

DEMOGRAPHIC PATTERNS AND PROCESSES IN *MAZZAELLA SPLENDENS*
(GIGARTINALES, RHODOPHYTA) AT SECOND BEACH, BARKLEY SOUND.

by

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ABSTRACT

In this research I examined the demography of *Mazzaella splendens* (Setchell *et* Gardener) Fredericq at Second Beach, Barkley Sound. A set of demographic patterns consistent with all previous studies of *M. splendens* was hypothesized and tested in a new location to determine the generality of these patterns. To that end seasonal changes in density of genets and modules of gametophytes vs. tetrasporophytes were measured approximately monthly over three years. Survival, new blade production, blade size and reproduction were also measured to determine the demographic mechanisms underlying changes in population density.

Patterns consistent with all previous studies of *Mazzaella splendens* are: 1) change from high summer to low winter population density in wave-sheltered areas with 2) a decreasing magnitude in this fluctuation as wave exposure increases and 3) a change from summer haploid to diploid dominance as wave exposure increases. These patterns may be common throughout the species range. Seasonal alternation in phase dominance in wave-sheltered areas, consistent with all previous studies, did not occur at Second Beach. Differential survival was not present between life history phases, but there was evidence of differential production of new blades. These results do not support a previous hypothesis that the alternate isomorphic life history phases of *M. splendens* are diverging ecologically along *r* and *K* lines.

In a wave-sheltered area, 85 – 90% of modules were smaller than the size for which previous studies had predicted differential survival between phases, but even within the appropriate size class differential survival was absent. In a wave-exposed area, haploid modules lost more tissue than diploid modules, apparently reconfiguring surface area in response to wave force.

Seasonally restricted reproduction, previously observed in other populations, was not present at Second Beach. Reproduction did not negatively affect survival. Evidence for slowing of growth after the onset of reproduction, and a time requirement before onset of reproduction, were mixed.

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Chapter 1. *Mazzaella splendens*: an introduction to the organism and its demography.

The place of local scale studies within population ecology.

Population ecology is widely defined as the investigation of dynamic patterns of distribution and abundance in a single species, but the term *population* itself has proved resistant to precise definition. Some have argued that population boundaries may be determined by an investigator's purpose or convenience (Begon *et al.* 1986). Others attempt to discover and define a natural unit to which the term *population* can be rigorously applied (Berryman 2002, Camus & Lima 2002).

Berryman (2002) formally defines the natural population as “a group of individuals of the same species that live together in an area of sufficient size to permit normal dispersal and/or migration behaviour and in which numerical changes are largely determined by birth and death processes.” This concept is similar to that of a metapopulation (Hanski 1997). In both cases the fundamental demographic equation, $N_{t+1} = N_t + B - D + I - E$ (where N_t = the number of individuals present at a particular time t , B = births, D = deaths, I = immigration, E = emigration and N_{t+1} = the number of individuals present after some interval Δt), is reduced to $N_{t+1} = N_t + B - D$. The area occupied by the natural population is determined by the dispersal biology of the species in question and geographic barriers to that dispersal.

For each of the smaller patches making up the natural population the full demographic equation applies. These patches are termed “local” populations and are considered more ephemeral than the natural population, being subject to the vagaries of changing dispersal vectors and local conditions. While the natural population may be in equilibrium the local population is less likely to be so, and Berryman (2002) has questioned the degree to which studies at local scales can adequately inform us of the processes stabilising (or destabilising) natural populations.

One immediate practical difficulty arises when examining a natural population defined in this way. The logistics of adequately sampling an area large enough to eliminate the effects of dispersal can be unmanageable. This is particularly true of marine organisms (motile and sessile) with free drifting pelagic stages. Some investigators have addressed this problem by defining populations as open or closed

(Caley *et al.* 1996, Cowen *et al.* 2000). This approach is rejected by Berryman (2002) implying that for many marine systems, in the absence of effective barriers producing geographic isolates, species with pelagic dispersal consist of a single population. The practical difficulties associated with adequately sampling such a population to determine the processes acting at this scale are apparent to any working field ecologist.

Though the natural population can be defined in terms of the dispersal properties of the species in question, there is no such parameter to define the scale at which a group of conspecifics becomes a “local” population (Camus & Lima 2002). The vast majority of studies take place at local scales and meaningful demographic information on the natural population is usually lacking. It is unclear, therefore, how processes observed at local scales (chosen largely as a function of available time and funding) relate to, or to what extent they are important in, dynamics at the larger scale.

A natural population is often patchy in a fractal manner. The sort of patchiness observed in the distribution of a particular species along a coastline, for example, often recurs within each of the general areas where it is found (possibly due to availability of suitable habitat) and then there is patchiness within these areas (perhaps because of microhabitat differences). The term “local” has been applied at all these scales (Camus & Lima 2002), but the demographic processes at one scale need not be representative of those at another as new properties of the larger groupings emerge. Rather than attempt to define “local population” in a precise way, Camus and Lima (2002) argue that the objective should be an understanding of how processes at one spatial scale map into those at another. This can only be accomplished by a number of investigators working at different spatial and temporal scales in a co-ordinated effort.

It is arguable whether any such co-ordinated studies have yet occurred in population ecology. One way of moving in this direction, however, is replication and extension of the work of previous investigators, in new geographic locations, within the overall range of the species of interest. Over time a spatio-temporal mosaic of information will be created which can raise interesting questions, hopefully attracting increasing numbers of investigators. As this mosaic builds, those demographic patterns that remain relatively invariant, or vary systematically with spatial and/or temporal gradients, will become more apparent. In these patterns we get the first glimpses of the behaviour of the natural population.

For algal population ecology on the west coast of North America, *Mazzaella splendens* (Setchell *et* Gardner) Fredericq has great potential to become such a species of interest. Studies of the distribution and abundance of *M. splendens* have accumulated steadily since interest first began in the late 1960's. Demographic studies of *M. splendens* have now occurred over the area from Vandenberg, California to Barkley Sound, British Columbia (Figure 1.1). This represents approximately the southern half of its range from the Gulf of Alaska to northern Baja California (Abbott & Hollenberg 1976 as *Iridaea cordata*, Scagel *et al.* 1989 as *Iridaea splendens*). As data have accumulated, demographic patterns have emerged, and with each new study the generality of these patterns is challenged or supported.

The life-history of *Mazzaella splendens*.

Mazzaella splendens is a red alga in the order Gigartinales. It has a sporic life-history with an alternation of isomorphic free living haploid and diploid generations. An individual consists of one or more ovoid to moderately lanceolate blades, each with a short stipe and apophysis, arising from a small basal crust. It has long been assumed that each basal crust is the result of recruitment from a single spore and therefore a genetically distinct individual, so a group of blades arising from a common spot on the substratum has been called a genet and each of its blades, a module of that genet. However, the discovery that sporeling coalescence occurs in early stages of development for many Rhodophyta (Santelices *et al.* 1999) has called into question the assumption that each basal crust is the product of a single spore. In coalescence, neighbouring germlings, each the result of a single spore, establish secondary pit connections between adjacent cells, forming a single crust of interconnected cells which is a genetic chimera. Therefore a clump of blades arising from a single crust may be the result of several spores. A recent attempt at redefinition of the genet *per se* (Scrosati 2002) has not addressed the problem of identifying one in the field, and Santelices (1999) has argued that the definition of an individual may be as variable, given the biology of the species of interest and the question being asked, as that of a population.

What is observed in the field when conducting a census of *Mazzaella splendens*, are groups of one or more blades projecting from a central basal disk usually 3 – 5 mm in diameter. The bases of these groups of blades are often obscured by encrusting marine

organisms. These groups are spatially discrete. It is these small "clumps" of blades that have, in previous studies of *M. splendens* (DeWreede & Green 1990 as *Iridaea splendens*, Dyck et al. 1985 as *Iridaea cordata*, Dyck & DeWreede 1995), been referred to as individuals or genets. I am retaining that terminology for the purposes of this dissertation, with the problems noted, rather than coining a new term. Genet here will refer to the observed discrete clumps of blades. Questions about the kind of individuality they represent must await an investigation of the frequency of sporeling coalescence in the field. Genets of *M. splendens* are each made up of one or more blades. Each blade constitutes a module of the genet in which it occurs.

It has been established for some time (Hansen 1977 as *Iridaea cordata*) that most new blades of *Mazzaella splendens*, arising in a given area, are the result of perennation (the production and loss of shorter lived blades from the longer lived basal crust) rather than recruitment. The relative contribution of recruitment to population density has been estimated at 20 % by May (1986 as *Iridaea cordata*) working on San Juan Island, Washington. Because other organisms frequently obscure the basal crusts of *M. splendens*, an individual of *M. splendens* is visible only when it has produced one or more blades and does not appear in a census if it is bladeless at that time. Because of this I will refer to changes in module density as gain and loss, but to changes in genet density as appearance and disappearance, reflecting uncertainty over the degree to which observed changes are due to recruitment and death or to perennation.

The distribution and abundance of both gametophytes (the free living haploid stage of the life history) and tetrasporophytes (the free living diploid stage) of *Mazzaella splendens* may vary seasonally and/or spatially. This can produce a greater complexity of demographic pattern than is present for most terrestrial plants, where the alternate generations are more intimately associated. The free-living sexual gametophytes of *M. splendens* are dioecious and the ratio of males to females may vary. After fertilisation *in situ* on the female blade, each zygote undergoes amplification to form diploid carpospores. These are dispersed and develop into diploid tetrasporophytes. Meiosis, in tetrasporangial initials throughout the diploid blade, produces haploid tetraspores, which are dispersed to complete the cycle (Figure 1.2). Between different habitats and between the alternate life history phases there may be variation in rates of growth, survival, reproduction, dispersal and recruitment. From the studies of *M. splendens* demography

to date, it is possible to examine which parts of the patterns found at local scales remain when larger parts of the species range and longer time frames are considered.

The natural population of *Mazzaella splendens*.

Barriers to immigration may be present or absent at different times. So the number of natural populations as defined by Berryman (2002) will likely vary over time within a species range. Groups will be split as barriers arise and merge with other groups as barriers fall.

For the algae in general, free floating spores normally remain viable for only a few days and dispersal shadows tend to be short (see Santelices 1990) for review). For *Mazzaella splendens* spore density drops by an order of magnitude 100 cm away from the spore releasing blade (Adams 1979, as *Iridaea cordata*). For *Mazzaella laminarioides* in central Chile, genetic differentiation increased with distance such that, for locations separated by 60 km, individuals could be assigned to their original population through discriminant analysis (Faugeron *et al.* 2001).

Algal spores remain viable for considerable lengths of time within detached fragments of the thallus and dispersal of such fragments can cover much larger distances (see Santelices 1990) for review). In North America and northern Europe the current distributions of macroalgal species represent postglacial colonization from refugia and from below the southern extent of the ice.

For *Palmaria mollis* on the Northeast Pacific coast, genetic relationships among populations did not reflect geographic proximity (Lindstrom *et al.* 1997). Plants were associated in two groups. An outer coastal group included individuals from the northwestern end of Vancouver Island and the Queen Charlotte Islands. This group was associated with sites from Prince William Sound, the Alaska Peninsula and Sitka, Alaska. An inner coastal group included individuals from the eastern side of Vancouver Island and Ketchikan, Alaska. This group was associated with sites near Juneau, Alaska and the eastern end of the Strait of Juan de Fuca. The pattern seen in *Palmaria mollis* is suggestive of similarities due to long distance dispersal by different patterns of currents on the outer vs. the inner coast.

Berryman (2002) does not address the time scale over which immigration is to be considered important. Immigration is clearly responsible for the postglacial presence of

much of the northern macroalgal flora and is probably ongoing. The frequency and extent of this long distance dispersal is not known. Therefore, that to assign boundaries to the natural populations of *Mazzaella splendens*, given the current level of understanding, would be arbitrary. There is every reason to suppose that spores do not travel a great distance and that populations separated by tens of kilometers would be genetically distinct. But there is also reason to believe that individuals on the outer coast separated by hundreds of kilometers may be more closely related than they are to individuals from less distant inner coast sites.

A note on the taxonomic history of *Mazzaella splendens*.

The information presented here, particularly regarding the early taxonomic work on *Mazzaella splendens*, is primarily that found in the Synopsis of the Benthic Marine Algae of British Columbia, Southeast Alaska, Washington and Oregon (Scagel *et al.* 1989). References to earlier work cited in Scagel *et al.* (1989) are included here for the sake of completeness.

The taxon currently known as *Mazzaella splendens* was first described by Turner (1809) as *Fucus cordatus*. This name was changed to *Iridaea cordata* by Bory de Saint Vincent (1826). Setchell and Gardner (1937) proposed changing *Iridaea cordata* to *Iridophycus cordatum* and also proposed a new species *Iridophycus splendens*. Papenfuss (1958) retained the genus *Iridaea* with two species, *I. cordata* and *I. splendens* (Setchell *et Gardner*) Papenfuss. Abbott (1971) recognised one species, *Iridaea cordata* (Turner) Bory, with two varieties; var. *cordata* and var. *splendens*. *Iridaea lilacina* Postels and Ruprecht (1840) was considered by Abbott (1971) to be a synonym of *Iridaea cordata*. Experimental work involving removal of competitors, grazer exclusion and transplants of *Iridaea cordata* and *Iridaea flaccida* (Setchell *et Gardner*) Silva (Foster 1982) suggested that these two taxa were conspecific, and in their Synopsis Scagel *et al.* (1989) listed *Iridaea splendens* with *I. cordata* var. *cordata*, *I. cordata* var. *splendens* and *I. flaccida* as synonyms. Hommersand *et al.* (1993) revised the Gigartinaceae and proposed a new genus, *Mazzaella*, to take the place of *Iridaea* in much of its global distribution including the west coast of North America. Hommersand *et al.* (1993) proposed *Mazzaella lilacina* (Postels *et Ruprecht*) Leister as the new name for *Iridaea splendens* and recognised *Mazzaella flaccida* (Setchell *et Gardner*) Fredericq

as a separate species. In their subsequent treatment of the Gigartinaceae (Hommersand *et al.* 1994) the name *Mazzaella lilacina* could not be linked to any presently recognised species. *Mazzaella splendens* (Setchell *et* Gardener) Fredericq now takes the place of *Iridaea splendens*. *Mazzaella flaccida* is once again recognised as a separate taxon.

Patterns of distribution of *Mazzaella splendens* on the west coast of North America: an accumulation of evidence.

In the Strait of Georgia, British Columbia, *Mazzaella splendens* has shown a distinct seasonal cycle for both biomass and density with a peak in May and June, and lows from December to February (Adams 1979, as *Iridaea cordata*). This pattern was consistent over three sites, two of them 5 km apart and the third some 36 km from the other two. In both biomass and density there was a general predominance of cystocarpic (carpospore producing haploid) individuals early in summer followed by a later predominance of tetrasporic (tetraspore producing diploid) plants. There were relatively high numbers of non-reproductive individuals in spring and early summer, giving way to nearly fully reproductive populations in fall and winter. Studies on growth rates at two sites near Friday Harbor, Washington, found growth to be minimal until early May when a rapid increase began which did not abate until mid August (Fralick 1971, as *Iridaea cordata*).

In central California, Hansen (1977, as *Iridaea cordata*) found seasonal changes in biomass with lows in winter and highs in summer. Growth rates in late winter and early spring were 1 – 2 orders of magnitude greater than at other times. These rates did not differ between cystocarpic and tetrasporic individuals. Density did not change appreciably over the year, with seasonal variation in biomass resulting from changes in size class frequencies (Hansen & Doyle 1976, as *Iridaea cordata*). Peak abundance of cystocarpic thalli occurred earlier (spring) than peak abundance of tetrasporangial thalli (fall) just as it did in the Strait of Georgia, but in central California tetrasporangial individuals predominated throughout the year. This constant diploid dominance raised questions about ecological differences between isomorphic phases and how the observed patterns might relate to the advantages of diploidy vs. haploidy. It also suggested the possibility of a latitudinal cline in summer population structure, from haploid dominance in the north to diploid dominance in the south.

In July 1982, 12 sites from northern Oregon to central California were sampled to see if such a cline could be detected (Dyck *et al.* 1985, as *Iridaea cordata*). This was the first population study of *Mazzaella splendens* to enumerate all haploids and diploids in the population, using carrageenan analysis, rather than estimating their proportions from the proportions of fertile individuals. Haploid plants of *M. splendens* contain primarily K-carrageenan while diploids contain primarily λ -carrageenan (McCandless *et al.* 1975, as *Iridaea cordata*), and the difference can be observed by subjecting a small amount of air dried tissue to heat and resorcinol reagent (Dyck *et al.* 1985, as *Iridaea cordata*, Shaughnessy & DeWreede 1991, as *Iridaea cordata*).

The pattern found was the inverse of the expected cline. Tetrasporophyte dominance was generally strongest in northern Oregon, grading to gametophyte dominance in central California. The population at Pigeon Point, California, reported as having diploid dominance by Hansen and Doyle (1976, as *Iridaea cordata*), was 86% gametophyte at the site sampled by Dyck *et al.* (1985 as *Iridaea cordata*). Work in Barkley Sound, British Columbia showed a trend (during the summer) of gametophyte dominance in relatively wave-sheltered habitats grading to tetrasporophyte dominance in wave-exposed locations (Dyck *et al.* 1985, as *Iridaea cordata*).

Recent sampling of *Mazzaella splendens* during three consecutive summers (from 1997 to 2000) at 21 locations from Cape Meares, Oregon, to Vandenberg, California, by Thornber (2001) found consistent gametophyte dominance (although interannual variation produced one year of diploid dominance at a few sites). As with the differences at Pigeon Point, the differences between the results of Dyck *et al.* (1985) and Thornber (2001) could be a reflection of processes operating either over longer periods of time, or site specific processes acting at relatively small scales.

DeWreede and Green (1990, as *Iridaea splendens*), working in Vancouver Harbour, British Columbia, first demonstrated a seasonal shift in phase dominance for *Mazzaella splendens*, and also showed that enumerating only reproductive individuals gave similar results to a complete survey using carrageenan analysis (Garbary & DeWreede 1988, Shaughnessy & DeWreede 1991) to differentiate between nonfertile isomorphic haploids and diploids. Differences in demographic behaviour of *M. splendens* between southern British Columbia, where carrageenan analysis was used, and central California (and also differences over time in central California) where

haploids and diploids were identified only when reproductively mature, were not simply due to the change in technique.

DeWreede and Green (1990, as *Iridaea splendens*) used random sampling of equal numbers of individuals in each season. This technique found the seasonal alternation in phase dominance but did not examine the underlying changes in density producing it. Working at the same location, Dyck and DeWreede (1995) followed density changes in permanent quadrats. The seasonal cycle in overall density, seen by Adams (1979, as *Iridaea cordata*) in the Strait of Georgia, was also present in Vancouver Harbour. Both gametophytes and tetrasporophytes increased in density during spring and summer, and declined during fall and winter. But Dyck & DeWreede (1995) found that haploids both increased and decreased in density at a greater rate than diploids, resulting in a fall crossover from summer gametophyte dominance to tetrasporophyte dominance in winter.

Studies of recruitment in *Mazzaella splendens* began on San Juan Island, Washington. Mapping of individuals in an extant population over three consecutive summers (May 1986, as *Iridaea cordata*) showed a consistent gametophyte dominance of about 83%. Perennation accounted for 80% of new production and recruitment 20%. Reproductive rates and survival of mature blades did not vary between phases during the summer months. Given equal spore production by both phases (and assuming a 1:1 ratio of males to females) approximately 2.4 times as many carpospores should be produced in this population as tetraspores (reflecting the cost of males and the degree of haploid dominance). The population structure, however, remained nearly constant over three consecutive summers, suggesting that selection pressures at the recruitment stage were maintaining gametophyte dominance. Sampling by May (1986 as *Iridaea cordata*) took place only in summer, so seasonal alternation in phase dominance was not addressed.

Similar results were found by Phillips (1994, as *Mazzaella lilacina*) at Second Beach in Barkley Sound, British Columbia. The number of spores produced per blade was not significantly different between phases in spring or fall but did differ, favouring tetraspore production, at the end of summer. Plots were cleared in both wave-sheltered and wave-exposed habitats and recruitment was measured. In wave-sheltered areas, where haploids predominated, gametophytes recruited in greater proportions than the number of reproductive diploids in the surrounding population should permit (assuming

recruitment to be a direct function of available tetraspores). The opposite occurred in wave-exposed areas where a greater proportion of tetrasporophytes recruited relative to the cystocarpic component in the parent population. This result was consistent with the hypothesis that different habitats select for a particular population structure at the recruitment stage. Phillips (1994, as *Mazzaella lilacina*) noticed another trend, however, in which population structure changed over time in the cleared plots. In wave-sheltered areas these plots became increasingly haploid dominant over and above the proportion present after the first wave of recruitment. A similar pattern in tetrasporophyte dominance emerged in wave-exposed areas.

The parent populations of *Mazzaella splendens* outside the cleared plots, in both sheltered and exposed sites at Second Beach (Phillips 1994, as *Mazzaella lilacina*), showed little change in proportion haploid over time. If the proportions of reproductive individuals in the parent populations were also relatively constant, the observed trend over time, to even greater predominance of the dominant recruit within the cleared plots, could point to selection acting on perennating individuals as well.

Phillips (1994, as *Mazzaella lilacina*) initiated biomechanical studies of *Mazzaella splendens* in an effort to explain differences in population structure at sites with different wave exposures. Examination of drag forces and the force required to break the stipe-holdfast junction did not find any significant differences between phases. But more detailed work, combining variation in surface area between life-history phases with the attendant hydrodynamic forces and the force required to break the stipe-holdfast junction (Shaughnessy *et al.* 1996), did predict a predominance of the diploid phase of *M. splendens* at wave-exposed sites. Shaughnessy *et al.* (1996) extended that work to explain the relative distributions of *Mazzaella splendens* and *Mazzaella linearis* along gradients of wave exposure. Further morphological examination (Shaughnessy 1996) and reciprocal transplant studies (Shaughnessy & DeWreede 2001) of these species demonstrated a trade-off in ability to withstand hydrodynamic forces vs. tolerance of other abiotic stresses such as high irradiance and desiccation.

A demographic pattern common to all previous studies.

Collectively, results from all the studies cited above are consistent with a particular dynamic pattern in density and population structure in *Mazzaella splendens*.

There is a seasonal change in biomass and density, with highs in summer and lows in winter, for both life history phases. The magnitude of seasonal change becomes less pronounced with increasing wave exposure. There is also a seasonal alternation between summer gametophyte and winter tetrasporophyte dominance in wave-sheltered areas. This pattern changes into complete diploid dominance as wave exposure increases. Changes in phase dominance along wave exposure gradients can occur over relatively short distances (Dyck *et al.* 1985, as *Iridaea cordata*) and are the most likely explanation for phase dominance reversals at nearby sites and over time along the Oregon and California coasts (Hansen & Doyle 1976 as *Iridaea cordata*, Dyck *et al.* 1985, as *Iridaea cordata*, Thornber 2001).

Both the seasonal alternation in phase dominance and the trend toward diploid dominance with increasing wave exposure are potentially widespread patterns within natural populations of *Mazzaella splendens*. Seasonal alternation has been observed in the Strait of Georgia (Adams 1979, as *Iridaea cordata*) and Vancouver Harbour (DeWreede & Green 1990, as *Iridaea splendens*, Dyck & DeWreede 1995). Summer haploid dominance, compatible with a seasonal alternation, has been observed in Barkley Sound (Phillips 1994, as *Mazzaella lilacina*), on San Juan Island (May 1986, as *Iridaea cordata*), on the Oregon coast (Thornber 2001) and at sites from northern to central California (Dyck *et al.* 1985, as *Iridaea cordata*, Thornber 2001).

A fundamental addition to understanding the overall picture of dynamic patterns in natural populations of *Mazzaella splendens* would involve examining changes in population density at a site exhibiting summer gametophyte dominance but distant from Vancouver Harbour. If seasonal alternation in phase dominance were found in Barkley Sound, on the outer coast of Vancouver Island it would increase the likelihood that it occurs generally in wave-sheltered areas throughout the Pacific Northwest and that this may be a feature of natural populations of *M. splendens*.

The potential roles of recruitment and perennation in producing demographic patterns.

Both recruitment and perennation are involved in establishing a particular population structure in a particular habitat. The evidence suggests that recruitment occurs primarily in early spring and does not, at least in extant populations, significantly

change the local phase ratio (May 1986, as *Iridaea cordata*, Phillips 1994, as *Mazzaella lilacina*). There appears to be strong selection on recruits before the juvenile stage, perhaps acting directly on spores.

This is supported by the hydrodynamic work of Shaughnessy *et al.* (1996), which indicated that juvenile blades should be much less impacted by wave action than mature blades. At wave-exposed sites Shaughnessy *et al.* (1996) found fewer small gametophytes of *M. splendens* than should have been present if hydrodynamic forces were the primary factor determining survival. Similarly, small blades of both phases of *M. splendens* should survive for a time in areas dominated by *Mazzaella linearis* (the most wave-exposed sites in which a species of *Mazzaella* survives), yet they were absent. In Barkley Sound, sites at which *M. linearis* is exclusively present can be as little as 10 – 15 m from sites containing *M. splendens*, and it seems likely that spores could travel this distance, allowing for *M. splendens* recruitment in these exposed areas. Again, some selection appears to take place at this early stage.

A differential response to hydrodynamic forces between the alternate phases of *Mazzaella splendens* would involve the removal of larger blades. These forces would act on established individuals. The trends seen by Phillips (1994, as *Mazzaella lilacina*) suggest that differential loss of established plants also has a role in altering population structure between wave-sheltered and wave-exposed sites. Moreover, the timing and amount of recruitment in extant populations (May 1986, as *Iridaea cordata*) suggests that a seasonal alternation in phase dominance (DeWreede & Green 1990, as *Iridaea splendens*, Dyck & DeWreede 1995) is primarily due to differences in module survival and production between perennating individuals.

When hydrodynamic forces remove modules from an individual, breakage usually occurs in the stipe (Phillips 1994, as *Mazzaella lilacina*, Shaughnessy *et al.* 1996), although parts of the blade may be lost before this happens. The prevalence of perennation in maintaining populations from year to year (Hansen 1977, as *Iridaea cordata*) suggests that the perennial crust or holdfast often is not removed when blades are lost, so the relationship between module death and genet death is not a direct one. It seems reasonable though, that consistently higher rates of blade loss by one life history phase would increase the percentage of times the holdfast of that phase is lost as well. There may also be more subtle effects. Removal of a blade produces a wound at the

blade-stipe junction and this breaks the cuticle, one of the plant's primary anti-herbivore defences (Gaines 1985). It is likely, therefore, that crusts with recently lost blades would be more susceptible to herbivores or pathogens, and that this could translate greater rates of module loss into greater rates of genet loss.

There are many interesting questions that could be asked about the process of selection, both during the early stages of recruitment and among established perennating individuals. But the demographic behaviour of perennating adults is more readily observed in the field (and therefore more likely to yield results) and is backed by a larger body of literature. This provides an opportunity to ask increasingly detailed questions about the ecological differences between phases that may contribute to changes in population structure. Seasonal alternation in phase dominance is particularly interesting because the mechanism producing it could also contribute to changes in population structure along wave exposure gradients. Winter in the Pacific Northwest is frequently marked by higher levels of wave action due to storms (Milligan & DeWreede 2000). Differential responses to hydrodynamic forces between phases of *Mazzaella splendens* (Shaughnessy *et al.* 1996) could, therefore, play a role in changes in population structure along both wave exposure and seasonal gradients.

The roles of genets and modules in producing a seasonal alternation in phase dominance.

Changes in population density of *Mazzaella splendens* at Brockton Point, Vancouver Harbour, (Dyck & DeWreede 1995) followed the usual pattern for wave-sheltered sites with marked highs in summer and lows in winter. Both gametophytes and tetrasporophytes followed this pattern, but rates of density increase in spring, and decrease in fall, were both greater for the haploid phase resulting in an alternation from summer haploid to winter diploid dominance. This pattern was similar for both genets (Figure 1.3) and modules (Figure 1.4) indicating that appearances and disappearances of genets, and not differential module production by genets of one phase over those of the other, were producing the alternation. The number of modules per genet varied seasonally. It was generally highest in early spring and lowest in late winter (Figure 1.5) for both life history phases. Tetrasporophytes often showed numerical predominance in modules per genet, but it was rarely a significant difference, reinforcing the idea that

dynamic changes in population structure are driven by appearances and disappearances of genets.

The spatial dynamics of *Mazzaella splendens* at Brockton Point, Vancouver Harbour.

Some seasonal fluctuation in spatial dynamics of *Mazzaella splendens* occurred among the permanent quadrats at Brockton Point, Vancouver Harbour (Dyck 1991, as *Iridaea splendens*). 80 - 85% of quadrats contained one or more individuals in winter, rising to 95 - 100% in summer (Figure 1.6). This suggests that the spring density increase and fall density decline were primarily the result of a general increase and decrease in population density across the spectrum of microhabitats represented by individual quadrats. It was only during the last part of winter that larger numbers of quadrats become empty, and even here it was not so much quadrats being emptied *per se* but quadrats with an absence of gametophytes. This reflected the extremely low densities ($2.8 - 1.4$ genets per m^2) to which haploids fell in winter. Increases and decreases in density generally took place over Brockton Point as a whole, and did not begin in certain microhabitats and proceed over time to others.

The objectives of this present study undertaken at Second Beach, Barkley Sound.

My initial objective was to examine the generality of those patterns that appear common to natural populations of *Mazzaella splendens* by repeating aspects of previous demographic work in a new area. At the same time I intended to measure the key demographic parameters most likely to be involved in producing these patterns. By following simultaneous changes in population density, survival, production of new modules, changes in size and shape and reproduction, the underlying mechanisms responsible for these broader patterns would be made clearer. This would allow the nature of ecological differences between the alternate isomorphic phases to be examined in greater detail than in any previous study.

I intended to follow these demographic parameters over three years at both a wave-sheltered and a nearby wave-exposed site in Barkley Sound. The amount of detail obtained, however, and the frequency of observation were modified early on by the physical conditions encountered, particularly at the wave-exposed site and in winter. As

a result, only density was measured at the wave-exposed site during the first two years of study, and this only in summer. In the third year survival was measured at the exposed site. In the wave-sheltered site simultaneous changes in density, new blade production, survival, blade size and reproduction were obtained for all seasons during all three years.

The beginning of data collection, in November 1997, coincided with the peak of the 1997 – 1998 El Niño event. This was followed, in early summer 1998, by the onset of the 1998 – 1999 La Niña. When large scale climatic changes may also be affecting demography, it is more difficult to attribute differences in patterns of population density to differences between environments (i.e., comparing previous observations from Vancouver Harbour to this study on the outer coast). On the other hand, those population dynamic patterns that remain constant, while both physical location and climate are altered, are likely to be the ones most widespread in the natural populations. A more detailed picture of the demographic mechanisms producing these patterns should increase our understanding of the population ecology of *Mazzaella splendens* at the largest scale, linking the most common patterns with the local changes that produce them.

The objectives of this study, in their general form, are as follows:

1. To compare seasonal changes in population density of gametophytes and tetrasporophytes of *Mazzaella splendens* between Vancouver Harbour and a summer gametophyte dominant population in a wave-sheltered area in Barkley Sound in order to examine seasonal alternation in phase dominance in wave-sheltered habitats as a common feature of natural populations of *M. splendens*. (Chapter 2)
2. To compare seasonal changes in population density of gametophytes and tetrasporophytes of *Mazzaella splendens* between a wave-sheltered and a wave-exposed habitat in Barkley Sound to examine change in population structure from summer gametophyte dominance in wave-sheltered areas to summer tetrasporophyte dominance in wave-exposed areas as a common feature of natural populations of *M. splendens*. (Chapter 2)

3. To examine the roles of survival and new blade production in altering the population structure of *Mazzaella splendens* along both seasonal and wave exposure gradients. (Chapter 3)
4. To examine the alternate isomorphic phases of *Mazzaella splendens* for size differences, which might contribute to differential survival in different habitats. (Chapter 4)
5. To compare patterns of reproduction of gametophytes and tetrasporophytes of *Mazzaella splendens* between Vancouver Harbour and a summer gametophyte dominant population in a wave-sheltered area in Barkley Sound to assess similarities in phenology, which might also be common to natural populations of *M. splendens*. (Chapter 5)
6. To compare reproductive behaviour of gametophytes and tetrasporophytes of *Mazzaella splendens* between a wave-sheltered and a wave-exposed habitat in Barkley Sound for differences that might have a potential impact on recruitment and for indications of potential costs involved in reproduction. (Chapter 5)

Each of these objectives has been realized to some degree, and in many instances unexpected results have led in new and interesting directions. Variability is one of the fundamental properties of life in all its forms, and finding common threads within that (sometimes overwhelming) variation is the central challenge in biology. Common demographic patterns, as well as variation in these patterns, are found in *Mazzaella splendens*, and as each new piece of evidence accumulates the mechanisms underlying these patterns come into sharper focus.

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Figures to accompany Chapter 1.

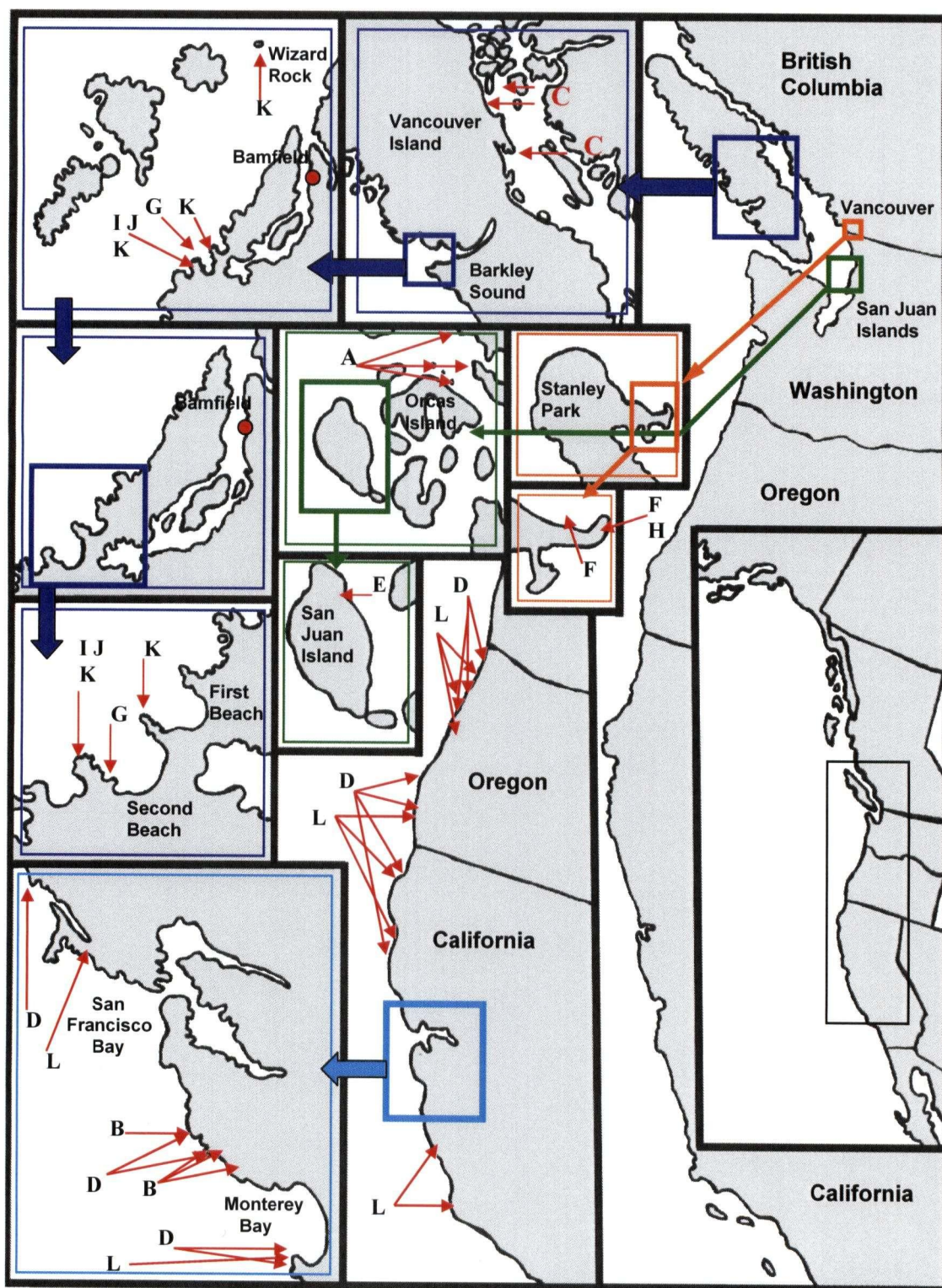


Figure 1.1: Sites of demographic studies of *Mazzaella splendens* on the west coast of North America. **A:** Fralick 1971. **B:** Hansen & Doyle 1976, Hansen 1977. **C:** Adams 1979. **D:** Dyck *et al.* 1985. **E:** May 1986. **F:** DeWreede & Green 1990. **G:** Phillips 1994. **H:** Dyck & DeWreede 1995. **I:** Shaughnessy 1996. **J:** Shaughnessy *et al.* 1996. **K:** Shaughnessy & DeWreede 2001. **L:** Thornber 2001.

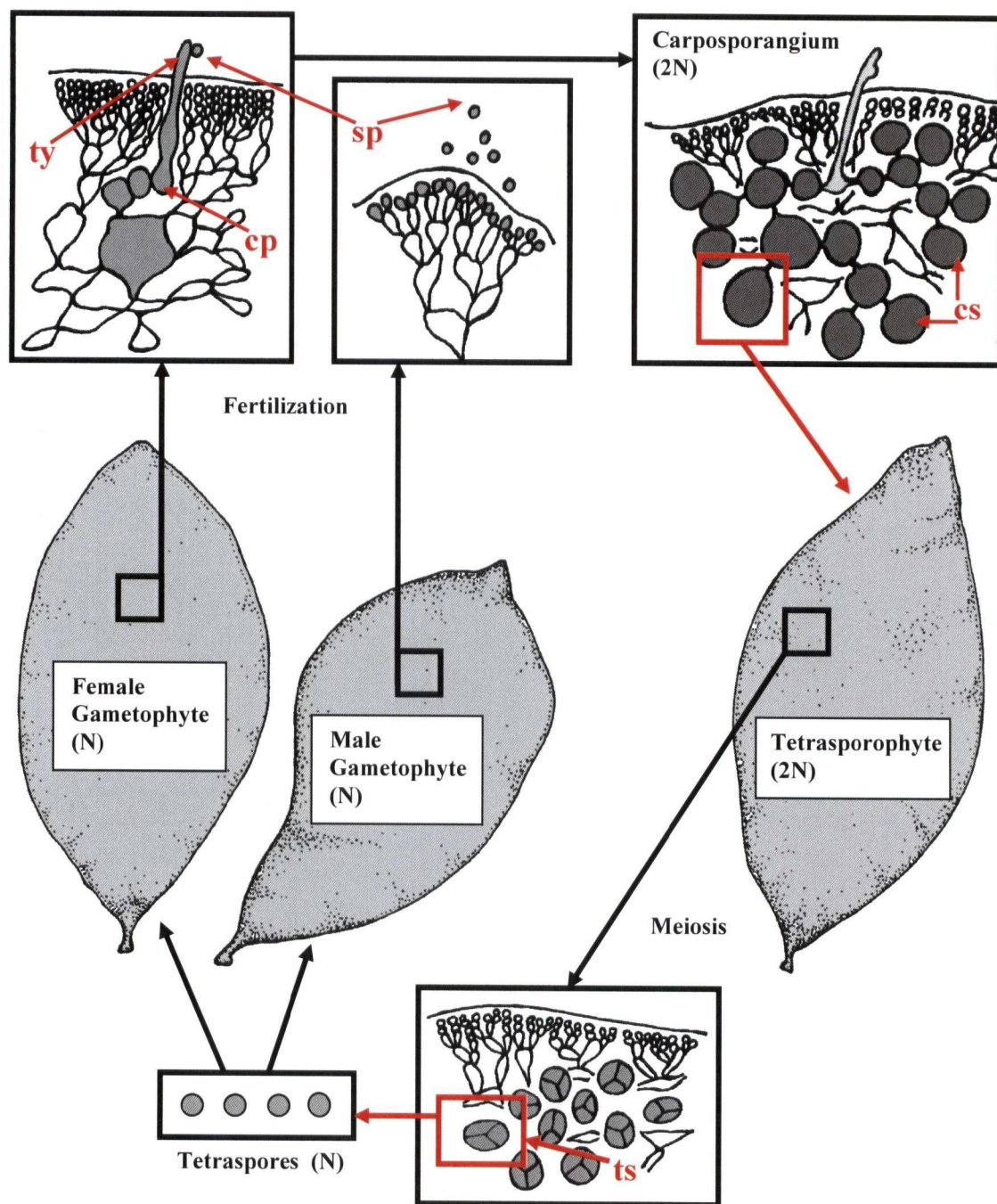


Figure 1.2: Fertilization, zygote amplification, and tetraspore production in the life history of *Mazzaella splendens*. ty = trichogyne, cp = carpogonium, sp = spermatium, cs = carposporangium, ts = tetrasporangium.

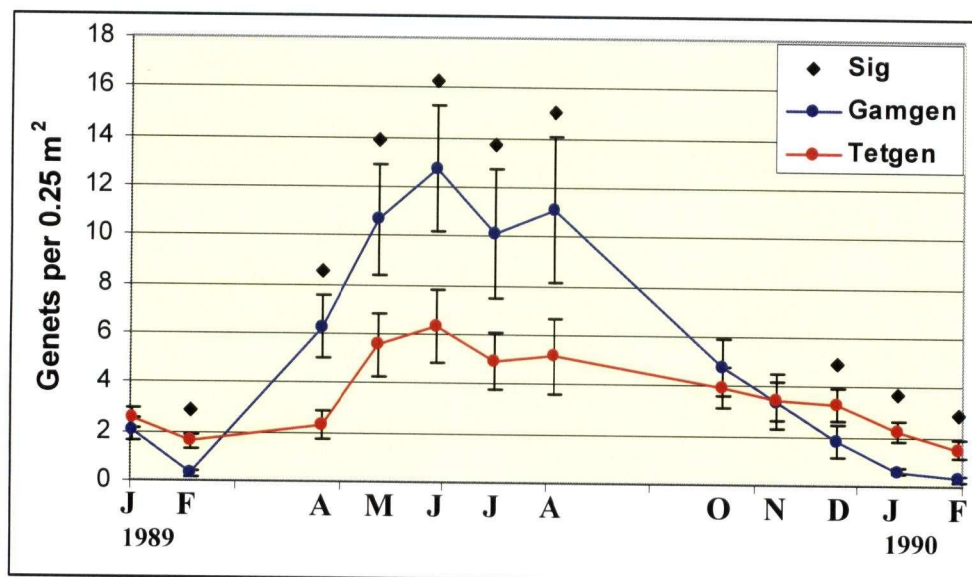


Figure 1.3: Seasonal changes in genet density for the alternate phases of *Mazzaella splendens* at Brockton Point, Vancouver Harbour (January 1989 to February 1990). Means (± 1 S E). Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets. Sig = Statistical significance: Mann-Whitney U Test, $P \leq 0.05$. Redrawn from Dyck & DeWreede 1995.

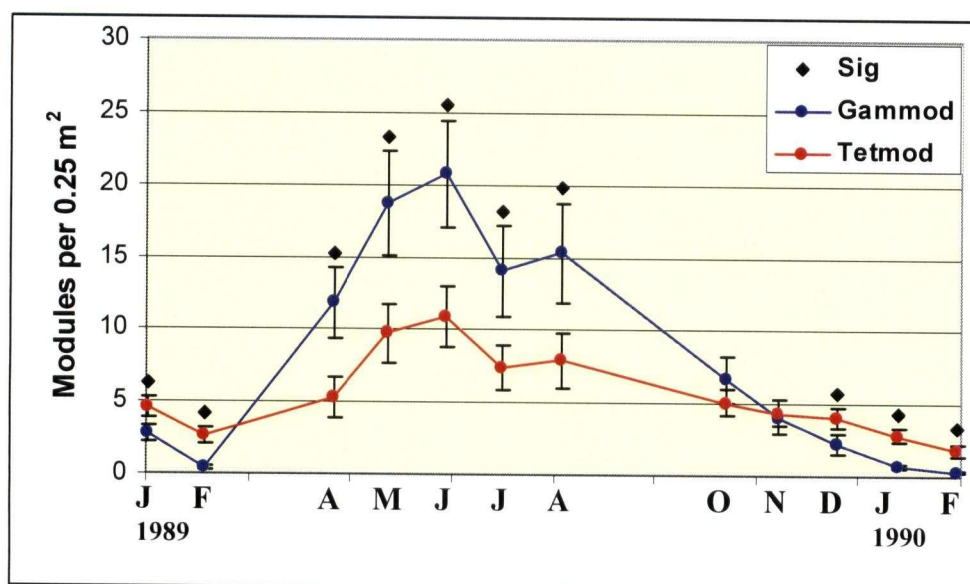


Figure 1.4: Seasonal changes in module density for the alternate phases of *Mazzaella splendens* at Brockton Point, Vancouver Harbour (January 1989 to February 1990). Means (± 1 S E). Gammod = gametophyte modules. Tetmod = tetrasporophyte modules. Sig = Statistical significance: Mann-Whitney U Test, $P \leq 0.05$. Redrawn from Dyck & DeWreede 1995.

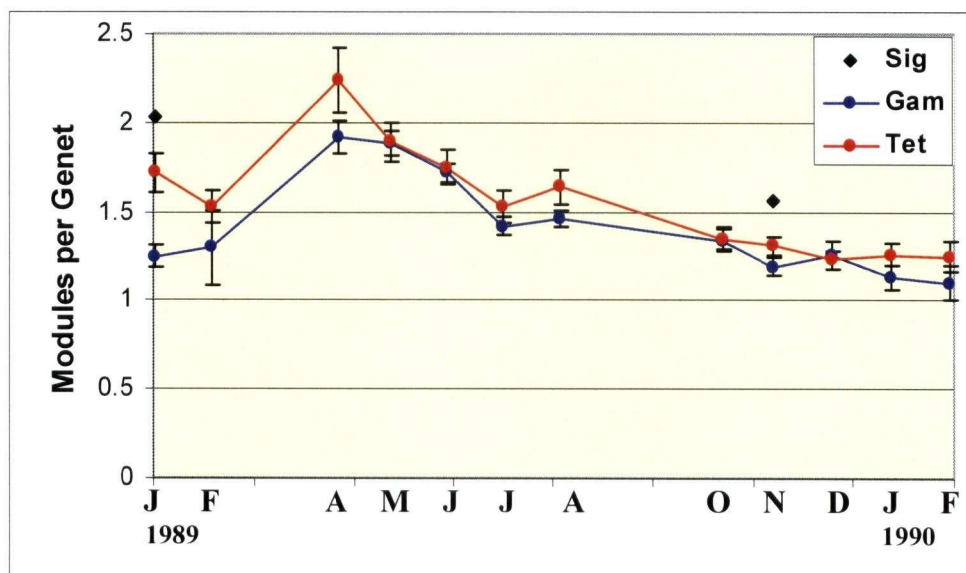


Figure 1.5: Seasonal changes in modules per genet for the alternate phases of *Mazzaella splendens* at Brockton Point, Vancouver Harbour (January 1989 to February 1990). Means (± 1 S E). Gam = gametophytes. Tet = tetrasporophytes Sig = Statistical significance: Mann-Whitney U Test, $P \leq 0.05$. Redrawn from Dyck & DeWreede 1995.

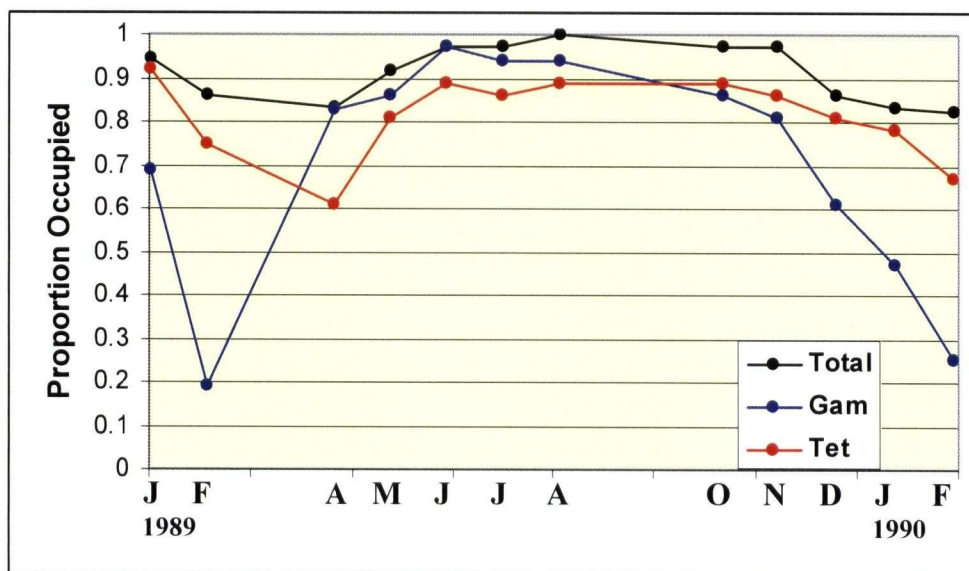


Figure 1.6: Seasonal changes, in proportion of 36 permanent 0.25 m² quadrats occupied by *Mazzaella splendens*, at Brockton Point, Vancouver Harbour (January 1989 to February 1990). Total = occupied by either phase or both. Gam = occupied by gametophytes. Tet = occupied by tetrasporophytes.

Chapter 2. Changes in population density of *Mazzaella splendens*: seasonal and spatial patterns.

Abstract

An understanding of the demographic processes operating at larger scales can be achieved through the study of local populations when a particular species of interest is studied over time by many investigators in a variety of locations. On the west coast of North America, *Mazzaella splendens* is such a species of interest. A synthesis of demographic studies of *M. splendens* from the late 1960s to the present reveals a set of demographic patterns that may be common to the larger natural populations. The pattern is this: population density is high in summer and low in winter for both alternate free-living life history phases of *M. splendens*. The magnitude of this seasonal change decreases in increasingly wave-exposed habitats. In wave-sheltered habitats there is a seasonal alternation from summer haploid to winter diploid dominance that grades to constant diploid dominance as wave exposure in the habitat increases. Changes in density are primarily a function of appearances and disappearances of perennating basal crusts (genets), as modules are produced or lost, rather than differential module production by genets of one phase over those of the other.

To test the generality of these patterns in a new location, I examined seasonal changes in density, in local populations of *Mazzaella splendens*, in a wave-sheltered and a wave-exposed habitat at Second Beach, Barkley Sound. Greater seasonal fluctuation in population density at wave-sheltered rather than wave-exposed habitats is supported as a pattern potentially common to the natural populations of *M. splendens*. The change from summer haploid dominance in wave-sheltered areas to summer diploid dominance in wave-exposed ones is similarly supported. All changes in population density were the result of appearances and disappearances of genets rather than differential module production by haploid vs. diploid basal crusts, in common with previous observations. A seasonal alternation in phase dominance, however, was absent from the wave-sheltered site at Second Beach, Barkley Sound for three consecutive years. This feature of the demography of *M. splendens* appears dependent on local conditions and is not common to all natural populations.

Introduction

Most studies in population ecology are conducted at local scales, but the degree to which any such study can accurately reflect patterns operating in the larger natural population is uncertain (Berryman 2002). There are many practical constraints on large scale demographic work, but an understanding of the patterns at these scales can be approached through replicating and extending the work of previous investigators, in novel situations, for a particular species of interest. Each investigator is able to observe the degree to which a demographic pattern, common to previous studies, is realized in a new environment, and can also examine some new aspect of the mechanisms underlying this pattern. This approach has the dual advantages of advancing a broad scale study and mapping processes important at local scales into those important at higher scales (Camus & Lima 2002).

Mazzaella splendens, a red alga in the Gigartinales with an alternation of free living isomorphic haploid and diploid generations, has great potential as such a species of interest on the west coast of North America. From the late 1960s to the present, demographic information about *M. splendens* has accumulated (Chapter 1). Collectively, this work points to a set of consistent demographic patterns which may be characteristic of the natural populations of *M. splendens*.

The patterns are as follows; standing crop and population density are high in summer and low in winter for both gametophytes and tetrasporophytes (Adams 1979 as *Iridaea cordata*, Dyck & DeWreede 1995). The magnitude of this change becomes less in increasingly wave-exposed habitats, particularly for population density (Hansen 1977 as *Iridaea cordata*). In wave-sheltered habitats there is a seasonal alternation in population structure from summer haploid to winter diploid dominance (DeWreede & Green 1990 as *Iridaea splendens*). This alternation is the result of greater rates of population density increase for gametophytes over tetrasporophytes in spring and summer and greater rates of decrease in fall and winter (Dyck & DeWreede 1995). This seasonal alternation changes to constant diploid dominance in increasingly wave-exposed habitats. Changes in density are a function of appearances and disappearances of genets in the population and not a result of differential module production by genets of one phase over those of the other (Dyck & DeWreede 1995). Evidence from Vancouver Harbour, British Columbia, suggests that increases and decreases in

population density of *Mazzaella splendens* occur more or less evenly over a larger area and are not the result of greater mortality in certain microhabitats over others (Dyck 1991 as *Iridaea splendens*).

In this chapter I report seasonal and spatial changes in population density of the alternate life history phases of *M. splendens* in a wave-sheltered habitat and a wave-exposed habitat at Second Beach, Barkley Sound, a location geographically and ecologically distant from Vancouver Harbour and the Strait of Georgia where these patterns have already been observed. The patterns of population density change from this new location are compared to the consistent demographic patterns from previous studies of *M. splendens*. This comparison is used to modify the set of common demographic patterns derived from previous studies and, in doing so, more accurately describe the demographic properties of the natural populations of *M. splendens* as a whole.

Methods and Materials

A survey of locations in Barkley Sound, Vancouver Island, British Columbia was undertaken from June to August 1997. Site selection was done using the assumption that new sites with a pronounced summer gametophyte dominance were likely wave-sheltered enough to be capable of producing the seasonal dynamics previously seen in Vancouver Harbour (Dyck & DeWreede 1995). In August 1997 a wave-sheltered area at Second Beach, with summer haploid dominance, was selected as the primary study site (Figure 2.1). On October 15 – 18, 1997, twenty 0.0625 m² permanent quadrats were placed within this area, at random, in locations supporting growth of *Mazzaella splendens*. At each of the four corners defining a quadrat, a hole was drilled into the underlying rock and a bolt inserted. Bolts were marked with flagging tape. An additional 20 quadrats were placed, in the same way, at a nearby wave-exposed site where summer diploid dominance was observed. At some point between February 3 and April 15, 1999, 8 quadrats at the wave-sheltered site were covered by sand. During May 14 – 20, 1999, eleven new 0.0625 m² permanent quadrats were placed at random within this site.

Measurements in the permanent quadrats at the sheltered site consisted of counting the number of genets (basal crusts) with visible modules (blades) in each quadrat. A 0.5

cm diameter disk of tissue was removed from each blade with a single hole paper punch. The tissue was used in carrageenan analysis to determine life history phase in the absence of reproductive structures (Garbary & DeWreede 1988, Shaughnessy & DeWreede 1991). This provided a record over time of changes in genet and module density of haploids vs. diploids.

Censuses of *Mazzaella splendens* at the wave-sheltered site were conducted as often as low tides would allow sufficient access to the population (approximately monthly) from November 1997 to January 2001. There were 35 censuses during this time (Table 2.1).

Additional measurements were taken to compare data from the population outside the permanent quadrats with the part inside, providing an assessment of the degree to which the sample in the permanent quadrats resembled the population at large. These additional measurements consisted of seven transects of contiguous 0.0625 m² quadrats run between randomly chosen permanent quadrats. In each contiguous quadrat along a transect the density of haploid and diploid genets, with the number of modules in each genet, were counted (as for the permanent quadrats), and tissue samples were taken from each blade for carrageenan analysis. These transects of contiguous quadrats, by crossing and recording sandy areas in which *Mazzaella splendens* was not present, also provided an estimate of the prevalence of *M. splendens* over all substrata and of the patchiness of its distribution.

The determining factor in doing these transects was availability of time in the face of uncertain conditions. The dates on which these measurements took place (Table 2.1), as well as the number of quadrats sampled on each date, reflect this contingency (and stochasticity) rather than a particular seasonal sampling strategy.

It became evident in November 1997 that winter conditions at the wave-exposed site would not permit detailed work in winter. In June 1998, 12 of the original 20 permanent quadrats placed at the wave-exposed site were rediscovered. These were examined for density of haploids vs. diploids. Number of genets and modules per genet were counted, and each blade had a 0.5 cm diameter tissue sample removed for carrageenan analysis. Seven censuses were conducted in the summers of 1998 and 1999. Sampling dates are given in Table 2.1.

For both the wave-sheltered and wave-exposed areas, differences between phase densities and differences between phases in number of modules per genet, within each sampling period, were assessed with the Mann-Whitney U test using SPSS 9.0. This test was also used to compare densities between the wave-sheltered and wave-exposed areas. The distribution of *Mazzaella splendens* is patchy and the parametric assumptions of homogeneity of variance and normality of distribution were often not met, even after various transformations of the data. Rather than present a combination of parametric tests where parametric assumptions could be met and non-parametric tests where they could not, I have decided to use one test throughout as a common yardstick in all cases. The Mann-Whitney U test is particularly useful in this regard. It is a two-sample rank test, applicable wherever a *t*-test is appropriate. The efficiency of this test relative to a two-sample *t*-test is 0.955 (Fisher & van Belle 1993), so greater applicability is achieved at a relatively small cost.

Since the same set of permanent quadrats was followed through time, concerns about statistical independence prevent discussion of significant differences between seasons and between years. I will, however, discuss apparent trends or tendencies in the data without attributing significance. To examine these trends without relying on parametric measures of variation about the means, I used a cubic spline. This is a nonparametric nonlinear regression that emphasises local over global fit (Hastie & Tibshirani 1990, Silverman 1986) and reveals structure that is obscured when the function to be fit is specified *a priori* (Schluter 1988). Intuitively, the process is analogous to a running regression that strongly weights local values around a particular point on the X-axis, carries out a regression, and then does the same for each of the following X-values. This curve reveals more or less local structure depending on the size of the "window" in which values are most heavily weighted (Schluter 2000). Standard errors on each cubic spline were calculated using 100 bootstrap samples drawn from the original data. All cubic spline calculations were done using glmsWIN 1.0 available at www.zoology.ubc.ca/~schluter/splines.html.

Results

Population density of genets and modules in the permanent quadrats.

Population density of *Mazzaella splendens* genets and modules in the wave-sheltered site at Second Beach, Barkley Sound, increased rapidly for gametophytes and tetrasporophytes in spring of each year (Appendix A, Figures A.1 - A.6), beginning in mid February and peaking in May. Late spring gametophyte densities were significantly larger than tetrasporophyte densities (Figure 2.2 & 2.3). From May to September in all three years there was a precipitous decline in population density of both phases, resulting in no significant differences in density during late summer/early fall. In the fall of 1998 (the El Niño year) there was a marked increase in gametophyte density but not in density of tetrasporophytes. Haploid density remained significantly higher from October 1998 to February 1999. This fall increase in density was much less pronounced in the second and third years.

Modules per genet in the permanent quadrats.

Mean number of modules per genet at the wave-sheltered site ranged between 1 and 3.5, often with large variances. Diploids had a numerical advantage in number of modules per genet on 21 out of 34 occasions, but only twice was this statistically significant (Figure 2.4). There was a general tendency for the number of modules per genet, for both life history phases, to rise as population density rose and fall as population density fell (Appendix A, Figures A.7 & A.8). In the first two years, however, the pattern of changes in number of modules per genet was more erratic for diploids than for haploids. In the third year both phases followed a similar pattern. Peak population density of both gametophytes and tetrasporophytes was lowest in the third year, but the peak number of modules per genet was highest in this year for both phases.

Quadrat occupancy in the permanent quadrats.

The pattern of quadrat occupancy at the wave-sheltered site (Figure 2.5) showed occupancy rising and falling synchronously with increases and decreases in population density. Both gametophytes and tetrasporophytes followed this general pattern.

The transects in the wave-sheltered site.

The pattern of significant differences between phases in the transects confirmed those in the permanent quadrats (Table 2.2). Sampling done on November 30 – December 8, 1998, December 31, 1998 – January 5, 1999, December 20 – 22, 1999, July 30 – August 3, 2000, August 26 – 31, 2000 and December 9 – 15, 2000 showed the same pattern of density as their counterparts in the permanent quadrats. On November 11 – 13, 2000, the results from the transects showed no significant difference between phases for both genets and modules while the permanent quadrats showed a significantly greater density of haploid than diploid modules.

Modules per genet were never significantly different between gametophytes and tetrasporophytes in the transects (Table 2.3). This result was identical to that obtained in the permanent quadrats for the dates in question.

The wave-exposed site.

At the wave-exposed site, tetrasporophyte genet densities were significantly higher than gametophyte densities at all sampling times (Figure 2.6). Population density at the wave-exposed site tended to be more stable than at the wave-sheltered site, with the sharp summer decline in density, seen at the wave-sheltered site, less prominent at the exposed site. Some decline in population density was observed at the wave-exposed site during the summer of 1998, but this was confined mainly to the diploid phase (Appendix A, Figures A.9 – A.11). During the summer of 1999 there was very little population decline (Appendix A, Figures A.12 – A.14). The pattern of change in module density at the wave-exposed site paralleled the pattern of genet density. Tetrasporophyte blades were significantly dominant at all times (Figure 2.7). Population decline was more obvious in modules than in genets, with a 47% decline in tetrasporophyte mean module density from June to September, 1998 (Appendix A, Figures A.15 – A.17). Decline in module density was less in the summer of 1999 (Appendix A, Figures A.18 – A.20).

At the wave-exposed site the number of modules per genet was consistently greater for the diploid phase, but this was statistically significant on only two occasions (Figure 2.8). Mean number of modules per genet varied from 1.3 to 1.5 times greater for diploids vs. haploids. Modules per genet tended to decline gradually from June to October, 1998, primarily among diploid individuals (Appendix A, Figures A.21 &

A.22). This trend was not apparent from June to August, 1999 (Appendix A, Figures A.23 & A.24).

All quadrats at the wave-exposed site were occupied by one or more individuals in each census.

A comparison of population density between the wave-sheltered and wave-exposed areas.

Genet and module density, for both phases combined, was significantly higher at the wave-exposed site than at the wave-sheltered site during all sampling periods (Table 2.4). This was also true for tetrasporophyte genets and modules. Gametophyte modules and genets, however, were not significantly different between these two habitats in June 1998, June 1999, and in July 1999 (for genets only). Gametophyte densities at all other times were significantly higher at the wave-exposed site.

Discussion

Similarities in population dynamics between wave-sheltered areas at Second Beach and at Brockton Point.

In comparing the patterns previously observed at Brockton Point (Dyck & DeWreede 1995) to those at the wave-sheltered site, Second Beach, some aspects of the demography of *Mazzaella splendens* were similar. At both locations there was a marked seasonal change in genets and modules of both life-history phases, with considerably higher population densities in summer than in winter. At both Brockton Point and Second Beach the number of modules per genet showed no significant overall predominance for either phase. In both areas, therefore, changes in population density were primarily the result of appearances and disappearances of genets and not of differential module production by genets of one phase over those of the other.

These two patterns are common to populations of *Mazzaella splendens* in all wave-sheltered areas studied to date, and are consequently the ones most likely to be characteristic of the natural populations of *M. splendens* as a whole. The pattern of high density in summer and low in winter has also been observed for *Mazzaella capensis*

(Bolton & Joska 1993 as *Iridaea capensis*) on the Cape Peninsula in South Africa and for *Mazzaella laminarioides* and *Mazzaella ciliata* in central Chile (Hannach & Santelices 1985 as *Iridaea laminarioides* and *Iridaea ciliata*). This pattern was variable, however, for *Mazzaella flaccida* in central California (Thornber 2001), where it was present in certain years and locations but was reversed in others. High summer and low winter densities at relatively wave-sheltered sites may be common in this genus as a whole, although clearly some variation in this pattern is to be expected.

Differences in population dynamics between wave-sheltered habitats at Second Beach and at Brockton Point.

The expected seasonal alternation in phase dominance, previously observed at Brockton Point, Vancouver Harbour (DeWreede & Green 1990, Dyck & DeWreede 1995), and in the Strait of Georgia (Adams 1979), did not occur in the wave-sheltered site at Second Beach, Barkley Sound. During the entire three year period, only the first and last censuses hinted at anything resembling a winter shift to tetrasporophyte dominance. Haploids predominated each spring and early summer, and often at some point in the fall density increase. A seasonal alternation in phase dominance is clearly not a consistent feature of all local populations of *Mazzaella splendens* in wave-sheltered areas.

Other aspects of the seasonal population dynamics of *Mazzaella splendens* also differed between the two sites. At Second Beach the spring population increase was usually under way each year in February and reached peak density by May. May to September was a period of rapid decline, with densities in August and September often as low as those at the end of winter. In October population density rebounded somewhat, primarily within the haploid phase. In contrast, at Brockton Point, February marked the winter low in density and the population peak was in June. Density then declined gradually from June to February without a fall increase (Dyck & DeWreede 1995).

When patterns of change in population density are compared, between Second Beach on the outer coast and Brockton Point in the relatively sheltered environment of Vancouver Harbour, the absence of a seasonal alternation in phase dominance at Second Beach appears to be primarily a function of the fall density increase. Even with the earlier and more dramatic summer decline at Second Beach, a crossover to winter

diploid dominance could still have occurred if the respective rates of decline in summer, greater for the haploid phase than for the diploid, had continued beyond September of each year. The fall increase however, with its boost in haploid density, seems to have prevented this even though rates of haploid decrease after November appear generally greater than diploid rates.

Some speculation about the relative influences of location and year on the differences in population dynamic patterns between Second Beach, Barkley Sound and Brockton Point, Vancouver Harbour.

Differences associated with geographical location, and with the 1997 – 1998 El Niño event, may both have influenced the differences in population dynamics between Brockton Point in Vancouver Harbour and Second Beach. Interannual variation in the pattern of population density changes would also be expected within each location, reflecting variation in biotic and abiotic parameters from year to year. To ascribe particular differences in the population dynamics of *Mazzaella splendens* observed between Brockton Point and Second Beach to one or the other of the above causes is of course difficult without more extensive data from both locations for the times in question. I would, however, like to suggest where I think the available data are pointing.

Peak spring density of *Mazzaella splendens* at Second Beach in 1998 was approximately twice the peak density previously observed at Brockton Point (Dyck & DeWreede 1995) and declined over the following two summers approaching the level observed in Vancouver Harbour (Figures 2.9 & 2.10). This could potentially represent the process of returning to the normative pattern after the El Niño disturbance. Winter low densities showed a similar trend for density of both phases combined, but not within phases (Figures 2.11 & 2.12), reflecting the presence of a seasonal alternation in phase dominance at Brockton Point but not at Second Beach.

If one allows the assumption that, under normal conditions, similar ranges of interannual variation characterise both geographic locations, there are some changes at Second Beach that could arguably fall outside the normal range. In particular, the period from January 1998 to February 1999 is different from the other two seasonal cycles. This first cycle had a greater fall density increase than the other two (Appendix A, Figure A.1) and was preceded, in November 1997, by the only significant diploid

dominance (for modules only) in the three years of study. It is possible that this cycle represents a response to the 1997 – 1998 El Niño, with an aborted shift to winter tetrasporophyte dominance followed by enhanced production of gametophytes (Figures 2.2 & 2.3). This could potentially occur if gametophyte growth was faster and more sensitive to temperature than tetrasporophyte growth.

The above interpretation is, of course, conditional on the assumption of similar ranges of interannual variation in the demography of *Mazzaella splendens* at both locations, and there are reasons why the normal range of this variation might differ between Brockton Point and Second Beach. It seems unlikely that there would be no abiotic differences between these two locations, and any abiotic parameter varying more widely at one location relative to the other could potentially increase the range of interannual demographic variation at that site. The biotic community at Second Beach is also richer, with many algae and invertebrates that are not found at Brockton Point. This increases the potential number of competitive and herbivore interactions with *M. splendens* at Second Beach. Changes in the impacts of these interactions, as other species fluctuate in numbers from year to year, could also contribute to greater interannual variation in the dynamics of *M. splendens* at Second Beach.

Unlike the patterns discussed above, the pattern of spring density increase and summer decline at Second Beach was consistent over the course of the study and consistently different from its counterpart at Brockton Point. At Second Beach (Figures 2.2 & 2.3) both the spring density increase and the summer decline began earlier than at Brockton Point (Dyck & DeWreede 1995). At Second Beach the summer decline was steep, ending in September, while at Brockton Point a gradual decline in population density proceeded from August to February.

The pattern of seasonal changes in spatial distribution of *Mazzaella splendens* at Second Beach, as seen in proportion of quadrats occupied (Figure 2.5), was also consistent between years and different from that previously seen at Brockton Point (Dyck 1991, as *Iridaea splendens*, see also Chapter 1, Figure 1.6). At Second Beach the proportion of quadrats occupied usually increased with increasing population density and decreased as population density declined. This pattern was similar for both life history phases. Quadrat occupancy at Second Beach was often low, falling into the range from 0.4 to 0.2 on about 30 % of the times population density was measured.

At Brockton Point quadrat occupancy never fell below 0.8 at any time of year. The patterns of occupancy here were different between gametophytes and tetrasporophytes, with occupancy by one phase sometimes declining less rapidly, or increasing relative to the other. But occupancy by diploids at Brockton Point did not fall below 0.6, even at the winter density minimum. Haploid occupancy remained relatively constant from April to November and then fell to 0.2 during the winter part of the population decline (Chapter 1, Figure 1.6).

Reduction in population density at Brockton Point, therefore, appears to have been more a general decrease over all quadrats at the site, while population density at Second Beach declined, to a greater degree, by all individuals disappearing from certain quadrats. This may reflect a greater heterogeneity of microhabitats for *Mazzaella splendens* at Second Beach, with plants in some quadrats reacting to the effects of seasonal changes before others.

The consistency of the above patterns between years at Second Beach, and their marked difference from those at Brockton Point, suggests that these differences in the demography of *Mazzaella splendens* are more likely to be due to differences of some kind between the two locations. What these differences may be is not yet clear. But the nature of the differences in population dynamics between the two locations suggests that some rethinking of the assumed roles of wave force and desiccation, in altering population density, is required.

Waves on the outer coast, even in summer, are larger than any waves usually found, even in winter storms, in Vancouver Harbour. If the seasonal change from summer haploid to winter diploid dominance at Brockton Point is indeed due to greater diploid survival in response to greater wave force in winter, why was such a shift not seen at Second Beach? If wave force is indeed acting in this process, there is clearly no standard response of *Mazzaella splendens* to wave force *per se*. If there were, haploid blades should not predominate, even in summer, in any outer coast habitats except the most sheltered inlets. Wave force may be less important in changing population density of established blades than previously thought.

Summer low tides at Second Beach typically occur early in the morning, sometimes accompanied by fog. At Brockton Point summer low water is usually in the middle of the day and fog is relatively rare. Because of this, desiccation stress on blades

of *Mazzaella splendens* during summer low tides should be generally higher at Brockton Point than at Second Beach. The summer decline in population density at Brockton Point (from June to July 1989) was accompanied by bleaching of blades (Dyck 1991 as *Iridaea splendens*), but there followed a subsequent recovery (in August) before the slow decline to the winter minimum. That this pattern is observed in a location like Brockton Point, which should produce greater desiccation stress compared to Second Beach, while at Second Beach there is a more precipitous decline with an earlier onset, would seem to indicate that desiccation also plays less of a role in summer population decline than has been previously supposed.

The seasonal alternation from summer gametophyte to winter tetrasporophyte dominance has proved variable, whether due to climatic anomaly or to differences in environment between Vancouver Harbour and the outer coast. On this point it is important to note that seasonal alternations, with summer haploid and winter diploid dominance, are not absent from Barkley Sound. Sunday (2001) found such alternations for the period of May 2000 – March 2001 at Seppings Island, Scott's Bay, Wizard Island and Prasiola Point, all in Barkley Sound. The Prasiola Point site used by Sunday (2001) was across the bay from the Second Beach site used in my study, at a distance of about 500 m. That a significant winter diploid dominance was found at Prasiola Point in the same winter (2000-2001) that no significant difference between phases was observed at my site indicates that there are likely local differences, even at this scale, that affect the degree to which seasonal alternation is expressed.

Population density at the wave-exposed site.

The previously reported pattern of change, from gametophyte dominance in relatively wave-sheltered areas to tetrasporophyte dominance in wave-exposed areas (Dyck *et al.* 1985, as *Iridaea cordata*, Phillips 1994, as *Mazzaella lilacina*), was also observed at Second Beach. This pattern, like seasonal fluctuation in density in wave-sheltered areas remains a potential common feature of the natural populations of *Mazzaella splendens*.

The pattern of change in population density at the wave-exposed site was markedly different from that at the wave-sheltered site. Comparatively little population decline was observed at the wave-exposed site while the population at the wave-

sheltered site was undergoing its annual summer crash. These two areas were about 30 m distant from each other, illustrating again the importance of local environmental differences in structuring populations of *Mazzaella splendens*. One potential explanation of this difference in population dynamics could be that increased wave activity at the exposed site reduces desiccation stress, keeping blades wetter during low tides. Doubts about the importance of desiccation stress have been raised, however, through comparing patterns at Second Beach and Brockton Point.

Wave force and desiccation are the two most obvious environmental variables that will vary over such short distances. But there could also be biotic differences between these two habitats that might contribute to the different population dynamic patterns. Gaines (1985 as *Iridaea cordata*) has shown that changes in the assemblage of herbivores can affect the distribution of *Mazzaella splendens*. Gaines (1985 as *Iridaea cordata*) found feeding preferences for reproductive over non-reproductive blades of *M. splendens* in *Lacuna marmorata* and *Idotea wosnesenskii*, but he did not examine whether there were feeding preferences for one life history phase over the other. The summer population decline in *M. splendens* at the wave-sheltered site at Second Beach could conceivably be due to an herbivore, not present at Brockton Point or at the wave-exposed site, that experiences a seasonal population increase in summer. It is even possible that there may be different micrograzers between the two habitats, with those at the wave-sheltered sites preferring diploid over haploid recruits of *M. splendens*, and those at the wave-exposed site having the opposite preference. Very little is known in this area, and with abiotic factors apparently not as important in structuring populations of *M. splendens* as previously supposed, biotic differences between these two habitats may prove a useful line of inquiry.

The available evidence (Hansen 1977, as *Iridaea cordata*, May 1986, as *Iridaea cordata*) suggests that seasonal change in population density of *Mazzaella splendens* is primarily the result of perennation, with more basal crusts producing blades (and therefore "appearing" in the population) when conditions are favourable and losing those blades ("disappearing") as conditions become unfavourable. In this case peak genet density, in any habitat, should be the best available estimator of the size of the population of basal crusts. Based on this, the density of haploid individuals (basal crusts) at the wave-sheltered site was not significantly different than at the wave-exposed site,

while the density of diploid individuals was always significantly higher at the wave-exposed site. The difference between the two habitats appears more a function of increasing the population of diploids in wave-exposed areas and less of reducing the population of haploids. In terms of the underlying population of basal crusts, haploids may do equally well in both habitats, although they lose modules at a greater rate and disappear more rapidly in summer at the wave-sheltered site. Diploids, however, appear to have a much larger density of basal crusts in the wave-exposed vs. the wave-sheltered habitat (Table 2.4).

Phillips (1994 as *Mazzaella lilacina*) found that recruitment by tetrasporophytes of *Mazzaella splendens* in wave-exposed areas was higher than expected based on local densities of cystocarpic gametophytes, and that gametophyte recruitment was greater than expected in wave-sheltered areas based on available fertile tetrasporophytes. May (1986 as *Iridaea cordata*) found that annual recruitment of 20% did not significantly alter the proportion haploid in a wave-sheltered population. If the relative densities of basal crusts are reflected by the peak densities of visible genets, and if these densities of basal crusts are a reflection of relative success at recruitment, then the differences in densities observed between the wave-sheltered and wave-exposed areas at Second Beach suggest that haploids may have similar recruitment success in both habitats while diploids recruit more successfully in wave-exposed areas.

Modules per genet at the wave-exposed site.

The number of modules per genet for *Mazzaella splendens* at the wave-exposed site was larger for tetrasporophytes at all times (Figure 2.8), but this advantage was only significant twice (July 1998 and June 1999). These results appear less variable than those at the wave-sheltered site at Second Beach. It is conceivable that these differences might be the beginnings of a trend toward significantly greater numbers of modules per genet for diploids, with a consistently significant difference appearing at wave exposures greater than those at the wave-exposed site at Second Beach. Nevertheless, the infrequency of significant differences in both habitats examined in this study leaves us unable to reject the hypothesis that the same essential mechanism is operating all along a wave exposure gradient. Like the populations at Brockton Point (Dyck & DeWreede 1995) and the sheltered site at Second Beach, changes in density among

perennating individuals at the wave-exposed site are primarily the result of appearances and disappearances of genets, and not differential module production by genets of one phase over those of the other. This final pattern is common to *Mazzaella splendens* at all times and in all habitats studied so far.

Conclusions

Demographic patterns potentially common to natural populations of *Mazzaella splendens* are:

- 1.) Seasonal fluctuation with high population density in summer and low density in winter for both life history phases in wave-sheltered habitats, with the magnitude of this fluctuation decreasing as wave force in the habitat increases.
- 2.) A change from summer gametophyte dominance to summer tetrasporophyte dominance as wave force in the habitat increases.
- 3.) Changes in population density are the result of appearances and disappearances of genets rather than differential module production by haploid vs. diploid genets.

Seasonal alternation in phase dominance at wave-sheltered sites, consistent with all previously published studies, was not present at Second Beach and appears dependent on local conditions.

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Figures to accompany Chapter 2.

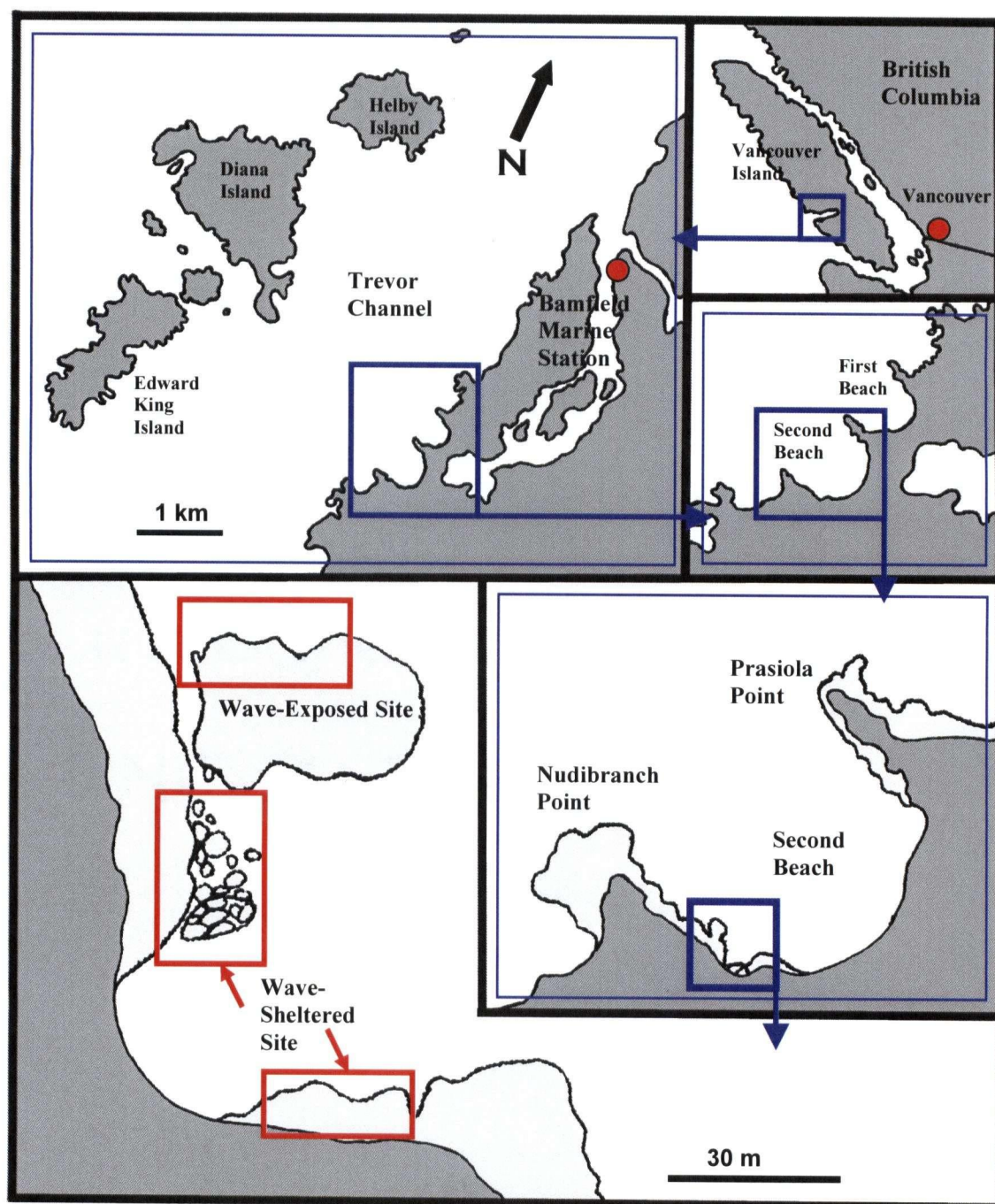


Figure 2.1: Location of the wave-sheltered and wave-exposed study sites for *Mazzaella splendens* at Second Beach, Barkley Sound. Shaded areas: dark = above high tide, light = intertidal.

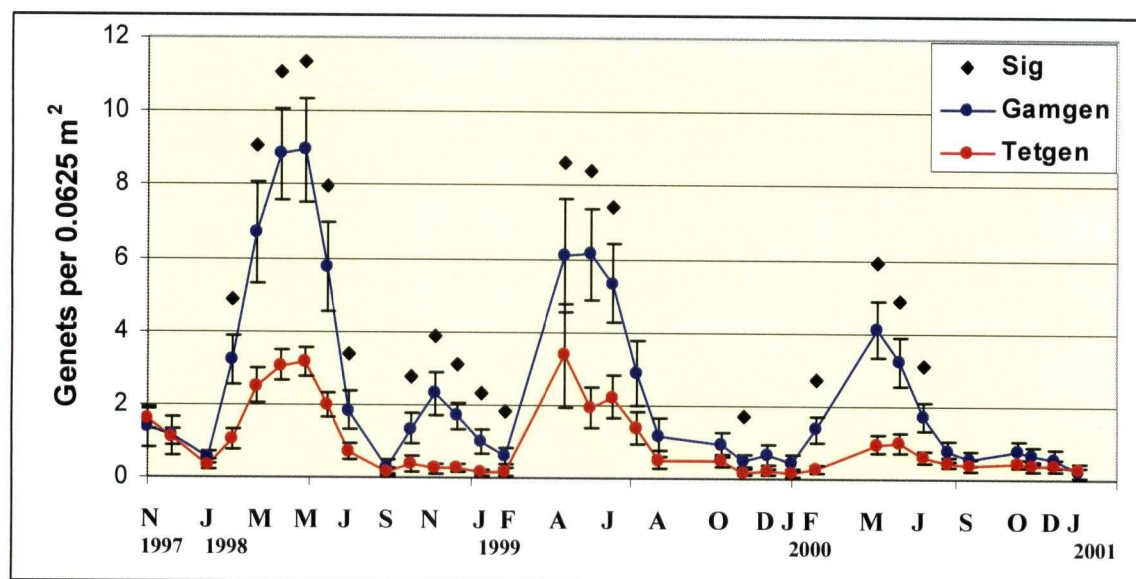


Figure 2.2: Seasonal changes in genet density for the alternate phases of *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Means (± 1 S E). Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets. Sig = Statistical significance: Mann-Whitney U Test, $P \leq 0.05$.

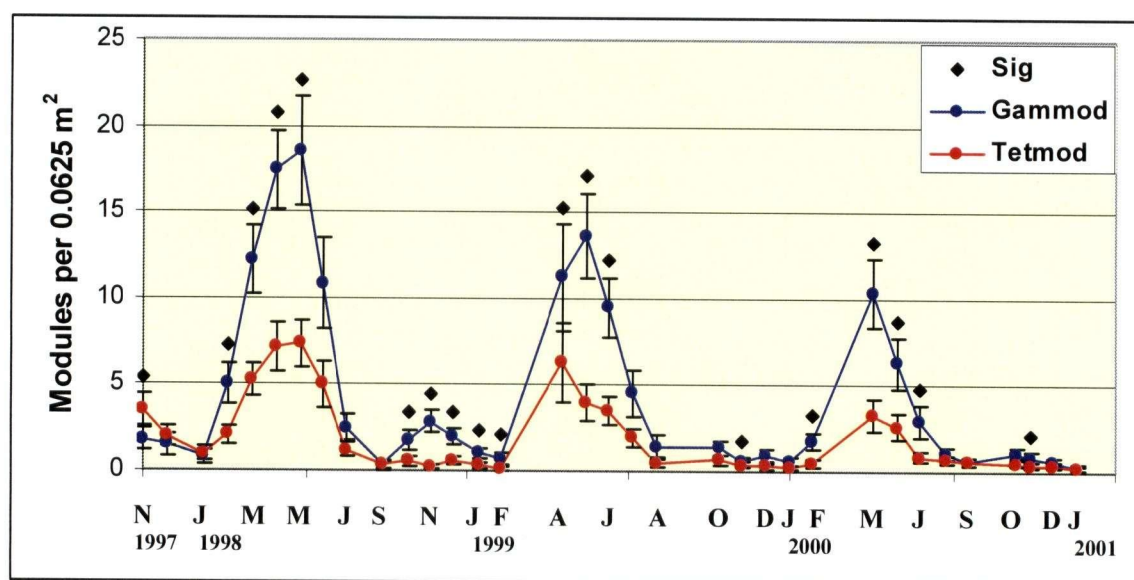


Figure 2.3: Seasonal changes in module density for the alternate phases of *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Means (± 1 S E). Gammod = gametophyte modules. Tetmod = tetrasporophyte modules. Sig = Statistical significance: Mann-Whitney U Test, $P \leq 0.05$.

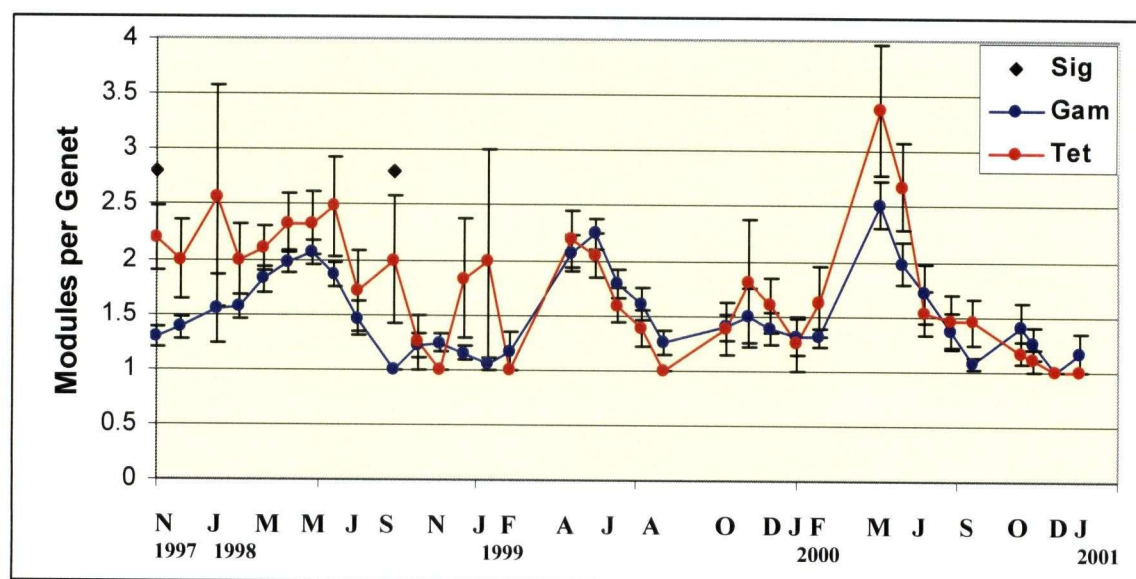


Figure 2.4: Seasonal changes in modules per genet for the alternate phases of *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Means (± 1 S.E.). Gam = gametophytes. Tet = tetrasporophytes. Sig = Statistical significance: Mann-Whitney U Test, $P \leq 0.05$.

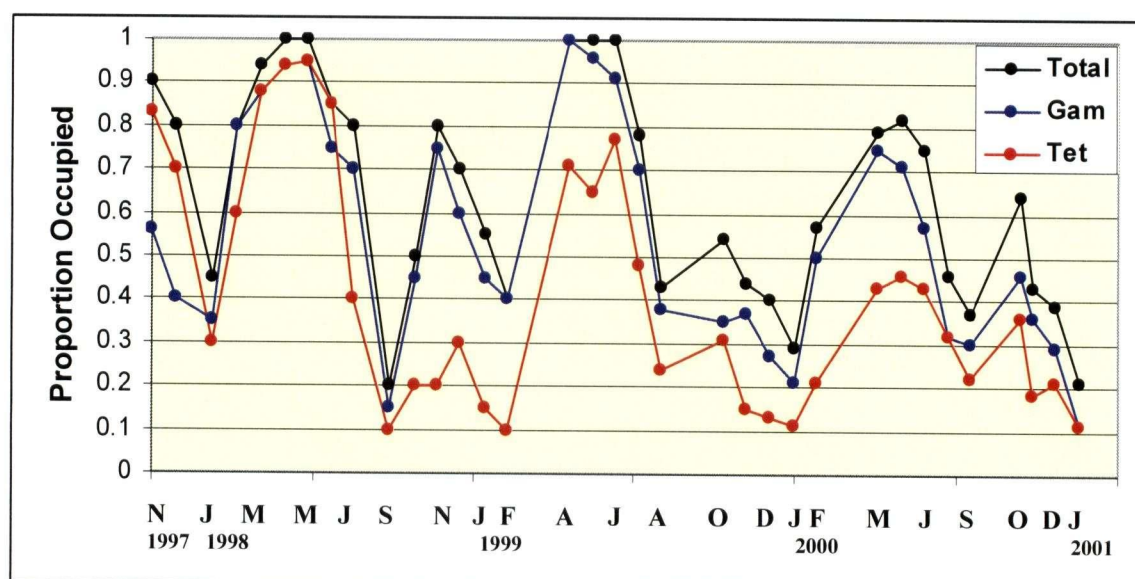


Figure 2.5: Seasonal changes, in proportion of total quadrats occupied by *Mazzaella splendens*, among 20 – 31 permanent 0.0625 m² quadrats at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Total = occupied by either phase or both. Gam = occupied by gametophytes. Tet = occupied by tetrasporophytes.

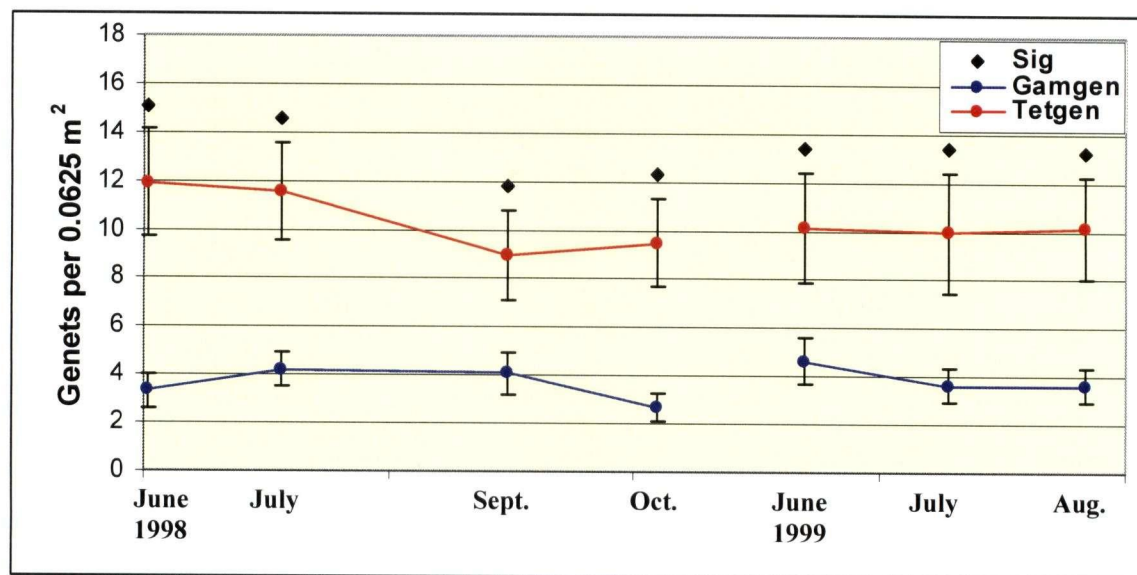


Figure 2.6: Seasonal changes in genet density for the alternate phases of *Mazzaella splendens* at the wave-exposed site, Second Beach, Barkley Sound (June to October 1998 and June to August 1999). Means (± 1 S E). Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets. Sig = Statistical significance: Mann-Whitney U Test, $P \leq 0.05$.

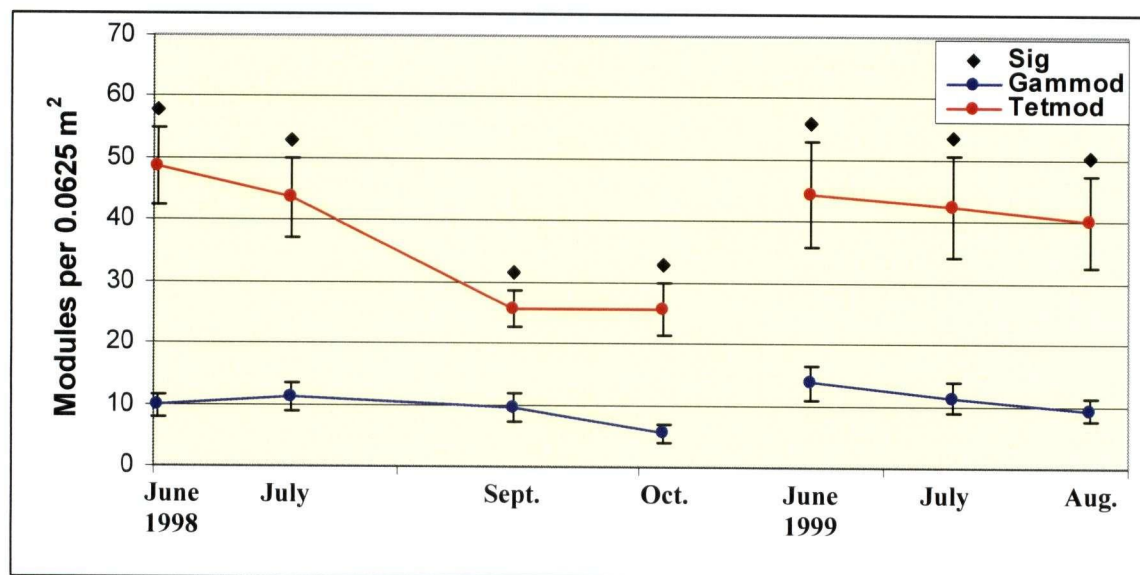


Figure 2.7: Seasonal changes in module density for the alternate phases of *Mazzaella splendens* at the wave-exposed site, Second Beach, Barkley Sound (June to October 1998 and June to August 1999). Means (± 1 S E). Gammod = gametophyte modules. Tetmod = tetrasporophyte modules. Sig = Statistical significance: Mann-Whitney U Test, $P \leq 0.05$.

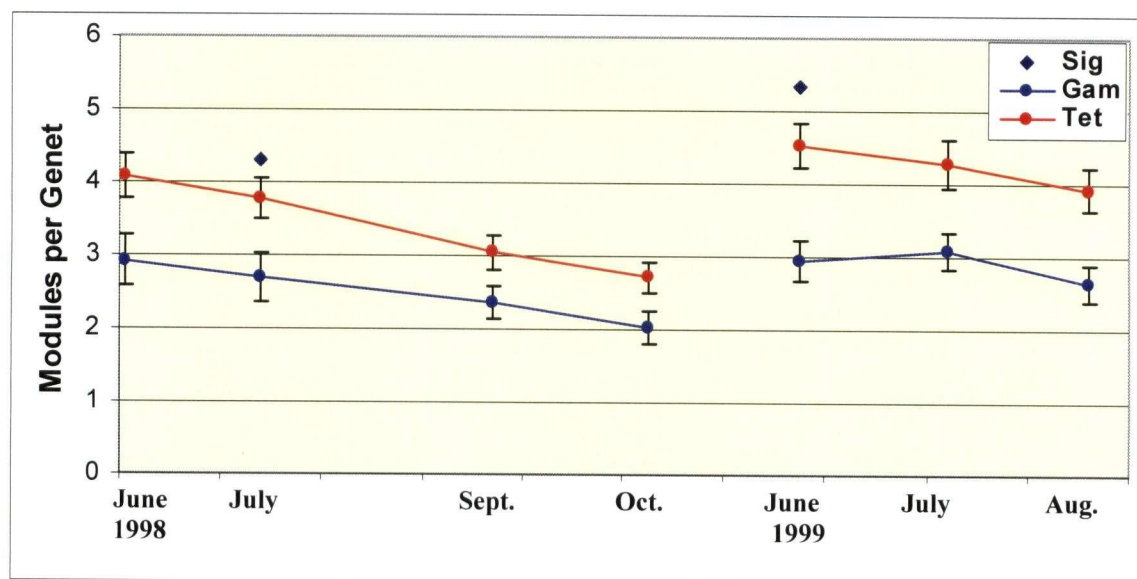


Figure 2.8: Seasonal changes in modules per genet for the alternate phases of *Mazzaella splendens* at the wave-exposed site, Second Beach, Barkley Sound (June to October 1998 and June to August 1999). Means (± 1 S E). Gam = gametophytes. Tet = tetrasporophytes. Sig = Statistical significance: Mann-Whitney U Test, $P \leq 0.05$.

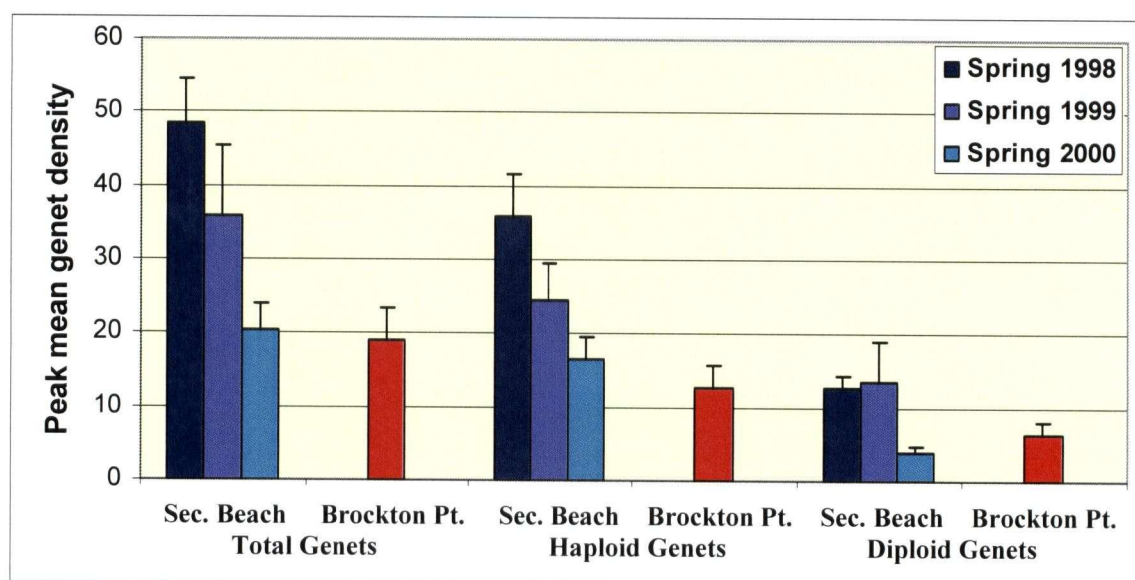


Figure 2.9: Peak mean genet density of *Mazzaella splendens* (genets per 0.25 m²) in three consecutive springs (1998–2000) at Second Beach, Barkley Sound compared to the spring peak mean genet density at Brockton Point, Vancouver Harbour (1989). Means (± 1 S E).

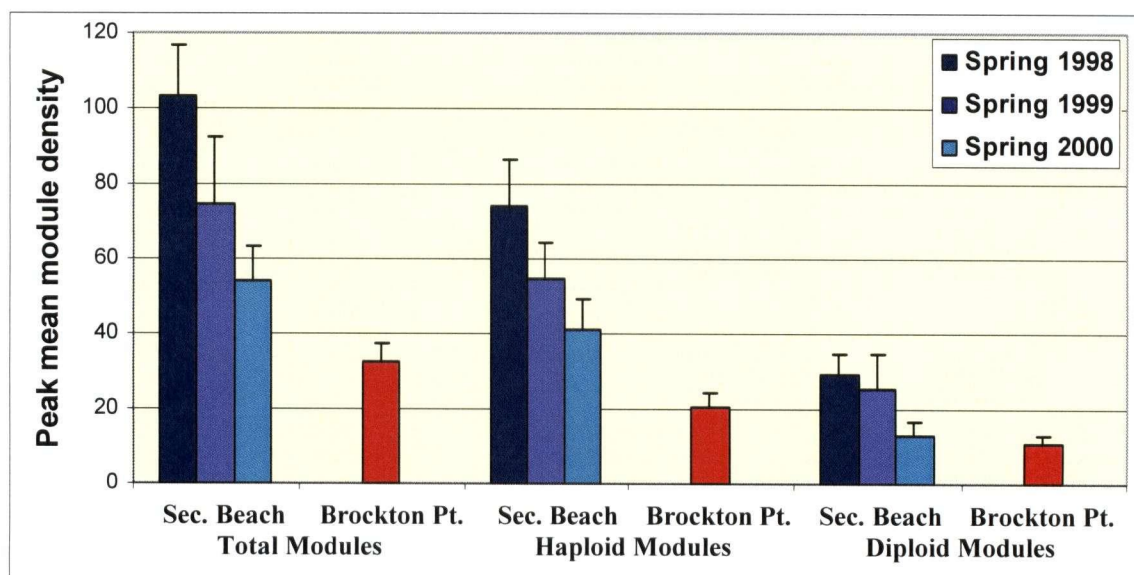


Figure 2.10: Peak mean module density of *Mazzaella splendens* (modules per 0.25 m²) in three consecutive springs (1998 – 2000) at Second Beach, Barkley Sound compared to the spring peak mean module density at Brockton Point (red bar), Vancouver Harbour (1989). Means (± 1 S E).

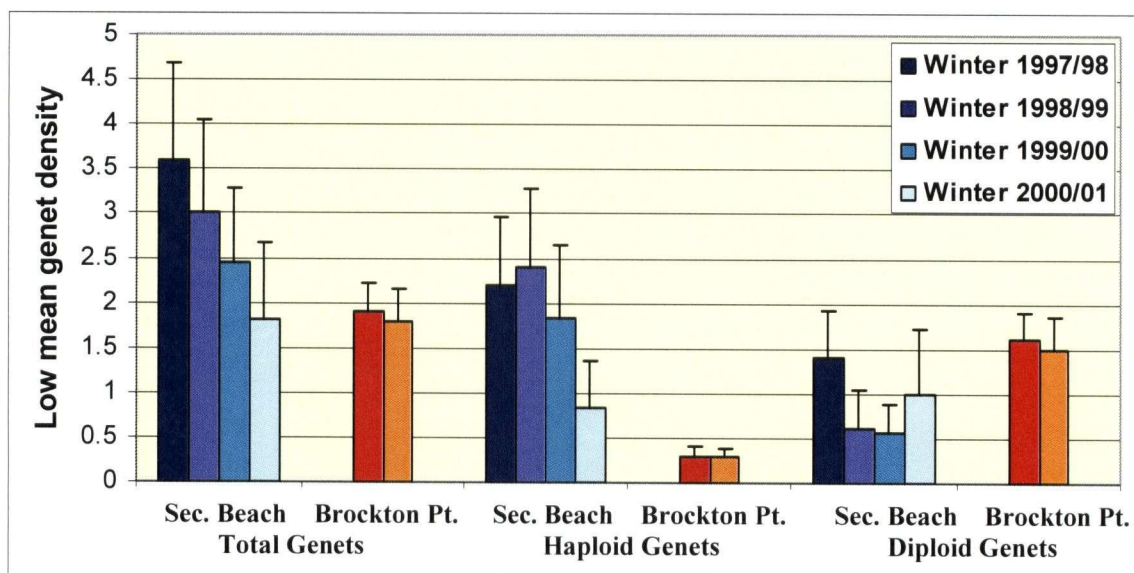


Figure 2.11: Low mean genet density of *Mazzaella splendens* (genets per 0.25 m²) in four consecutive winters (1997/98 – 2000/01) at Second Beach, Barkley Sound compared to the winter low mean genet density at Brockton Point, Vancouver Harbour in 1988/89 (red bar) & 1989/90 (orange bar). Means (± 1 S E).

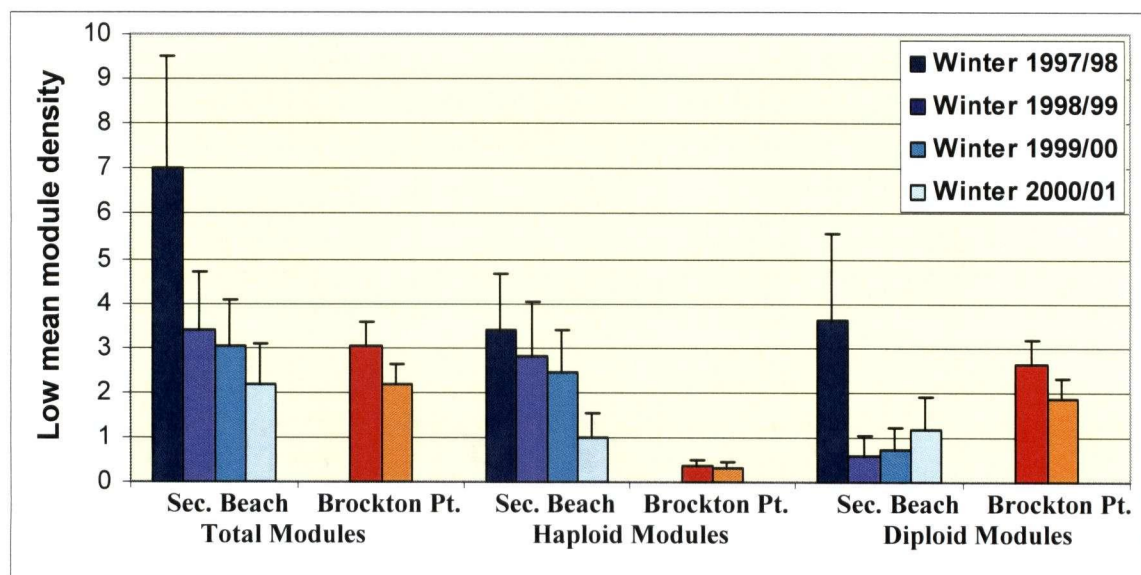


Figure 2.12: Low mean module density of *Mazzaella splendens* (modules per 0.25 m²) in four consecutive winters (1997/98 – 2000/01) at Second Beach, Barkley Sound compared to the winter low mean module density at Brockton Point, Vancouver Harbour in 1988/89 (red bar) & 1989/90 (orange bar). Means (± 1 S.E.).

Tables to accompany Chapter 2.

Table 2.1: Dates of censuses of *Mazzaella splendens* at Second Beach, Barkley Sound.

Permanent Quadrats, Wave-Sheltered Site.			
Year	Census dates.	Year	Census dates.
1997	November 11 - 18	1999	July 11 - 18
	December 11 - 16		August 8 - 13
1998	January 26 - 30		October 24 - 27
	February 24 - 28		November 21
	March 26 - April 1		December 20 - 22
	April 25 - May 1	2000	January 20 - 22
	May 23 - 30		February 17 - 19
	June 22 - 28		April 6 - 8
	July 20 - 26		May 3 - 9
	September 3 - 7		June 1 - 8
	October 5 - 10		June 29 - July 6
	November 2 - 8		July 30 - August 3
	November 30 - December 8		August 26 - 31
1999	December 31, 1998 - January 5		October 26 - 30
	January 28 - February 3		November 11 - 13
	April 14 - 12		December 9 - 15
	May 14 - 20	2001	January 7 - 8
	June 11 - 18		
Transects, Wave-Sheltered Site.			
Year	Census dates.	Year	Census dates.
1998	November 30 - December 8	2000	July 30 - August 3
1999	December 30, 1998 - January 5		August 26 - 31
	December 20 - 22		November 11 - 13
			December 9 - 15
Permanent Quadrats, Wave-Exposed Site.			
Year	Census dates.	Year	Census dates.
1998	June 22 - 28	1999	June 11 - 18
	July 20 - 26		July 11 - 18
	September 3 - 7		August 8 - 13
	October 5 - 10		

Table 2.2: Descriptive and inferential statistics for genets and modules of *Mazzaella splendens* gametophytes and tetrasporophytes in the transects at the wave-sheltered site, Second Beach, Barkley Sound. December 1998 to December 2000. Given are sample size (= N), mean population density per 0.0625 m² (= Mean), the standard error of the mean (= S.E.) and the P value from the Mann-Whitney U test (= M.W.-U) comparing densities of haploid vs. diploid genets and haploid vs. diploid modules. Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

Date	N		Mean	S.E.	M.W.-U
Dec. 1998	31	Gamgen	4.58	0.756	P < 0.001
		Tetgen	0.35	0.143	
		Gammod	6.61	1.203	P < 0.001
		Tetmod	0.35	0.127	
Jan. 1999	173	Gamgen	0.21	0.049	P = 0.001
		Tetgen	0.07	0.021	
		Gammod	0.27	0.064	P = 0.003
		Tetmod	0.09	0.031	
Dec. 1999	199	Gamgen	0.27	0.055	P = 0.102
		Tetgen	0.20	0.047	
		Gammod	0.44	0.097	P = 0.182
		Tetmod	0.36	0.088	
Aug. 2000	9	Gamgen	3.0	1.109	P = 0.075
		Tetgen	1.22	0.760	
		Gammod	5.89	2.031	P = 0.064
		Tetmod	2.56	2.069	
Sept. 2000	18	Gamgen	1.67	0.676	P = 0.274
		Tetgen	0.89	0.387	
		Gammod	2.56	1.079	P = 0.218
		Tetmod	1.22	0.769	
Nov. 2000	26	Gamgen	0.37	0.097	P = 0.153
		Tetgen	0.25	0.079	
		Gammod	0.58	0.171	P = 0.397
		Tetmod	0.47	0.149	
Dec. 2000	145	Gamgen	0.27	0.055	P = 0.183
		Tetgen	0.20	0.047	
		Gammod	0.44	0.097	P = 0.286
		Tetmod	0.36	0.088	

Table 2.3: Descriptive and inferential statistics for modules per genet in *Mazzaella splendens* gametophytes and tetrasporophytes in the transects at the wave-sheltered site, Second Beach, Barkley Sound. December 1998 to December 2000. Given are sample size (= N), mean population density per 0.0625 m² (= Mean), the standard error of the mean (= S.E.) and the P value from the Mann-Whitney U test (= M.W.-U) comparing densities of haploid vs. diploid genets and haploid vs. diploid modules. Gam = gametophyte. Tet = tetrasporophyte.

Date		N	Mean	S.E.	M.W.-U
Dec. 1998	Gam	141	1.45	0.08	P = 0.133
	Tet	11	1.09	0.09	
Jan. 1999	Gam	36	1.28	0.09	P = 0.156
	Tet	12	1.75	0.30	
Dec. 1999	Gam	53	1.62	0.13	P = 0.625
	Tet	39	1.82	0.20	
Aug. 2000	Gam	26	1.96	0.20	P = 0.943
	Tet	11	2.09	0.39	
Sept. 2000	Gam	30	1.63	0.16	P = 0.820
	Tet	13	1.69	0.24	
Nov. 2000	Gam	37	1.54	0.13	P = 0.471
	Tet	25	1.88	0.25	
Dec. 2000	Gam	33	1.33	0.11	P = 0.341
	Tet	27	1.52	0.17	

Table 2.4: Descriptive and inferential statistics for comparing densities of *Mazzaella splendens* at the wave-sheltered and wave-exposed sites, Second Beach, Barkley Sound. June to October 1998 and June to August 1999. Given are the mean population density per 0.0625 m² (= Mean), the standard error of the mean (= S.E.) and the P value from the Mann-Whitney U test (= M.W.-U). Genets = genets of both phases. Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets. Modules = modules of both phases. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

June 1998					
	Wave-sheltered		Wave-exposed		M.W.-U
	Mean	S.E.	Mean	S.E.	
Genets	7.75	1.380	15.25	2.508	P = 0.015
Gamgen	5.75	1.214	3.33	0.700	P = 0.431
Tetgen	2.00	0.348	11.92	2.190	P < 0.001
Modules	13.83	3.093	22.20	6.409	P < 0.001
Gammod	11.80	2.639	6.27	1.810	P = 0.803
Tetmod	6.18	1.382	21.87	6.313	P < 0.001

July 1998					
	Wave-sheltered		Wave-exposed		M.W.-U
	Mean	S.E.	Mean	S.E.	
Genets	2.55	0.667	15.79	2.330	P < 0.001
Gamgen	1.85	0.530	4.21	0.712	P = 0.011
Tetgen	0.70	0.219	11.57	2.029	P < 0.001
Modules	3.70	1.013	54.79	6.129	P < 0.001
Gammod	2.50	0.783	11.21	2.382	P = 0.004
Tetmod	1.20	0.401	43.57	6.312	P < 0.001

September 1998					
	Wave-sheltered		Wave-exposed		M.W.-U
	Mean	S.E.	Mean	S.E.	
Genets	0.45	0.235	13.00	2.425	P < 0.001
Gamgen	0.30	0.207	4.07	0.880	P < 0.001
Tetgen	0.15	0.109	8.93	1.841	P < 0.001
Modules	0.60	0.320	35.21	4.246	P < 0.001
Gammod	0.30	0.207	9.57	2.404	P < 0.001
Tetmod	0.30	0.252	25.64	3.032	P < 0.001

October 1998					
	Wave-sheltered		Wave-exposed		M.W.-U
	Mean	S.E.	Mean	S.E.	
Genets	1.75	0.507	12.21	2.149	P < 0.001
Gamgen	1.35	0.399	2.71	0.578	P = 0.045
Tetgen	0.40	0.222	9.50	1.778	P < 0.001
Modules	2.35	0.779	31.21	4.945	P < 0.001
Gammod	1.80	0.569	5.50	1.402	P = 0.023
Tetmod	0.55	0.328	25.71	4.232	P < 0.001

Table 2.4: Continued.

June 1999					
	Wave-sheltered		Wave-exposed		M.W.-U
	Mean	S.E.	Mean	S.E.	
Genets	7.55	1.395	14.79	2.776	P = 0.012
Gamgen	5.32	1.078	4.62	0.941	P = 0.974
Tetgen	2.23	0.570	10.14	2.282	P < 0.001
Modules	13.00	2.021	58.00	9.877	P < 0.001
Gammod	9.45	1.724	13.64	2.655	P = 0.235
Tetmod	3.55	0.824	44.36	8.462	P < 0.001

July 1999					
	Wave-sheltered		Wave-exposed		M.W.-U
	Mean	S.E.	Mean	S.E.	
Genets	4.26	1.192	13.57	2.832	P = 0.001
Gamgen	2.87	0.870	3.64	0.753	P = 0.171
Tetgen	1.39	0.043	9.93	2.460	P < 0.001
Modules	6.48	1.700	53.50	9.609	P < 0.001
Gammod	4.52	1.317	11.21	2.445	P = 0.033
Tetmod	1.96	0.557	42.29	8.199	P < 0.001

August 1999					
	Wave-sheltered		Wave-exposed		M.W.-U
	Mean	S.E.	Mean	S.E.	
Genets	1.67	0.794	13.79	2.468	P < 0.001
Gamgen	1.14	0.540	3.64	0.723	P = 0.001
Tetgen	0.52	0.273	10.14	2.070	P < 0.001
Modules	1.95	0.950	49.36	8.534	P < 0.001
Gammod	1.43	0.692	9.36	1.903	P < 0.001
Tetmod	0.52	0.273	40.00	7.378	P < 0.001

Chapter 3. Seasonal and spatial change in population density of *Mazzaella splendens*: survival and new blade production.

Abstract

Mazzaella splendens, a red alga with an alternation of isomorphic generations has shown a seasonal alternation from summer gametophyte to winter tetrasporophyte dominance. This alternation is the result of greater rates of density increase in spring and summer, and greater rates of decrease in fall and winter, for the haploid phase. Dyck & DeWreede (1995) hypothesized that this pattern, among perennating adults, was due to greater production of new modules coupled with lesser survival in haploids, and lesser production with greater survival in diploids. The alternate isomorphic phases would, therefore, be diverging ecologically with gametophytes following an *r* strategy relative to a more *K* selected tetrasporophyte.

A trade-off in ability to withstand hydrodynamic forces vs. resistance to desiccation, between alternate phases of *Mazzaella splendens*, has been suggested by the work of Shaughnessy *et al.* (1996). This hypothesis has the potential to explain aspects of both a seasonal alternation in phase dominance and constant diploid dominance in wave-exposed habitats. Different patterns in probability of loss between phases are predicted depending on whether primarily wave force or desiccation is controlling changes in density or whether these two factors are acting together.

In this study I examined survival and new production for the alternate phases of *Mazzaella splendens* in a wave-sheltered habitat at Second Beach, Barkley Sound. I also examined survival at a nearby wave-exposed habitat. There was no evidence of a significant difference in survival between phases in either habitat. This does not support the hypothesis that the alternate life history phases of *M. splendens* are diverging ecologically along the lines proposed by Dyck & DeWreede (1995). In the absence of survival differences the relative importance of wave force vs. desiccation in controlling changes in population density cannot be addressed. Without significant differences in survival, seasonal changes in the density of *M. splendens* are most likely due to differential new production, during perennation, between gametophytes and tetrasporophytes. The absence of differential survival between phases in the wave-exposed habitat suggests that the same process may be important here as well.

Introduction

Seasonal patterns of density change in *Mazzaella splendens*.

Mazzaella splendens, a red alga in the Gigartinales with an alternation of isomorphic generations, has shown a seasonal shift from summer haploid to winter diploid dominance within a broader pattern of high summer and low winter population density for both phases (DeWreede & Green 1990 as *Iridaea splendens*, Dyck & DeWreede 1995). Working at Brockton Point, Vancouver Harbour, Dyck and DeWreede (1995) showed that the mechanism of this alternation was greater density increase by haploids during spring and summer and greater decrease in fall and winter. Gametophyte densities fluctuated above and below the more stable tetrasporophyte densities, becoming dominant in the seasons favourable to growth (spring and summer) and losing that dominance in winter conditions.

For *Mazzaella splendens*, this seasonal alternation in phase dominance appears to be the result of mechanisms acting through the process of perennation. Most new blades are produced from longer-lived perennating basal crusts (Hansen 1977 as *Iridaea cordata*). May (1986 as *Iridaea cordata*) found recruitment accounted for approximately 20% of new blades each year. May (1986 as *Iridaea cordata*) also found the population structure (83% gametophyte, 17% tetrasporophyte at this site) remained virtually unchanged over three consecutive summers. This finding suggested that selection among recruits occurred in the early stages and produced, among recruits in a particular area, a phase ratio similar to that of the surrounding population.

Genets of *Mazzaella splendens* can be readily observed only when they have produced one or more blades. The seasonal alternation in phase dominance, seen at Brockton Point in Vancouver Harbour, was the result of genets appearing whenever one or more modules were produced by a basal crust, or disappearing whenever all modules were lost, and did not involve a greater number of modules per genet for one life history phase over the other (Dyck & DeWreede 1995).

Ecological differences between phases of *Mazzaella splendens* may reflect *r* and *K* selection.

On the basis of the pattern of changes in population density, underlying the seasonal alternation in phase dominance of *Mazzaella splendens* at Brockton Point, Dyck and DeWreede (1995) hypothesized that greater production of new blades (resulting in appearances of genets) may be coupled with lower blade survival in gametophytes, and lower rates of production with higher survival in tetrasporophytes. This would allow gametophyte density to outstrip tetrasporophyte density in spring and summer (in conditions conducive to maximal survival of both phases) but would give tetrasporophytes an advantage later in the year as conditions increasingly favour the ability to withstand harsher abiotic forces.

Greater production with lower survival is generally characteristic of *r* selection, while lesser production with greater survival is more characteristic of *K* selection (Begon *et al.* 1986). Dyck and DeWreede (1995) have proposed that such differences could represent ecological divergence between life history phases, with gametophytes tending to an *r* strategy, and tetrasporophytes to a *K* strategy, relative to each other. As a theory, *r* and *K* selection has been criticised (Stearns 1977) for its lack of predictive ability and for generalization beyond its original context in the work of MacArthur and Wilson (1967) and Pianka (1970). In spite of this it remains a useful tool for summarizing and comparing different life history strategies (Begon *et al.* 1986), and it is in this capacity that it is employed here.

Purely genetic models of the advantages of haploidy vs. diploidy have not produced an evolutionarily stable haploid-diploid life-history, but models including ecological differences between the alternate phases have done so (Mable & Otto 1998, Hughes & Otto 1999). Finding ecological divergence between the alternate isomorphic phases of *Mazzaella splendens* would support the idea that such differences are important in maintaining haploid-diploid life histories, and also give an indication of the amount of difference needed to produce this stability, since gross morphological differences between phases are not present.

The fact that gametophytes and tetrasporophytes dominate in different habitats (Dyck *et al.* 1985 as *Iridaea cordata*, Phillips 1994 as *Mazzaella lilacina*, see also Chapter 2) or seasons (DeWreede & Green 1990 as *Iridaea splendens*, Dyck &

DeWreede 1995), apparently with haploids predominating in less harsh conditions, may enable *Mazzaella splendens* to expand its habitat. As such ecological divergence continues, the range of conditions the species could inhabit would expand, but the degree to which both phases could occupy the same habitat might decline. It has been argued that the disruptive selection necessary to drive such a divergence would act only where gross morphological differences between phases are of the kind found in an alternation of heteromorphic generations (Klinger 1993). However, since the alternate isomorphic phases of *M. splendens* have been observed to preferentially occupy different habitats and seasons, it appears that some degree of disruptive selection already has taken place. By examining the changes in survival and new blade production underlying these changes in phase density, the magnitude of ecological difference allowing disruptive selection to act could be determined. Disruptive selection between phases may act on much smaller phenotypic differences than previously thought.

The demographic mechanism underlying the changes in phase density that produce a seasonal alternation in phase dominance would, acting mainly through perennation (Hansen 1977 as *Iridaea cordata*, May 1986 as *Iridaea cordata*), involve primarily differential production of new blades between life history phases, primarily differential blade survival, or some combination of these two. There are a number of ways that production and survival could vary with phase and season to produce the particular pattern observed in Vancouver Harbour. Only a pattern that shows greater production dominating in gametophytes and greater survival in tetrasporophytes would lend support to the hypothesis that the alternate phases are ecologically different with haploids following an *r* strategy relative to a more *K* selected diploid.

Seasonal alternation in phase dominance at wave-sheltered sites is, however, not a consistent feature of *Mazzaella splendens*. A demographic study from November 1997 to January 2001 at Second Beach, Barkley Sound, detected no alternation in phase dominance (Chapter 2). In this relatively wave-sheltered site at Second Beach there was marked seasonal change in density for both life history phases, but gametophytes dominated at most times. Another study in Barkley Sound (Sunday 2001), however, found a seasonal alternation with summer haploid and winter diploid dominance at four sites, including one approximately 500 m from the Second Beach Site, for the period of May 2000 to March 2001.

During the summers of 1998 and 1999 at a wave-exposed site approximately 30 meters from the wave-sheltered site, the population was consistently diploid dominant (Chapter 2). Fluctuation in population density was much less at the wave-exposed site than at the wave-sheltered one.

The pattern of seasonal changes in population density at Second Beach also differed from that observed previously at Brockton Point (Chapter 2). In the wave-sheltered site at Second Beach, maximum population density arrived early in spring and density declined rapidly in summer, reaching very low levels in September. A recovery followed in early fall and then a second decline to winter minimum density. In contrast, population density at Brockton Point peaked in mid-summer and then gradually declined to a minimum density in February (Dyck & DeWreede 1995). These differences in population dynamics suggest responses to different environmental conditions either over time (much of the study at Second Beach took place during an El Niño – La Niña cycle) or between geographic locations (Chapter 2).

A seasonal alternation in phase dominance has been observed for *Mazzaella splendens* in the Strait of Georgia (Adams 1979, as *Iridaea cordata*), in Vancouver Harbour (DeWreede & Green 1990 as *Iridaea splendens*, Dyck & DeWreede 1995), and at four locations in Barkley Sound (Sunday 2001). Changes from gametophyte dominance in wave-sheltered areas to tetrasporophyte dominance in wave-exposed areas have also been observed in Barkley Sound (Dyck *et al.* 1985 as *Iridaea cordata*, Phillips 1994 as *Mazzaella lilacina*). This temporal and spatial partitioning of the environment is commonly observed in *M. splendens*, and it seems reasonable to assume that it is the result of similar ecological differences between the alternate phases operating in each location. Fundamental ecological differences between phases, such as relatively greater blade survival and lesser new blade production for diploids and the reverse for haploids, should be present even in local areas, or at times, when environmental conditions are such that a seasonal alternation does not occur. A detailed study of new blade production and survival in the wave-sheltered site at Second Beach would, therefore, test the hypothesis of coupled characteristics reflecting *r* and *K* strategies and would also show how these parameters interact to produce the seasonal fluctuations in population density, which are a general feature of *M. splendens* populations in relatively wave-sheltered areas (Chapter 2).

Inferring the relative importances of wave force and desiccation from patterns of differential survival between phases of *Mazzaella splendens*.

Changes in the population structure of *Mazzaella splendens* have been observed along gradients of wave exposure. In the summer, populations in relatively wave-sheltered areas generally exhibit gametophyte dominance while at more wave-exposed sites there is tetrasporophyte dominance (Dyck *et al.* 1985 as *Iridaea cordata*, Phillips 1994 as *Mazzaella lilacina*, Shaughnessy *et al.* 1996). If the alternate isomorphic phases of *M. splendens* differ ecologically, with greater production and lesser survival characteristic of gametophytes and lesser production with greater survival characteristic of tetrasporophytes, the correlation of diploid dominance with increasingly wave-exposed habitat suggests that greater ability to withstand hydrodynamic forces is one factor contributing to greater diploid survival. As fall and winter progress, storms typically increase in severity with an accompanying increase in wave action (Milligan & DeWreede 2000). This same mechanism, then, has the potential to also explain seasonal alternation in phase dominance.

Phillips (1994 as *Mazzaella lilacina*) examined drag forces and the force required to break the stipe-holdfast junction in *Mazzaella splendens* but reported no significant differences between life history phases. Shaughnessy *et al.* (1996) modeled how these forces would interact with observed differences in surface area between the alternate phases. The results predicted a tetrasporophyte predominance in more wave-exposed areas and also predicted the observed distributions of *M. splendens* and *Mazzaella linearis* along gradients of wave exposure. This work was extended through further morphological examination (Shaughnessy 1996) and reciprocal transplant studies (Shaughnessy & DeWreede 2001). In the transplant studies both *M. splendens* and *M. linearis* showed a trade off in ability to withstand hydrodynamic forces vs. tolerance of high irradiance and desiccation. *Mazzaella splendens*, with its wider blade, was more tolerant of the increased levels of desiccation at wave-sheltered sites than the narrower *M. linearis*. Shaughnessy & DeWreede (2001) reported changes in the physical appearance of *M. linearis* when transplanted from its natural habitat (the most extreme wave exposure occupied by any species of *Mazzaella*) into areas of lesser wave exposure dominated by *M. splendens*. *M. linearis* showed no signs of bleaching in its natural habitat, but transplanted individuals showed extensive bleaching and blade

deterioration. Bleached individuals of *M. linearis* were more likely to die or lose biomass than bleached individuals of *M. splendens*. At wave-exposed sites, where desiccation pressure was less due to greater wave wash, *M. splendens* exhibited lower survival than *M. linearis* (Shaughnessy & DeWreede 2001), presumably due to the hydrodynamic disadvantages of a wider blade.

Gametophyte blades of *Mazzaella splendens* are, on average, larger than tetrasporophyte blades (Shaughnessy *et al.* 1996) and a similar trade off between desiccation tolerance and ability to withstand hydrodynamic forces may be operating between phases. Such a mechanism has the potential to explain how differential survival of modules from perennating individuals of *M. splendens* contributes to changes in population structure that occur with season or along wave exposure gradients.

For *Mazzaella splendens* in Vancouver Harbour (Dyck & DeWreede 1995) summer densities (when desiccation stress is maximal) were highest and winter densities (when wave force is maximal) were lowest for both phases. This suggests that, at wave-sheltered sites, wave force exerts a greater overall effect on survival than desiccation does. Given this difference, and the fact that these two factors operate largely in different seasons, the pattern of differential survival between alternate phases of *M. splendens*, in the case where either wave force or desiccation alone acts on survival, should be distinguishable in principle from one where both wave force and desiccation play a part.

For wave force acting alone, little difference in probability of loss between phases would be expected during the summer when wave force is presumably below the threshold needed to preferentially remove haploids. Probability of loss would then diverge between phases in fall and winter as wave force increases. Probability of module loss (or of genet disappearance) would be greatest for both phases in winter (with haploid loss greater than diploid loss) and then in spring, these values would converge again to summer equality (Figure 3.1). For desiccation acting alone, probability of loss would be greatest for both phases in summer, with diploid loss greater than haploid loss. These values would converge in winter (Figure 3.2). If both wave force and desiccation are acting to change population structure, probability of loss should be higher for diploids in summer when conditions generally contribute to higher desiccation levels. Haploid probability of loss would then increase and cross over the diploid value as

increasing wave action differentially affected haploid over diploid survival and provided relief from desiccation during low tides (Figure 3.3). At a wave-exposed site, where frequent wave wash ensures shorter periods of desiccation, wave force would be the predominant factor and haploid probability of loss should be consistently higher.

An examination of new blade production and survival at Second Beach, Barkley Sound.

Transplant studies suggesting that *Mazzaella splendens* had a greater tolerance for desiccation while *Mazzaella linearis* had greater resistance to hydrodynamic forces took place in Barkley Sound (Shaughnessy & DeWreede 2001). In the area at Second Beach, Barkley Sound, there are wave-sheltered and wave-exposed habitats in close proximity to each other, often 20 to 30 meters apart. This provides some measure of control for other abiotic factors, which may vary over longer distances, and ensures that differences in demographic behaviour between habitats are due to factors correlated with increasing or decreasing wave exposure.

Examining the production of new blades and their survival in a wave-sheltered habitat and a nearby wave-exposed habitat would test the hypothesis that the alternate isomorphic generations of *Mazzaella splendens* differ ecologically with greater new blade production and lesser survival characteristic of the haploid phase and with lesser production and greater survival characteristic of the diploid (Dyck & DeWreede 1995). Finding a pattern consistent with this hypothesis at both the wave-exposed and wave-sheltered sites would suggest that the same mechanism is responsible for controlling seasonal changes in population structure and those occurring along a wave exposure gradient. The most likely candidate for this mechanism is greater resistance to hydrodynamic forces by the sporophyte (Shaughnessy *et al.* 1996). If differential survival between alternate life history phases of *M. splendens* is found, the particular pattern of probability of loss, seen in each of the two habitats, should indicate whether these survival differences are a function of wave force primarily or if both wave force and desiccation play a substantial role (Figures 1 – 3).

Methods and Materials

Site selection, quadrat size and placement, and sampling dates were as outlined in Chapter 2.

In the wave-sheltered site, the number of genet (basal crusts) with visible modules (blades) present in each quadrat was counted. Each module was tagged around the stipe with a colour-coded plastic electrical tie strap. A 0.5 cm diameter disk of tissue was removed from each blade with a single hole paper punch. This tissue was used in carrageenan analysis to determine life history phase in the absence of reproductive structures (Garbary & DeWreede 1988, Shaughnessy & DeWreede 1991). At each subsequent census this same procedure was applied to all newly grown blades, and all surviving blades were noted. This provided a record over time of changes in genet and module density of haploids vs. diploids, and for each genet, the timing of production and survival for each of its modules.

For modules, new production in a particular census was simply the number of previously untagged blades, and loss from the population was the absence of previously tagged blades. A genet without any previously tagged modules was also considered new when encountered in a census. This leaves open the possibility that genets that had lost all their tagged blades and grew new ones in the interval between censuses would be considered new genets when they were encountered. The absence of any of the blades previously tagged for that genet would be counted as a genet lost from the population. Error due to counting genets that had lost all previously tagged blades as new genets could not be controlled short of explicit spatial mapping of all genets in a quadrat, for which there was insufficient time during a low tide series. During the first year of measurement all modules were double tagged to estimate rate of tag loss in the absence of module loss. Subsequently all modules received only one tag.

Whenever time was available pairs of blades matched as closely as possible for size and life history phase were mapped outside the permanent quadrats and had tissue samples removed for carrageenan analysis. In each pair one blade was tagged and the other left untagged. Untagged blades were recognised in subsequent censuses by two round holes punched in the blade above the apophysis. This provided an estimate of the effect of tagging on survival of blades. The dates of tagged/untagged pair selection were

January 1999, April 1999, December 1999, January 2000, August 2000, November 2000 and December 2000. A total of 63 pairs were examined.

In November 1997 it became obvious that winter conditions at the wave-exposed site would not permit detailed work. In June 1998, 12 of the original 20 permanent quadrats placed at that site were rediscovered. During the summers of 1998 and 1999 these were examined for density of haploids vs. diploids but no tagging was done. During June 1 – 8, 2000, a cohort of individuals was tagged at the wave-exposed site to examine survival. In each of the 12 quadrats, the largest blade in each genet was selected and tagged around the stipe with a colour coded plastic electrical tie strap; in total, 178 blades were tagged. Forty-eight of these were haploid and 130 diploid. A tissue sample was removed from each blade for carrageenan analysis. Subsequent censuses were on June 29 – July 6, July 29 – August 3, August 26 – 31, November 11 – 13 and December 9 – 11, 2000.

Within each sampling period differences between haploid and diploid densities, for newly produced blades and for blades surviving from the previous census, within each sampling period, were assessed with the Mann-Whitney U test. The Mann-Whitney U test was also used to examine within phase differences in densities of genets and modules due to survival vs. new production, and for differences in genet and module survival time, between phases, for each new cohort tagged in each census at the wave-sheltered site.

Differences in per capita rates of module loss and new module production, between gametophytes and tetrasporophytes, were tested with 2 X 2 contingency tables (Zar, 1996). In per capita survival, the number of individuals surviving and number of individuals not surviving was compared, for gametophytes and tetrasporophytes, for each census. In per capita new production the number present in the previous census was compared with newly arisen individuals, for gametophytes and tetrasporophytes, for each census.

Overall differences in probability of genet disappearance and probability of module loss, between phases, was tested with the Wicoxon Signed Ranks test. Mann-Whitney U and Wicoxon Signed Ranks tests were performed using SPSS 6.0.

Cohorts from the wave-exposed and wave-sheltered sites were tested for survival differences between phases using the Kaplan-Meier estimate of the survival curve

(Fisher & van Belle 1993). The Kaplan-Meier analysis was performed using JMP IN 4 which assesses statistically significant differences between Kaplan-Meier product limit survival curves in two ways: with a log-rank test that places greater weight on larger survival times, and with a Wilcoxon test that places greater weight on early survival times. Survival curves were classified as Type I, II, or III (Deevey 1947) by a linear regression of μ_x (the absolute value of the natural logarithm of the probability of survival from one census to the next) on current age (as estimated from the census of first appearance). A graph of μ_x over time tends to rise in the case of Type I survival, is flat throughout for Type II survival, and tends to fall for Type III survival. In each case the regression of μ_x on age was compared to a flat line through the mean value of μ_x to determine if the deviation from a flat line was significant. This analysis was performed using JMP IN 4.

Due to concerns about statistical independence of samples from one month to the next, I will discuss apparent trends or tendencies over time without attributing statistical significance. To examine these trends I used a cubic spline, a nonparametric nonlinear regression that emphasises local over global fit (Hastie & Tibshirani 1990, Silverman 1986, Chapter 2). All cubic spline calculations were done using glmsWIN 1.0 available at www.zoology.ubc.ca/~schluter/splines.html.

Results

Results of the estimates of error.

Error in survival estimates at the wave-sheltered site, due to loss of tags when blades were not lost, was low. Out of 1000 blades that were double tagged, 18 lost one of the tags before mortality of the blade and 982 blades retained both tags until mortality, indicating a 1.8 % overestimation of mortality. Error associated with identification of genets (both haploid and diploid blades found within a unit presumed to be a genet) was also small. Over the course of the study there were 2708 opportunities for such an error, either with new blades arising in an existing clump, or with development of a new clump of two or more blades. Of these opportunities, 101 presumed genets were of mixed phase, an error of 3.7 %. With total genets over the

course of the study present in a ratio of 2.83 haploids to 1 diploid, the density of haploid genets would be underestimated by approximately 5.3% and diploid genet density by 0.65%.

The effect of the tags on mortality was more substantial. In the 63 tagged/untagged pairs there were 37 tagged gametophytes. These were reduced in the next census (approximately 1 month later) to 12, a loss of 68 %. By contrast there were 40 untagged gametophytes, which were reduced in the next census to 29, a loss of 28%. The tagged/untagged pairs contained 26 tagged tetrasporophytes. These were reduced to 11 in the next census, a loss of 58 %. There were 23 untagged tetrasporophytes, 17 of which survived to the next census, a loss of 26 %. Overall, tagged haploid blades showed 40 % greater mortality than untagged haploid blades, and tagged diploid blades showed 32 % greater mortality than their untagged counterparts. This was a significantly higher loss for haploids (chi-square test, $P = 0.002$) but not for diploids (chi-square test, $P = 0.053$). The effect of tagging did not significantly depend on life history phase (chi-square test, $P = 0.809$). These results were used as correction factors in adjusting population density on a quadrat by quadrat basis.

Density of survivors and new production in the wave-sheltered site.

Within the process of perennation, density of observed genets at any particular time will be a function of survival of modules from the previous census and production of new modules in the interval. These two processes could potentially interact in a number of ways to produce a given population density and there is no reason to presume, *a priori*, that survival and new production would both increase and decrease concurrently with population density.

In fact, changes in density of individuals surviving from the previous census tended to follow the same general pattern seen in population density (Chapter 2), rising sharply in early spring and declining just as sharply in late spring and summer (Appendix B, Figures B.1 – B.6). Density of survivors was significantly haploid dominant each year in summer, and in the fall increase of 1998 (Figure 3.4 & 3.5).

These patterns changed when loss was measured on a per capita basis. Per capita rate of loss in both life history phases of *Mazzaella splendens* generally rose and fell in synchrony for both genets and modules (Figure 3.6 & 3.7) but not in synchrony with

rising and falling population density (Appendix C, Table C.1). There were few significant differences between gametophytes and tetrasporophytes. These significant differences did not follow a seasonal pattern and favoured gametophytes at some times and tetrasporophytes at others (Figure 3.6 & 3.7).

Population density of genets and modules appearing since the previous census, also tended to follow the seasonal pattern observed for population density (Chapter 2) and for density of survivors. The fall density increase tended to be more prominent in newly apparent genets and modules than it was in survivors, and more prominent in haploids than in diploids (Appendix B, Figures B.7 – B.12). Density of new genets and modules was significantly haploid dominant each year in summer, and in the fall increase of 1998 year (Figure 3.8 & 3.9).

For appearances of new genets and production of new modules, per capita rates of new production peaked sharply each year in late winter to early spring and in early fall of 1998 (Figures 3.10 & 3.11). Gametophyte per capita rate of new production was approximately twice that of tetrasporophytes in early spring and fall of 1998. The reverse occurred in early spring 1999, and in early spring 2000 haploid and diploid per capita rates of new production were similar. There were few significant differences between gametophytes and tetrasporophytes. These significant differences did not follow a seasonal pattern and favoured tetrasporophyte genets. Gametophyte modules were favoured at some times and tetrasporophyte modules at others (Figure 3.10 & 3.11).

The relative contributions of survival vs. new production to population density.

For genets and modules of both phases (Figure 3.12 – 3.15), the contribution of new production to population density was significantly larger than that of survival each early spring, but the contribution of survival was significantly greater each summer. New production also contributed a significantly larger amount to each fall density increase.

A comparison of per capita rate of new production with per capita rate of loss, for haploid and diploid genets and modules of *Mazzaella splendens*, showed these processes operating at different scales (Figures 3.16 – 3.19). Per capita rate of new production showed much more seasonal periodicity than per capita rate of loss and, during its

peaks, a much greater magnitude of effect. Per capita rate of loss varied less regularly and over a smaller range.

Probability of loss in the permanent quadrats.

There were no apparent differences in the pattern of probability of disappearance for haploid vs. diploid genets and modules of *Mazzaella splendens* (Figure 3.20 & 3.21). There were times of diploid advantage and times of haploid advantage, but probability of disappearance tended to rise and fall concurrently for both phases, with one phase sometimes rising or falling farther than the other. There was a general tendency for probability of disappearance to fall as population density increased and rise as population density decreased. But even this pattern was not consistent, with probability of disappearance remaining relatively high during the fall increase each year, relatively low during the late winter population decrease of 1999, and relatively high during the early part of the 2000 spring population increase.

Mean probability of genet disappearance, when the probabilities from each census were summed over the course of the study, differed little between haploid and diploid genets or modules (Table 3.1). A Wilcoxon Signed Ranks test detected no significant differences between gametophytes and tetrasporophytes in either probability of genet disappearance ($P = 0.482$) or probability of module loss ($P = 0.713$).

Survival time at the wave-sheltered site.

Kaplan-Meier analysis of a static cohort of all 2747 blades (1952 haploid, 795 diploid) tagged at the wave-sheltered site from November 1997 to December 2000 found no significant difference between gametophytes and tetrasporophytes (log rank test, $P = 0.458$; Wilcoxon Signed Ranks test, $P = 0.994$). A Mann-Whitney U test comparing gametophyte to tetrasporophyte survival times also found no significant difference ($P = 0.247$). A graph of survival in this static cohort is given in Appendix B, Figure B.13. The slope of a regression of μ_x on current age was not significantly different from flat for either gametophytes ($r^2 = 0.297$, $P = 0.263$) or tetrasporophytes ($r^2 = 0.210$, $P = 0.361$), indicating that the survivorship curves are Type II with random loss of blades from the population over time.

Changes in survival time with seasonal time of origin.

At each census a cohort representing individuals arising in that particular month was established as all newly produced modules were tagged. The size of these cohorts varied in relation to population density and were relatively large in spring, but often quite small in late summer and winter. Fall cohorts were larger than those from late summer and winter but were still small compared to spring cohorts. Variation in cohort size with season is shown in Appendix B (Figures B.14 & B.15).

The proportion of genets and modules disappearing by the census after their first appearance (Figures 3.22 & 3.23) was generally highest in late summer and lowest in spring. Winter values were most variable, likely due to stochastic events in small cohorts (1999 – 2000, for example, was dominated by a single long-lived diploid individual).

Gametophyte and tetrasporophyte genets and modules of *Mazzaella splendens* appearing in early spring tended to have a greater mean survival time. Mean survival time declined steeply for those appearing later in spring and throughout summer. Very few plants appearing in August, and none from September, survived to the next census (Appendix B, Figures B.16 – B.21). There was only one significantly different mean survival time between haploid and diploid phases in any of the cohorts (Figures 3.24 & 3.25).

Survival times from all censuses, from November 1997 to December 2000, were used in the analysis in spite of the fact that total survival times for individuals tagged in November 1997 and some individuals from the winter of 2000 are not known. This may introduce a bias, but population density was small in winter and survival time was relatively short, so the bias should be slight.

A Kaplan-Meier analysis of survival was performed on the 9 largest spring and summer cohorts; February, March, April, May and June, 1998; April, May and June, 1999, and May 2000. Only the cohort tagged in February 1998 showed a significant difference between phases, and this difference appeared only in the log rank test and not in the Wilcoxon test, indicating that the difference was primarily among the longer lived blades (Table 3.2).

Graphs of survival in the 9 cohorts listed above are given in Appendix B, Figures B.22 – B.30. A regression of μ_x on current age was performed on 6 of these cohorts; February, March and April 1998, April and May 1999, and May 2000. The remaining 3

cohorts had less than 3 μ_x values, and regression would not be meaningful. There were only 3 occasions when the slope of the regression differed significantly from a flat line through the mean of the μ_x values. These were all for genet disappearance rather than module loss and occurred in February 1998 for tetrasporophyte genets, in March 1998 for gametophyte genets, and in April 1998 for tetrasporophyte genets (Appendix C, Table C.2). These three survival curves may be classified as Type III, but the rest fit best into the Type II category (Deevey 1947) suggesting that blade loss is random with respect to time in the population

Survival at the wave-exposed site.

A Kaplan-Meier analysis of the cohort of *Mazzaella splendens* modules tagged in June, 2000 at the wave-exposed site at Second Beach, Barkley Sound, found no significant difference in survival between phases (log rank test, $P = 0.431$; Wilcoxon test, $P = 0.257$). No significant difference in survival time between phases was detected by a Mann-Whitney U test ($P = 0.136$). Regression of μ_x on current age found no significant difference between the slope of the regression line and a flat line through the mean of the μ_x values for gametophytes ($r^2 = 0.793$, $P = 0.110$) or tetrasporophytes ($r^2 = 0.431$, $P = 0.229$) indicating that both are Type II. The survival curves are given in Figure 3.26.

Discussion

The r & K hypothesis reconsidered: survival and new blade production in *Mazzaella splendens* at the wave-sheltered site, Second Beach.

The hypothesis that greater survival is coupled with lesser new blade production in perennating diploids and lesser survival with greater new blade production in haploid individuals of *Mazzaella splendens* (Dyck & DeWreede 1995) is not supported by the observations at the wave-sheltered site, Second Beach. Differential survivorship of some kind, between life history phases, must be present for ecological divergence between the alternate isomorphic phases to be proceeding along r & K lines. At the wave-sheltered site, Second Beach, there was no evidence of such differential survival overall, or during

the different times of year that could be analyzed (those months with cohorts large enough to yield useful information). The behaviour of survival curves was also similar between phases (23 out of 26 curves analyzed were Type II).

In comparing per capita rates of genet disappearance and module loss with per capita rates of genet appearance and new module production at the same scale the differences between these two processes became readily apparent (Figures 3.16 – 3.19). Per capita new production showed much more seasonal periodicity than per capita loss and, during its peaks, a much greater magnitude of effect. While there appeared to be no regularity in the pattern of per capita loss with increasing and decreasing population density (Figures 3.6 & 3.7), per capita new production increased sharply in times of rising population density (Figures 3.10 & 3.11).

The evidence at this site suggests that ecological differences between the alternate isomorphic life history phases of *Mazzaella splendens*, pertaining to the process of perennation, are much more likely to be a function of differential new production than of differential survivorship. It is unclear, however, how to apply the evidence from this site to the larger question of haploid vs. diploid advantage (Hughes & Otto 1999). Per capita new production was greater for haploids in the first year, greater for diploids in the second, and very similar for both phases in the third, yet each year the result was spring gametophyte dominance. It would be useful to replicate this work in an area with a persistent seasonal alternation in phase dominance in order to better address the way in which differential new production may contribute to this alternation.

The *r* & K hypothesis reconsidered: survival of *Mazzaella splendens* at Brockton Point, Vancouver Harbour.

The population of *Mazzaella splendens* at the wave-sheltered site, Second Beach, was gametophyte dominant each spring and early summer, and often in fall, with periods of no significant difference between phases in late summer and in winter (Chapter 2). It could be argued that differential survival occurs between phases in some areas and not in others, producing a seasonal alternation where and when it is present. This could potentially account for the absence of a seasonal alternation at the wave-sheltered site, Second Beach, when an alternation between summer gametophyte and winter tetrasporophyte dominance was present at Brockton Point, Vancouver Harbour.

Some data on survival at Brockton Point are available to address this conjecture. During work in Vancouver Harbour two cohorts of *Mazzaella splendens* blades were tagged in order to test the usefulness of a new kind of tag (Dyck 1991 as *Iridaea splendens*), one in June 1989, the other in November 1989. Blades in these cohorts were of mixed phases and sizes chosen at random. The survival curves for these cohorts are given in Appendix B, Figures B.31 & B.32.

Re-analysis of the survival curves from both these cohorts, using the Kaplan-Meier method, found no significant difference between life history phases in either cohort (Appendix C, Table C.3). A regression of μ_x on current age found no significant difference between the slope of the regression line and a flat line through the mean of the μ_x values for gametophytes ($r^2 = 0.169$, $P = 0.311$) or tetrasporophytes ($r^2 = 0.182$, $P = 0.400$) in the June cohort, or for gametophytes ($r^2 = 0.694$, $P = 0.373$) or tetrasporophytes ($r^2 = 0.087$, $P = 0.810$) in November, suggesting that all are Type II.

The survival behaviour of gametophytes and tetrasporophytes of *Mazzaella splendens* at Brockton Point is very similar, in all aspects measured, to that observed at the wave-sheltered site, Second Beach. Finding the same survival pattern at Brockton Point, where a seasonal alternation in phase dominance occurred, as in the wave-sheltered site at Second Beach, that remained primarily gametophyte dominant, suggests that something other than differential survival was responsible for the seasonal alternation. Differential new production is the most likely candidate.

Survival of *Mazzaella splendens* in the wave-exposed site at Second Beach.

Survival curves of gametophytes vs. tetrasporophytes in the cohort of *Mazzaella splendens* blades tagged at the wave-exposed site in June 2000 were also Type II. Once again, as in the wave-sheltered site at Second Beach and at Brockton Point, there was no significant difference in survival between life history phases. Shaughnessy *et al.* (1996) found that as *Mazzaella splendens* blades grow longer, gametophytes become wider than sporophytes, presenting a greater planform area on which hydrodynamic forces can act. They predicted that, among the larger size classes at least, there would be higher survival among sporophytes. The cohort at the wave-exposed site consisted of the largest blade present in each genet found in the 12 permanent quadrats. Survival in this

cohort should be representative of the size class for which Shaughnessy *et al.* (1996) made their predictions, however the predicted advantage to diploids did not appear.

This result could imply that a relative tetrasporophyte survival advantage in conditions of increasing wave exposure may not be as important as has often been assumed. On the other hand, this effect may be subtle, requiring a larger cohort to detect a significant difference. On this point, it is worth noting that at the wave-exposed site, Second Beach, tetrasporophyte survival was always clearly above gametophyte survival (Figure 3.26), while at the wave-sheltered site, Second Beach, (Appendix B, Figures B.13 & B.22 – B.30) and at Brockton Point (Appendix B, Figures B.31 & B.32) survival was sometimes higher for gametophytes, sometimes higher for tetrasporophytes, and often very similar.

Although models indicate that survival of tetrasporophyte blades should exceed survival of gametophyte blades as wave-exposure increases, there is no survival advantage predicted for either life history phase among smaller blades (Shaughnessy *et al.* 1996). Measurements of population density at the wave-exposed site at Second Beach, during the summers of 1998 and 1999, included all blades in the 12 permanent quadrats (Chapter 2). The observed diploid dominance was not a result of bias toward larger blades.

At a wave-sheltered site, Phillips (1994 as *Mazzaella lilacina*) found recruitment of *Mazzaella splendens* gametophytes was greater than expected based on the proportion of reproductively mature tetrasporophytes in the surrounding population, although the proportion haploid among recruits was usually not as large as among the surrounding adults. The same occurred for tetrasporophytes at a wave-exposed site. In both habitats he also found that the phase ratio among individuals in the cleared quadrats tended to become even closer to that in the surrounding population over time. It is possible that the underlying haploid or diploid dominance in the population of perennial crusts is determined primarily by events surrounding recruitment, with further differential survival between modules of gametophytes and tetrasporophytes influencing survival within the population of crusts to a lesser degree.

Hughes and Otto (1999) speculated that competition during the spore/recruitment stage was likely to be important in maintaining an isomorphic alternation of generations over evolutionary time. This is consistent with the speculation here, that the events

surrounding recruitment are of primary importance in determining population structure at a particular site. On the other hand, Engel *et al.* 2001, in a four year study of *Gracilaria gracilis*, found that subtle changes in survival rates had a significant impact on the projected population structure, even though these changes were too minor to detect statistically in the field. Further modelling, using the parameters obtained in this study, may determine if a similar situation is present in *M. splendens*.

The relative importance of wave force vs. desiccation in the survival of the alternate life history phases of *Mazzaella splendens*.

Given the absence of significant differential survival between life history phases of *Mazzaella splendens* in all habitats and locations examined in this study, the question of the relative importance of wave forces and desiccation in structuring the population is unanswerable. Like the differences in population dynamics between Vancouver Harbour and the outer coast (Chapter 2), the apparent absence of differential survival raises questions about the importance of desiccation and wave force in producing seasonal changes in population density. Although field experiments have shown that both these factors should have an effect (Shaughnessy 1996, Shaughnessy *et al.* 1996, Shaughnessy & DeWreede 2001) that effect may be subtle, or may only become significant in more extreme conditions than those routinely encountered by the plants observed in this present study.

A comparison of the contributions of survival and new blade production to the population density of *Mazzaella splendens* at Second Beach, Barkley Sound.

Changes in density of survivors and newly produced blades.

Changes in density of surviving genets and modules, and of newly appearing genets and newly produced modules for both life history phases of *Mazzaella splendens*, followed a similar seasonal pattern. Both the loss of modules and the production of new modules operated in such a way that genets appeared and disappeared as the observable density changed, but neither phase developed more modules per genet than the other. Both density of survivors and density of new production had their peaks at the same general times as the peaks in overall population density (Chapter 2) indicating that

generally survival and new production were responding favourably to similar environmental conditions.

Both survival and newly appearing genets and newly produced modules contributed substantially to spring and summer densities at the wave-sheltered site. The early spring and fall density increases tended to be driven primarily by new production, coming as they did after periods of low survival for both life history phases. But while haploids and diploids were both engaged in substantial new production in spring, during the fall density increase the haploid phase tended to account for most of the new density (Appendix B, Figures B.1 – B.12). In the first two years this resulted in a larger proportion of haploid plants during fall than was present in spring (Chapter 2).

It is possible that conditions influencing the spring density increase at the wave-sheltered site, Second Beach, may be different from those influencing the fall increase, and that these differences may work in a way that boosts new blade production by gametophytes in the later season. Differential production of new blades in October, favouring haploids, would not only produce fall gametophyte dominance at Second Beach, but would provide a density buffer against decreasing rates of new production as winter progressed.

A temporal segregation of new blade production and survival.

Production of new modules and appearances of new genets made a significantly larger contribution to population density in early spring while survival made a significantly larger contribution in summer (Figures 3.12 – 3.15). Conditions at Second Beach appeared conducive to a sudden increase in production of new modules and appearances of new genets for a relatively brief period each spring (Figures 3.10 & 3.11). As new production declined with the onset of summer, population density was increasingly maintained by survivors from this original burst of growth. Subsequent declines in both new production and survival produced the late summer decline in population density. New production was also the important factor in the fall density increase, where its contribution to the total density was significantly larger than the contribution of survivors for both gametophytes and tetrasporophytes.

Demographic patterns at the wave-sheltered site, Second Beach vs. Brockton Point, Vancouver Harbour.

A key difference between the changes in population density of *Mazzaella splendens* at Second Beach vs. at Brockton Point is the late summer population crash, present on the outer coast but not in Vancouver Harbour (Chapter 2). At Second Beach, the proportion of a cohort disappearing before the next census consistently rises to one at some point between June and September (Figures 3.20 & 3.21). September conditions here form a barrier through which few survivors pass. This is very different from the gradual population decline (August to February) at Brockton Point (Dyck & DeWreede 1995).

It seems that the combination of conditions causing the late summer population crash at the wave-sheltered site, Second Beach, was as difficult to survive (or even more so) than the conditions prevailing in the middle of winter. It was also a set of conditions that was not conducive to new blade production. The factors responsible for the late summer decline must be capable of changing substantially over relatively short distances, as the population decline at the wave-exposed site was slight by comparison (Chapter 2).

The available evidence on survival suggests that seasonal changes in the ratio of gametophytes to tetrasporophytes in the wave-sheltered site at Second Beach and at Brockton Point were primarily a result of differential new production. At the wave-sheltered site, Second Beach, conditions in fall favoured haploid new production which would contribute to continued haploid dominance in winter. For a seasonal alternation to occur due to differential new production within the process of perennation, as may have happened at Brockton Point, haploid new blade production would proceed at a greater rate than diploid production in spring and at a lesser rate throughout the long August to February decline. For this to occur, however, the conditions at Brockton Point would need to be different, in some crucial way, than those at the wave-sheltered site, Second Beach, with fall conditions favouring new blade production among tetrasporophytes over gametophyte production.

Seasonal changes in certain abiotic parameters may influence the pattern of survival and new blade production in *Mazzaella splendens* at Second Beach.

I have called into question the importance of wave force and desiccation stress, which have previously been considered important in structuring populations of *Mazzaella splendens*. Having done this, I would now like to engage in some speculation as to which of the many other factors potentially impinging on these populations might prove important in controlling changes in density, and what directions for future study might prove fruitful in this regard. Two other factors that may affect population density are nutrients and temperature, and there may be potential relationships between fluctuations in these parameters and changes in density of new individuals and density of survivors in *M. splendens*. Sunday (2001) has demonstrated differential uptake of dissolved nitrate between the life history phases of *M. splendens*, and dissolved nitrate is the nutrient I will be focusing on in this section.

Since dissolved nitrate and temperature data coinciding with the dates and sites of the population studies at the wave-sheltered site, Second Beach, and at Brockton Point is not available, I will be utilizing data from other times or nearby areas. I am not attempting to say definitively that either dissolved nitrate or temperature is acting here, but rather to suggest how factors other than wave-exposure and desiccation stress might contribute to changes in population density of *Mazzaella splendens*.

Dissolved nitrate concentration and temperature.

Some measurements of temperature and dissolved nitrate, taken in Bamfield Inlet near Second Beach, are available from a previous ecophysiological study of *Macrocystis integrifolia* (Wheeler & Srivastava 1984). Monthly changes in surface water temperature were available from the Cape Beale Lighthouse in Barkley Sound for 1994 - 2000. Using these data as a general picture of changes in these parameters for this area, it appears that temperature peaks in summer (July) and is lowest in winter (late December to early February). The range is approximately 6 to 16 °C (Appendix B, Figure B.33). Nitrate concentration peaked in winter (January to February) then declined steeply in early spring (March to April) and remained low until late summer when it began to rise again and increased steadily during fall and early winter. The range was approximately

0.3 to 12.5 μ moles/litre. Generally temperature and nitrate concentration appear inversely related, with one rising while the other falls.

Nitrate levels will fluctuate with differences in location and timing of upwelling from year to year (or within a particular year) and the amount of this fluctuation occurring at Second Beach is not known. The particular levels found by Wheeler and Srivastava (1984) could shift upwards or downwards over time, and variation of this kind could potentially account for some of the differences in per capita new production between years.

While the particular maximum and minimum concentrations may vary, the seasonal cycle of higher nitrate concentrations in fall and winter, alternating with lower concentrations in late spring and summer, appears generally similar in a variety of times and temperate locations. This pattern in dissolved nitrate concentration was also observed at Brockton Point in Vancouver Harbour (Druehl & Hsiao 1977), at two locations in Shag Bay, Nova Scotia (Gerard & Mann 1979) and at Newcastle, Portsmouth and Dover in New Hampshire (Burns & Mathieson 1972).

When the nitrate concentrations obtained by Wheeler and Srivastava (1984) and the temperatures from Cape Beale are superimposed on a graph of changes in density of survivors and newly produced individuals (Figures 3.27 & 3.28), population density of new plants peaks shortly after the peak in dissolved nitrate concentration as temperature is rising from its winter minimum. New production then declines steeply, as does nitrate concentration. The density of survivors, however, continues to climb as blades are lost slowly at first. Then, with dissolved nitrate scarce, both new production and survival decline together. The end of this process is the late summer population minimum when dissolved nitrate is at its lowest concentration and both survival and new blade production are minimal.

At this point nitrate concentration begins to rise again and the fall density increase occurs. The fall density increase may occur in response to increasing nitrate concentration while temperatures and daylength remain conducive to growth. Sensitivity to decreasing temperature and light availability, as winter continues, could then account for the decline in density while nitrate concentration continues to rise. With ambient dissolved nitrate near its maximum concentration in February, it may be that there is a

temperature or irradiance threshold which, once exceeded, allows the spring burst of growth to proceed.

Abiotic factors and interannual variation in population dynamics.

During the three spring population increases that occurred over the course of this study, per capita rate of new production exhibited each of the three possible permutations of difference between phases. The rate was higher for haploids in 1998, higher for diploids in 1999, and similar for both phases in 2000. Only the first fall population increase (1998), showed a spike in per capita rate of new production similar to those seen in the spring population increases.

Since this study began in an El Niño year, it might be suggested that increased temperature contributed in some way to the differences between fall population increases, providing a better growing environment in the fall of 1998. However, a comparison of changes in surface water temperature at Cape Beale from November 1997 to January 2001, with per capita rates of new production in *Mazzaella splendens* at the sheltered site, Second Beach, during the same time period (Figures 3.29 & 3.30), presents mixed evidence. The peak temperature in (September) 1998 was higher than the peak temperature in either of the following years and the peak in per capita new production during the fall population increase of 1998 coincided with this peak in temperature. But all three peaks in per capita new production during spring population increases coincided with temperature minima, and the rates dropped rapidly as temperature rose. Higher temperatures *per se* do not appear to be a sufficient cause of increased per capita new production.

Sunday (2001) found that gametophytes showed significantly more nitrate uptake than tetrasporophytes at concentrations similar to the spring peak values reported by Wheeler and Srivastava (1984). At dissolved nitrate concentrations three times higher, this difference disappeared. At the higher nitrate concentration, gametophytes showed much greater variability in rate of uptake than tetrasporophytes. Mean rate of uptake at the higher nitrate concentration was significantly different from the mean rate of uptake at the lower concentration for diploids, but not for haploids.

If this trend continues as dissolved nitrate concentration increases above the levels measured by Sunday (2001), there could conceivably be a diploid advantage in rate of

nitrate uptake at higher concentrations. And, if a greater rate of nitrate uptake translates into a greater per capita rate of new production during perennation, variation in ambient nitrate concentration could potentially contribute to differences in the behaviour of per capita rate of new production between life history phases, years, and times of year.

Ambient nitrate and demographic differences between the wave-sheltered and wave-exposed sites.

The degree of water motion present in an area can indirectly influence productivity by altering the supply of dissolved nutrients (Jones 1959, Whitford & Schumacher 1961, 1964, Conover 1968, Steever *et al.* 1976). Large differences in ambient dissolved nitrate concentration do not seem likely between the wave-sheltered and wave-exposed sites at Second Beach, Barkley Sound, but increased water motion would more continuously replenish the layer of water next to each blade from which nitrate is taken up. In areas of greater wave action this could enhance nitrate uptake by making it continuously available even at low ambient concentrations.

The differences in demographic behaviour during late summer, with the population at the wave-exposed site declining slightly while the population at the wave-sheltered site crashed, could be equally well explained by the above mechanism as by decreased desiccation stress due to more continuous moistening by wave action. Both of these mechanisms, however, are subject to other interactions between the plant and increasing wave exposure. Gerard and Mann (1979) found that *Laminaria longicuris* changed its blade morphology in response to increasing wave exposure. For plants with a similar morphology increased water motion did enhance nutrient uptake. But plants exposed to increased wave force developed much thicker narrower blades making nutrient uptake more difficult. Consequently growth rates in the wave-exposed areas were not enhanced over those in wave-sheltered ones. Further work on morphological differences between phases of *Mazzaella splendens* along wave-exposure gradients, and differences in uptake rates between different blade morphologies, may uncover a similar complex interaction occurring in *M. splendens*.

Abiotic differences between Vancouver Harbour and the outer coast and associated differences in population dynamics between locations.

It may be that differences in ambient dissolved nitrate also have the potential to explain aspects of the differences in seasonal population dynamics between the wave-sheltered site at Second Beach and Brockton Point. Temperature at both locations showed a similar seasonal pattern (Appendix B, Figure B.34), but ambient nitrate concentrations, while exhibiting the same seasonal periodicity, were generally much higher at Brockton Point (Appendix B, Figure B.35). While the measurements of dissolved nitrate (Druehl & Hsiao 1977) were not for the same time period in which Dyck & DeWreede (1995) measured changes in population density of *Mazzaella splendens*, they are in keeping with the general expectation that dissolved nitrate levels will be higher in areas affected by urban development and the runoff of a large river (the Fraser) with substantial agriculture in its watershed.

Assuming a pattern of ambient nitrate availability at Brockton Point during the study by Dyck & DeWreede (1995) similar to that observed by Druehl & Hsiao (1977), the change from winter diploid to summer haploid dominance at Brockton Point would have coincided with a decrease in ambient nitrate to levels at which differential uptake rates should favour gametophytes (Sunday 2001).

In the absence of differential survival between phases, changing from summer gametophyte to winter tetrasporophyte dominance would require greater rates of new production during perennation by diploids during fall and winter. This would have coincided with an increase in available nitrate to concentrations at which no significant difference was present between phases (Sunday 2001). Whether this alone could provide the advantage in new production needed by tetrasporophytes to achieve winter dominance is unclear. It would be interesting to examine the interaction of nutrient cycles, desiccation stress and water motion on the population dynamics of *Mazzaella splendens*, as there may be synergistic effects of certain combinations of these factors.

Much remains to be explained concerning the mechanisms by which the environment controls population density in *Mazzaella splendens*. These mechanisms will probably be complex, as the morphology and physiology of the organism may change with habitat or season, as well as different habitats or seasons bringing changes in biotic and abiotic variables.

Conclusions.

The hypothesis that greater new blade production is coupled with lesser survival in gametophytes, and lesser production with greater survival in tetrasporophytes, reflecting an ecological divergence between isomorphic life history phases of *Mazzaella splendens* along *r* and *K* lines (Dyck & DeWreede 1995) is not supported. Significant differences in survival between the alternate isomorphic life history phases were not observed at the wave-sheltered site, Second Beach, or in a re-analysis of cohorts from Brockton Point. This suggests that differential appearances of genets between phases, as new blades are produced by basal crusts, is the primary mechanism controlling seasonal changes in the ratio of haploids to diploids during perennation.

The absence of differential survival between phases at the wave-exposed site, Second Beach, runs counter to predictions made by models of hydrodynamic forces acting on gametophyte vs. tetrasporophyte blades (Shaughnessy *et al.* 1996). If the absence of this effect proves common, it appears that differential recruitment between haploids and diploids, rather than differences between perennating adults, is the primary factor determining *Mazzaella splendens* population structure in wave-exposed habitats.

Seasonal changes in wave force and desiccation pressure may be less important than previously thought for controlling seasonal changes in population density in wave-sheltered areas. Availability of nutrients could potentially play a role here and continued work on physiological differences between the alternate life history phases of *Mazzaella splendens* is needed. Understanding the interaction of water motion, desiccation and nutrient uptake in the growth of this alga may help to pinpoint where selection is acting to produce the spatial and temporal changes in phase dominance that have been observed.

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Figures to accompany Chapter 3.

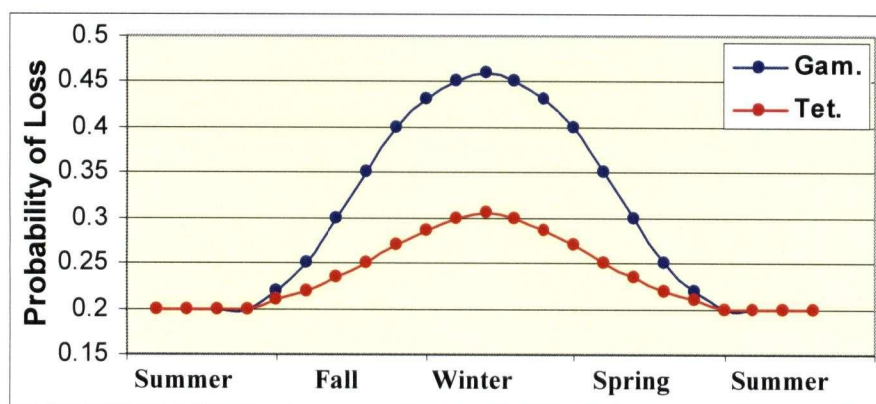


Figure 3.1: Expected pattern of divergence in probability of blade loss with season, between alternate phases of *Mazzaella splendens* in a wave-sheltered site, if wave force alone is producing survival differences. Gam. = gametophytes. Tet. = tetrasporophytes.

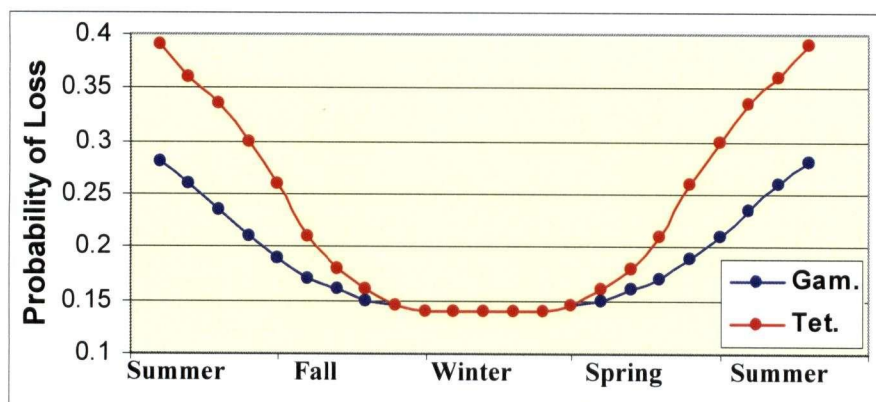


Figure 3.2: Expected pattern of divergence in probability of blade loss with season, between alternate phases of *Mazzaella splendens* in a wave-sheltered site, if desiccation alone is producing survival differences. Gam. = gametophytes. Tet. = tetrasporophytes.

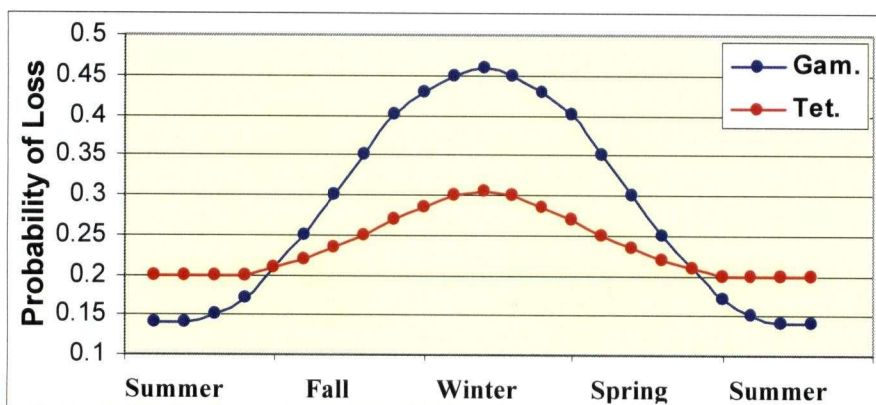


Figure 3.3: Expected pattern of divergence in probability of blade loss with season, between alternate phases of *Mazzaella splendens* in a wave-sheltered site, if wave force and desiccation together are producing survival differences. Gam. = gametophytes. Tet. = tetrasporophytes.

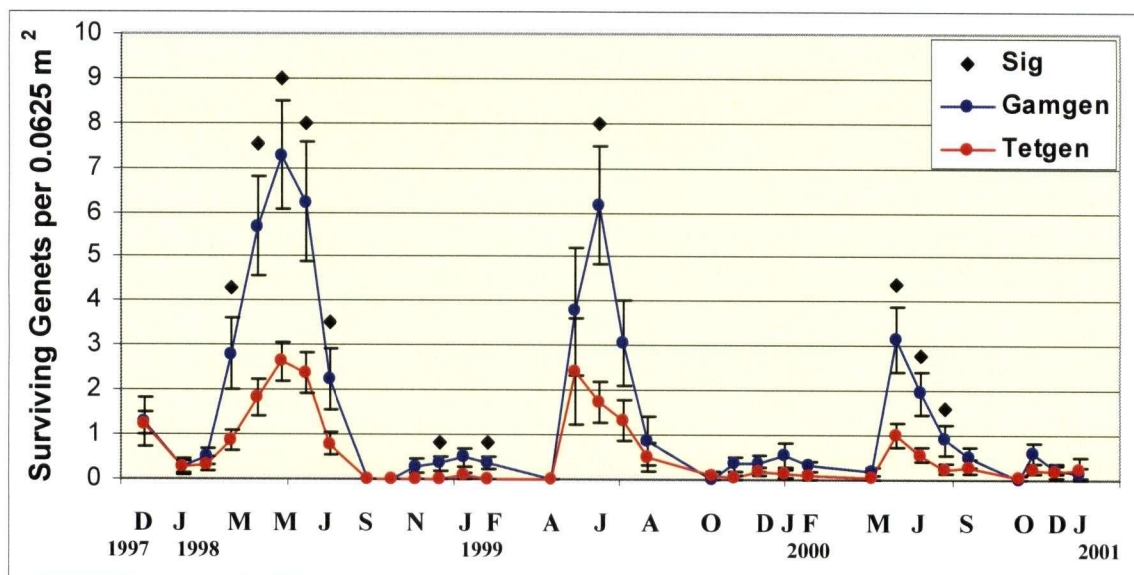


Figure 3.4: Seasonal changes in density of genets remaining from the previous census for the alternate phases of *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Means (± 1 S E). Sig = Significance: Mann-Whitney U Test, $P \leq 0.05$. Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets.

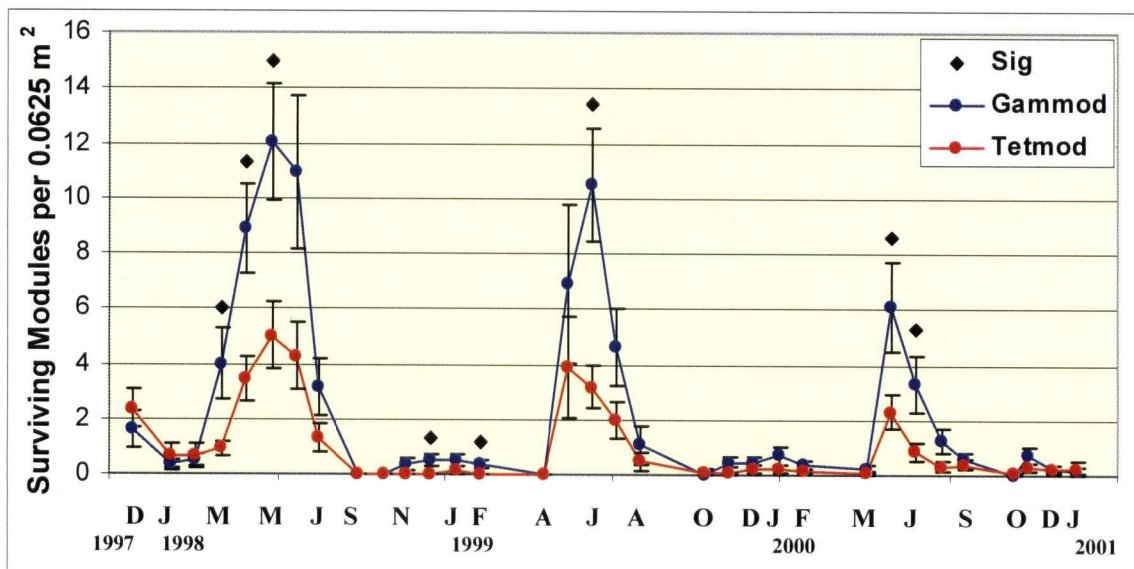


Figure 3.5: Seasonal changes in density of modules surviving from the previous census for the alternate phases of *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Means (± 1 S E). Sig = Significance: Mann-Whitney U Test, $P \leq 0.05$. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

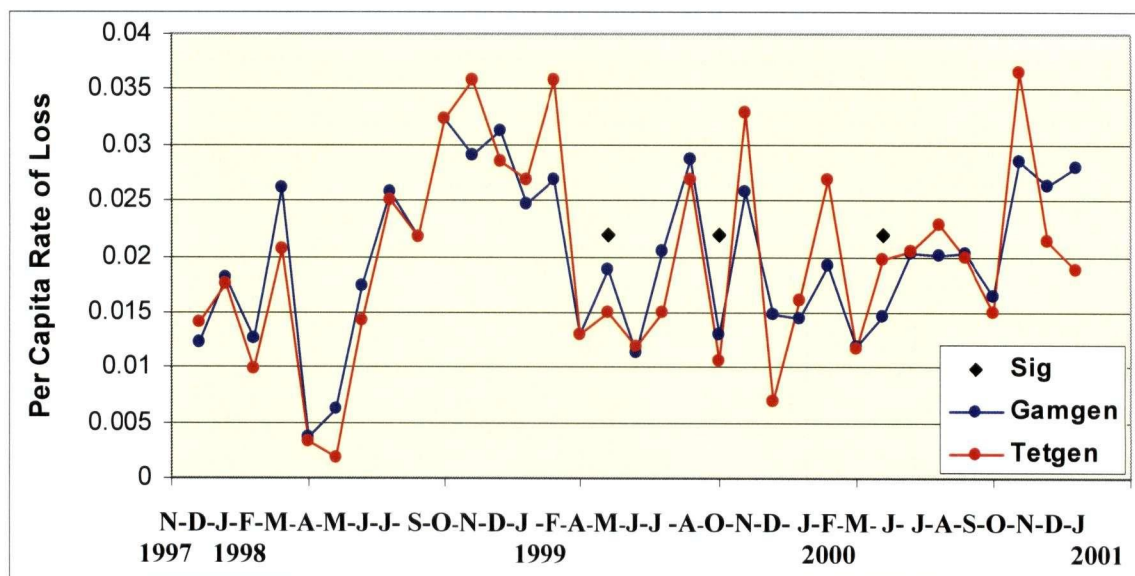


Figure 3.6: Per capita rate of loss (per day) for haploid vs. diploid genets of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets. Sig = statistical significance (2 X 2 Contingency Table, $P \leq 0.05$)

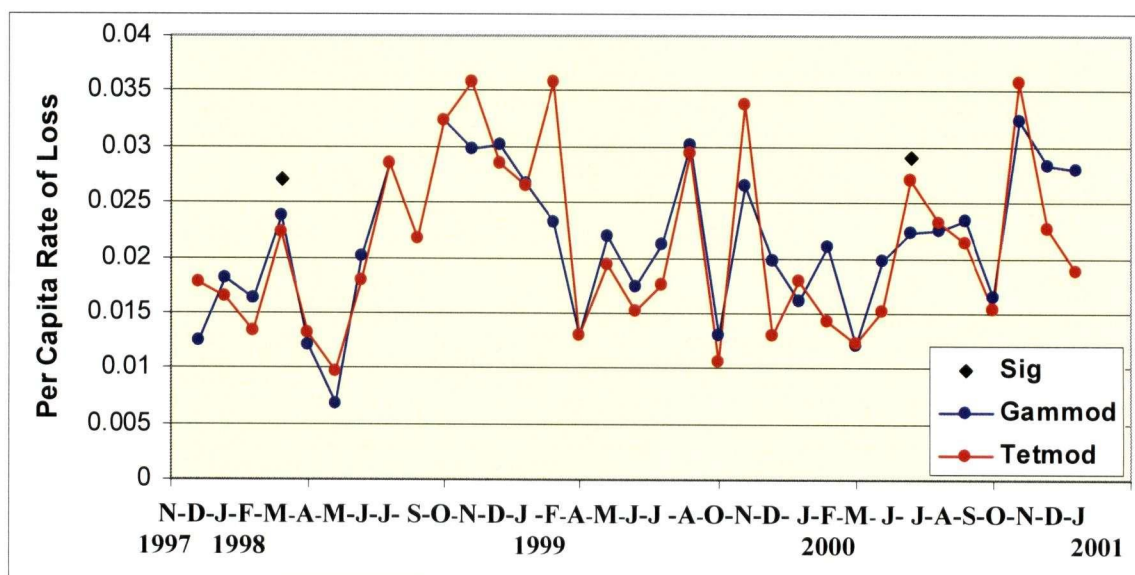


Figure 3.7: Per capita rate of loss (per day) for haploid vs. diploid modules of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). Gammod = gametophyte modules. Tetmod = tetrasporophyte modules. Sig = statistical significance (2 X 2 Contingency Table, $P \leq 0.05$)

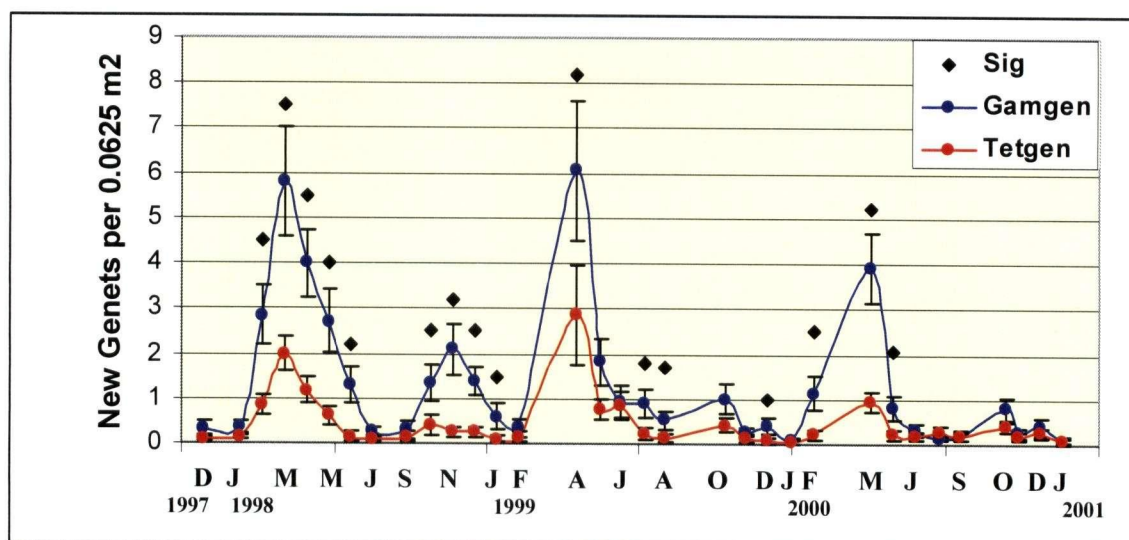


Figure 3.8: Seasonal changes in density of new genets appearing since the previous census for the alternate phases of *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Means (± 1 S E). Sig = Significance: Mann-Whitney U Test, $P \leq 0.05$. Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets.

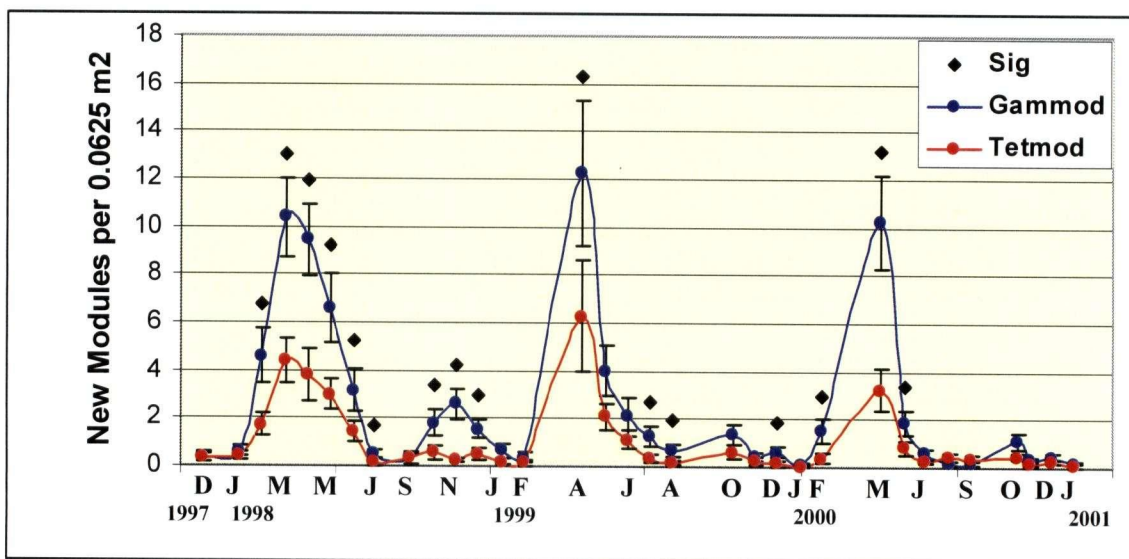


Figure 3.9: Seasonal changes in density of new modules appearing since the previous census for the alternate phases of *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Means (± 1 S E). Sig = Significance: Mann-Whitney U Test, $P \leq 0.05$. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

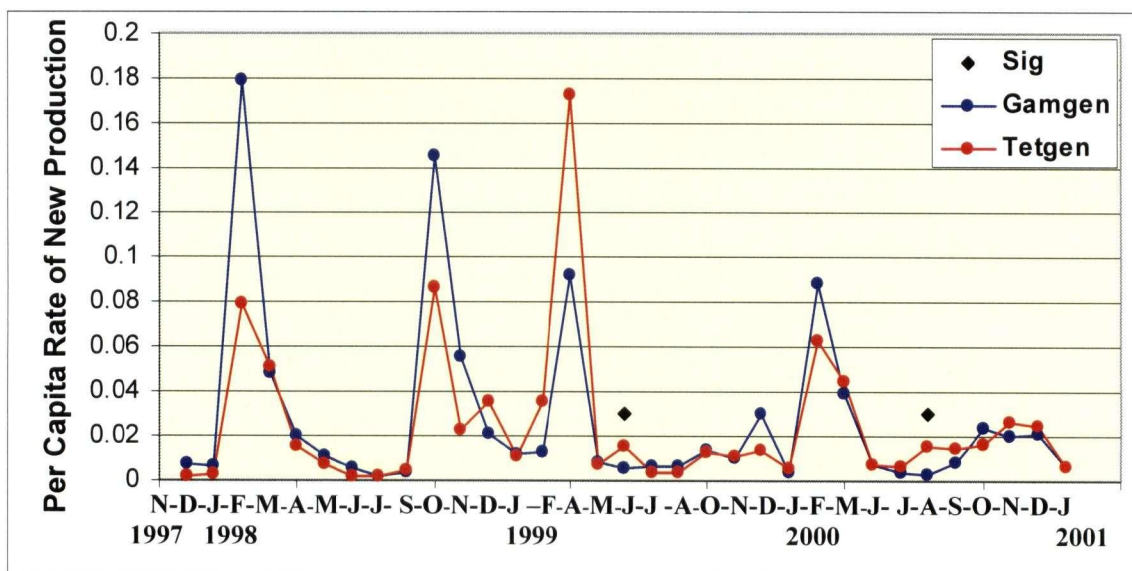


Figure 3.10: Per capita rate of new production (per day) for genets of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets. Sig = statistical significance (2 X 2 Contingency Table, $P \leq 0.05$)

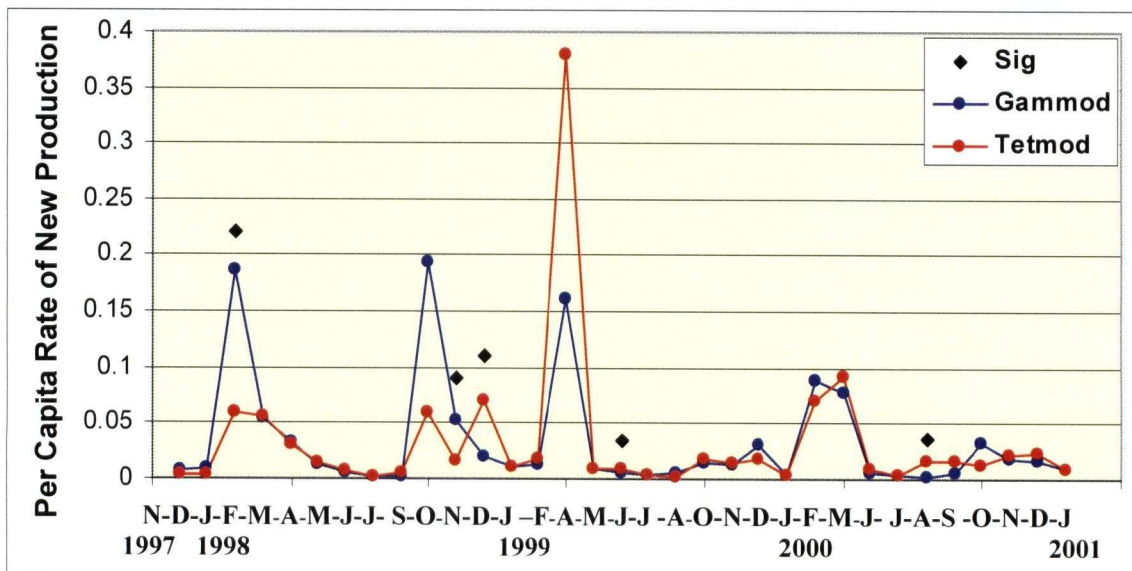


Figure 3.11: Per capita rate of new production (per day) for modules of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). Gammod = gametophyte modules. Tetmod = tetrasporophyte modules. Sig = statistical significance (2 X 2 Contingency Table, $P \leq 0.05$)

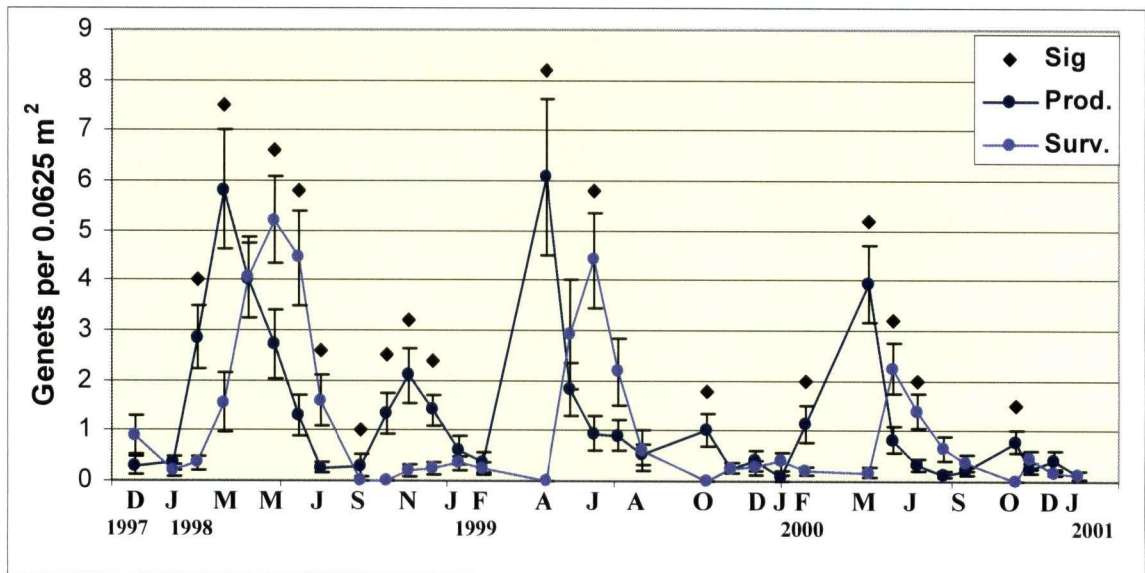


Figure 3.12: A comparison of population densities of survivors and new production for haploid genets of *Mazzaella splendens*, at Second Beach, Barkley Sound (November 1997 to January 2001). Means (± 1 S E). Sig = Significance: Mann-Whitney U Test, $P \leq 0.05$. Prod. = new genets. Surv. = surviving genets.

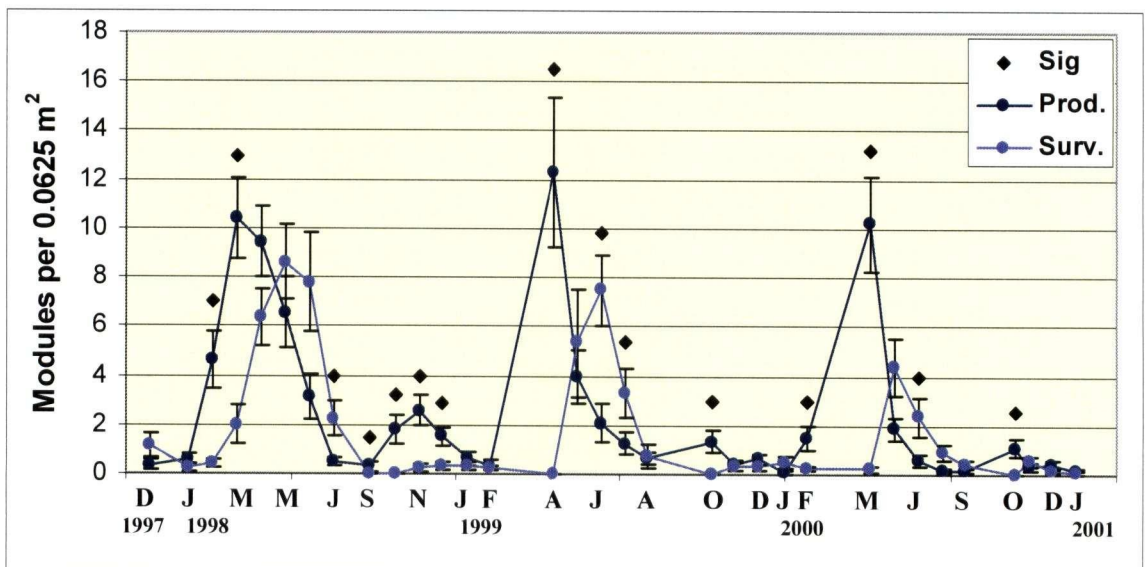


Figure 3.13: A comparison of population densities of survivors and new production for haploid modules of *Mazzaella splendens*, at Second Beach, Barkley Sound (November 1997 to January 2001). Means (± 1 S E). Sig = Significance: Mann-Whitney U Test, $P \leq 0.05$. Prod. = new modules. Surv. = surviving modules.

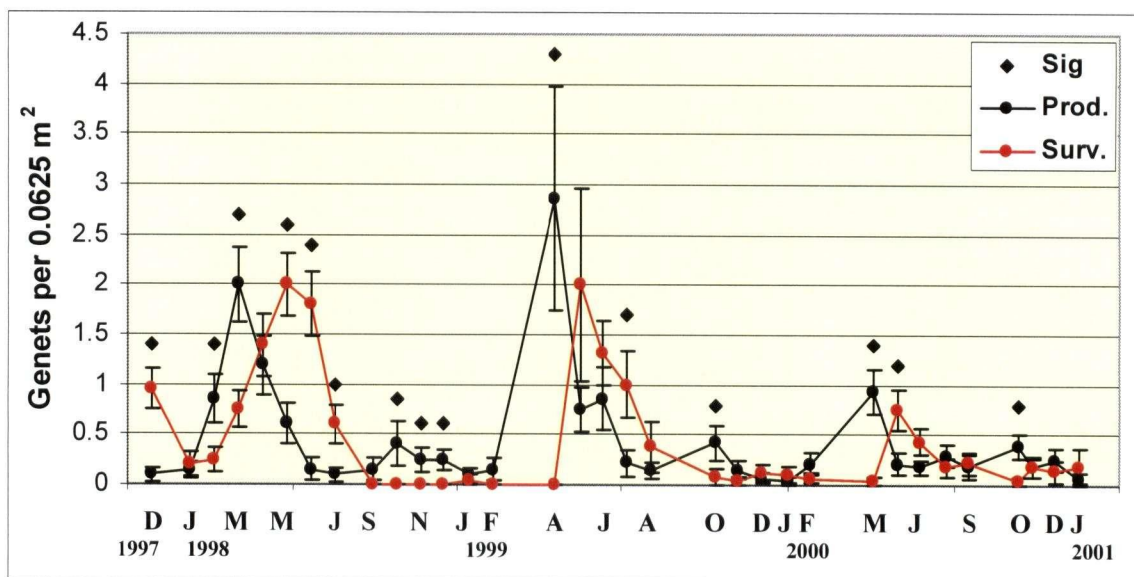


Figure 3.14: A comparison of population densities of survivors and new production for diploid genets of *Mazzaella splendens*, at Second Beach, Barkley Sound (November 1997 to January 2001). Means (± 1 S.E.). Sig = Significance: Mann-Whitney U Test, $P \leq 0.05$. Prod. = new genets. Surv. = surviving genets.

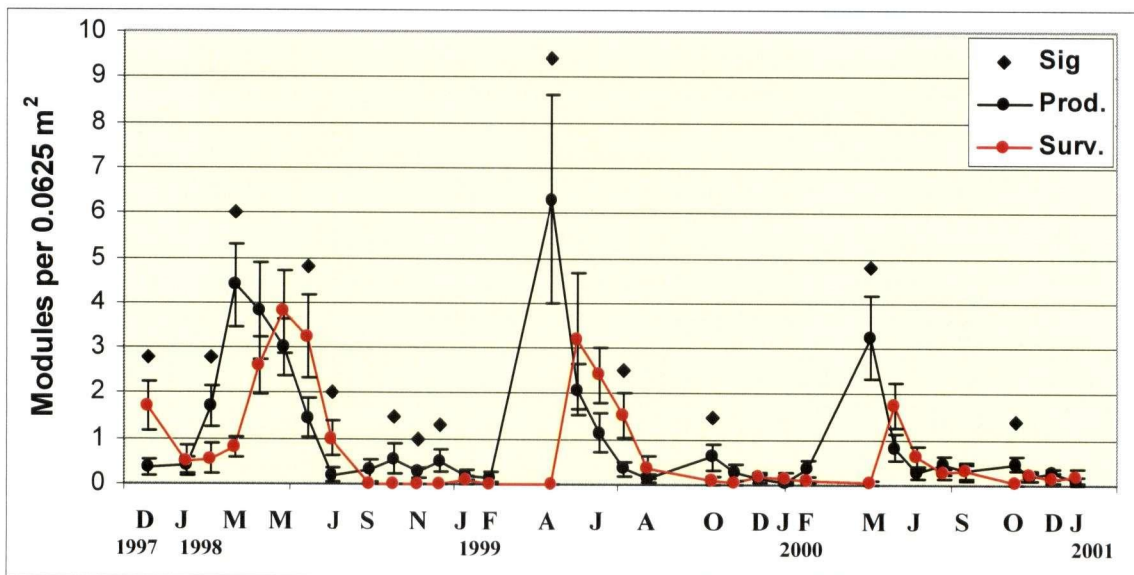


Figure 3.15: A comparison of population densities of survivors and new production for diploid modules of *Mazzaella splendens*, at Second Beach, Barkley Sound (November 1997 to January 2001). Means (± 1 S.E.). Sig = Significance: Mann-Whitney U Test, $P \leq 0.05$. Prod. = new modules. Surv. = surviving modules.

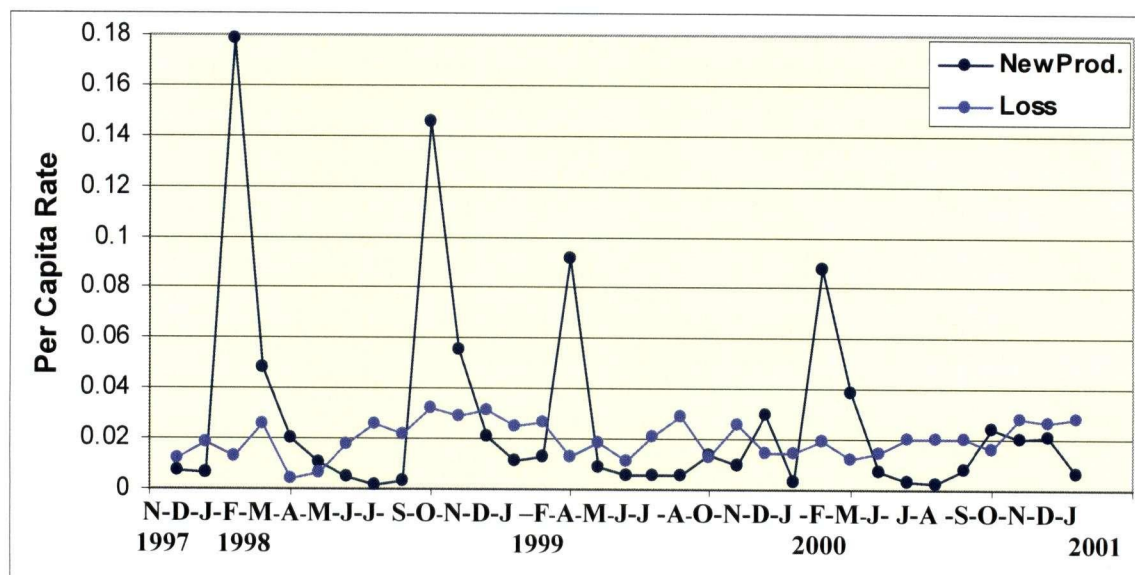


Figure 3.16: Per capita rate of new production (per day) vs. per capita rate of loss (per day) for gametophyte genets of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). NewProd. = per capita rate of new genet appearance. Loss = per capita rate of genet disappearance.

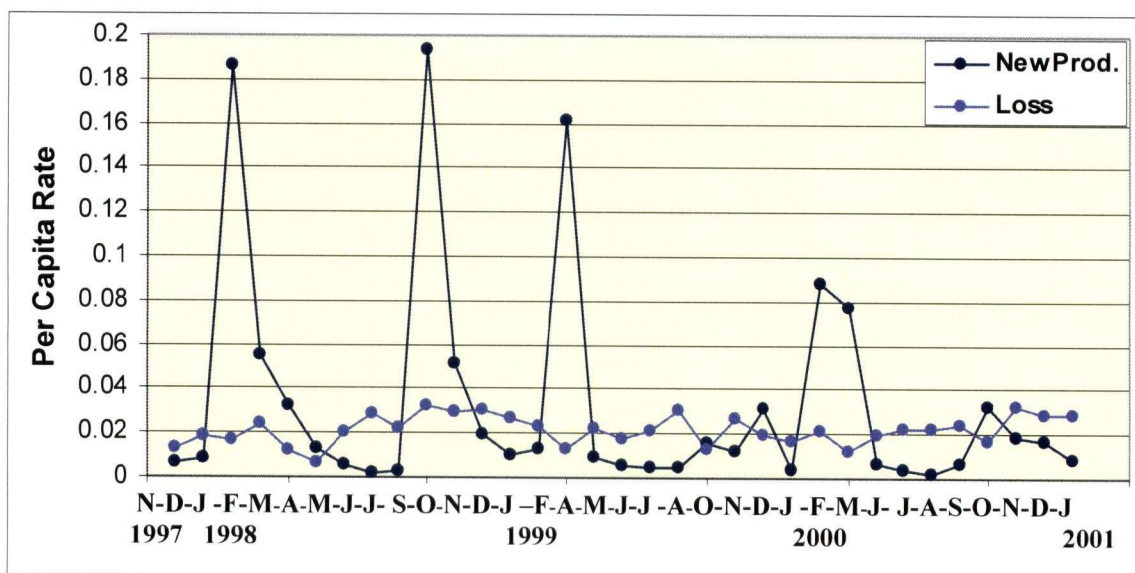


Figure 3.17: Per capita rate of new production (per day) vs. per capita rate of loss (per day) for gametophyte modules of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). NewProd. = per capita rate of new module production. Loss = per capita rate of module loss.

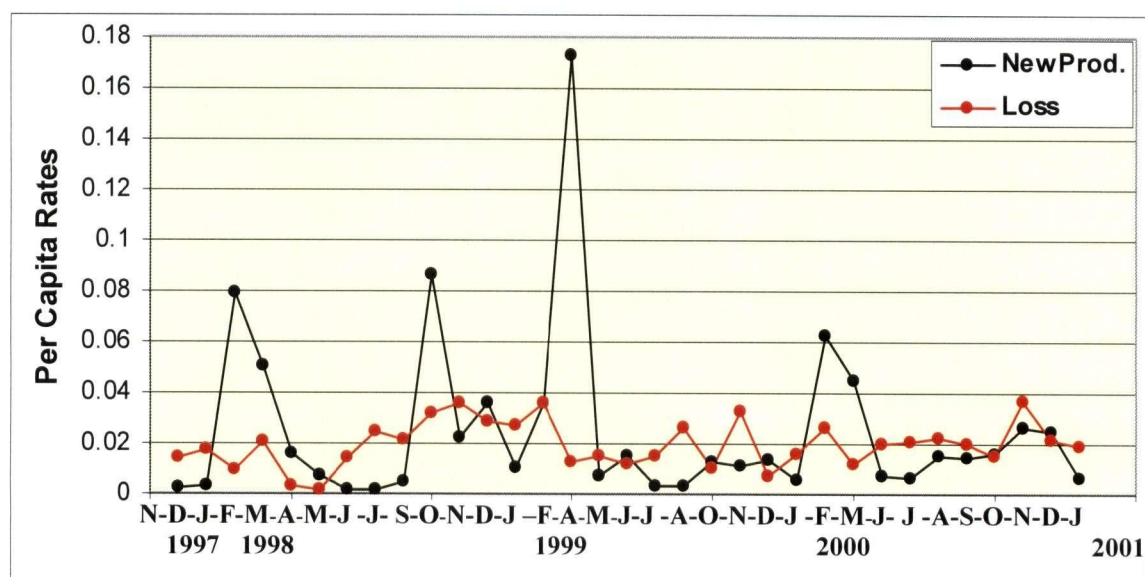


Figure 3.18: Per capita rate of new production (per day) vs. per capita rate of loss (per day) for tetrasporophyte genets of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). NewProd. = per capita rate of new genet appearance. Loss = per capita rate of genet disappearance.

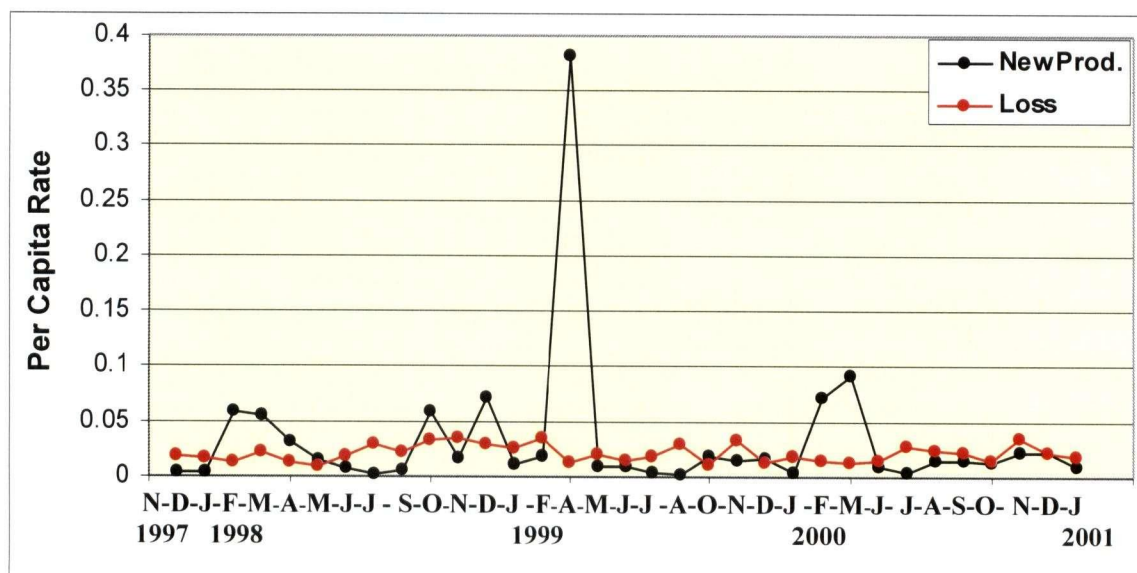


Figure 3.19: Per capita rate of new production (per day) vs. per capita rate of loss (per day) for tetrasporophyte modules of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). NewProd. = per capita rate of new module production. Loss = per capita rate of module loss.

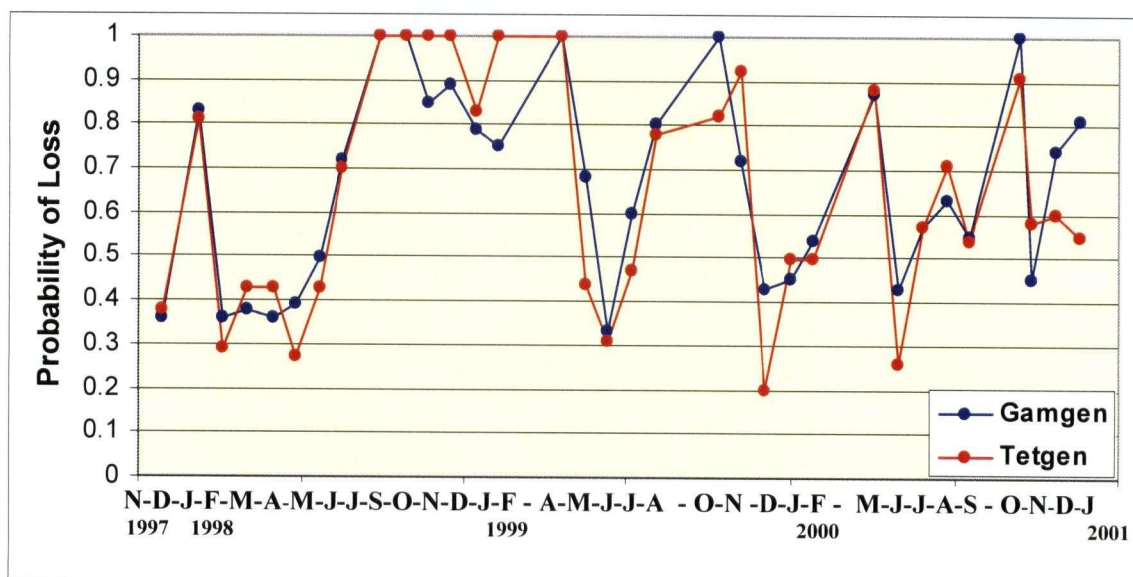


Figure 3.20: Probability of disappearance for haploid vs. diploid genets of *Mazzaella splendens*, at Second Beach, Barkley Sound (November 1997 to January 2001). Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets.

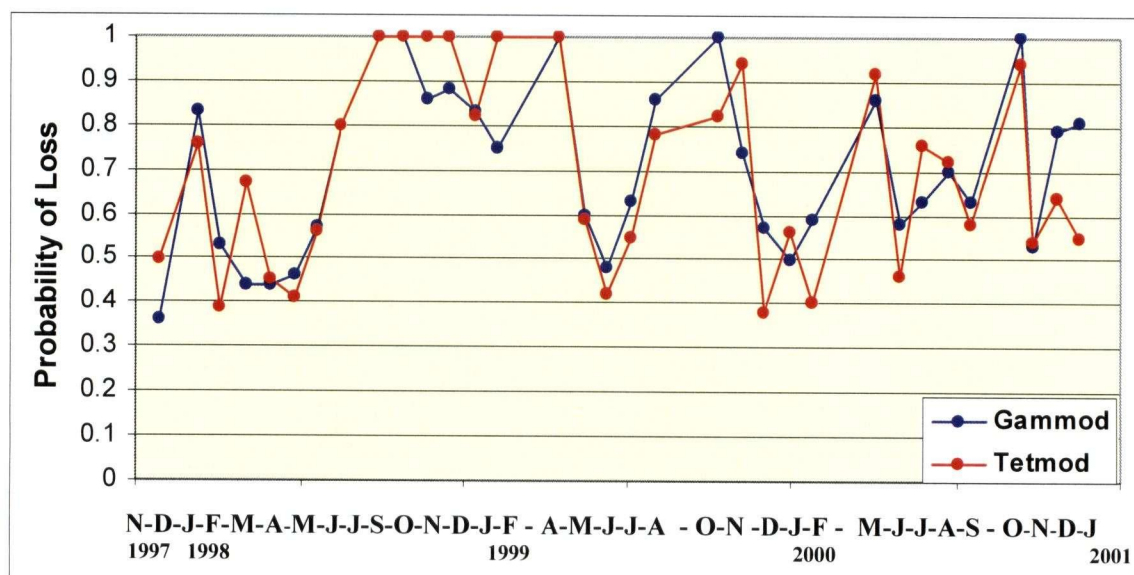


Figure 3.21: Probability of loss for haploid vs. diploid modules of *Mazzaella splendens*, at Second Beach, Barkley Sound (November 1997 to January 2001). Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

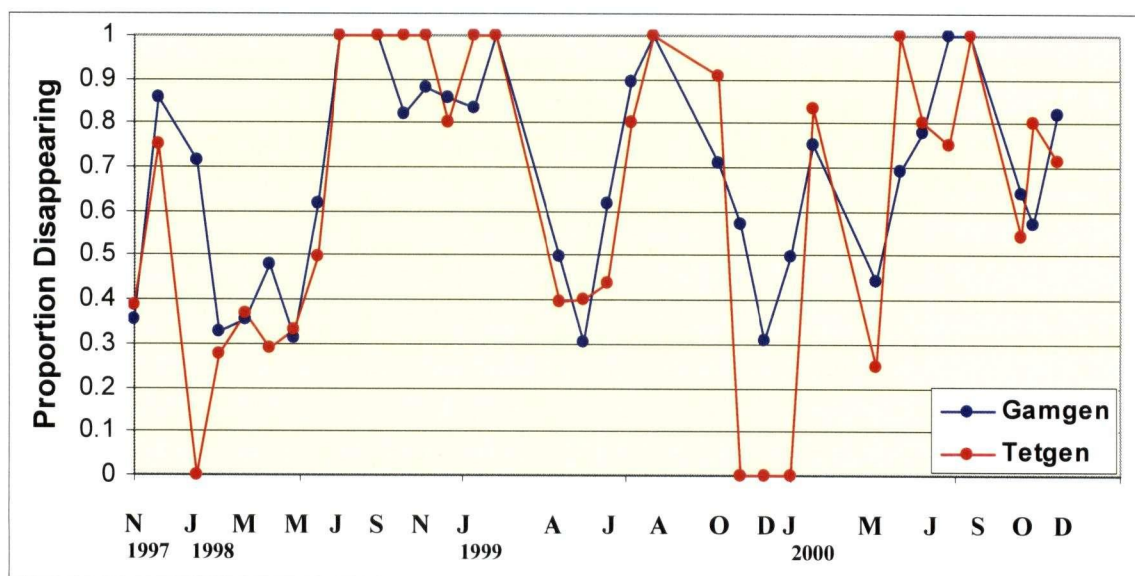


Figure 3.22: Proportion disappearing between the first and second censuses for each cohort of genets of *Mazzaella splendens*, at Second Beach, Barkley Sound (November 1997 to December 2000). Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets.

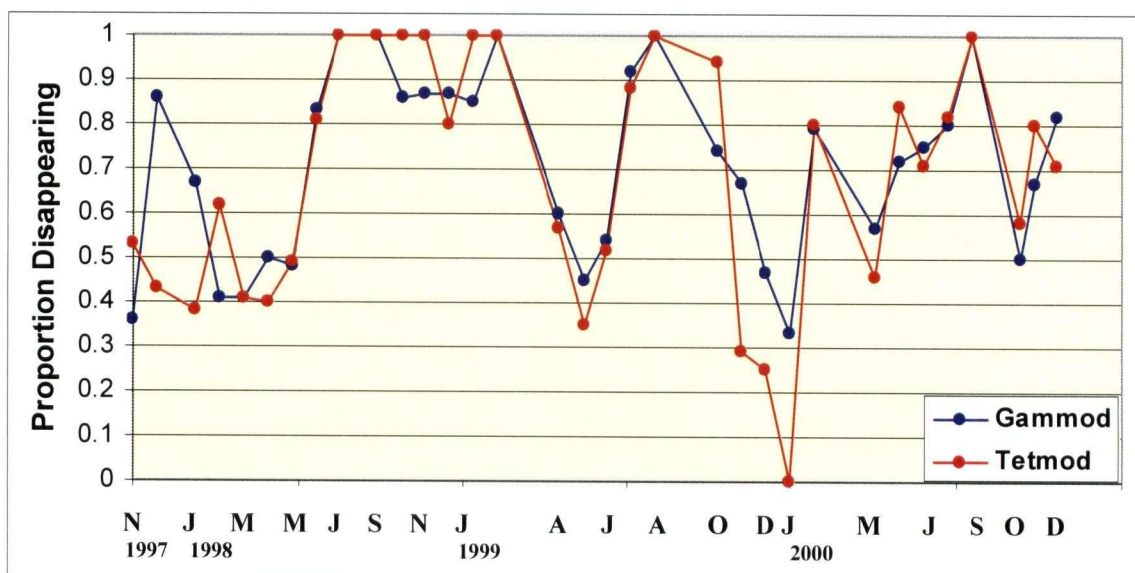


Figure 3.23: Proportion lost between the first and second censuses for each cohort of modules of *Mazzaella splendens*, at Second Beach, Barkley Sound (November 1997 to December 2000). Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

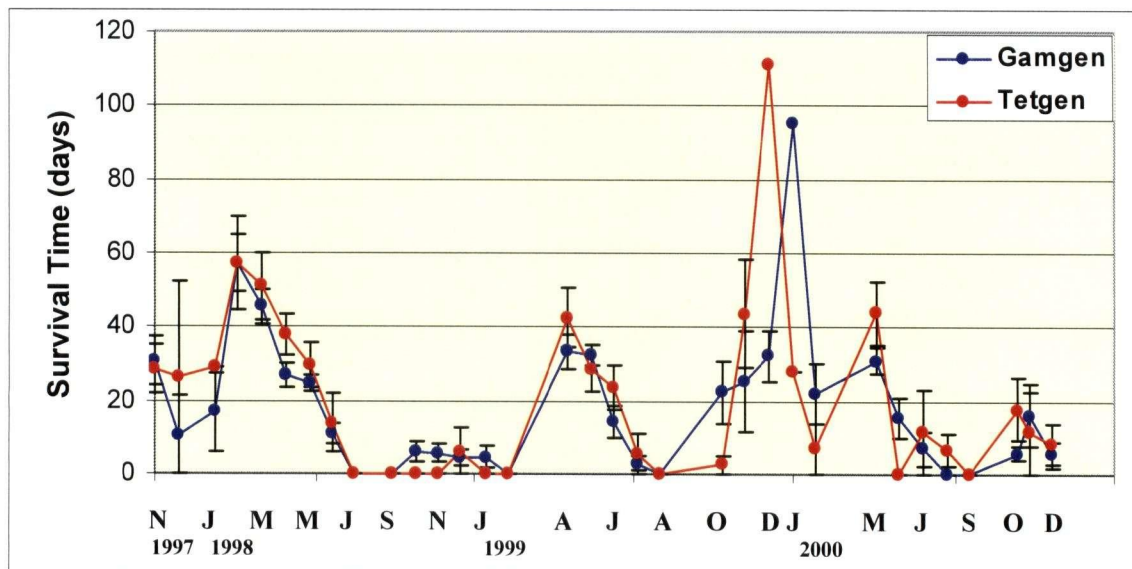


Figure 3.24: Genet survival time for each cohort of *Mazzaella splendens*, at Second Beach, Barkley Sound (November 1997 to December 2000). Means (± 1 S.E.). Sig = Significance: Mann-Whitney U Test, $P \leq 0.05$. Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets. The S.E. bars were removed from diploids for December 1999 (S.E. = 80.0) and from haploids for January 2000 (S.E. = 95.0) to reduce the scale.

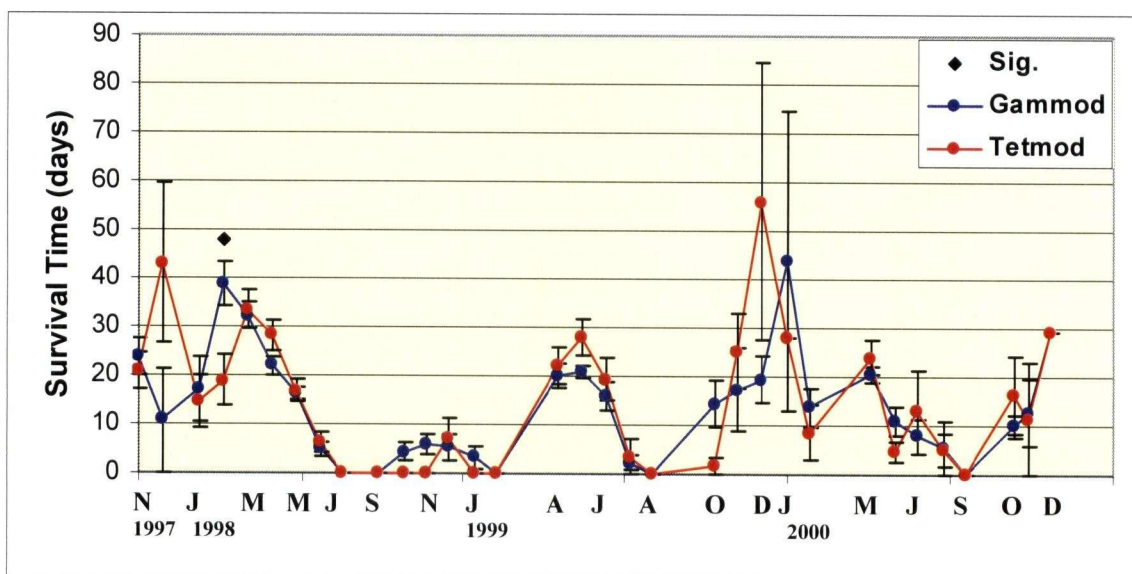


Figure 3.25: Module survival time for each cohort of *Mazzaella splendens*, at Second Beach, Barkley Sound (November 1997 to December 2000). Means (± 1 S.E.). Sig = Significance: Mann-Whitney U Test, $P \leq 0.05$. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

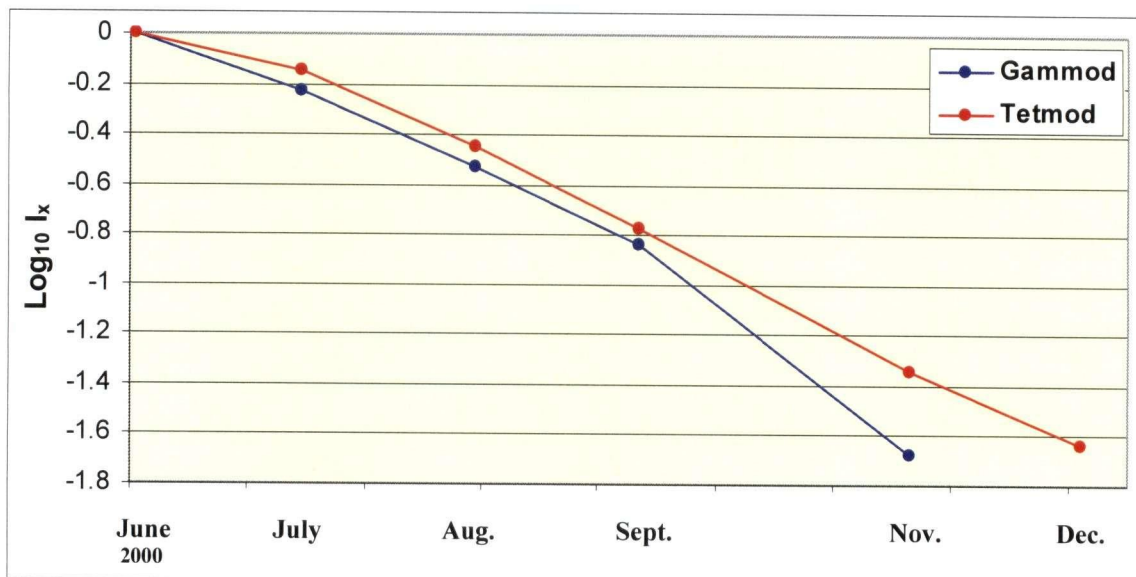


Figure 3.26: Survival ($\log_{10} l_x$) for the alternate phases of *Mazzaella splendens* at the wave-exposed site, Second Beach, Barkley Sound (June to December 2000). Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

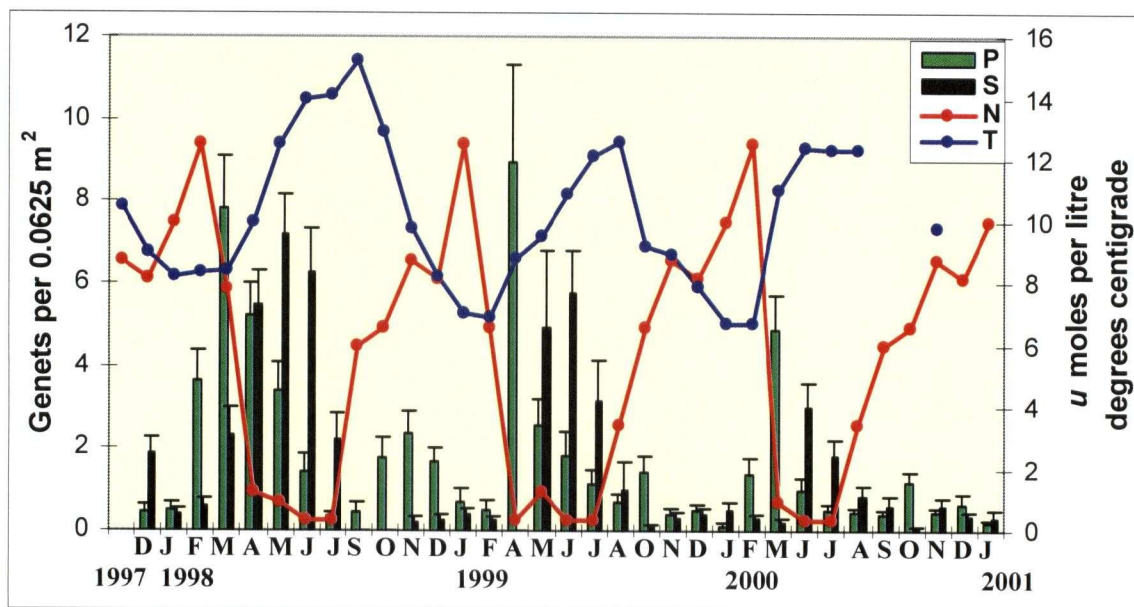


Figure 3.27: Population densities of survivors and new production for genets of *Mazzaella splendens*, at Second Beach, Barkley Sound, with seasonal changes in surface water temperature and dissolved nitrate (November 1997 to January 2001). P = genet density due to new production (mean + 1 S E). S = genet density due to survival (mean + 1 S E). N = Nitrate concentrations (μ moles l^{-1}) for 1981 – 1982 from Wheeler and Srivastava (1984). T = temperature ($^{\circ}C$) for 1997 – 2000 from Cape Beale Lighthouse.

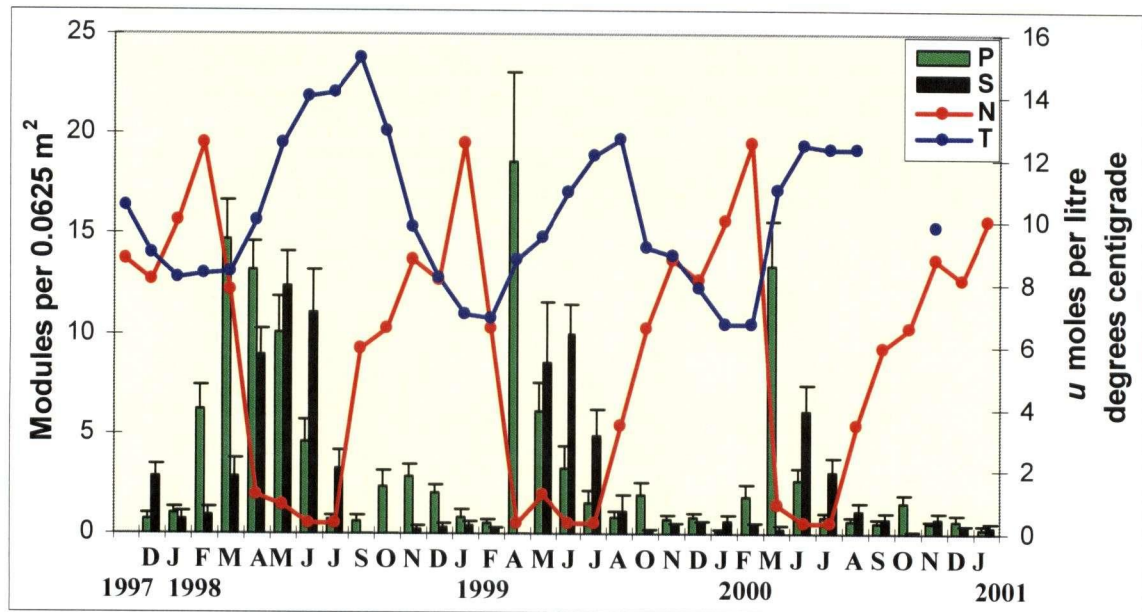


Figure 3.28: Population densities of survivors and new production for modules of *Mazzaella splendens*, at Second Beach, Barkley Sound, with seasonal changes in surface water temperature and dissolved nitrate (November 1997 to January 2001). P = module density due to new production (mean + 1 S E). S = module density due to survival (mean + 1 S E). N = Nitrate concentrations (μ moles l^{-1}) for 1981 – 1982 from Wheeler and Srivastava (1984). T = temperature ($^{\circ}C$) for 1997 – 2000 from Cape Beale Lighthouse.

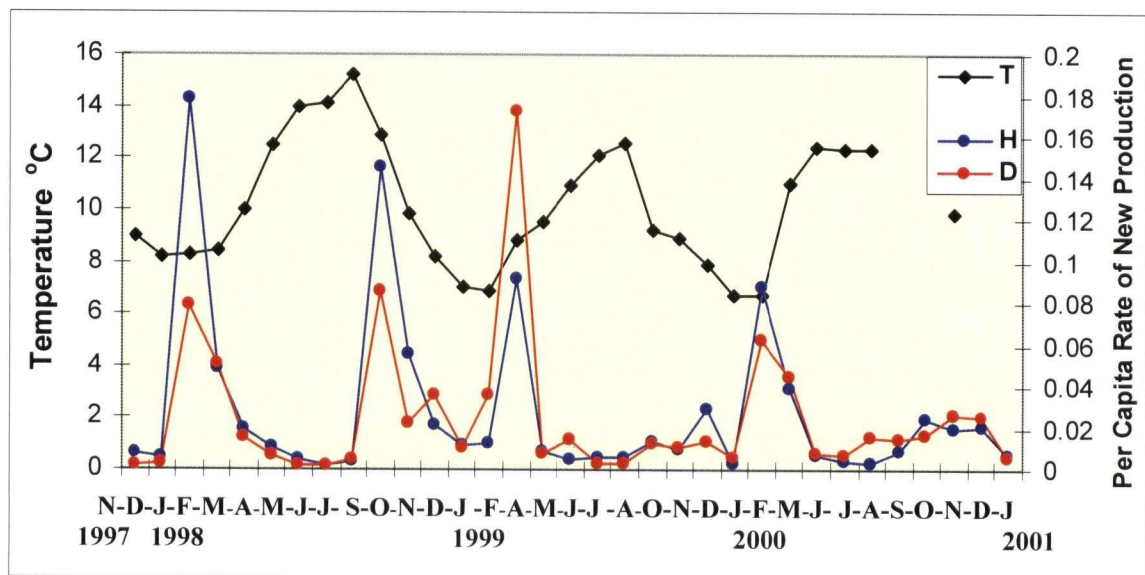


Figure 3.29: A comparison of surface water temperature at Cape Beale and per capita rate of new production (per day) for haploid vs. diploid genets of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). T = Temperature ($^{\circ}C$). H = gametophyte genets. D = tetrasporophyte genets.

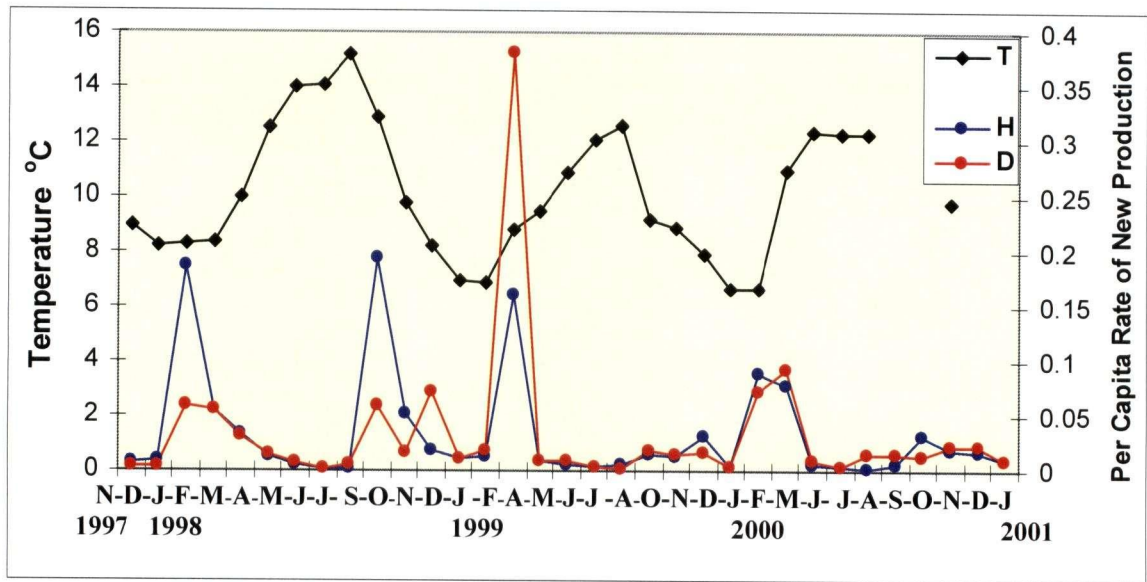


Figure 3.30: A comparison of surface water temperature at Cape Beale and per capita rate of new production (per day) for haploid vs. diploid modules of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). T = Temperature (°C). H = gametophyte modules. D = tetrasporophyte modules.

Tables to accompany Chapter 3.

Table 3.1: Descriptive statistics for probability of loss (proportion lost from previous census) for genets and modules of *Mazzaella splendens* gametophytes and tetrasporophytes at the wave-sheltered site, Second Beach, Barkley Sound. November 1997 to January 2001.

Gametophyte				Tetrasporophyte			
Genets		Modules		Genets		Modules	
Mean	St. Error	Mean	St. Error	Mean	St. Error	Mean	St. Error
0.6585	0.03977	0.7036	0.03315	0.6458	0.0452	0.7009	0.03757

Table 3.2: Kaplan-Meier analysis of survival differences in haploid vs. diploid genets and modules of *Mazzaella splendens* in nine cohorts tagged at the wave-sheltered site, Second Beach, Barkley Sound.

Date		Log-Rank test	Wilcoxon test
February 1998	Genets	P = 0.022	P = 0.065
	Modules	P = 0.001	P = 0.100
March 1998	Genets	P = 0.471	P = 0.567
	Modules	P = 0.939	P = 0.801
April 1998	Genets	P = 0.365	P = 0.287
	Modules	P = 0.411	P = 0.422
May 1998	Genets	P = 0.516	P = 0.495
	Modules	P = 0.810	P = 0.785
June 1998	Genets	P = 0.475	P = 0.475
	Modules	P = 0.962	P = 0.962
April 1999	Genets	P = 0.462	P = 0.668
	Modules	P = 0.990	P = 0.915
May 1999	Genets	P = 0.395	P = 0.347
	Modules	P = 0.125	P = 0.152
June 1999	Genets	P = 0.591	P = 0.697
	Modules	P = 0.692	P = 0.889
May 2000	Genets	P = 0.462	P = 0.388
	Modules	P = 0.431	P = 0.257

Chapter 4. Seasonal changes in surface area and biomass in *Mazzaella splendens*.

Abstract

On the basis of a significantly larger planform area in gametophytes vs. tetrasporophytes of *Mazzaella splendens* within the size category of 15 – 30 cm long, Shaughnessy *et al.* (1996) predicted greater survival of the diploid tetrasporophyte stage in response to increased hydrodynamic force. It was also suggested that such a difference could be instrumental in maintaining diploid dominance in wave-exposed habitats and producing seasonal alternations from summer haploid to winter diploid dominance in wave-sheltered habitats as wave force increased due to winter storms. Differential survival, however, was not detected in either habitat at Second Beach, Barkley Sound (Chapter 3).

In this study I examined surface area of *Mazzaella splendens* in a wave-sheltered and a wave-exposed area at Second Beach, Barkley Sound. Most modules in the population at the wave-sheltered site were smaller than the size category for which differential survival was predicted. But at this site and at the wave-exposed site differential survival was also absent from the larger size class.

At the wave-sheltered site modules of both phases, in both size classes gained significantly more tissue than they lost. Larger blades were present primarily in spring and early summer, after the decline of winter storms and before the late summer/early fall population crash (Chapter 2). This suggests that modules at this site may never encounter hydrodynamic forces large enough to exert a differential effect on the alternate phases.

At the wave-exposed site modules of both phases gained significantly more tissue than they lost while in the smaller size class. But in the size class for which differential survival between phases was predicted by Shaughnessy *et al.* (1996) tissue gain continued to significantly exceed tissue loss for tetrasporophytes but not for gametophytes. This suggests that gametophytes are losing parts of their blades, reconfiguring their surface area in response to wave action. This may result in similar chances of removal at the stipe for both life history phases.

Introduction

Population density, biomass and surface area in *Mazzaella splendens*.

Population density of *Mazzaella splendens* often changes with season, though the pattern of this change varies with habitat. In wave-sheltered sites at Brockton Point in Vancouver Harbour (Dyck & DeWreede 1995), the Strait of Georgia (Adams 1979 as *Iridaea cordata*) and at Second Beach in Barkley Sound (Chapter 2) *M. splendens* has shown a regular pattern of high summer and low winter density. At Brockton Point and the Strait of Georgia a seasonal alternation from summer haploid to winter diploid dominance was observed. At Second Beach gametophytes were dominant in summer but significant differences in density, between life history phases, were absent in late summer/early fall and in winter.

This study is the first detailed examination of seasonal changes in blade surface area for *Mazzaella splendens*. It is reasonable to hypothesize that the sudden increase in per capita production of new blades each spring at the wave-sheltered site, Second Beach, (Chapter 3) reflects increased growth rates, and that mean blade size would increase from winter to summer. The high mortality of *M. splendens* at this site in late summer implies that most fall and winter blades will be new growth, begun after September as growing conditions become less favourable in fall and winter. Mean surface area should be generally lower in these months than in spring and early summer.

Biomass will increase as surface area increases, and there is some information on the relationship of biomass to density in *Mazzaella splendens*. Adams (1979 as *Iridaea cordata*) reported, for wave-sheltered sites in the Strait of Georgia, that biomass (as fresh weight per 0.5 m²) of *M. splendens* was, like density, high in summer and low in winter. Both life history phases followed this pattern and, like density, haploid biomass predominated in summer and diploid biomass in winter.

In central California Hansen and Doyle (1976 as *Iridaea cordata*) found a different situation. In a population dominated year round by tetrasporophytes, density changed little with season. Biomass, however, was high in summer and low in winter as perennating crusts lost larger blades and produced new smaller ones. Diploid dominance in summer is characteristic of wave-exposed habitats (Dyck *et al.* 1985 as *Iridaea cordata*, Phillips 1994 as *Mazzaella lilacina*, Chapter 2). At Second Beach, Barkley Sound, population density of *M. splendens* in a wave-exposed habitat remained

relatively stable during summer, while density at a nearby wave-sheltered site dropped dramatically (Chapter 2). It is likely, although degree of wave exposure was not mentioned in the study, that the work of Hansen and Doyle (1976 as *Iridaea cordata*) described the dynamics of density and biomass in a wave-exposed area.

The finding that biomass in gametophytes and tetrasporophytes of *Mazzaella splendens* follows the same pattern as density on a per unit of habitat basis, in wave-sheltered sites (Adams 1979 as *Iridaea cordata*), indicates that size differences between phases, if present, are not large enough for phase dominance in biomass to behave differently from phase dominance in density. In the population of *M. splendens* at the wave-sheltered site, Second Beach, Barkley Sound, the density of gametophytes during periods of significant haploid dominance was usually several times the respective diploid density (Chapter 2). Size differences between phases would need to be substantial for biomass to reverse this dominance in density, and no such differences were obvious in the field. It seems unlikely, therefore, that biomass at Second Beach would produce a pattern of phase dominance different from the one already observed for density (Chapter 2). It is expected that module surface area, increasing as biomass increases, should also produce this pattern.

Sunday (2001) has shown that biomass increases with surface area at a significantly greater rate for tetrasporophytes of *Mazzaella splendens* than it does for gametophytes. The most likely reason for this difference is that tetrasporophytes increase in thickness at a greater rate than gametophytes. Shaughnessy (1996) found no difference in blade thickness between gametophytes and tetrasporophytes 5 cm in length or less, but for blades 15 – 25 cm long diploids were significantly thicker than haploids. The resulting lower surface area to volume ratio in diploids vs. haploids may be one reason for the higher rate of dissolved nitrate uptake in gametophytes (Sunday 2001). If the relationship between surface area and biomass described by Sunday (2001) is strong one might expect to see mean biomass of tetrasporophytes exceed mean biomass of gametophytes during the main growing season, though total biomass at the site would reflect population density.

Individual differences in surface area between phases.

There may, however, be individual differences in surface area between gametophytes and tetrasporophytes that reflect different growth responses to season or are a product of more fundamental developmental differences. Shaughnessy *et al.* (1996) found significant differences in surface area between gametophytes and tetrasporophytes of *Mazzaella splendens*. The larger planform area of gametophytes formed part of the basis for predicting that tetrasporophytes would exhibit greater survival as wave force increased.

Differential survival between phases of *Mazzaella splendens*, however, was not found at either the wave-sheltered or wave-exposed sites at Second Beach, Barkley Sound (Chapter 3). There are several possibilities that could reconcile this result with the predictions of Shaughnessy *et al.* (1996). Differential survival was predicted to take place for a particular size class of individual (blades 15 – 30 cm long). Shaughnessy *et al.* (1996) reported significantly larger gametophytes within this size class but not among smaller blades. It would be useful to replicate this result and also to extend it by examining seasonal variability in mean surface area. The greatest proportion of large blades would be expected in spring and early summer when population density is highest. If this occurs the larger blades, which are predicted to exhibit differential survival between phases (Shaughnessy *et al.* 1996), would be present primarily during the seasons when wave force is at its lowest, and one would not expect to see much of an effect. In fall and winter nearly all blades may be in the smaller size category, for which differential survival is not predicted.

Loss of the entire blade is not the only possible response of a seaweed to increasing wave force. Blanchette (1997) found that *Fucus gardneri* transplanted from wave-sheltered to wave-exposed habitats lost parts of their blades, conforming their morphology to the new habitat. There were no significant survival differences between transplanted and control individuals. Shaughnessy and DeWreede (2001) found severe loss of tissue in *Mazzaella splendens* among those individuals surviving transplantation into the extremely wave-swept habitat of *Mazzaella linearis*. In habitats with less extreme water motion, survival of *M. splendens* blades may be facilitated by loss of tissue rather than breaking at the stipe. This could also contribute to the absence of

significant differences in survival between modules of gametophytes and tetrasporophytes in both wave-sheltered and wave-exposed areas at Second Beach.

An examination of changes in size in both these habitats will determine the size class structure present at different times of year and the amount of tissue loss that occurs before modules are lost from the population. Both of these factors have the potential to account for the absence of predicted differential survival between gametophyte and tetrasporophyte modules of *Mazzaella splendens*.

Methods and Materials

Site selection, quadrat placement and census dates were as described in chapter 2.

In each of the permanent quadrats at the sheltered site, the number of genets (basal crusts) with visible modules (blades) was enumerated. Each module was tagged around the stipe with a colour coded plastic electrical tie strap. A 0.5 cm diameter disk of tissue was removed from each blade with a single hole paper punch. This tissue sample was used in carrageenan analysis to determine life history phase in the absence of reproductive structures (Garbary & DeWreede 1988, Shaughnessy & DeWreede 1991). The outline of each blade was traced on acetate, and at each subsequent census this procedure was applied to all new blades. The outline of each surviving blade was traced at each census. This produced a record over time of changes in genet and module density for haploids vs. diploids. For each genet, the timing of new production, survival and changes in size and shape of each of its modules was recorded.

As conditions permitted, transects of contiguous 0.0625 m² quadrats were run between randomly chosen permanent quadrats. In each quadrat along a transect the density of haploid and diploid genets, with the number of modules in each genet, were counted (as for the permanent quadrats). The outline of each blade was traced on acetate. No tagging was done in these transects. Dates of sampling the transects were as described in chapter 2 (Table 2.1).

Surface area was not measured in the permanent quadrats at the wave-exposed site during 1998 and 1999 when population density was examined at this site. Surface area was measured in a cohort tagged at the wave-exposed site in June, 2000. This cohort consisted of the largest blade in each genet within the permanent quadrats and was not representative of the underlying size class structure in the population.

Biomass was not measured directly at Second Beach. Surface area was converted into biomass (g. dry wt.) using equations for a regression of surface area on \log_{10} dry weight (g.), for gametophytes and tetrasporophytes of *Mazzaella splendens*, done by Sunday (2001). These equations produced reasonable biomass values from surface areas within the sizes (10 – 120 cm²) examined by Sunday (2001). For greater individual surface areas, however, biomass values derived from these equations soon became unrealistically large. Since the individual biomasses of modules larger than 120 cm² could not be calculated, their contribution could only be assessed in the context of the total biomass at the wave-sheltered site. This was calculated for modules larger than 120 cm² by setting the ratio of total biomass to total surface area in the size class of blades greater than 120 cm², equal to the ratio of total biomass to total surface area in the size class of blades 120 cm² or less. Conclusions from these estimates of biomass will be tentative as error is introduced both in the measurement of surface area and in the use of a linear equation to convert this surface area to dry weight. Nevertheless the work done by Sunday (2001) has made it possible to examine this parameter, and it may suggest some relationships between surface area and biomass in the alternate phases that would bear further examination.

Significant differences between life history phases, in mean surface area, mean biomass, survival time between size classes, and tissue gain and loss were determined with the Mann-Whitney U test. Differences in size class distributions between gametophytes and tetrasporophytes were tested with contingency tables (Fischer & van Belle, 1993).

Concerns about statistical independence of samples from one month to the next prevent attributing statistical significance to apparent trends or tendencies over time. I will, however, discuss what I believe these trends to be without attributing statistical significance. To examine these trends I used a cubic spline. This is a nonparametric nonlinear regression that emphasises local over global fit (Hastie & Tibshirani 1990, Silverman 1986, Chapter 2). All cubic spline calculations were done using glmsWIN 1.0 available at www.zoology.ubc.ca/~schluter/splines.html.

Results

Changes in surface area at the wave-sheltered site.

Maximum size attained, for all modules tagged at the sheltered site during the course of the study, showed 90 % of modules fell in the 120 cm² surface area or less category, which corresponds approximately to the lower boundary of the size class in which Shaughnessy *et al.* (1996) predicted differential survival between phases would take place (Figure 4.1). The distributions of gametophytes and tetrasporophytes across these size classes were significantly different ($\chi^2 = 45.208$, d.f. = 24, $P = 0.006$). This difference persisted when only blades 100 cm² or less were considered ($\chi^2 = 21.23$, d.f. = 9, $P = 0.012$) and also for blades 50 cm² or less ($\chi^2 = 12.4$, d.f. = 4, $P = 0.016$). Maximum size was significantly greater for gametophytes (mean = 66.64 cm², SE = 2.203) vs. tetrasporophytes (mean = 42.87 cm², SE = 2.093) as determined by a Mann-Whitney U test ($P < 0.001$).

The trend for seasonal changes in mean module surface area over the three years of study, for modules of all size classes combined, showed mean surface area was generally higher in summer and lower in winter for both life history phases. There was a tendency for peak mean surface area to increase in each consecutive summer for gametophytes, but this tendency was not clearly apparent for tetrasporophytes (Appendix D, Figures D.1 & D.2).

Mean surface area of tetrasporophyte modules was significantly greater than that of gametophytes in November 1997 and June 1998. During March, May and June 1998, gametophyte mean surface area was significantly larger. This was the only year in which there was a crossover from greater haploid mean surface area to greater diploid mean surface area (June to July). In 1999 and 2000 either haploid surface area was significantly greater or there was no significant difference between phases (Figure 4.2).

When only modules 120 cm² or smaller were considered the trend of higher mean surface area in summer and lower mean surface area in winter remained for both phases, but the tendency for peak mean surface area to increase over time was not apparent in either life history phase (Appendix D, Figures D.3 & D.4). Many of the significant differences in mean surface area between life history phases were no longer present. The crossover from greater haploid mean surface area to greater mean diploid surface area in summer, 1998, remained. But there were no significant differences in surface area

between phases in 1999 and only one (August) with significantly greater gametophyte mean surface area in 2000 (Figure 4.3).

Total surface area (all modules in the permanent quadrats at the sheltered site, Second Beach) was much greater each spring and summer than in fall and winter (Appendix D, Figure D.5) as expected from the observed seasonal changes in density (Chapter 2). Spring peak values of total surface area for gametophytes were generally 3.5 to 4.5 times those for tetrasporophytes. Peak total surface area declined slightly each consecutive spring for tetrasporophytes but rose each time for gametophytes. When only modules 120 cm² or less were considered (Appendix D, Figure D.6), peak total surface area for both life history phases declined over the three consecutive summers. Modules greater than 120 cm² consistently contributed a greater proportion of the total surface area, during the spring and summer periods, than under 120 cm² for both gametophytes (Figure 4.4) and tetrasporophytes (Figure 4.5).

In the transects at the wave-sheltered site, Second Beach, mean surface area tended to be higher in summer and lower in winter for both life history phases (Table 4.1). Mean surface area was not significantly different between haploid and diploid modules in December 1998, January 1999, December 1999, August 2000, or September 2000. In November and December 2000, tetrasporophytes showed significantly larger mean surface areas. Over 90% of haploid and diploid modules were in the size classes 120 cm² or less (Figure 4.6). The distributions of gametophytes and tetrasporophytes across these size classes were significantly different ($\chi^2 = 47.69$, d.f. = 22, $P = 0.001$). The distributions of gametophytes were significantly different between the permanent quadrats and the transects ($\chi^2 = 67.32$, d.f. = 22, $P < 0.001$) as were the distributions of tetrasporophytes ($\chi^2 = 44.76$, d.f. = 22, $P = 0.001$). This difference was not significant when only blades 100 cm² or less were considered ($\chi^2 = 11.39$, d.f. = 9, $P = 0.250$).

Changes in biomass at the wave-sheltered site.

Seasonal changes in total biomass for all size classes combined showed spring and summer haploid predominance with peak values for gametophytes generally twice those for tetrasporophytes. Peak biomass for both phases declined over the three consecutive summers (Appendix D, Figure D.7). Among those modules 120 cm² or less the pattern was similar (Appendix D, Figure D.8).

The pattern of mean biomass was opposite to that for mean surface area. Gametophyte biomass was significantly greater than tetrasporophyte biomass on only two occasions, January 1998 and January 1999. Tetrasporophyte biomass was significantly greater each spring (Figure 4.4).

Survival time in large and small blades of *Mazzaella splendens*.

The wave-sheltered site.

The comparison of survival time in blades which never became larger than 120 cm² (size class 1) vs. blades that grew larger than 120 cm² (size class 2) at some point in their lifespan was conducted on blades produced during the favourable period from February to July each year because the fall and winter months tended to be dominated by small blades with short survival times which could bias the outcome. The total lifespans of size class 2 haploids and diploids were significantly longer than their respective size class 1 counterparts. Subsequent mean survival time after reaching size class 2, for both gametophyte and tetrasporophyte modules, was not significantly different from their respective mean survival times for size class 1 (Table 4.2).

When examining differences between tissue gain and loss within each life history phase, tissue gain was significantly greater than tissue loss for gametophytes and for tetrasporophytes, of both size classes, when their entire lifespan was considered. Tissue gain was also significantly greater than tissue loss for size class 2 modules of both life history phases when considering gain and loss that occurred only after the blades had reached 120 cm² (Table 4.3). When examining differences between life history phases in size class 1, both mean tissue gain and mean tissue loss were significantly greater for gametophytes than for tetrasporophytes. In size class 2 gametophyte tissue gain was significantly higher than tetrasporophyte tissue gain but there was no significant difference between phases in tissue loss. Tissue gain after reaching 120 cm² also showed no significant difference between gametophytes and tetrasporophytes (Table 4.4).

The wave-exposed site.

At the wave-exposed site, the total lifespan of size class 2 tetrasporophytes was significantly longer than for size class 1, but for gametophytes the difference was not significant. For both life history phases subsequent survival after reaching size class 2 was not significantly different from survival in size class 1 (Table 4.5).

When the entire lifespan of the modules was considered, tissue gain was significantly greater than tissue loss for both size classes in both life history phases. When considering tissue gain and loss that occurred only after modules had reached 120 cm², gain was significantly greater than loss for tetrasporophytes but gametophytes showed no significant difference (Table 4.6). Within size class 1 there were no significant differences in tissue gain or loss between gametophytes and tetrasporophytes. In size class 2, gametophyte tissue gain and loss were both significantly greater than for tetrasporophytes. Gametophyte tissue gain was also significantly greater than tetrasporophyte tissue gain after modules had reached 120 cm² (Table 4.7).

Discussion

Size class structure, tissue gain and loss, and the absence of differential survival.

The wave-sheltered site.

Maximum size of gametophyte modules of *Mazzaella splendens* at the wave-sheltered site, Second Beach, was significantly larger than tetrasporophyte maximum size as previously observed by Shaughnessy *et al.* (1996). Of the modules that were produced by *M. splendens* at this site during the three years of study, 85% of gametophytes and 93% of tetrasporophytes did not grow larger than 120 cm². Modules that reached 120 cm² or larger (size class 2) were significantly longer lived than those in the smaller size class, as would be expected if size were a function of age.

Only a small proportion of *Mazzaella splendens* blades at the wave-sheltered site grew large enough for the hydrodynamic model of Shaughnessy *et al.* (1996) to apply, and even among these larger blades size had no significant effect on survival (as survival time after reaching 120 cm² was not significantly different from survival time for size class 1 modules). Survival was not facilitated by tissue loss as it was for *Fucus*

gardneri (Blanchette 1997). Growth continued to outstrip tissue loss in *M. splendens*, even after size class 2 was reached. Since most large blades are produced during spring and summer, when wave force is in general decline, and lost in the September population crash before winter storms begin (Chapter 2), it may be that large blades of *M. splendens* at the wave-sheltered site rarely encounter waves of sufficient magnitude to produce significant tissue loss or differential survival. At the wave-sheltered site, Second Beach, the fact that most blades of *M. splendens* are less than 120 cm² and the fact that size confers no significant disadvantage in module survival both contribute to the observed absence of differential survival (Chapter 3) between life history phases.

The wave-exposed site.

Mazzaella splendens also showed no significant survival difference between gametophytes and tetrasporophytes at the wave-exposed site, Second Beach (Chapter 3). The cohort at this site consisted of the largest blade present in each genet, so an evaluation of the size class structure of the population was not possible.

Survival time with respect to size was different, however, at this site compared to the wave-sheltered site. Size class 2 tetrasporophyte modules at this site were, as at the wave-sheltered site, significantly longer lived than those remaining in size class 1, but for gametophytes this difference was not significant. This suggests that while size is generally a function of age in tetrasporophytes at this site, the relationship between size and age for gametophytes is less clear. It may be that certain gametophyte modules grow much more rapidly than others at this site. There was, however, no negative effect of large size on survival for either phase. Tissue gain and loss was also different at the wave-exposed vs. the wave-sheltered site, with growth after reaching size class 2 significantly greater than tissue loss for tetrasporophytes but with no significant difference for gametophytes. At the wave-exposed site it is likely that tissue loss assisted gametophyte survival more than tetrasporophyte survival, since gametophyte tissue loss was significantly greater than tetrasporophyte tissue loss.

The observation that tetrasporophyte blades are thicker than gametophyte blades in size class 2 (Shaughnessy 1996) may explain this difference if a thicker blade confers greater resistance to tissue loss. Gametophyte blades may grow larger than tetrasporophyte blades during times when wave force is not strong enough to remove

tissue, producing the differences in planform area observed by Shaughnessy *et al.* (1996). When wave force is sufficient to remove blades, gametophytes may lose more tissue than tetrasporophytes, modifying their surface area, so that both life history phases present similar planform areas resulting in similar survival times.

Differences in tissue gain and loss between life history phases and between wave-sheltered and wave-exposed habitats.

In the wave-sheltered site gametophyte modules both grew faster and lost more tissue in the process than tetrasporophyte modules, yet achieved significantly larger size as tissue gain was always significantly greater than loss. This difference between phases was no longer significant, however, after blades had grown into size class 2.

In the wave-exposed site there was no significant difference in growth or tissue loss when blades were smaller, but after growing to size class 2, gametophytes both gained and lost significantly more tissue than tetrasporophytes.

This is a subtle difference in behaviour between phases of *Mazzaella splendens* in these two different habitats, and interpreting it within the context of speculations in chapter 3 about the importance of dissolved nitrate in producing changes in population density yields some contradictions. If dissolved nitrate at the wave-exposed site is less of a limiting factor than at the wave-sheltered site due to increased water motion (Chapter 3), the fact that smaller blades at this site show no significant differences in tissue gain is consistent with the observation (Shaughnessy, 1996) that there are no significant differences in thickness of smaller blades. Nitrate would have similar distances to diffuse within blades of each phase and would contribute to growth at a similar rate in gametophytes and tetrasporophytes. With larger tetrasporophytes significantly thicker than larger gametophytes (Shaughnessy, 1996) this would change, with gametophytes adding more tissue per unit time, but also losing more tissue due to lesser blade strength, as was observed in this present study.

If the increased biomass per unit area for tetrasporophytes reported by Sunday (2001) is due to the greater thickness of tetrasporophyte blades reported by Shaughnessy (1996), the significantly greater mean biomass calculated for tetrasporophytes (Figure 4.4), which appeared during the same seasons as significantly greater mean surface area was measured for gametophytes (Figure 4.2), suggests that tetrasporophytes became

thicker than gametophytes at the wave-sheltered site, Second Beach. Here, however, smaller gametophytes added tissue more quickly than smaller tetrasporophytes, which would not be expected if blade thickness was similar between phases, and these differences became insignificant upon reaching the larger size when blade thickness should have been significantly different. It seems that something other than wave force, dissolved nitrate, and the interaction of the two is at work producing these differences between phases, but it is difficult at this point to suggest what this might be.

The proportion of total surface area contributed by modules in size class 2.

At the wave-sheltered site, a relatively small proportion of the total population of both gametophytes and tetrasporophytes of *Mazzaella splendens* contributed a relatively large proportion of the total surface area for each life history phase (Figures 3.4 & 3.5). This would not be the case if modules in size class 1 tended to grow to nearly the limit of their size class before being lost and modules in the larger size class were lost shortly after entering it. In fact, mean maximum surface area in size class 2 was 7.1 times larger than mean maximum surface area in size class 1 for gametophytes, and 6.8 times larger for tetrasporophytes (Table 4.8).

DeWreede and Klinger (1988) have listed one of the expected outcomes of reproductive cost in the algae as the necessity of blades reaching a certain critical (relatively large) size before reproduction will begin. If reproduction in *M. splendens* were to take place primarily in larger blades, the fact that these few large blades contributed so much to the total available surface area could potentially allow substantial spore production by both phases, at this site, even if only these few blades became fertile. In the next chapter I will be examining various aspects of reproduction and its interactions with population density and size at the wave-sheltered site.

Conclusions

In both the wave-sheltered site and wave-exposed sites at Second Beach, Barkley Sound, differential survival between gametophytes and tetrasporophytes of *Mazzaella splendens*, predicted by Shaughnessy *et al.* (1996), was absent within the size class for which it was predicted.

At the wave-sheltered site tissue gain significantly exceeded tissue loss in both smaller and larger modules. It may be that modules at this site never encounter hydrodynamic forces large enough to exert a differential effect on the alternate phases, since large blades appear in the population only after winter storms have subsided and a population crash each year in late summer/early fall ensures that no large blades survive to encounter increased wave force in winter.

At the wave-exposed site tissue gain significantly exceeded tissue loss in smaller modules, but within the size class for which differential survival due to hydrodynamic forces was predicted tissue gain significantly exceeded tissue loss for tetrasporophytes but not for gametophytes. The absence of differential survival at this site may be due to gametophytes losing parts of their blades, reconfiguring their surface area in response to wave action, and resulting in similar chances of removal at the stipe for both life history phases.

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Figures to accompany Chapter 4.

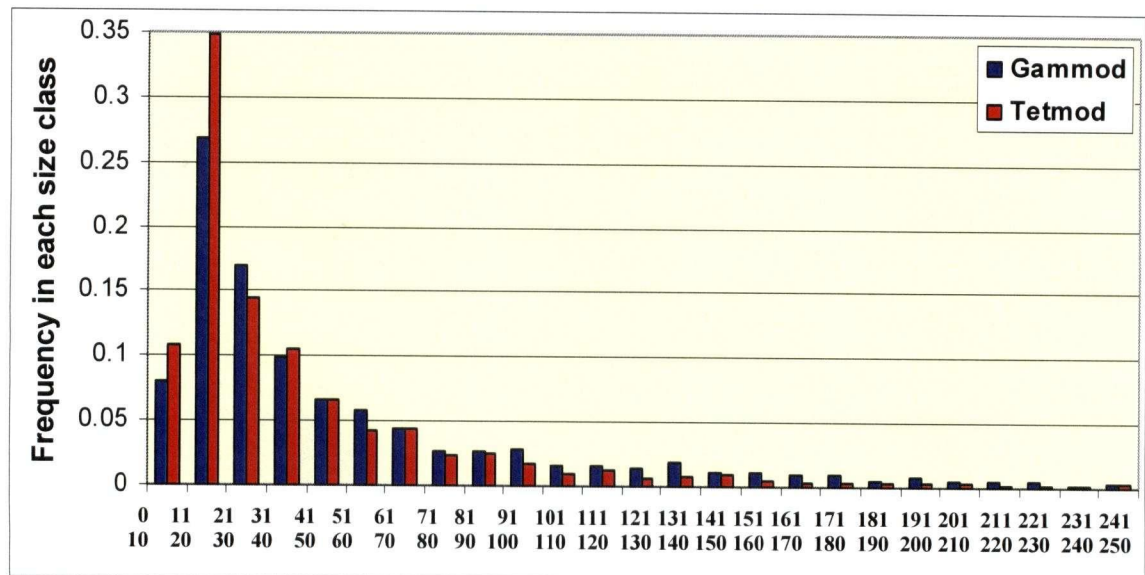


Figure 4.1: Size class frequency of modules (maximum size attained in cm²) in the alternate phases of *Mazzaella splendens* in 20 (November 1997 – April 1999) and 31 (May 1999 - January 2001) 0.0625 m² permanent quadrats at Second Beach, Barkley Sound (November 1997 to January 2001). Gammod = gametophyte modules. Tetmod = tetrasporophyte modules. (size classes above 250 cm² listed in Appendix E, **Table E.1**)

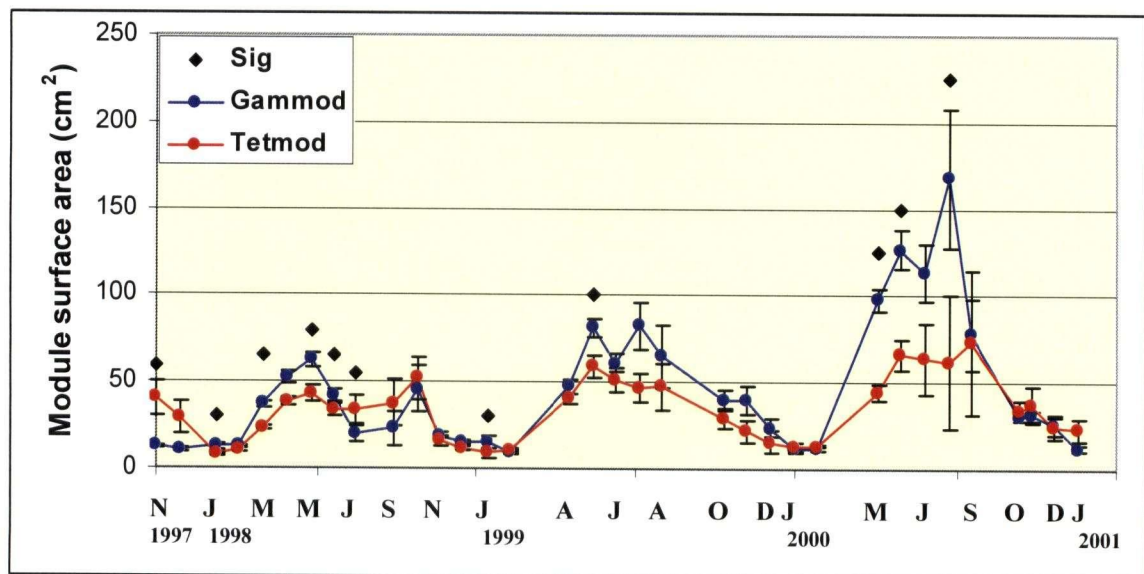


Figure 4.2: Seasonal changes in module surface area (all blades) for the alternate phases of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). Means (± 1 S.E.). Gammod = gametophyte modules. Tetmod = tetrasporophyte modules. Sig. = Statistical significance: Mann-Whitney U Test, $P \leq 0.05$.

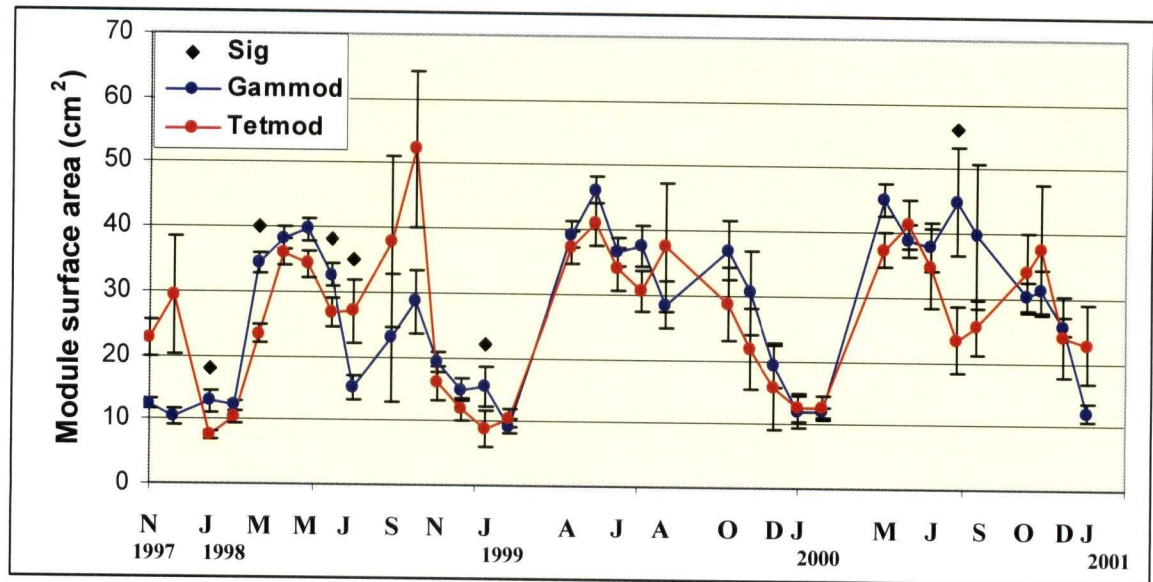


Figure 4.3: Seasonal changes in module surface area (blades 120 cm² or less) for the alternate phases of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). Means (± 1 S.E.). Gammod = gametophyte modules. Tetmod = tetrasporophyte modules. Sig. = Statistical significance: Mann-Whitney U Test, $P \leq 0.05$.

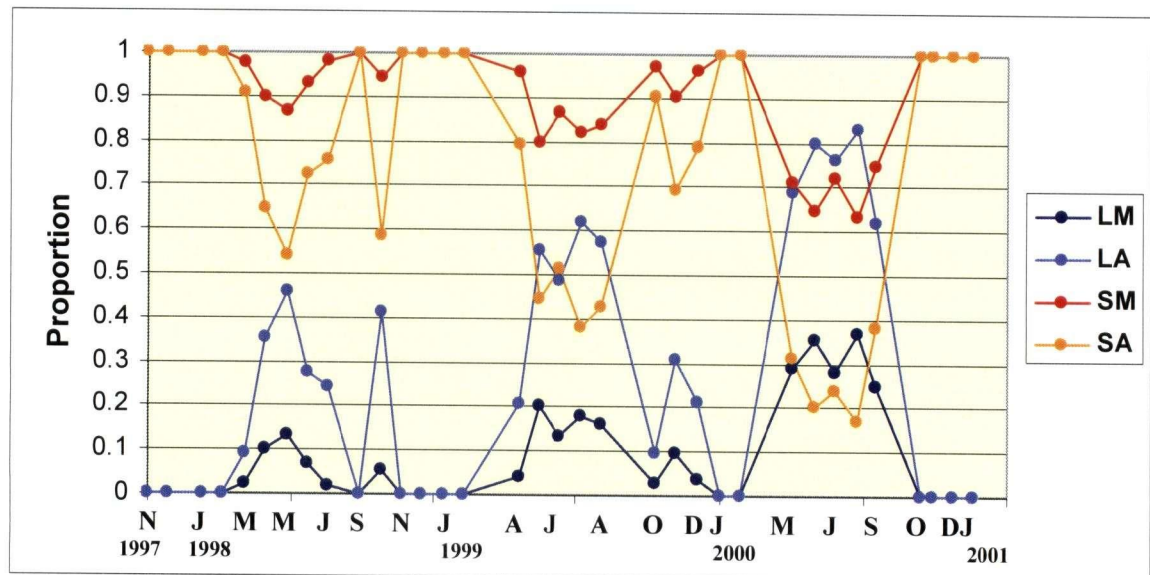


Figure 4.4: Proportion of total modules which are greater than 120 cm² vs. modules 120 cm² or less and proportion of total surface area within the larger size class vs. the smaller size class for gametophytes of *Mazzaella splendens* in 20 (November 1997 – April 1999) and 31 (May 1999 - January 2001) 0.0625 m² permanent quadrats at Second Beach, Barkley Sound (November 1997 to January 2001). LM = modules greater than 120 cm². LA = surface area in the larger size class. SM = modules 120 cm² or less. SA = surface area in the smaller size class.

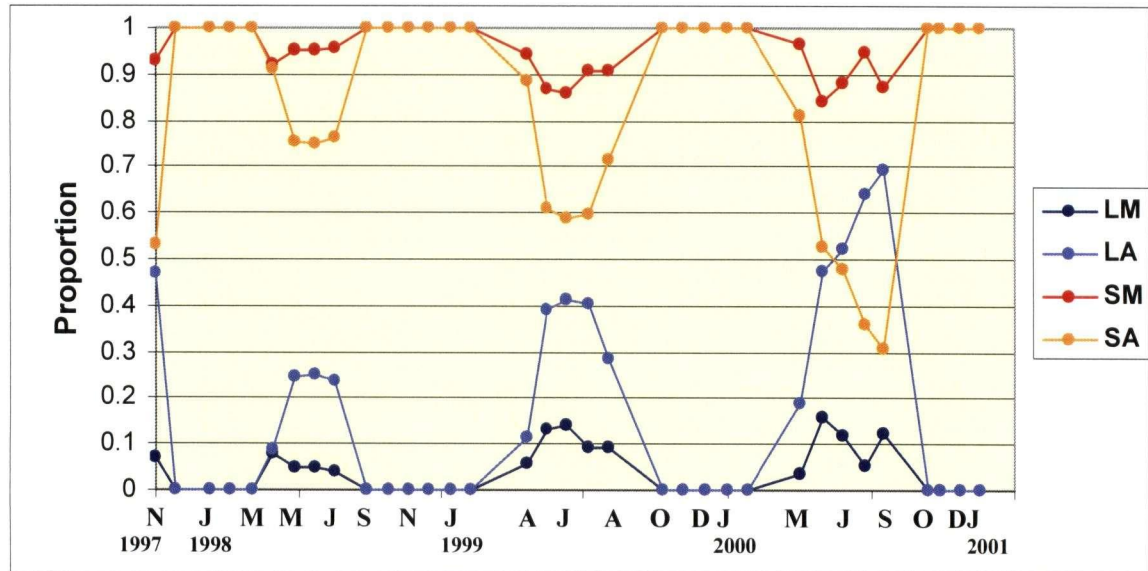


Figure 4.5: Proportion of total modules which are greater than 120 cm² vs. modules 120 cm² or less and proportion of total surface area within the larger size class vs. the smaller size class for tetrasporophytes of *Mazzaella splendens* in 20 (November 1997 – April 1999) and 31 (May 1999 - January 2001) 0.0625 m² permanent quadrats at Second Beach, Barkley Sound (November 1997 to January 2001). LM = modules greater than 120 cm². LA = surface area in the larger size class. SM = modules 120 cm² or less. SA = surface area in the smaller size class.

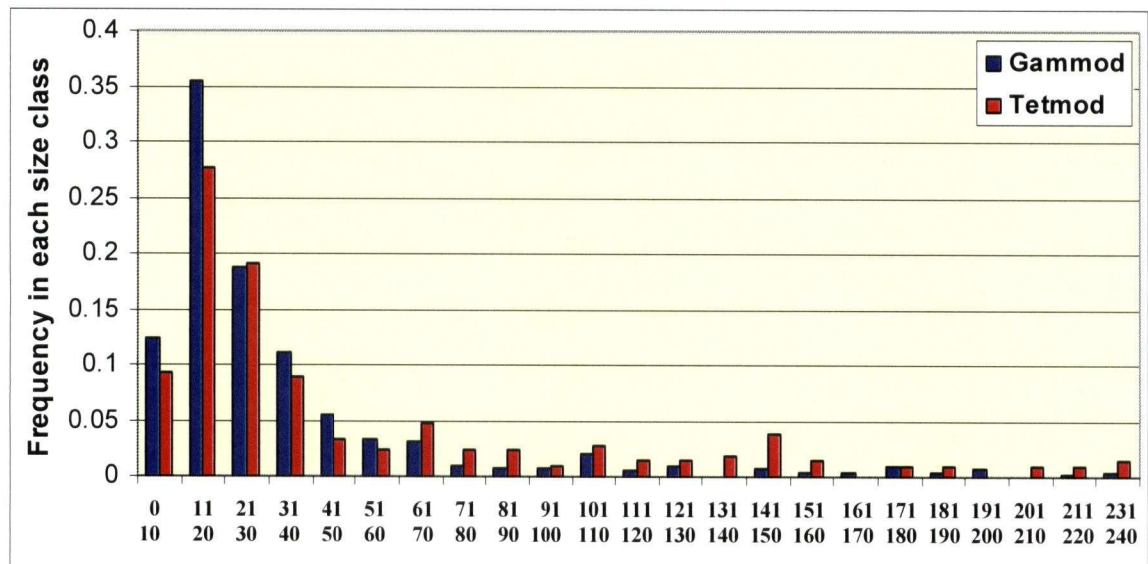


Figure 4.6: Size class frequency of modules (cm²) in the alternate phases of *Mazzaella splendens* in the transects at Second Beach, Barkley Sound. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules. (size classes above 250 cm² listed in Appendix E, Table E.2)

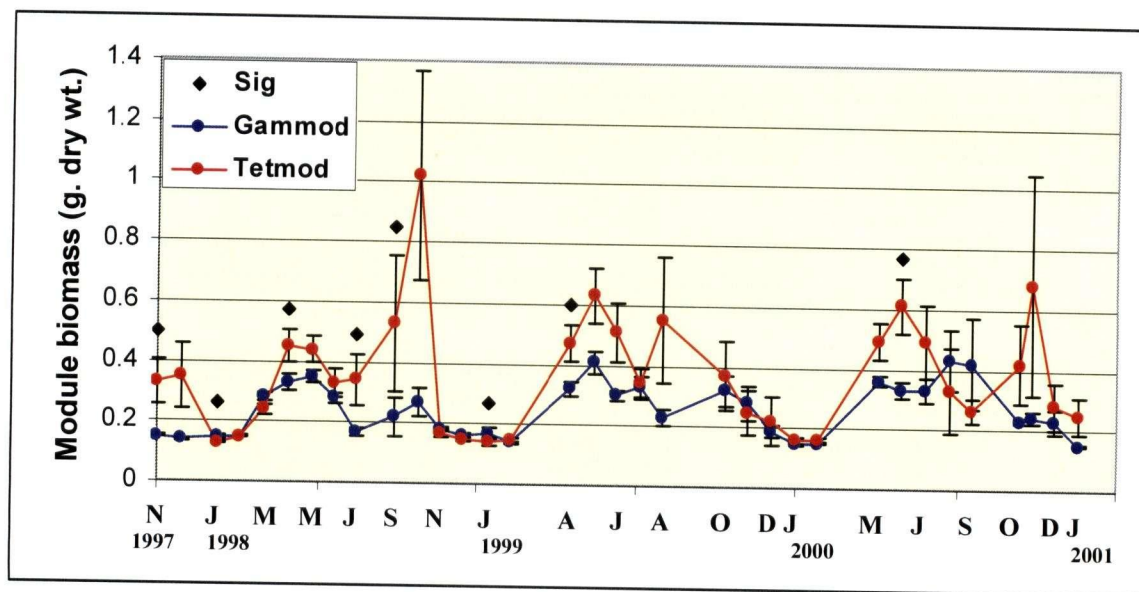


Figure 4.7: Seasonal changes in module biomass (blades 120 cm² or less) for the alternate phases of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). Means (± 1 S.E.). Gammod = gametophyte modules. Tetmod = tetrasporophyte modules. Sig. = Statistical significance: Mann-Whitney U Test, $P \leq 0.05$.

Tables to accompany Chapter 4.

Table 4.1: Descriptive and inferential statistics for modules of *Mazzaella splendens* gametophytes and tetrasporophytes in the transects at the wave-sheltered site, Second Beach, Barkley Sound. December 1998 to December 2000. Given are mean surface area (cm^2) (= Mean), the standard error of the mean (= S.E.) and the P value from the Mann-Whitney U test (= M.W.-U) comparing surface areas of haploid vs. diploid modules.

Date		Mean	S.E.	M.W.-U
Dec. 1998	Gametophyte	20.62	0.937	P = 0.270
	Tetrasporophyte	15.18	1.446	
Jan. 1999	Gametophyte	20.43	1.968	P = 0.250
	Tetrasporophyte	47.90	10.711	
Dec. 1999	Gametophyte	29.21	3.413	P = 0.188
	Tetrasporophyte	39.29	5.212	
Aug. 2000	Gametophyte	186.66	26.292	P = 0.209
	Tetrasporophyte	133.82	24.130	
Sept. 2000	Gametophyte	141.07	23.374	P = 0.911
	Tetrasporophyte	147.75	27.03	
Nov. 2000	Gametophyte	35.34	4.036	P = 0.003
	Tetrasporophyte	84.89	14.424	
Dec. 2000	Gametophyte	24.52	3.070	P < 0.001
	Tetrasporophyte	83.19	15.018	

Table 4.2: Descriptive and inferential statistics for survival time, in modules of different size classes, for *Mazzaella splendens* in the permanent quadrats at the wave-sheltered site, Second Beach, Barkley Sound. The size classes are: modules 120 cm² or less (= size class 1) and modules larger than 120 cm² (= size class 2). Given are mean survival time (days) (= Mean), the standard error of the mean (= S.E.), the sample size (= N), and the P value from the Mann-Whitney U test (= M.W.-U) comparing survival times between size classes.

Comparison		Size Class	N	Mean	S.E.	M.W.-U
Total survival time for modules reaching 120 cm ² or more (size 2) vs. modules less than 120 cm ² throughout their life span (size 1).	All	1	1840	17.59	0.579	P < 0.001
	Modules	2	278	40.76	2.055	
	All	1	1298	16.72	0.664	P < 0.001
	Haploids	2	278	39.75	2.220	
	All	1	542	19.68	1.151	P < 0.001
	Diploids	2	48	46.79	5.394	
	All	1	1840	17.59	0.579	P = 0.357
	Modules	2	278	19.98	1.533	
Total survival time for modules in size 1 vs. survival time after reaching 120 cm ² for modules in size 2.	All	1	1298	16.72	0.664	P = 0.091
	Haploids	2	278	20.33	1.636	
	All	1	542	19.68	1.151	P = 0.394
	Diploids	2	48	17.90	4.366	

Table 4.3: Descriptive and inferential statistics for tissue gain and loss, in modules of different size classes, for *Mazzaella splendens* in the permanent quadrats at the wave-sheltered site, Second Beach, Barkley Sound. The size classes are: modules 120 cm² or less (= size class 1) and modules larger than 120 cm² (= size class 2). Given are mean tissue gain and loss (cm²) (= Mean), the standard error of the mean (= S.E.), the sample size (= N), and the P value from the Mann-Whitney U test (= M.W.-U) comparing tissue loss vs. gain.

Comparison		N	Mean	S.E.	M.W.-U
Total lifespan of all haploid modules in size class 1.	Gain	605	45.89	1.166	P < 0.001
	Loss		9.35	0.749	
Total lifespan of all haploid modules in size class 2.	Gain	195	244.64	10.427	P < 0.001
	Loss		65.08	8.678	
Total lifespan of all diploid modules in size class 1.	Gain	304	40.64	1.773	P < 0.001
	Loss		4.93	0.847	
Total lifespan of all diploid modules in size class 2.	Gain	44	220.22	20.736	P < 0.001
	Loss		19.56	11.295	
Haploids in size class 2 after reaching 120 cm ² .	Gain	304	126.05	10.578	P < 0.001
	Loss		65.42	8.716	
Diploids in size class 2 after reaching 120 cm ² .	Gain	44	100.98	20.276	P < 0.001
	Loss		22.76	11.485	

Table 4.4: Descriptive and inferential statistics for tissue gain and loss between the alternate life history phases, in modules of different size classes, for *Mazzaella splendens* in the permanent quadrats at the wave-sheltered site, Second Beach, Barkley Sound. The size classes are: modules 120 cm² or less (= size class 1) and modules larger than 120 cm² (= size class 2). Given are mean tissue gain or loss (cm²) (= Mean), the standard error of the mean (= S.E.), the sample size (= N), and the P value from the Mann-Whitney U test (= M.W.-U) comparing haploid vs. diploid modules.

Comparison		N	Mean	S.E.	M.W.-U
Tissue gain during the total lifespan in size class 1.	Haploid	606	45.39	1.165	P < 0.001
	Diploid	304	39.92	1.623	
Tissue loss during the total lifespan in size class 1.	Haploid	606	9.44	0.761	P < 0.001
	Diploid	304	4.32	0.678	
Tissue gain during the total lifespan in size class 2.	Haploid	195	244.64	10.427	P = 0.010
	Diploid	43	221.17	20.271	
Tissue loss in size class 2.	Haploid	195	65.08	8.678	P = 0.380
	Diploid	43	22.76	11.485	
Tissue gain after reaching 120 cm ² .	Haploid	195	126.05	10.578	P = 0.358
	Diploid	43	100.98	20.276	

Table 4.5: Descriptive and inferential statistics for survival time, in modules of different size classes, for *Mazzaella splendens* in the permanent quadrats at the wave-exposed site, Second Beach, Barkley Sound. The size classes are: modules 120 cm² or less (= size class 1) and modules larger than 120 cm² (= size class 2). Given are mean survival time (days) (= Mean), the standard error of the mean (= S.E.), the sample size (= N), and the P value from the Mann-Whitney U test (= M.W.-U) comparing survival times between size classes.

Comparison		Size Class	N	Mean	S.E.	M.W.-U
Total survival time for modules reaching 120 cm ² or more (size 2) vs. modules less than 120 cm ² throughout their life span (size 1).	All	1	85	31.00	4.033	P = 0.008
	Modules	2	91	44.81	4.375	
	All	1	15	26.80	8.641	P = 0.460
	Haploids	2	31	34.74	6.831	
	All	1	70	31.90	4.553	P = 0.002
	Diploids	2	60	50.02	5.539	
	All	1	85	31.00	4.033	P = 0.264
	Modules	2	91	36.92	4.174	
Total survival time for modules in size 1 vs. survival time after reaching 120 cm ² for modules in size 2.	All	1	15	26.80	8.641	P = 0.691
	Haploids	2	31	31.06	6.901	
	All	1	70	31.90	4.553	P = 0.180
	Diploids	2	60	39.95	5.230	

Table 4.6: Descriptive and inferential statistics for tissue gain and loss, in modules of different size classes, for *Mazzaella splendens* in the permanent quadrats at the wave-exposed site, Second Beach, Barkley Sound. The size classes are: modules 120 cm² or less (= size class 1) and modules larger than 120 cm² (= size class 2). Given are mean tissue gain and loss (cm²) (= Mean), the standard error of the mean (= S.E.), the sample size (= N), and the P value from the Mann-Whitney U test (= M.W.-U) comparing tissue loss vs. gain.

Comparison		N	Mean	S.E.	M.W.-U
Total lifespan of all haploid modules in size class 1.	Gain	7	74.68	10.943	P = 0.001
	Loss		2.50	2.501	
Total lifespan of all haploid modules in size class 2.	Gain	21	281.11	26.721	P = 0.002
	Loss		138.94	32.596	
Total lifespan of all diploid modules in size class 1.	Gain	45	67.52	4.513	P < 0.001
	Loss		4.28	2.101	
Total lifespan of all diploid modules in size class 2.	Gain	50	199.06	11.382	P < 0.001
	Loss		51.87	9.011	
Haploids in size class 2 after reaching 120 cm ² .	Gain	21	172.54	30.468	P = 0.252
	Loss		138.94	32.596	
Diploids in size class 2 after reaching 120 cm ² .	Gain	50	86.26	11.830	P = 0.002
	Loss		51.87	9.011	

Table 4.7: Descriptive and inferential statistics for tissue gain and loss between the alternate life history phases, in modules of different size classes, for *Mazzaella splendens* in the permanent quadrats at the wave-exposed site, Second Beach, Barkley Sound. The size classes are: modules 120 cm² or less (= size class 1) and modules larger than 120 cm² (= size class 2). Given are mean tissue gain or loss (cm²) (= Mean), the standard error of the mean (= S.E.), the sample size (= N), and the P value from the Mann-Whitney U test (= M.W.-U) comparing haploid vs. diploid modules.

Comparison		N	Mean	S.E.	M.W.-U
Tissue gain during the total lifespan in size class 1.	Haploid	7	74.68	10.943	P = 0.445
	Diploid	45	67.52	4.513	
Tissue loss during the total lifespan in size class 1.	Haploid	7	2.50	2.501	P = 0.624
	Diploid	45	4.28	2.101	
Tissue gain during the total lifespan in size class 2.	Haploid	21	281.11	26.721	P = 0.005
	Diploid	50	199.06	11.382	
Tissue loss in size class 2.	Haploid	21	138.94	32.596	P = 0.022
	Diploid	50	51.87	9.011	
Tissue gain after reaching 120 cm ² .	Haploid	21	172.24	30.468	P = 0.010
	Diploid	50	86.26	11.830	

Table 4.8: Descriptive and inferential statistics for mean maximum size between two size classes of *Mazzaella splendens* in the permanent quadrats at the wave-exposed site, Second Beach, Barkley Sound. The size classes are: modules 120 cm² or less (= size class 1) and modules larger than 120 cm² (= size class 2). Given are mean maximum size (cm²) (= Mean), the standard error of the mean (= S.E.), the sample size (= N), and the P value from the Mann-Whitney U test (= M.W.-U).

Comparison		N	Mean	S.E.	M.W.-U
Size class 1 vs. size class 2 for gametophyte modules.	Size 1	1657	34.96	0.660	P < 0.001
	Size 2	291	247.06	8.488	
Size class 1 vs. size class 2 for tetrasporophyte modules.	Size 1	744	31.07	0.916	P < 0.001
	Size 2	52	211.70	16.488	
Gametophytes vs. tetrasporophytes in size class1.	Haploid	1657	34.96	0.660	P < 0.001
	Diploid	744	31.07	0.916	
Gametophytes vs. tetrasporophytes in size class2.	Haploid	291	247.06	8.488	P = 0.124
	Diploid	52	211.70	16.488	

Chapter 5. Reproduction in *Mazzaella splendens*.

Abstract

The hypothesis of reproductive cost forms the foundation of current life history theory but often impacts of reproduction on survival, or on subsequent reproduction, are not found. The physiological tradeoffs that enforce reproductive cost in allocating resources to reproduction vs. somatic growth do not appear common in the algae where reproductive structures are usually pigmented and capable of photosynthesis during development.

A population of *Mazzaella splendens* at Brockton Point, Vancouver Harbour (Dyck 1991, as *Iridaea splendens*) has shown a pattern of temporally restricted reproduction suggestive of the kind of life history optimization resulting from a cost to reproduction. This same population, however, showed no survival cost to reproductive individuals.

In this study I examined populations of *Mazzaella splendens* in a wave-sheltered and a wave-exposed habitat at Second Beach, Barkley Sound, for three of the signs of reproductive cost predicted by DeWreede and Klinger (1988): 1.) That probability of death increases after the onset of reproduction, 2.) That growth slows or stops after the onset of reproduction and, 3.) That individuals must attain a certain size before reproduction will begin.

There was no evidence of reduced survival due to reproduction in either habitat at Second Beach, Barkley Sound. At the wave-exposed site reproductive tetrasporophytes survived significantly longer than their non-reproductive counterparts by losing parts of the thallus rather than the entire blade. In the wave-sheltered site growth slowed significantly for both life history phases after the onset of reproduction, but at the wave-exposed site this occurred only for gametophytes. In the wave-sheltered site, cystocarpic gametophytes were significantly larger than their non-reproductive counterparts but reproductive tetrasporophytes were not. The reverse occurred at the wave-exposed site. Overall, evidence for a cost of reproduction in *Mazzaella splendens* is mixed. Differences between habitats may play a role in whether such a cost is incurred and which phase of the life history is most impacted by it.

Introduction

The hypothesis of reproductive cost in relation to the algae.

The foundation of current life history theory is the hypothesis of reproductive cost (Bell 1984a), which follows from the idea that resources are available in limited quantity and that increased allocation to current reproduction causes reduced allocation to individual growth or general maintenance (Bell 1984b, Obeso 2002). If current reproductive output results in reduced future reproduction, either by reducing future fecundity or survival, then age specific reproduction can be optimised by natural selection. Reproductive cost does not ensure the evolution of intermediate levels of reproductive output, but without it there is no reason for reproduction to be restricted to a particular time within the life cycle of an organism.

DeWreede and Klinger (1988) identify five predictions, for the algae, which result from the assumption of a resource trade-off between vegetative growth and reproduction: 1.) The organism must attain a certain size in order to begin reproduction; 2.) Growth is likely to stop at the onset of reproduction; 3.) Probability of death is increased after producing and releasing reproductive structures or propagules; 4.) For perennials: greater reproduction in a given year is inversely correlated with growth in that year or with survival or growth the following year; 5.) If greater numbers of gametes or spores are produced from a given quantity of resource, there will be fewer offspring or decreased growth or survival of these offspring due to less resource being allocated to each gamete or spore.

When organisms have been examined for evidence of reproductive cost, the results have been mixed (Bell 1984a,b, DeWreede & Klinger 1988, Obeso 2002). Negative correlations between present and future fecundity, or between fecundity and survival, are often weak. Such correlations can also be absent entirely, and even consistently positive correlations between present and future fecundity have been found (Bell 1984a). Bell (1984a) argues that the reproductive cost hypothesis may need restating. Present and future reproduction may be positively correlated within any given niche, reflecting reproductive adaptation to a particular set of conditions, but age specific reproduction will be negatively correlated between niches. If the organism inhabits a single niche, selection will simply favour maximal reproduction. But if offspring are dispersed to different niches there will be a negative effect on heritability of

reproductive rate. Selection in this case should be towards some intermediate rate of reproduction.

The physiological cost of algal reproductive structures.

An important premise of the hypothesis of reproductive cost is a physiological trade-off between resource allocation to vegetative growth and allocation to reproduction (Harper & Ogden 1970). Gillespie and Critchley (2001) found significantly greater biomass allocation to the holdfast and significantly less biomass allocation to reproductive structures in the brown alga *Sargassum elegans* compared to *Sargassum incisifolium* indicating that such a trade-off could be taking place. This may not apply generally to the macroalgae, however, since most produce female gametes and spores that are usually pigmented and capable of photosynthesis during development (DeWreede & Klinger 1988). In *Mazzaella splendens* carpospores and tetraspores are visible in the blade as areas even darker than the pigmented vegetative cells among which they are growing.

Hansen (1977 as *Iridaea cordata*) observed that blades of *Mazzaella splendens* in the field continued to grow after the onset of reproduction. Again results are mixed, as this did not occur in culture (Waaland 1973 as *Iridaea cordata*). The observations from the field, however, do run counter to the prediction of cessation of growth with the onset of reproduction (DeWreede & Klinger 1988) and suggest at least a diminished cost of reproduction.

Temporal restriction of reproduction in *Mazzaella splendens* suggests optimization of the life history.

In this chapter I will be examining the patterns of reproduction in *Mazzaella splendens* that were observed at the wave-sheltered site, Second Beach, in Barkley Sound, comparing seasonal changes in reproductive output at this site to patterns from other sites. I will also examine whether the local population at this site shows any evidence of three of the expected patterns that DeWreede and Klinger (1988) predict should result from the assumption of a resource trade-off between vegetative growth and reproduction: 1.) That the organism must attain a certain size in order to begin reproduction; 2.) That growth is likely to stop at the onset of reproduction; 3.) That the

probability of death is increased after producing and releasing reproductive structures or propagules.

A temporal restriction of reproduction suggests optimization of the life history through some kind of reproductive cost (Bell 1984a). Santelices (1990) has argued that a compromise between the optimum time for recruitment and the optimum time for adult growth would temporally restrict spore production and release to those seasons best suited for recruits. Such a restriction, however, could also be a result of reproductive cost. If there is no cost to producing spores, it seems reasonable that maximal reproduction at all times of year would increase the chances of producing new variants of *Mazzaella splendens* capable of recruiting in non-optimal conditions. This would increase population size and facilitate adaptation to new habitats. Even a small amount of additional recruitment, at no cost, should be beneficial, and in the absence of a cost associated with reproduction, a compromise between reproductive activity and growth or recruitment need not occur.

Temporal restriction of reproduction has been observed in intertidal red algae. In *Mastocarpus stellatus* (Burns & Mathieson 1972, as *Gigartina stellata*) and in *Gelidium sequepedale* (Santos & Duarte 1996) reproduction was restricted in time, but without a definite seasonal pattern. Norall *et al.* (1981) found that only one of four subtidal red algae studied showed seasonal restriction of reproduction while two showed reduced reproduction in shallower water.

Temporal restriction of reproduction has also been observed in *Mazzaella splendens* at Brockton Point, Vancouver Harbour (Dyck 1991 as *Iridaea splendens*). As a further introduction to the questions being examined in the population of *M. splendens* at the wave-sheltered site, Second Beach, I will present here a re-analysis of some data on reproduction in *M. splendens* at Brockton Point.

During spring and summer at Brockton Point, when population density of *Mazzaella splendens* was highest, reproduction by both haploid and diploid genets and modules was minimal (Appendix F, Figures F.1 & F.2). Density of reproductive individuals increased when population density declined in fall and was maximal during winter when population density was lowest. This is in contrast to the pattern reported for *Chondrus canaliculatus*, also in the Gigartinaceae. For *C. canaliculatus* reproductive output increased and decreased in proportion to population increase and decrease (Vega

& Meneses 2001). For both genets and modules of *M. splendens*, density of carpospore-producing female gametophytes peaked earlier in the year than density of tetraspore-producing sporophytes (Appendix F, Figures F.3 & F.4).

Changes in module density of *Mazzaella splendens* at Brockton Point were the result of appearances and disappearances of genets rather than differential module production by genets of one phase over those of the other (Dyck & DeWreede 1995). There were also no significant differences in number of reproductive modules per reproductive genet (Appendix F, Figure F.5) indicating that changes in the density of reproductive modules was the result of genets becoming or ceasing to be reproductive, rather than greater numbers of modules per genet becoming reproductive in one phase of the life cycle vs. the other.

At Brockton Point, the proportion of *Mazzaella splendens* that became reproductive rose steadily from June 1989 to February 1990, following a similar pattern for genets and modules (Appendix F, Figures F.6 & F.7). The proportion of cystocarpic (carpospore producing) gametophytes was greater than for tetrasporic (tetraspore producing) sporophytes from June to October, at which time both reached 20 – 25 % of current population density. From October onward the proportion of cystocarpic gametophytes declined while that of fertile tetrasporophytes continued to increase.

Peak densities of reproductive genets and modules, when they occurred, were only a fraction of the peak population densities present earlier in the year (Appendix F, Figures F.8 & F.9). The much higher densities available earlier in the year were not utilized for reproduction; reproductive activity was restricted to seasons when population density was in decline. This is suggestive of the sort of trade-off between conditions favourable to growth and conditions favourable to recruitment discussed by Santelices (1990).

At Brockton Point, Vancouver Harbour, the proportion of haploids that became cystocarpic was similar to the proportion of diploids that became tetrasporic from June to October 1989 (allowing for the later onset of reproduction in tetrasporophytes). From October 1989 onward, the proportion of gametophytes that became cystocarpic did not rise above 50%, while the proportion of fertile tetrasporophytes rose steadily to over 90%. This pattern was similar for genets and modules (Appendix F, Figures F.10 & F.11). The failure of cystocarpic gametophytes to rise above 50% could be the result of a

1:1 ratio of males to females. This is the most commonly observed sex ratio among algal species (DeWreede & Klinger 1988). In this case gametophytes would have maximised reproduction within the female part of the population by October and then remained at that level throughout winter. If there is a 1:1 sex ratio among gametophytes and the proportion of spermatia producing males follows the same pattern through time as the proportion of carpospore producing females, the proportion of reproductive gametophytes (male and female combined) would be similar to the proportion of reproductive tetrasporophytes.

Does reproduction incur a survival cost in *Mazzaella splendens*?

The phenology of *Mazzaella splendens* at Brockton Point, Vancouver Harbour (Dyck 1991) has shown a pattern of temporally restricted reproduction at odds with the pattern of optimum growth, suggesting some kind of reproductive cost. One potential cost may involve the presence of reproductive structures weakening blades and contributing to blade mortality. The isopod *Idotea wosnesenskii* and the coiled snail *Lacuna marmorata* both feed preferentially on fertile tissues of *Mazzaella splendens* (Gaines 1985), and while this may assist in spore release it also creates numerous patches of wounded tissue that may weaken the blade, potentially contributing to earlier loss.

Two cohorts of modules were tagged in 1989 at Brockton Point, Vancouver Harbour (Dyck 1991), one on June 18 and the other on November 13. Survival curves in both cases were Type II (Deevey 1947) indicating random loss of modules over time (Chapter 3) and the survival curves of haploids vs. diploids were not significantly different (see below). Within the June cohort, only 11 gametophyte modules developed cystocarps and only 4 tetrasporophytes developed tetrasporangia. The gametophytes that developed cystocarps were significantly longer lived than those that did not, but this was not true for tetrasporophytes (Appendix G, Table G.1).

A Kaplan-Meier analysis found no survival differences between life history phases for either reproductive (log rank test, $P = 0.601$; Wilcoxon test, $P = 0.454$) or non-reproductive modules (log rank test, $P = 0.550$; Wilcoxon test, $P = 0.366$), and no significant difference between phases in a static cohort of survival time after the onset of reproduction (log rank test, $P = 0.185$; Wilcoxon test, $P = 0.403$).

Survival curves for the June 1989 cohort are given in Appendix F (Figures F.12 – F.14). The slope of a regression of μ_x ($\ln p_x$) on current age was not significant for cystocarpic ($r^2 = 0.452$, $P = 0.328$) or non-reproductive gametophytes ($r^2 = 0.112$, $P = 0.463$), or for non-reproductive tetrasporophytes ($r^2 = 0.161$, $P = 0.503$). The same was true for cystocarpic gametophytes after the onset of reproduction ($r^2 = 0.529$, $P = 0.164$). This suggests that the survivorship curves are Type II with random loss of blades from the population over time. For reproductive diploid modules there were too few μ_x values to give a meaningful result.

The November 1989 cohort, although smaller overall, was better balanced in terms of representatives of both phases, and reproductive vs. non-reproductive modules. In this cohort neither fertile tetrasporophytes nor cystocarpic gametophytes were significantly longer lived than their non-reproductive counterparts. Survival time after the onset of reproduction was not significantly lower, in either life history phase, than survival time in blades which never developed reproductive structures (Appendix G, Table G.1).

A Kaplan-Meier analysis of the November 1989 cohort found no survival differences between life history phases for either reproductive (log rank test, $P = 0.614$; Wilcoxon test, $P = 0.688$) or non-reproductive modules (log rank test, $P = 0.734$; Wilcoxon test, $P = 0.774$), and no significant difference between phases in a static cohort of survival time after the onset of reproduction (log rank test, $P = 0.277$; Wilcoxon test, $P = 0.222$).

Survival curves for the November 1989 cohort are given in Appendix F (Figures F.15 – F.17). The slope of a regression of μ_x on current age was not significantly different from flat for cystocarpic ($r^2 = 0.937$, $P = 0.162$) or non-reproductive gametophytes ($r^2 = 0.544$, $P = 0.472$), for reproductive tetrasporophytes ($r^2 = 0.201$, $P = 0.704$), or for cystocarpic gametophytes ($r^2 = 0.722$, $P = 0.353$) and fertile tetrasporophytes ($r^2 = 0.824$, $P = 0.276$) after the onset of reproduction. This suggests that these survivorship curves also are Type II with random loss of blades over time. The survival curve for non-reproductive tetrasporophytes ($r^2 = 0.999$, $P = 0.007$) showed significant Type I curvature indicating a tendency for greater mortality with advancing age.

Reproduction in *Mazzaella splendens* at Brockton Point was restricted mainly to fall and winter so only the longer lived modules in the June cohort would be likely to

become reproductive. With so few blades surviving to become reproductive, the June cohort provides little concrete information on the survival behaviour of reproductive vs. non-reproductive blades. The June cohort does show, however, that module loss during summer was 45 to 50 % per month. During this period, which was most conducive to growth, large numbers of blades of both phases were continuously lost without forming any reproductive structures.

Comparison of survival times between reproductive and non-reproductive individuals suggests that reproductive activity does not significantly decrease survival. Moreover, with higher rates of module loss in summer (at maximum population density when reproduction is negligible) the greatest mortality, in the population as a whole, is happening to non-reproductive blades. Not only is there no apparent survival cost to reproduction, but large numbers of blades which could contribute to reproductive effort, apparently at no additional cost, die without doing so.

It is possible that a pattern of seasonally restricted reproduction could arise for reasons other than a trade-off involving some cost of reproduction. The presence of a developmental constraint is one such explanation. If the intertidal *M. splendens* population at Brockton Point was recruited primarily from spores dispersed by *M. splendens* in a different environmental setting (e.g. a nearby subtidal population), reproduction in the subtidal habitat might be continuous (or nearly so) reflecting an absence of reproductive cost. But initiation of reproductive structures (or their subsequent development) could require environmental signals or nutritive factors that, while continuously available in the subtidal, are seasonally restricted in the intertidal. The result would be a temporally restricted pattern of reproduction, in the intertidal habitat, suggestive of the kind of compromise between reproduction and recruitment proposed by Santelices (1990) or of optimisation of reproduction within the life history due to its cost (Bell 1984a).

Objectives in examining the phenology of *Mazzaella splendens* at Second Beach, Barkley Sound.

Seasonal restriction of reproduction in *Mazzaella splendens* has been observed in areas other than Vancouver Harbour. Adams (1979 as *Iridaea cordata*) found a similar phenological pattern at three sites in the Strait of Georgia. Cystocarpic blades were first

present in April, increasing in abundance through July, and then declining to a minimum in December. Density of tetrasporic blades rose more slowly, peaking in September and then declining to a December minimum density higher than that for cystocarpic modules. The order of events and the separate peak densities of cystocarpic and tetrasporic blades were similar in Vancouver Harbour (Dyck 1991 as *Iridaea splendens*) and the Strait of Georgia, but the sequence in the Strait of Georgia was initiated approximately two months earlier than in Vancouver Harbour.

It would be a valuable addition to understanding common demographic patterns over the whole distribution of *Mazzaella splendens* (Chapter 2) to examine the degree to which phenology changes with geographic location. The studies already done in Vancouver Harbour (Dyck 1991 as *Iridaea splendens*) and the Strait of Georgia (Adams 1979 as *Iridaea cordata*) suggest that the temporal segregation of haploid and diploid peak reproductive output may be a common phenological feature, but that the onset of this reproductive sequence of events may vary with habitat.

The population of *Mazzaella splendens* in Vancouver Harbour showed no evidence of significantly reduced survival due to reproduction. It is important to replicate this result in a different habitat to further determine its generality.

It would also be interesting to examine, in a preliminary way, several of the predictions of DeWreede and Klinger (1988) simultaneously in one population. By following survival, size changes and reproduction on a monthly basis it is possible to address three specific predictions: 1.) That probability of death increases after the onset of reproduction, 2.) That growth slows or stops after the onset of reproduction and 3.) That modules must attain a certain size before reproduction will begin. These are different ways in which reproductive cost can manifest itself. A blade of *Mazzaella splendens* that first contributes resources to growth and strength, achieving a large enough size to ensure optimal reproductive output (a function of surface area over which sporangia can form), and then ceases further growth to contribute resources only to reproduction and maintenance of existing structure, may exhibit no cost in terms of survival relative to non-reproductive individuals. Here the differences in resource allocation between reproductive and non-reproductive individuals would appear only in size at onset of reproduction and in subsequent growth.

Methods and Materials

Site selection, quadrat placement and census dates were as described in Chapter 2.

In each of the permanent quadrats at the wave-sheltered site the number of genets (basal crusts) with visible modules (blades) were enumerated. Each module was tagged around the stipe with a colour coded plastic electrical tie strap. A 0.5 cm diameter disk of tissue was removed from each blade with a single hole paper punch. This tissue sample was used in carrageenan analysis to determine life history phase in the absence of reproductive structures (Garbary & DeWreede 1988, Shaughnessy & DeWreede 1991). The outline of each blade was traced on acetate. Onset of reproduction was noted for each blade. At each subsequent census this procedure was applied to all new blades. The outline of each surviving blade was traced at each census. This produced a record over time of changes in genet and module density in haploids vs. diploids, and for each genet the timing of production, survival, reproduction and changes in size and shape of each of its modules.

At the wave-exposed site, reproductive condition was noted in a single cohort of modules tagged in June 2000. Members of this cohort were selected by tagging the largest module in each genet in the permanent quadrats at this site. An outline of each blade was traced on acetate at each census (see chapter 3 for dates of subsequent censuses). One hundred and seventy-eight modules were tagged. Forty-eight of these were haploid and 130 diploid.

For the permanent quadrats in the wave-sheltered site, densities of cystocarpic vs. tetrasporic genets and modules were compared by month for the period from November 1997 to January 2001. Concerns about the statistical independence of samples from one month to the next prevent attributing statistical significance to apparent trends or tendencies over time. I will, however, discuss what I believe these trends to be using a cubic spline, a nonparametric nonlinear regression that emphasises local over global fit (Hastie & Tibshirani 1990, Silverman 1986, Chapter 2). All cubic spline calculations were done using glmsWIN 1.0 available at www.zoology.ubc.ca/~schluter/splines.html.

It is possible that blades of *M. splendens* may need time for certain developmental processes to take place, or resources to be accumulated, before reproduction can begin. If this is true then, on average, longer lived modules should be the ones that become reproductive. Total survival time of reproductive modules (non-reproductive +

reproductive time) at the wave sheltered site was compared to survival time of non-reproductive modules to determine if reproductive modules were longer lived.

Survival for gametophytes and tetrasporophytes of *Mazzaella splendens* at both the wave-sheltered and wave-exposed sites, Second Beach, was Type II (Chapter 3) indicating that the probability of being removed was not age dependant. At the wave-sheltered site, survival was not negatively affected by increasing size (Chapter 4). Subsequent survival after the onset of reproduction, therefore, should not differ from survival in non-reproductive modules simply because of increased age or size (if present) but because of effects arising from attaining reproductive maturity. Survival after the onset of reproduction was compared to survival in non-reproductive modules. Within the modules that became reproductive, time spent non-reproductive was compared to time spent reproductive.

Survival time was also compared between gametophytes and tetrasporophytes for non-reproductive modules, for reproductive modules (total survival time), and for modules after the onset of reproduction.

Survival curves in a static cohort of all non-reproductive modules observed at the wave-sheltered site, and in a static cohort of survival after the onset of reproduction, were compared, between phases, with a Kaplan Meier analysis (Fischer & van Belle, 1993) using JMP IN 4. Assignment of survival curves to Type I, II or III (Deevey 1947) was by a regression of μ_x (the absolute value of the natural logarithm of the probability of survival from one census to the next) on current age (as estimated from the census of first appearance). For Type I survival, a graph of μ_x over time tends to rise abruptly after a flat period. For Type II survival the graph is flat throughout, and for Type III survival the graph tends to fall sharply and then flatten. In each case the regression of μ_x on age was compared to a flat line through the mean value of μ_x to determine if the deviation from a flat line was significant. This analysis was performed using JMP IN 4.

To determine if growth slowed after the onset of reproduction, the relative growth rates before becoming reproductive were compared to those after the onset of reproduction in the reproductive modules.

The prediction that individuals must attain a certain size before reproduction will begin (DeWreede & Klinger 1988) was tested by examining whether a minimum size existed below which reproduction was not initiated. Since a very small reproductive

module could potentially be the result of tissue loss in a previously larger blade, the shape of each small reproductive module was examined for evidence of having had previous tissue loss.

Size may increase significantly with age. A regression of size on age was done, for gametophytes and for tetrasporophytes, to determine if size increases significantly with age for both phases. If so, a mean time to onset of reproduction that is significantly longer than the mean survival time for non-reproductive modules would suggest that, on average, modules attain a certain size before reproducing. To test this, time to onset of reproduction was compared to survival time in non-reproductive modules for each life history phase. Also, if size increases significantly with age, and longer lived modules are more likely to become reproductive, the maximum size achieved by reproductive modules is expected to be greater than for non-reproductive modules. Maximum size reached for reproductive modules was compared to maximum size for non-reproductive modules.

If the formation of reproductive structures weakens blades of *Mazzaella splendens*, more tissue loss would be expected from reproductive than from non-reproductive modules. Changes in surface area over time were used to estimate tissue gain and loss. Tissue loss before mortality was compared between reproductive and non-reproductive blades for each life history phase, and between phases for non-reproductive modules and for modules after the onset of reproduction. Within each category (non-reproductive gametophytes, reproductive gametophytes, non-reproductive tetrasporophytes, reproductive tetrasporophytes) tissue gain was compared to tissue loss.

For the wave-exposed site, the surface area of reproductive blades tagged in June 2000 was compared to the surface area of non-reproductive blades tagged at the same time. In July 2000, the surface area of blades that had become reproductive since the last census was compared to the surface area of the remaining non-reproductive modules. This was done again in August 2000, after which the number of modules in the cohort declined below a useful sample size.

To determine if growth slowed after the onset of reproduction in the wave-exposed site, the relative growth rates before becoming reproductive were compared to those after the onset of reproduction in the reproductive modules.

The same comparisons of tissue loss preceding mortality were made as for the wave-sheltered site.

The statistical significance of differences in densities, module sizes, survival times and tissue gain and loss were determined with the Mann-Whitney U test ($\alpha = 0.05$). Mann-Whitney U tests were performed using SPSS 6.0. Regressions were done using JMP IN 4. In cases where the analyses may be interpreted as constituting multiple testing, the alpha levels denoting statistical significance have not been adjusted. There is currently considerable debate surrounding the applicability and usefulness of a variety of corrections for perceived multiple comparisons (Perneger 1998, 1999, Aickin 1999, Bender & Lange 1999, Sterne & Smith 2001). Sterne & Smith (2001) argue that, in light of this debate, the best approach in publication is to include a description of each comparison made within a dataset giving the sample size, mean, a measure of variability and the p value itself. The reader then has more information with which to assess the authors arguments. This is the approach I have taken.

Results

The wave-sheltered habitat.

The density of reproductive individuals.

Density of reproductive individuals at the wave-sheltered site, Second Beach, Barkley Sound, was low, by comparison with Vancouver Harbour, throughout the three years of study, although density of non-reproductive individuals was higher than at Brockton Point. Density of tetrasporic genets and modules was highest in November 1997 at the beginning of the study (Figures 5.1 & 5.2). By January 1998 reproduction had dropped to approximately a quarter of the November 1997 level and continued thereafter to fluctuate within a smaller range.

Density of tetrasporic genets and modules was significantly greater than for cystocarpic genets and modules in November and December 1997, and in October 1999 (Figures 5.1 & 5.2). Variation in the data was such that cubic splines could be calculated only for density of reproductive genets of both phases and density of cystocarpic genets

and modules. There were no readily apparent seasonal trends in reproduction (Appendix F, Figures F.18 - F.20).

The proportion reproductive.

The proportion of available tetrasporophytes that became tetrasporic usually exceeded the proportion of available gametophytes that became cystocarpic (Figures 5.3 & 5.4) during the periods of maximum reproduction. For all modules observed over the course of the study (assuming a 1:1 sex ratio among gametophytes) the proportion of tetrasporophytes that became fertile significantly exceeded the proportion of female gametophytes that became cystocarpic ($\chi^2 = 44.8$, d.f. = 1, $P < 0.001$).

Survival after the onset of reproduction.

At the wave-sheltered site, Second Beach, the total survival time of those modules that became reproductive was significantly longer than that of non-reproductive modules for both phases (Table 5.1).

Mean survival time was not significantly different between gametophytes and tetrasporophytes for non-reproductive modules or for modules after the onset of reproduction. Within each life history phase, survival time after the onset of reproduction was not significantly different from survival time for non-reproductive blades (Table 5.2).

Among those modules that were non-reproductive when first tagged and subsequently became reproductive, the amount of time spent non-reproductive vs. the amount of time spent reproductive was not significantly different for gametophytes or tetrasporophytes (Table 5.3).

A Kaplan Meier analysis found no significant difference (log rank test, $P = 0.900$; Wilcoxon test, $P = 0.663$) between gametophyte and tetrasporophyte survival curves in a static cohort of all non-reproductive modules (Figure 5.5). A regression of μ_x on current age showed a significant positive slope relative to a line through the μ_x mean ($r^2 = 0.963$, $P = 0.003$) for gametophytes but not for tetrasporophytes ($r^2 = 0.013$, $P = 0.855$). This suggests that the gametophyte curve could be characterized as Type I while the tetrasporophyte curve is Type II.

A Kaplan Meier analysis also found no significant difference (log rank test, $P = 0.649$; Wilcoxon test, $P = 0.573$) between gametophyte and tetrasporophyte survival curves in a static cohort of survival time after the onset of reproduction (Figure 5.6). A regression of μ_x on current age did not show a significant positive slope relative to a line through the μ_x mean for either gametophytes ($r^2 = 0.966$, $P = 0.119$) or tetrasporophytes ($r^2 = 0.016$, $P = 0.918$), suggesting that both curves could be characterized as Type II.

Growth after the onset of reproduction.

There was no significant difference in relative growth rate between the period before the onset of reproduction and the period after onset of reproduction for either haploid or diploid modules (Table 5.4).

Surface area and age.

At the wave-sheltered site, Second Beach, the onset of reproduction in modules of *Mazzaella splendens* was first observed at sizes ranging from 6 cm² to 750 cm² for tetrasporophytes and 6 cm² to 620 cm² for gametophytes. Among gametophytes, 27 out of 54 blades were small (6 – 50 cm²) at the onset of reproduction. Of these 54, 11 showed no evidence of tissue loss. Among tetrasporophytes, 71 out of 105 blades were small (6 – 50 cm²) at the onset of reproduction. Of these 71, 31 showed no evidence of tissue loss.

Size increased slightly, but significantly, with age for both gametophytes (Figure 5.7; $N = 3165$, $r^2 = 0.0943$, $P < 0.001$) and tetrasporophytes (Figure 5.8; $N = 1320$, $r^2 = 0.0706$, $P < 0.001$). The equation for the regression line for gametophytes was: $\text{Area} = 39.16 + 0.91 \text{ Age}$. For tetrasporophytes: $\text{Area} = 29.43 + 0.51 \text{ Age}$. Mean time to onset of reproduction was significantly longer than mean survival time of non-reproductive modules for gametophytes but not for tetrasporophytes (Table 5.5).

The maximum size of non-reproductive haploid modules was significantly greater than that of non-reproductive diploid modules. This was also true for reproductive blades. Among haploids, the maximum size of reproductive modules was significantly larger than that of non-reproductive ones, but among diploids there was no such difference (Table 5.6).

Tissue loss after the onset of reproduction.

Tissue loss was significantly higher in non-reproductive gametophyte modules than in non-reproductive tetrasporophytes, but not between life history phases after the onset of reproduction. For both gametophytes and tetrasporophytes, tissue loss after the onset of reproduction was significantly greater than in their respective non-reproductive counterparts. Among non-reproductive haploids and among non-reproductive diploids tissue gain was significantly greater than tissue loss over the lifespan of the modules. Among diploids, after the onset of reproduction, tissue loss was significantly greater than tissue gain. This was not true for haploids (Table 5.7).

The wave-exposed habitat.

Survival after the onset of reproduction.

At the wave-exposed site, Second Beach, the total survival time of modules that became reproductive was significantly longer than the survival time of modules lost to mortality before becoming reproductive (Table 5.8).

Mean survival time was not significantly different between gametophytes and tetrasporophytes for non-reproductive modules or for modules after the onset of reproduction. For haploid modules, survival time after the onset of reproduction was not significantly different from survival time for modules lost to mortality before becoming reproductive. For diploid modules, survival after the onset of reproduction was significantly longer than survival in non-reproductive modules (Table 5.9).

Among blades that were not reproductive when initially tagged, but subsequently became reproductive, there was no significant difference in time spent reproductive vs. time spent non-reproductive within either of the alternate life history phases (Table 5.10).

A Kaplan Meier analysis found no significant difference (log rank test, $P = 0.551$; Wilcoxon test, $P = 0.629$) between gametophyte and tetrasporophyte survival curves in a cohort of all non-reproductive modules (Figure 5.9). A regression of μ_x on current age did not show a significant positive slope relative to a line through the μ_x mean for gametophytes ($r^2 = 0.975$, $P = 0.101$) or for tetrasporophytes ($r^2 = 0.058$, $P = 0.845$). This suggests that both curves could be characterized as Type II.

A Kaplan Meier analysis found no significant difference (log rank test, $P = 0.265$; Wilcoxon test, $P = 0.343$) between gametophyte and tetrasporophyte survival curves in a static cohort of survival time after the onset of reproduction (Figure 5.10). A regression of μ_x on current age did not show a significant positive slope relative to a line through the μ_x mean for either gametophytes ($r^2 = 0.046$, $P = 0.862$) or tetrasporophytes ($r^2 = 0.004$, $P = 0.923$), suggesting that both curves could be characterized as Type II.

Growth after the onset of reproduction.

There was no significant difference in relative growth rate between the period before the onset of reproduction and the period after onset of reproduction for gametophytes. For tetrasporophytes relative growth rate after the onset of reproduction was significantly lower than before reproduction (Table 5.11).

Size of reproductive and non-reproductive modules.

Comparisons of size for reproductive and non-reproductive modules in the cohort tagged at the wave-exposed site, Second Beach, in June 2000, are given in Table 5.12.

Non-reproductive gametophyte modules were significantly larger than non-reproductive tetrasporophytes in June, July and August 2000. For reproductive blades there were no significant differences in size, between life history phases, in June and August. This comparison could not be made in July as no previously non-reproductive gametophyte modules became reproductive this month.

Reproductive tetrasporophytes were significantly larger than their non-reproductive counterparts in June 2000. This was also true in the following months, when comparing reproductive diploid modules which had been non-reproductive the previous month with the remaining non-reproductive diploids. Reproductive gametophytes were not significantly different in size than non-reproductive gametophytes at any time.

Tissue loss after the onset of reproduction.

Tissue loss was significantly higher in non-reproductive gametophytes than in non-reproductive tetrasporophytes but not between phases after the onset of reproduction. There was no significant difference in tissue loss between reproductive

and non-reproductive gametophyte modules. Among tetrasporophytes, however, tissue loss was significantly higher in blades after the onset of reproduction than in non-reproductive blades. Tissue loss significantly exceeded tissue gain after the onset of reproduction for both gametophytes and tetrasporophytes. There was no significant difference between loss and gain among non-reproductive haploids, but among non-reproductive diploid modules tissue gain significantly exceeded tissue loss (Table 5.13).

Discussion

Patterns of reproductive activity between Vancouver Harbour and Barkley Sound.

The levels of reproductive activity at Second Beach, Barkley Sound, were lower than those in Vancouver Harbour (Dyck 1991 as *Iridaea splendens*) and seemed very low given the population density at Second Beach. In November – December 1997, at the beginning of the study, density of reproductive individuals of both phases at the wave-sheltered site, Second Beach, was similar to that observed in mid-winter at Brockton Point (Dyck 1991 as *Iridaea splendens*) and the Strait of Georgia (Adams 1979 as *Iridaea cordata*). But following this there was only one significant difference between cystocarpic and tetrasporic individuals at the wave-sheltered site, Second Beach, (October 1999) which favoured tetrasporic diploids. There was no consistent seasonal trend to reproduction at this site, and temporal segregation of reproduction, like that observed at Brockton Point (Dyck 1991 as *Iridaea splendens*), was not clearly evident.

Onset of reproduction was earlier in the Strait of Georgia (Adams 1979 as *Iridaea cordata*) than in Vancouver Harbour (Dyck 1991 as *Iridaea splendens*). However, a potential trend toward earlier onset of reproduction as geographic location changed from the very sheltered environment of Vancouver Harbour to the less sheltered outer coast of Vancouver Island was not clearly supported by observations in the wave-sheltered site at Second Beach.

Some modules at the wave-sheltered site, Second Beach, became reproductive as early as May of each year (a similar result to the Strait of Georgia) while the first reproductive blades at Brockton Point appeared in June. However, at the wave-sheltered

site, Second Beach, reproduction in spring and early summer was erratic in the first two years. A few reproductive individuals appeared in May and then were lost. Reproductive individuals were absent in June, with a few appearing again in July or August.

In the cohort at the wave-exposed site at Second Beach, however, reproduction was already well under way in June. Conditions between these two habitats affect both population density and population structure (Chapter 2), and now appear to affect onset and extent of reproduction as well.

A similarity between the wave-sheltered site at Second Beach and Brockton Point emerged when the proportion of reproductive individuals was examined. In both locations, tetrasporophytes committed a significantly larger proportion of their available density to tetraspore production than female gametophytes did to producing carposporangia. This suggests that, in spite of the differences in reproductive behaviour, some of the same factors may be at work structuring reproductive activity in both locations, and that the examination of reproductive cost at Second Beach, Barkley Sound may have relevance to other areas.

Nutrient levels and the timing of reproduction.

In Chapter 3 I speculated about the possible role of ambient dissolved nitrate in changing population densities of *Mazzaella splendens* in both the wave-sheltered and wave-exposed sites at Second Beach, Barkley Sound. Nitrate levels have been implicated in the onset and extent of reproduction in algae (Santelices 1990), and I will speculate here on the possibility that ambient nitrate concentrations may also explain aspects of the reproductive behaviour of *M. splendens*.

Maximum reproductive effort at the wave-sheltered site, Second Beach, often coincided with seasons when dissolved nitrate would have been at higher concentrations given the seasonal pattern of dissolved nitrate concentration discussed in Chapter 3. Increased water motion at the wave-exposed site, replenishing nutrients in the boundary layer next to the algal thallus, is a potential difference between the wave-sheltered and wave-exposed habitats which could contribute to the increased population density in wave-exposed areas (Chapter 3). This could also potentially contribute to proportionately greater reproductive activity at the exposed vs. the sheltered sites.

Reproduction and survival.

Gametophytes and tetrasporophytes of *Mazzaella splendens* at the wave-sheltered site, Second Beach, showed no evidence of decreased survival after the onset of reproduction (Tables 5.2 & 5.3). This result is similar to that previously obtained for Brockton Point, Vancouver Harbour. This similarity between widely separated wave-sheltered locations, together with the absence of a negative effect of reproduction on survival in the wave-exposed site at Second Beach (Table 5.9) suggests that it is a common feature of *M. splendens* populations.

A positive relationship between reproduction and survival for tetrasporophytes in the wave-exposed habitat.

At the wave-exposed site, Second Beach, the onset of reproduction did not negatively affect survival in gametophytes of *Mazzaella splendens*. For tetrasporophytes, however, mean survival time after the onset of reproduction was significantly longer than mean survival time in non-reproductive blades. In this case the onset of reproduction was followed by enhanced survival.

A potential reason for greater survival time after the onset of reproduction appears in the patterns of tissue loss. For non-reproductive modules in both wave-sheltered and wave-exposed habitats, tissue loss by gametophytes was significantly higher than by tetrasporophytes, suggesting that diploid blades are generally stronger than haploid blades (Chapter 4). After the onset of reproduction, however, this difference between phases was not found in either habitat (Tables 5.7 & 5.13). At the wave-sheltered site, in gametophytes and in tetrasporophytes, tissue loss was greater for reproductive blades than for their non-reproductive counterparts. This suggests that, at the wave-sheltered site, the onset of reproduction weakens blades of both life history phases. At the wave-exposed site this happened only to tetrasporophytes.

Tetrasporophyte modules at the wave-exposed site may have survived significantly longer after the onset of reproduction (than non-reproductive modules) because reproductive tetrasporophytes more frequently lost part of their blades rather than losing the whole blade to mortality. Non-reproductive gametophytes and tetrasporophytes may have lost the entire blade more frequently than reproductive tetrasporophytes.

The picture for tissue loss in reproductive gametophytes at the wave-exposed site is less clear. The absence of a significant difference in tissue loss between gametophytes and tetrasporophytes after the onset of reproduction at this site (Table 5.13) suggests that a similar mechanism should be operating in both life history phases. The absence of a significant difference in tissue loss between non-reproductive and reproductive gametophytes suggests the opposite. There were relatively few reproductive gametophytes at the wave-exposed site and variances were large, reducing the power of the analysis to resolve differences. Further work is needed to determine what is happening with respect to tissue loss and survival, after the onset of reproduction, in the haploid phase.

The wave-exposed site, with its greater numbers of fertile tetrasporophytes, was approximately 30 m from the wave-sheltered site, where reproduction was minimal but gametophytes predominated. It is possible that a source-sink relationship may exist between these sites, with reproductive diploids at the wave-exposed site providing the source for much of the haploid recruitment at the wave-sheltered site.

The viability of free floating algal spores is reported to be of short duration, typically a few hours to a few days (Santelices 1990). Even so, the wave-sheltered site should be within the dispersal area of tetraspores from the wave-exposed site. Moreover, it is common for detached fragments containing functional reproductive structures to remain viable while drifting over much longer times and distances, and this seems to constitute a natural method of spore dispersal (see Santelices 1990 for review). The discovery that fertile tetrasporophytes at the wave-exposed site lose substantial amounts of tissue supports the possibility of source-sink relationship between these sites.

Growth after the onset of reproduction.

Growth after the onset of reproduction did not decline significantly for either gametophytes or tetrasporophytes of *Mazzaella splendens* at the wave-sheltered site (Table 5.4). At the wave-exposed site growth after the onset of reproduction declined significantly for tetrasporophytes but not for gametophytes (Table 5.11). The sample size for gametophytes at the wave-exposed site was very small and this particular result should be treated with caution. There is some evidence here that growth after the onset of reproduction in *Mazzaella splendens* may behave differently between the wave-

sheltered and wave exposed sites, but further work is necessary to establish if this is the case.

Size, age and reproduction.

The range of sizes at which the onset of reproduction occurred, and the range of times to the onset of reproduction for both gametophytes and tetrasporophytes of *Mazzaella splendens*, indicate that reproduction can take place at any size above 6 cm² and less than 28 days after the blade is initiated. Within this variation there were results suggesting that, on average, time was required (possibly for development or resource accumulation) before the onset of reproduction was initiated, but there were also contradictory results that weakened this argument. I will discuss the evidence for and against this trend, beginning with the wave-sheltered site.

It was significantly longer lived blades, both gametophytes and tetrasporophytes, that became reproductive (Table 5.1), suggesting that a certain period of time was required, on average, for both phases before reproduction was initiated.

Mean time to onset of reproduction was significantly longer than the mean survival time of non-reproductive modules only for gametophytes (Table 5.5), while mean survival time of non-reproductive modules did not differ significantly between life history phases. Reproductive gametophytes also had a significantly longer total survival time than reproductive tetrasporophytes (Table 5.1). This suggested that gametophytes had a greater time requirement, before reproduction was initiated, than tetrasporophytes.

Size increased significantly with age for both gametophytes and tetrasporophytes (Figures 5.7 & 5.8). The result that maximum size of reproductive blades was significantly larger than non-reproductive blades for gametophytes but not for tetrasporophytes, and that reproductive gametophytes were significantly larger than reproductive tetrasporophytes (Table 5.6), therefore supports the hypothesis that gametophytes, on average, require more time before onset of reproduction than tetrasporophytes.

It is possible that there is a physiological reason for a longer time to onset of reproduction in gametophytes than in tetrasporophytes. Although both carpospores and tetraspores are photosynthetic and this may provide their own energy requirements, the carpogonium, trichogyne and carpogonial branch develop from non-photosynthetic

medullary tissue (Van Den Hoek *et al.* 1995) and this may result in an energetic cost for female gametophytes that would not be present in tetrasporophytes.

Certain results, however, contradicted the above scenario. Maximum size in non-reproductive gametophytes was also significantly larger than in non-reproductive tetrasporophytes (Table 5.6) even though mean survival time was not significantly different between phases (Table 5.1). This suggests that differences in growth rates between phases may be involved as well. And finally, a direct comparison of time to onset of reproduction between gametophytes and tetrasporophytes showed no significant difference (Table 5.5). The variance around both means in this last comparison was high, and it could be argued that a larger sample size would reveal a significant difference, but this would be true only if the difference between means in the sample is an accurate representation of the difference between means in the population. Only resampling will resolve this question.

At the wave-exposed site non-reproductive gametophytes were, as at the wave-sheltered site, significantly larger than non-reproductive tetrasporophytes. This suggests that gametophytes may grow more rapidly than tetrasporophytes in both habitats. At the wave-exposed site, however, there was no significant difference in maximum size between reproductive gametophytes and tetrasporophytes (Table 5.12). The present data do not provide a clear reason for this difference between sites. Tissue loss by reproductive tetrasporophytes was not significantly greater than by reproductive female gametophytes (Table 5.13). Relative growth rate slowed significantly after the onset of reproduction for tetrasporophytes but not gametophytes at the wave-exposed site (Table 5.11). This has potential to explain the similarity in maximum size between reproductive gametophytes and tetrasporophytes at the wave-exposed site since such slowing did not occur at the wave-sheltered site. But once again the small sample sizes and large variances do not allow this mechanism to be proposed with confidence.

The above results, on time to onset of reproduction and size at reproduction, should be considered a preliminary examination of whether gametophytes require more developmental time than tetrasporophytes before reproduction can begin. Contradictions prevent a clear answer, but subsequent work in a location where a greater proportion of the population becomes reproductive, may uncover a consistent difference in onset of reproduction between the life history phases of *Mazzaella splendens*. There is reason to

suspect that female gametophytes face an energetic cost (the production of carpogonial branches) that tetrasporophytes do not face, and that time to onset of reproduction may be longer for gametophytes than for tetrasporophytes. As a result, in a population with Type II survival for blades of both phases before and after the onset of reproduction, reproductive gametophytes would be longer lived than reproductive tetrasporophytes. In a population where size increases with age, this difference in time to onset of reproduction would account for cystocarpic blades being significantly larger than tetrasporic ones.

Conclusions

A temporal restriction of reproduction in *Mazzaella splendens*, like that seen at Brockton Point, Vancouver Harbour (Dyck 1991, as *Iridaea splendens*), is not a pattern common to all populations of *Mazzaella splendens* in wave-sheltered habitats. Proportion reproductive, however, tends generally to increase in winter and is significantly greater for tetrasporophytes than for gametophytes in all wave-sheltered areas examined to date.

Reproduction did not significantly affect survival of either life history phase in wave-sheltered or wave-exposed habitats. Growth did not slow after the onset of reproduction for either life history phase in the wave-sheltered site, but did for tetrasporophytes in the wave exposed site. The onset of reproduction in modules of *Mazzaella splendens* can begin at any size above 6 cm² and at ages less than 28 days for both life history phases. Gametophytes in the wave-sheltered site require, on average, a period of time significantly longer than the mean survival time of non-reproductive gametophytes before onset of reproduction.

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Figures to accompany Chapter 5.

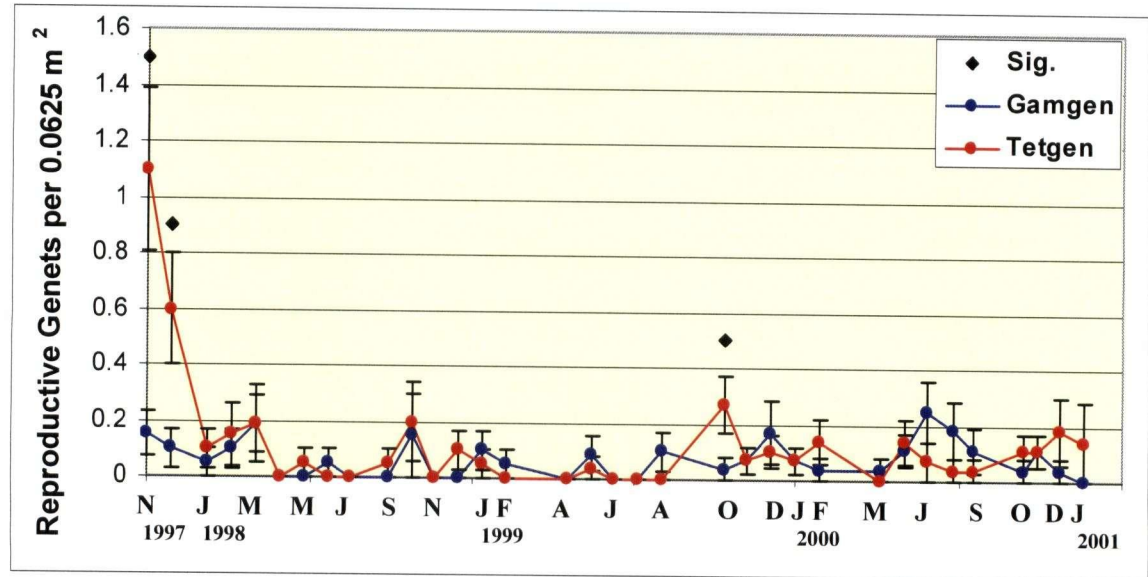


Figure 5.1: Seasonal changes in reproductive genet density for the alternate phases of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). Means (± 1 S.E.). Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets. Sig. = Statistical significance: Mann-Whitney U Test, $P \leq 0.05$.

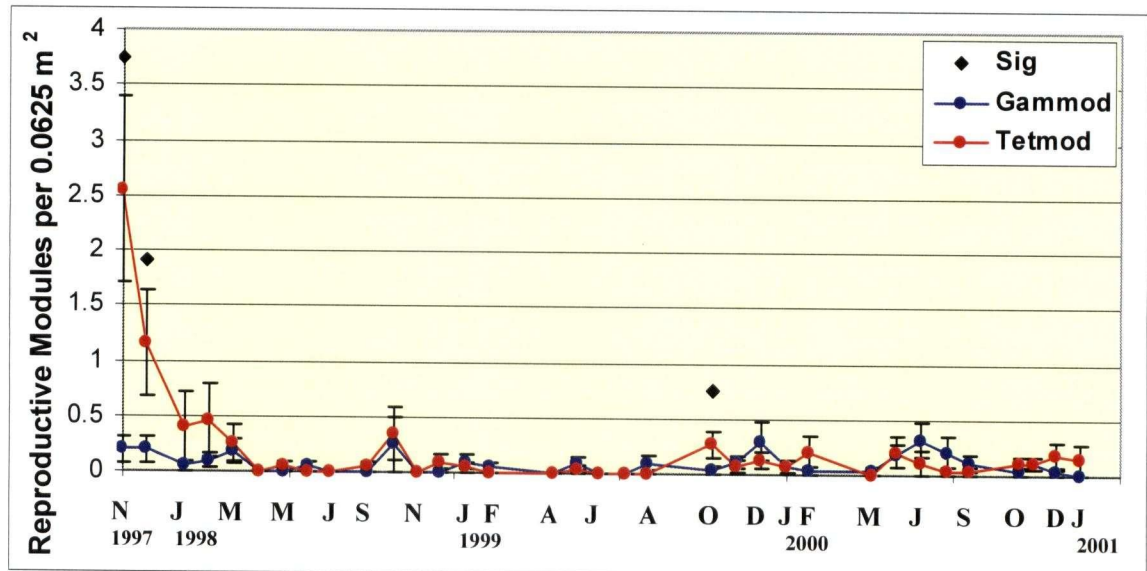


Figure 5.2: Seasonal changes in reproductive module density for the alternate phases of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). Means (± 1 S.E.). Gammod = gametophyte modules. Tetmod = tetrasporophyte modules. Sig. = Statistical significance: Mann-Whitney U Test, $P \leq 0.05$.

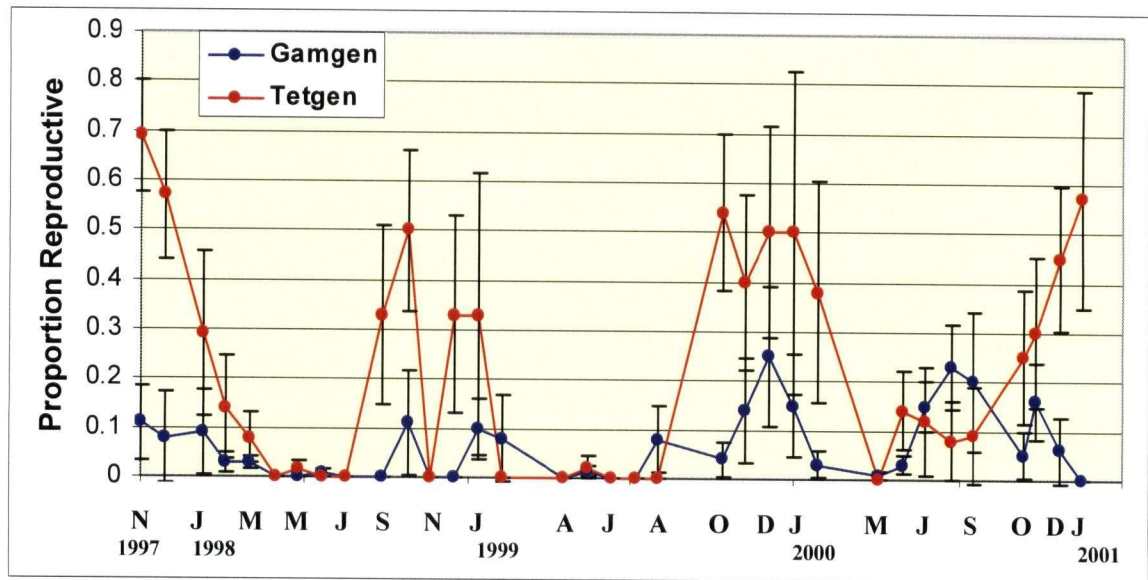


Figure 5.3: Seasonal changes in reproductive genets as a proportion (± 1 S E) of within phase population density of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets.

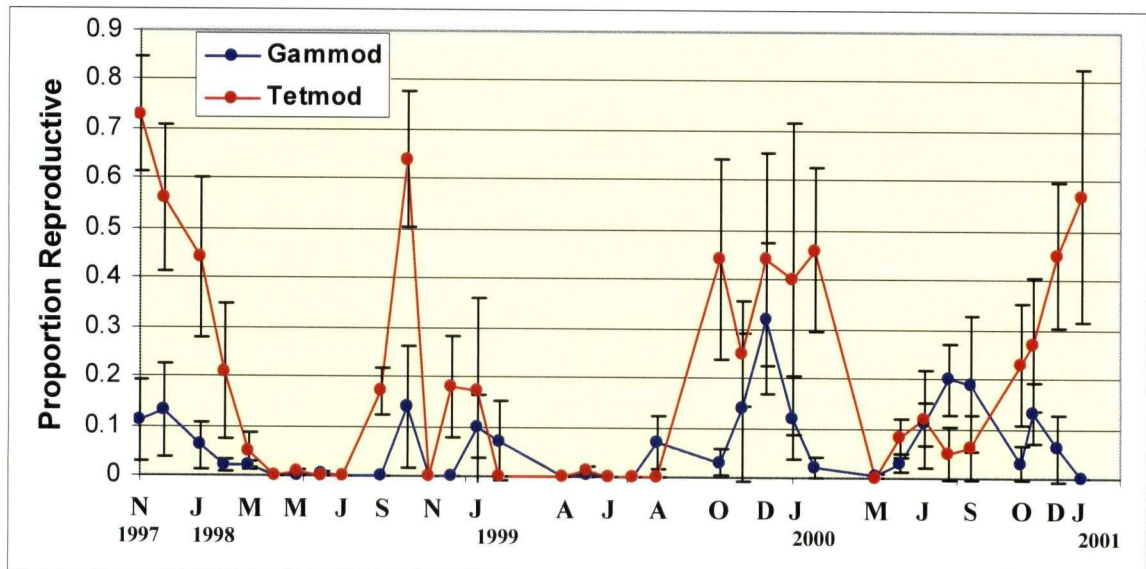


Figure 5.4: Seasonal changes in reproductive modules as a proportion (± 1 S E) of within phase population density of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

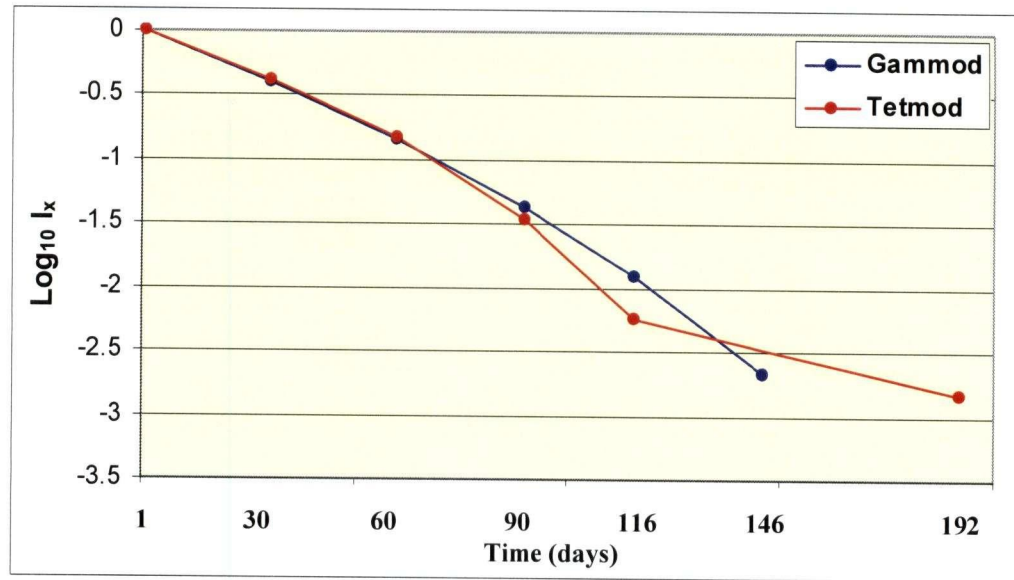


Figure 5.5: Survival ($\log_{10} l_x$) in a static cohort of 2588 non-reproductive modules (690 diploid, 1898 haploid) of *Mazzaella splendens* tagged at the sheltered site, Second Beach, Barkley Sound from November 1997 to December 2000. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

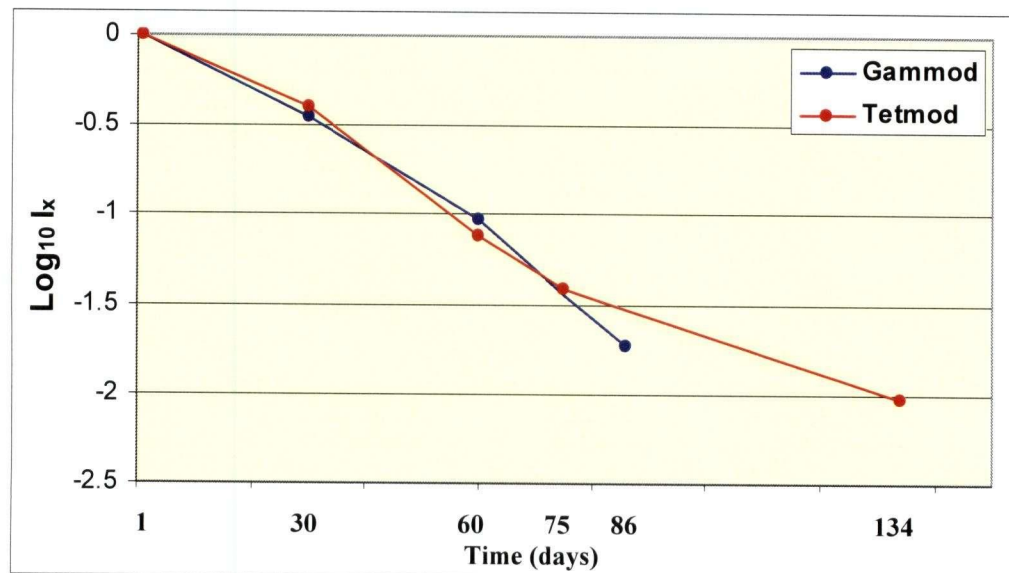


Figure 5.6: Survival ($\log_{10} l_x$) following onset of reproduction in a static cohort of 159 reproductive modules (105 diploid, 54 haploid) of *Mazzaella splendens* tagged at the sheltered site Second Beach, Barkley Sound from November 1997 to December 2000. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

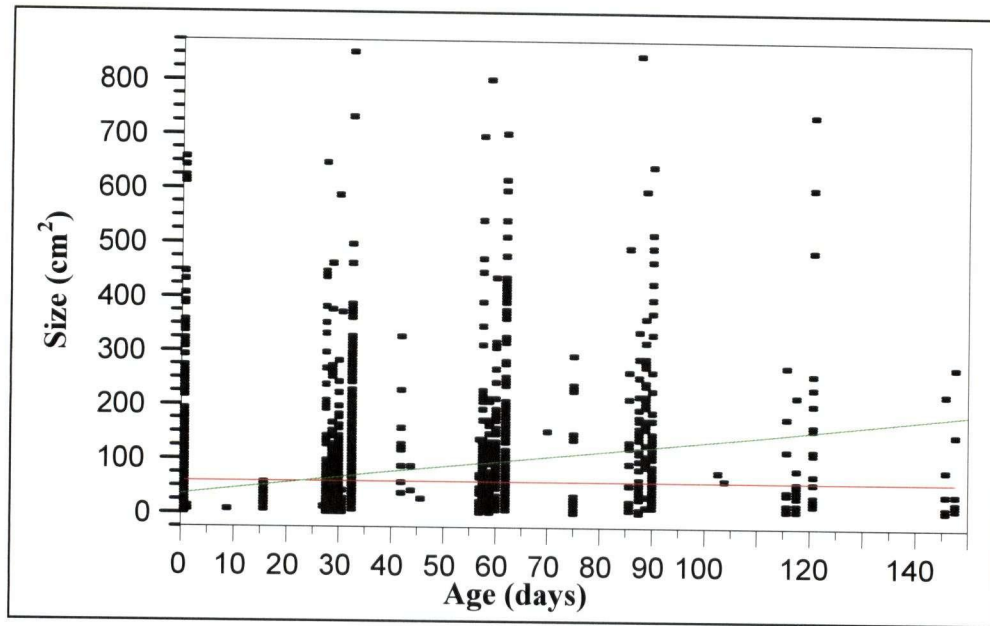


Figure 5.7: Regression of size on age for gametophyte modules of *Mazzaella splendens* tagged at the sheltered site Second Beach, Barkley Sound from November 1997 to January 2001. Red line = the line through the mean of the ratio. Green line = the regression line through the data.

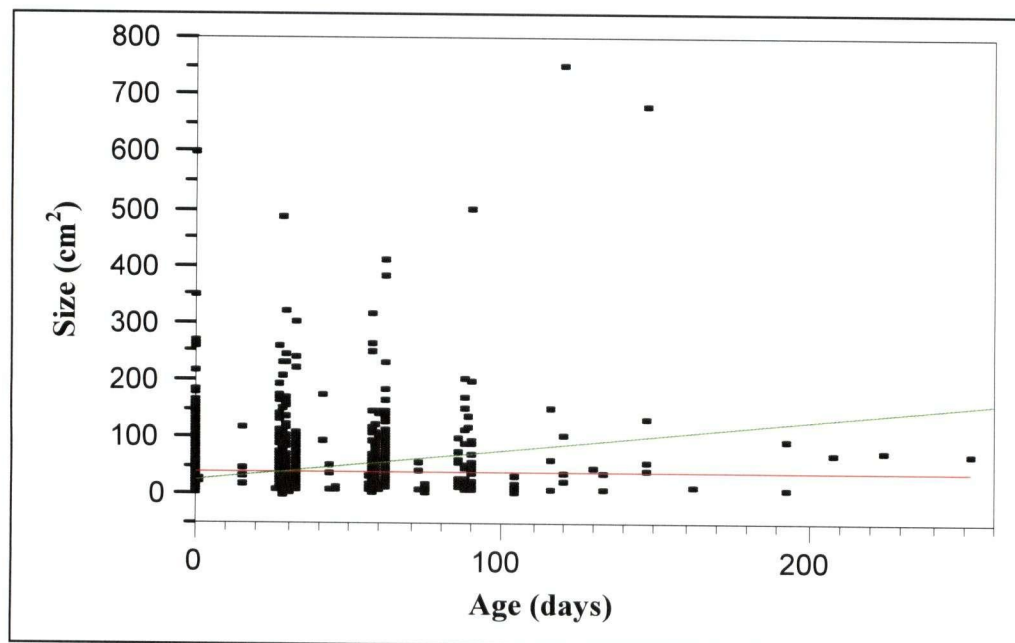


Figure 5.8: Regression of size on age for tetrasporophyte modules of *Mazzaella splendens* tagged at the sheltered site Second Beach, Barkley Sound from November 1997 to January 2001. Red line = the line through the mean of the ratio. Green line = the regression line through the data.

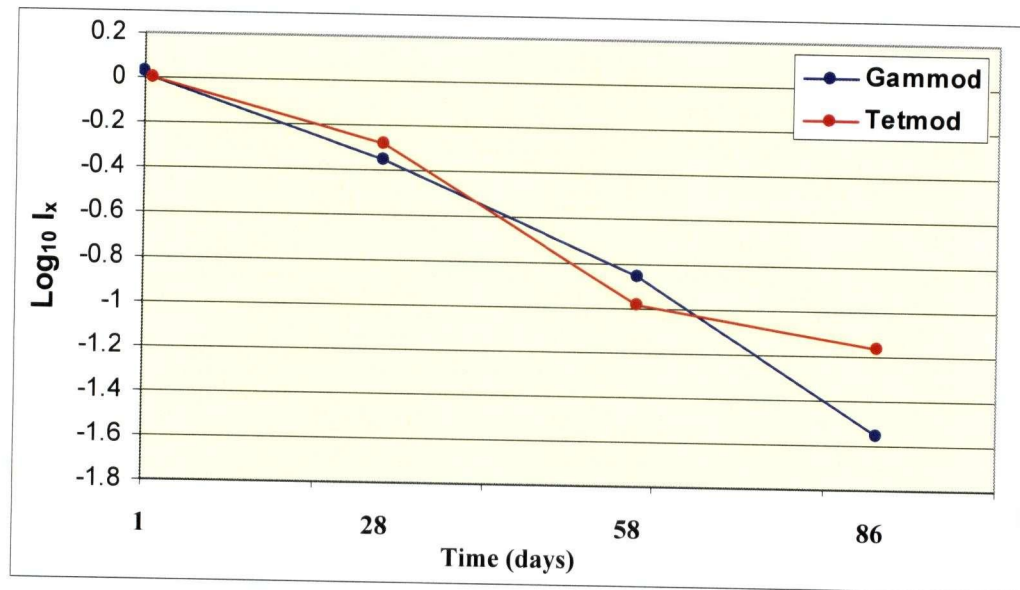


Figure 5.9: Survival ($\log_{10} l_x$) in a cohort of 94 non-reproductive modules (58 diploid, 36 haploid) of *Mazzaella splendens* tagged at the exposed site, Second Beach, Barkley Sound in June 2000. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

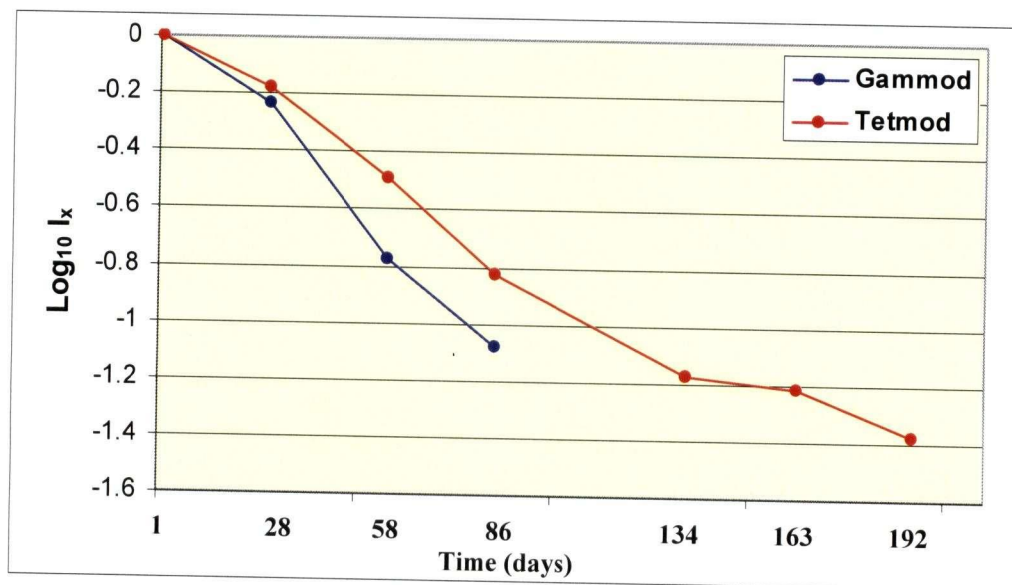


Figure 5.10: Survival after the onset of reproduction ($\log_{10} l_x$) in a static cohort of 86 reproductive modules (74 diploid, 12 haploid) of *Mazzaella splendens* tagged at the exposed site, Second Beach, Barkley Sound in June 2000. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

Tables to accompany Chapter 5.

Table 5.1: Comparisons of total survival time (days) for non-reproductive vs. reproductive modules in the alternate phases of *Mazzaella splendens* in the permanent quadrats, sheltered site, at Second Beach, Barkley Sound. November 1997 to January 2001. Rep = reproductive. Nrep = non-reproductive. MW-U = Mann-Whitney U test.

Comparison		N	Mean	S.E.	MW-U
Reproductive vs. non-reproductive haploids	Nrep	1898	18.01	0.60	P < 0.001
	Rep	54	47.76	5.96	
Reproductive vs. non-reproductive diploids	Nrep	690	17.98	0.96	P = 0.014
	Rep	105	29.51	3.95	
Non-reproductive haploids vs. diploids	Haploid	1898	18.01	0.60	P = 0.457
	Diploid	690	17.98	0.96	
Reproductive haploids vs. diploids	Haploid	54	47.76	5.96	P = 0.006
	Diploid	105	29.51	3.95	

Table 5.2: Comparisons of survival time (days) of non-reproductive modules and survival after the onset of reproduction for reproductive modules for the alternate phases of *Mazzaella splendens* in the permanent quadrats, sheltered site, at Second Beach, Barkley Sound. November 1997 to January 2001. Rep = reproductive. Nrep = non-reproductive. MW-U = Mann-Whitney U test.

Comparison		N	Mean	S.E.	MW-U
Non-reproductive haploids vs. diploids	Haploid	1898	18.01	0.60	P = 0.457
	Diploid	690	17.96	0.96	
Reproductive haploids vs. diploids	Haploid	54	13.54	2.85	P = 0.754
	Diploid	105	14.6	2.16	
Reproductive vs. non-reproductive haploids	Nrep	1898	18.01	0.60	P = 0.334
	Rep	54	13.54	2.85	
Reproductive vs. non-reproductive diploids	Nrep	690	17.98	0.96	P = 0.204
	Rep	105	14.6	2.16	

Table 5.3: Comparisons of time spent non-reproductive vs. time spent reproductive (days) for reproductive modules for the alternate phases of *Mazzaella splendens* in the permanent quadrats, sheltered site, at Second Beach, Barkley Sound. November 1997 to January 2001. Rep = reproductive time. Nrep = non-reproductive time. MW-U = Mann-Whitney U test.

Comparison		N	Mean	S.E.	MW-U
Reproductive vs. non-reproductive time in haploids	Nrep	31	40.02	6.13	P = 0.287
	Rep	31	31.81	4.51	
Reproductive vs. non-reproductive time in diploids	Nrep	29	36.48	6.69	P = 0.861
	Rep	29	33.72	4.51	

Table 5.4: Comparisons of relative growth rate (cm²/day) for non-reproductive vs. reproductive periods in gametophyte and tetrasporophyte modules of *Mazzaella splendens* in the permanent quadrats, sheltered site, at Second Beach, Barkley Sound. November 1997 to January 2001. Rep = reproductive period. Nrep = non-reproductive period. MW-U = Mann-Whitney U test.

Comparison		N	Mean	S.E.	MW-U
Gametophyte	Nrep	24	0.022	0.0020	P = 0.241
	Rep	10	0.014	0.0096	
Tetrasporophyte	Nrep	19	0.018	0.0022	P = 0.063
	Rep	24	0.014	0.0037	

Table 5.5: Comparisons of time to onset of reproduction (days) with survival time in non-reproductive modules for gametophytes and tetrasporophytes of *Mazzaella splendens* in the permanent quadrats, sheltered site, at Second Beach, Barkley Sound. Plants tagged December 1997 to December 2000. Rep = time to onset of reproduction. Nrep = survival time in non-reproductive modules. MW-U = Mann-Whitney U test.

Comparison		N	Mean	S.E.	MW-U
Gametophyte	Nrep	1843	17.63	0.606	P < 0.001
	Rep	49	34.65	5.400	
Tetrasporophyte	Nrep	669	17.32	0.936	P = 0.198
	Rep	52	25.75	5.500	
Between life history phases	Haploid	49	34.65	5.400	P = 0.138
	Diploid	52	25.75	5.500	

Table 5.6: Comparisons of maximum size (cm²) of non-reproductive and reproductive modules for the alternate phases of *Mazzaella splendens* in the permanent quadrats, sheltered site, at Second Beach, Barkley Sound. November 1997 to January 2001. Rep = reproductive. Nrep = non-reproductive. MW-U = Mann-Whitney U test.

Comparison		N	Mean	S.E.	MW-U
Non-reproductive haploids vs. diploids	Haploid	1894	64.77	2.15	P < 0.001
	Diploid	689	40.91	1.91	
Reproductive haploids vs. diploids	Haploid	54	132.38	23.97	P = 0.001
	Diploid	107	55.51	9.48	
Reproductive vs. non-reproductive haploids	Nrep	1894	64.77	2.15	P = 0.007
	Rep	54	132.38	23.97	
Reproductive vs. non-reproductive diploids	Nrep	689	40.91	1.91	P = 0.730
	Rep	107	55.51	9.48	

Table 5.7: Comparisons of tissue loss (cm²) in non-reproductive modules and after the onset of reproduction for the alternate phases of *Mazzaella splendens* in the permanent quadrats, sheltered site, at Second Beach, Barkley Sound. November 1997 to January 2001. Rep = reproductive. Nrep = non-reproductive. MW-U = Mann-Whitney U test.

Comparison		N	Mean	S.E.	MW-U
Non-reproductive haploids vs. diploids	Haploid	767	21.77	2.27	P < 0.001
	Diploid	287	6.47	1.83	
Reproductive haploids vs. diploids	Haploid	19	70.7	33.0	P = 0.243
	Diploid	41	23.72	13.93	
Reproductive vs. non-reproductive haploids	Nrep	767	21.77	2.27	P = 0.019
	Rep	19	70.7	33.0	
Reproductive vs. non-reproductive diploids	Nrep	287	6.47	1.83	P < 0.001
	Rep	41	23.72	13.93	
Within non-reproductive haploids: tissue loss vs. gain		767	91.39	3.91	P < 0.001
	Gain				
	Loss	767	21.77	2.27	
Within reproductive haploids: tissue loss vs. gain after the onset of reproduction		19	70.7	33.0	P = 0.141
	Gain				
	Loss	19	44.56	34.48	
Within non-reproductive diploids: tissue loss vs. gain		287	60.12	3.96	P < 0.001
	Gain				
	Loss	287	6.47	1.83	
Within reproductive diploids: tissue loss vs. gain after the onset of reproduction		41	5.17	23.72	P = 0.047
	Gain				
	Loss	41	23.72	5.17	

Table 5.8: Comparisons of total survival time (days) for non-reproductive vs. reproductive modules in the alternate phases of *Mazzaella splendens* in the permanent quadrats, exposed site, at Second Beach, Barkley Sound. June – December, 2000. Rep = reproductive. Nrep = non-reproductive. MW-U = Mann-Whitney U test.

Comparison		N	Mean	S.E.	MW-U
Reproductive vs. non-reproductive haploids	Nrep	34	20.12	4.46	P < 0.001
	Rep	12	66.25	9.11	
Reproductive vs. non-reproductive diploids	Nrep	58	19.52	3.16	P < 0.001
	Rep	74	53.49	4.55	

Table 5.9: Comparisons of survival (days) of non-reproductive modules and reproductive modules after the onset of reproduction for the alternate phases of *Mazzaella splendens* in the permanent quadrats, exposed site, at Second Beach, Barkley Sound. June – December, 2000. Rep = reproductive. Nrep = non-reproductive. MW-U = Mann-Whitney U test.

Comparison		N	Mean	S.E.	MW-U
Non-reproductive haploids vs. diploids	Haploid	34	20.12	4.46	P = 0.929
	Diploid	58	19.52	3.16	
Reproductive haploids vs. diploids	Haploid	12	30.42	11.38	P = 0.512
	Diploid	74	37.46	4.62	
Reproductive vs. non-reproductive haploids	Nrep	34	18.22	3.99	P = 0.298
	Rep	12	30.42	11.38	
Reproductive vs. non-reproductive diploids	Nrep	58	19.52	3.16	P = 0.003
	Rep	74	37.46	4.62	

Table 5.10: Comparisons of time spent non-reproductive vs. time spent reproductive (days) for reproductive modules for the alternate phases of *Mazzaella splendens* in the permanent quadrats, exposed site, at Second Beach, Barkley Sound. June – December, 2000. Rep = reproductive. Nrep = non-reproductive. MW-U = Mann-Whitney U test.

Comparison		N	Mean	S.E.	MW-U
Reproductive vs. non-reproductive time in haploids	Nrep	11	32.45	5.9	P = 0.433
	Rep	11	39.91	10.65	
Reproductive vs. non-reproductive time in diploids	Nrep	28	29.36	4.9	P = 0.201
	Rep	28	33.39	5.65	

Table 5.11: Comparisons of relative growth rate (cm^2/day) for non-reproductive vs. reproductive periods in gametophyte and tetrasporophyte modules of *Mazzaella splendens* in the permanent quadrats, exposed site, at Second Beach, Barkley Sound. Cohort tagged June 2000. Rep = reproductive period. Nrep = non-reproductive period. MW-U = Mann-Whitney U test.

Comparison		N	Mean	S.E.	MW-U
Gametophyte	Nrep	6	0.006	0.0018	P = 0.096
	Rep	2	0.001	0.0013	
Tetrasporophyte	Nrep	13	0.008	0.0013	P = 0.019
	Rep	42	0.005	0.0006	

Table 5.12: Comparisons of size (cm^2) of non-reproductive and reproductive modules for the alternate phases of *Mazzaella splendens* in the permanent quadrats, exposed site, at Second Beach, Barkley Sound. Rep = reproductive. Nrep = non-reproductive. MW-U = Mann-Whitney U test.

June 2000					
Comparison		N	Mean	S.E.	MW-U
Non-reproductive haploids vs. diploids	Haploid	46	183.79	19.46	P < 0.001
	Diploid	83	81.83	6.17	
Reproductive haploids vs. diploids	Haploid	2	179.74	17.04	P = 0.178
	Diploid	44	144.69	9.37	
Reproductive vs. non-reproductive haploids	Nrep	46	183.79	19.46	P = 0.747
	Rep	2	179.74	17.04	
Reproductive vs. non-reproductive diploids	Nrep	83	81.83	6.17	P < 0.001
	Rep	44	144.69	9.37	
July 2000					
Comparison		N	Mean	S.E.	MW-U
Non-reproductive haploids vs. diploids	Haploid	20	165.09	27.64	P = 0.001
	Diploid	39	81.76	11.4	
Reproductive haploids vs. diploids	Haploid	None			
	Diploid	19	171.98	20.54	
Reproductive vs. non-reproductive haploids	Nrep	46	183.79	19.46	
	Rep	None			
Reproductive vs. non-reproductive diploids	Nrep	39	81.76	11.4	P < 0.001
	Rep	19	171.98	20.54	

Table 5.12: Continued.

August 2000					
Comparison		N	Mean	S.E.	MW-U
Non-reproductive haploids vs. diploids	Haploid	5	86.07	18.84	P = 0.053
	Diploid	9	41.57	6.19	
Reproductive haploids vs. diploids	Haploid	4	82.82	14.19	P = 0.308
	Diploid	8	104.5	15.64	
Reproductive vs. non-reproductive haploids	Nrep	5	86.07	18.84	P = 0.806
	Rep	4	82.82	14.19	
Reproductive vs. non-reproductive diploids	Nrep	9	41.57	6.19	P = 0.005
	Rep	8	104.5	15.64	

Table 5.13: Comparisons of tissue loss (cm²) in non-reproductive modules and after the onset of reproduction in reproductive modules for the alternate phases of *Mazzaella splendens* in the permanent quadrats, exposed site, at Second Beach, Barkley Sound. June - December, 2000. Rep = reproductive. Nrep = non-reproductive. MW-U = Mann-Whitney U test.

Comparison		N	Mean	S.E.	MW-U
Non-reproductive haploids vs. diploids	Haploid	15	92.13	35.32	P = 0.001
	Diploid	28	0.89	0.44	
Reproductive haploids vs. diploids	Haploid	7	117.8	37.8	P = 0.066
	Diploid	48	51.46	8.68	
Reproductive vs. non-reproductive haploids	Nrep	15	92.13	35.32	P = 0.299
	Rep	7	117.8	37.8	
Reproductive vs. non-reproductive diploids	Nrep	28	0.89	0.44	P < 0.001
	Rep	48	51.46	8.68	
Within non-reproductive haploids: tissue loss vs. gain		15	22.0	9.62	P = 0.182
	Gain				
	Loss	15	92.13	35.32	
Within reproductive haploids: tissue loss vs. gain after the onset of reproduction		7	0.68	0.68	P = 0.005
	Gain				
	Loss	7	117.8	37.8	
Within non-reproductive diploids: tissue loss vs. gain		28	24.27	8.26	P < 0.001
	Gain				
	Loss	28	0.89	0.44	
Within reproductive diploids: tissue loss vs. gain after the onset of reproduction		48	17.0	5.46	P = 0.009
	Gain				
	Loss	48	51.46	8.68	

Chapter 6. Summary: Advances and future directions in the demography of *Mazzaella splendens*.

Patterns in natural and local populations.

Advances in understanding how population dynamics at the natural population (Berryman 2002) or metapopulation (Hanski 1997) level are controlled come from understanding how processes at local scales map into those at larger scales (Camus & Lima 2002). The first step in this process is the identification of common demographic patterns that persist, over time and in different environments. Such a set of patterns has been identified for *Mazzaella splendens* in a synthesis of the work of a number of investigators over a period of years from 1969 to 2000 (Chapter 1). This present study has modified that set of patterns. It is now apparent that seasonal alternation in phase dominance at wave-sheltered sites is a local phenomenon (Chapter 2). The shift from summer haploid to summer diploid dominance as wave force increases remains a pattern potentially common to the species throughout its range, as does the fact that changes in population density among perennating adults are a function of appearances and disappearances of genets and not differential module production between life history phases (Chapter 2).

Changes in population density and phase dominance.

Previous hypotheses about the factors controlling changes in phase dominance of *Mazzaella splendens* along wave exposure gradients focused primarily on differential survival favouring tetrasporophytes as hydrodynamic forces increase (Shaughnessy *et al.* 1996). A similar underlying assumption, that stronger diploids were better able to withstand the increased wave force due to winter storms, led to the hypothesis of an ecological divergence between phases, with greater production of new blades by gametophytes in conditions conducive to growth coupled with greater loss in conditions requiring resistance to wave force, as an explanation of seasonal alternation in phase dominance (Dyck & DeWreede 1995).

The similarity in survival between life history phases of *Mazzaella splendens* in both the wave-exposed and wave-sheltered habitats at Second Beach, Barkley Sound,

suggests that hydrodynamic forces are less influential than previously thought in controlling phase dominance. For seasonal alternations in phase dominance this means that differential production of new modules, resulting in differential appearances and disappearances of genets, is the more important factor determining whether haploids or diploids predominate in a particular season. This is supported by the examination of new production at Second Beach, Barkley Sound, where differences in per capita rates of new production between gametophytes and tetrasporophytes were markedly greater, and more seasonally regular, than differences in per capita rates of loss (Chapter 3).

The alternate isomorphic phases of *Mazzaella splendens* are not diverging ecologically along the lines hypothesised by Dyck & DeWreede (1995), with a relatively *r* selected gametophyte and *K* selected sporophyte. But the alternate phases apparently do respond differently to seasonal changes in the environment by altering rates of module production (Chapter 3). This is a more subtle difference than previously suspected. It would be useful to replicate this study within a population that does undergo seasonal alternation in phase dominance, both to test this result in a different population and to determine the way in which new production changes with season in the alternate life history phases.

For wave-exposed habitats, the absence of differential survival between perennating adult phases (Chapter 3) shifts the focus in explaining population structure back to the events surrounding recruitment (Phillips 1994). Further work examining the relationship between spore production, release and viability, and resulting levels of recruitment in wave-exposed and wave-sheltered habitats, would help to pinpoint where selection is acting in this process.

The general population dynamics of *Mazzaella splendens* at the wave-sheltered site, Second Beach, have shown that large population declines are not necessarily coincident with winter conditions (Chapter 2). Nutrient levels have been suggested as a potentially important determinant of population density (Chapter 3). Differences in uptake abilities of gametophytes vs. tetrasporophytes (Sunday 2001) may be involved in differential production between phases. Further work is needed to more closely examine the relationship between nutrient concentration, water motion and uptake rates in the alternate phases. Such work would ideally be done in a laboratory flow or wave tank where all parameters could be controlled. This could provide the ecophysiological

mechanism underlying differential production between life history phases, and with it an understanding of the magnitude of difference between isomorphic phases on which selection can act to produce a temporal or spatial segregation of gametophytes and tetrasporophytes as they adapt to different conditions.

Changes in size.

The majority of blades of *Mazzaella splendens* produced at the wave-sheltered site, Second Beach, were below the size category for which differential survival due to increased tetrasporophyte resistance to hydrodynamic force (Shaughnessy *et al.* 1996) was predicted. But at the wave-sheltered site and at the wave-exposed site differential survival was also absent from the larger size class (Chapter 4).

At the wave-sheltered site, larger blades were present primarily in spring and early summer (Chapter 4), after the decline of winter storms and before the late summer/early fall population crash (Chapter 2), and modules of both phases, in both size classes, gained significantly more tissue than they lost (Chapter 4). Modules at this site may never encounter waves large enough to affect survival between the alternate phases.

At the wave-exposed site modules of both phases, in the smaller size class, gained significantly more tissue than they lost. But in the size class for which differential survival between phases was predicted by Shaughnessy *et al.* (1996) tissue gain significantly exceeded tissue loss for tetrasporophytes, but not for gametophytes (Chapter 4). This suggests that gametophytes are losing parts of their blades, reconfiguring their surface area in response to wave action. This may result in similar chances of removal at the stipe for both life history phases.

The above suggests that wave force may be operating to generally limit the size of *M. splendens* modules in wave-exposed habitats, even though survival differences are not evident between life history phases (Chapter 3). Seasonal changes in size class structure of *M. splendens* should be examined in wave-exposed habitats to determine if this is the case.

Reproduction in *Mazzaella splendens*.

Mazzaella splendens at Brockton Point, Vancouver Harbour has shown a pattern of temporally restricted reproduction (Dyck 1991, as *Iridaea splendens*) suggestive of

optimization of the life history due to reproductive cost, but a survival cost to reproduction was not evident. Temporal restriction of reproductive activity was less apparent in the wave-sheltered site, Second Beach, than at Brockton Point and patterns of this kind may be responses to local conditions and not a general feature of *M. splendens* populations (Chapter 5).

A comparison of seasonal reproductive patterns of *Mazzaella splendens* in intertidal wave-exposed and subtidal habitats with intertidal populations in nearby wave-sheltered areas would provide an understanding of how these patterns may change over relatively small spatial scales. Simultaneous monitoring of key environmental factors associated with the onset of reproduction in algae (see Santelices 1990 for review) in these habitats might provide a correlation between abiotic changes and reproductive patterns. Seasonal variation, between habitats, in factors important to the reproductive process could produce temporally restricted reproduction in certain areas without the presence of a reproductive cost.

The absence of a negative effect of reproduction on survival in *Mazzaella splendens* is supported by results from both the wave-sheltered and wave-exposed habitats at Second Beach, Barkley Sound. Other evidence for reproductive cost is mixed. Growth did not slow after the onset of reproduction, for gametophytes or tetrasporophytes, in the wave-sheltered habitat. In the wave-exposed area growth slowed after the onset of reproduction in tetrasporophytes, but not for gametophytes. Modules of both phases became reproductive at a wide variety of sizes and times to onset of reproduction without any apparent absolute threshold requirement. Gametophytes in the wave-sheltered site, however, required a mean period of time to onset of reproduction significantly longer than the mean survival time of non-reproductive gametophytes.

Although the evidence is mixed, time to onset of reproduction may be longer for gametophytes than for tetrasporophytes. This would explain the result that reproductive gametophytes were significantly longer lived than reproductive tetrasporophytes. Those blades that live longer tend to be the ones that reproduce. In the absence of survival differences between phases before or after the onset of reproduction, a significantly longer time to onset of reproduction in gametophytes than in tetrasporophytes would select longer lived gametophytes than tetrasporophytes for the reproductive group. In a population where size increased with age, this difference in time to onset of

reproduction would account for cystocarpic blades being significantly larger than tetrasporic ones.

Haploid vs. diploid advantage.

Another area of inquiry, to which studies of *Mazzaella splendens* can contribute, is the question of the adaptive advantages of diploidy vs. haploidy. Alternation between haploid and diploid phases is a necessary consequence of eukaryotic sexual reproduction with its cycles of meiosis and syngamy, but the degree to which either phase predominates in the life-history varies enormously among taxa. This variation is expressed in the proportion of time a phase occupies during the life-cycle and in morphological differences between phases. There are species with gametes as the only haploid stage, and others where the only diploid phase is the zygote. Some taxa have free living alternate phases distinguishable only by microscopic differences in reproductive structures. Some have alternate stages with radically different gross morphologies.

Some evolutionary lineages apparently eliminated much of this variation at an early time, while others retained it. Haploidy is considered by many to be the phylogenetically primitive condition (Margulis 1968, Raper & Flexer 1970) from which biphasic and diploid cycles were derived, with diploidy becoming fixed early in animal evolution (Raper & Flexer 1970, Mable & Otto 1998). For most animal life histories, only gametes are haploid. The exceptions are mainly arrhenotokous species that produce haploid males by parthenogenesis (see Mable & Otto 1998, for review) and parthenogenesis of haploid females from haploid females in certain spider mites (Weeks *et al.* 2001, Perrot 2002), both derived from diploidy.

All plants have, in some form, retained an alternation of haploid and diploid generations. In terrestrial plants there is (in broad terms) a temporal sequence in the fossil record. Increased size and complexity of development is correlated with a reduction in both longevity and structural complexity of the haploid phase, from gametophyte dominance in bryophytes to functional diploidy in angiosperms. This trend, in combination with the predominance of purely diploid cycles in animals, has long dominated thinking on the evolutionary advantages of haploidy vs. diploidy (Valero *et al.* 1992, Hughes & Otto 1999) and with diploidy seen as evolutionarily

preferred, the primary motivation has been to discover the advantages inherent in diploidy.

Several mechanisms have been proposed to explain diploid predominance. Masking of deleterious recessives could increase diploid fitness (Crow & Kimura 1965, Kondrashov & Crow 1991, Perrot *et al.* 1991). Such masking could also permit these mutations to be retained in the population for longer times, providing a pool of potentially advantageous variation for adaptation to changing environments (Raper & Flexer 1970). Also, with twice the DNA, diploids could accumulate beneficial mutations at twice the haploid rate (Orr & Otto 1994).

There are, however, potential disadvantages to diploidy as well. Masking leaves a diploid population with a large deleterious mutation load. Those individuals homozygous for the worst of these mutations are continuously being lost and incomplete dominance may reduce fitness in heterozygotes. Haploid populations are better at purging deleterious mutations. Individuals are more likely to die, but the survivors pass fewer mutations forward, resulting, at equilibrium, in haploid populations with a higher mean fitness than diploid populations (Crow & Kimura 1965). Masking also covers the effects of beneficial mutations. These spread less rapidly in diploid populations and are more susceptible to loss by chance while they are still rare. Beneficial mutations only increase the rate of diploid adaptation when they are dominant (Orr & Otto 1994).

Haploidy is favoured only when its advantages are not shared with diploid members of a population. When there is a high degree of genetic mixing, diploid individuals gain the benefits of both masking and purging. Models of this process have concluded that haploid cycles are favoured when sex and recombination are relatively rare or when selfing or assortative mating are common (Mable & Otto 1998).

These genetic models favour haploidy in certain conditions and diploidy in others, but have not found a balance of conditions within which haploid-diploid cycles are evolutionarily stable (Mable & Otto 1998, Hughes & Otto 1999). This is consistent with the traditional view in which a haploid-diploid cycle is evolutionarily transitional, existing as the conduit between primitive haploidy and preferred diploidy. It is not entirely consistent, however, with the available evidence.

Sporic life cycles, consisting of an alternation of free living haploid and diploid generations, are common among eukaryotic algae, particularly red algae. With a few

arguable exceptions, the whole phylum Rhodophyta is haploid-diploid in life-history type. One phase or the other may be reduced in size, structural complexity, longevity or some combination of these, but there is little evidence of reduction to either true haploid or diploid cycles (Hawkes 1990). Fossils which can reasonably be identified as red algae are corallines from the Cambrian, approximately 500 mya. (van den Hoek *et al.* 1995). The persistence of this life-history type over evolutionary time constitutes considerable circumstantial evidence that haploid-diploid cycles are adaptive and evolutionarily stable.

While purely genetic models of the advantages of haploidy vs. diploidy have not produced an evolutionarily stable haploid-diploid life-history, models including ecological differences between the alternate phases have done so (Mable & Otto 1998, Hughes & Otto 1999). Disruptive selection acting on alternate phenotypes in spatially and/or temporally variable environments has been proposed as a mechanism capable of producing this stability (Klinger 1993). But Klinger (1993) also argues that this would account only for the stability of an alternation of heteromorphic generations, where gross morphology between phases is different enough for selection to act, and that other mechanisms would account for the stability of an alternation of isomorphic phases.

Ecological differences between heteromorphic phases have been found in each of the three major macroalgal groups and are particularly evident in differential responses to herbivory (Lubchenco & Cubit 1980, Slocum 1980). But evidence is mixed on the presence of ecological differences between phases of isomorphic species. There are detailed studies of isomorphic red (Littler *et al.* 1987, Sosa *et al.* 1993) and brown (Klinger 1988) algae where no significant differences between phases have been found.

Within the red algae, some members of the Gigartinales have shown biochemical (McCandless *et al.* 1973, 1975; Pickmere *et al.* 1973; Waaland 1975) or photosynthetic (Mathieson & Norall 1975) differences between isomorphic phases. Others have shown differential growth rates and desiccation tolerances among juveniles in laboratory conditions (Hannach & Santelices 1985). Differential survival has been demonstrated for juveniles in the laboratory (Destombe *et al.* 1993), although this has been more difficult to establish in the field (Destombe *et al.* 1989). Differences in dispersal abilities and survival of haploid vs. diploid spores have also been observed in vitro (Destombe *et al.* 1992).

One kind of evidence from the field, suggestive of ecological differences between isomorphic phases, has been observed changes in the ratio of haploids to diploids along a spatial or temporal environmental gradient. Such changes were observed in *Chondrus crispus* Stackhouse in some areas (Mathieson & Burns 1975, Craigie & Pringle 1978) but not in others (Lazo *et al.* 1989). For the isomorphic brown alga *Zonaria farlowii*, Klinger (1988) found consistent sporophyte dominance, invariant with site and season. Diploids had higher growth rates in both culture and field. In addition, diploid recruitment and survival rates were higher. This trend continued when diploids and haploids were transplanted into novel environments.

Early work on *Mazzaella splendens* showed a similar pattern, with four sites near Monterey, California (Hansen 1977, Hansen & Doyle 1976, as *Iridaea cordata*) dominated by diploids throughout the year. Changes in phase dominance along spatial and temporal gradients, however, were observed for *Mazzaella laminarioides* (Luxoro & Santelices 1989, as *Iridaea laminarioides*) in central Chile, and *Mazzaella splendens* on the west coast of Vancouver Island (Dyck *et al.* 1985, as *Iridaea cordata*) and in Vancouver Harbour (DeWreede & Green 1990, as *Iridaea splendens*, Dyck & DeWreede 1995).

A seasonal alternation in phase dominance of the kind reported for *Mazzaella splendens* (Adams 1979, as *Iridaea cordata*, DeWreede & Green 1990, as *Iridaea splendens*, Dyck & DeWreede 1995) or changes in phase dominance along a wave exposure gradient (Dyck *et al.* 1985, as *Iridaea cordata*) are good systems in which to examine the degree of ecological difference between isomorphic phases (and by extension the amount of difference required to evolutionarily stabilize an alternation of isomorphic generations) and to illustrate how the advantage to haploids vs. diploids changes with environment.

The absence of differential survival between phases and the greater magnitudes of seasonal change in per capita rates of new production over per capita rates of loss, found in this present study (Chapter 3), suggests that the key difference between phases for *Mazzaella splendens*, within the process of perennation, is likely to be differential new blade production from basal crusts. Combined with the absence of differences in survival between life history phases of *M. splendens* at Brockton Point (Chapter 3), it seems likely that differential new blade production is responsible for seasonal

alternations in phase dominance. This present study has not, however, been able to show how this difference provides an advantage to one phase over the other as conditions change.

A seasonal alternation in phase dominance was not observed at the wave-sheltered site, Second Beach, and differential new production of the kind favouring haploids in spring and summer and diploids in fall and winter was not found. The pattern of per capita new production in spring did not consistently favour one phase over the other. During the three years of study, haploids were favoured in the first spring, diploids in the second, and spring per capita rates of new production were similar for both phases in the third (Chapter 3). The question of how new production changes with season to produce a seasonal alternation in phase dominance remains open. The pattern of seasonal changes in population density at Brockton Point (Dyck & DeWreede 1995) strongly suggests, however, that both phases should respond similarly to seasonal changes, increasing in spring and summer, and decreasing in fall and winter, but with rates of new production increasing and decreasing more rapidly for gametophytes.

Differential recruitment is also an important determinant of population structure in *Mazzaella splendens* (May 1986, as *Iridaea cordata*, Phillips 1994, as *Mazzaella lilacina*) in both wave-sheltered and wave-exposed habitats. It is here that important new ecological differences between the isomorphic phases could potentially be discovered. Recruitment in both habitats examined by Phillips (1994) did not reflect the proportions of carpospores and tetraspores that should be present in the spore rain if recruitment was from local sources, and reproductive output was similar between phases. There are potential differences between phases at many levels here. Spore production, timing of release, viability, attachment, and interactions of juveniles with different biotic and abiotic variables could differ between gametophytes and tetrasporophytes of *M. splendens*.

Considerable work remains to be done in differential recruitment between phases and how this changes with environment to favour haploids or diploids. This line of inquiry may be more applicable to the questions surrounding the evolutionary stabilization of isomorphic life histories than work on perennation is. Hughes and Otto (1999) have speculated that competition during the spore recruitment stage is especially likely to maintain an alternation of isomorphic generations over evolutionary time. For

Mazzaella splendens (May 1986 as *Iridaea cordata*), and for both *M. splendens* and *M. flaccida* (Thornber & Gaines 2003), the ratio of gametophytes to tetrasporophytes at a particular site did not change significantly from one summer to the next over 3 to 4 years, yet there were significant differences between sites (Thornber & Gaines 2003). Even in populations where differences in the behaviour of modules during perennation produces a seasonal alternation in phase dominance, it may be that the underlying ratio of haploids to diploids is determined primarily by differential recruitment. In this case the ratio of haploids to diploids, between which the population alternates from summer haploid to winter diploid dominance, may also be relatively stable over time within a particular site. If the events surrounding recruitment are contributing most to the stability of the population structure from year to year in a particular habitat, then differences in recruitment between life history phases may be the differences most important in stabilizing an isomorphic alternation of generations over evolutionary time by favouring gametophytes in one kind of habitat and tetrasporophytes in another.

With each new local study for a particular species, our understanding of how local processes interact to produce patterns at larger scales is enhanced. In each new study the possible mechanisms underlying a previously discovered pattern can be examined. As such a mosaic of information builds, it enables increasingly detailed questions about the way in which individuals interact with components of their environment to give rise to disruptive selection between phenotypes, and of the potentially subtle differences capable of producing divergence. The accumulation of studies of *Mazzaella splendens* has made it a useful species in this regard, and it is hoped that the advances presented here and the questions they raise will trigger further interest and continue the process.

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APPENDIX A

Additional figures to accompany Chapter 2.

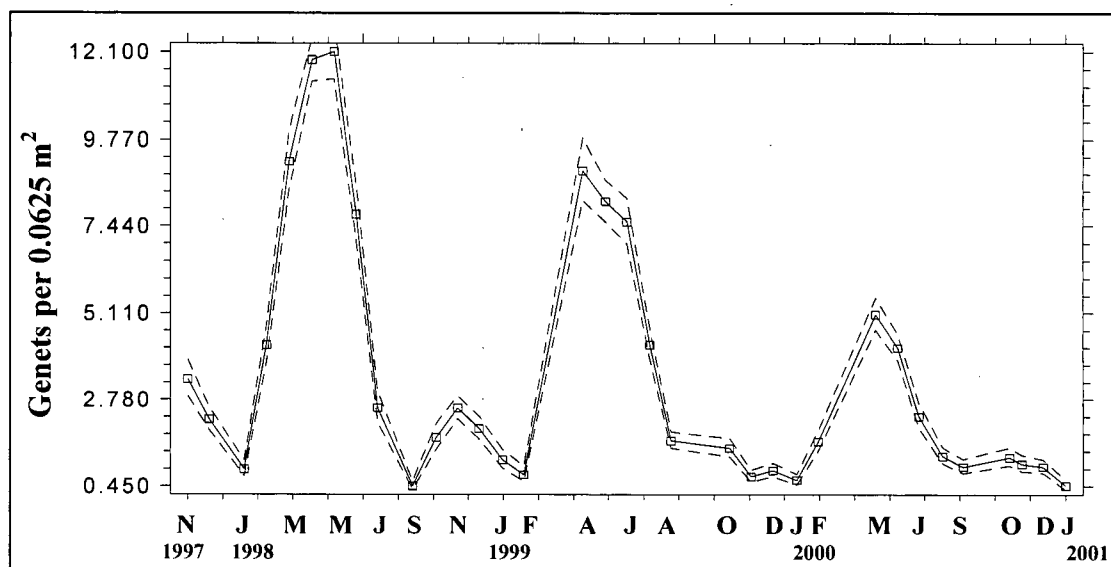


Figure A.1: Cubic spline graph of seasonal changes in genet density for *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

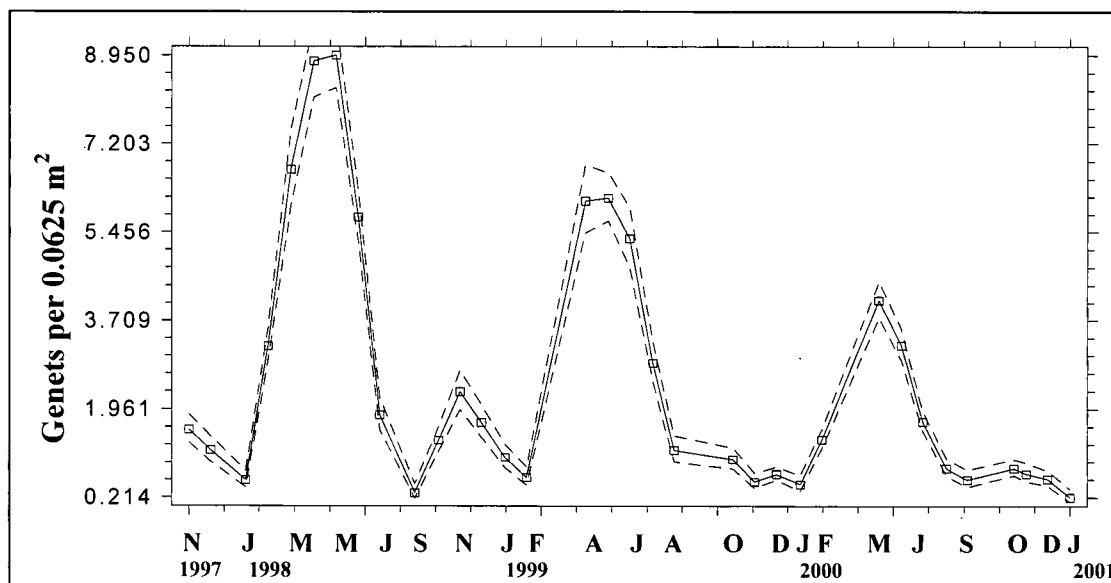


Figure A.2: Cubic spline graph of seasonal changes in haploid genet density for *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

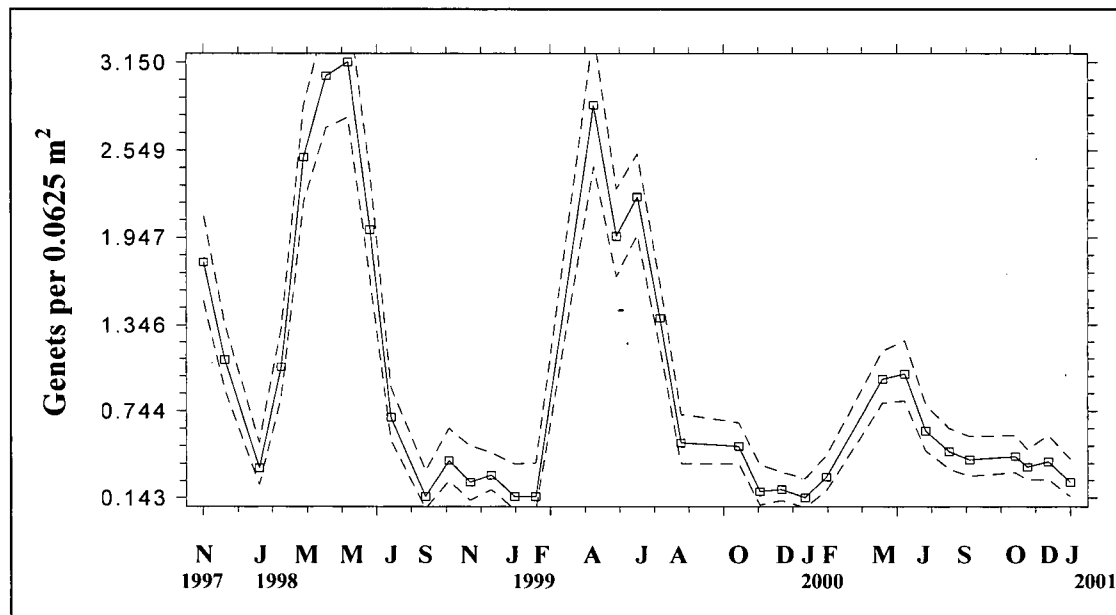


Figure A.3: Cubic spline graph of seasonal changes in diploid genet density for *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

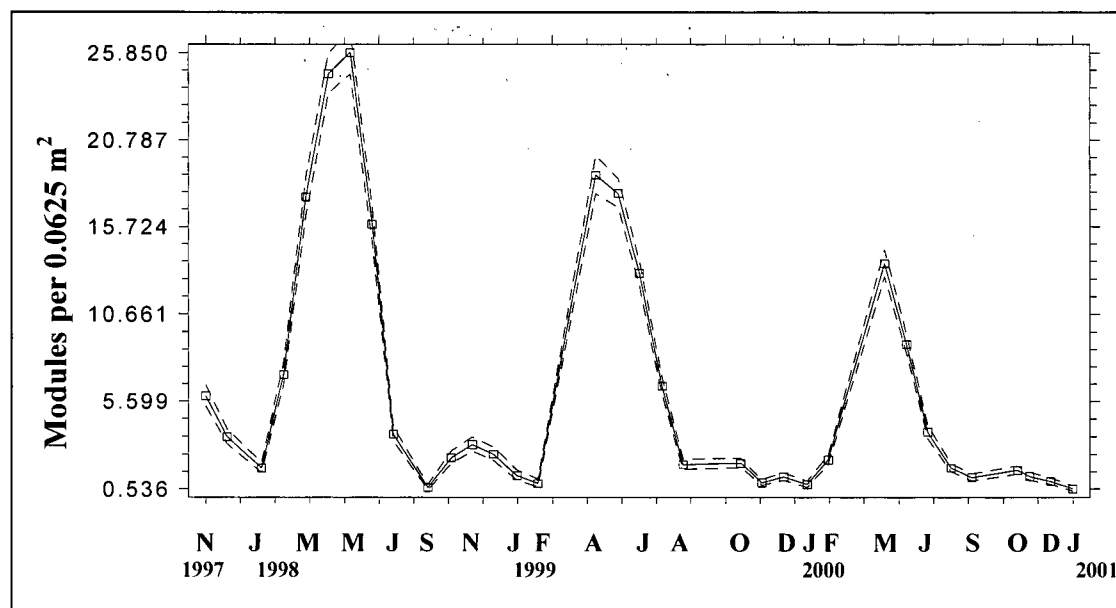


Figure A.4: Cubic spline graph of seasonal changes in module density for *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

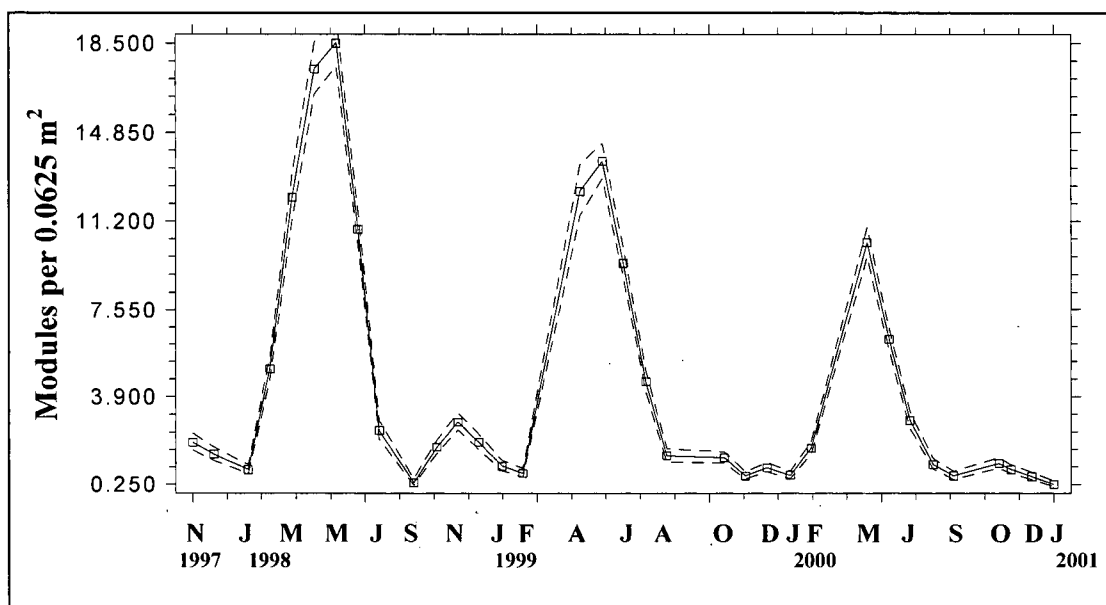


Figure A.5: Cubic spline graph of seasonal changes in haploid module density for *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S.E.

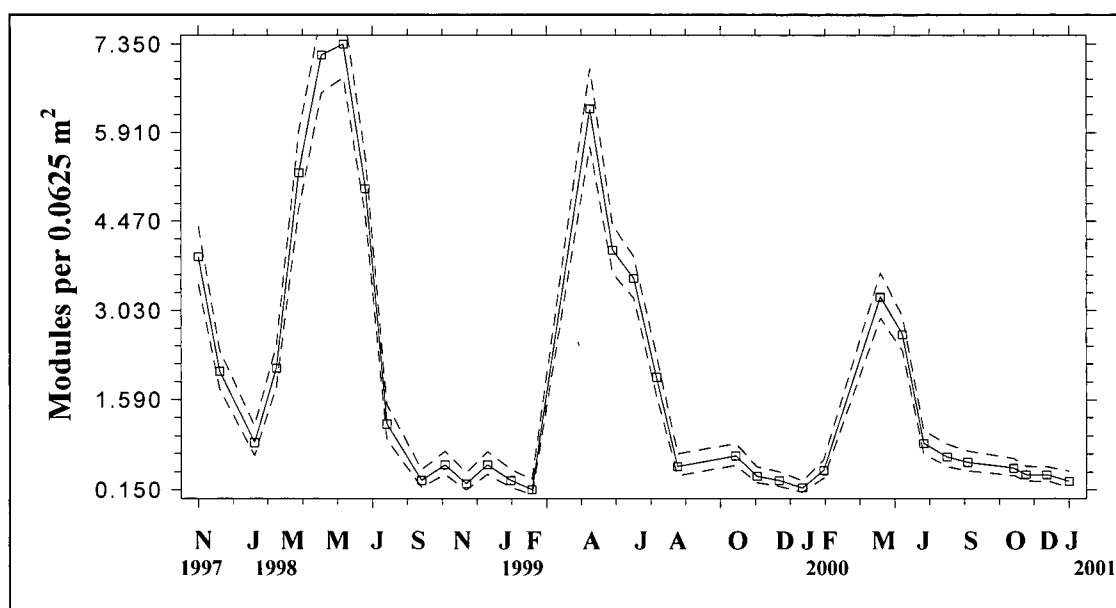


Figure A.6: Cubic spline graph of seasonal changes in diploid module density for *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S.E.

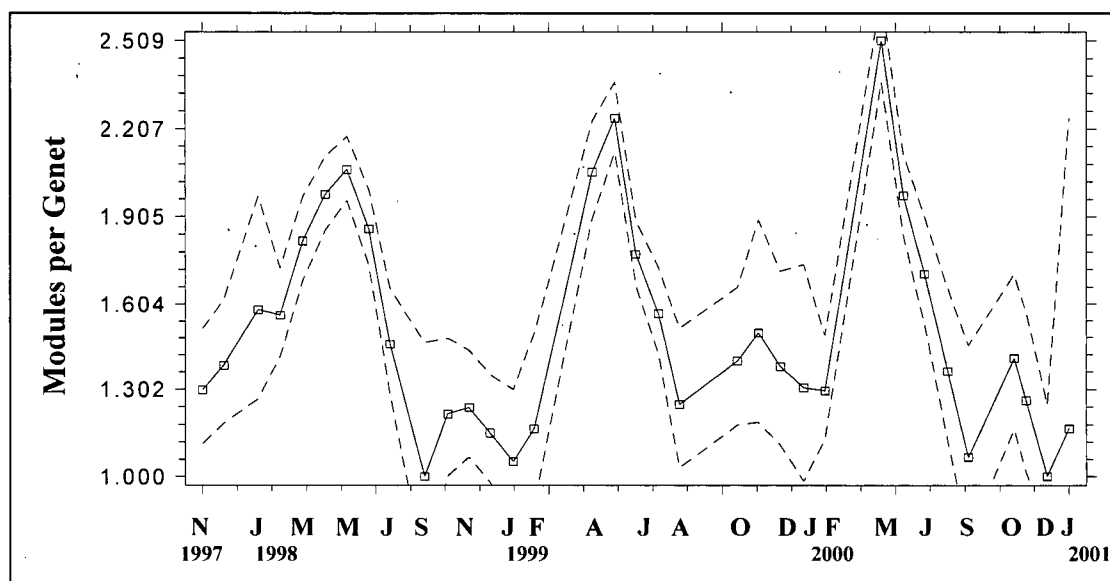


Figure A.7: Cubic spline graph of seasonal changes in haploid modules per genet for *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S.E.

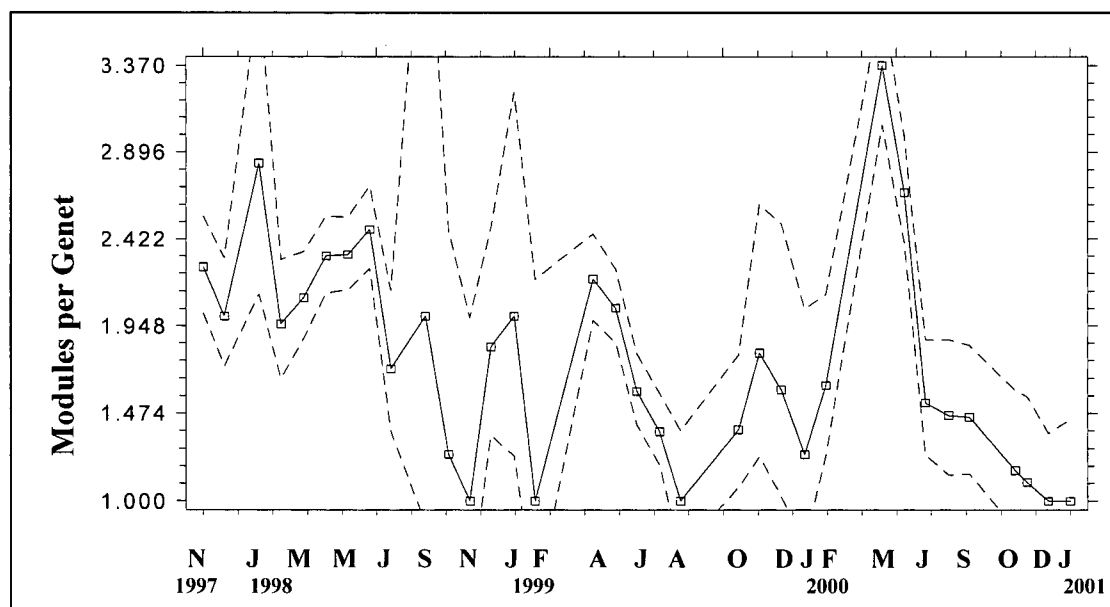


Figure A.8: Cubic spline graph of seasonal changes in diploid modules per genet for *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S.E.

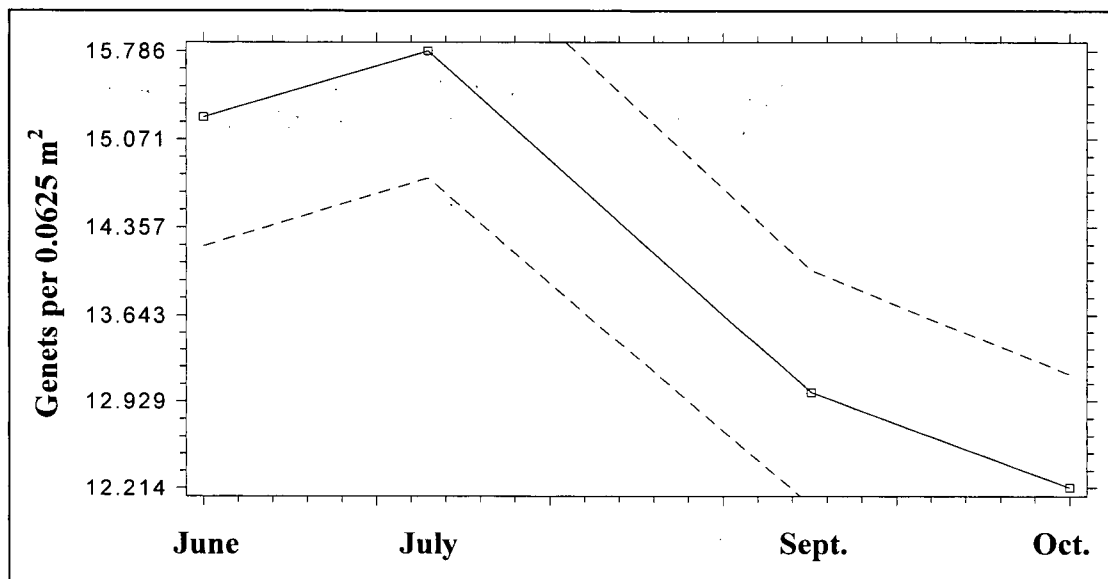


Figure A.9: Cubic spline graph of seasonal changes in genet density for *Mazzaella splendens* at the wave-exposed site, Second Beach, Barkley Sound (June to October 1998). Solid line = curve fit through mean densities. Dashed lines = ± 1 S.E.

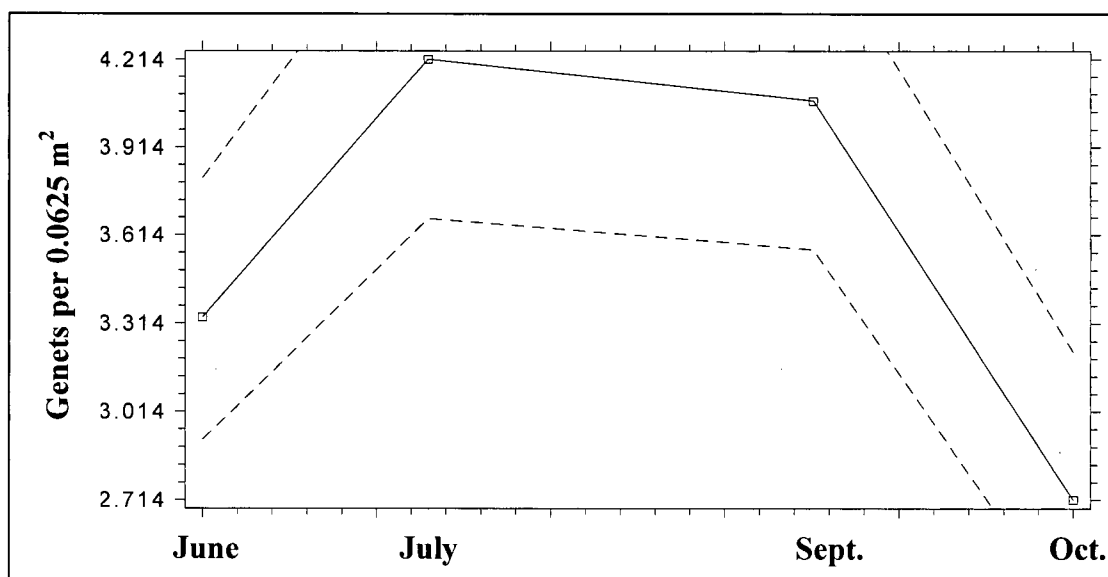


Figure A.10: Cubic spline graph of seasonal changes in haploid genet density for *Mazzaella splendens* at the wave-exposed site, Second Beach, Barkley Sound (June to October 1998). Solid line = curve fit through mean densities. Dashed lines = ± 1 S.E.

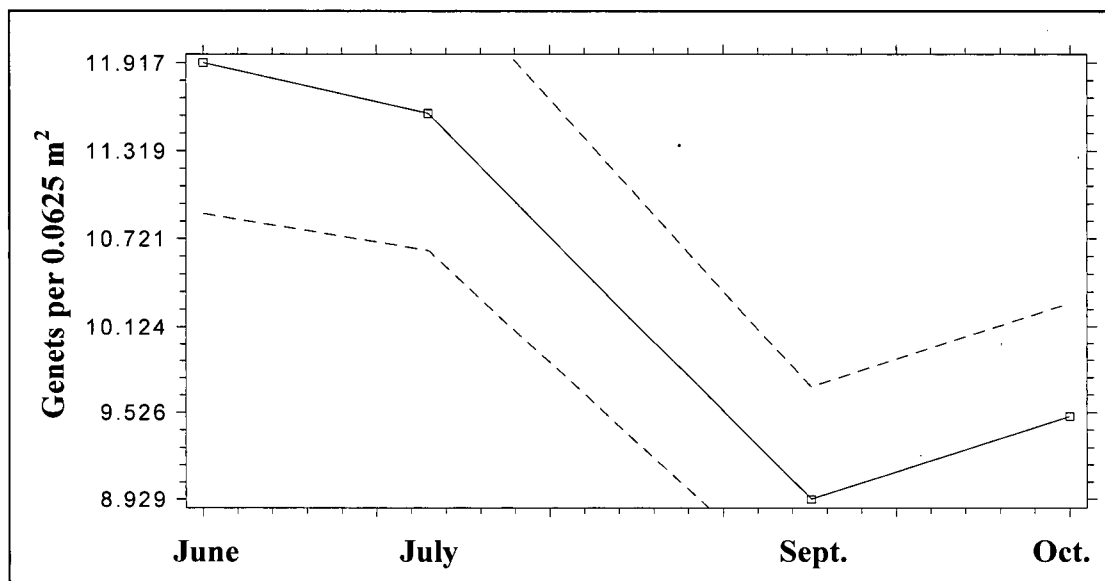


Figure A.11: Cubic spline graph of seasonal changes in diploid genet density for *Mazzaella splendens* at the wave-exposed site, Second Beach, Barkley Sound (June to October 1998). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

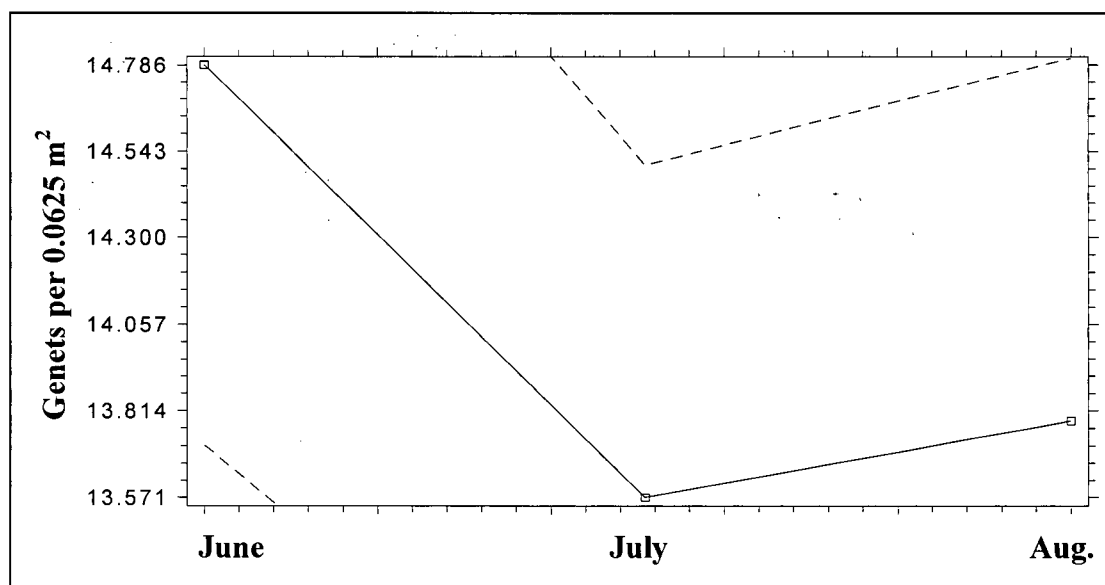


Figure A.12: Cubic spline graph of seasonal changes in genet density for *Mazzaella splendens* at the wave-exposed site, Second Beach, Barkley Sound (June to August 1999). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

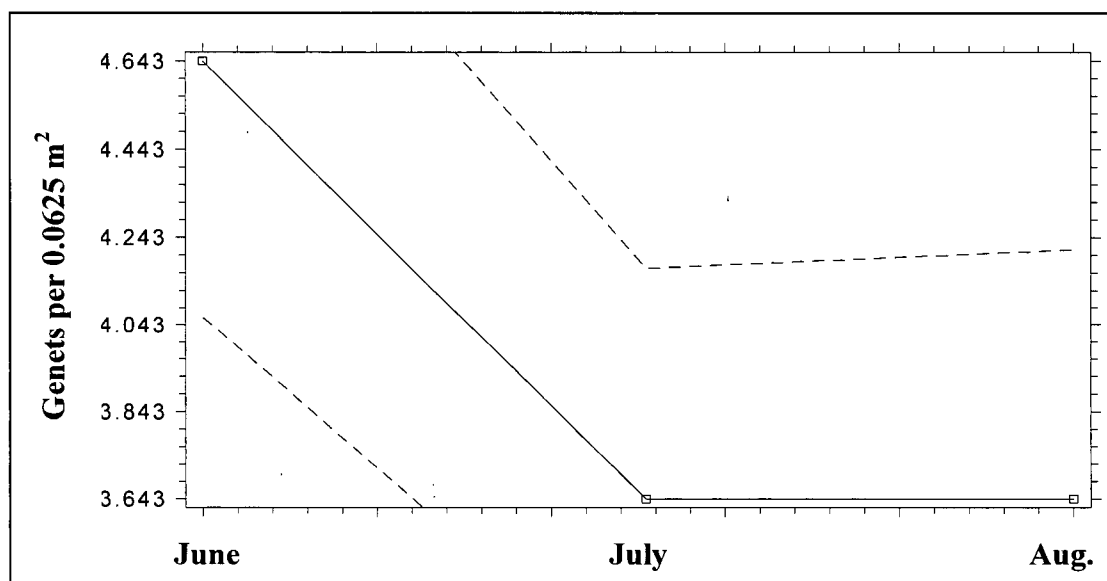


Figure A.13: Cubic spline graph of seasonal changes in haploid genet density for *Mazzaella splendens* at the wave-exposed site, Second Beach, Barkley Sound (June to August 1999). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

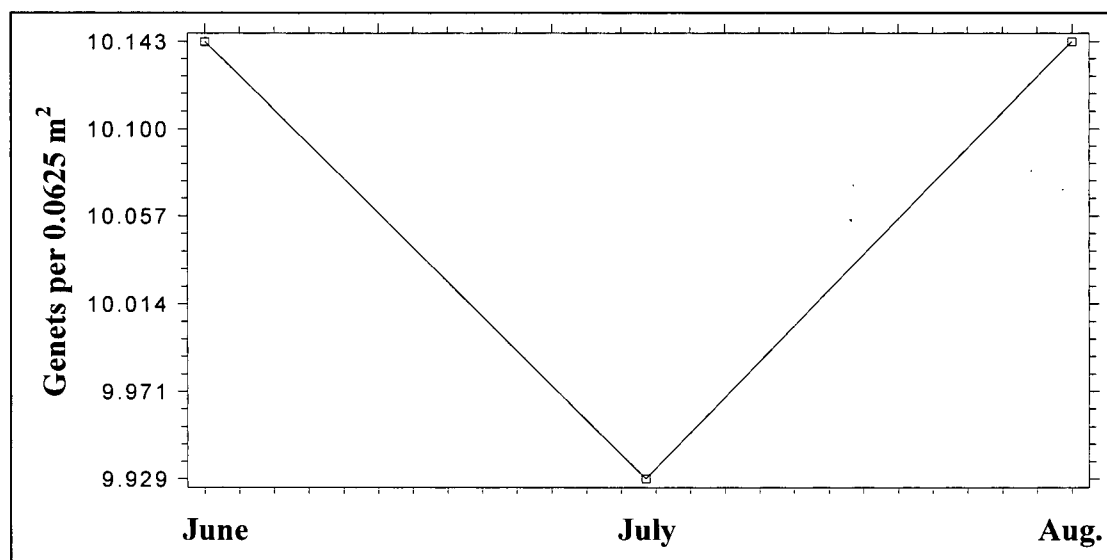


Figure A.14: Cubic spline graph of seasonal changes in diploid genet density for *Mazzaella splendens* at the wave-exposed site, Second Beach, Barkley Sound (June to August 1999). Solid line = curve fit through mean densities. Dashed lines (outside available frame) = ± 1 S E.

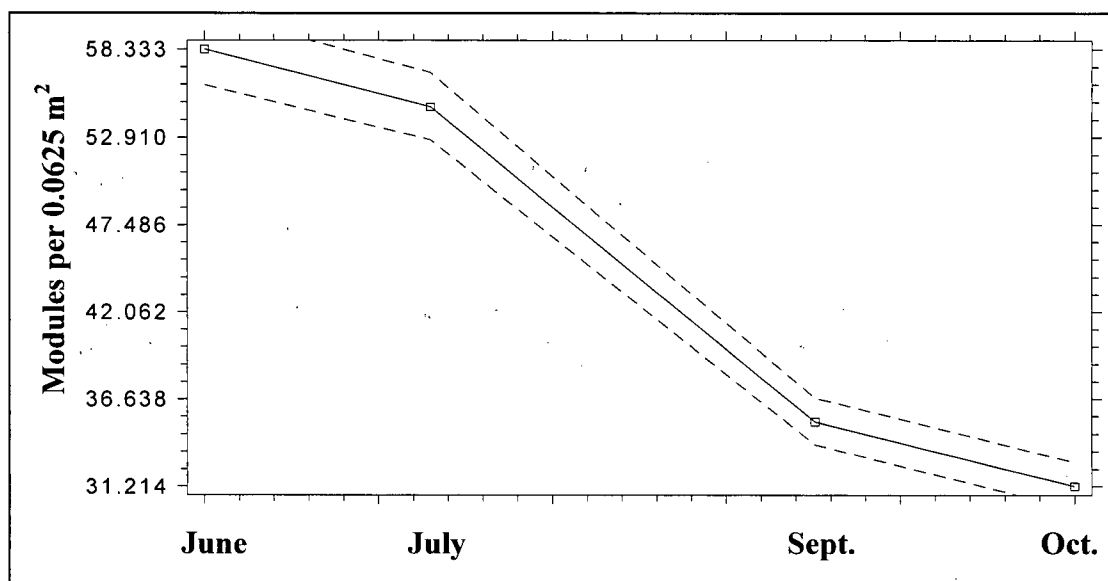


Figure A.15: Cubic spline graph of seasonal changes in module density for *Mazzaella splendens* at the wave-exposed site, Second Beach, Barkley Sound (June to October 1998). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

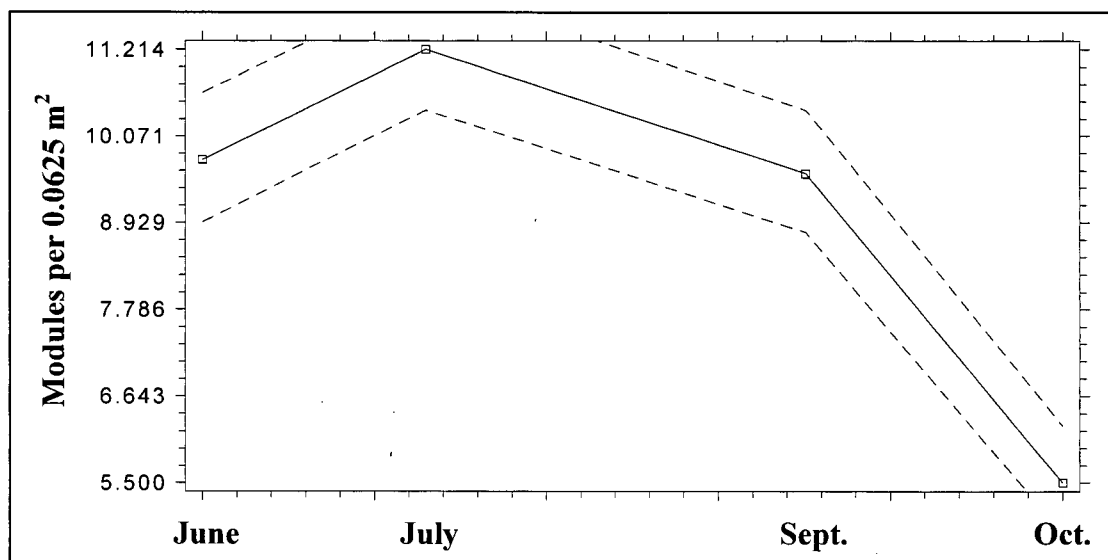


Figure A.16: Cubic spline graph of seasonal changes in haploid module density for *Mazzaella splendens* at the wave-exposed site, Second Beach, Barkley Sound (June to October 1998). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

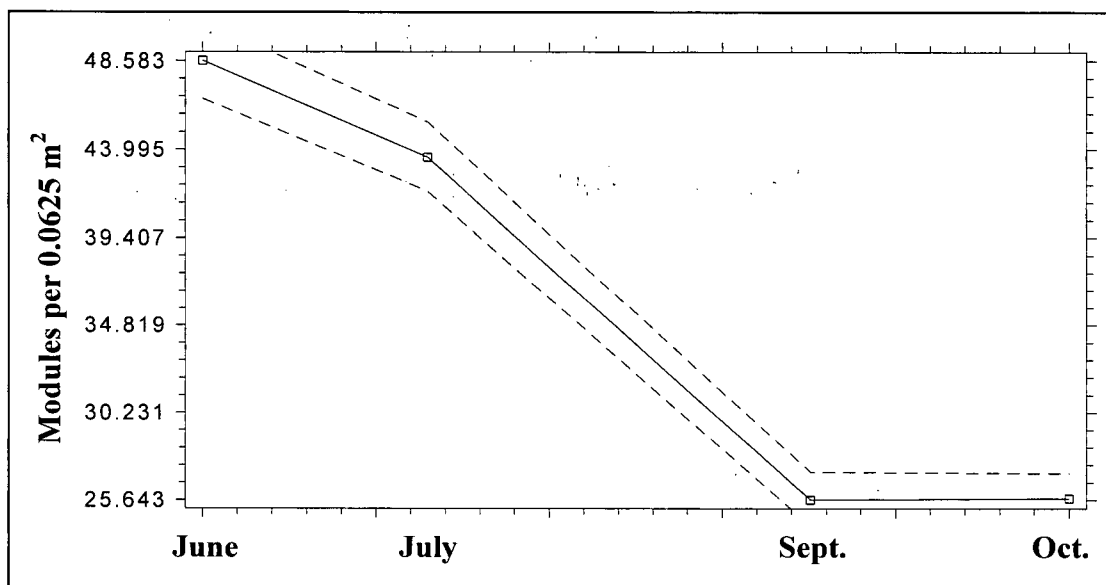


Figure A.17: Cubic spline graph of seasonal changes in diploid module density for *Mazzaella splendens* at the wave-exposed site, Second Beach, Barkley Sound (June to October 1998). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

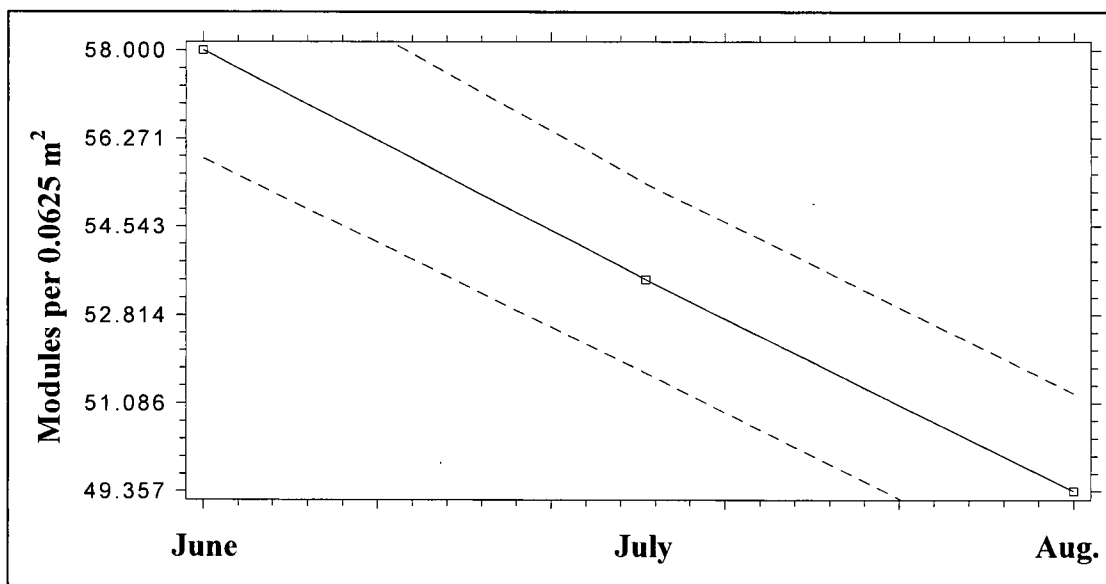


Figure A.18: Cubic spline graph of seasonal changes in module density for *Mazzaella splendens* at the wave-exposed site, Second Beach, Barkley Sound (June to August 1999). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

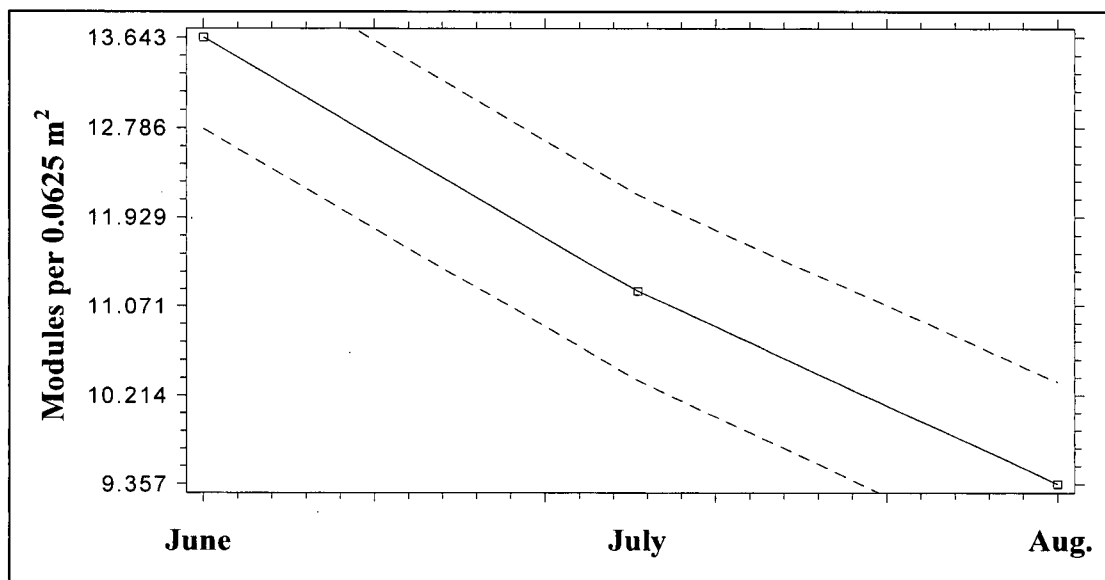


Figure A.19: Cubic spline graph of seasonal changes in haploid module density for *Mazzaella splendens* at the wave-exposed site, Second Beach, Barkley Sound (June to August 1999). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

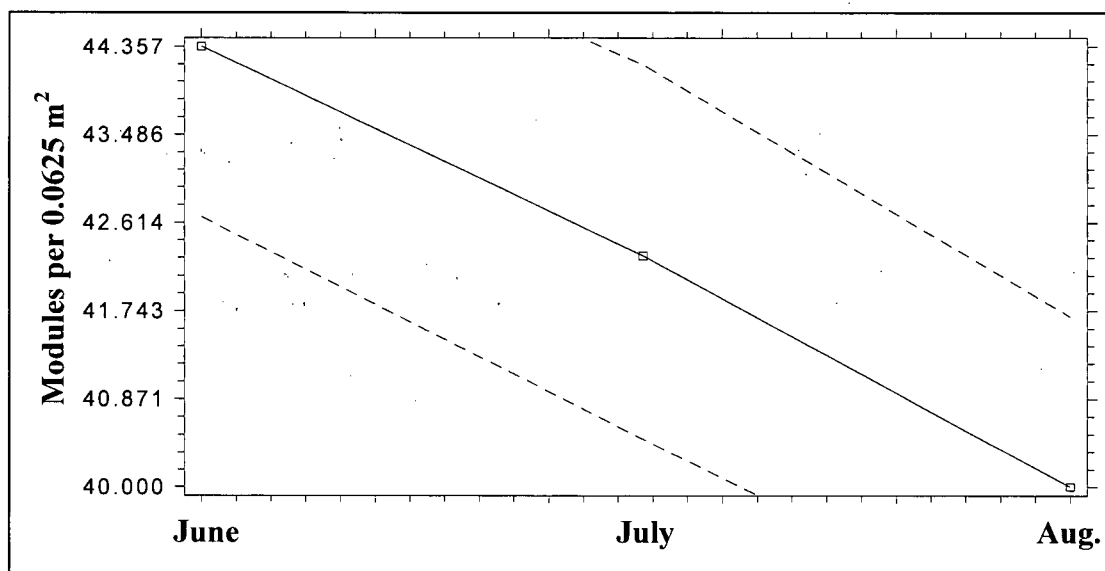


Figure A.20: Cubic spline graph of seasonal changes in diploid module density for *Mazzaella splendens* at the wave-exposed site, Second Beach, Barkley Sound (June to August 1999). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

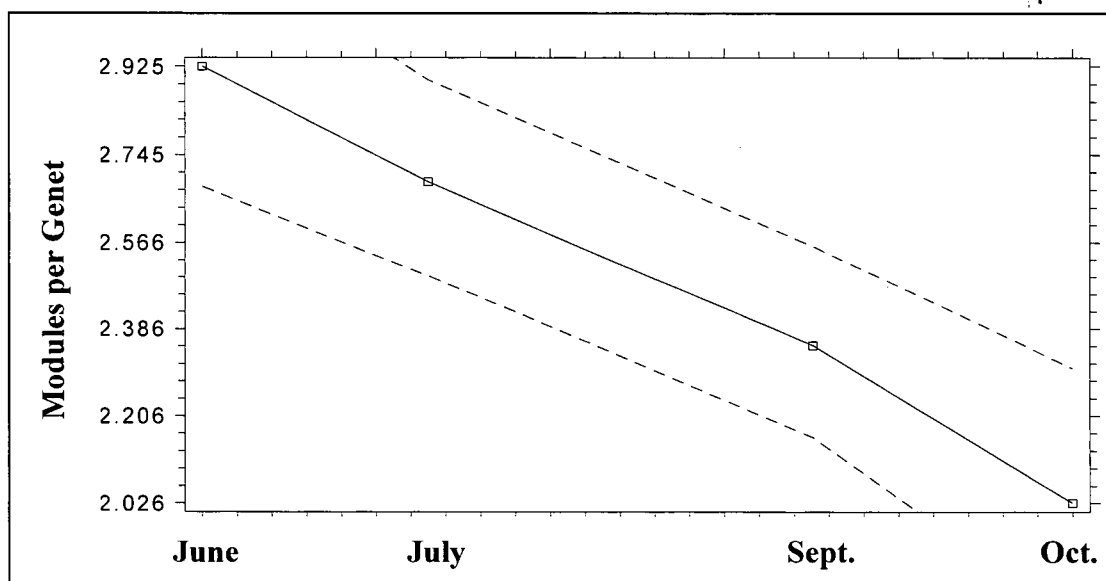


Figure A.21: Cubic spline graph of seasonal changes in haploid modules per genet for *Mazzaella splendens* at the wave-exposed site, Second Beach, Barkley Sound (June to October 1998). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

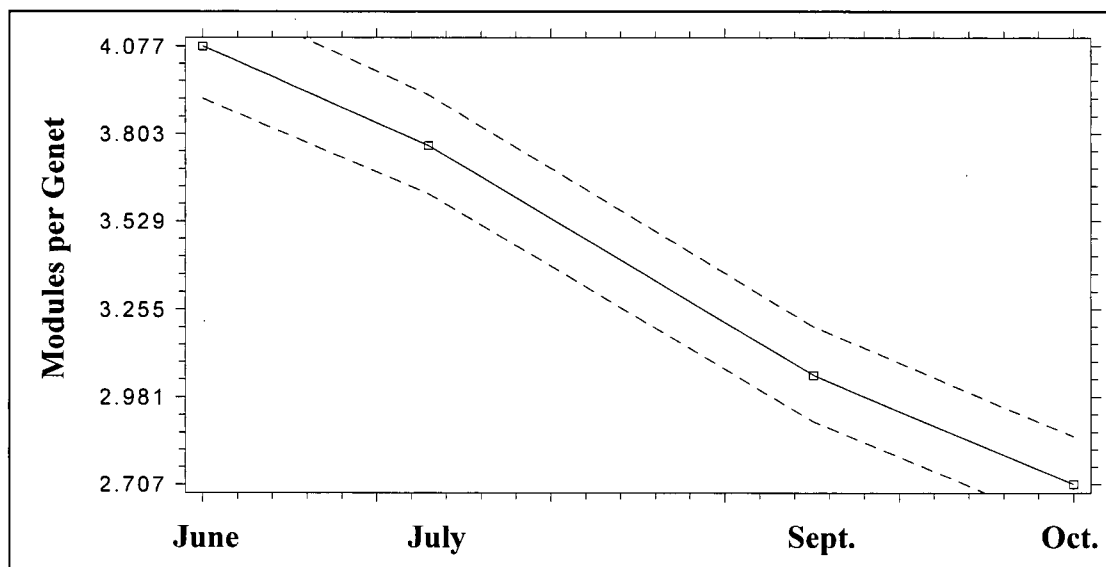


Figure A.22: Cubic spline graph of seasonal changes in diploid modules per genet for *Mazzaella splendens* at the wave-exposed site, Second Beach, Barkley Sound (June to October 1998). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

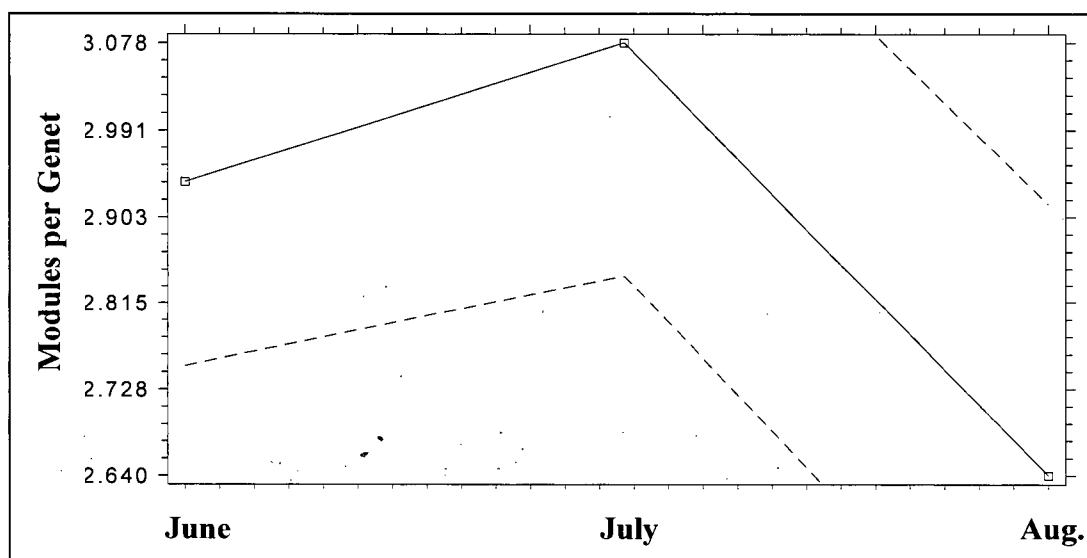


Figure A.23: Cubic spline graph of seasonal changes in haploid modules per genet for *Mazzaella splendens* at the wave-exposed site, Second Beach, Barkley Sound (June to August 1999). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

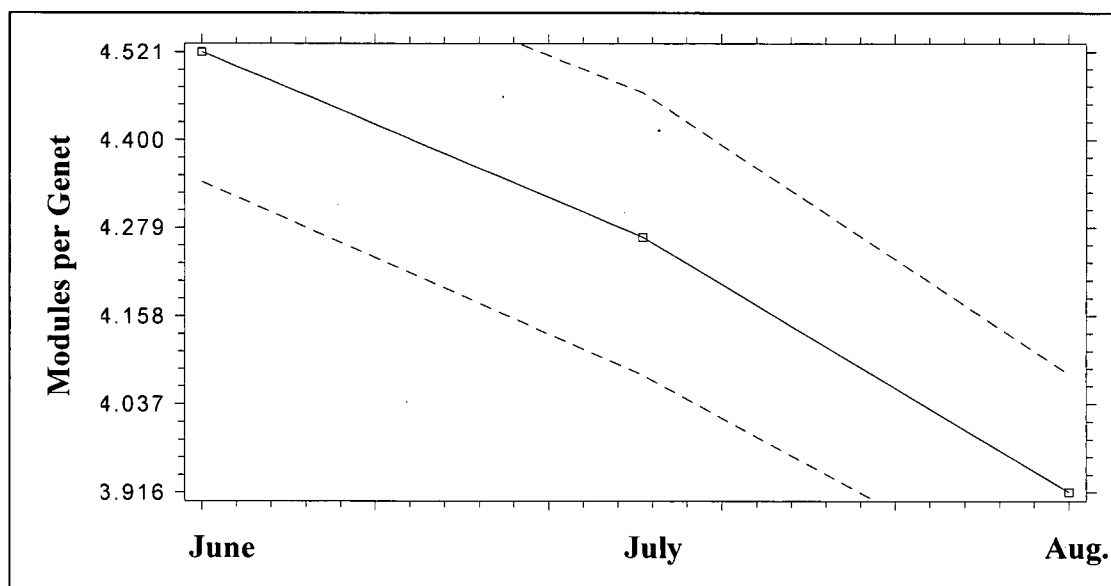


Figure A.24: Cubic spline graph of seasonal changes in diploid modules per genet for *Mazzaella splendens* at the wave-exposed site, Second Beach, Barkley Sound (June to August 1999). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

APPENDIX B

Additional figures to accompany Chapter 3.

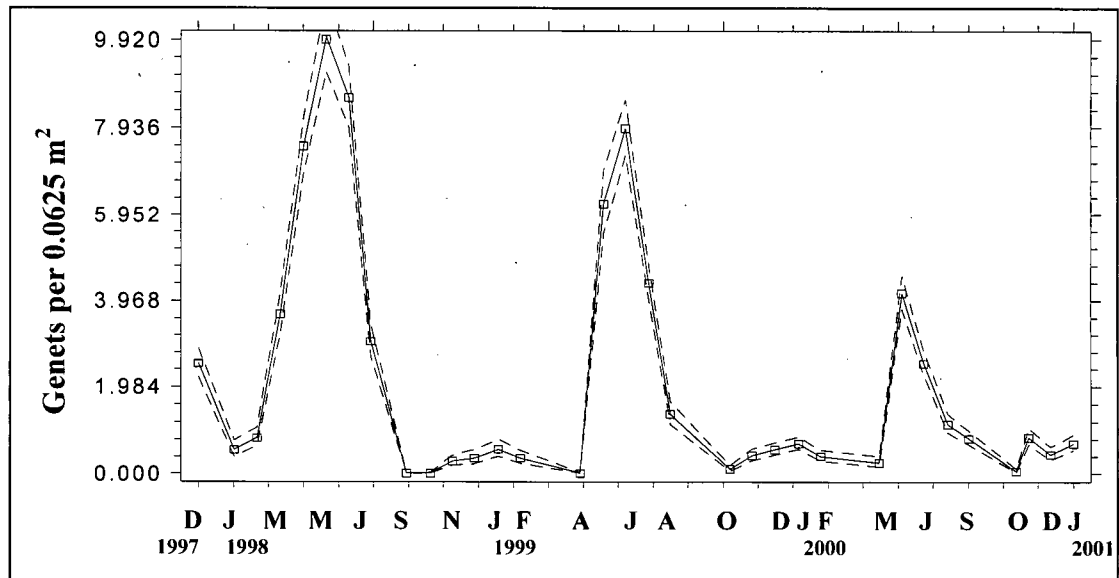


Figure B.1: Cubic spline graph of seasonal changes in density of genets remaining from the previous census for *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

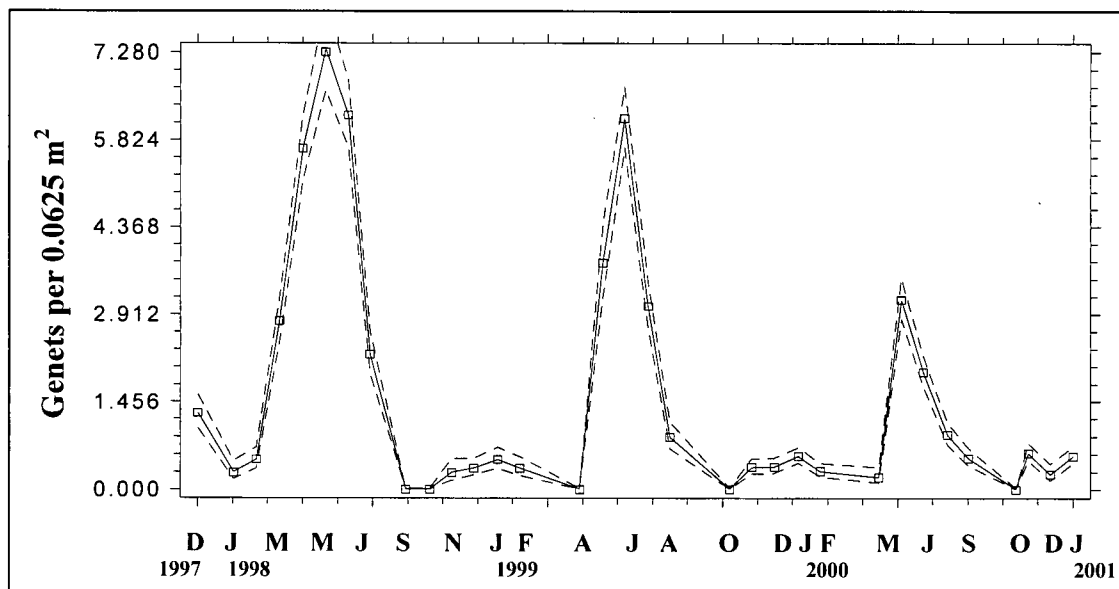


Figure B.2: Cubic spline graph of seasonal changes in density of haploid genets remaining from the previous census for *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

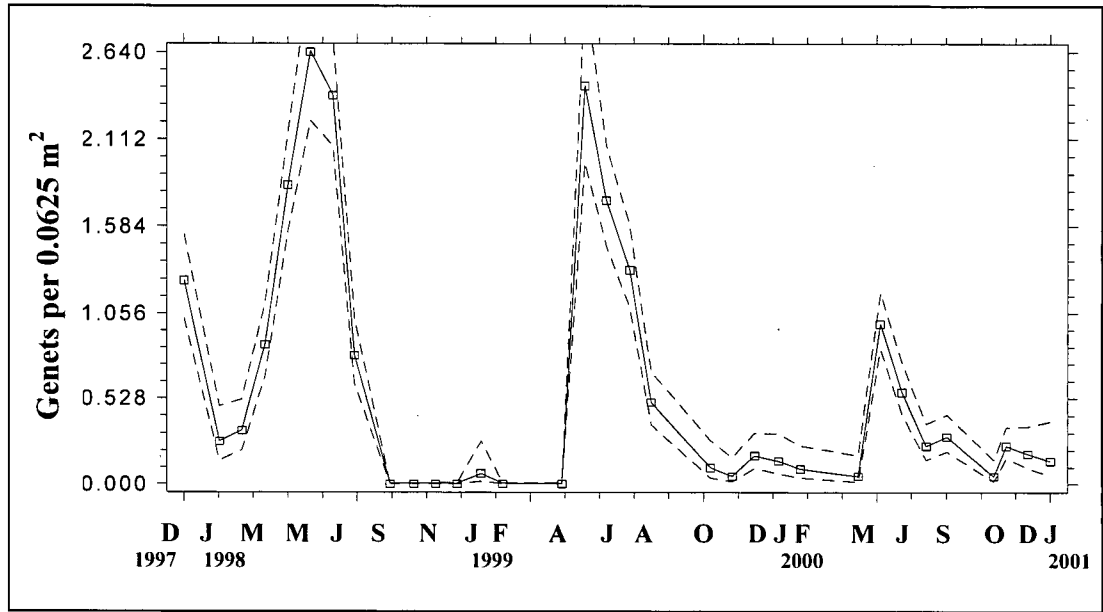


Figure B.3: Cubic spline graph of seasonal changes in density of diploid genets remaining from the previous census for *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

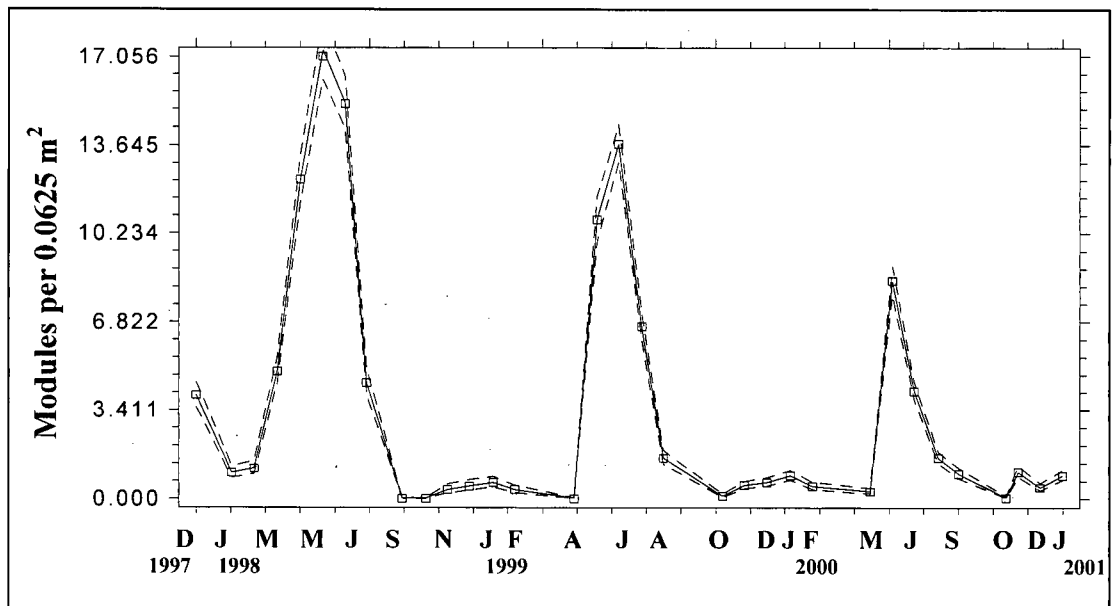


Figure B.4: Cubic spline graph of seasonal changes in density of modules remaining from the previous census for *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

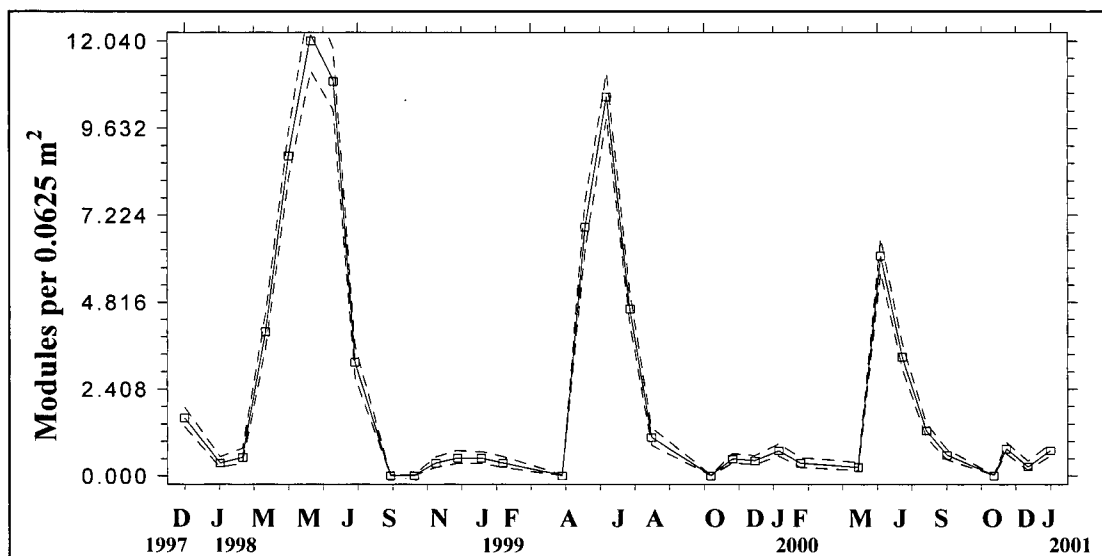


Figure B.5: Cubic spline graph of seasonal changes in density of haploid modules remaining from the previous census for *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

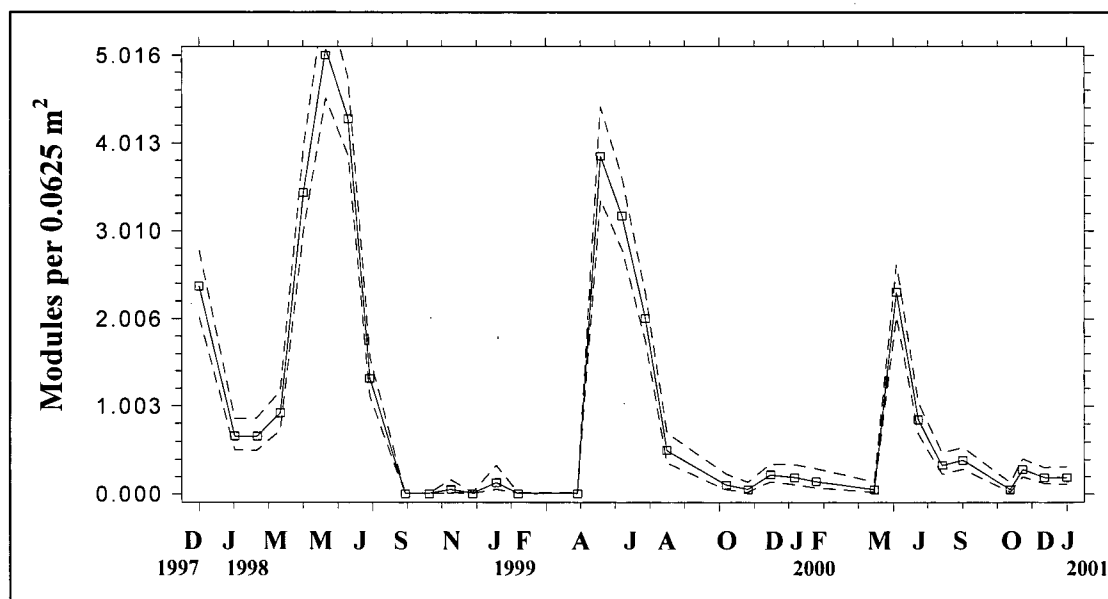


Figure B.6: Cubic spline graph of seasonal changes in density of diploid modules remaining from the previous census for *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

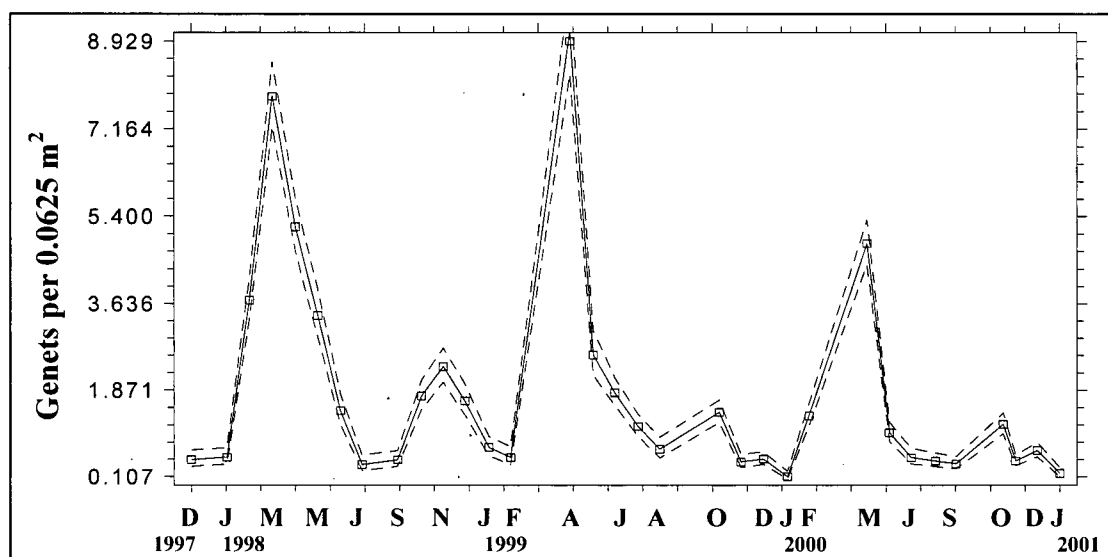


Figure B.7: Cubic spline graph of seasonal changes in density of new genets appearing since the previous census for *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

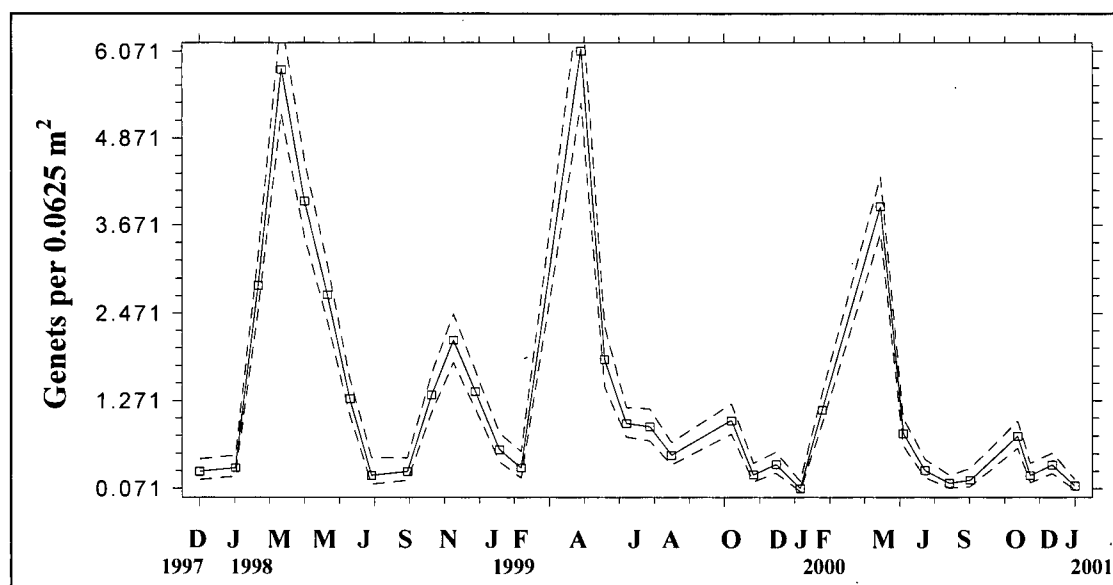


Figure B.8: Cubic spline graph of seasonal changes in density of new haploid genets appearing since the previous census for *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

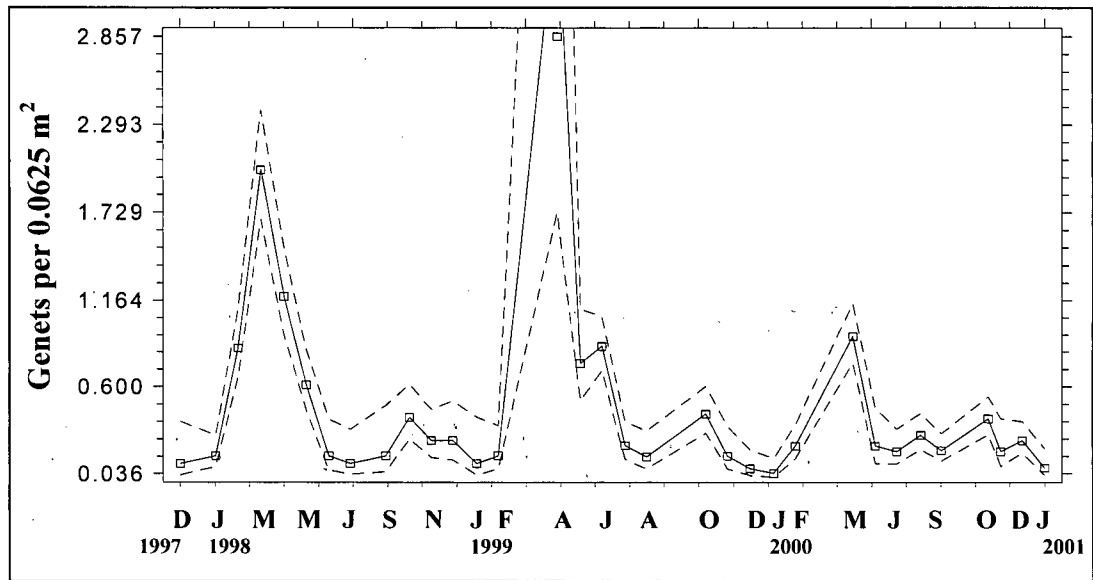


Figure B.9: Cubic spline graph of seasonal changes in density of new diploid genets appearing since the previous census for *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

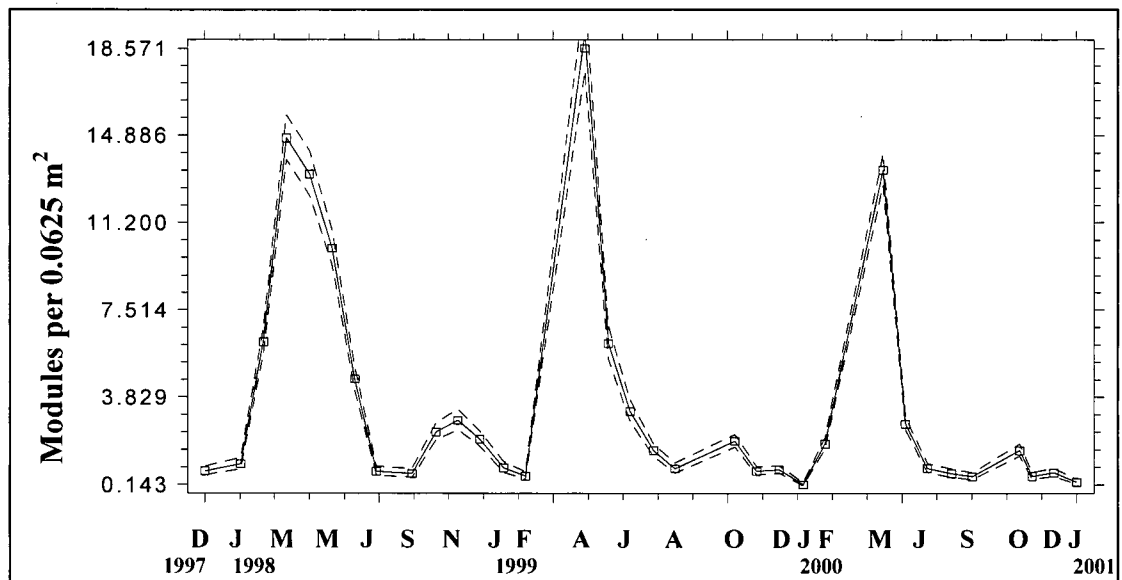


Figure B.10: Cubic spline graph of seasonal changes in density of new modules appearing since the previous census for *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

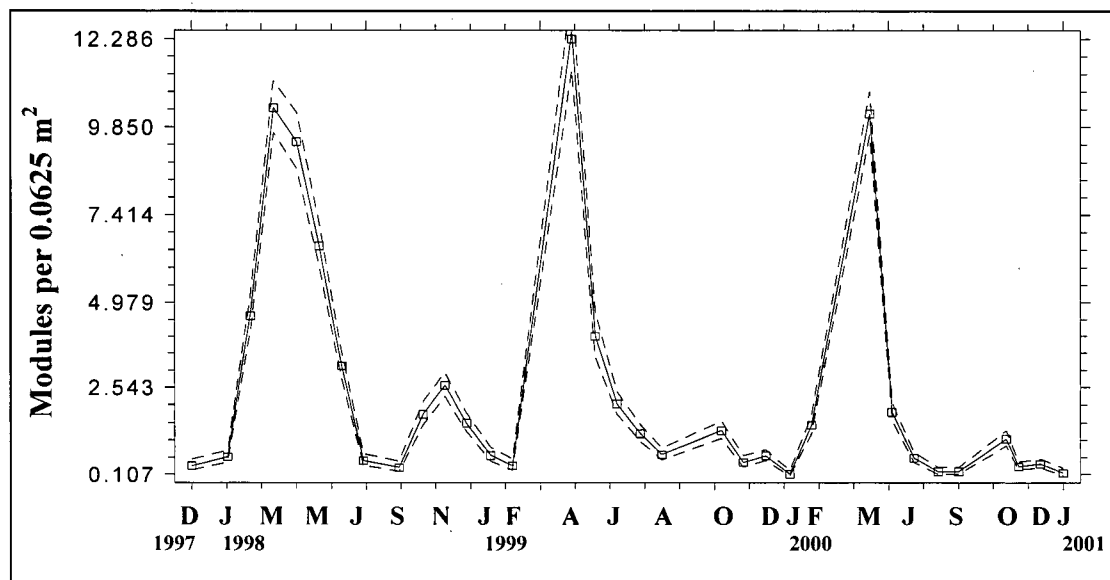


Figure B.11: Cubic spline graph of seasonal changes in density of new haploid modules appearing since the previous census for *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

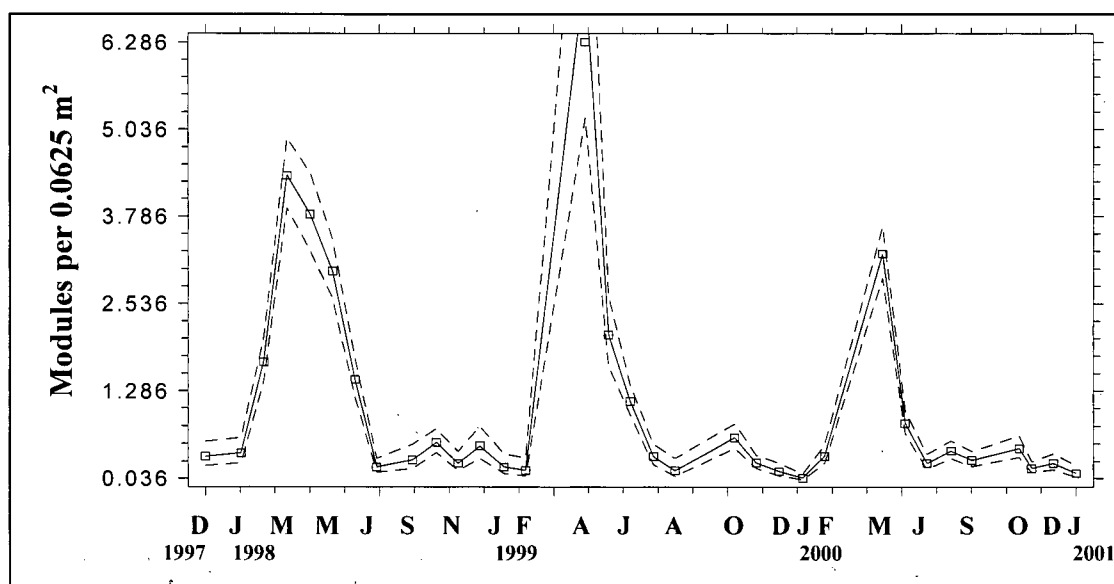


Figure B.12: Cubic spline graph of seasonal changes in density of new diploid modules appearing since the previous census for *Mazzaella splendens* at the wave-sheltered site, Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

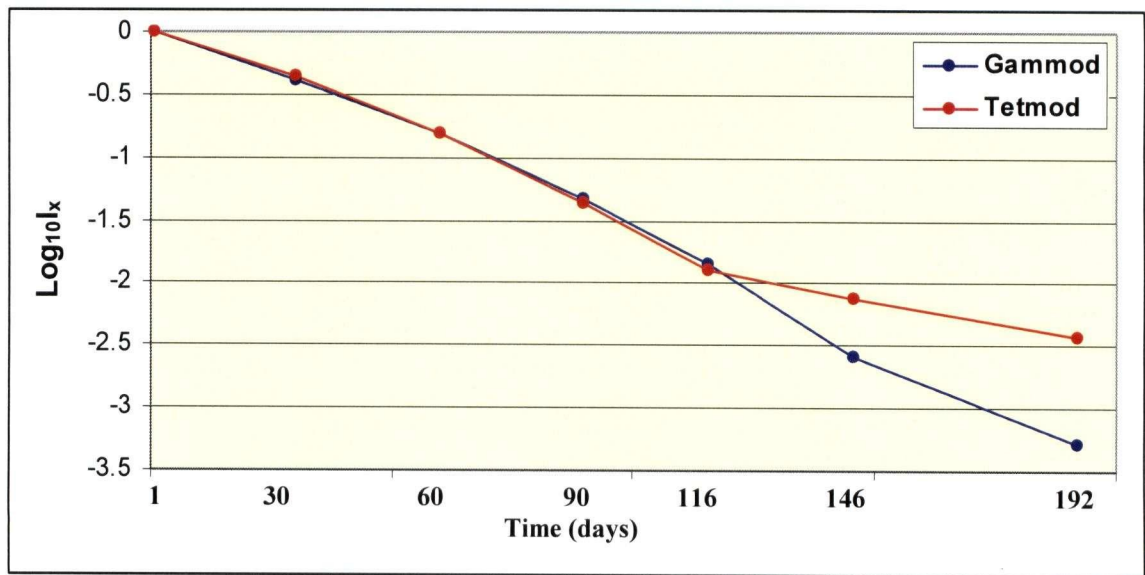


Figure B.13: Survival ($\log_{10} l_x$) in a static cohort of 2747 modules (1952 haploid, 795 diploid) of *Mazzaella splendens* tagged at Second Beach, Barkley Sound from November, 1997 to December 2000. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

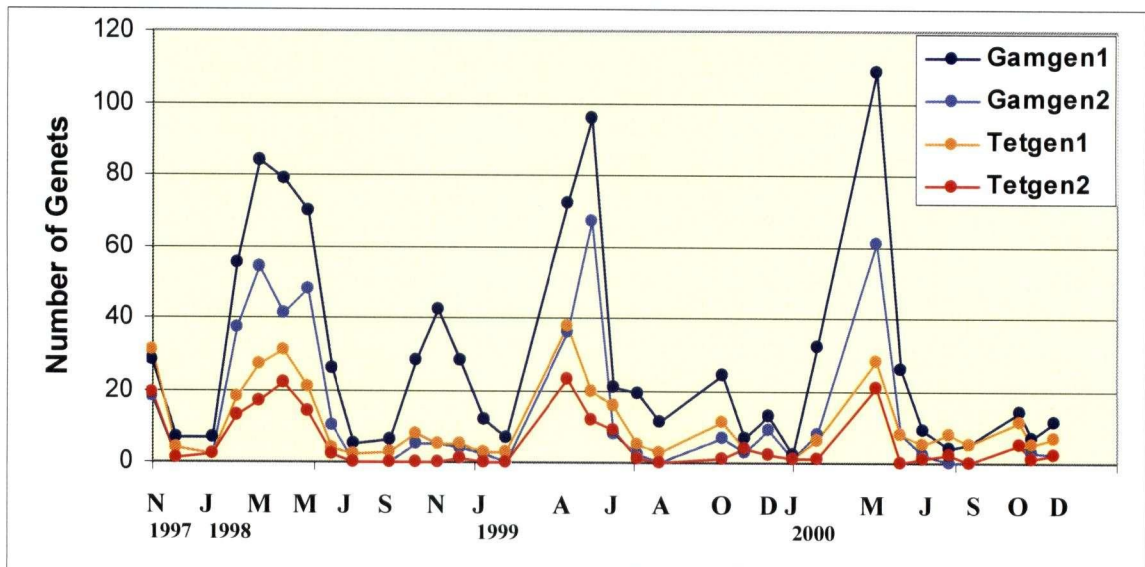


Figure B.14: Cohort size (new genets appearing in each census) for *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to December 2000). Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets. For each life history phase, 1 denotes the number in the cohort and 2 denotes the number surviving from the first to the second census.

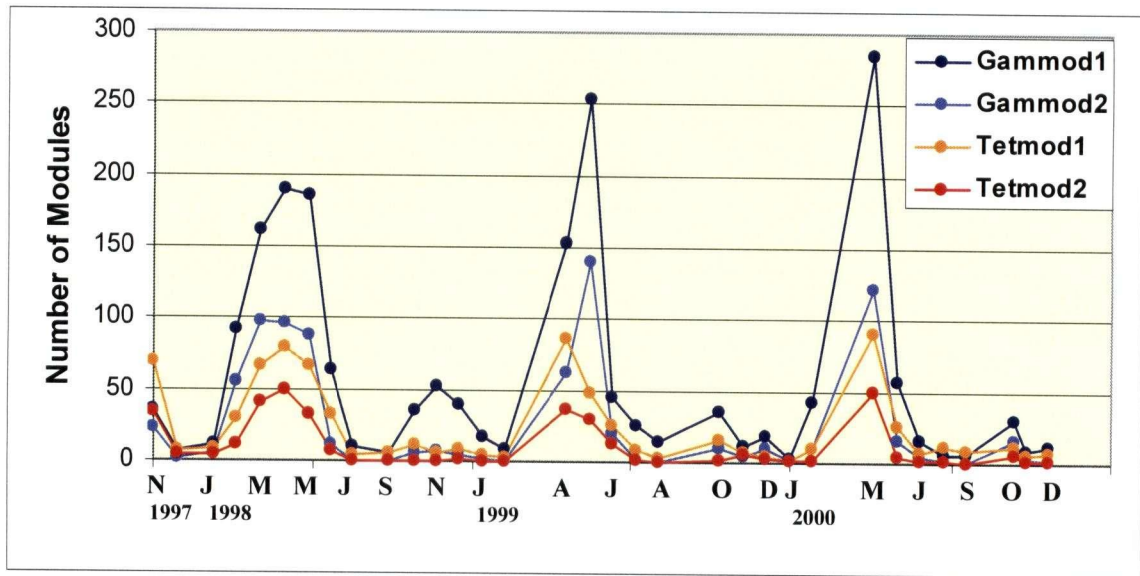


Figure B.15: New modules appearing in each census of *Mazzaella splendens*, at Second Beach, Barkley Sound (November 1997 to December 2000). Gammod = gametophyte modules. Tetmod = tetrasporophyte modules. For each life history phase, 1 denotes the number in the cohort and 2 denotes the number surviving from the first to the second census.

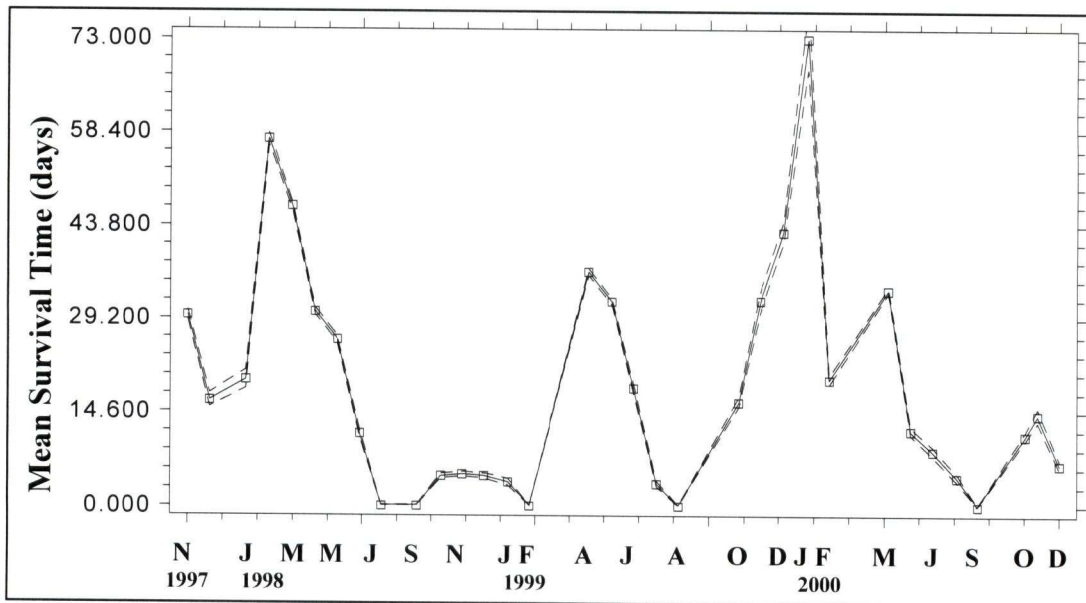


Figure B.16: Cubic spline graph of seasonal changes in mean survival time for genets of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to December 2000). Solid line = curve fit through mean areas. Dashed lines = ± 1 S.E.

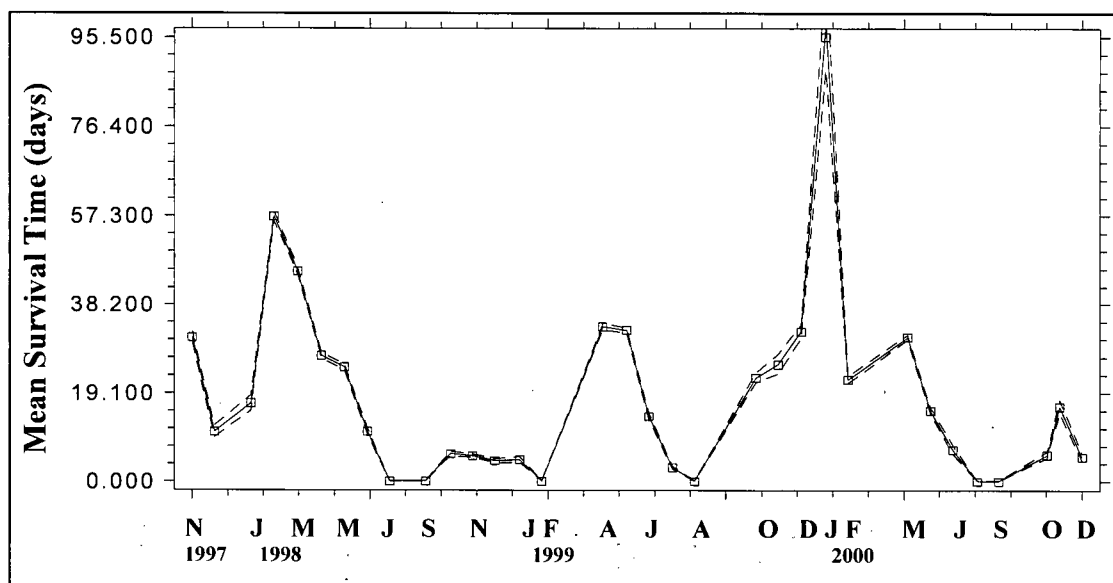


Figure B.17: Cubic spline graph of seasonal changes in mean survival time for haploid genets of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to December 2000). Solid line = curve fit through mean areas. Dashed lines = ± 1 S.E.

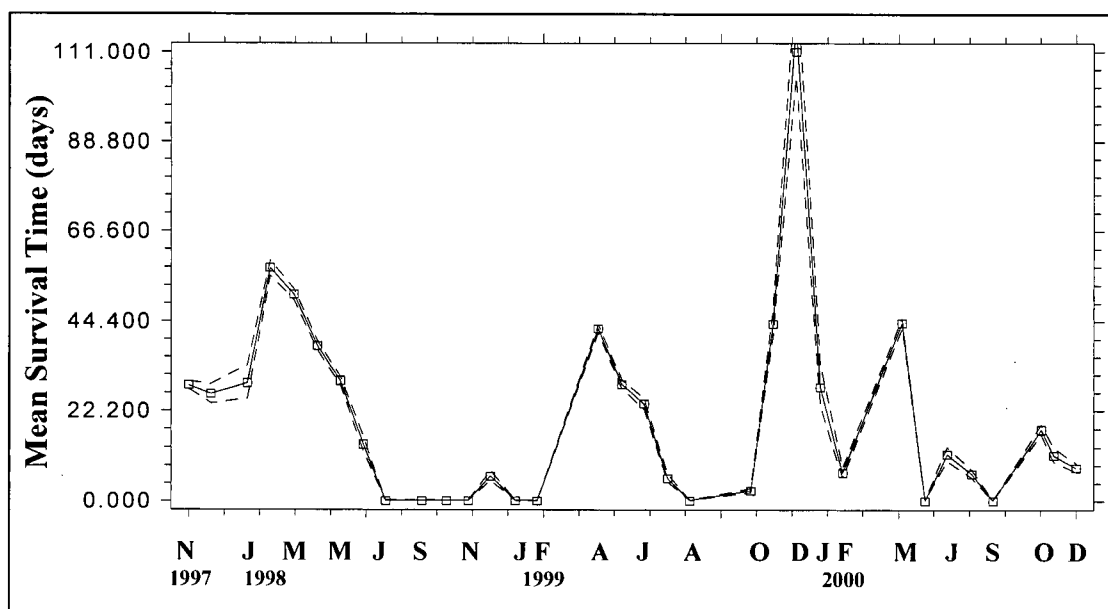


Figure B.18: Cubic spline graph of seasonal changes in mean survival time for diploid genets of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to December 2000). Solid line = curve fit through mean areas. Dashed lines = ± 1 S.E.

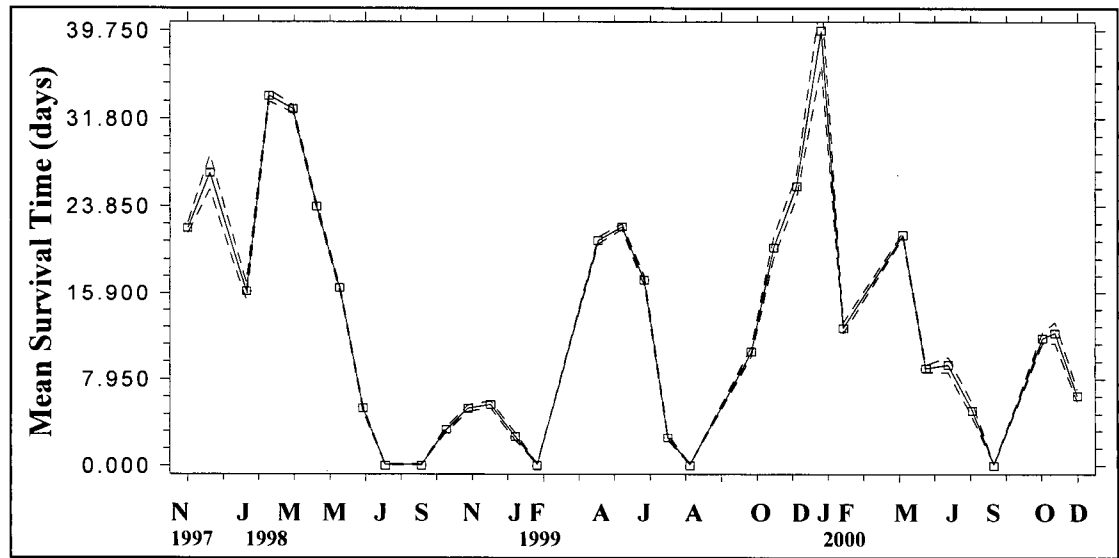


Figure B.19: Cubic spline graph of seasonal changes in mean survival time for modules of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to December 2000). Solid line = curve fit through mean areas. Dashed lines = ± 1 S E.

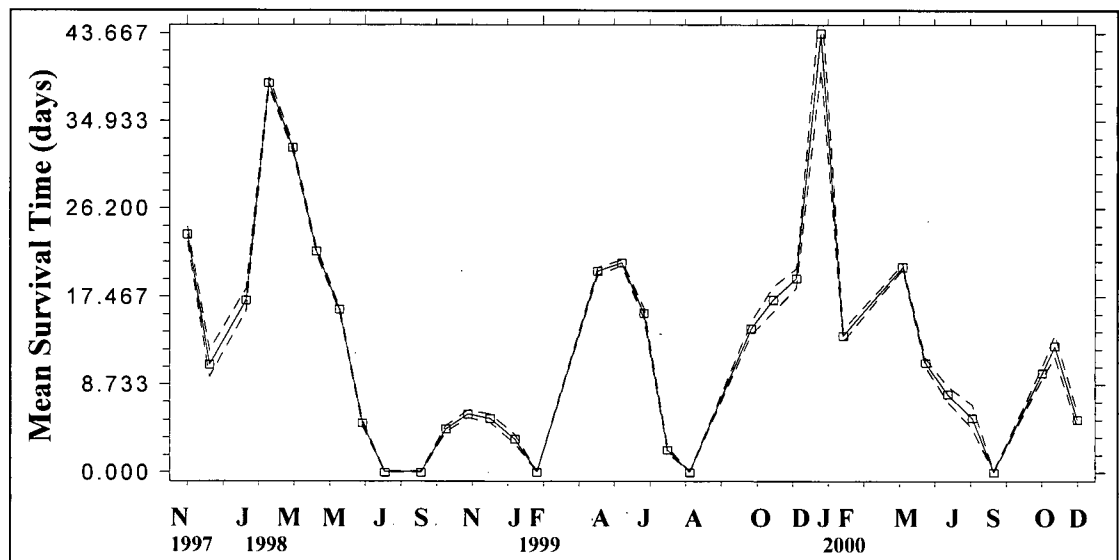


Figure B.20: Cubic spline graph of seasonal changes in mean survival time for haploid modules of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to December 2000). Solid line = curve fit through mean areas. Dashed lines = ± 1 S E.

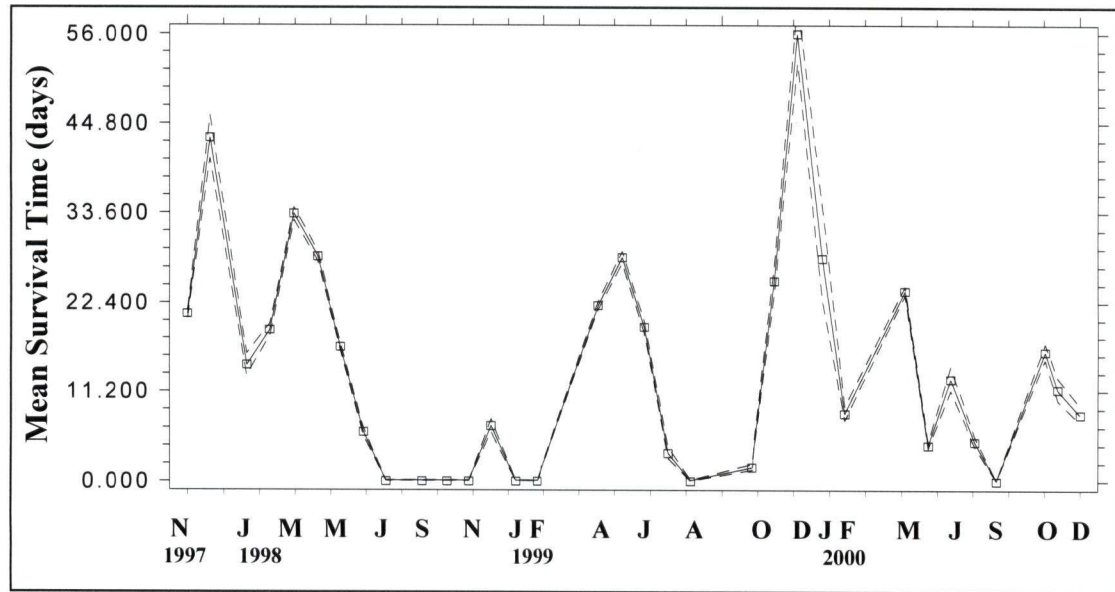


Figure B.21: Cubic spline graph of seasonal changes in mean survival time for diploid modules of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to December 2000). Solid line = curve fit through mean areas. Dashed lines = ± 1 S.E.

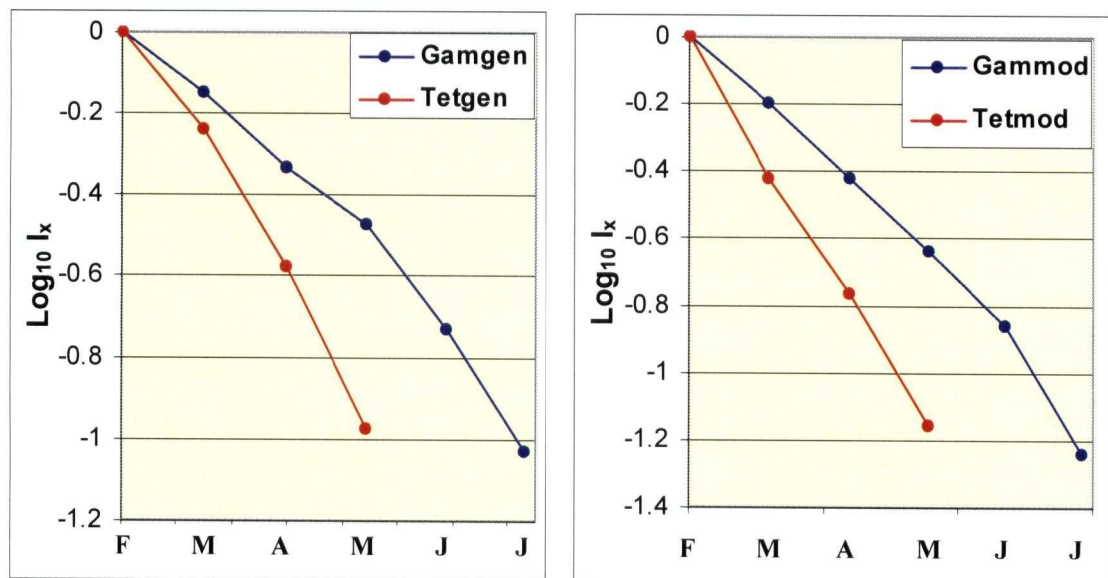


Figure B.22: Survival ($\log_{10} l_x$) in a cohort of 77 genets (58 haploid, 19 diploid) and 123 modules (94 haploid, 29 diploid) of *Mazzaella splendens* tagged at Second Beach, Barkley Sound in February, 1998. Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

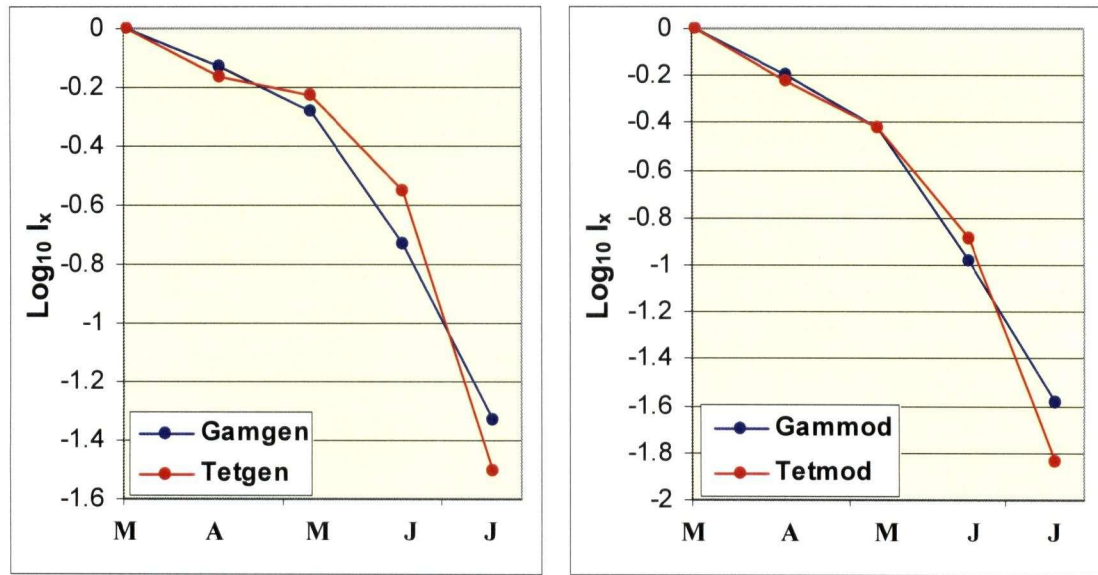


Figure B.23: Survival ($\log_{10} l_x$) in a cohort of 125 genets (93 haploid, 32 diploid) and 234 modules (165 haploid, 69 diploid) of *Mazzaella splendens* tagged at Second Beach, Barkley Sound in March, 1998. Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

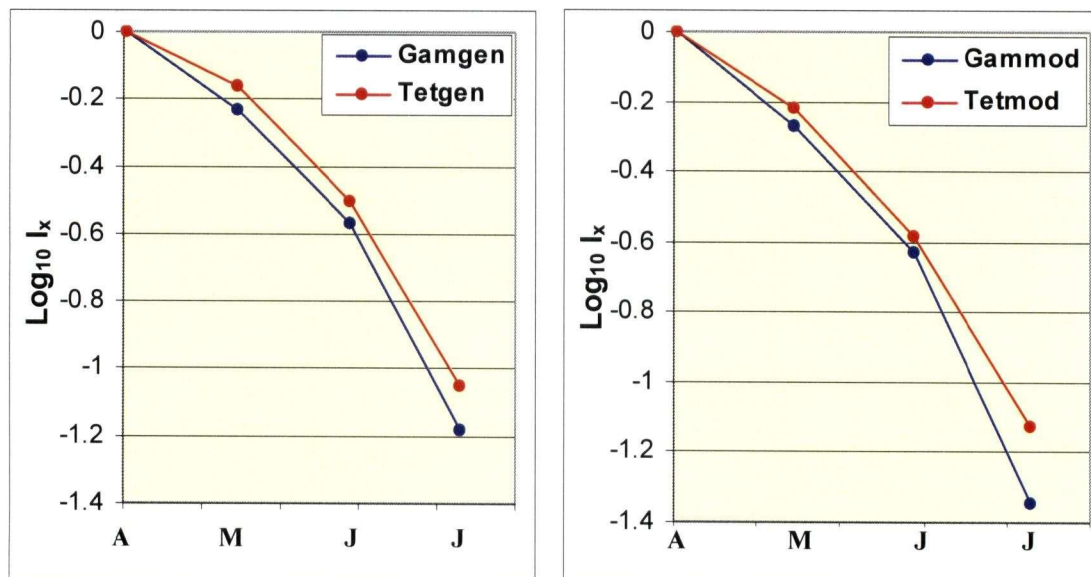


Figure B.24: Survival ($\log_{10} l_x$) in a cohort of 161 genets (116 haploid, 45 diploid) and 274 modules (193 haploid, 81 diploid) of *Mazzaella splendens* tagged at Second Beach, Barkley Sound in April, 1998. Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

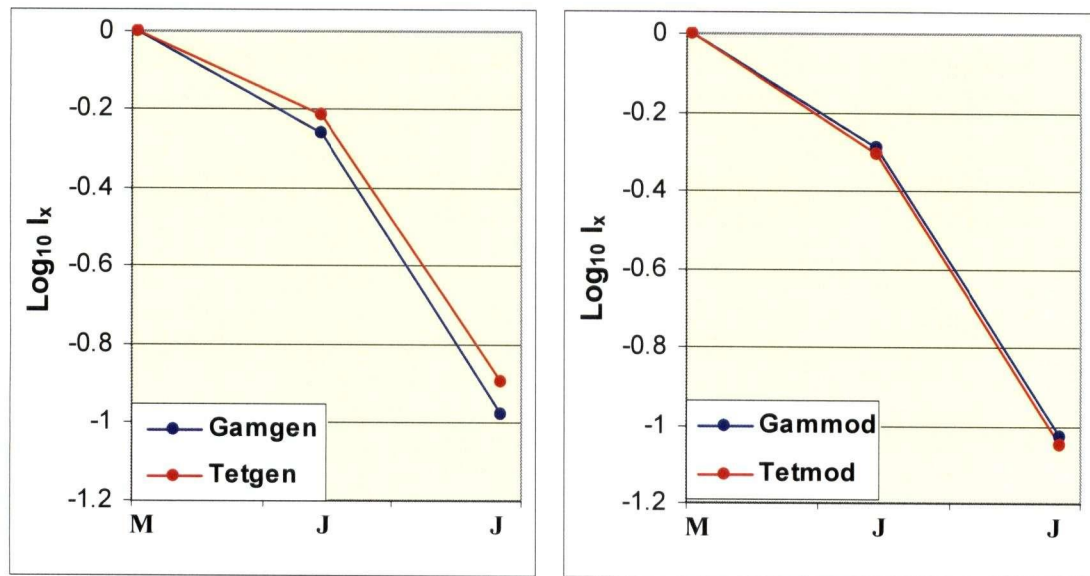


Figure B.25: Survival ($\log_{10} l_x$) in a cohort of 151 genets (112 haploid, 39 diploid) and 252 modules (185 haploid, 67 diploid) of *Mazzaella splendens* tagged at Second Beach, Barkley Sound in May, 1998. Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

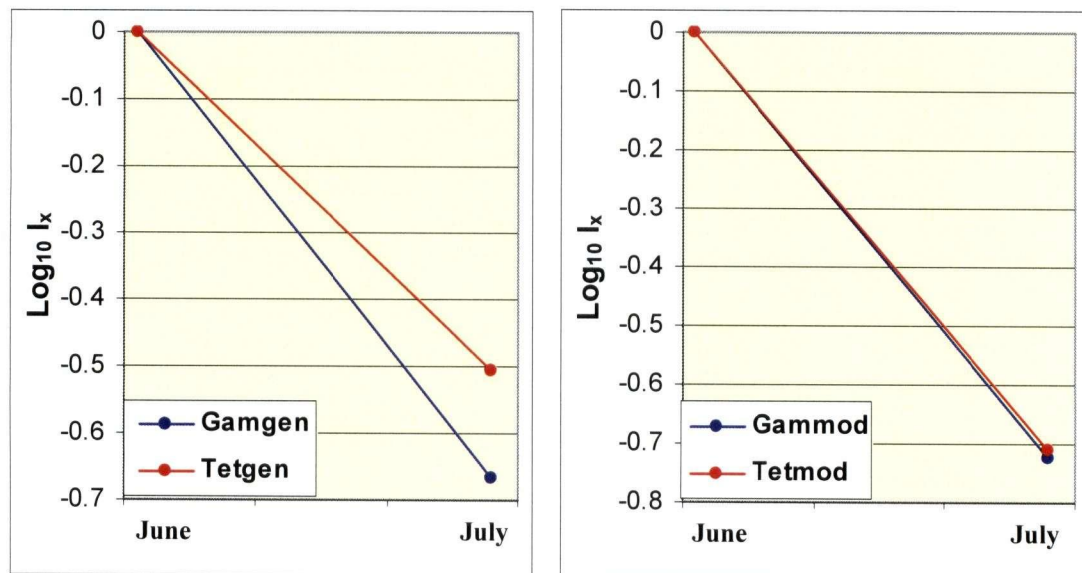


Figure B.26: Survival ($\log_{10} l_x$) in a cohort of 61 genets (45 haploid, 16 diploid) and 99 modules (63 haploid, 36 diploid) of *Mazzaella splendens* tagged at Second Beach, Barkley Sound in June, 1998. Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

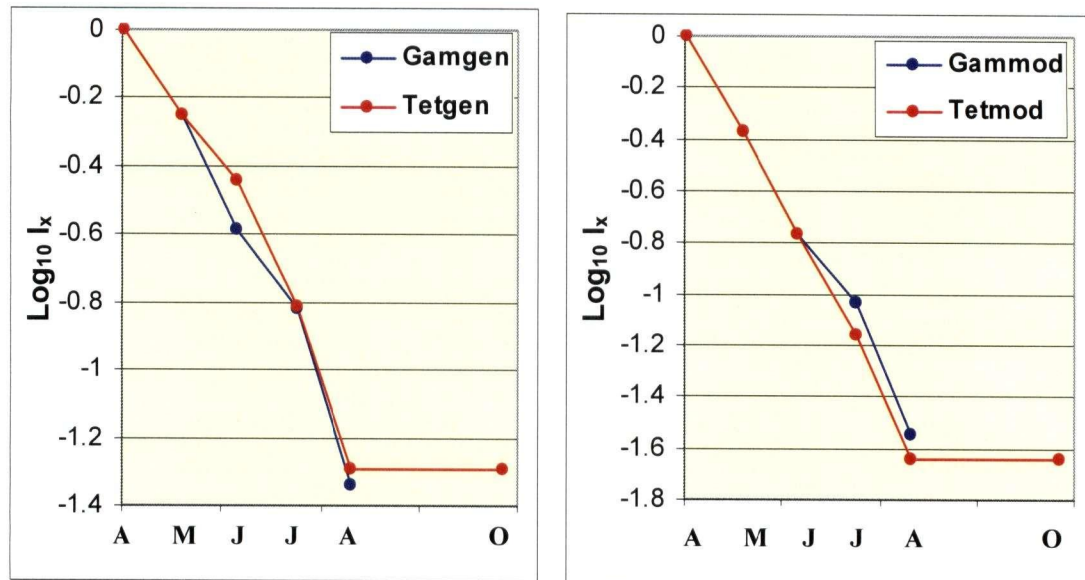


Figure B.27: Survival ($\log_{10} l_x$) in a cohort of 110 genets (71 haploid, 39 diploid) and 238 modules (151 haploid, 87 diploid) of *Mazzaella splendens* tagged at Second Beach, Barkley Sound in April, 1999. Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

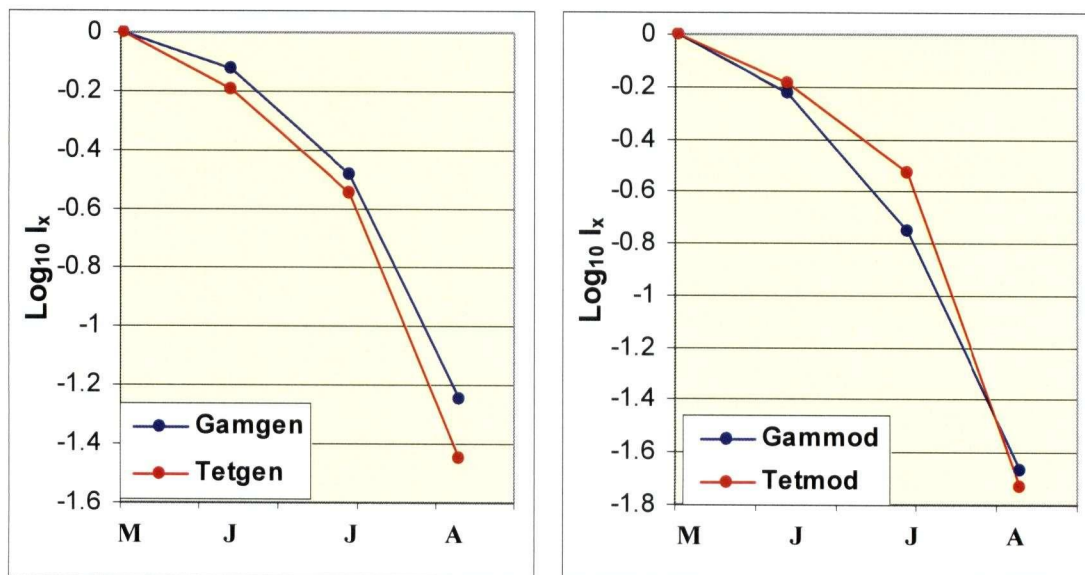


Figure B.28: Survival ($\log_{10} l_x$) in a cohort of 142 genets (114 haploid, 28 diploid) and 306 modules (252 haploid, 54 diploid) of *Mazzaella splendens* tagged at Second Beach, Barkley Sound in May, 1999. Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

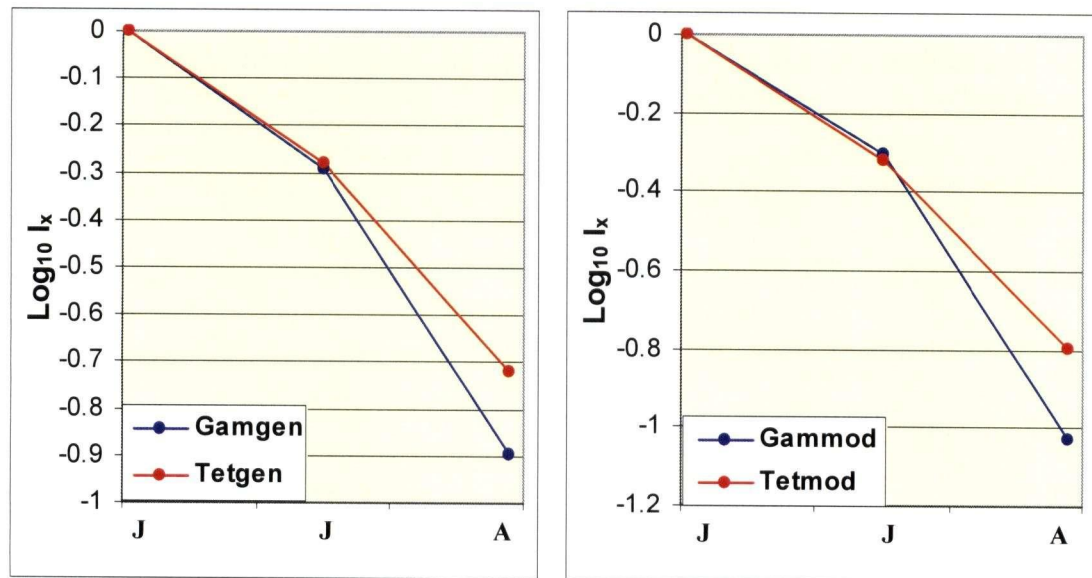


Figure B.29: Survival ($\log_{10} l_x$) in a cohort of 55 genets (34 haploid, 21 diploid) and 71 modules (46 haploid, 25 diploid) of *Mazzaella splendens* tagged at Second Beach, Barkley Sound in June, 1999. Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

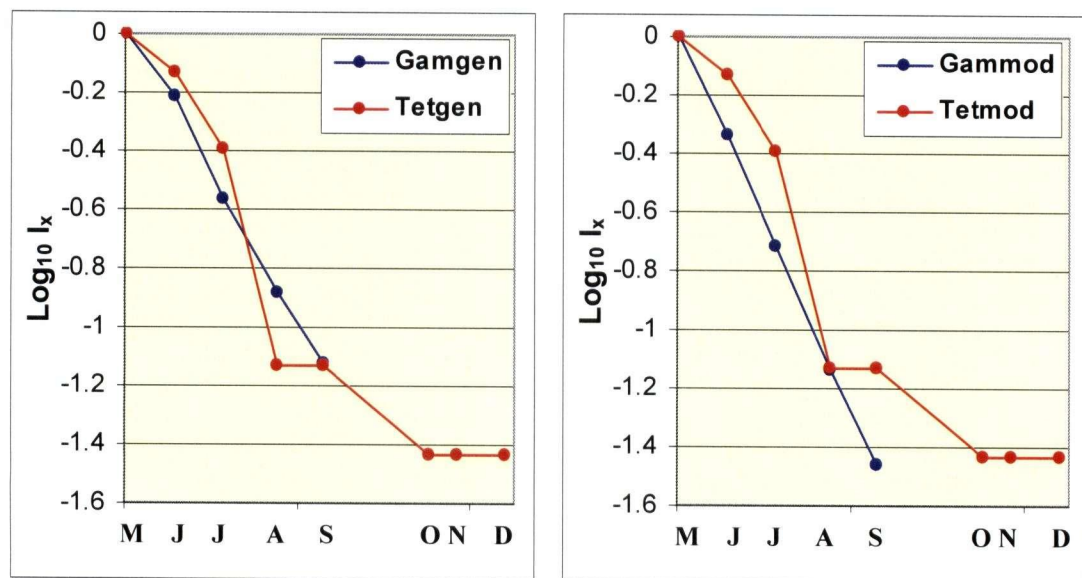


Figure B.30: Survival ($\log_{10} l_x$) in a cohort of 142 genets (115 haploid, 27 diploid) and 373 modules (283 haploid, 90 diploid) of *Mazzaella splendens* tagged at Second Beach, Barkley Sound in May, 2000. Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

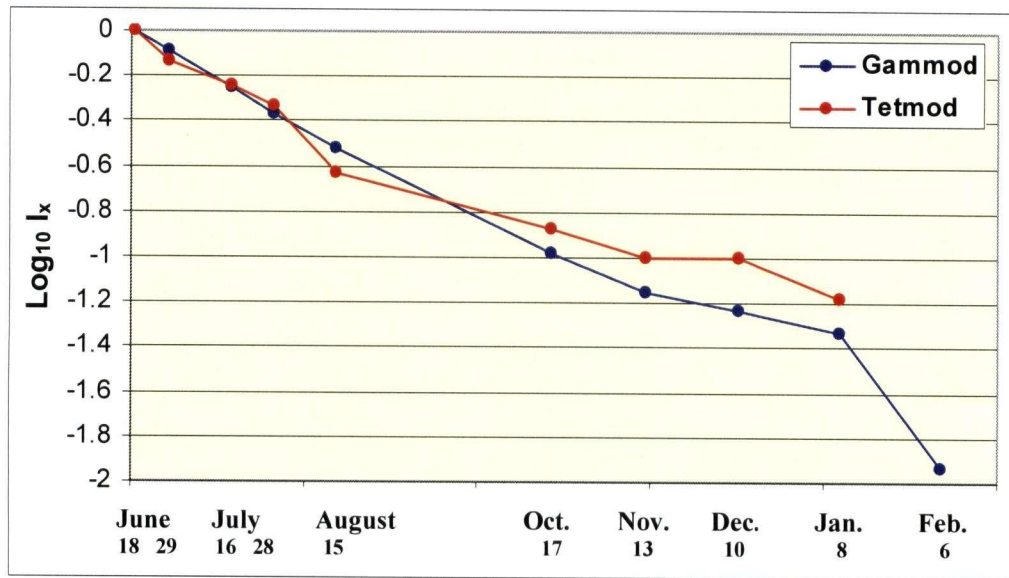


Figure B.31: Survival ($\log_{10} l_x$) in a cohort of 116 modules (86 haploid, 30 diploid) of *Mazzaella splendens* tagged at Brockton Point, Vancouver Harbour on June 18, 1989. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

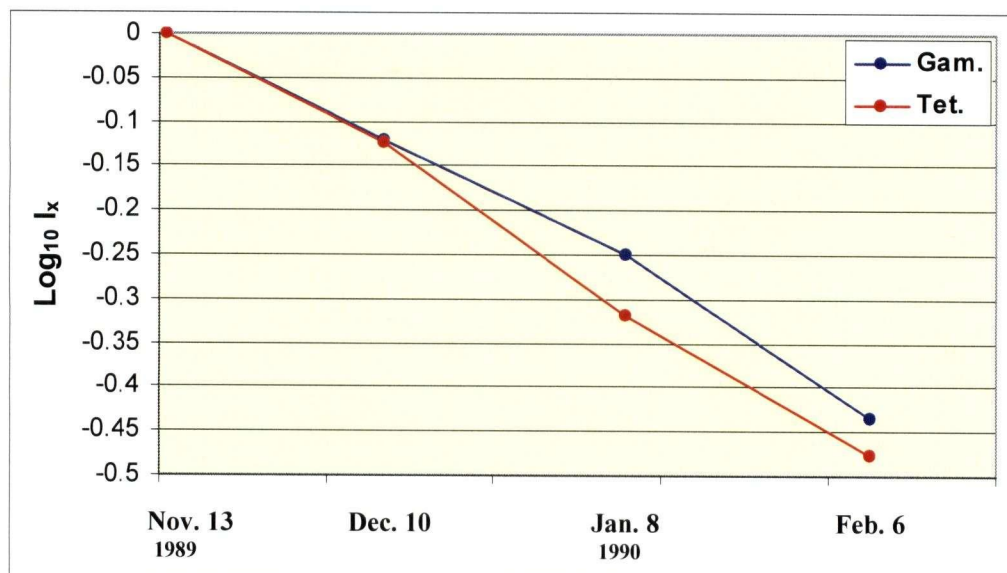


Figure B.32: Survival ($\log_{10} l_x$) in a cohort of 89 modules (41 haploid, 48 diploid) of *Mazzaella splendens* tagged at Brockton Point, Vancouver Harbour on November 13, 1989. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

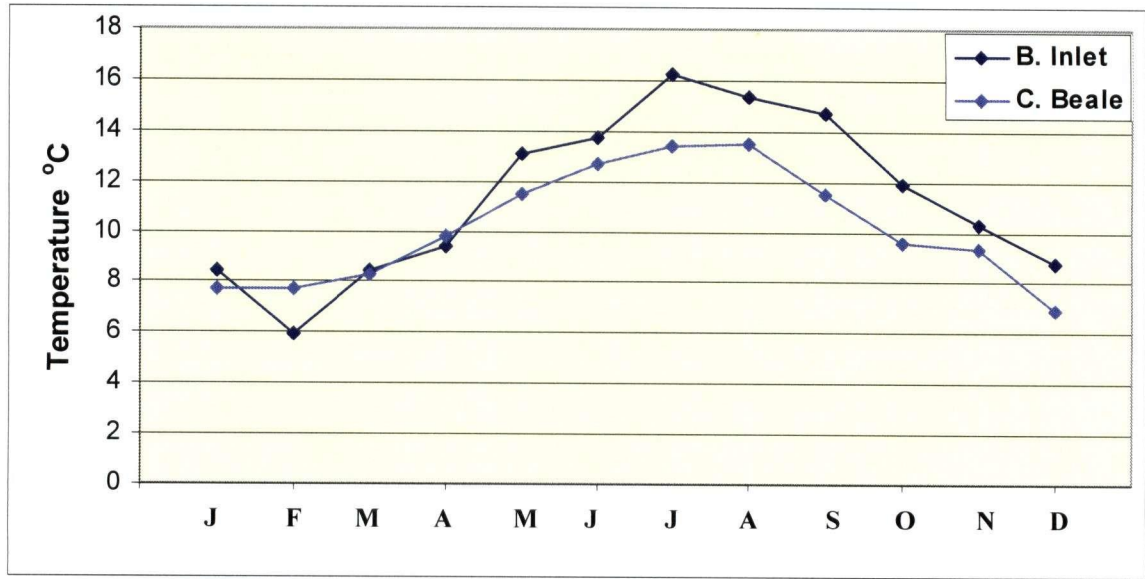


Figure B.33: Surface water temperature in the vicinity of Second Beach, Barkley Sound. B. Inlet = surface water temperatures from Bamfield Inlet (from Wheeler & Srivastava 1984). C. Beale = mean surface water temperature for the years 1994 – 2000 at the Cape Beale Lighthouse.

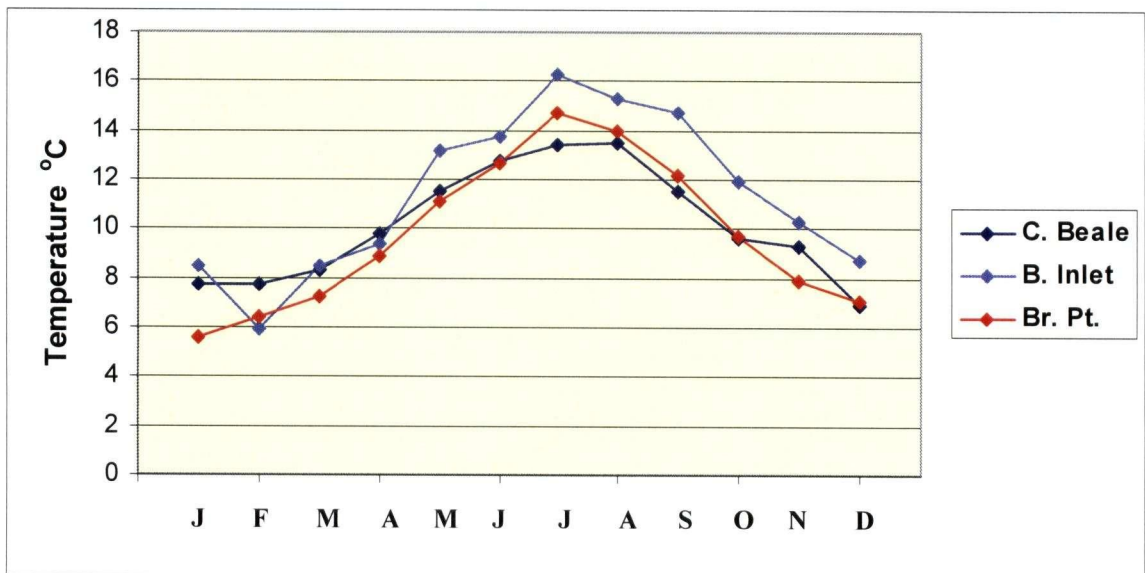


Figure B.34: A comparison of seasonal changes in surface water temperature at Cape Beale, in Bamfield Inlet (Wheeler & Srivastava 1984) and at Brockton Point (Druehl & Hsiao 1977). C. Beale = Cape Beale (mean temperatures for January 1994 – December 2000). B. Inlet = Bamfield Inlet (temperatures for January – December 1981) Br. Pt. = Brockton Point (mean temperatures for July 1968 – June 1971).

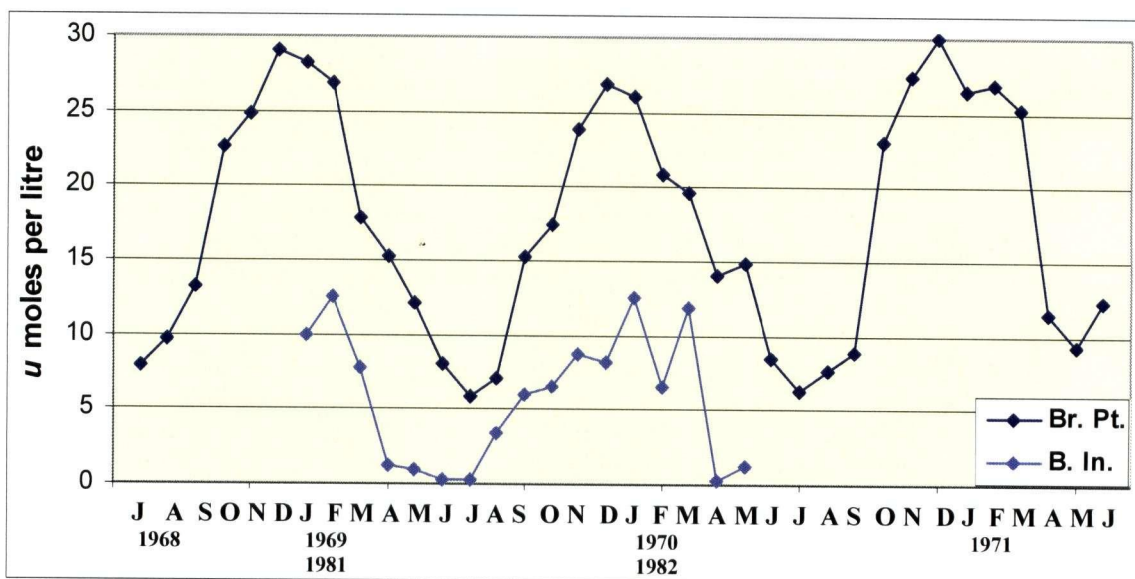


Figure B.35: A comparison of seasonal changes in nitrate concentration in Bamfield Inlet, January 1981 – May 1982 (Wheeler & Srivastava 1984) and at Brockton Point, Vancouver Harbour, July 1968 – June 1971 (Druehl & Hsiao 1977). Br. Pt. = Brockton Point. B. In. = Bamfield Inlet.

APPENDIX C

Additional tables to accompany Chapter 3.

Table C.1: Changes in population density with concurrent changes in per capita rate of loss for gametophyte vs. tetrasporophyte genets and modules of *Mazzaella splendens* at Brockton Point, Vancouver Harbour. November 1997 to January 2001.

Coinciding Events	Genets		Modules	
	Haploid	Diploid	Haploid	Diploid
Number of times that population density increased with a concurrent increase in per capita rate of loss	5	4	4	2
Number of times that population density increased with a concurrent decrease in per capita rate of loss	7	9	8	8
Within the periods of population density increase; the proportion of concurrent increases in per capita rate of loss	0.42	0.31	0.33	0.2
Within the periods of population density increase; the proportion of concurrent decreases in per capita rate of loss	0.58	0.69	0.67	0.8
Number of times that population density decreased with a concurrent decrease in per capita rate of loss	7	6	9	9
Number of times that population density decreased with a concurrent increase in per capita rate of loss	13	13	11	12
Within the periods of population density decrease; the proportion of concurrent decreases in per capita rate of loss	0.35	0.32	0.45	0.43
Within the periods of population density decrease; the proportion of concurrent increases in per capita rate of loss	0.65	0.68	0.55	0.57

Table C.2: Regression of μ_x on current age in six cohorts of *Mazzaella splendens* tagged at the wave-sheltered site, Second Beach, Barkley Sound.

Date			r^2	P value
February 1998	Genets	Haploid	0.745	0.060
		Diploid	0.998	0.009
	Modules	Haploid	0.592	0.128
		Diploid	0.056	0.848
March 1998	Genets	Haploid	0.992	0.040
		Diploid	0.720	0.151
	Modules	Haploid	0.883	0.060
		Diploid	0.808	0.101
April 1998	Genets	Haploid	0.924	0.177
		Diploid	0.998	0.031
	Modules	Haploid	0.880	0.225
		Diploid	0.993	0.052
April 1999	Genets	Haploid	0.460	0.321
		Diploid	0.789	0.112
	Modules	Haploid	0.155	0.607
		Diploid	0.669	0.182
May 1999	Genets	Haploid	0.968	0.115
		Diploid	0.901	0.203
	Modules	Haploid	0.989	0.070
		Diploid	0.861	0.243
May 2000	Genets	Haploid	0.009	0.907
		Diploid	0.001	0.967
	Modules	Haploid	0.001	0.971
		Diploid	0.031	0.823

Table C.3: Kaplan-Meier analysis comparing survival for gametophytes vs. tetrasporophytes of *Mazzaella splendens* at Brockton Point, Vancouver Harbour.

Date	Log rank test	Wilcoxon test
June 18, 1989	P = 0.988	P = 0.814
November 13, 1989	P = 0.615	P = 0.739

APPENDIX D

Additional figures to accompany Chapter 4.

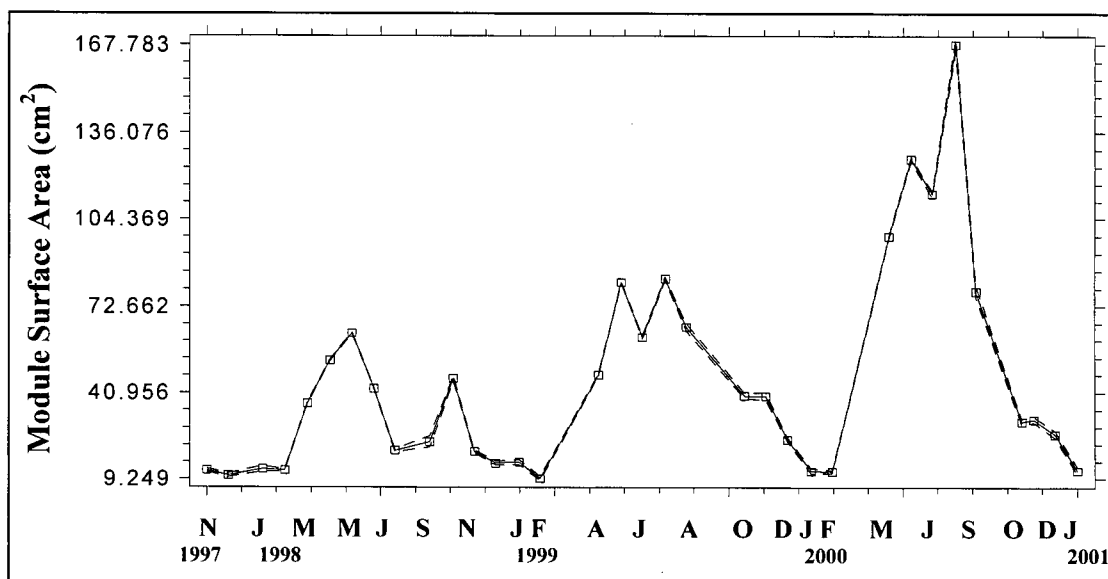


Figure D.1: Cubic spline graph of seasonal changes in surface area for haploid modules (all size classes) of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean areas. Dashed lines = ± 1 S E.

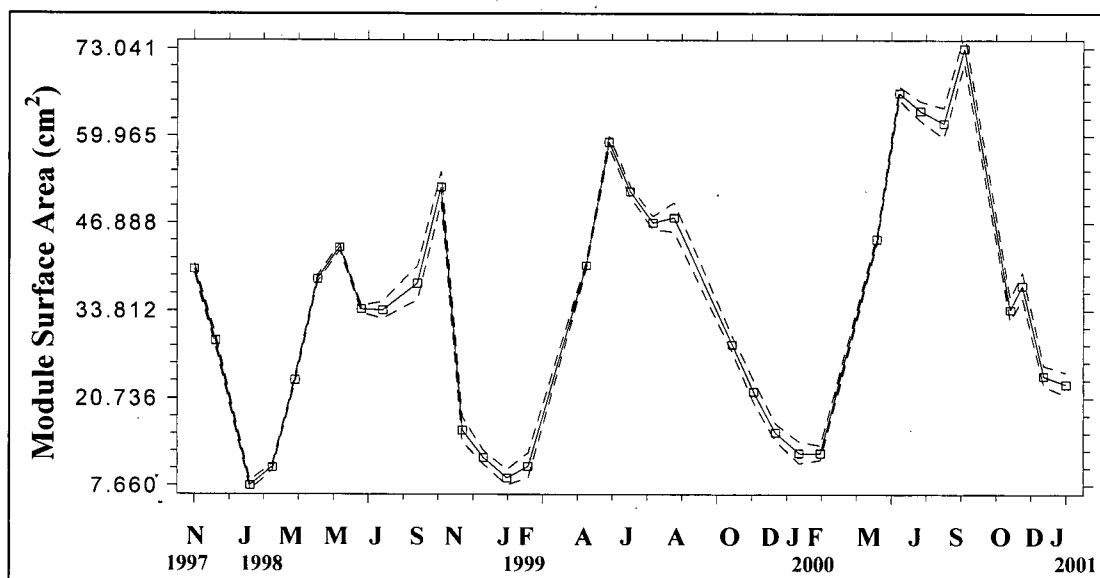


Figure D.2: Cubic spline graph of seasonal changes in surface area for diploid modules (all size classes) of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean areas. Dashed lines = ± 1 S E.

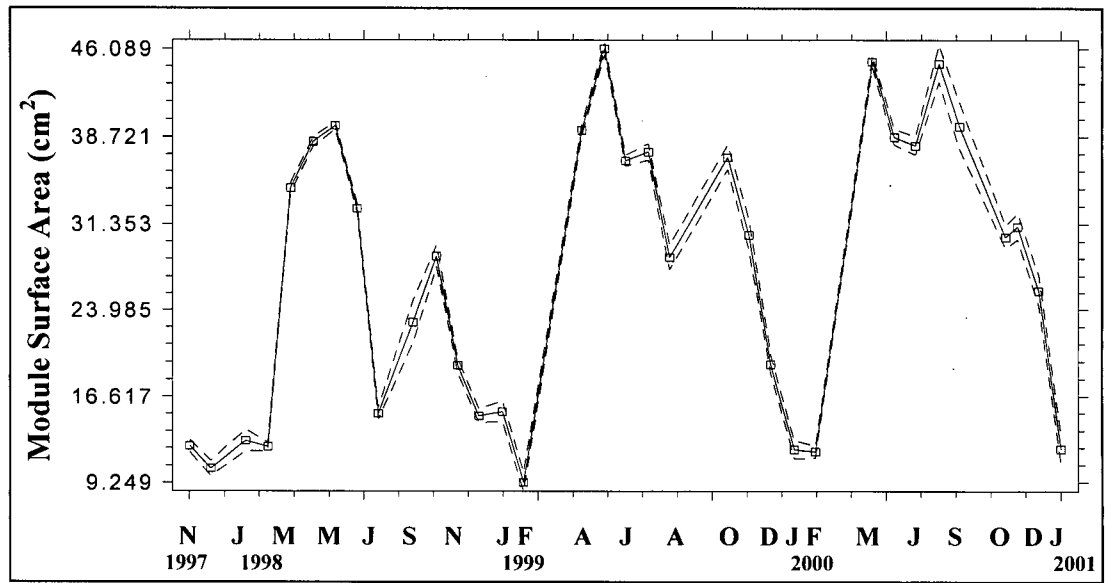


Figure D.3: Cubic spline graph of seasonal changes in surface area for haploid modules (120 cm^2 or less) of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean areas. Dashed lines = ± 1 S E.

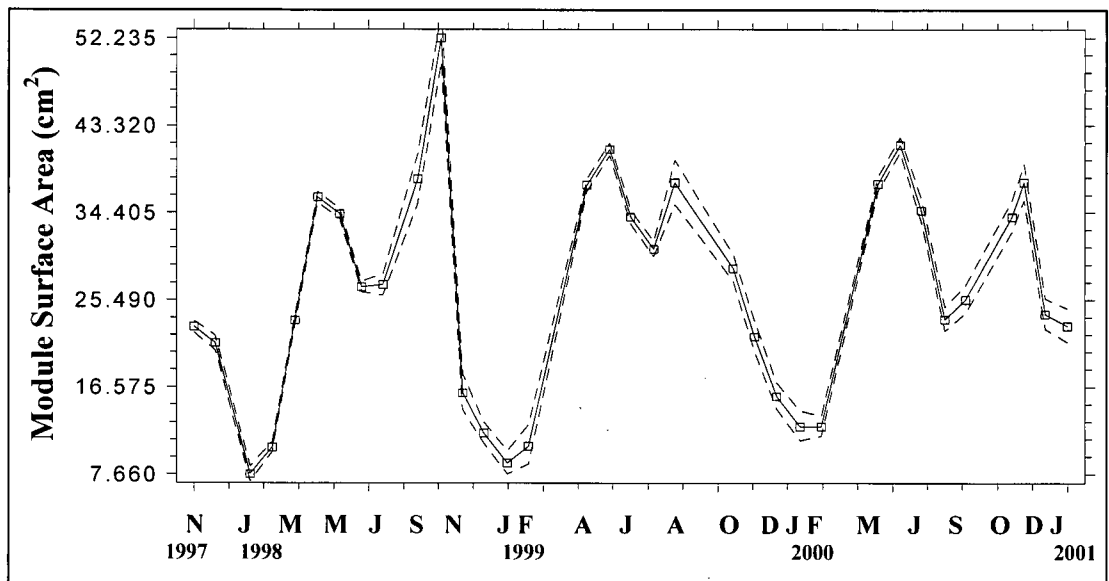


Figure D.4: Cubic spline graph of seasonal changes in surface area for diploid modules (120 cm^2 or less) of *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean areas. Dashed lines = ± 1 S E.

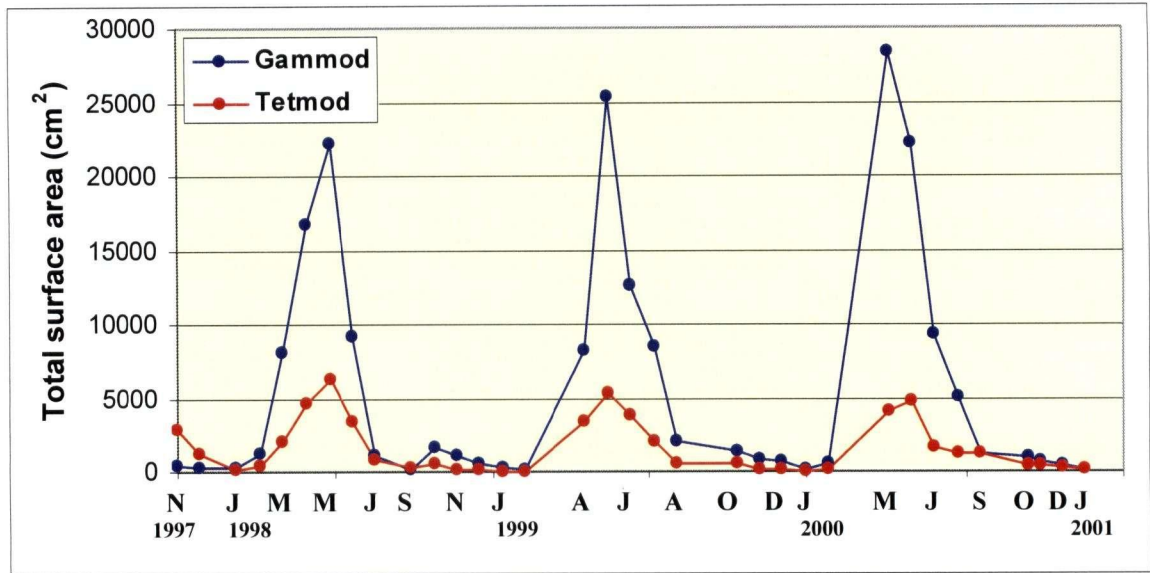


Figure D.5: Seasonal changes in total surface area for the alternate phases of *Mazzaella splendens* in 20 (November 1997 – April 1999) and 31 (May 1999 - January 2001) 0.0625 m² permanent quadrats at Second Beach, Barkley Sound (November 1997 to January 2001). Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

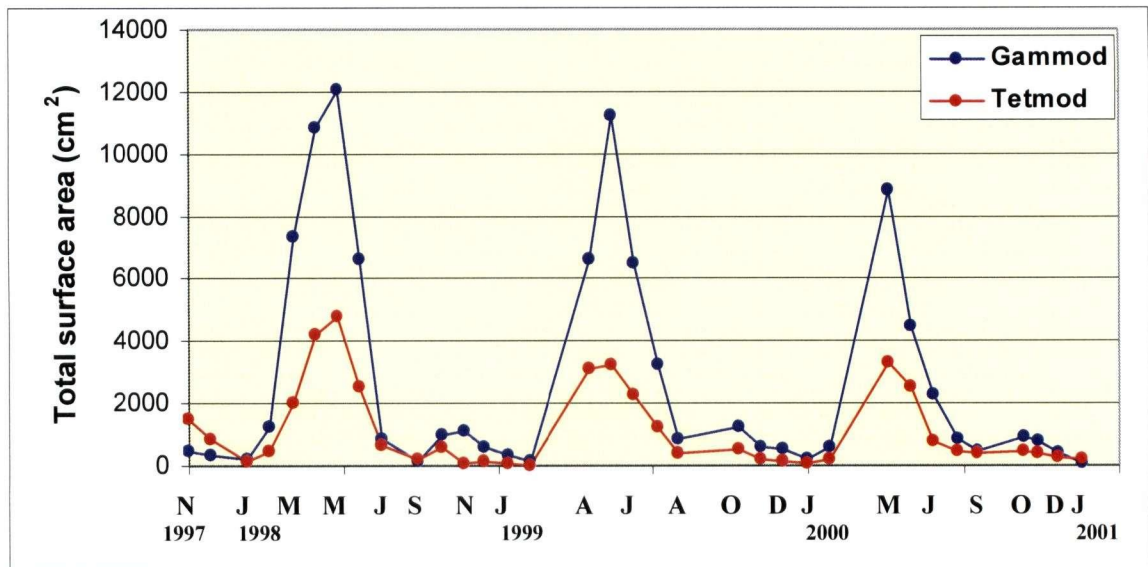


Figure D.6: Seasonal changes in total surface area (modules 120 cm² or less) for the alternate phases of *Mazzaella splendens* in 20 (November 1997 – April 1999) and 31 (May 1999 - January 2001) 0.0625 m² permanent quadrats at Second Beach, Barkley Sound (November 1997 to January 2001). Gammod = gametophyte modules Tetmod = tetrasporophyte modules.

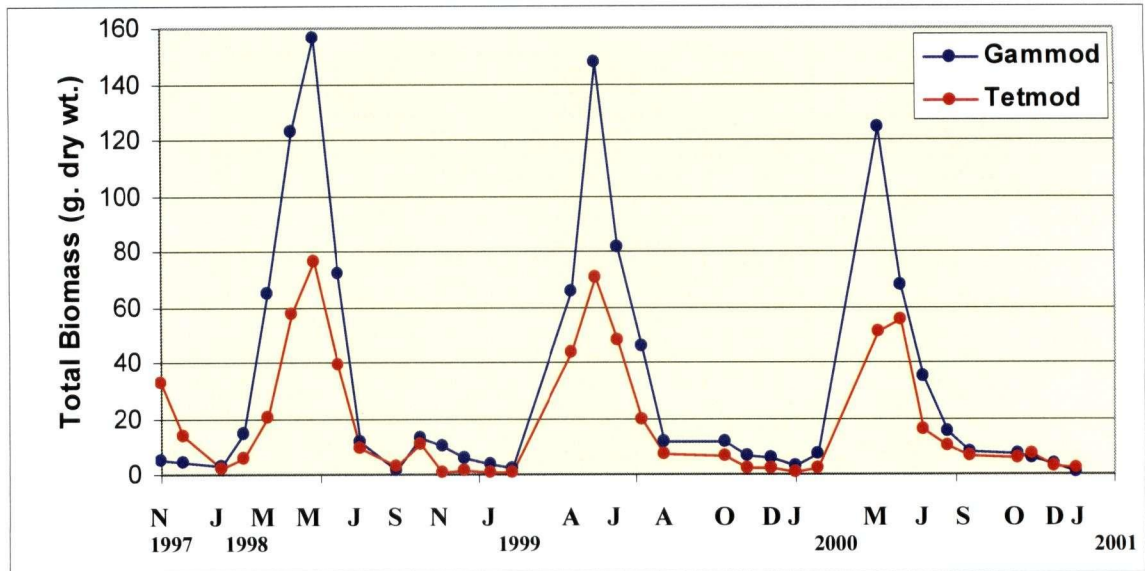


Figure D.7: Seasonal changes in total biomass (all modules) for the alternate phases of *Mazzaella splendens* in 20 (November 1997 – April 1999) and 31 (May 1999 - January 2001) 0.0625 m² permanent quadrats at Second Beach, Barkley Sound (November 1997 to January 2001). Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

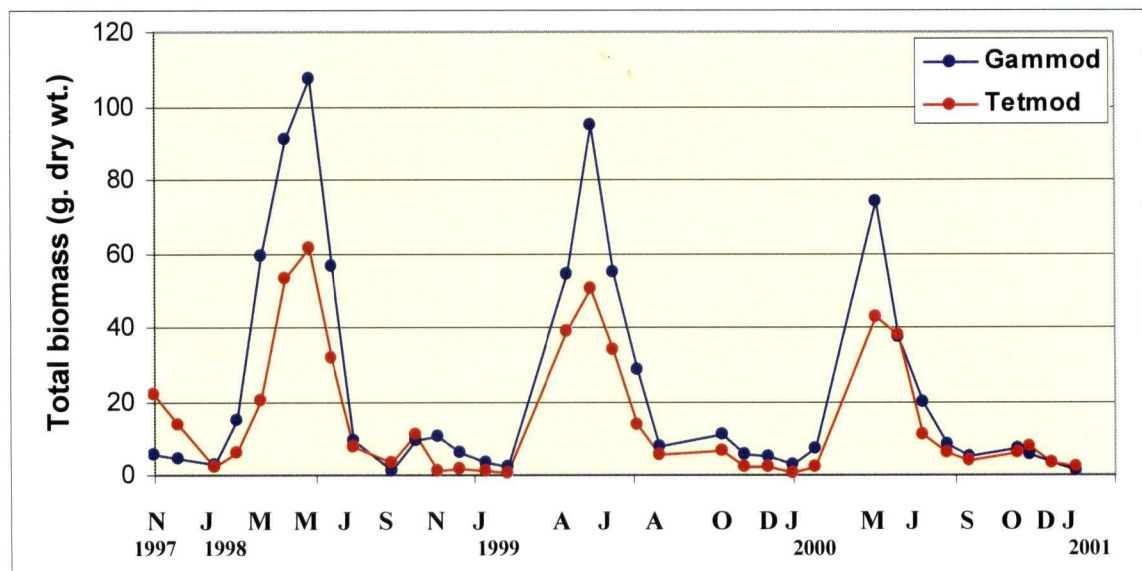


Figure D.8: Seasonal changes in total biomass (modules 120 cm² or less) for the alternate phases of *Mazzaella splendens* in 20 (November 1997 – April 1999) and 31 (May 1999 - January 2001) 0.0625 m² permanent quadrats at Second Beach, Barkley Sound. November 1997 to January 2001. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

APPENDIX E

Additional tables to accompany Chapter 4.

Table E.1: Size classes of modules above 250 cm² (maximum size attained) in the alternate phases of *Mazzaella splendens* in 20 (November 1997 – April 1999) and 31 (May 1999 - December 2000) 0.0625 m² permanent quadrats at Second Beach, Barkley Sound. November 1997 to January 2001. Haploid = gametophyte. Diploid = tetrasporophyte.

Number of Modules			Number of Modules		
Size Class (cm ²)	Haploid	Diploid	Size Class (cm ²)	Haploid	Diploid
251-260	6	1	481-490	1	1
261-270	4	3	491-500	1	
271-280	9		581-590	1	
281-290	5		591-600	2	1
291-300	2		601-610	1	
301-310	3		611-620	2	
311-320	6	1	621-630	1	
321-330	5		631-640	1	
331-340	3		641-650	1	
341-350	1		651-660	1	
351-360	3	1	691-700	1	
361-370	2		701-710	1	
371-380	3		731-740	2	
381-390	3	1	751-760		1
391-400	3		801-810	1	
401-410	4		841-850	1	
411-420	1		851-860	1	
421-430	2				
431-440	3				
441-450	3				

Table E.2: Size classes of modules above 250 cm² in the alternate phases of *Mazzaella splendens* in the transects at Second Beach, Barkley Sound. Haploid = gametophyte. Diploid = tetrasporophyte.

Number of Modules			Number of Modules		
Size Class (cm ²)	Haploid	Diploid	Size Class (cm ²)	Haploid	Diploid
251-260		2	401-410	1	1
261-270	2	1	431-440	3	1
301-310	2	3	441-450	1	
311-320		2	461-470	1	
331-340	3	2	521-530	1	
341-350	2		581-590	1	
351-360	2	1	951-960	1	
381-390	2	1	1061-1070	1	

APPENDIX F

Additional figures to accompany Chapter 5.

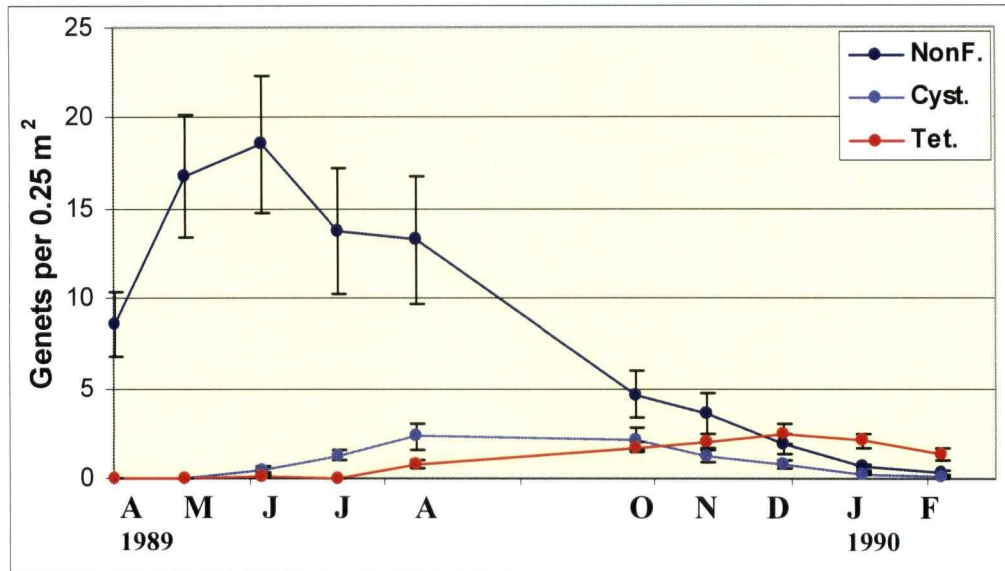


Figure F.1: Seasonal changes in nonfertile and reproductive genet density of *Mazzaella splendens* at Brockton Point, Vancouver Harbour (April 1989 to February 1990). Means (± 1 S.E.). NonF. = Non-fertile genets. Cyst. = Cystocarpic genets. Tet. = Tetrasporic genets.

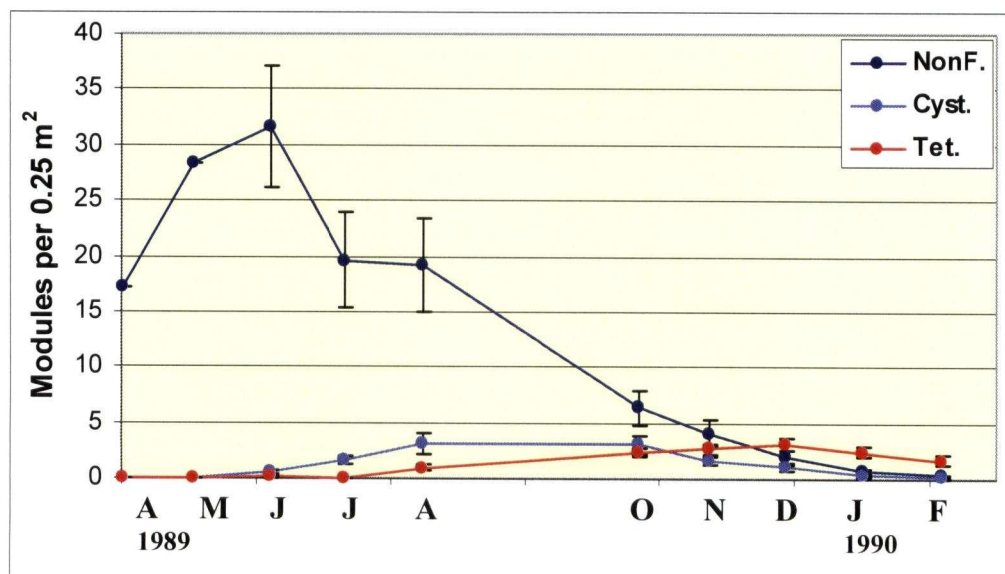


Figure F.2: Seasonal changes in nonfertile and reproductive module density of *Mazzaella splendens* at Brockton Point, Vancouver Harbour (April 1989 to February 1990). Means (± 1 S.E.). NonF. = Non-fertile modules. Cyst. = Cystocarpic modules. Tet. = Tetrasporic modules.

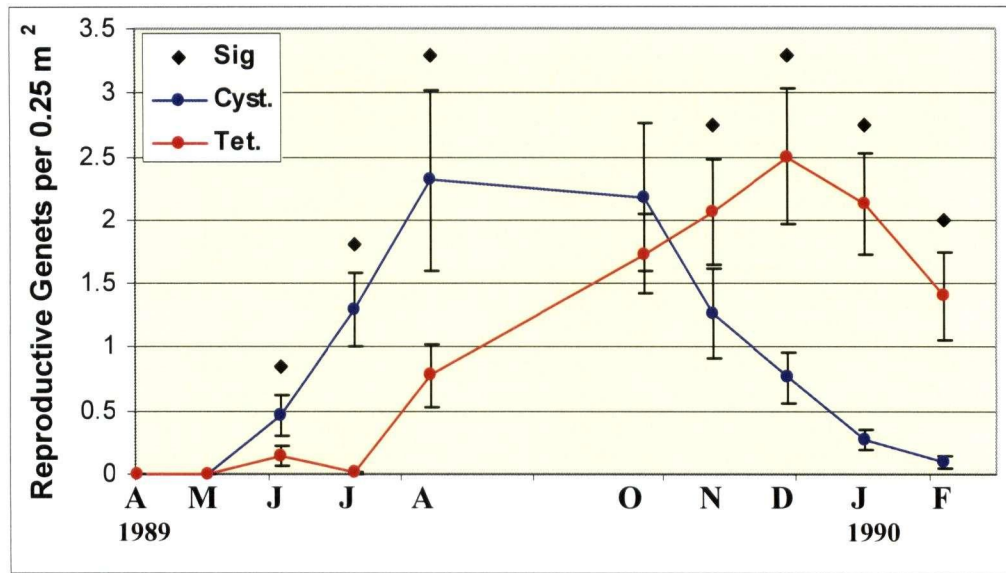


Figure F.3: Seasonal changes in reproductive genet density for the alternate phases of *Mazzaella splendens* at Brockton Point, Vancouver Harbour (April 1989 to February 1990). Means (± 1 S E). Cyst. = Cystocarpic genets. Tet. = Tetrasporic genets. Sig. = Statistical significance: Mann-Whitney U Test, $P \leq 0.05$.

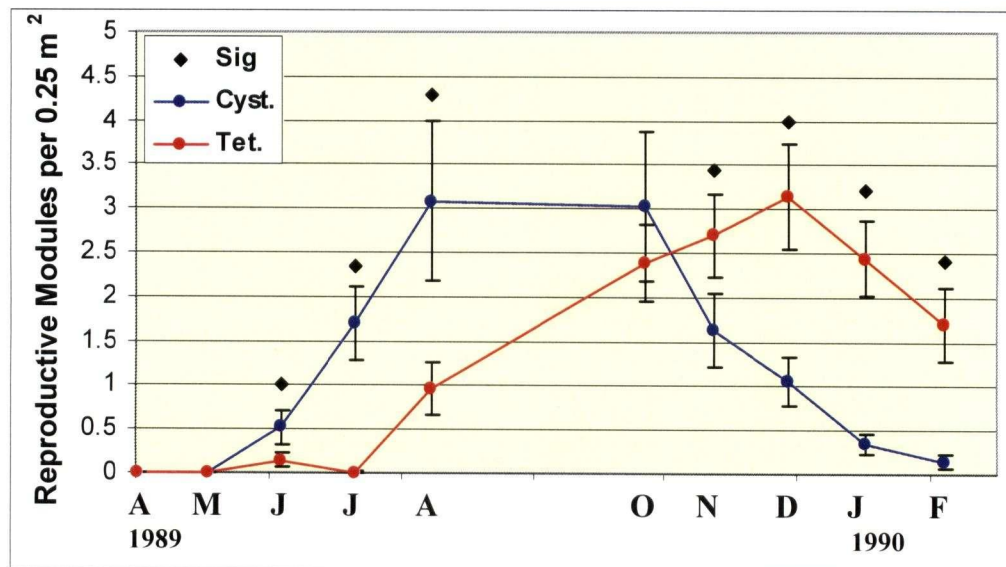


Figure F.4: Seasonal changes in reproductive module density for the alternate phases of *Mazzaella splendens* at Brockton Point, Vancouver Harbour (April 1989 to February 1990). Means (± 1 S E). Cyst. = Cystocarpic modules. Tet. = Tetrasporic modules. Sig. = Statistical significance: Mann-Whitney U Test, $P \leq 0.05$.

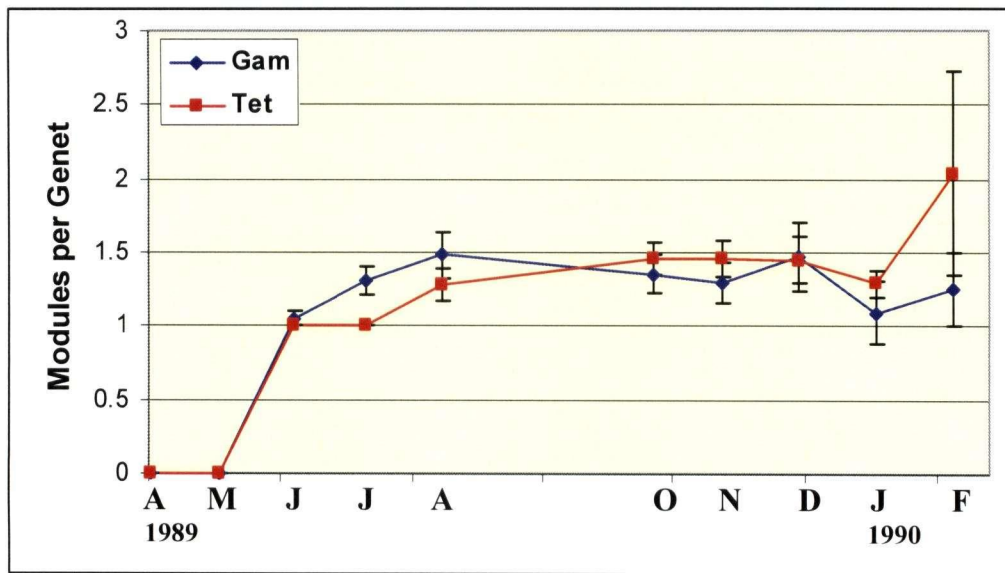


Figure F.5: Seasonal changes in reproductive modules per reproductive genet for the alternate phases of *Mazzaella splendens* at Brockton Point, Vancouver Harbour (April 1989 to February 1990). Means (± 1 S E). Cyst. = Cystocarpic modules. Tet. = Tetrasporic modules. There were no significant differences between life history phases (Mann-Whitney U test, $\alpha = 0.05$).

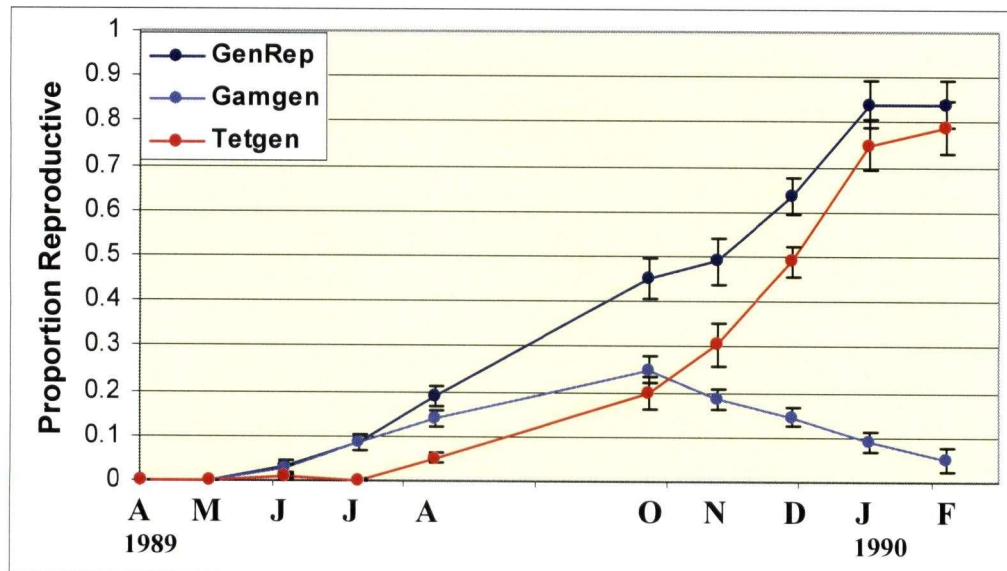


Figure F.6: Seasonal changes in reproductive genets as a proportion (± 1 S E) of total population density of *Mazzaella splendens* at Brockton Point, Vancouver Harbour (April 1989 to February 1990). GenRep = reproductive genets of both phases. Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets.

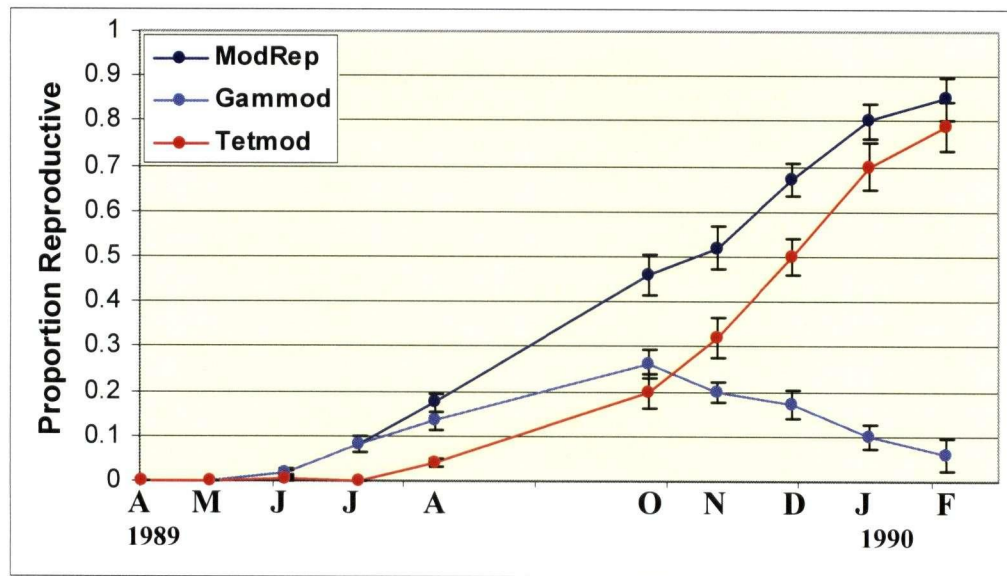


Figure F.7: Seasonal changes in reproductive modules as a proportion (± 1 S E) of total population density of *Mazzaella splendens* at Brockton Point, Vancouver Harbour (April 1989 to February 1990). ModRep = reproductive modules of both phases. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

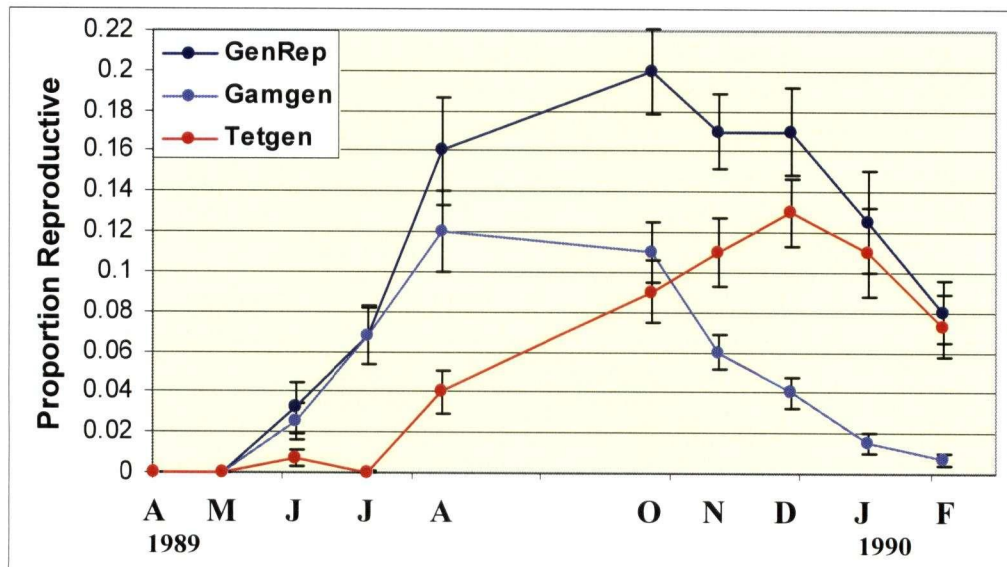


Figure F.8: Seasonal changes in reproductive genets as a proportion (± 1 S E) of peak population density of *Mazzaella splendens* at Brockton Point, Vancouver Harbour (April 1989 to February 1990). GenRep = reproductive genets of both phases. Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets.

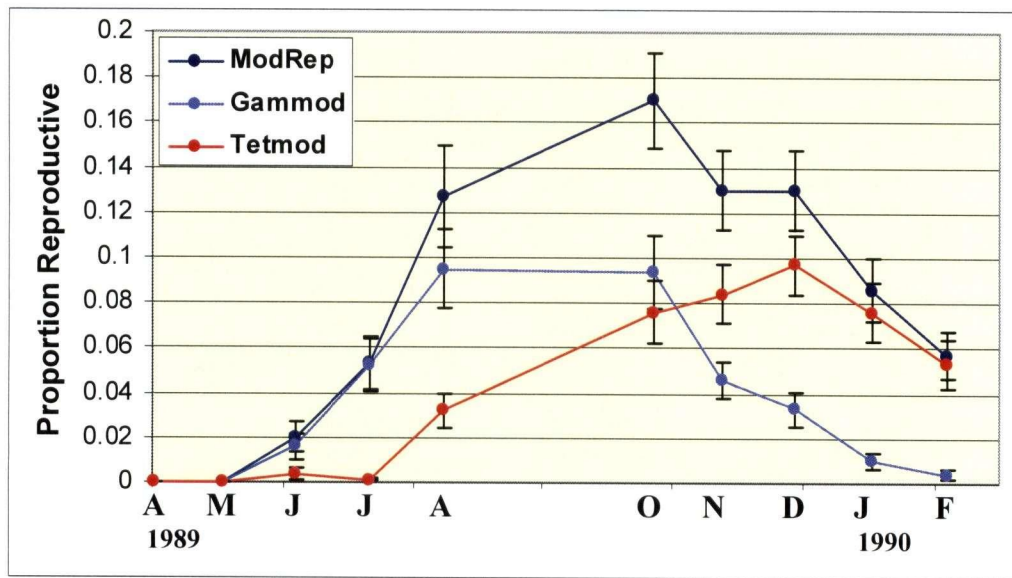


Figure F.9: Seasonal changes in reproductive modules as a proportion (± 1 S E) of peak population density of *Mazzaella splendens* at Brockton Point, Vancouver Harbour (April 1989 to February 1990). ModRep = reproductive modules of both phases. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

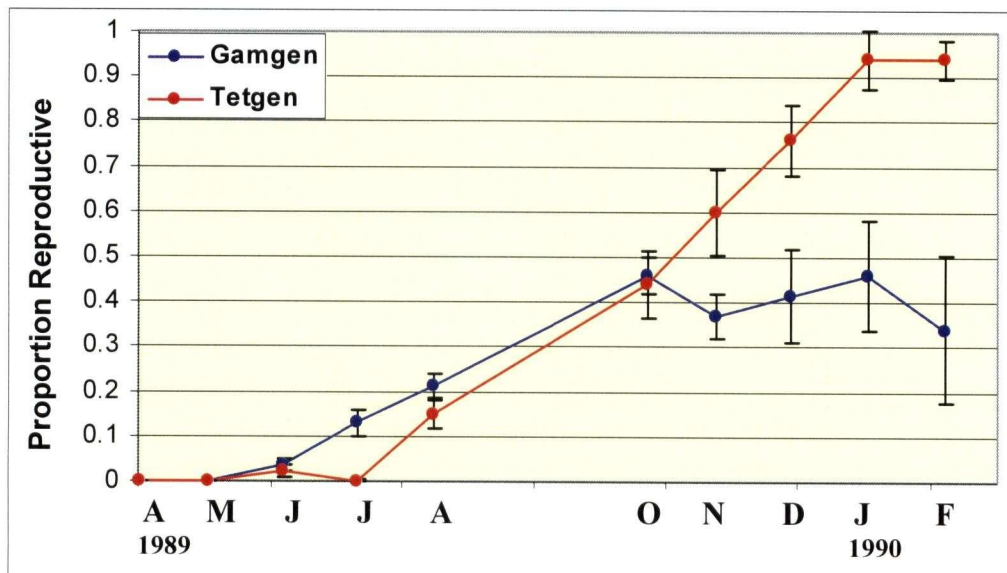


Figure F.10: Seasonal changes in reproductive genets as a proportion (± 1 S E) of within phase population density of *Mazzaella splendens* at Brockton Point, Vancouver Harbour (April 1989 to February 1990). Gamgen = gametophyte genets. Tetgen = tetrasporophyte genets.

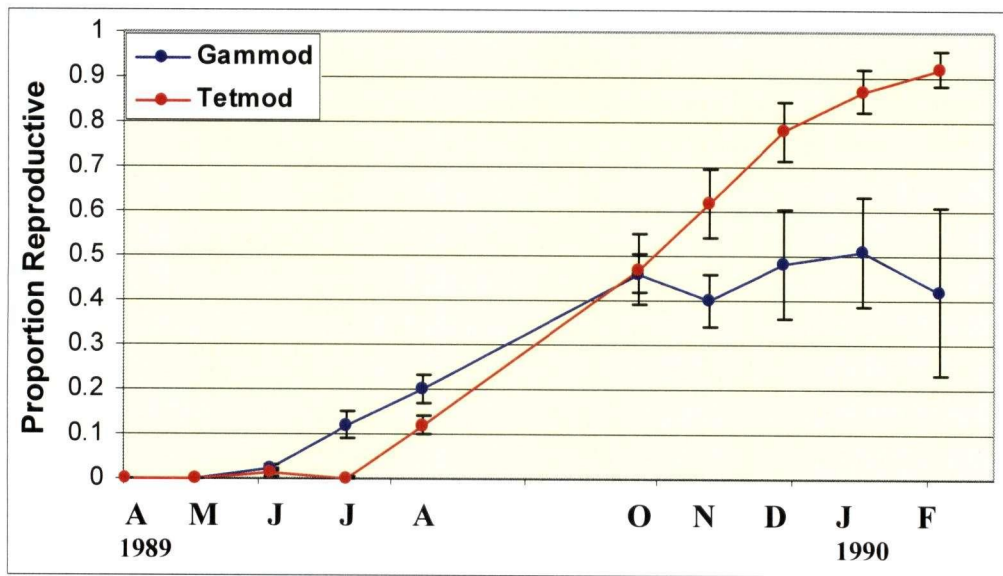


Figure F.11: Seasonal changes in reproductive modules as a proportion (± 1 S E) of within phase population density of *Mazzaella splendens* at Brockton Point, Vancouver Harbour (April 1989 to February 1990). Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

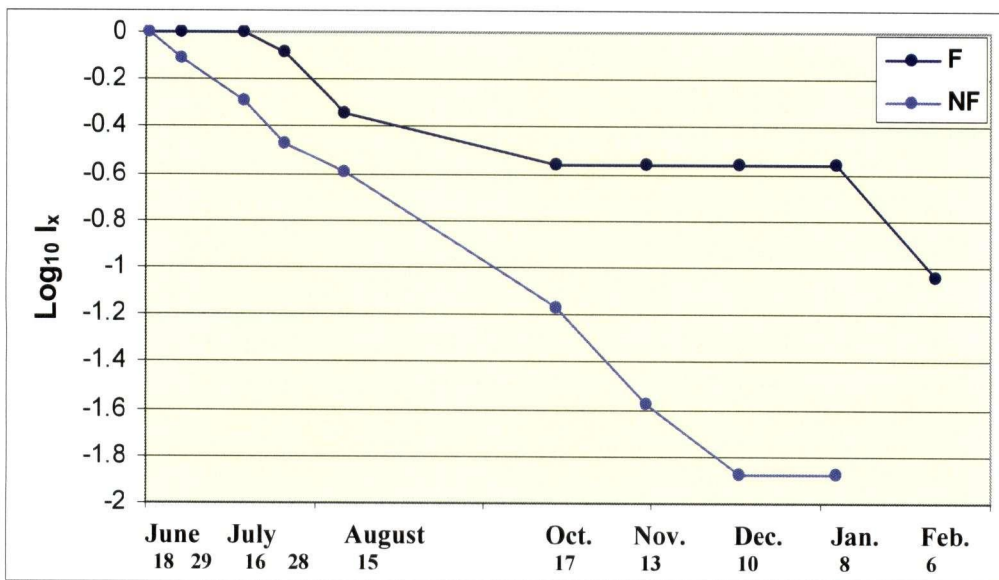


Figure F.12: Survival ($\log_{10} l_x$) between fertile and non-fertile blades in a cohort of 86 haploid modules (11 fertile, 76 non-fertile) of *Mazzaella splendens* tagged at Brockton Point, Vancouver Harbour on June 18, 1989. F = haploids developing cystocarps before loss from the population. NF = haploids which never developed cystocarps.

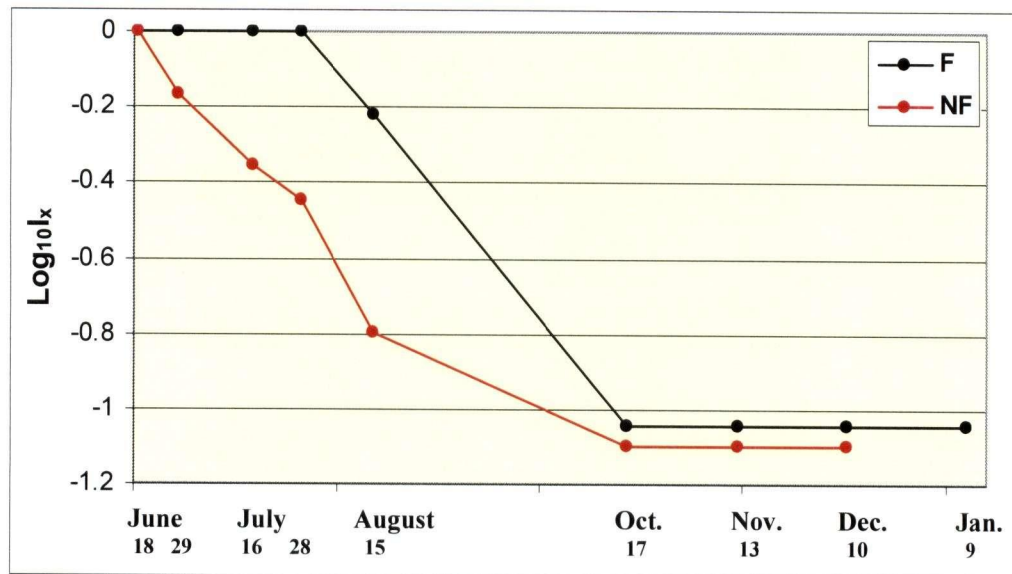


Figure F.13: Survival ($\log_{10} l_x$) between fertile and non-fertile blades in a cohort of 30 diploid modules (4 fertile, 26 non-fertile) of *Mazzaella splendens* tagged at Brockton Point, Vancouver Harbour on June 18, 1989. F = diploids developing tetrasporangia before loss from the population. NF = diploids which never developed tetrasporangia.

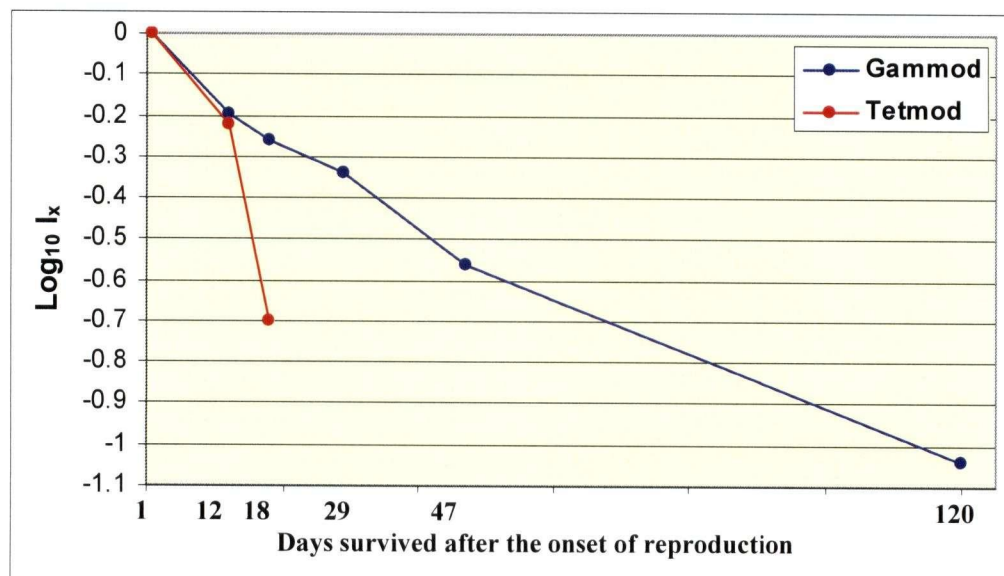


Figure F.14: Survival ($\log_{10} l_x$) following onset of reproduction in a static cohort of 15 fertile modules (4 diploid, 11 haploid) of *Mazzaella splendens* tagged at Brockton Point, Vancouver Harbour on June 18, 1989. Gammod = gametophyte modules. Tetmod = tetrasporophyte modules.

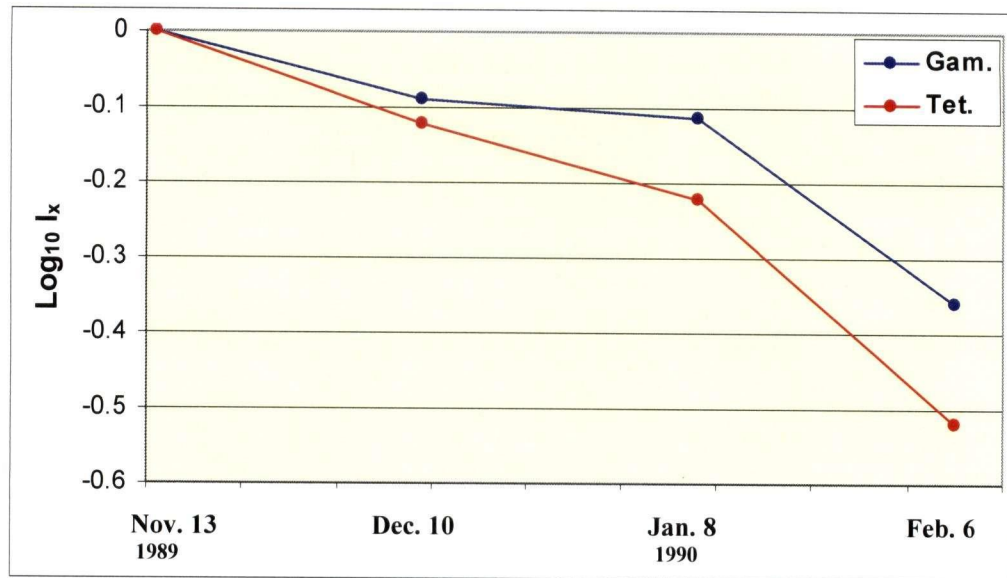


Figure F.15: Survival ($\log_{10} l_x$) in a cohort of 48 fertile modules (16 haploid, 32 diploid) of *Mazzaella splendens* tagged at Brockton Point, Vancouver Harbour on November 13, 1989. Gammod = cystocarpic gametophyte modules. Tetmod = fertile tetrasporophyte modules.

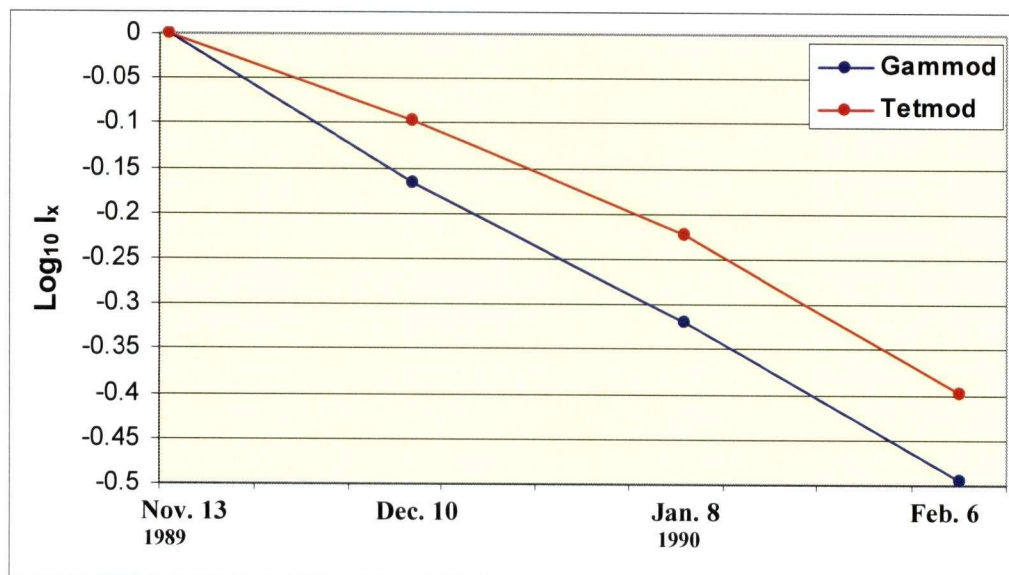


Figure F.16: Survival ($\log_{10} l_x$) in a cohort of 40 non-fertile modules (25 haploid, 15 diploid) of *Mazzaella splendens* tagged at Brockton Point, Vancouver Harbour on November 13, 1989. Gammod = non-cystocarpic gametophyte modules. Tetmod = non-fertile tetrasporophyte modules.

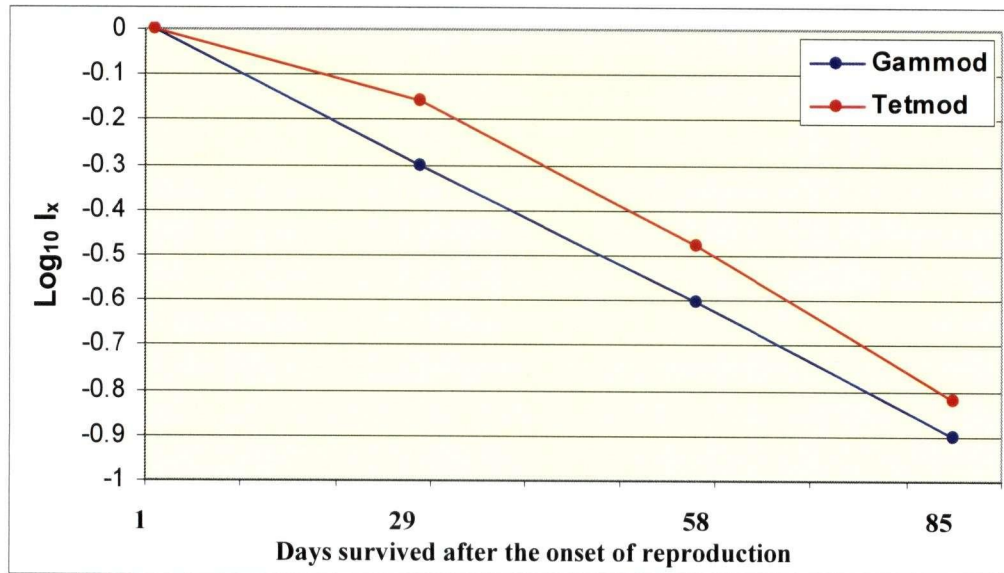


Figure F.17: Survival ($\log_{10} l_x$) following onset of reproduction in a static cohort of 48 fertile modules (32 diploid, 16 haploid) of *Mazzaella splendens* tagged at Brockton Point, Vancouver Harbour on November 13, 1989. Gammod = cystocarpic gametophyte modules. Tetmod = fertile tetrasporophyte modules.

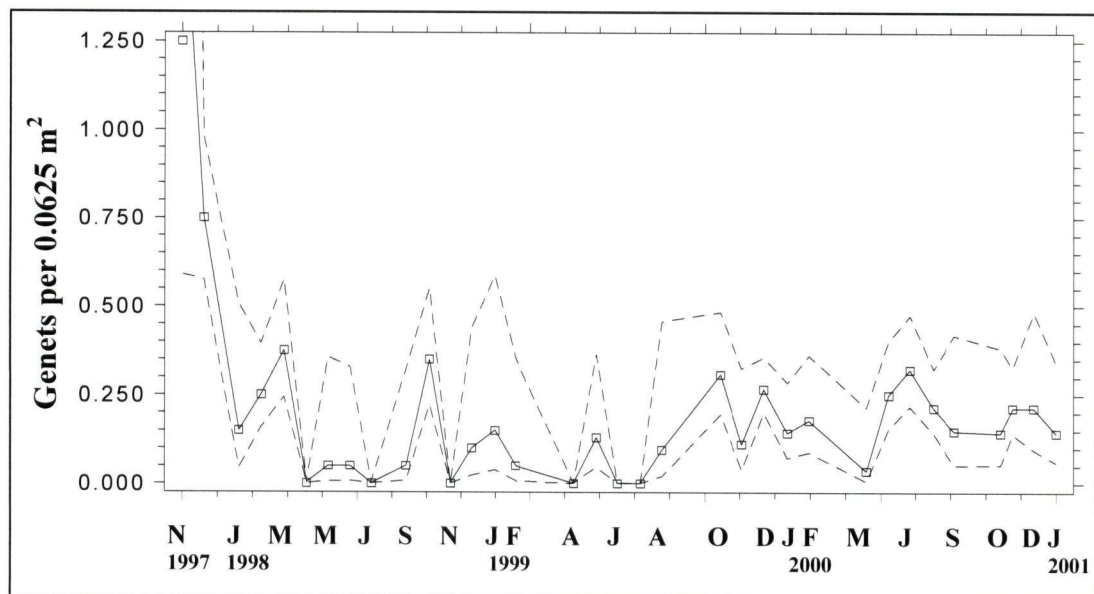


Figure F.18: Cubic spline graph of seasonal changes in reproductive genet density for *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S.E.

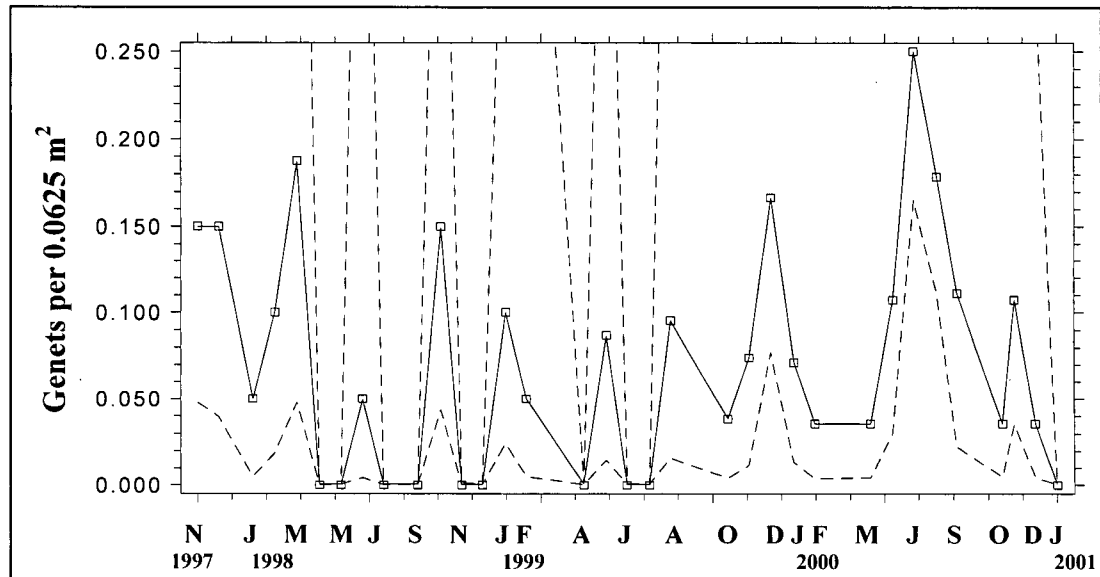


Figure F.19: Cubic spline graph of seasonal changes in reproductive haploid genet density for *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

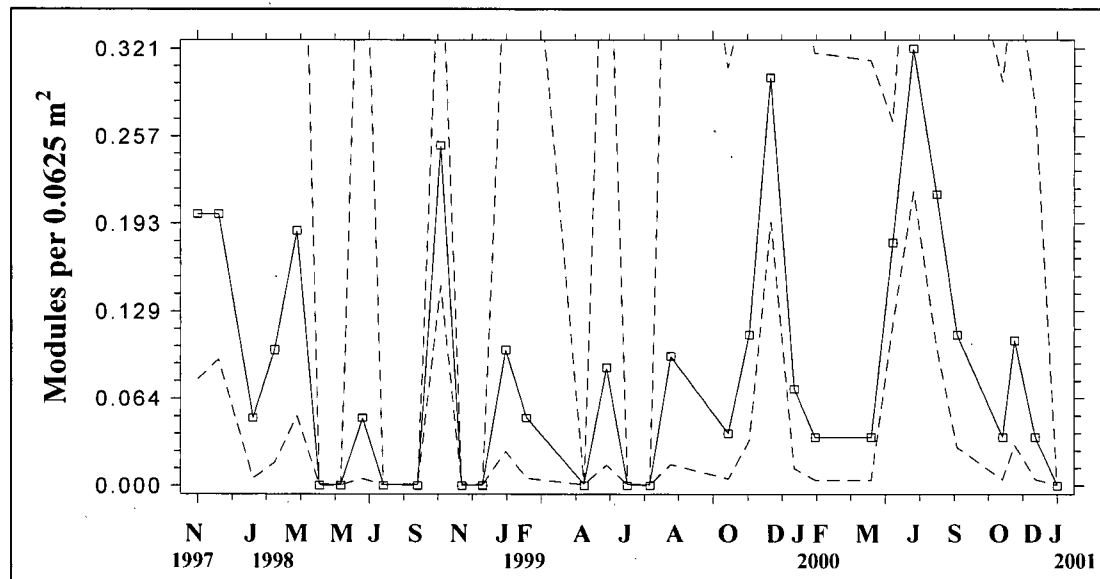


Figure F.20: Cubic spline graph of seasonal changes in reproductive haploid module density for *Mazzaella splendens* at Second Beach, Barkley Sound (November 1997 to January 2001). Solid line = curve fit through mean densities. Dashed lines = ± 1 S E.

APPENDIX G

Additional tables to accompany Chapter 5.

Table G.1: Descriptive and inferential statistics for survival time, in two cohorts of modules of *Mazzaella splendens* from Brockton Point, Vancouver Harbour. Given are mean survival time in days (= Mean), the standard error of the mean (= S.E.), the sample size (= N), and the P value from the Mann-Whitney U test (= M.W.-U) comparing survival times (total lifespan) between reproductive and non-reproductive blades.

Comparison	N	Mean	S.E.	M.W.-U
Cohort tagged June 1989.				
Cystocarpic gametophytes	11	85.36	25.36	P = 0.008
Non-fertile gametophytes	76	32.33	4.46	
Tetrasporic tetrasporophytes	4	49.00	5.20	P = 0.071
Non-fertile tetrasporophytes	26	38.46	11.19	
Cohort tagged November 1989.				
Cystocarpic gametophytes	25	52.56	8.39	P = 0.676
Non-fertile gametophytes	16	48.00	7.00	
Tetrasporic tetrasporophytes	32	44.23	5.89	P = 0.874
Non-fertile tetrasporophytes	15	42.93	8.95	
Non-fertile gametophytes	16	48.00	7.00	P = 0.384
Cystocarpic gametophytes after the onset of reproduction.	25	37.13	8.67	
Non-fertile tetrasporophytes	15	42.93	8.95	P = 0.554
Tetrasporic tetrasporophytes after the onset of reproduction	32	34.52	5.57	