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Effects of wave exposure on the proportion of gametophytes and tetrasporophytes of *Mazzaella oregona* (Rhodophyta: Gigartinales) from Pacific Canada

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The proportion of life history phases in red seaweeds is an important descriptor of population structure. This paper describes the relative abundance of gametophytes and tetrasporophytes of *Mazzaella oregona* (Rhodophyta: Gigartinales; formerly *M. heterocarpa*), focusing particularly on the effects of wave exposure on the proportion of both life history phases. In two different rocky points in Barkley Sound (Pacific Canada), gametophytes were, in proportion to tetrasporophytes, relatively more abundant under low wave exposure than under high wave exposure in July 2002, during the period of highest abundance for this species. The inverse relationship between the G:T ratio and the degree of wave exposure also occurs for local *M. splendens*, but not for local *M. parksii*. Differences in frond size and population density between these three sympatric species are related to the effects of wave exposure on their G:T ratio.

INTRODUCTION

The life history of most red seaweeds (Rhodophyta) includes two independent reproductive phases namely gametophytes and tetrasporophytes. A third reproductive phase, the carposporophyte, is smaller and develops within the female gametophyte. Variability among species of the Gigartinaceae (Gigartinales) ranges from gametophyte predominance to tetrasporophyte predominance, depending on the species, abiotic factors, and/or time (Scrosati & DeWreede, 1999).

For the Gigartinaceae, studies of the proportion of life history phases (hereafter referred to as the G:T ratio) have been particularly carried out on the north-western coast of North America. In this region, studies were mostly focused on two species: *Mazzaella splendens* (Setchell & Gardner) Fredericq (Dyck et al., 1985; May, 1986; Phillips, 1994; Dyck & DeWreede, 1995) and *M. parksii* (Setchell & Gardner) Hughey, P.C. Silva & Hommersand (Scrosati, 1998; formerly *M. cornucopiae*, according to Hughey et al., 2001). Another species of this genus, *M. oregona* (Doty) Hughey, P.C. Silva & Hommersand (Figure 1; formerly *M. heterocarpa*, according to Hughey et al., 2001), is also common in this region, but there are no published data on its G:T ratio. A comparison of several species will allow to assess the generality of patterns found so far for this family. Therefore, the G:T ratio for *M. oregona* from a number of sites in Barkley Sound, on the Pacific coast of Canada, was measured.

Several population traits determine the G:T ratio in nature (Scrosati & DeWreede, 1999), but there is no species for which all traits have been measured. A few abiotic factors including wave exposure have been shown to be related to changes in the G:T ratio for some species. In Barkley Sound, tetrasporophytes of *Mazzaella splendens* are more abundant than gametophytes under relatively high wave exposure, gametophytes predominating at low exposure (Dyck et al., 1985; Phillips, 1994). For *M. parksii* from this region, however, gametophytes predominate regardless of the degree of wave exposure (Scrosati, 1998). Such interspecific differences have been attributed to differences in frond size and density and their interaction with wave action. *Mazzaella parksii* fronds are much smaller and occur in extensive, dense turfs, which would make fronds less sensitive to hydrodynamic forces and, therefore, possible biomechanical differences between phases (shown only for *M. splendens* so far). The main objective of this study is to compare *M. oregona* with the above two species to test for the generality of the observed relationship between frond size/density, wave exposure, and G:T ratio. Since *M. oregona* fronds grow relatively large and occur in low densities across the substrate, resembling more *M. splendens* than *M. parksii*, we predicted that the G:T ratio for *M. oregona* would be inversely related to wave exposure.

Many ecological patterns vary spatially for seaweeds. Therefore, within limits imposed by logistics, we determined the spatial consistency of the G:T ratio for *M. oregona* by comparing two nearby sites, each with a similar gradient of wave exposure from east to west. Because of such environmental similarity, a similar spatial difference in the G:T ratio, depending on wave exposure, was predicted for each site.

MATERIALS AND METHODS

The 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 about 0.5 km from one another on southern Barkley Sound, Vancouver Island, British Columbia, Canada (Figure 2). Both sites have a rocky substrate and are washed by cold-temperate waters, with mean monthly

Figure 1. Thallus (clump) of *Mazzaella oregona* from Prasiola Point. The frond to the right (containing tetrasporic sori) was about 9 cm long. *Fucus gardneri* appears in the background, whereas *Endocladia muricata* appears in the foreground. Photograph taken by R. Scrosati on 20 September 2002.

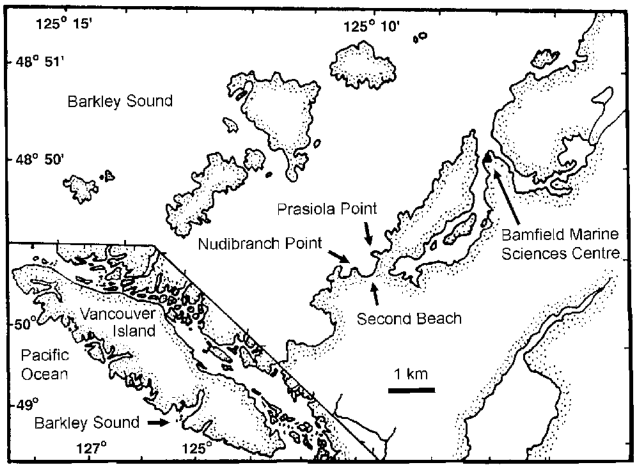

Figure 2. Map showing the location of the study sites.

temperatures between 8.6°C and 16.1°C (Scrosati, 2001). At these sites, the highest tidal amplitude is about 4 m and *Mazzaella oregona* occurs approximately at the mid-intertidal zone across a vertical range of about 1 m. It is a highly seasonal species, since biomass and reproduction peaks occur in spring and early summer and fronds are absent in autumn and early winter (R. Scrosati, personal observation). The identification to the species level was done following the keys made by Gabrielson et al. (2000), considering the nomenclatural change from *M. heterocarpa* to *M. oregona* proposed by Hughey et al. (2001) for specimens between southern Alaska and California.

The west side of both studied points is frequently exposed to intense wave action, since they face the open ocean (Figure 3A), while the east sides are more sheltered (Figure 3B). Biological indicators are related to wave exposure in a similar way at both points. For example, total seaweed cover is higher at both 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. We determined the G:T ratio

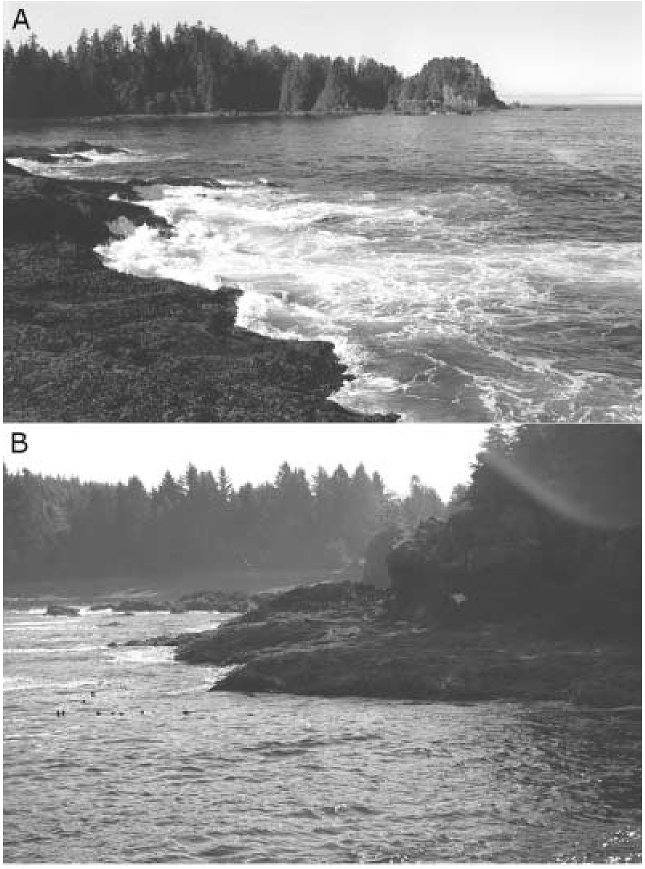

Figure 3. (A) Wave-exposed side (west) of Prasiola Point seen at mid-tide; note the direct exposure to the open ocean; (B) wave-protected side (east) of Prasiola Point seen at mid-tide. Nudibranch Point, which is located closer to the open ocean, has a similar difference in wave exposure between its west and east sides. Photographs taken by R. Scrosati on 20 September 2002.

for *Mazzaella oregona* separately for the exposed and for the protected side of both Prasiola Point and Nudibranch Point. The two Prasiola Point sampling sites were the same as those sampled for *M. parksii* previously (Scrosati, 1998).

To determine the G:T ratio for any rhodophyte population, counts of genets (each individual that develops from one spore; Scrosati, 2002) of gametophytes and tetrasporophytes should be done. At the study sites, *M. oregona* occurs as spatially separated clumps (=thalli) composed each of a variable number of fronds arising from a small holdfast. We collected only one frond sample per clump to determine its life history phase. Although coalescence of genets might have occurred during early stages, we followed the best existing field method to ensure that a given genet was sampled only once. When at least some of the fronds of a clump were reproductive, determining its life history phase was straigthforward. When they were all vegetative, however, frond samples were subjected to the resorcinol test in the laboratory (Shaughnessy & DeWreede, 1991). This test is based on the fact that gametophytes and tetrasporophytes have different carrageenans in cell walls, which results in reagent solutions with gametophyte samples turning red and those with tetrasporophyte samples remaining colourless. Fronds were haphazardly sampled at each site in early and mid-July 2002. The samples were subjected to the resorcinol test simultaneously

Table 1. *Relative abundance of gametophytes (G) and tetrasporophytes (T) of* Mazzaella oregona *from four sites in Barkley Sound in July 2002. Data are summarized as the G:T ratio and as the relative per cent abundance of each phase.*

Site	Wave-exposed side (west)	Wave-protected side (east)
Prasiola Point	G:T=0.6 39% G–61% T (N=95 fronds)	G:T=0.8 45% G–55% T (N=107 fronds)
Nudibranch Point	G:T=1.1 52% G–48% T (N=135 fronds)	G:T=1.4 58% G–42% T (N=103 fronds)

with frond samples of known life history phase, due to their reproductive condition (using three fronds per phase per run), thus acting as controls for colour.

RESULTS AND DISCUSSION

The resorcinol test on *Mazzaella oregona* always gave clearcut results: solutions with gametophyte samples turned dark red, whereas those with tetrasporophyte samples remained colourless. This is remarkable, as our trials with *M. splendens* and *M. parksii* samples, done for other purposes, always included some doubtful results due to intermediate colours. The clearcut results for *M. oregona* likely occurred because its tetrasporophytes do not contain κ-carrageenan (Waaland, 1975). This compound is dominant in gametophytes and is the cause of test solutions turning red (Shaughnessy & DeWreede, 1991). Tetrasporophytes of *M. splendens* and *M. parksii* do contain small amounts of κ-carrageenan (Waaland, 1975).

The G:T ratios for *Mazzaella oregona* from the four studied sites are shown in Table 1. Either gametophytes or tetrasporophytes predominated, depending on the site. However, phase predominance was always mild, never as high as for some populations of other species of the Gigartinaceae also studied with the resorcinol test, such as *M. splendens* from western North America (Dyck et al., 1985; May, 1986; DeWreede & Green, 1990; Phillips, 1994), *M. parksii* from Prasiola Point (Scrosati, 1998), *Chondrus crispus* Stackhouse from eastern Canada (Scrosati et al., 1994) and Sweden (Lindgren & Åberg, 1996), *Chondracanthus squarrulosus* (Setchell & Gardner) Hughey, P.C. Silva & Hommersand from north-western Mexico (Pacheco-Ruiz & Zertuche-González, 1999; formerly *Chondracanthus pectinatus*, according to Hughey et al., 2001), *Gigartina skottsbergii* Setchell & Gardner from Chile (Westermeier et al., 1999), and *Sarcothalia crispata* (Bory de Saint-Vincent) Leister from Chile (Otaíza et al., 2001). Full explanations of such interspecific differences must consider several population traits at the same time (Scrosati & DeWreede, 1999), but such information is currently unavailable for any of the above species.

As predicted, the G:T ratio for *Mazzaella oregona* was inversely related to the degree of wave exposure. Moreover, such pattern was spatially consistent, since it occurred at both Prasiola Point and Nudibranch Point. For each point, gametophytes were, in proportion to tetrasporophytes, relatively more abundant at the wave-protected side than at the wave-exposed side. Such a pattern is representative of mature populations, since early to mid-July is within the period of highest abundance for this species. For *M. splendens*, tetrasporophytes are more resistant than gametophytes to the hydrodynamic forces generated by waves (Phillips, 1994; Shaughnessy et al., 1996). Since *M. splendens* fronds are large (up to 35 cm long) and thallus density across the substrate is low, the fronds are relatively exposed to waves, so the biomechanical differences between phases are expected to shape its G:T ratio. Effectively, tetrasporophytes are more abundant than gametophytes at the exposed side of a rocky area west of Second Beach (Figure 1) than at its protected side, where gametophytes predominate (Phillips, 1994). Gametophytes of *M. parksii*, however, always predominate strongly over tetrasporophytes regardless of the degree of wave exposure at Prasiola Point (Scrosati, 1998). The biomechanical properties of *M. parksii* life history phases are unknown. However, even if phases differed in this respect, its G:T ratio would not vary much with wave exposure as a result, because fronds grow tightly packed in extensive turfs no higher than 5 cm, which would divert the main water flow over the turf. Given that *M. oregona* fronds are relatively large (up to 15 cm) and occur in low densities across the substrate, and that its G:T ratio is inversely related to wave exposure (all traits shared with *M. splendens*), the next logical step is to test for possible biomechanical differences between *M. oregona* phases. This will help to establish the mechanistic basis explaining G:T ratios across gradients of wave exposure for members of the Gigartinaceae.

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