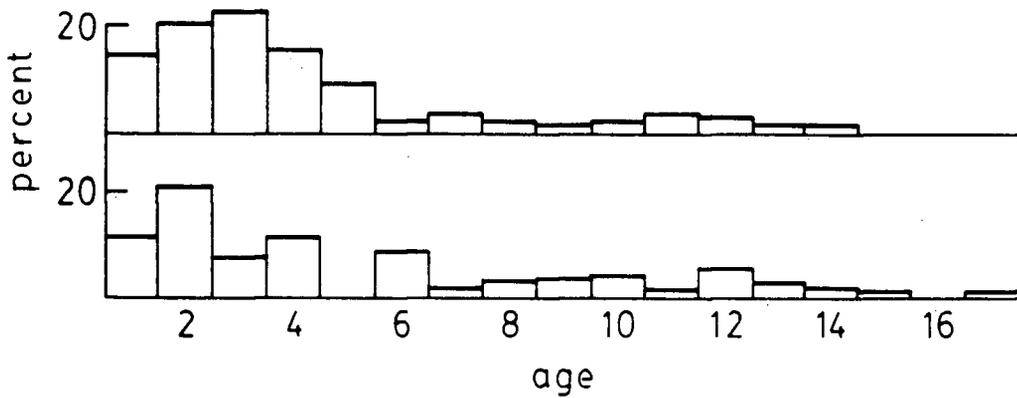


Figure 5.6. Age class distribution among each of two pooled samples from Execution Bay. Above: November, 1981, and January, March, 1982; below: May, July, Septemeber, and October, 1982.

CHAPTER 6

GENERAL DISCUSSION

A synthetic discussion of results gained from investigation of congeneric species suffers from problems of simplification inherent in comparison of dissimilar taxa. However, the hypothesis formulated for the purposes of this study allowed the testing of three predictions put forth in Chapter 1. These will be addressed in turn.

1. Estimated fecundity (as meiospore production) was not different between the two species (L. ephemera: 1.49×10^8 (Cable Beach) and 2.90×10^8 (Execution Bay); L. setchellii: 1.91×10^8 (Wizard Rock) and 1.80×10^8 (Execution Bay)). This result is contrary to the prediction of increased fecundity in the semelparous sporophyte. It should be noted, however, that sporic contribution to overall fitness may be very different between the two species, even in the absence of statistical differences in fecundity. As Fisher (1931) has discussed, offspring produced early in the parents' lifetime may be more valuable (e.g. make a greater contribution to population rate of increase) than the same number of offspring produced later in the parents' lifetime. On this basis, one might predict a greater 'r' for Laminaria ephemera (producing 10^8 spores at an age of 6 to 8 weeks) than for Laminaria setchellii (producing 10^8 spores at 2 or more years of age).

2. Developmental time to maturity was observed to be shorter for the semelparous than for the iteroparous sporophyte, as predicted. Individuals of Laminaria ephemera were estimated to become reproductive at an age of 6 to 8 weeks. Conversely, Laminaria setchellii did not become reproductive at less than 1 year of age, and seldom before the second or even third year. Delayed

maturity in the iteroparous sporophyte possibly results from partitioning of available resources between the alternative processes of reproduction and of stipe growth and maintenance.

3. There is no evidence in these data that annual reproductive effort (as the mean ratio of sorus surface area to vegetative surface area) is greater for the semelparous than for the iteroparous sporophyte. The ratio of sorus surface area to vegetative surface area in Laminaria ephemera varied from 13% to 19% (Cable Beach) and from 14% to 32% (Execution Bay); in Laminaria setchellii, this ratio varied from 1% to 18% (Wizard Rock) and from 2% to 32% (Execution Bay). Between species, the maximum mean values (L. ephemera: 32%; L. setchellii: 30%) are nearly identical, and therefore do not support the expectation of increased reproductive effort in the semelparous species. Between-species differences in maximum individual reproductive effort are smaller (L. ephemera, Execution Bay: 92%; L. setchellii, Execution Bay: 84%) than are intraspecific differences in reproductive effort (L. setchellii, Wizard Rock: 44%; L. setchellii, Execution Bay: 84%). These data indicate that reproductive effort is variable both within and between populations of a single species, and such variability may preclude any comparisons of reproductive effort between species.

The prediction of increased reproductive effort with age among populations of the iteroparous species was not supported by these data. This result may be attributable to the observed high variability in individual reproductive effort, which may obscure overall trends within populations. Alternatively, the discrete method of sampling used in this study may have precluded identification of age-specific trends in reproductive effort among individuals.

For a stable population in which birth rate equals death rate, any individual must replace itself once during its lifetime. The high sporic fecundities exhibited by Laminaria ephemera are sufficient to allow for a successful rate of replacement, and alternative mechanisms of population increase (i.e. enhanced gametophyte longevity or fecundity) need not be invoked in order to account for the observed population processes. Laminaria setchellii, however, exhibits an annual sporic fecundity of the same magnitude as as L. ephemera, but maintains an annual sporophyte replacement rate much smaller than that of L. ephemera. This suggests the existence of species-specific differences in the contribution of the gametophyte to observed population processes. Such differences may be effected by alteration of gametophyte life history characteristics.

The problem of alteration of gametophyte life history characteristics must be approached intuitively. Inherent in all non-vegetative reproductive events is the risk of offspring mortality, or lack of success; the magnitude of risk is variable between reproductive events. Reproduction-associated risk in a single zygote-to-zygote cycle increases as the product of the risk terms associated with each phase of the cycle. For those complex life histories maintaining only a single reproductive episode per zygote-to-zygote cycle (i.e. diplontic organisms), the relevant risk term is simply that of the observed reproductive episode. However, for complex life histories with more than one reproductive episode per zygote-to-zygote cycle, reproduction-associated risk may be significantly increased.

In order for complex-life-history populations to remain stable or to increase in size, the enhanced risk associated with complexity must be compensated for or exceeded by an increase in fecundity. For complex life

histories, overall (zygote-to-zygote) fecundity increases as the product of the individual fecundities of between-stage reproductive events. It is attractive to predict mean fecundities of greater than one for all stages in the complex life history: this would afford the greatest potential for compensation of mortality accruing to reproduction-associated risk. Alternatively, if reproduction-associated risk accrues to more than one phase, but fecundity is greater than one in only a single phase, then fecundity within that single phase must increase multiplicatively over a comparable value for the non-complex condition.

Data presented above do not bear directly on the problem of gametophyte life history characteristics, and no estimates are available for processes of gametophyte survivorship and fecundity in the field. Observed sporophyte life history characteristics do not strictly confirm the predictions made at the outset of this study, and the importance of gametophyte dynamics to the overall kelp life history is implicated. The nature and magnitude of gametophyte contribution to population processes remains unidentified.

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APPENDIX 1

STIPE RING FORMATION IN LAMINARIA SETCHELLII

INTRODUCTION

Visible concentric rings at the base of some kelp stipes have been used by various authors (Novaczek, 1981; Kain, 1971, 1963; Parke, 1948) to determine minimum age of the individual. Correlational evidence has been invoked to show that these rings are annual. Kain (1963) and Novaczek (1971) relate ring formation in Laminaria hyperborea and in Ecklonia radiata to seasonal periods of fast and slow growth, coupled with observation of periods of annual hapteron initiation. Direct observation of stipe ring formation has not been reported in the literature.

The results of a 12 month in situ tagging study are given below. These results constitute direct evidence that ring formation in Laminaria setchellii is annual.

MATERIALS AND METHODS

One hundred individuals of Laminaria setchellii at Wizard Rock were tagged and numbered on 27 October 1981 for the purpose of repeated observation. Tags were securely fastened by nylon cable ties positioned at the base of each stipe. Subsequent observations showed that most tags did not remain in place, but moved freely up and down the stipe with water motion.

All tagged individuals were harvested from Wizard Rock on 19 November 1982. Plants were returned to the laboratory, where longitudinal- and cross-

sections of some stipes were made.

RESULTS AND DISCUSSION

In only 17% of the surviving tagged plants did the cable tie remain in place at the stipe base for an entire year. These ten plants had developed localized 'saddles' from constraint of lateral growth in the region of the cable tie. In every case, the increase in girth of surrounding tissues corresponded, in longitudinal section, to one cortical growth ring (Figure A.1).

The observed girdling phenomenon can be explained according to growth patterns reported for perennial species of Laminaria. Increase in stipe girth results from meristodermal cell divisions, and subsequent production of a secondary cortex interior to the meristoderm. Artificial constraint of lateral expansion may allow the occurrence of limited cell divisions, but precludes increase in cross-sectional area of the stipe. The meristoderm would therefore remain intact, but would undergo no development of secondary cortex and no increase in stipe girth in the girdled region.

Seasonal harvesting and sectioning of kelp stipes from two sites (re: Materials and Methods, Chapter 4) indicated that meristodermal division rates are greatest in the months of March and April; this corresponded to a time of observable stipe 'peeling', and to initiation of new rings. Cross-sections of stipes made during these months showed a distinct, dense outer tissue layer, succeeded by a narrow, incipient layer of loosely-arranged secondary cortex.

It is apparent, then, that Laminaria setchellii stipe rings are produced annually, and that new rings are initiated synchronously within a population.

Generally, ring widths become successively narrower with increasing age or with increasing stipe diameter; accuracy of observation consequently decreases with increasing number of rings. Visible rings are therefore an indication of minimum age, in years, in discrete time, and resulting data should be interpreted accordingly.

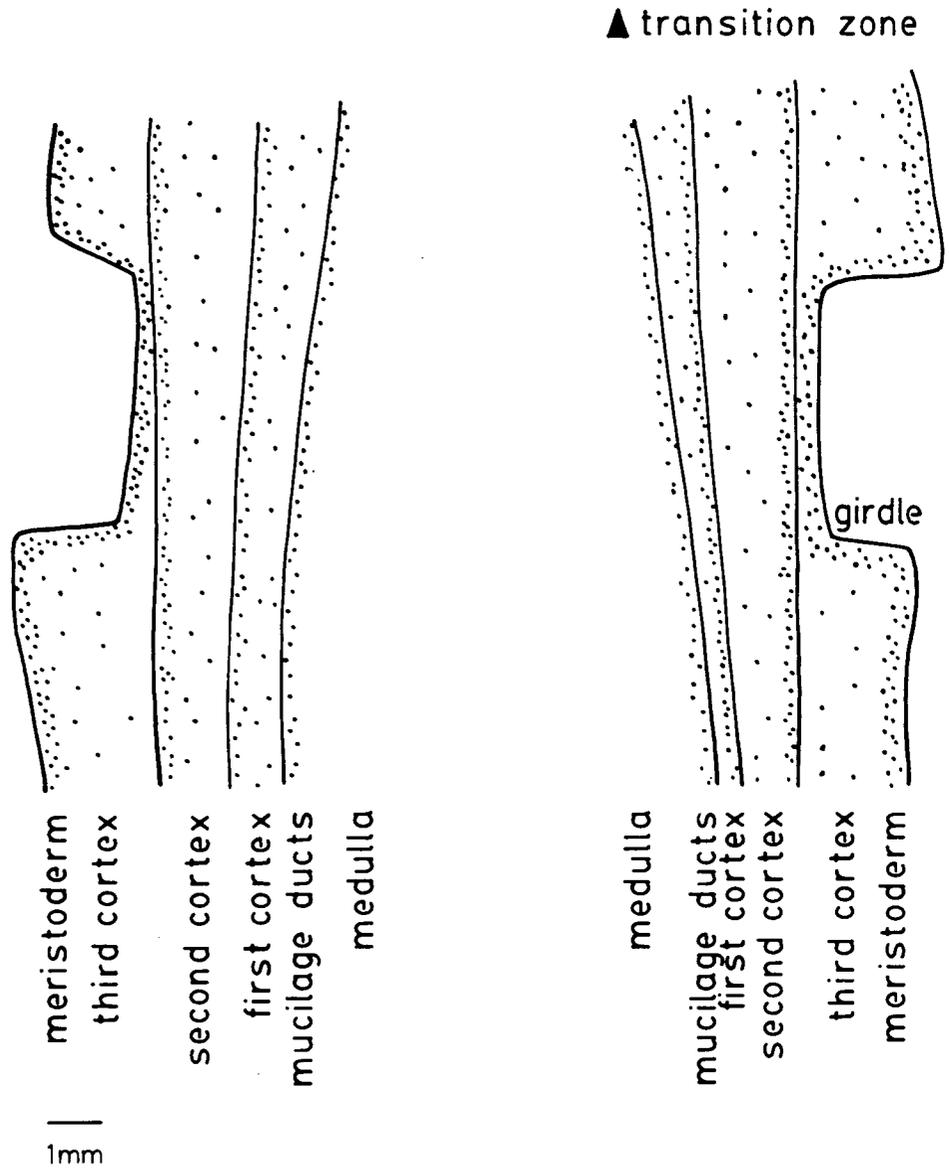


Figure A.1. Longitudinal cross-section of stipe base, showing girdled region and increase in girth of adjacent tissues. (Drawn from a photograph).

APPENDIX 2

GAMETOPHYTE CULTURE OF LAMINARIA EPHEMERA AND L. SETCHELLII

MATERIALS AND METHODS

More than 60 replicate gametophyte cultures each of Laminaria ephemera and Laminaria setchellii were established during the period May through July, 1981. All cultures were initiated as follows: fertile fronds were collected and immediately returned to the laboratory, where they were maintained in flowing sea water for a maximum of 24 hours before use. Fronds or portions of fronds were surface-sterilized (0.1% Betadine solution in sterile sea water), and partially dessicated. Soral tissues were then reimmersed in sterile sea water at 10°C; after zoospore release, 1 ml of spore suspension was pipetted into each 60 X 15 mm petri dish already containing 15 mls Provasoli's enriched sea water (PES). All dishes were sealed with Parafilm to avoid salinity increase by evaporation. Dishes were stacked 5 deep and placed in Percival incubators at 5, 10, and 15°C, under long-day (16L:8D) conditions, at irradiance of about 100 $\mu\text{E}/\text{cm}^2/\text{sec.}$, cool white fluorescent light. Medium was replaced at approximate bi-weekly intervals. Germanium dioxide was added to cultures at a concentration of 5 mg/l (Lewin, 1966).

Each frond selected for culture initiation was used to establish 5 replicate cultures. No two fronds were from the same parent sporophyte. The products of 12 or more parental genotypes were therefore represented among the cultures of each species. All study sites (Laminaria ephemera: Cable Beach and Execution Bay; Laminaria setchellii: Wizard Rock and Execution Bay) were represented. Results were pooled within species.

Observations are presented in Table A.1. Results are qualitative, and no statistical inferences are made. For each combination of treatment, character, and time, a '+' is recorded if that character was present in at least some cultures; a '-' indicates that no cultures exhibited that character.

RESULTS

Laminaria ephemera germinated and grew vegetatively at 5, 10, and 15°C. Gametophytes were strictly isomorphic, and their morphology was more similar to females of other species of Laminaria than to males of other species. Oogonium development was observed only after the ninth week at 10 and 15°C. No sexuality was observed at 5°C. Antheridia were never identified among the cultures, but were presumed to be present in cultures which produced sporophytes. There was sparse development of sporophytes at 10 and 15°C. Some sporophytes were isolated from the dishes and removed to bubble culture, or to greenhouse culture, where they attained overall lengths of 15 to 25 cm. Gentle grinding of vegetatively-growing gametophytes after the second month often initiated production of oogonia.

Laminaria setchellii germinated and grew vegetatively at 5, 10, and 15°C. Gametophytes were heteromorphic. At 10 and 15°C, oogonia and antheridia were observed among some cultures by the end of the second week, and among most cultures by the fourth week. Dense production of sporophytes was observed within sexual cultures. Ten and 15°C treatments were terminated after 4 weeks. Cultures held at 5°C were maintained for 4 months; these grew vegetatively, but produced neither oogonia nor antheridia.

T°C	WEEKS	<u>LAMINARIA EPHEMERA</u>					<u>LAMINARIA SETCHELLII</u>				
		1-2	3-4	5-8	9-12	13-16	1-2	3-4	5-8	9-12	13-16
05°C	GERMINATION	+					+				
	VEGETATIVE GROWTH	+	+	+	+	+	+	+	+	+	
	OOGONIA	-	-	-	-	-	-	-	-	-	
	ANTHERIDIA	-	-	-	-	-	-	-	-	-	
	SPOROPHYTES	-	-	-	-	-	-	-	-	-	
10°C	GERMINATION	+					+				
	VEGETATIVE GROWTH	+	+	+	+	+	+	+	TERMINATED		
	OOGONIA	-	-	-	+	+	+	+	TERMINATED		
	ANTHERIDIA	-	-	-	-	-	+	+	TERMINATED		
	SPOROPHYTES	-	-	-	+	+	-	+	TERMINATED		
15°C	GERMINATION	+					+				
	VEGETATIVE GROWTH	+	+	+	+	+	+	+	TERMINATED		
	OOGONIA	-	-	-	+	+	+	+	TERMINATED		
	ANTHERIDIA	-	-	-	-	-	+	+	TERMINATED		
	SPOROPHYTES	-	-	-	+	+	+	+	TERMINATED		

Table A.1. Results of gametophyte culture experiments. See text for explanation of symbols.