

## Reproduction strategies of *Macrocystis pyrifera* (Phaeophyta) in Southern Chile: The importance of population dynamics

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### Abstract

*Macrocystis pyrifera* is an ecologically dominant species along the temperate Northern and Southern Pacific Coast of America, showing some similarities and differences at population and community level. In general, this kelp is reported to be reproductive all year round. Annual populations present in wave-protected areas of southern Chile suggest that the reproductive strategies of this population can be different. In this study we explore the reproductive strategies of annual *M. pyrifera* present in wave-protected areas and perennial populations encountered in exposed areas of southern Chile (41°S). Our results show that *M. pyrifera* present in wave-exposed locations has a reproductive strategy that is similar to populations in the northern hemisphere. These populations reproduce all year round and their strategy is to produce high numbers of sporophylls and ensure that most of them (over 90%) become sporogenous. On the other hand, the protected populations with an annual life cycle, produce more spores per area of sorus. In a few months, they are able to produce sufficient propagules to recolonize areas before the adult plants disappear in autumn.

### Introduction

*Macrocystis pyrifera* (L.) C. Ag. is abundant along the Chilean coastline from Cape Horn up to Valparaíso (33°S), but has also been reported on the Peruvian coast (Hoffmann & Santelices, 1997). Abundant populations are located south of Concepción (37°S) down to Patagonia in protected bays open to the Pacific Ocean, as well as in channels and fjords, forming conspicuous belts along the coastline. In this southern region, fluctuation of environmental parameters, especially temperature, salinity and nutrients, are greater in the inner waters than in bays open to the Pacific Ocean (Buschmann et al., 2004). Also, the morphology of plants from these populations differs significantly. Plants present in the inner sea (the most wave-protected populations) have broader blades, smaller pneumatocysts, and more ribbed blades, among other characteris-

tics suggesting that the environmental conditions have considerable individual and population consequences for this brown alga (Buschmann, 1992; Vásquez & Buschmann, 1997).

Previous results indicate that wave-exposed sites produce fewer perennial populations than wave-protected sites (e. g. Seymour et al., 1989; Harrold & Reed, 1985). Studies of the reproduction ecology of *Macrocystis pyrifera* in the North Pacific show that this species is reproductive all year round (Reed et al., 1996), as has also been established in protected areas of the Beagle Channel (Santelices & Ojeda, 1984). However, the wave-protected populations of *M. pyrifera* in the northern limit (41–44°S) of the archipelago area of southern Chile show a different trend (Buschmann, 1992; Vásquez & Buschmann, 1997). These are annual, raising several questions regarding factors that produce these unusual patterns and how these populations

manage to recruit successfully year after year. In consequence, wave-protected and exposed kelp populations have important ecological differences that have not yet received attention for a more comprehensive understanding of *M. pyrifera* population dynamics.

This study outlines the annual population dynamics and reproductive patterns in areas with different water movement regimes that represent different reproductive strategies. We describe the reproductive strategy of *Macrocystis pyrifera* with respect to the size of the parent plants, indicating size of first reproduction and reproductive effort in relation to different (annual and perennial) population dynamics.

## Material and methods

### Study areas

This study was carried out in southern Chile (40–41°S) where different water movement regimes can be found as a consequence of the presence of channels, fjords and wave-protected bays (Figure 1). In this region a wave exposed locality (Bahía Mansa; 40°34'S, 73°44'W) and a protected locality (Metri; 41°36'S, 72°43'W) were identified on the basis of carbonate-block dissolution rates, as described by Buschmann et al. (2004). The study was carried out, within each locality, at two sites separated by <500 m to assure the representation of the variability of each locality. The exposed area, Bahía Mansa (Figure 1), is characterized by variable depths between 0 to 12 m, with a substratum mostly composed of compact rock and boulders and where carbonate dissolution rates varied from 0.6 to 0.9 g h<sup>-1</sup>. At exposed localities, the giant kelp *Macrocystis pyrifera* populations are perennial, but show fluctuations in abundance due to increased water movement in winter (Westermeier & Möller, 1990). This kelp is the only subtidal canopy-forming species in the area, while the main understory species are *Ulva* sp. and *Sarcothalia crispata*. In wave-protected locations, such as Metri (Figure 1), *M. pyrifera* forests are present from the low intertidal down to 10 m depth and have typical annual population dynamic (Buschmann, 1992). Carbonate dissolution rates at Metri varied from 0.12 to 0.18 g h<sup>-1</sup>, which is significantly lower ( $P < 0.001$ ) than the exposed locality. The bottom is mainly granite-consolidated rock, with some boulder patches. The most abundant understory species are the red alga *Sarcothalia crispata* and the green alga *Ulva* sp. At both Bahía Mansa and Metri the most conspicuous grazer

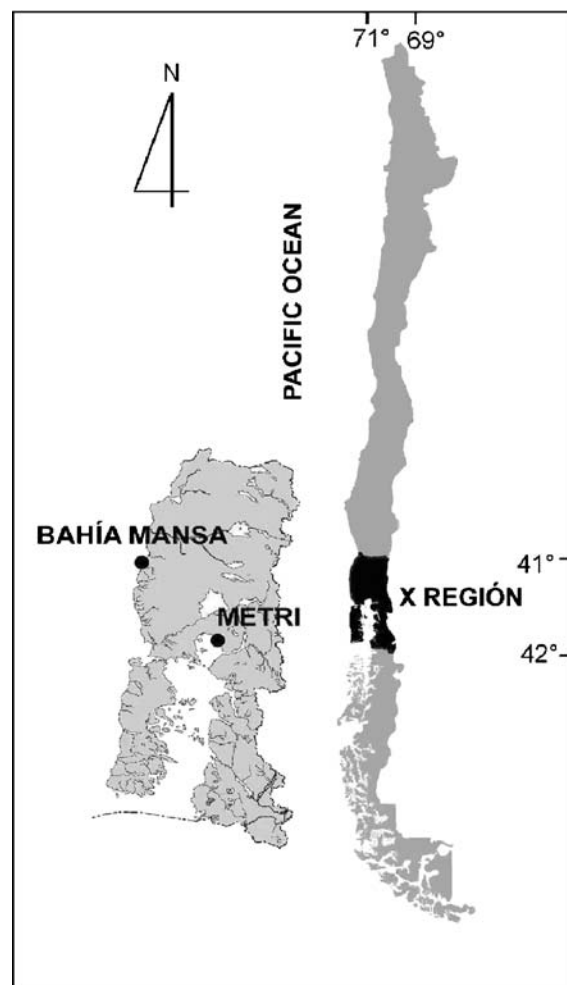


Figure 1. Map showing the study sites in southern Chile. Bahía Mansa is an exposed area and Metri is a protected area.

is the snail *Tegula atra*, but a lower number of sea urchins, chitons and limpets are also found. In general, it has been demonstrated that *Tegula* has no effect on the population dynamics of *Macrocystis*, but does have a moderate effect on the abundance of understory algal species (Moreno & Sutherland, 1982). The main difference between these areas is the absence in the protected areas of the kelp *Lessonia*, lower species diversity, and high abundance of the filter-feeding gastropod *Crepidula*.

### Population and reproduction patterns

In each study area, eighteen 0.25 m<sup>2</sup> random samples (9 per location) were taken by scuba diving, to include a range of depths. Each location had a coastline length of

at least 250 m. In each area, locations were duplicated to ensure better representation of the population dynamics of *M. pyrifer*. The diameter ( $\pm 0.5$  cm) of all holdfasts inside each quadrat was measured *in situ* with a plastic ruler, and the number of sporophylls on each plant was counted. A previous study demonstrated that the holdfast diameter correlates well with plant length (Buschmann, unpublished). This procedure was repeated monthly throughout one year and only interrupted twice due to dangerous diving conditions. This allowed us to describe the annual variation in plant size and reproductive tissue production for both populations (Metri & Bahía Mansa).

For each sampling date, the holdfasts with sporophylls ( $n > 100$ ) were sorted by size, and a random number of 50 sporophylls from each location was collected monthly. In the laboratory, the area of each sporophyll was measured by digitizing the shape using an image analyzer. The sorus area ( $A$ ) was measured by using the equation given by Reed et al. (1996) where  $A = 2slw$ , ( $s$  = total number of sporophylls containing sori;  $l$  = mean length of sori and  $w$  = mean width of the sori). These data were pooled and allowed the calculation of the following variables for each plant: size (holdfast diameter in cm), plant density (no.  $m^{-2}$ ), sporophyll abundance (no.  $plant^{-1}$ ) and the reproduction frequency (%). Also, the ratio of sorus to sporophyll area and the total sorus area per plant, for two different size classes (small plants 0–6 cm and large plants 6–12 cm of holdfast diameter) were determined. Statistical analysis was by two-way ANOVA where the factors were plant size (holdfast diameter) and life history type (annual and perennial), using SYSTAT, after ensuring normality and homoscedasticity of the data.

### Spore release

An additional reproductive variable, the number of spores per  $cm^2$  of fertile tissue, was determined by cutting five independent  $1\text{ cm}^2$  discs from different sori every month. Each disc was rinsed with tap water, gently brushed and placed in a Petri dish filled with 10 mL of filtered ( $0.2\ \mu\text{m}$ ) and sterilized Provasoli culture medium (according to McLachlan, 1973). After 1.5 h, the disc was removed from each dish. Immediately, an aliquot was placed in a  $1/10\text{ mm}$  deep Neubauer cell-counting chamber to determine the number of spores, under an inverted Nikon microscope. These data were used to calculate the number of spores per sorus area, which was later related to plant size to calculate the total release of spores per plant. Furthermore, the number of

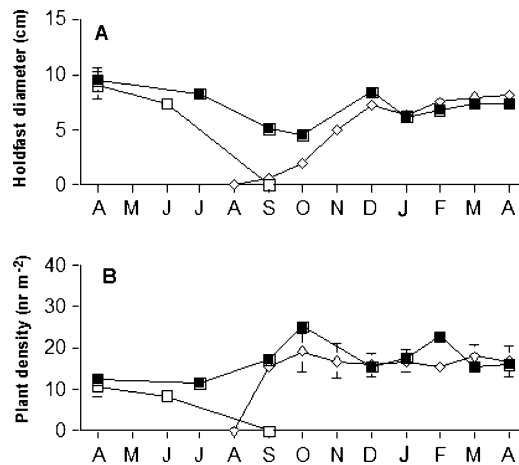


Figure 2. Mean ( $\pm 1$  SE;  $n = 18$ ) annual variation of the (A) plant size (holdfast diameter; cm) and the (B) plant density (Nr.  $m^{-2}$ ) in Bahía Mansa ( $\nu$ ; exposed) and Metri ( $\square$  and  $\diamond$ ; protected). The  $\square$  represents the 2001 cohort and  $\diamond$  the 2002 *M. pyrifer* cohort. Absence of error bars indicates small variation of the data.

spores released per sorus area and the total number of spores released per plant for different sorus size classes was also determined. Using a one-way ANOVA, we performed pairwise comparisons between the numbers of spores released per fertile sorus.

## Results

Average plant size of *Macrocystis pyrifer* (as holdfast diameter) varies seasonally in both protected and exposed areas (Figures 2A). In protected areas, the size variation is greater because the 1-year old cohort disappears in September (Figures 2A). The protected populations recover again through massive recruitment during the following spring (September), reaching the highest holdfast diameter (similar to exposed populations), in summer. The exposed *M. pyrifer* populations have a rather constant population density (varying between 12 and 25 individuals per  $m^2$ ), however, the protected population is lost in September and a new cohort starts in August-September (Figure 2B).

Due to this annual abundance pattern, the sporophylls disappear during winter (June to September), in Metri (Figure 3A). In contrast, the exposed population of *Macrocystis pyrifer* produce sporophylls throughout the year, although numbers of sporophyllic plants decreases strongly towards winter (Figure 3A). The percentage of plants carrying sporophylls shows a similar pattern to the above (Figure 3B). In exposed

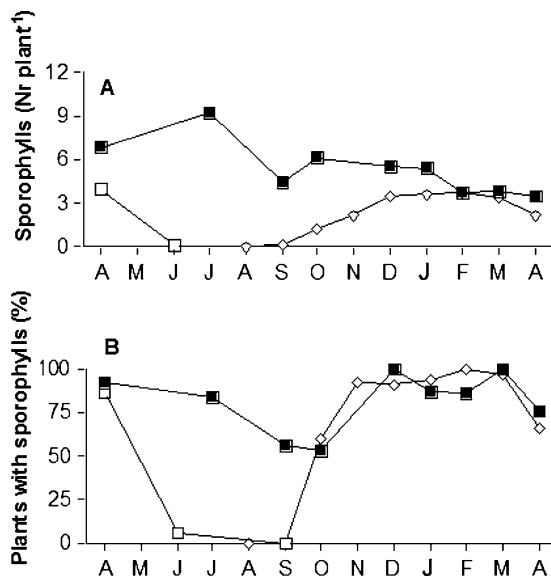


Figure 3. Mean ( $\pm 1$  SE;  $n=18$ ) annual variation of (A) sporophyll production and the (B) plants with sporophylls (%) in Bahia Mansa ( $\nu$ ; exposed) and Metri ( $\square$  and  $\diamond$ ; protected). The  $\square$  represents the 2001 cohort and  $\diamond$  the 2002 *M. pyrifera* cohort. Absence of error bars indicates small variation of the data.

*M. pyrifera* locations 50% of the plants carry sporophylls in October and the number increases to almost 100% during the rest of the year. In contrast, during the winter there are no plants in the protected locations and thus no sporophylls. In spring, Metri again shows a high (ca. 100%) number of plants with sporophylls (Figures 3B).

The average number of sporophylls per plant varies from 3 to 13 (Figure 4A). Smaller plants show a significantly ( $F = 16.49$ ;  $P \ll 0.001$ ) lower sporophyll number than the bigger plants at both sites. Also, the annual populations produce significantly ( $F = 22.82$ ;  $P \ll 0.001$ ) fewer sporophylls per plant than perennial ones (Figure 4A). The total sporophyll area per plant is significantly ( $F = 5.76$ ;  $P < 0.017$ ) higher in smaller plants, in sheltered conditions, but the significant ( $F = 5.91$ ;  $P < 0.015$ ) interaction between plant size and type of life history (annual and perennial) indicates that this difference is due mainly to the increased sporophyll area of plants collected from the annual population (Figure 4B). For the total sorus area per plant, the statistical analysis showed that the perennial populations produce significantly ( $F = 35.64$ ;  $P \ll 0.001$ ) more fertile tissue than the annual population from the protected locations (Figure 4C). However, the significant ( $F = 11.17$ ;  $P < 0.001$ ) interaction of plant size

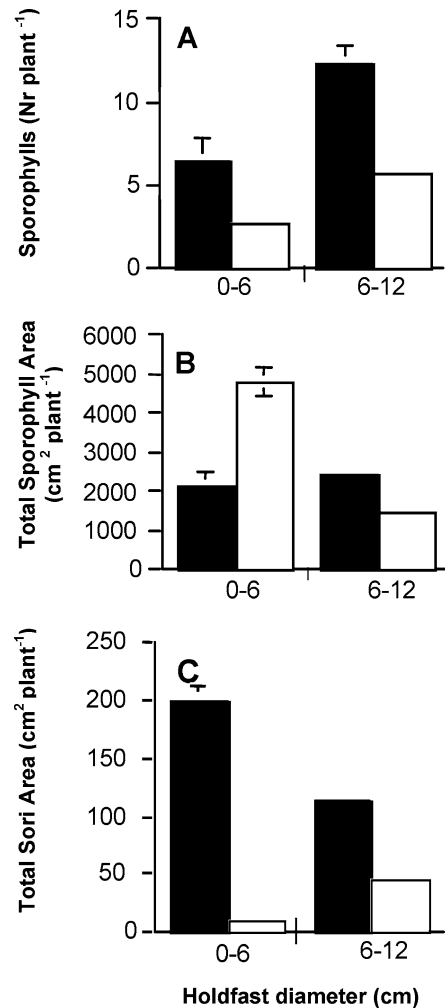


Figure 4. Mean ( $\pm 1$  SE;  $n \geq 10$ ) values of two reproduction variables: (A) number of sporophylls per plant; (B) total sporophyll area per plant and (C) total sori area per plant in relation to two plant size categories, 0–6 cm and 6–12 cm holdfast diameter. White bars represent Metri (wave protected) and the black bars Bahía Mansa (wave exposed population). Absence of error bars indicates small variation of the data.

and type of life history indicates that the effect is due to the greater sorus area present in the exposed kelp populations (Figure 4C).

The annual release of spores for the Metri and Bahía Mansa populations was calculated at 760,000 and 480,000 spores cm<sup>-2</sup>, respectively. Spore release of annual *Macrocystis pyrifera* is low in small plants and is equal to perennial populations for taller plants (Figure 5). However, a significant ( $F = 330.4$ ;  $P \ll 0.001$ ) difference exists between perennial and annual protected kelp populations, determined mainly by the

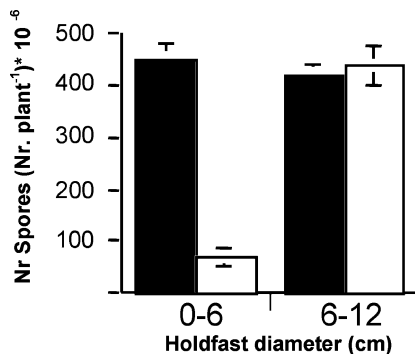


Figure 5. Mean ( $\pm 1$  SE;  $n = 15$ ) values of the number of spores produced per plant in relation to two plant size categories, 0–6 cm and 6–12 cm holdfast diameter. White bars represent Metri (wave protected with annual populations) and the black bars Bahía Mansa (wave exposed with perennial populations).

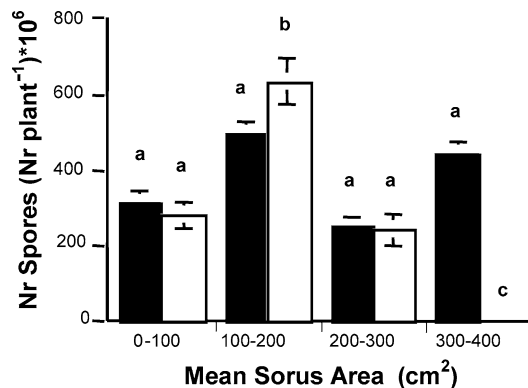


Figure 6. (A) Number of spores produced per plant in relation to sorus size. All data represent mean values ( $\pm 1$  SE;  $n = 15$ ). White bars refer to Metri (wave protected with annual populations) and the black bars to Bahía Mansa (wave exposed with perennial populations). The letters over the bars indicate statistical differences ( $p < 0.05$ ) between exposed and protected populations.

significant ( $F = 75.3$ ;  $P \ll 0.001$ ) interaction of kelp size and life history strategy (Figure 5). The total spore release per plant for sori of the size class 100 to 200 cm<sup>2</sup> from the annual kelp populations is also significantly ( $P < 0.024$ ) higher than for the perennial populations (Figure 6). It should be emphasized that the perennial populations produce larger sori with spores, whereas the annual kelps release significantly more spores in smaller sori, especially in medium-sized sori (Figure 6).

## Discussion

In our study, we demonstrate that wave-protected and exposed populations have different reproduc-

tive strategies. Wave protected areas with annual populations have a very distinctive strategy compared to perennial populations in exposed localities. These annual populations recruit in September (Figure 2A) and, within months, start to produce sporophylls and allocate biomass to fertile tissues. The spore production takes place in plants with smaller sori, and perhaps in younger plants than in the perennial populations. In contrast, perennial populations reproduce all year round, with a similar reproductive pattern to those described for the northern hemisphere (e.g. Reed et al., 1996).

It is clear that the potential reproductive effort can vary in space and time due to biological and abiotic factors. Because canopy density is related to water movement (e.g. Tegner & Dayton, 1987; Seymour et al., 1989; Graham et al., 1997) and grazing activity (e.g. Harrold & Pearse, 1987; Dayton, 1985; Dayton et al., 1992) causing a loss of the blades, the vegetative regrowth of the sporophyte is induced in spite of a reduction in the production of sporophylls (e.g. Graham, 2002). The removal of *Macrocystis pyrifera* canopy affects sporophyll production, since the experimental removal of 75% of the canopy resulted in a significant reduction in the sporophyll production (Reed, 1987). However, the expected responses between exposed and protected locations of *M. pyrifera* in southern Chile are different. The annual population in protected areas should not lose its canopy due to wave action or herbivory (Dayton, 1985; Vásquez & Buschmann, 1997), but the high summer mortality of this population seems to be related to higher temperature and low nutrient concentration (Buschmann, unpublished data; Buschmann et al., 2004; Muñoz et al., 2004). For these reasons the growth and reproduction of the kelp population in Metri is tightly coupled: when reproduction finishes in June recruitment and growth will start in late winter again. The perennial populations can lose part of their canopy, but still maintain a remaining sporophyll stock and reproduce all year round.

The contrasting life history strategies of *M. pyrifera* in protected and exposed sites described above, raises the question as to whether these differences have some genetic basis. There are no significant genetic differences between them in term of ITS1 and ITS2 sequences, indicating that we are dealing with one species (Coyer et al., 2001). On the other hand, ropes seeded from mother plants collected in exposed sites and transplanted for cultivation in protected environments did not survive (Gutierrez et al., 2006). This result

suggests that not only phenotypical characters differ between these *M. pyrifera* populations, but that there are some intra-population genetic differences in this kelp in southern Chile.

Another general thought related to the reproduction strategy of kelps is that environmental conditions exert a much greater effect on the reproduction strategy of species like *Macrocystis*, which reproduce continuously, than on other strictly seasonal species (Reed et al., 1996). This suggests that short-lived species should reproduce during the complete growth period rather than risk delaying reproduction. Here we present data for an annual kelp that produces significantly fewer sporophylls, and spores, and less sorus tissue. These protected kelp populations present a paradox, by enhancing the risk of collapsing through reduction of their reproductive potential, as their recovery depends on a successful spore production and sporophytic recruitment. The strategic advantage of this protected population is related to an increased sporophyll area produced by a smaller number of sporophylls. However, this strategy alone cannot counterbalance the reduction of the reproduction potential of this kelp as the sorus area does not reach over 75% of the sporophyll area. The only reproductive strategy capable of increasing the reproductive success of these annual kelp populations seems to be an increase in the number of spores produced by middle-sized sori. Nevertheless, this strategy raises the question: why invest energy in producing large sporophylls with a high proportion of non-reproductive tissues?

This leads us to ask how these annual populations recover regularly year after year, even during a four to five month period without the presence of a seed bank? It has been suggested that the strategy followed by these protected populations involves massive spore production during summer and autumn (Buschmann et al., 2004). Annual comparisons show that spore release per adult plant of the Metri population reaches the same numbers as the exposed population (Figures 5 and 6). Thus, the higher release of spores per area unit of the annual population in Metri compensates for its prolonged absence of spore production. The annual population produces spores massively during summer and autumn, presenting a high number of spores per sorus area, which may produce sufficient gametophytes to ensure the recovery of populations during the following spring (Buschmann et al., 2004). This strategy suggests that the *M. pyrifera* propagules or more likely the resulting gametophytes have the capability of dormancy (Kinlan et al., 2003), and effectively cre-

ate a seed bank (Hoffmann & Santelices, 1991; Santelices et al., 1995). This capability has also been suggested for *M. pyrifera* from the northern hemisphere (Ladah et al., 1999), but still needs to be tested. It is also important to mention that *M. pyrifera* plasticity constitutes a great ecological advantage by permitting the colonization of more variable environments such as Metri (Buschmann et al., 2004). It is important to mention that the number of spores released per sori area (20,000 to 80,000 spores  $\text{cm}^{-2}$ ; Buschmann et al., 2004) in *Macrocystis*, is considerably lower than for *Laminaria* spp. (Chapman, 1984). This difference may be related to differences in the estimation method employed, as we estimated the release of spores instead of the total spore production counted microscopically in sections of the sorus (Chapman, 1984).

We need not only to determine the success of seed banks in order to understand these annual populations, but also to understand the role of mortality factors in determining the numbers of the new recruits. Physical (e.g. Deysher & Dean, 1986; Amsler & Neushul, 1990; Graham, 1996) and biotic factors appear to be important in the northern hemisphere (e.g. Reed & Foster, 1984; Harrold & Pearse, 1987; Reed, 1990; Reed et al., 1991; Dayton et al., 1992) to promote or reduce the successful recruitment of *M. pyrifera*. In the southern hemisphere, there is some controversy regarding the regulatory function of sea urchins and gastropods (see Dayton, 1985; Castilla & Moreno, 1982; Moreno & Sutherland, 1982). Whether the present distribution success of *Macrocystis* is related to over-fishing of sea urchins in these protected areas (Dayton, 1985) or failure of consumption, as claimed by Castilla and Moreno (1982), remains to be studied. The extent to which recruitment success is influenced by abiotic and biotic factors in the Chilean coast is another question that requires further attention.

Based on our results, we propose that our exposed and perennial *M. pyrifera* populations in the southern and southernmost part of the Chilean Coast (Santelices & Ojeda, 1984) show a reproductive strategy similar to that of the northern hemisphere populations, in contrast to protected and annual populations in southern Chile. The exposed populations reproduce all year round and their strategy is to produce high numbers of sporophylls to ensure sufficient reproductive tissue and to transform most of the sporophyll (over 90%) into fertile sorus tissue. On the other hand, the annual populations of protected sites invest in greater production of spores

per sorus area, so that they are able to produce, in a few months, sufficient propagules to recolonize areas where the adult plants will disappear in the next months.

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