## Seasonal and spatial patterns of population density in the marine macroalga *Mazzaella splendens* (Gigartinales, Rhodophyta)

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#### SUMMARY

Insight into demographic processes that operate at larger spatial scales can be achieved through studying local populations when a particular species of interest is examined over time, by many investigators, in a variety of locations. On the west coast of North America, Mazzaella splendens (Setchell et Gardner) Fredericq is such a species of interest. A synthesis of local demographic studies of *M. splendens* from the late 1960s to the present reveals a pattern that is potentially common to the larger natural populations. This is the pattern: 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 waveexposed habitats. In wave-sheltered habitats there is a seasonal alternation from summer haploid to winter diploid dominance. This alternation gradually changes to constant diploid dominance as wave exposure in the habitat increases. Changes in population 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 this pattern, we examined seasonal changes in density, in local populations of *M. splendens*, in both a wave-sheltered and a wave-exposed habitat at Second Beach, Barkley Sound. Greater seasonal fluctuation in population density at wave-sheltered, compared to wave-exposed habitats is supported as a pattern potentially common to the natural populations of *M. splendens*. A change from summer haploid dominance in wave-sheltered areas to summer diploid dominance in wave-exposed areas is similarly supported. All changes in population density were the result of appearances and disappearances of genets rather than differential module production by haploid versus diploid basal crusts, also consistent with previous observations. A seasonal alternation in phase dominance, however, was absent from the wave-sheltered site at Second Beach, Barkley Sound for 3 consecutive years. Seasonal alternation in phase dominance of *M. splendens* appears

dependent on local conditions and is not common to all natural populations.

Key words: demography, ecology, *Mazzaella splendens*, population, seasonality.

### INTRODUCTION

# Integrating local scale into larger patterns in 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 remains resistant to precise definition. Some contend that population boundaries might be determined simply by an investigator's purpose or convenience (Begon et al. 1986). Others resist this arbitrariness and seek a natural unit of population (Berryman 2002; Camus & Lima 2002). For Berryman (2002) this 'natural population' is that unit of population where demographic behavior is determined only by births and deaths and not by dispersal, a concept similar to the metapopulation (Hanski 1997). Smaller patches, subject to the vagaries of changing dispersal vectors and local conditions, are termed 'local populations' and are considered more ephemeral than the natural population. The natural population might be in equilibrium whereas this is less likely in a local population, and Berryman (2002) has questioned how well 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. Most ecologic studies take place at local scales and meaningful demographic information on the larger natural population is lacking.

The practical difficulties involved in adequately sampling an area large enough to eliminate the effects of

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dispersal, particularly for marine organisms (motile and sessile) with free drifting pelagic stages, is apparent to any working field ecologist. In the absence of effective barriers producing geographic isolates, species with pelagic dispersal consist of a single natural population. Some investigators have defined populations as open or closed regarding dispersal (Caley et al. 1996; Cowen et al. 2000), but this is essentially the same distinction as Berryman's (2002), with local populations being 'open' and the natural population being 'closed'. There is no parameter to define the scale at which a group of conspecifics becomes a local population, and so this term has been applied at a variety of scales (Camus & Lima 2002). In local populations as well, the demographic processes at one scale need not be representative of those at another as new properties of the larger groupings emerge.

Rather than defining local population in a precise way, Camus and Lima (2002) argue that the proper objective is to understand how processes at one spatial scale map into those at another. For any species that occupies a large geographic range this can only be accomplished by several investigators working at different spatial and temporal scales in a coordinated effort. Studies of this kind are rare, but can be accomplished through replication and extension of previous work, in new locations, by investigators with a common interest in a particular species. Over time a spatio-temporal mosaic of information is created, generating new hypotheses and hopefully attracting increasing numbers of investigators. As this mosaic builds, demographic patterns that are relatively invariant, or that vary systematically with spatial and/or temporal gradients, become apparent. In these patterns we see the behavior of the natural population and the way that the dynamics of local populations interact to produce large scale patterns.

For algal population ecology on the west coast of North America, *Mazzaella splendens* (Setchell et Gardner) Fredericq, a red alga with an alternation of free living isomorphic generations, is becoming such a well studied species. Studies of the distribution and abundance of *M. splendens* have accumulated steadily since the late 1960s, and have now occurred at various sites from Vandenberg, California to Barkley Sound, British Columbia, 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*).

# The natural population of *Mazzaella splendens*

In any attempt to designate a group of individuals as a natural population by Berryman's (2002) criteria, it is important to note that barriers to immigration change with time. As these barriers come and go the number of natural populations as defined by Berryman (2002) will vary within a species range. Berryman (2002) does not address the time scale in which the presence or absence of dispersal is to be considered important when defining the natural population, and here arbitrariness creeps back into the definition. Dispersal vectors are also non-uniform, and certain combinations of events can result in occasional dispersal of propagules over greater distances than what is usual.

The current distributions of macroalgal species in North America and northern Europe represent postglacial colonization from refugia and from below the southern extent of the ice. Immigration is clearly responsible for the postglacial presence of much of the northern macroalgal flora and this immigration is probably ongoing. The importance of long distance dispersal in recolonization is illustrated by a study of Palmaria mollis (Setchell et Gardner) van der Meer and C. J. Bird by Lindstrom et al. (1997) on the west coast of North America. Genetic relationships among local populations of *P. mollis* did not reflect geographic proximity. Instead, individuals on the outer coast were more closely associated with each other than with individuals on the inner coast. Individuals separated by only hundreds of kilometers were less genetically similar than individuals separated by thousands. This suggests long distance dispersal along prevailing currents is structuring the relatedness of local populations.

In general, free floating algal spores remain viable for only a few days and dispersal shadows tend to be short (see Santelices 1990 for review). Spore density in *M. splendens* drops by an order of magnitude 100 cm away from spore releasing blades (Adams 1979, as *I. cordata*). In central Chile, genetic differentiation of *Mazzaella laminarioides* (Bory de Saint Vincent) Fredericq increased with distance such that individuals 60 km apart could be assigned to their source population with discriminant analysis (Faugeron *et al.* 2001). Algal spores, however, remain viable much longer within detached thallus fragments and dispersal of such fragments can cover much larger distances (see Santelices 1990 for review).

The frequency and extent of long distance dispersal is not known for *M. splendens*. There is reason to suppose that released spores do not travel far and that populations separated by tens of kilometers would be genetically distinct. But there is also reason to believe that individuals along the outer coast of British Columbia might be more closely related to each other than they are to individuals from less distant inner coast sites. To define natural populations of *M. splendens* based on dispersal patterns would require an arbitrary timescale, defeating the purpose of defining populations in natural rather than arbitrary units. Instead of attempting this definition, we will use the information currently available on *M. splendens* to derive demographic patterns common to all existing studies. These common patterns form a hypothesis concerning the amount of differentiation in demographic behavior that has occurred, among local populations of *M. splendens*, as both short-distance and long-distance dispersal have expanded its range to the present post-glaciation limits. We will examine the generality of these patterns and contribute another local study to the emerging picture of interacting local and large scale demographic processes in *M. splendens*.

# A demographic pattern common to all previous studies of *Mazzaella splendens*

In relatively wave-sheltered areas, *M. splendens* has shown a distinct seasonal cycle. Biomass and population density are high in summer and low in winter for both gametophytes and tetrasporophytes (Adams 1979, as *I. cordata*; Dyck & De Wreede 1995). In wavesheltered areas there is a seasonal alternation between summer gametophyte and winter tetrasporophyte dominance (Adams 1979, as *I. cordata*; De Wreede & Green 1990, as *I. splendens*; Dyck & De Wreede 1995). Other studies of life history phase dominance in *M. splendens*, where observations were made only in spring and summer, have found consistent gametophyte dominance during this season (May 1986, as *I. cordata*; Thornber & Gaines 2003).

Summer gametophyte dominance in wave-sheltered habitats changes to tetrasporophyte dominance as the habitat becomes more wave-exposed (Dyck et al. 1985, as I. cordata; Phillips 1994, as Mazzaella lilacina). In central California, Hansen (1977, as Iridaea cordata) observed populations of *M. splendens* that were predominantly tetrasporophytic throughout the year. Here there were seasonal changes in biomass, from high in summer to low in winter, but density did not change appreciably. Seasonal variation in biomass resulted from changes in size class frequencies (Hansen & Doyle 1976, as I. cordata). Sites relatively close to each other, along the Oregon and California coastline, can differ substantially in phase ratio (Dyck et al. 1985, as I. cordata). At Pigeon Point, California, Hansen and Doyle (1976, as I. cordata) found tetrasporophyte dominance, but Dyck et al. (1985, as I. cordata) later found gametophyte dominance. These observations are consistent with nearby sites differing sufficiently in wave-exposure to support different life history phase predominance.

A particular demographic pattern, consistent with all previously published studies of *M. splendens*, emerges from the above studies. The pattern is this: gametophytes and tetrasporophytes generally cycle between high biomass and density in summer and low biomass and density in winter. For population density, taken separately, the magnitude of this seasonal change decreases as wave exposure in the habitat increases. In wave-sheltered habitats there is a seasonal alternation between summer gametophyte dominance and winter tetrasporophyte dominance. This changes to year-round tetrasporophyte dominance in more wave-exposed habitats. Changes in population density are the result of appearances and disappearances of genets, not greater module production by genets of one life history phase over those of the other (Dyck & De Wreede 1995). A re-analysis of data collected by Dyck (1991, as I. splendens) showed that 80% or more of the guadrats were occupied by one or more individuals throughout the year (Fig. 1), although gametophyte presence/ absence varied more widely than tetrasporophyte presence/absence (primarily in winter). Given that these quadrats represent a range of microhabitats in which *M. splendens* grows, the pattern suggests that changes in population density of *M. splendens* occur more or less evenly among patches in an area and are not a result of greater growth or mortality in certain microhabitats versus others.

In the present paper we report 3 years of seasonal and spatial changes in population density of the alternate life history phases of *M. splendens* in a wavesheltered habitat and a wave-exposed habitat at Second Beach, Barkley Sound. This location is geographically distant from Vancouver Harbour and the Strait of Georgia, sites of studies used in deriving the common demographic pattern. We compare the patterns of population density change at Second Beach to the common demographic pattern. This comparison is used to modify the common demographic pattern and, in doing so, to more accurately describe the demographic properties of *M. splendens* populations at larger scales.



**Fig. 1.** Seasonal changes, in proportion of 36 permanent 0.25 m<sup>2</sup> 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. ( $\blacklozenge$ ) Total; ( $\blacksquare$ ) Gem; ( $\blacktriangle$ ) Tet.

#### MATERIALS AND METHODS

Various locations in Barkley Sound, Vancouver Island, British Columbia were surveyed from June to August 1997. In selecting sites, our working assumption was that areas with a pronounced summer gametophyte dominance were capable of a seasonal alternation in phase dominance. In August 1997, a relatively wavesheltered area at Second Beach with haploid dominance, and a nearby more wave-exposed area with diploid dominance, were selected as the primary study sites (Fig. 2).

On 15-18 October 1997, 20 0625 m<sup>2</sup> permanent quadrats were placed at random within the wavesheltered site, in locations supporting growth of M. 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. Twenty quadrats were positioned, in the same way, at the wave-exposed site. Between 3 February and 15 April 1999, 8 guadrats at the wave-sheltered site were covered by sand and on 14-20 May 1999, 11 new 0.0625 m<sup>2</sup> permanent quadrats were placed at random within this site. Censuses of *M. splendens* at the wavesheltered site were conducted as often as low tides allowed access to the population (approximately monthly) from November 1997 to January 2001. All months were sampled except August 1998, March and September 1999, and March and September 2000, for a total of 35 censuses.

In November 1997 it became apparent that 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 waveexposed site were rediscovered. Seven censuses of these quadrats were conducted during the summers of 1998 and 1999. The months sampled were June, July, September and October 1998, and June, July and August 1999.

In each quadrat the number of genets and the number of modules in each genet were counted. We considered each distinct basal crust of *M. splendens*, from which several blades emerged, as a genet, and each blade as a module of that genet. Genet, as we use it here, is an operational definition. What we observed in the field, when conducting a census of M. splendens, were 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 (De Wreede & Green 1990, as I. splendens; Dyck et al. 1985, as I. cordata; Dyck & De Wreede 1995), been referred to as individuals or genets. We have retained this functional terminology, bearing in mind that the possibility of sporeling coalescence (Santelices 1999; Santelices *et al.* 1999) does not allow the assumption that each basal crust is necessarily the product of a single spore. We discuss 'appearances' and 'disappearances' of genets, because the loss of all blades from a basal crust need not indicate its loss from the population, and reserve the terms 'gain' and 'loss' for modules.

A 0.5 cm diameter disk of tissue was removed from each module 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 & De Wreede 1988; Shaughnessy & De Wreede 1991). This provided a record over time of changes in genet and module density for haploids versus diploids.

Within each sampling period, differences in density between gametophytes and tetrasporophytes, and differences between phases in the number of modules per genet, were assessed with the Mann–Whitney *U*-test (Fisher & van Belle 1993) using SPSS 9.0.

### RESULTS

#### Population density

At the wave-sheltered site, population density of *M. splendens* genets and modules increased rapidly for both gametophytes and tetrasporophytes each spring, beginning in mid February and peaking in May. Late spring gametophyte densities were significantly larger than tetrasporophyte densities. Each year from May to September there was a decline in density of both life history phases. There were no significant differences in density during late summer/early fall. In October 1998, there was an increase in gametophyte density but not in density of tetrasporophytes. Haploid density remained significantly higher from October 1998 to February 1999. This October increase in density was much less pronounced in the second and third years (Figs 3,4).

At the wave-exposed site, tetrasporophyte genet and module densities were significantly higher than gametophyte densities at all sampling times. Population density at the wave-exposed site did not show the sharp summer decline seen at the wave-sheltered site. There was some decline in population density at the wave-exposed site in the summer, 1998, but this was confined mainly to the diploid phase. During the summer of 1999 there was very little decline (Figs 5,6).

#### Modules per genet

At the wave-sheltered site there was a general tendency for the number of modules per genet, for both life



Fig. 2. Location of the wave-sheltered and wave-exposed study sites for *Mazzaella splendens* at Second Beach, Barkley Sound. Shaded areas: dark, above mean high tide; light, intertidal.

history phases, to rise with increasing population density and to fall with decreasing population density. On only 2 out of the 35 dates was there a significant difference between life history phases. On both of these occasions tetrasporophytes had the greater number of modules per genet (Fig. 7).

At the wave-exposed site, the number of modules per genet was significantly different between life history



**Fig. 3.** 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 standard error). Gamgen, gametophyte genets; Tetgen, tetrasporophyte genets; Sig, Statistical significance: Mann–Whitney *U*-test,  $P \le 0.05$ . (\*) Total; (**■**) Gamgen; (**▲**) Tetgen.



**Fig. 4.** 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 ( $\pm$ 1 standard error). Gammod, gametophyte modules; Tetmod, tetrasporophyte modules; Sig, Statistical significance: Mann–Whitney *U*-test, P ≤ 0.05. (\*) Sig; (**■**) Gammod; (**△**) Tetmod.



**Fig. 5.** 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 ( $\pm$ 1 standard error). Gamgen, gametophyte genets; Tetgen, tetrasporophyte genets; Sig, Statistical significance: Mann–Whitney *U*-test, P ≤ 0.05. (\*) Sig; (**■**) Gamgen; (**▲**) Tetgen.



**Fig. 6.** 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 ( $\pm$ 1 standard error). Gammod, gametophyte modules; Tetmod, tetrasporophyte modules; Sig, Statistical significance: Mann–Whitney *U*-test, P  $\leq$  0.05. (\*) Sig; (**II**) Gammod; (**A**) Tetmod.



**Fig. 7.** 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 standard error). Gam, gametophytes; Tet, tetrasporophytes; Sig, Statistical significance: Mann–Whitney *U*-test,  $P \le 0.05$ . (\*) Tet; (**II**) Gam; (**A**) Tet.

phases once in 1998 and once in 1999 (Fig. 8). Both times tetrasporophytes had more modules per genet. Modules per genet tended to decline gradually from June to October 1998, and from June to August 1999.

#### Quadrat occupancy

Quadrat occupancy is that proportion of the total number of quadrats at a site that had one or more individuals of *M. splendens* present. At the wave-sheltered site occupancy rose and fell synchronously with increases and decreases in population density. Both gametophytes and tetrasporophytes followed this general pattern (Fig. 9). All quadrats in the wave-exposed site were occupied at each census.

	1998				1999		
	June	July	September	October	June	July	August
Genets	0.015	< 0.001	< 0.001	< 0.001	0.012	0.001	< 0.001
Gamgen	0.431	0.011	< 0.001	0.045	0.974	0.171	0.001
Tetgen	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Modules	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Gammod	0.803	0.004	< 0.001	0.023	0.235	0.033	< 0.001
Tetmod	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

 Table 1. Inferential statistics comparing densities of Mazzaella splendens at the wave-sheltered versus wave-exposed sites, Second Beach, Barkley Sound. June to October 1998 and June to August 1999

Given are *P*-values from the Mann–Whitney *U*-test. Gamgen, gametophyte genets; Gammod, gametophyte modules; Genets, genets of both phases; Modules, modules of both phases; Tetgen, tetrasporophyte genets; Tetmod, tetrasporophyte modules.



**Fig. 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 ( $\pm$ 1 standard error). Gam, gametophytes; Tet, tetrasporophytes; Sig, Statistical significance: Mann–Whitney *U*-test, P  $\leq$  0.05. (\*) Tet; ( $\blacksquare$ ) Gam; ( $\blacktriangle$ ) Tet.

#### 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. 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 (Table 1).

#### DISCUSSION

#### Differences between the hypothesized common demographic patterns and the patterns at Second Beach, Barkley Sound

One part of the demographic pattern that we hypothesized as common to all populations of *M. splendens* 



**Fig. 9.** Seasonal changes, in proportion of total quadrats occupied by *Mazzaella splendens*, among 20–31 permanent 0.0625 m<sup>2</sup> 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. (\*) Total; ( $\blacksquare$ ) Gam; ( $\blacktriangle$ ) Tet.

was a seasonal alternation, from summer gametophyte to winter tetrasporophyte dominance, in wave-sheltered habitats. But this did not occur in the wave-sheltered site at Second Beach, Barkley Sound. During the entire 3 year period, only the first and last censuses hinted at anything resembling a winter shift to tetrasporophyte dominance. Haploids predominated significantly each spring and early summer, and often at some point in the fall density increase. Therefore, seasonal alternations in phase dominance, in wave-sheltered areas, must be considered variable, influenced by local conditions and not a common feature of all populations of *M. splendens*.

In a wave-sheltered population in Vancouver Harbour, previously observed by Dyck and De Wreede (1995), the lowest population density was in February and the peak in June. Density declined gradually from June to February. In contrast, at Second Beach, population increase usually began in February and peak density was in May. May to September was a period of rapid decline, with densities in August and September often as low as at the end of winter. Each October population density rebounded somewhat, primarily within the haploid phase, and then declined through January.

The absence of an alternation in phase dominance at Second Beach appears primarily to be a result of the fall density increase, which was not present in Vancouver Harbour. Even with the earlier and more dramatic summer population decline, a crossover to winter diploid dominance could still have happened if the respective rates of decline (greater for the haploid phase than for the diploid) had continued beyond September. The fall increase, with its boost in gametophyte density, prevented this, although rates of haploid decrease after November appear generally greater than diploid rates.

The timing of population density increase and decrease, and the absence of a seasonal alternation in phase dominance at Second Beach was consistent over 3 years. The first year coincided with the 1997-1998 El Niño event. This was followed by the 1998-1999 La Niña. It is possible that these events influenced the demography of *M. splendens*, causing differences from the hypothesized common pattern. However, these differences persisted in the third year of study, which did not have a major climatic event associated with it. Also, Sunday (2001) found seasonal alternations, with summer haploid and winter diploid dominance, during the period of May 2000 to March 2001. These occurred 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 the present study, at a distance of approximately 500 m. There are local differences, even at this scale, affecting the degree to which seasonal alternation is expressed.

In the wave-sheltered population previously observed by Dyck (1991, as *I. splendens*) quadrat occupancy never fell below 0.8 at any time of year. The patterns of occupancy were different between gametophytes and tetrasporophytes. Occupancy by tetrasporophytes remained higher during population decline (never falling below 0.6), but gametophyte occupancy (although relatively constant from April to November) fell to 0.2 in winter (Fig. 1). Overall reduction in population density, however, is more of a general decrease over all quadrats at the site.

At Second Beach the proportion of quadrats occupied (Fig. 9) increased with increasing population density, and decreased as population density declined, to a greater degree than in the population observed by Dyck (1991, as *I. splendens*). Between life history phases the pattern was variable with, except for the first spring and summer, gametophytes generally occupying a greater number of quadrats. At Second Beach, population density declined more by the disappearance of all individuals from certain quadrats than by a general decrease in density over all quadrats. This might reflect a greater heterogeneity of microhabitats occupied by *M. splendens* at Second Beach versus the habitat examined by Dyck (1991, as *I. splendens*) in Vancouver Harbour, with plants in some quadrats at Second Beach reacting to the effects of seasonal change before those in other quadrats.

#### Similarities between the hypothesized common demographic patterns and the patterns at Second Beach, Barkley Sound

In the wave-sheltered site at Second Beach, Barkley Sound, there was a marked seasonal change in density of genets and modules of both life-history phases, with considerably higher population densities in summer than in winter. This is consistent with the hypothesized common demographic pattern. High density in summer and low in winter is often observed in populations of Mazzaella. It has been observed for Mazzaella capensis (J. Agardh) Fredericq (Bolton & Joska 1993, as I. capensis) on the Cape Peninsula in South Africa and for M. laminarioides and Mazzaella ciliata in central Chile (Hannach & Santelices 1985, as I. laminarioides and I. ciliata). This pattern was variable, however, for Mazzaella flaccida (Setchell et Gardner) Fredericg in central California (Thornber 2001), where high summer and low winter density was present in certain years and locations but the reverse in others. High summer and low winter densities might be relatively common in this genus as a whole, although clearly some variation is to be expected.

Also consistent with the hypothesized common pattern were higher population density and summer tetrasporophyte dominance in the wave-exposed site at Second Beach. Whereas the population of modules at the wave-sheltered site was undergoing its annual summer crash, comparatively less population decline was observed at the wave-exposed site. The wavesheltered and wave-exposed areas were approximately 30 m distant from each other, illustrating the importance of local environmental differences in structuring populations of *M. splendens*. It is possible that the increased wave activity at the exposed site reduces desiccation stress, keeping blades wetter during spring tides.

In both the wave-sheltered and wave-exposed sites at Second Beach the number of modules per genet showed no significant overall predominance for either life history phase. In both areas changes in visible 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. This pattern is consistent with all studies of *M. splendens* to date.

# Differences between the wave-sheltered and wave-exposed habitats at Second Beach

The available evidence (Hansen 1977, as *I. cordata*; May 1986, as *I. cordata*) suggests that seasonal change in population density of *M. splendens* is primarily the result of perennation, with more basal crusts producing blades (and, therefore, 'appearing' in the population) when conditions are favorable and losing those blades ('disappearing') as conditions become unfavorable. Peak genet density, therefore, is the best available estimator of the size of the underlying population of basal crusts. Peak density of haploid individuals (basal crusts) at the wave-sheltered site was not significantly different from peak density at the wave-exposed site, whereas peak density of diploid individuals was always significantly higher at the wave-exposed site than in the wave-sheltered site.

This implies that the population of tetrasporophyte basal crusts was significantly larger in the waveexposed site than in the wave-sheltered site, whereas the population of haploids was not significantly different. In terms of the underlying population of basal crusts, haploids might 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, do best in numerical terms in the wave-exposed habitat (Table 1). Shaughnessy et al. (1996) found generally greater planform areas in adult gametophyte blades of *M. splendens* than in adult tetrasporophytes and suggest that tetrasporophyte blades could better resist hydrodynamic force than gametophyte blades. This hypothesis has the potential to explain both the spatial change from gametophyte to tetrasporophyte dominance as wave exposure increases, and the seasonal change from summer gametophyte to winter tetrasporophyte dominance in wave-sheltered areas, given that the onset of winter storms increases wave activity and preferentially culls gametophytes.

The above is a powerful hypothesis, but general differences between the habitat in Vancouver Harbour where a seasonal alternation in phase dominance was found, and that on the outer coast at Second beach where it was not, raise certain questions. Waves on the outer coast, even in summer, are larger than any waves usually found, even during winter storms, in Vancouver Harbour. If the seasonal change from summer haploid to winter diploid dominance in Vancouver Harbour is a result of greater diploid survival in winter, why was such a shift not seen at Second Beach? The differences in demographic pattern between the two locations suggest that, if wave force is indeed acting in this process, there is clearly no standard response of *M. splendens* to wave force per se that can be applied across habitats. If the winter hydrodynamic forces in Vancouver Harbour are sufficient to preferentially cull gametophytes, haploid blades should not predominate, even in summer, in any outer coast habitats except the most sheltered inlets. The role of wave force, in changing the population density of established adult blades, is less clear than previously thought.

Differences between Vancouver Harbour and Second Beach also raise questions about the role of desiccation in altering population density of adult blades. Summer low tides at Second Beach typically occur very early in the morning, usually beginning before dawn, and are 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, one would expect the desiccation stress on blades of *M. splendens* during summer low tides to be generally higher at Brockton Point than at Second Beach.

There was a summer decline in population density at Brockton Point (from June to July 1989), accompanied by bleaching of blades (Dyck 1991, as *I. splendens*), but the population recovered (in August) before a slow decline to the winter minimum density. In contrast, population density at Second Beach declined precipitously from May through September each year, recovering somewhat in October. This more dramatic summer population decline, with an earlier onset, occurred in a habitat where desiccation pressure should be less than at Brockton Point, as a result of both less direct sunlight and greater water motion. It seems unlikely that the immediate cause of summer population decline at Second Beach is desiccation stress. This is also suggested by Shaughnessy and De Wreede (2001) who found a positive relationship between elevation in the intertidal and bleaching of blades in *M. splendens*, but a weak relationship between elevation and loss of blades by genets. They conclude that loss of blades is not primarily a function of bleaching in *M. splendens*, although they found bleaching to be an important source of mortality for Mazzaella linearis (Setchell et Gardner) Fredericq.

The consistency of the seasonal demographic pattern at Second Beach and its marked difference from the pattern at Brockton Point suggest that these differences in the demography of *M. splendens* are a result of environmental differences between the two locations rather than climatic differences between the years in which the two studies took place. What these differences are is not yet clear. But the evidence suggests that some rethinking of the roles of wave force and desiccation in altering population density is required.

These questions concerning the underlying mechanisms by which differences in seasonal demographic patterns arise will hopefully spur further interest in population studies of *M. splendens*. Each examination of a new local population can contribute both to a better understanding of these mechanisms and to a greater understanding of the common patterns that characterize *M. splendens* populations at much larger spatial scales. Short-term small scale studies, useful in their own right, can also serve to address long-term large scale phenomena, as interest in *M. splendens* as a

### CONCLUSIONS

A demographic pattern, potentially common to natural populations of *M. splendens* is: (i) 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; (ii) a change from summer gametophyte dominance to summer tetrasporophyte dominance as wave force in the habitat increases; and (iii) that changes in population density are the result of appearances and disappearances of genets rather than differential module production by haploid versus diploid genets.

model species for algal demography continues to grow.

Seasonal alternation in phase dominance at wavesheltered sites, consistent with all previously published studies, was not present at Second Beach and is dependent on local conditions. Local conditions also influence the pattern of appearances and disappearances of genets. This occurs relatively evenly among microhabitats in some areas, but much more unevenly in others.

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