



Short research note

Effects of elevation, wave exposure, and year on the proportion of gametophytes and tetrasporophytes in *Mazzaella parksii* (Rhodophyta, Gigartinaceae) populations

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Received 15 September 2003; in revised form 17 December 2003; accepted 22 December 2003

Key words: elevation, gametophyte, Gigartinaceae, *Mazzaella*, tetrasporophyte, wave exposure

Abstract

We investigated the effects of elevation, wave exposure, and year on the proportion of gametophytes and tetrasporophytes in populations of the intertidal red seaweed *Mazzaella parksii* (= *M. cornucopiae*, Gigartinaceae) from the Pacific coast of Canada. In July 2002, we determined the life-history phase of 864 frond samples from four populations from Barkley Sound, using the resorcinol-acetal test. For these populations, gametophytes were significantly more numerous than tetrasporophytes, and the proportion of gametophytes was significantly higher at higher elevations. The proportion of gametophytes varied directly (although less markedly) with the degree of wave exposure, but significance could not be assessed for this factor. All of these patterns were spatially consistent, as they held for two different rocky points with similar physical characteristics. One of these points had also been surveyed in 1994–1995, which allows us to conclude that the population-wise gametophyte predominance and the positive relationship between elevation and the proportion of gametophytes are stable features of this species in this area. However, the average proportion of gametophytes was similar between the studied levels of wave exposure in 1994–1995; such a difference revealed as non-significant when data were combined with those for 2002. This suggests that wave exposure is not important in determining the proportion of life-history phases for this species. Comparisons with other species are done in search of general patterns for the Gigartinaceae.

The identification of spatial and temporal patterns of population structure is fundamental in population ecology (Underwood et al., 2000). Seaweeds are significant components of many coastal marine communities, because they provide food and habitat for many animals. The life history of most seaweeds includes an alternation between phases of different ploidy levels. In particular, species of the Gigartinaceae (Rhodophyta) alternate between macroscopic gametophytes and tetrasporophytes, with a third phase (the carposporophyte) being microscopic and developing inside the female gametophyte after syngamy (Graham & Wilcox, 2000). An important descriptor of population structure for these algae is, therefore, the

relative abundance of gametophytes and tetrasporophytes. Knowing this sets the base for studies of population dynamics (Scrosati & DeWreede, 1999).

Variability in the proportion of life-history phases (sometimes referred to as the ratio of gametophytes to tetrasporophytes, the G:T ratio) occurs across spatial and temporal scales for the Gigartinaceae (Scrosati & DeWreede, 1999; Thornber & Gaines, 2003). Thus, it is important to identify factors that are associated with such variability. One spatial factor that affects the proportion of phases in some species is depth. For example, for *Chondrus crispus* Stackhouse from northeastern North America, studies have shown, with varying degrees of conclusiveness, that tetrasporo-

phytes are relatively more common in deeper waters, while gametophytes are so in shallower waters (Mathieson & Burns, 1975; Craigie & Pringle, 1978; Lazo et al., 1989). Another spatial factor that affects the proportion of phases in some species is wave exposure. For example, for *Mazzaella splendens* (Setchell & Gardner) Fredericq and *M. oregona* (Doty) Hughey, P. C. Silva & Hommersand (formerly *M. heterocarpa*, according to Hughey et al., 2001) from southwestern Canada, the proportion of gametophytes is inversely related to the degree of wave exposure (Dyck et al., 1985; Phillips, 1994; Mudge & Scrosati, 2003). Temporal variability in the proportion of phases has also been detected for a number of species, for which seasonal shifts in phase predominance may occur, such as for *M. splendens* from southwestern Canada (DeWreede & Green, 1990; Dyck & DeWreede, 1995) and *M. capensis* (J. Agardh) Fredericq from South Africa (Bolton & Joska, 1993). Comparisons have also been made for some species between a few consecutive years (Otaíza et al., 2001; Morley et al., 2003; Thornber & Gaines, 2003). Comparisons after several years, however, are almost lacking for the Gigartinaceae. One such study was done on *M. splendens*, which was sampled with a difference of 10 years at Pigeon Point, California (Hansen & Doyle, 1976; Dyck et al., 1985). However, it is uncertain whether the exact same area was sampled in both occasions because of the difference in survey teams, which might explain the high interdecadal difference observed in the proportion of each life-history phase (L. Dyck, pers. comm.). Another study on the subject was recently done on *Chondrus crispus*, which was sampled after an interval of 12 years at the same site in Tor Bay (Nova Scotia, Canada). This study indicated a persistence of gametophyte predominance after this period, which had been predicted based on the stable nature of the rocky substrate and the perennial nature of the species (Scrosati & Mudge, 2004). It is progressively becoming evident that reliable data describing changes after long periods are needed to better understand ecological systems (Barry et al., 1995; Inchausti & Halley, 2001; Sousa, 2001; Haddad et al., 2002).

In search of general patterns for the Gigartinaceae, we investigated in 2002 the variability in the relative abundance of gametophytes and tetrasporophytes for the intertidal species *Mazzaella parksii* (Setchell & Gardner) Hughey, P. C. Silva & Hommersand (formerly *M. cornucopiae*, according to Hughey et al., 2001) from southwestern Canada. On a spatial scale, changes in the proportion of phases were studied

across gradients of elevation and wave exposure. On a temporal scale, the results for one of our study sites were compared with those obtained 7–8 years earlier at that same site (Scrosati, 1998a), thus constituting one of the longest intervals for which G:T data became available unequivocally for the same site for the Gigartinaceae. In 1994–1995, the proportion of *M. parksii* gametophytes varied directly with elevation. Wave exposure was found to have more variable effects, however, with average values for both years being similar between the two studied levels of exposure (Scrosati, 1998a). Since *M. parksii* is perennial (Scrosati, 1998a) and the rocky substrate at the re-sampled site is mostly stable on a long-term basis (small-scale disturbances involving the loss of surface rock layers are infrequent), we predicted similar spatial patterns for the G:T ratio in 2002. In addition, in 2002 we also determined the spatial consistency of such patterns by comparing the re-sampled site with another site with similar physical characteristics. Because of the environmental similarity between both sites, we predicted similar patterns for the G:T ratio across their respective gradients of elevation and wave exposure.

The thallus of *Mazzaella parksii* is composed of a crustose holdfast and many foliose fronds, which are equivalent to ramets in this clonal alga (Scrosati & DeWreede, 1997). Its biogeographic range is from Alaska to California (Hughey et al., 2001), although this species has been mostly studied in British Columbia (Kim & DeWreede, 1996; Scrosati, 1998a, b; Scrosati & DeWreede, 1998), Washington (Harley, 2003), and Oregon (Olson, 1985, 1990). Our study sites were Prasiola Point (48° 49' 6" N, 125° 10' 6" W) and Nudibranch Point (48° 48' 54" N, 125° 10' 24" W), located approximately 0.5 km from one another (separated by a sandy beach) on southern Barkley Sound, on the west coast of Vancouver Island, British Columbia, Canada (see map in Mudge & Scrosati, 2003). Both sites have a rocky substrate and are washed by cold-temperate waters, with mean monthly temperatures between 8.6 °C in winter and 16.1 °C in summer (Scrosati, 2001). At these sites, the highest tidal amplitude is approximately 4 m. *M. parksii* occurs at the high intertidal zone, across a vertical range of about 1 m (between approximately 3–4 m above the lowest normal tide at the east side of Prasiola Point; Scrosati, 1998a). The west side of both points is frequently exposed to intense wave action, since they face the open ocean, while the east sides are more sheltered (see such exposure differences in the

photographs appearing in Mudge & Scrosati, 2003). Biological indicators are related to wave exposure in a similar way at both points. For example, total seaweed cover is higher at both the protected sides, whereas the mussel *Mytilus californianus* Conrad and the gooseneck barnacle *Pollicipes polymerus* Sowerby, characteristic of exposed habitats, are larger and more abundant at the exposed sides. Sampling more similar sites was not possible in the time available for this study for logistical reasons, as rocky intertidal sites in southern Barkley Sound are topographically challenging and accessible mostly only by sea.

To determine the proportion of life-history phases for any rhodophyte population, counts of genets (defined as the thallus that develops from a single spore; Scrosati, 2002) of gametophytes and tetrasporophytes should be done. At the study sites, *Mazzaella parksii* generally occurs as extensive turfs with fronds no longer than 5 cm. High frond densities (up to 21 fronds cm^{-2} ; Scrosati & Servi re-Zaragoza, 2000), the possible coalescence among neighboring sporelings (Santelices et al., 1999) and older thalli (Santelices et al., 2003), and the possible fragmentation of a genet into two or more clonal fragments (sensu Eriksson & Jerling, 1990) prevented the unequivocal identification of genets in these populations. The proportion of life-history phases was determined for the protected and exposed sides of Prasiola Point and Nudibranch Point by identifying the life-history phase of frond samples collected at random in July 2002. Fronds were sampled separately from the upper and lower halves of each *M. parksii* population. To ensure as much as possible that genets were not sampled twice, the sampled fronds were never less than 10 cm from one another. The life-history phase of a frond can be easily determined visually when it is reproductive (Fig. 1), but not when it is vegetative, since both phases are morphologically similar. We determined the phase of our frond samples through the resorcinol-acetal test in the laboratory (Garbary & DeWreede, 1988; Shaughnessy & DeWreede, 1991). This test is based on the fact that gametophytes and tetrasporophytes have different carrageenans in cell walls, which, for *M. parksii*, results in reagent solutions with gametophyte samples turning red and those with tetrasporophyte samples turning pink. We tested our samples simultaneously with samples of known life-history phase, due to their reproductive condition (using three fronds per phase per run), thus acting as controls for colour. The frond samples were air-dried immediately after collection and stored in that

condition until analyzed with the resorcinol-acetal test. Whenever appropriate, results were tested for significance using 95% confidence intervals (Howell, 1992).

Overall, we tested 864 fronds with the resorcinol-acetal test. A small percentage of the samples ($4 \pm 2\%$, mean $\pm$ S. E., $n = 8$ runs) could not be accurately identified, because they showed intermediate colours between the two control types. Such unidentified samples were excluded from calculations of the proportion of life-history phases.

The results of our tests are shown in Table 1. Overall, gametophytes predominated over tetrasporophytes in the four populations studied in July 2002: the mean relative abundance of gametophytes was 65% (60–70% as confidence limits; $n = 4$ populations). The relative abundance of gametophytes was, for the four populations, higher at the upper half of the *Mazzaella parksii* belt (mean relative abundance = 81%, with 65–97% as confidence limits; $n = 4$) than at the lower half (mean relative abundance = 49%, with 41–56% as confidence limits; $n = 4$). Wave exposure had less marked effects than elevation: the relative abundance of gametophytes was higher under high wave exposure (mean relative abundance = 67.5%) than under low exposure (mean relative abundance = 62%); confidence intervals were not calculated due to the low site replication for exposure ($n = 2$). There was an apparent interaction between elevation and wave exposure, as the vertical difference in the proportion of gametophytes was more pronounced under high exposure than under low exposure (Table 1). It must be stressed that all of these patterns were spatially consistent, as they occurred similarly at Prasiola Point and Nudibranch Point.

The temporal comparison can only be done for Prasiola Point, since this was the only site surveyed in 1994–1995; see Scrosati (1998a) for results of those years. Then, an overall gametophyte predominance had also been found for both populations (east and west of the point), regardless of the sampled season. Elevation (investigated only at the west side in 1995) had also been found to be directly related to the proportion of gametophytes. In 1994–1995, however, the effects of wave exposure had been more variable, with the mean (considering all of the 1994–1995 sampling dates) relative abundance of gametophytes being similar between the exposed and protected sides of Prasiola Point. Combining all of the existing data sets for *Mazzaella parksii* (1994, 1995, and 2002), wave exposure did not have a significant effect on



Figure 1. Top photograph: cystocarpic fronds (female gametophytic fronds with cystocarps) of *Mazzaella parksii*; the scars indicate the position of old cystocarps that lost all of the carpospores. Bottom photograph: tetrasporic fronds (tetrasporophytic fronds with tetrasporic sori); the sori are the dark spots. The largest fronds depicted here are 3–4 cm long. Both photographs were taken by R. Scrosati at Prasiola Point.

the proportion of life-history phases: the mean relative abundance of gametophytes was 69% (55–83% as confidence limits; $n = 4$), under high exposure, and 68% (60–76% as confidence limits; $n = 5$), under low exposure.

The resorcinol-acetal test distinguished life-history phases adequately for *Mazzaella parksii*. Gametophytes of members of the Gigartinaeaceae have κ -carrageenan in cell walls, which is responsible for

solutions containing gametophytic samples turning red with the resorcinol-acetal test (Shaughnessy & DeWreede, 1991). Unlike other species of this family, tetrasporophytes of *M. parksii* have small amounts of κ -carrageenan (Waaland, 1975), which might explain the intermediate colours that we found for some samples. However, intermediate colours could also have resulted from smaller-than-adequate amounts of gametophytic tissues placed in test tubes. Such pos-

Table 1. Relative abundance of gametophytes (G) and tetrasporophytes (T) of *Mazzaella parksii* in four populations from Barkley Sound in July 2002. Data are summarized as the relative percent abundance of each phase and as the G:T ratio. Relative levels of wave exposure are denoted as 'Exposed' and 'Protected', whereas relative levels of intertidal elevation are denoted as 'High' and 'Low', with 'All' combining all of the data for each exposure level. The number of frond samples considered for each calculation is denoted by *n*.

	Prasiola point			Nudibranch point		
	% G - % T	G:T ratio	<i>n</i>	% G - % T	G:T ratio	<i>n</i>
Exposed - High	87 - 13	6.6	114	91 - 9	9.6	106
Exposed - Low	47 - 53	0.9	110	44 - 56	0.7	120
Exposed - All	67 - 33	2.1	224	68 - 32	2.1	226
Protected - High	68 - 32	2.1	90	78 - 22	3.6	105
Protected - Low	55 - 46	1.2	88	48 - 52	0.9	97
Protected - All	61 - 39	1.6	178	63 - 37	1.7	202

sibilities should be investigated further to increase the accuracy of this test for *M. parksii*. In any case, the proportion of unknowns was small in our analyses, and such samples were not included to calculate the proportion of life-history phases.

Overall, gametophytes predominated over tetrasporophytes in the four populations of *Mazzaella parksii* studied in Barkley Sound in July 2002. Since a similar pattern was found in 1994–1995, we conclude that gametophyte predominance is a stable feature of *M. parksii* in this area. This agrees with the general pattern observed for the Gigartinaceae, for which the predominance of gametophytes is common on a whole-habitat or an annual basis. At smaller spatial (or shorter temporal) scales, however, tetrasporophytes may predominate in this family (Scrosati & DeWreede, 1999). Such was the case at the lower half of three of our four *M. parksii* populations, although tetrasporophyte predominance was mild there. Explaining any given pattern of population structure requires knowledge on demographic features of the population. In the case of G:T ratios, explaining them needs data on rates of recruitment, mortality, and fertility for both life-history phases, as one phase depends demographically on the other via spores (Scrosati & DeWreede, 1999). Although some demographic information exists for *M. parksii* from Prasiola Point (Scrosati & DeWreede, 1997; Scrosati, 1998a, b), specific data for each life-history phase are lacking, therefore preventing us from explaining with certainty the reasons for the observed G:T ratios.

Elevation on the shore was directly related to the proportion of gametophytes in the four populations of *Mazzaella parksii* studied in July 2002 and also in that studied in May and October 1995 at the west side of

Prasiola Point (Scrosati, 1998a). Studies on *M. parksii* from the Oregon coast (Olson, 1990) found the same vertical pattern for its G:T ratio. Experiments indicated that a higher resistance to desiccation in gametophytes and a higher resistance to limpet herbivory in tetrasporophytes might explain such differential distribution of life-history phases with elevation (Olson, 1990). Assessing the effects of desiccation and limpet herbivory specifically on the demographic rates of both phases might confirm such hypotheses. The possible effects of herbivory by snails of the genus *Littorina* should also be assessed, as they actively consume *M. parksii* tissues (Kim & DeWreede, 1996; Heaven & Scrosati, 2003).

Based on counts of reproductive fronds and on the resorcinol-acetal test, the increased relative abundance of gametophytes higher up on a vertical gradient was also observed for subtidal *Chondrus crispus* from northeastern North America, with varying degrees of strength (Mathieson & Burns, 1975; Craigie & Pringle, 1978; Lazo et al., 1989). Based on counts of reproductive fronds, gametophytes were also concluded to be relatively more abundant at higher elevations for the intertidal species *Mazzaella laminarioides* (Bory de Saint-Vincent) Fredericq from central Chile (Hannach & Santelices, 1985). This vertical pattern is, however, not unique for the Gigartinaceae, as the opposite trend was found for intertidal *Sarcothalia crispata* (Bory de Saint-Vincent) Leister from the same site in Chile (Hannach & Santelices, 1985) and a general lack of vertical differences was found for *M. flaccida* (Setchell & Gardner) Fredericq from California (Thornber & Gaines, 2003).

Although not greatly, wave exposure was directly related to the proportion of *Mazzaella parksii* gamet-

ophytes at both the rocky points studied in 2002, but such a pattern was not evident considering average values for 1994–1995 (Scrosati, 1998a). Analyzing all of the data for these years together, wave exposure did not have a significant effect on the proportion of life-history phases. Then, the observed interannual differences (and the differences observed among sampling dates in 1994–1995) may have resulted mostly from the inherent variability in samplings. For other species of the Gigartinaeae from Barkley Sound, such as *M. splendens* and *M. oregona*, the proportion of gametophytes was found to be inversely related to the degree of wave exposure (Dyck et al., 1985; Phillips, 1994; Mudge & Scrosati, 2003). For *M. splendens*, such spatial differences are related to biomechanical differences between life-history phases, since tetrasporophytes are more resistant than gametophytes to the hydrodynamic forces generated by waves (Phillips, 1994; Shaughnessy et al., 1996). No biomechanical studies have been done for *M. parksii*, but wave forces would not affect differently the survival of gametophytes and tetrasporophytes. This might be so because, unlike those of *M. splendens*, fronds of *M. parksii* grow tightly packed in extensive turfs no higher than 5 cm (Scrosati & DeWreede, 1997), which would reduce drag forces and provide mechanical support for the fronds within the turf. Such protective effects were observed for fronds of *Chondrus crispus*, which experience milder hydrodynamic forces when in groups than when solitary (Johnson, 2001). Experimental work is needed to test this possibility for *M. parksii*, which might explain the lack of significant differences in the proportion of life-history phases between the studied levels of wave exposure.

Acknowledgements

This study was done as part of the Marine Ecology course given by R. Scrosati in the summer of 2002 at Bamfield Marine Sciences Centre. We are grateful to Brian Penney, Christine Heaven, and Jean-Paul Danko, for their help in different aspects of this study, to the staff of Bamfield Marine Sciences Centre, for their logistical support, to the Huu-ay-aht First Nation, for granting access to the study sites, to Robert DeWreede, for laboratory support through his NSERC (Natural Sciences and Engineering Research Council of Canada) grant, and to two anonymous reviewers, for their useful comments.

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