

Population Structure of *Codium amplivesiculatum* (Chlorophyta) Associated with Rhodolith Beds from the Southwestern Gulf of California

Rafael Riosmena-Rodríguez* and Elena Holguín-Acosta

Programa de Investigación en Botánica Marina, Departamento de Biología Marina, Universidad Autónoma de Baja California Sur, Apartado postal 19-B, La Paz B.C.S. 23080 México. Tel Int. 52-612-1238800 ext. 4812, FAX Int. 52-612-1280880

Populations of *Codium amplivesiculatum* were found in association with rhodolith beds. We present population trends of *C. amplivesiculatum* from surveys conducted in the southwestern Gulf of California based on monthly sampling from June 1999 to August 2000. Surveys were conducted at 2 sites in the San Lorenzo Channel at depths of 8 - 12 m. The parameters measured were percent cover, biomass and structure in relation to size of the thalli. From each thallus the following measurements were taken: length and diameter, proportion of each thallus with reproductive structures and the degree of fragmentation (measured as number of small thalli). Mean biomass and cover varied seasonally with the maximum (1036.6 g m⁻² and 100% cover) present in June 2000 and the minimum in winter (0 g m⁻² and 0% cover). The longest fronds (3 m) occurred during July 1999 and August 2000, while the maximum diameters of 1.0 cm were present during October and November 1999. There were no significant linear relationships between length and diameter of the fronds, suggesting independent growth. Reproductive structures were common in June and July 1999 with monoic and dioic thalli present. Most fronds were monoic, and this is the first record of this feature for this species. Fragmentation occurred in September, and may be associated with stress from early gametangial reproduction and the combination of high temperatures and low nutrients. A hypothetical life cycle for the species is presented.

Key Words: *Codium*, Gulf of California, morphology, population structure, reproduction

INTRODUCTION

The coenocytic green algal genus *Codium* is a good example of a clonal seaweed that is widely distributed over the world from temperate to tropical areas (Silva 1962), in muddy, sandy, rocky and rhodolith habitats. Several species widely distributed in rocky habitats (i.e. *Codium fragile* (Suringer) Hariot and *Codium fragile* ssp. *tomentosoides* Silva) have been studied because of their invasive strategies (Borden and Stein 1969a, b; Churchill and Moeller 1972; Fralick and Mathieson 1972; Malinowski and Ramus 1973; Prince 1988; Trowbridge 1996; Garbary *et al.* 1997; Hubbard and Garbary 2002; Garbary *et al.* 2004) linked to their massive fragmentation events. But there is no clear indication if there is any relationship between the fragmentation and the densities found. The population densities of those species seems to be related to their seasonal growth that starts in spring,

gametangial structures that develop during summer and maturation of the thalli and fragmentation that occurs in autumn after gametangial reproduction (Churchill and Moeller 1972; Malinowski and Ramus 1973; Prince 1988). However, the coenocytic organization of the thalli would seem to permit the same potential for biomass increase by elongation or diameter increase, the implications of which have not been evaluated in relation to fragmentation time.

There is no consensus about what might cause changes in biomass, morphology and reproduction. Some authors have suggested that sedimentation will produce high seasonal changes in biomass production (Garbary *et al.* 2004; Thomsen and Mcglathery 2006) because of burial and fragmentation. Other authors have suggested that a combination of changes in water temperature and salinity might influence the population structure and reproduction, producing earlier fragmentation (Churchill and Moeller 1972; Malinowski and Ramus 1973; Vidondo and Duarte 1995, 1998; Trowbridge 1996). Recently, the effect of wave exposure (D'Amours and Scheibling 2007) has

*Corresponding author (riosmena@uabcs.mx)

been shown to have an effect on morphology, strength of attachment of seaweed to substrata, and survival. However, in all cases it is clear that when fragmentation happens earlier in the year, fragments are produced near the dichotomies (in species with this type of branching) and causes the thalli to change in size and general morphology (Fralick and Mathieson 1972). Most of the studied species mentioned above are associated with rocky areas and only a few with sandy habitats. The frond dynamics and reproductive strategies of free living species are poorly known in rhodolith habitats.

In relation to reproduction, there is a clear trend that gamete production happens in spring in temperate habitats (Bulleri *et al.* 2007) but there is no information about when this might happen in tropical areas. Also, it has been suggested that nutrient availability might control gametangial structure production and thus, fragmentation (Vidondo and Duarte 1995, 1998). There are some suggestions that gametangial numbers are related to plant density in rocky areas as a consequence to low tide conditions (Bulleri *et al.* 2007). However, in subtidal areas the gametangial production might be not related with density.

Codium amplivesiculatum Setchell and Gardner is a widely distributed species along the Mexican Pacific in sandy habitats, where free living fronds can reach 10 m in length (Dawson 1950; Flores-Pedroche *et al.* 2002). It has been reported as occurring in spring and summer in Bahía de Los Angeles (Pacheco-Ruíz and Zertuche-González 1996) and from winter to summer in Bahía de La Paz (Paul-Chávez and Riosmena-Rodríguez 2000). Recently, Steller *et al.* (2003) found the species associated with rhodolith beds in the southwestern Gulf of California during summer and winter as one of the main biomass components of flora. Iglesias-Prieto *et al.* (2003) has found as one of the main species who might survive the ENSO conditions and Hilbert *et al.* (2005) and Lopéz-Mendilaharsu *et al.* (2005, 2008) determined as one of the main items who prefer the green turtle (*Chelonia mydas*) on its diet.

Our goals were to determine the populational patterns of *Codium amplivesiculatum* in relation to the gametangial and vegetative (fragmentation) reproductive strategies. We hypothesize that *Codium amplivesiculatum* population is strongly affected by oceanographic conditions (Álvarez-Borrego 1983; Cervantes-Duarte *et al.* 1991) in where the species has large seasonal variations in biomass, plant morphology in relation to size, maturity date of gametangial structures and fragmentation time.



Fig. 1. Range in morphology of *Codium amplivesiculatum* from a fragment of several centimeters (left) to an adult plant of several meters (right) Scale bar 1 m.

MATERIAL AND METHODS

Monthly sampling was carried out between June 1999 and August 2000 at two sites cover with rhodoliths 100%, in the San Lorezno channel (24°22'9.0"N, 110°18'49.2"W) at 12-15 m deep; with the exception of May and July 2000 because of logistical problems. In each site, two 50 m transect lines were used and in each transect five quadrats of 1 m² were selected using random numbers; a total of 10 quadrants per transect being analyzed. In each quadrat, we evaluated percent cover using the random point quadrat method of Cowen *et al.* (1982) and samples for biomass evaluation were taken by collecting all the plants in the quadrats and keeping them in separate, numbered bags. The collected material fitted into the *Codium amplivesiculatum* species according to Flores-Pedroche *et al.* (2002) (Fig. 1). After evaluation, all analyzed thalli were fixed in formalin and voucher material was deposited in the Phycological Herbarium of UABCS (FBCS) with the following catalog numbers: 6975, 6976, 6977, 6978, 6979, 6980, 6981, 6982, 6983, 6984, 6985, and 6986.

Samples from each quadrat were weighed using Ohaus scales (+/-0.02 g) and 10 randomly selected plants from each quadrat (depending on availability) were measured for frond length and width using calipers (+/-0.05 mm). Width was measured using the edges and the central part of the thalli. After analysis, all the data were analyzed for normality and homoscedasticity. Because these absent, Kruskal-Wallis non parametric methods were used to determine if there were significant changes

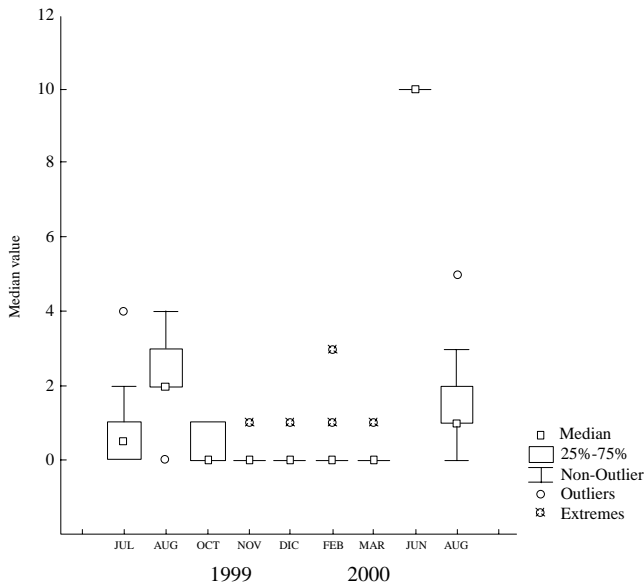


Fig. 2. Temporal variation of the median value of *Codium amplevesiculatum* cover in where significant variations were found in several months (asterisks). ND = no data.

in the percent cover, biomass and size (length and diameter) over time. After this, Duncan’s rank test was performed on data to determine which months were different from each other. To test the hypothesis to find out if thalli develop at the same rate in relation to cover and biomass, length or diameter, a simple linear regression was performed between percent cover and biomass. To do this, data were organized in pairs and were analyzed in Statistica 5.0 to get an r^2 , r and p value. Size intervals for the histogram analysis were obtained using the length/width data and were calculated using the Sturges relationship $K = 1 + 3.322 (\log_{10} n)$ while the size of the interval of size class was calculated using the formula:

$$W = R / K$$

in which K is the number of intervals n is the number of data collected, R is the difference in the outlying values observed.

The proportion of reproductive vs vegetative thalli was determined using the same plants selected from the quadrats. Each thallus was sectioned at the ends and in the middle of the thalli. Aniline blue was used to stain reproductive structures and semipermanent slides were made and housed with the collections in the Phycological Herbarium. As part of the analysis, monoic (both gametangial stages together) and dioic stages (only one gametangial stage) were observed in the samples and the proportion of each of them was recorded. The

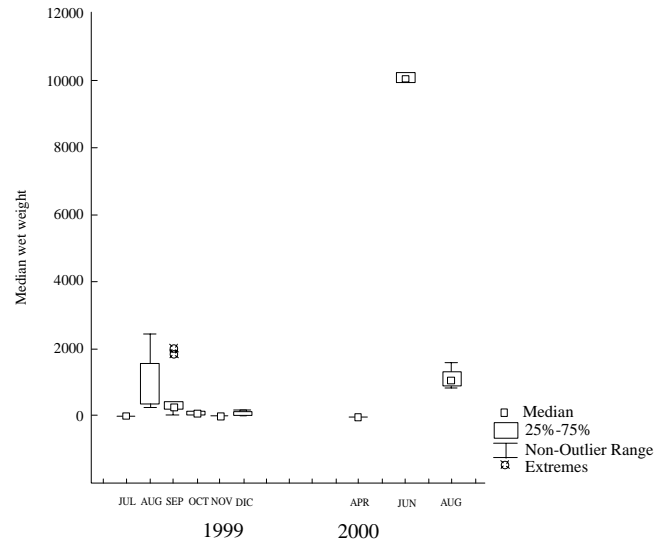


Fig. 3. Temporal variation of the median value of *Codium amplevesiculatum* wet weight in where significant variations are marked in asterisks.

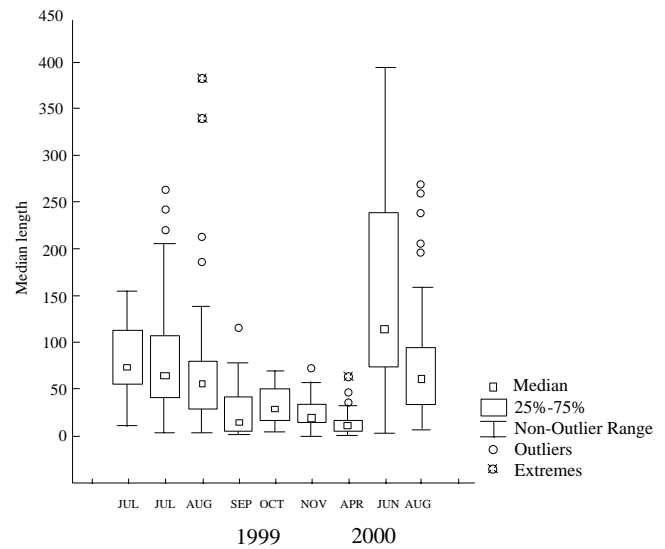


Fig. 4. Variation in median length value of *Codium amplevesiculatum* thalli in relation to months in where significant variations are marked in asterisks. based on Duncan tests.

proportion of mature reproductive structures along the thalli was analyzed based on 960 slides in which each of the gametangial stages was counted along the first 20 utricles (19,200 utricles measured in total). The monthly proportion of each life cycle stage was subjected to the same statistical analysis as described above to determine if and when significant changes occurred.

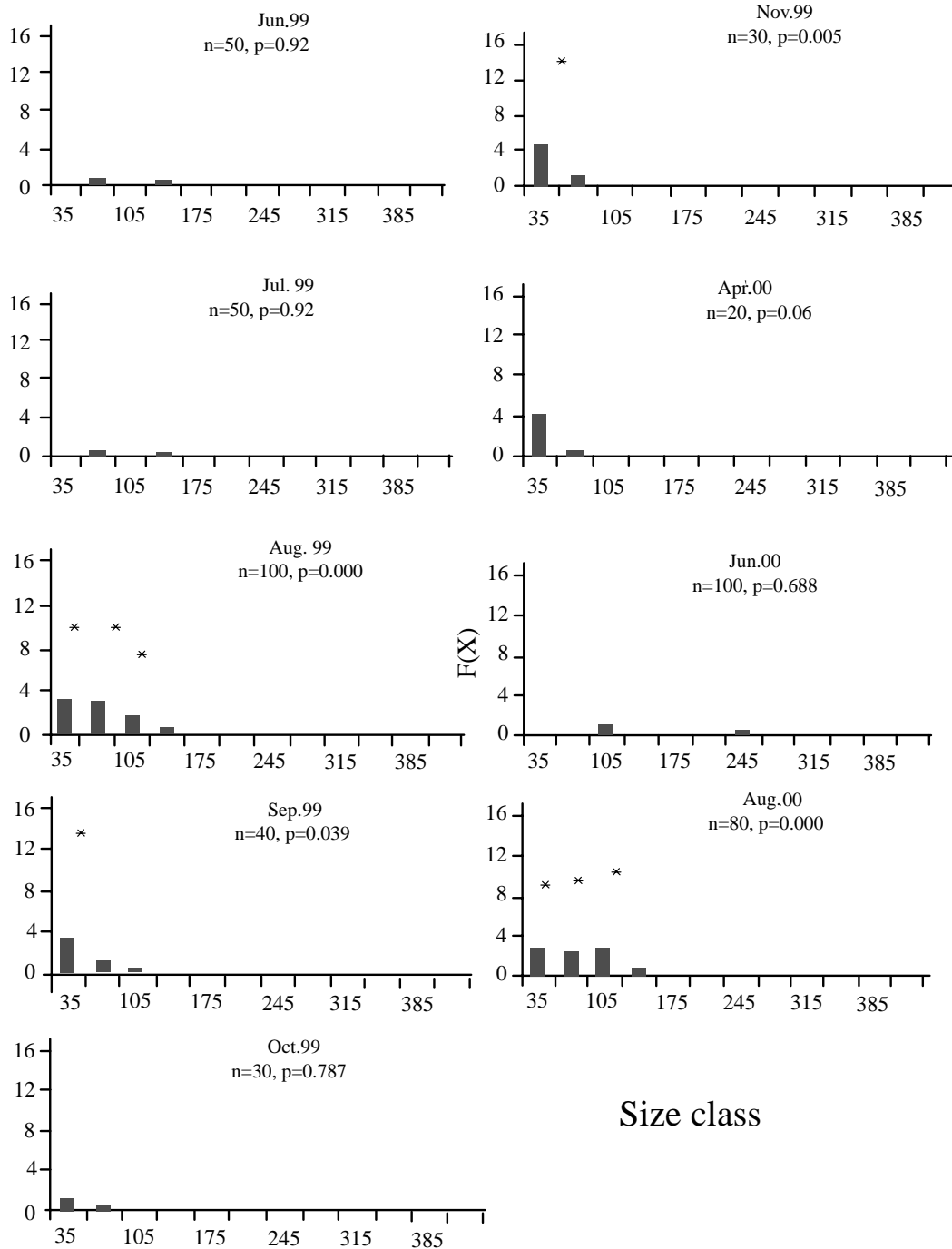


Fig. 5. Size frequency histograms of *Codium amplexiculatum* frond length in where more than one size class is dominant each month.

RESULTS

The presence of *Codium amplexiculatum* in the study area was very irregular, with peaks in the mean cover in August (both years) and June 2000 and very low cover in December (Fig. 2). The statistical analysis, with a Duncan range test comparison, showed significant differences ($H = 58.211, p < 0.001$) during August (both years) and June

2000. Wet weights showed a similar trend with August (both years) and June 2000 with high values, but in addition July 1999 also had high values (Fig. 3). The mean value observed in June 2000 is very noticeable ($10,097 \text{ g m}^{-2}$) in relation to the observed values in other months, which are lower by an order of one magnitude. The Kruskal-Wallis analysis showed significant differences between the months ($H = 38.102, p = 0.0000$) and the Duncan's rank test demonstrated that August and June

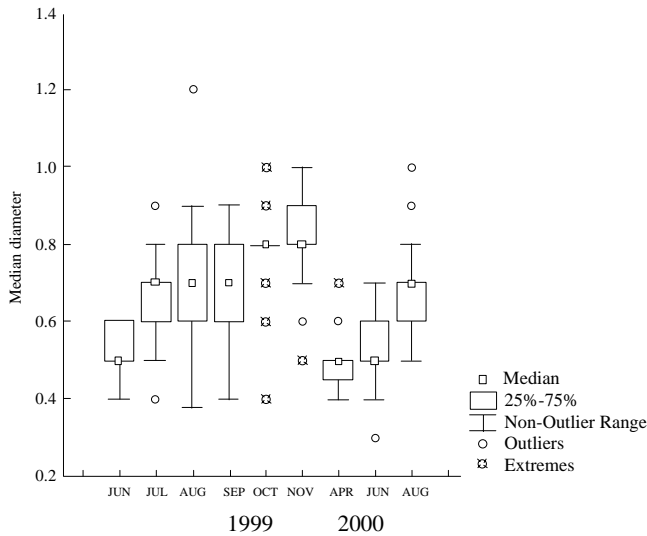


Fig. 6. Variation in median diameter of *Codium amplexicaule* thalli in relation to months in where significant variations are marked in asterisks.

are significantly different months with the exception of September ($p < 0.05$) 1999. The exploration of the linear relationship between cover and biomass showed very little relationship ($r^2 = 0.62$).

The monthly variation in frond length was very consistent over time with highest values between June and August (Fig. 4) and lowest values between September and May. The above trends were confirmed with statistical analysis ($H = 206.019$, $p = 0.0000$), and the significantly different months were detected with the Duncan's rank test ($p < 0.05$) that showed June, July and August (both years) as the most different months. The analysis of the size class over time has shown that most of the analyzed plants were shorter than 35 cm; with the exception of June 2000 in where fronds reached 300 cm and June, July, August and September 1999 in which fronds were 140 cm long or longer (Fig. 5) with a similar observation in June and August 2000. The Kruskal-Wallis analysis showed there was a dominant size class for July 1999 ($H = 45.451$, $p = 0.0000$), August 1999 ($H = 71.636$, $p = 0.0000$), September 1999 ($H = 12.582$, $p = 0.0396$), November 1999 ($H = 13.969$, $p = 0.0055$) and August 2000 ($H = 52.602$, $p = 0.0000$). The Duncan's rank test revealed that in July 1999 the dominant size class was 70 cm; while in August 1999 there were two dominant size classes (35 and 70 cm). In August 2000 a similar situation was observed, with 3 size classes (35, 75 and 105 cm).

Frond diameter revealed a seasonal change, with consistent increments from June (mean 0.51) to November 1999 (mean 0.81 cm; Fig. 6); a similar trend was observed

between April and August 2000. The above observation is statistically significant ($H = 221.733$, $p < 0.001$) and Duncan's rank test supports the difference observed in October and November 1999 ($p < 0.05$). Size frequency of the diameters has shown that the median value was localized between 0.8 and 1.0 cm (Fig. 7). During June 1999, and April and June 2000, it was clear that most of the diameters were over 0.6 cm (Fig. 7) and during July and August (both years) the diameters were 0.8 cm. The above observations were found statistically significant in July 1999 ($H = 52.092$, $p = 0.0000$), August 1999 ($H = 55.342$, $p = 0.0000$), September 1999 ($H = 12.582$, $p = 0.0396$), November 1999 ($H = 32.055$, $p = 0.0000$), April 2000 ($H = 19.441$, $p = 0.0011$), June 2000 ($H = 10.346$, $p = 0.0436$) and August 2000 ($H = 52.105$, $p = 0.0000$). Duncan's rank test showed that between 0.4 and 0.6 cm was a significant difference. There was no linear relationship between length and diameter ($r = 0.092$).

We observed the presence of dioic (Fig. 8A) and monoic fronds (Fig. 8B) in the same population. Female gametangia had larger gametes than males. This was most apparent in monoic thalli (Fig. 9) where five or more gametangia were observed per utricle. Most fronds were mature during 1999 and in August 2000 (Fig. 9), while thalli were mostly vegetative in April and June 2000. The Kruskal-Wallis analysis showed significant differences over the year ($H = 185.170$, $p < 0.01$). Duncan's rank test revealed that most of the months were different from each other ($p < 0.05$).

During the analysis of frond reproductive status, it became evident that the gametangial distribution differed over the length of the frond. This is because we separated the analysis of the proportion of reproductive structures in the central and the two extreme end areas of thalli. Accordingly, most gametangia were in the extreme ends of the thalli (Fig. 10) between June and August (1999), later developing in the central part of the thallus (September to December 1999). The proportion became more balanced in the three frond parts in August 2000. However, statistically significant differences in the proportion of the gametangia between the months in the ends ($H = 34.221$, $p = 0.005$) or in the center ($H = 36.664$, $p = 0.004$) were only observed during October (Fig. 10). The same result was determined by the Duncan's rank test ($p < 0.05$).

The presence of monoic fronds was dominant over the sampled period (Fig. 11) with the exception of June 2000 when the dioic fronds were more abundant. The above observations were confirmed with the Kruskal-Wallis

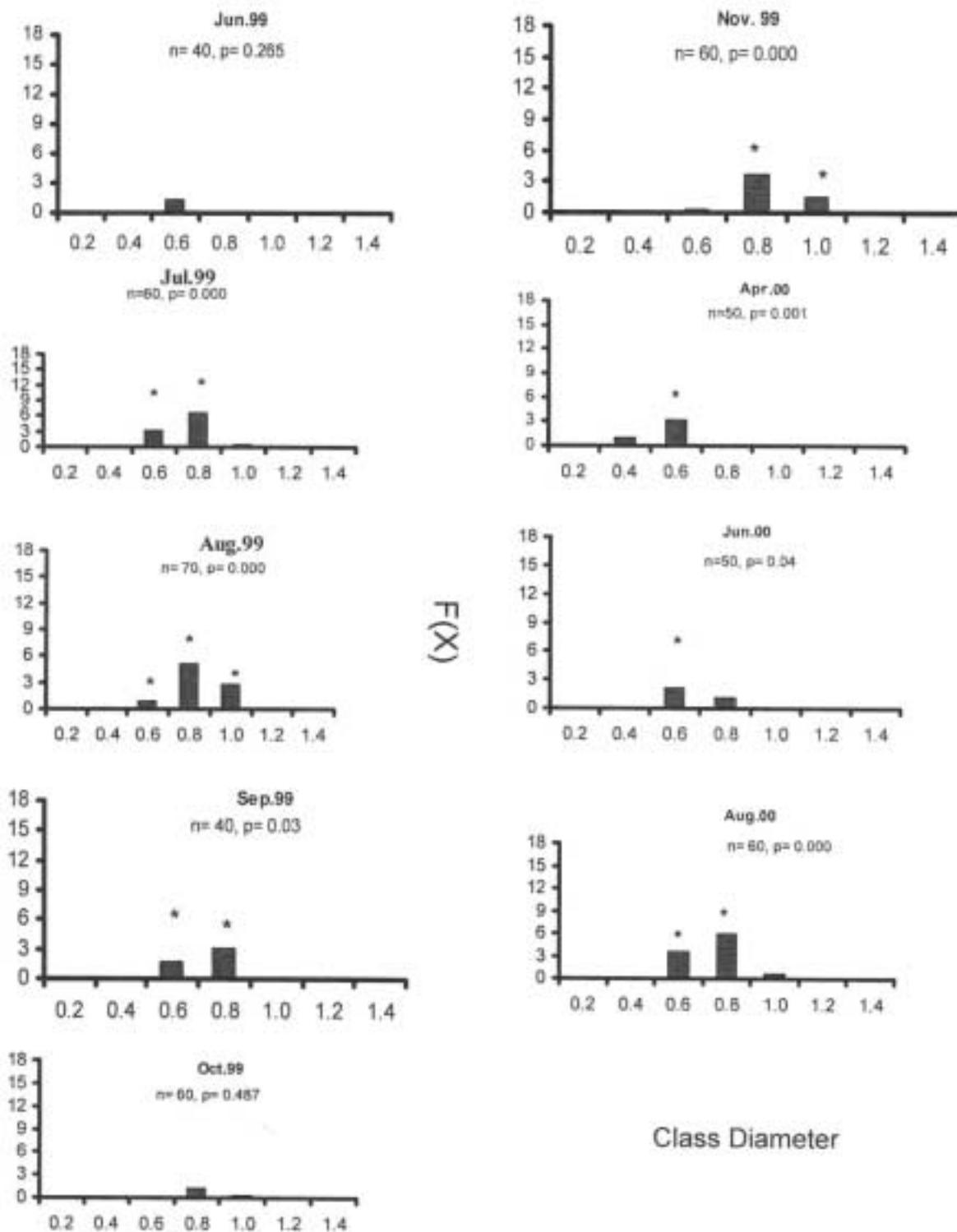


Fig. 7. Size frequency histograms of *Codium amplexiculatum* frond diameter in which more than one size class is dominant each month.

analysis ($H = 210.273$, $p < 0.001$). Duncan's comparison ($p < 0.05$) revealed significant differences in June, September, October and November 1999, and June and August 2000.

DISCUSSION

Codium amplexiculatum showed seasonal variations in percentage cover and biomass, but no relationship

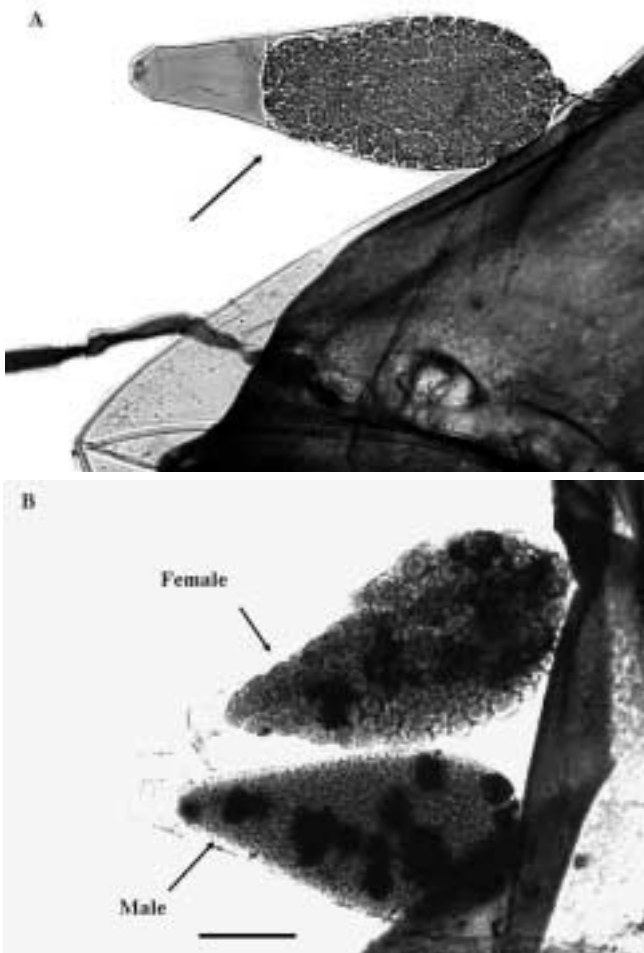


Fig. 8. A. Longitudinal section showing a female gametangia (arrow) rising from a utricle of a *Codium amplexiculatum* thallus. B. Longitudinal section showing the presence of male and female gametangia in the same utricle.

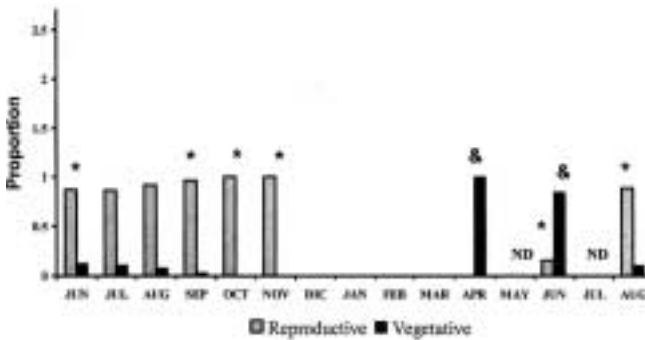


Fig. 9. Temporal variation in the proportion of reproductive and vegetative fronds in where significant variations are marked in asterisks and & symbol.

between them. Summer was statistically different ($p < 0.05$) from the other seasons, and this might be related to nutrient levels, especially reduced nitrogen and phosphorous compounds (Reyes-Salinas 1999), and the increase in surface water temperature by 9°C (Scrosati

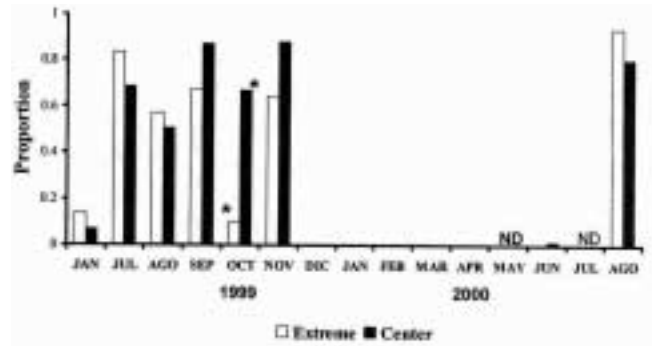


Fig. 10. Temporal variation of mature gametangial in relation to the position on a *Codium amplexiculatum* frond where significant variations were only observed in October 1999.

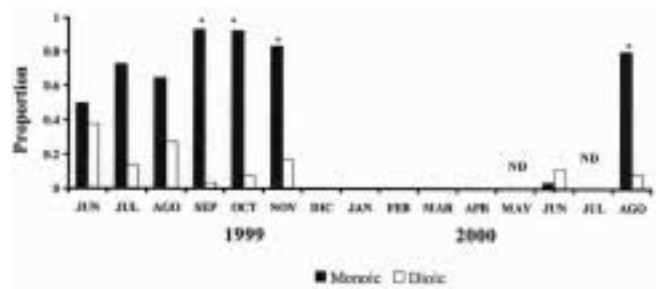


Fig. 11. Temporal variation of the monoic vs dioic thalli among the reproductive fronds of *Codium amplexiculatum* in where significant variations are marked in asterisks.

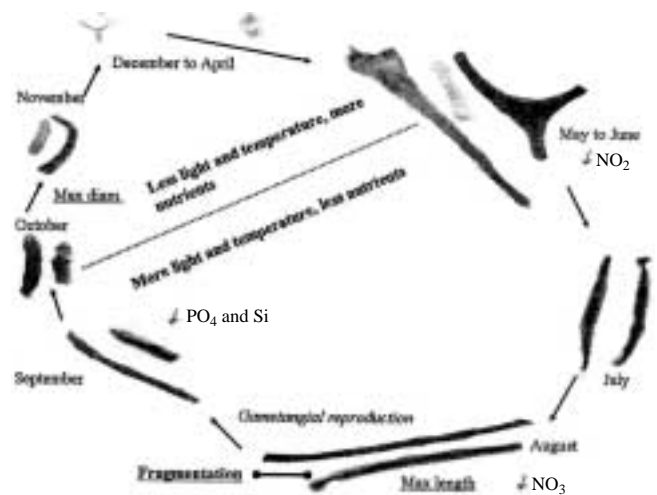


Fig. 12. Hypothetic life cycle of *Codium amplexiculatum* associated with rhodolith beds and the main environmental variables based on our data (population information and environmental data from Reyes-Salinas 1999).

2001) compared to the coolest period. The influence of the above factors has also been observed in *Caulerpa sertularioides* (Scrosati 2001) where maximum plant size was found in July and August 1999, and June and August

2000. This suggests density independence in population development. This was clearly observed by the presence of large and small fronds in the field (Riosmena-Rodriguez pers obs). Most thalli were anchored to individual rhodoliths which acted as physical traps, as suggested by Ceccherelli and Piazzini (2001) and Garbary *et al.* (2004).

It is clear that the summer (May to October as defined by Reyes-Salinas 1999) had higher light availability, higher water temperatures and lower nutrient levels than the other seasons, and this is when plants developed the largest populations. By the end of October, the population started a fragmentation process (Fig. 12) and began to disperse. During the winter (November to April) the population had a low percentage cover and biomass reflected by the development of young thalli only and changes in water motion especially resulted from storms (i.e. hurricanes). The above strongly suggests that *C. amplivesiculatum* responds like *C. bursa* J. Agardh (Vidondo and Duarte 1995) and *C. fragile* (Malinowski and Ramus 1973) to annual cycle.

Like *Codium setchelli* Gardner (Trowbridge 1996) and *Codium fragile* (Malinowski and Ramus 1973), *C. amplivesiculatum* showed one yearly peak in biomass. However, there are species, like *Codium bursa*, which have no seasonal pattern (Vidondo and Duarte 1998). High biomass value of *C. amplivesiculatum* were present in late spring (10,097 g m⁻² in June 2000), and were greater than those recorded for *C. fragile* with 3,500 g m⁻² (Malinowski and Ramus 1973).

The high values of biomass result from elongation of thalli because of the lack of a relationship between frond length and diameter. A similar observation was also reported for *C. fragile ssp. tomentosoides* (Trowbridge 1996). The growth rate probably changes seasonally based on changes in water temperature and nutrients (Trowbridge 1996; Vidondo and Duarte 1998). This is consistent with the large differences in plant size observed between April and June ($p < 0.05$) in both years. We did not find any morphological variants as Hubbard and Garbary (2002)

In June 2000 we found one of the highest thalli lengths in relation to cover and this corresponded to when reproductive structures appeared as observed by Bulleri *et al.* (2007) when nutritional conditions are optimal (Reyes-Salinas 1999). By late June and in August the length of thalli reached 300 cm and did not have reproductive structures. Between August and September a massive fragmentation of thalli occurred and simultaneous repro-

duction when is the peak of hurricane season. This was also observed by Malinowski and Ramus (1973).

Seasonal changes in the proportion of reproductive and vegetative thalli were found. Thalli were reproductive most of the year with a peak in October and November of 1999 (100%) and a minimum in April (0%), suggesting the growth rate changes in April. We observed differences in the proportion of fronds in reproduction between the sampled years. *Codium amplivesiculatum* is an iteroparous species that can reproduce continuously throughout the year. The presence of thalli with monoic and dioic reproductive structures are also noteworthy (Fig. 8). Our observations suggest a life cycle in which re-growth of plants occurs from fragments from November to April (Fig. 12). In June most of the fronds were in reproductive and were short thalli 35-70 cm. This pattern was prevalent and associated with monoic utricles. This is the first record of monoic utricles in this species.

Another interesting pattern observed was that *C. amplivesiculatum* had a more advanced level of maturity at the extreme ends of the thalli in the later months of the year, with some exceptions in September, October and November in which the central part of the thalli showed a higher level of maturity. A similar trend was observed in *C. fragile ssp. tomentosoides* (Churchill and Moeller 1972), in which central parts mature later in the year. The above trend might be related to the development of fragmentation in the thalli and utricle maturation. The utricle, a gametangial structure, developed in 6 months in a similar way to *C. fragile ssp. tomentosoides* (Churchill and Moeller 1972) and *C. fragile* (Malinowski and Ramus 1973).

The histograms demonstrate fragmentation in September, a form of asexual reproduction which may be in part a consequence of physical stress. In contrast, Trowbridge (1996) observed fragmentation in *C. fragile ssp. tomentosoides* in relation to herbivore density. But in our case seems to be more related with the hurricane season in late summer.

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