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Frond dynamics and reproductive trends of *Amphiroa beauvoisii* (Corallinales, Rhodophyta) from Isla Asunción, Baja California Sur, Mexico

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Abstract – *Amphiroa beauvoisii* (Corallinales, Rhodophyta) is distributed in tropical, subtropical and temperate regions, but little information is available about its demographics. We examined variation in wet weight, cover, frond size, length/width relation and proportion of life history stages in a study conducted at Isla Asunción, Mexico, from April 1998 to December 1998. The population of *A. beauvoisii* showed seasonal variation in cover, frond length and width, frond length frequency and percentage of reproductive fronds. These variations could not be associated with variation in temperature, daylength or nitrate concentration. Reproduction took place by production of tetrasporangia and bisporangia; no gametangial reproduction was observed. Recruitment by germination of bispores and re-growth from the holdfast are believed to play a major role in the persistence of the population.

***Amphiroa* / Baja California / geniculate corallines / population biology / reproduction**

Résumé – Dynamique des frondes et tendances de la reproduction chez Amphiroa beauvoisii (Corallinales, Rhodophyta) de l'île Asuncion, Baja California Sur, Mexique. *Amphiroa beauvoisii* (Corallinales, Rhodophyta) est présent dans les régions tropicales, subtropicales et tempérées, mais peu de renseignements sont disponibles sur ses caractéristiques démographiques. Lors d'une étude conduite à Isla Asunción (Mexique) entre les mois d'avril 1998 et décembre 1998, nous avons examiné la variabilité des caractéristiques suivantes : poids mouillé, couverture, taille des frondes, rapport longueur/largeur et des fréquences des stades du cycle réproductif. La population de *A. beauvoisii* montre des variations saisonnières de couverture, du rapport longueur/largeur des frondes, de la distribution des fréquences de la longueur des frondes et du pourcentage des frondes reproductrices. Ces variations ne dépendent pas de la température, ni de la longueur du jour ou de la concentration en nitrates. La reproduction a lieu par la production de

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tétrasporanges et de bisporanges ; aucune reproduction par gamétanges n'a été observée. On postule que le recrutement par germination des bispores et la nouvelle croissance à partir du crampon jouent un rôle essentiel dans la persistance de la population.

***Amphiroa* / Baja California / biologie des populations / corallines géniculées / reproduction**

INTRODUCTION

Geniculate coralline algae are among the most common marine algae on rocky shores all around the world; in kelp forests, in particular, they are the main understory species (Foster & Schiel, 1985). Their population dynamics are essential to provide insights into the mechanisms determining the long-term persistence of natural populations in their habitats, but they have been investigated in detail only in relatively few studies. In the intertidal zone of the western Mediterranean, growth of *Corallina elongata* Ellis & Solander and *Haliptilon virgatum* (Zanardini) Garbary & Johansen is associated with higher temperature conditions during the summer and the autumn (Benedetti-Cecchi & Cinelli, 1994). In subtidal habitats in central California, mean growth rates of *Calliarthron tuberculosum* (Postels & Ruprecht) Dawson are higher in winter (Johansen & Austin, 1970). Konar & Foster (1992) examined species composition and distribution of subtidal geniculate corallines at a site in central California and found different patterns of settlement and growth of fronds at different depths and in different seasons. At the same site, Goldberg & Foster (2002) found that recruitment and growth of *Calliarthron* were much higher on horizontal substrata than on vertical substrata. No studies carried out in kelp forest environments of the north-eastern Pacific have examined seasonal variation in frond size of individual populations, probably because species of *Calliarthron* and *Bossiella* do not show obvious variation in frond size related to season in central California and other shores of this region (Foster & Schiel, 1985).

Variation in frond length showed a seasonal pattern in *Corallina officinalis* Linnaeus in Japan (Baba *et al.*, 1988). Baba *et al.* (1988) found also that summer was the time of the year of maximal fertility in this species, and the presence of fertile tetrasporangial and gametangial fronds suggested the occurrence of the regular triphasic life history typical of most red algae. An alternative strategy of reproduction in the geniculate coralline algae is the regeneration of new fronds from the holdfast (Littler & Kauker, 1984; De Wreede & Vandermeulen, 1988; Tyrrell & Johansen, 1995). Presence of mitotic spores, known as bispores, is also commonly reported in both geniculate (Tyrrell & Johansen, 1995) and non-geniculate coralline red algae (Woelkerling 1996a, 1996b, 1996c, 1996d, 1996e). Chamberlain (1977) suggested that regeneration from holdfast and production of bispores are reproductive strategies typical of populations persisting at the geographic borders of the species, because it is assumed that these populations survive in environmental conditions unfavourable for sexual reproduction and causing low survivorship of gametangial plants, a phenomenon know as the border effect. Nevertheless, neither the contribution of bispores to persistence of individual populations and/or the importance of regeneration of new fronds have been evaluated in detail in the field. The existence of a border effect in species of red algae has been fully demonstrated only in very few cases [e.g., the presence of a non-sexual life history in which cystocarps were formed without fertilization in *Gigartina stellata* (Stackhouse) Batters (Guiry & West, 1983)].

Most corallines associated with kelp forests belong to the Corallinoideae, but there are also a few species from the Amphiroideae, such as species of *Amphiroa* [*i.e. A. beauvoisii* Lamouroux, *A. misakiensis* Yendo and *A. anceps* (Lamarck) Decaisne]. Species of *Amphiroa* are widely distributed in tropical, subtropical and temperate regions (Norris & Johansen, 1981; Choi & Lee, 1989; Riosmena-Rodríguez & Siqueiros-Beltrones, 1996; Womersley, 1996; Riosmena-Rodriguez, 2002). This genus has its centre of diversity in the tropics, where it is represented by a large number of species (Dawson, 1966). Very few demographic studies are available for the genus *Amphiroa*. The most detailed refers to a population of *Amphiroa vanbosseae* Lemoine from a subtropical region (Rivera-Campos & Riosmena-Rodríguez, 2003), where continuous growth and no seasonal variation in population size structure were detected (Rivera-Campos & Riosmena-Rodríguez, 2003).

A. beauvoisii is one of the species with largest geographical distribution, occurring in tropical, subtropical and temperate areas of the Atlantic, Pacific and Indian oceans (Riosmena-Rodríguez & Siqueiros-Beltrones, 1996; Riosmena-Rodríguez, 2002; Guiry & Guiry, 2007). In the Mexican Pacific the species ranges from tropical (state of Oaxaca) to subtropical regions (Bahía Asunción, state of Baja California Sur, which represent its northern limit of distribution: Dawson, 1952: Mateo-Cid & Mendoza-González, 1994).

No demographic studies are currently available for *A. beauvoisii*; previous investigations have only recorded the reproductive state. In subtropical regions, tetrasporangial, bisporangial and gametangial specimens have been recorded (Norris & Johansen, 1981; Choi, 1989: Mateo-Cid & Mendoza-González, 1994; Riosmena-Rodríguez, 2002). In tropical regions, three patterns are known: 1) presence of both gametangial and sporangial fronds in similar proportions, observed in tropical Pacific Mexico (Dawson, 1952); 2) a reduced percentage of gametangial fronds, observed in the Gulf of California, at the northern limit of the tropical region (Riosmena-Rodríguez, 2002); 3) presence of only tetrasporangial and bisporangial fronds, observed in the Caribbean area (Littler & Littler, 2000).

The aims of the present work are: 1) to evaluate if demographic parameters varied seasonally in a population of *A. beauvoisii* occurring at the northern limit of distribution of this species (Isla Asunción, Baja California Sur) by examining variation in frond size and abundance (measuring wet weight, cover, length and width of fronds and length/width ratio of fronds); and 2) to determine what mechanisms of reproduction take place in fronds of this species at Isla Asunción. Because the population of *A. beauvoisii* considered is located in a subtropical area and is at the northern limit of its distribution, we hypothesize that this population will show some border effects reflected in well structured cohorts, a seasonal peak in wet weight and the presence of a high proportion of tetraspores and bispores.

MATERIALS AND METHODS

Study Area

Isla Asunción is located off the Pacific coast of the Peninsula of Baja California Sur (27°07" N and 114°15"W) (see Hernández-Carmona *et al.* [2001] for further details). This region is influenced by the California current (< 20°C, 36 psu) in winter and spring, and by the Equatorial and North Equatorial counter currents (> 20°C, 34 psu; Cervantes-Duarte, 1988) in summer and autumn, with an intensive upwelling in spring. The most common benthic assemblage in the area is a kelp forest dominated by *Macrocystis pyrifera* (Linnaeus) C. Agardh, for which Isla Asunción is the southern limit of distribution in North America (Dawson *et al.*, 1960; Hernández-Carmona *et al.*, 2001). Daylength data were obtained from Robles-Gil (1998), the most accurate meteorological information available for the area. Information on sea temperature and nitrate concentration was obtained from Hernández-Carmona *et al.* (2001).

Fieldwork

Sampling was carried out monthly from April to December 1998, with the exception of July (when the fieldwork was made impossible by the rough conditions of the sea). For logistical problems, it was not possible to obtain cover data in April 1998, although scrapings from quadrants were taken. Three permanent sampling sites were located around Isla Asunción at 10 m depth; at each site, a transect 50 meters long was established with orientation parallel to shoreline. Samples were collected by scraping quadrats (25 × 25 cm) with hammer and chisel, as part of a restoration experiment developed by Hernández-Carmona *et al.* (2001). At each site, four quadrats were sampled; the quadrats were collected at 10 meters distance from each other. The number of quadrats to be sampled was determined by the iterative method (Brower *et al.*, 1998). Cover was recorded with the random points method (Cowen *et al.*, 1982). All fronds of *A. beauvoisii* were collected, placed in labelled plastic bags and fixed in a 4% solution of formaldehyde-seawater (Littler & Littler, 1985).

Laboratory work

The fronds of *A. beauvoisii* were identified using the key of Riosmena-Rodríguez & Siqueiros-Beltrones (1996), based on the apical intergenicula morphology. The wet weight was measured to the nearest ± 0.02 g, using an Ohaus LS5000 scale. Frond length (distance between basal and apical intergenicula) and width (the greatest distance between the tips of opposite lateral branches) were measured from each quadrat for 30 fronds removed in their full integrity (from the basal to the apical intergenicula), and the length/width ratio was subsequently calculated.

The following methodology was used to select the fronds: a) all fronds of a quadrat were laid over a surface, b) the fronds were evenly distributed, c) a black bag with a hole in the centre was used to pick each frond for measurement, d) the frond was examined, and only complete fronds were used for measurements. The number of fronds required for the sampling was calculated with the Performance method (Brower *et al.*, 1998).

The reproductive condition was assessed by examining conceptacles located in the intergenicula of the middle part of the fronds, since it has been reported that these section contain the highest percentage of conceptacles in other *Amphiroa* species (Rivera-Campos & Riosmena-Rodríguez, 2003). For each month, five quadrats were randomly selected, and six complete reproductive fronds were chosen from each quadrat using the methodology described for the selection of the fronds. One intergeniculum for each frond was examined; therefore, thirty intergenicula per month were utilized to determine the presence of fertile gametangia or sporangia, using the histological technique described by Riosmena-Rodríguez *et al.* (1999). Representative fronds were deposited at the

Phycological Herbarium of the UABCS [FBCS] with the collection numbers 7300, 7306, 7320, 7323, 7338, 7339, 7340, 7351, 7358, 7360, 7362, 7363, 7373 and 7380.

Statistical analyses

For all parameters measured, the values obtained for all quadrats for each site in a month were combined to give a mean value for the month. In this way, three replicates were obtained for spring (April, May and June, except for cover, for which only May and June were sampled), two for Summer (August, September) and three for Autumn (October, November, December). The Kolmogorov-Smirnov-Lilliefors and Bartlett tests were used respectively to test for normality and homogeneity of variances (Zar, 1996). Data for all sampling dates were normal and homoscedastic, except for wet weight and length/width frond relation that were heteroscedastic. To solve the problem, these data were log transformed by the proportional relation between their mean and variances (Underwood, 1997). After transformation, the data were reexamined with the Bartlett test and only the wet weight data were homoscedastic.

To test for seasonal differences in wet weight, frond length, frond width and percentage of vegetative, bisporangial and tetrasporangial fronds, an unbalanced one-way ANOVA and a non-balanced Tukey test were used (Zar, 1996). Mean values of cover were examined by a balanced one-way ANOVA and Tukey test (Zar, 1996). Length/width frond ratio was analyzed using Kruskal-Wallis and Dunn tests (Zar, 1996). A linear regression was calculated for wet weight, cover and proportions of vegetative, bisporangial and tetrasporangial fronds in relation to temperature, daylength and nutrients (Zar, 1996). The STATISTICA 6.0 (StatSoft) package was used for all analyses. To obtain seasonal histograms of the frond length, the number of size class and their dimension were calculated with the Sturges method (Daniel, 1999).

RESULTS

Wet weight varied with season with minimum mean values in spring (2.44 mgr/cm^2) and maximum in autumn (10.13 mgr /cm^2; Tab. I). The unbalanced one-way ANOVA and non-balanced Tukey test showed no significant seasonal differences in wet weight ($F_{0.05, 2} = 1.67$, $p > 0.05$). Variation in wet weight was not associated with daylength ($r = 0.85$, $p > 0.05$), nitrate concentration ($r = 0.99$, $p > 0.05$) and temperature ($r = 0.36$, $p > 0.05$).

Cover showed seasonal variation, with a significantly higher mean value in summer (13.33) than spring and autumn (4.58; 6.25) (Tab. 1; $F_{0.05, 2} = 26.64$,

Table 1. Seasonal wet weight (a) and coverage (b) of *Amphiroa beauvoisii*. Figures indicate mean ± standard error (number of replicates)

Parameter	*Spring*	*Summer*	*Autumn*
Wet weight (mgr/cm^2)	2.44 ± 1.27 (3)	6.94 ± 4.33 (2)	10.13 ± 1.14 (3)
Percentage cover (%)	4.58 ± 0.41 (2)	13.33 ± 0.83 (2)	6.25 ± 1.25 (3)

$p < 0.05$). The linear regressions between cover and temperature, daylength and nitrate concentration were not statistically significant ($r = 0.99$, $p > 0.05$; $r = 0.73$, $p > 0.05$: $r = 0.21$, $p > 0.05$).

Frond length and width increased significantly in size (length $F_{0.05,2} = 7.14$, $p < 0.05$ and width $F_{0.05,2} = 7.92$, $p < 0.05$) from spring to summer and autumn (Fig. 1). The length/width relationship showed no significant seasonal changes ($F_{0.05,2} = 3.8$, $p > 0.05$). Seasonal variation in frond length class frequency was observed (Fig. 2). In spring the dominant size classes were lower size-classes (0 – 0.29 to 1.20 – 1.49 cm; Fig. 2). In summer and autumn the dominant size classes were the intermediate classes (0.6 – 0.89 cm to 2.4 – 2.69 cm) (Fig. 2).

Reproductive fronds were recorded in all three seasons. In the reproductive fronds both tetrasporangia (Fig. 3 A) and bisporangia (Fig. 3 B) were observed, but no gametangial conceptacles were found. The percentage of vegetative fronds showed seasonal differences, with significantly lower values in summer than spring and autumn ($F_{0.05,2} = 19.01$, $p < 0.05$; Fig. 4). The percentage of vegetative fronds was not significantly associated with temperature ($r = 0.99$, $p > 0.05$), daylenght ($r = 0.65$, $p > 0.05$) or nutrients ($r = 0.10$, $p > 0.05$). The percentage of tetrasporangial and bisporangial fronds showed similar mean values in spring, summer and autumn ($F_{0.05,2} = 2.51$, $p > 0.05$; $F_{0.05,2} = 0.53$, $p > 0.05$). The percentage of bisporangial fronds was not significantly associated with temperature ($r = 0.85$, $p > 0.05$), daylength or nitrate concentration ($r = 0.37$, $p > 0.05$; $r = 0.22$, $p > 0.05$, respectively). The same pattern was found between tetrasporangial fronds and daylength ($r = 0.87$, $p > 0.05$), nitrate concentration ($r = 0.99$, $p > 0.05$) and temperature ($r = 0.412$, $p > 0.05$).

DISCUSSION

Our results showed a significant seasonal variation in cover but not in wet weight of *A. beauvoisii* in Isla Asunción. This was an unexpected result, which is presumably due to the unbalanced sampling used in the study. This pattern differs from the situation observed in other species of red algae, in which these parameters are usually positively correlated (Scrosati, 2005). The maximum values in cover in summer occurred at the time of the year with the highest water temperatures, and probably resulted from recruitment from spores and growth (or regrowth from holdfasts) in spring, as suggested by the smaller size of fronds in spring than in summer and autumn (Fig. 1, Fig. 2). The seasonal variation in size related to cover is similar to that reported for *Mazzaella cornucopiae* (Postels & Ruprecht) Hommersand by Scrosati & DeWreede (1997). An alternative explanation would be that the species maintain by lateral growth instead of regular recruitment.

The importance of re-growth versus spore-recruitment was not measured in the present. Nevertheless, evidence of successful recruitment from spores (tetra or bispores) was the presence of new small fronds in cleared areas in the seeding experiments done by Hernández-Carmona *et al.*, (2000; unpublished data). No gametangial fronds were found in the present study.

The recruitment and high growth in spring may be related to the combination of the highest nitrate reported (4.8 – 18.8 μM/L) (Hernández-Carmona *et al.*, 2001) and the substratum availability caused by the reduction of *Eisenia* and *Macrocystis* density, both from El Niño-Southern Oscillation (ENSO) (97-98) effects (Edwards, 2004; Edwards & Hernández-Carmona, 2005). This

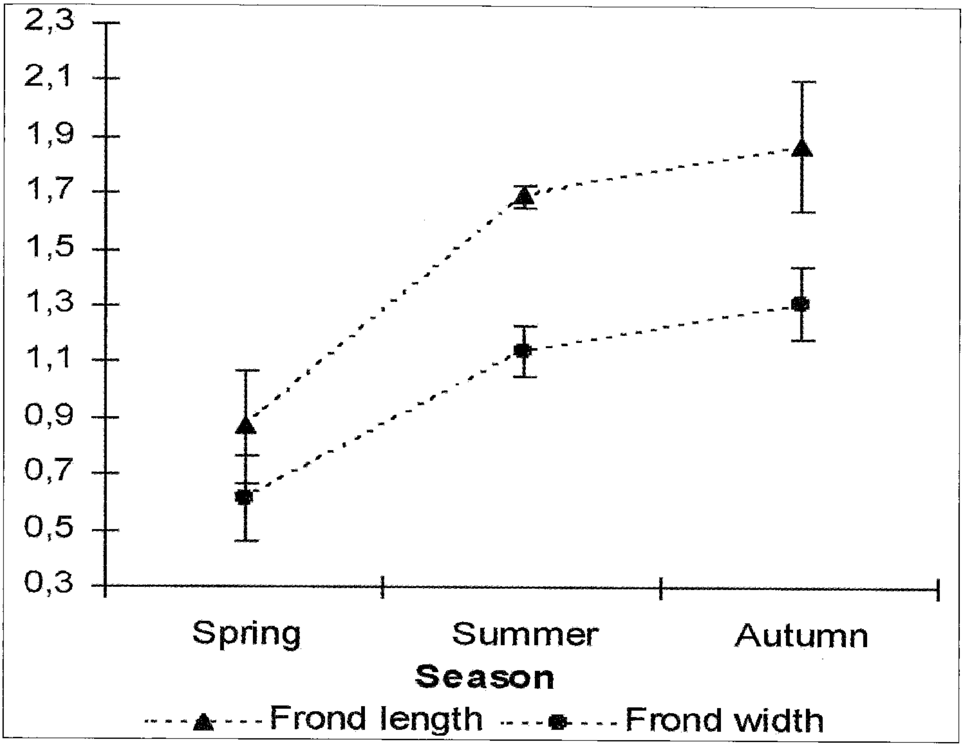

Fig. 1. Frond length and width (mean + se: Spring and Autumn n = 3, Summer n = 2) showing a significant increment in size between spring and summer-autumn (length -$F_{0.05,2} = 7.14$, $p < 0.05$ and width- $F_{0.05,2} = 7.92$, $p < 0.05$). Bars indicate standard errors.

trend is similar to the recruitment of geniculate coralline algae in temperate zones (Konar & Foster, 1992; Goldberg & Foster, 2002) related to light.

Seasonal variation, with the highest bisporangial and tetrasporangial proportion in summer, has been reported for *A. vanbosseae* in a subtropical area (Rivera-Campos & Riosmena-Rodríguez, 2003). The absence of gametangial phases and the high proportion of vegetative fronds suggest that the population probably is long-living, with few recruits from bisporangial (mitotic) reproduction as suggested by Chamberlain (1977) for the northern geographic distribution of *A. beauvoisii.* The survival of tetrasporangial (meiotic) spores should be evaluated in a further study.

The dominance of tetrasporangial-bisporangial fronds is common for *A. beauvoisii* (Norris & Johansen, 1981) and other coralline algae of temperate affinity in temperate regions (Baba *et al.*, 1988) where the summer isotherm is 20°C (Lüning, 1990). Nevertheless in the summer of 1997 in Isla Asunción, a temperature of 27.4°C (September) was recorded (ENSO phenomenon) (Hernández-Carmona *et al.*, 2001), a condition closer to that of tropical regions, in which gametangial fronds are present (Dawson, 1952). Hernandez-Carmona *et al.* (2001) suggested that the temperature is not the only or principal factor influencing the development of gametangia, and detailed laboratory studies are necessary to understand what factors affect the development of the reproductive structures in the life history.

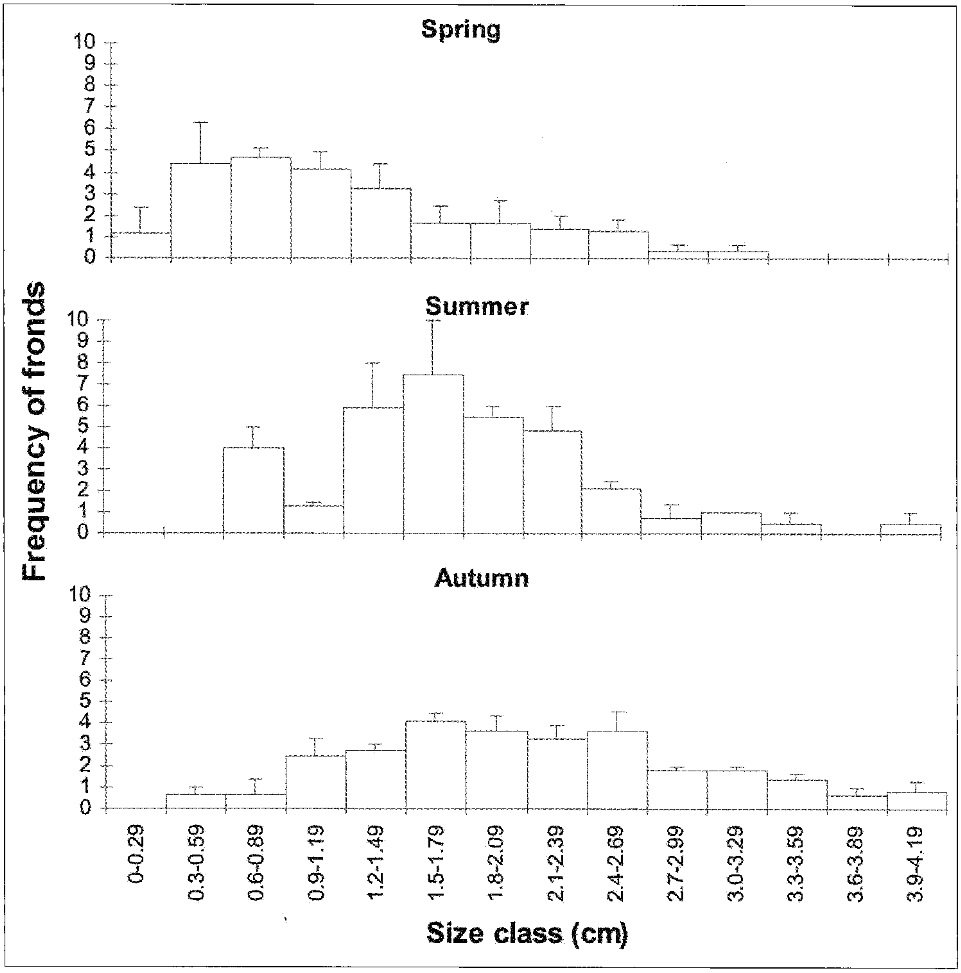

Fig. 2. Seasonal size-frequency histograms of fronds length, (mean + se: Spring and Autumn n = 3, Summer n = 2), note that the frequency of small fronds (first size-class) is highest in spring than summer and autumn. Bars indicate standard errors.

On the other hand, an overall predominance of reproductive tetrasporophytic fronds over reproductive gametophyte fronds has been recorded in many groups of red algae, for example the Gelidiaceae (Serviere-Zaragoza & Scrosati, 2002), whereas a consistent alternation of phases has been observed in species of other families, such as the Gigartinaceae (Thornber & Gaines, 2003).

In conclusion, the population of *A. beauvoisii* from Isla Asunci6n showed seasonal variation in cover, frond length and width, frond length frequency and percentage of reproductive fronds. The changes in these parameters could not be associated with variations in temperature, daylength or nitrate concentration. The persistence of the population is believed to be due to recruitment through germination of bispores and potential re-growth from the holdfast.

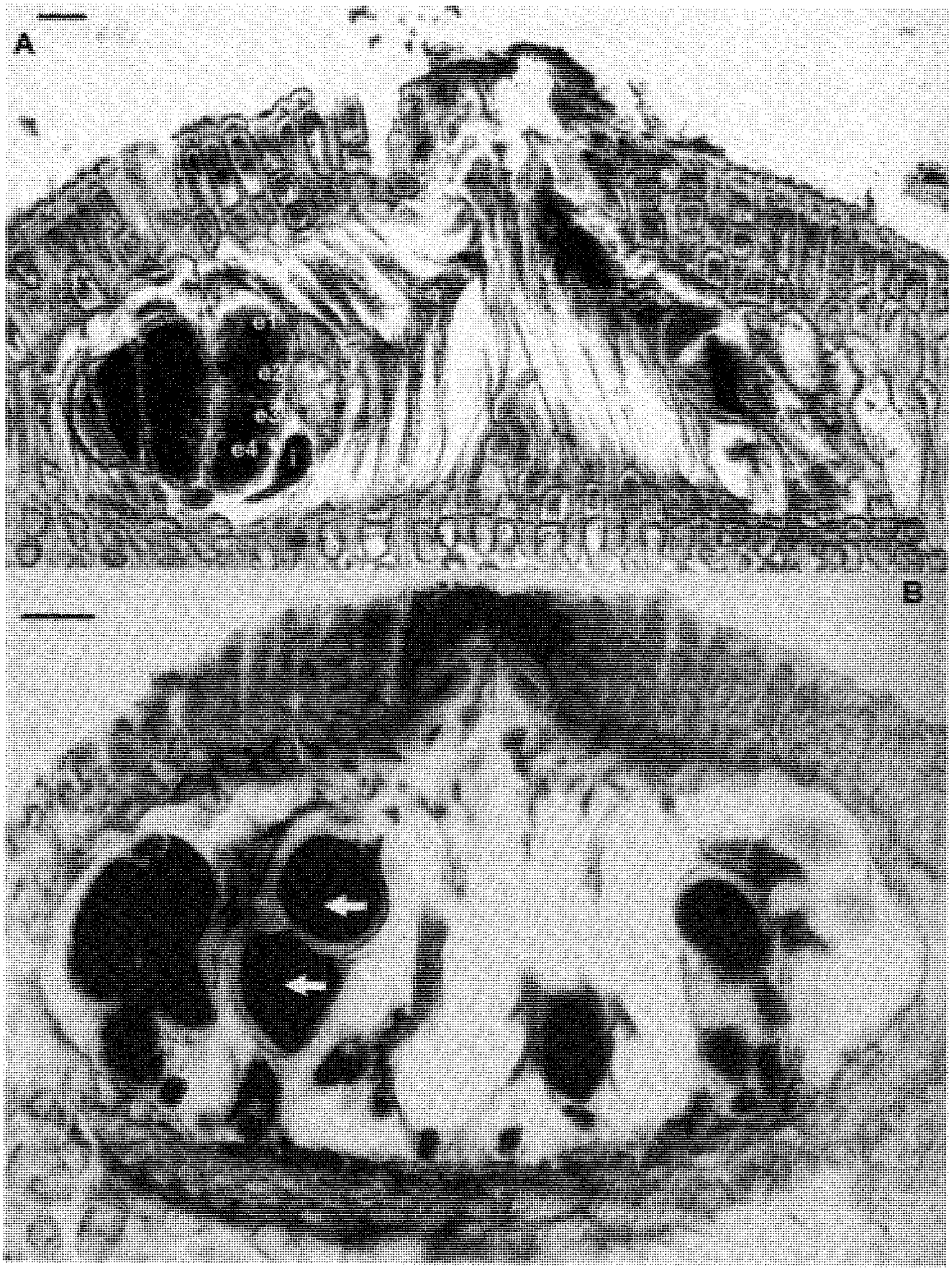

Fig. 3. Reproductive structures of *A. beauvoisii* from Isla Asunción. **A.** Tetrasporangial conceptacle showing mature tetrasporangium with spores (e1,e2,e3,e4) and immature tetrasporangium (i). **B.** Bisporangial conceptacle showing mature sporangium with bispores (white arrows). Bar scale 20 μm.

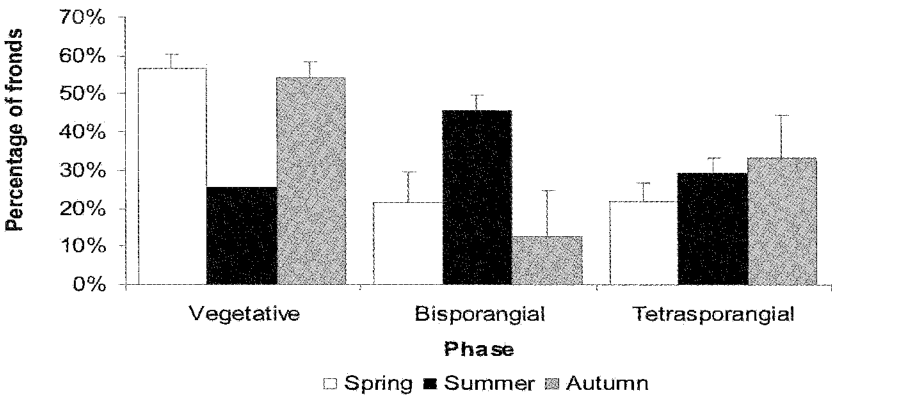

Fig. 4. Percentage of reproductive plants by season (mean + se: Spring and Autumn n = 3, Summer n = 2). Vegetative fronds were dominant in spring, autumn and winter. Bisporangial and tetrasporangial phases occurred in less proportion, but were dominant during the summer months. Bars indicate standard errors.

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