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FIELD STUDIES IN *CHONDRACANTHUS CHAMISSOI* (C. AGARDH) KÜTZING: SEASONAL AND SPATIAL VARIATIONS IN LIFE-CYCLE PHASES

ESTUDIOS DE *CHONDRACANTHUS CHAMISSOI* (C.AGARDH) KÜTZING EN TERRENO: VARIACIONES ESTACIONALES Y ESPACIALES EN FASES DEL CICLO DE VIDA

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ABSTRACT

Chondracanthus chamissoi (C. Ag.) Kützing is a commercial resource in certain areas of the Chilean coast and is becoming increasingly important due to its food value in Asian countries. This species grows only in natural beds that require to be rationally exploited in order to avoid their depletion. Since the first step necessary to develop this exploitation is a knowledge of the dynamics of the populations, the study of seasonal and spatial variations in abundance and reproduction of a natural bed in the locality of Puerto Aldea has been carried out. Samples taken bimonthly at four different depths during an entire year resulted in the detection of a sharp seasonality of biomass of sterile as well as reproductive plants with its maximum in summer months due mainly to the increase in growth of plants rather than in density. Reproductive plants only contributed 30% of the total biomass. Reproductive sporophytes were more abundant throughout the year. Reproductive gametophytes and sporophytes behaved differently over depth, with cystocarpic plants being more abundant at shallower depths and tetrasporophytes showing no differences along the bathymetric profile. Nevertheless, phase ratios calculated considering sterile and reproductive plants resulted in a higher proportion of haploid (gametophytes) plants. Differences appear to be due to phase-specific behavior at early stages of development or to differential rates of attachment to the sustrate by drifting frond pieces.

Key words: Gametophytes, sporophytes, seasonal variation, depth variation, phase ratio.

RESUMEN

Chondracanthus chamisshoi (C. Ag.) Kützing es un recurso comercial en ciertas áreas de la costa chilena que se ha vuelto paulatinamente importante debido a su valor alimenticio en países asiáticos. Esta especie crece sólo en praderas naturales que requieren de manejo racional con el fin de evitar su sobreexplotación. Como el primer paso para desarrollar un sistema de manejo racional es el conocimiento de las dinámicas poblacionales, se ha realizado el estudio de variaciones estacionales y espaciales de la abundancia y reproducción de una pradera natural de esta especie ubicada en la localidad de Puerto Aldea. A partir de muestras bimensuales colectadas a cuatro profundidades distintas durante el curso de un año se detectó una marcada estacionalidad en la biomasa de plantas tanto estériles como reproductivas con un máximo en los meses de verano debido principalmente al crecimiento de las plantas más que a su densidad. Las plantas reproductivas sólo contribuyeron con el 30% de la biomasa total. Los esporofitos fértiles fueron los más abundantes a lo largo de todo el año. Gametofitos y esporofitos fértiles se comportaron de forma distinta con la profundidad, las plantas cistocárpicas fueron siempre más abundantes a profundidades someras, mientras que los tetrasporofitos no presentaron diferencias a lo largo del perfil batimétrico. Sin embargo, la proporción de fases calculada considerando plantas tanto estériles como fértiles reveló una proporción mayor de plantas haploides (gametofitos). Estas diferencias parecen deberse a un comportamiento específico para cada fase en las etapas tempranas de su desarrollo o bien a la adhesión diferencial al sustrato de frondas a la deriva.

Palabras clave: Gametofitos, esporofitos, variaciones estacionales, variaciones en profundidad, proporción de fases.

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INTRODUCTION

Chondracanthus chamissoi (C. Agardh) Kützing is present on the coasts of Perú and Chile (Santelices, 1989) forming subtidal beds (up to 15 m depth) in protected bays with hard (shells, pebbles, stones) substrata. This species is a carrageenan-producer, therefore commercially utilized in the elaboration of food and pharmacological products. In recent years, the direct consumption of this alga in Asian countries resulted in an increase in harvesting for exports.

In Chile, there are three main regions where *C. chamissoi* is produced: Caldera (27° 4' S, 70° 50' W), Bahía La Herradura (29° 58' S, 71° 22' W) and Tongoy (30° 15' S, 71° 35' W). None of these has man-made cultures and the estimates of production of the alga are based on the harvesting of natural beds. Two of these beds are located in the region comprised between 29 and 32° S, one of them is located at the South extreme of Tongoy bay next to Puerto Aldea, a small fishing village, and it has the highest extraction volumes (more than 120 metric tons year^{-1}) recorded for the region. Although *C. chamissoi* is one of the seasonal major economic resources for the people living in Puerto Aldea, the lack of knowledge about the dynamics of the algal population in this locality (and several others), frequently impacts on the production due to indiscriminate extraction.

The goal of this study is to describe the seasonal and spatial variations in abundance and reproductive behaviour of the *C. chamissoi* population of Puerto Aldea, which could be helpful in order to develop and apply a management plan for this resource at this locality.

MATERIALS AND METHODS

All measurements were made in *C. chamissoi* beds located at Puerto Aldea (30 16' S, 71 38' W) a fishing cove at the southward end of Tongoy Bay (Fig.1). The study area comprises the bathymetric limits of the *C. chamissoi* beds between 4 and 10 m of depth.

Samples were taken in stations located at 4, 6, 8 and 10 m deep. Stations were marked with buoys along each of three 50 m long transects perpendicular to the shore line. Estimation of abundance, size frequency and reproductive stage of plants was done by removing all plants included in two quadrats of 25 cm side (at opposite sides of the transect line) at each depth station. Samples were taken bimonthly from November 1991 until November 1992 by SCUBA diving. The corresponding 24 samples of each month were carried to the laboratory in labelled plastic bags and frozen until later manipulation.

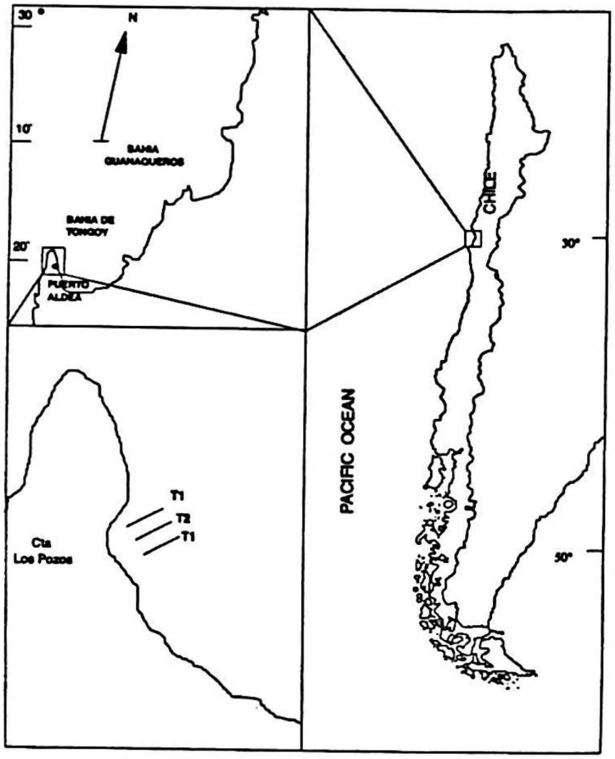

Figure 1. Study site located at Puerto Aldea (30°16' S; 71° 38' W) calm cove within a larger bay (Tongoy).

Sitio de estudio ubicado en Puerto Aldea (30°16' S; 71° 38' W), caleta protegida al interior de una bahía de mayor tamaño (Tongoy).

Reproductive (those with visible reproductive structures) and non-reproductive fronds were washed and weighed separately in the laboratory. To standardize the rather complex morphology of *C. chamissoi*, only those fronds found attached to a single basal disc were considered belonging to the same individual in order to evaluate total density as well as density of reproductive plants. Therefore, density is expressed in algal units per square meter, where different algal units correspond to the longest fronds attached to different and independent basal discs. The length of the longest frond within each individual was measured and plants were classified into one of the four length classes: less than 4 cm, 4.1 to 8 cm long, 8.1 to 12 cm long and longer than 12 cm.

A subsample of 90 sterile plants (ranging between less than 4 cm and 16 cm long) for each sampling station was taken bimonthly and separated into haploid and diploid thalli according to the acetal-resorcinol reaction (Craigie & Pringle, 1978) in order to evaluate the phase ratio of the population. Reproductively mature material of each phase was used as a control.

Results were submitted to a Bartlett's test of homogeneity of variance. AG-test (Steel & Torrie 1988) was used to compare the phase ratios recorded in time and depth. Density and biomass values were analysed with a multifactorial ANOVA (Sokal & Rohlf, 1981) and a *a posteriori* Tukey test.

RESULTS

Seasonal distribution of plant biomass

C. chamissoi occupied most of the available sustratum of the cove all year round. Figure 2A shows the patterns of total biomass and biomass of reproductive plants in time. A two-way ANOVA between depth and time (months) shows significance of total biomass along the sampling time, at different depths, and at the interaction of the two variables. A sharp seasonality is detected in total biomass with a maximum in January decreasing significantly ($P<0.01$) during the winter months until a minimum was reached in July. In the month of September biomass increased again and reached, in November of the second year, a significantly higher value than in the same month of the preceding year.

Reproductive plants did not show significant variation in biomass between the two phases in their seasonal pattern except in January (Fig. 2A), when tetrasporic plants had an average biomass value of 62g m^{-2} whereas cystocarpic plants had a biomass of 30g m^{-2}. Although January was the month with the greatest biomass of reproductive plants, both phases contributed only with 30% of the total population biomass. Reproductive plants decreased in biomass during the winter months disappearing in September (spring). Both phases increased again during November of the second year although not reaching the values observed in January.

Seasonal distribution of plant density

The only significant changes ($P<0.01$) in total density of plants were detected in both years during November (Fig. 2B). The increase between November of the first year and January of the second year (ca. 60 algal units m^{-2}) was due to the increase recorded at 6 m depth (see

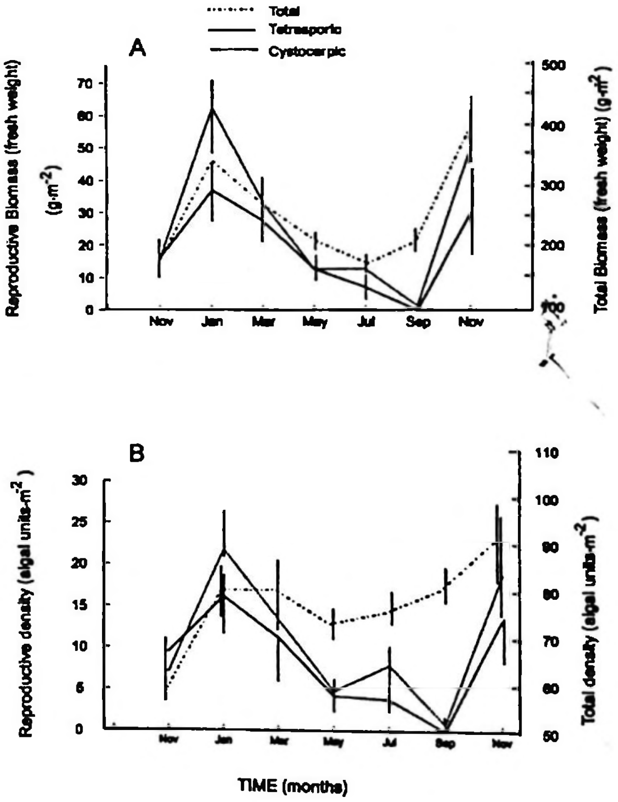

Figure 2. **Seasonal variations in biomass (A) and (B) density of *C. chamissoi*. Left-side axis corresponds to variations in reproductive plants and right-side axis corresponds to total variations. Bar= 2 standard errors.**

Variaciones estacionales en (A) biomasa y (B) densidad de *C. chamissoi*. Eje del lado izquierdo corresponde a variaciones de plantas reproductivas y eje de lado derecho corresponde a variaciones totales. Barra = 2 errores estándar.

Fig 4), whereas the increase from September to November corresponded to an increase detected at 4 m depth (see Fig. 4). During the rest of the months, densities did not change significantly contrasting with the variations in biomass.

Density of reproductive plants of both phases had the same trend with time as biomass (Fig. 2B). Tetrasporic plants were significantly more abundant than cystocarpic plants only in January without significant differences in the rest of the sampling months.

Bathymetric and seasonal variation of total biomass and biomass of reproductive plants

Total biomass showed a reduction of almost half its average value between depths of less than 6 m and those deeper than 6 m (Fig. 3A). These differences were mainly due to the large biomass observed at 4 m during January and March and at 6 m during September and November of the second year. These seasonal variations were not detected at lower depths (8 and 10 m) where, in addition to a more uniform distribution of biomass along the seasons, this never reached values higher than 400 g m^{-2}. This trend was partially followed by cystocarpic plants, except that the second maximum of biomass was not at 6 but at 4 m depth during November of the second sampling year (Fig. 3B). Biomass of tetrasporic plants (Fig. 3C) was also significantly different depending on the season of the year and the sampling depth ($P<0.01$), although these plants behaved similarly at 6 and 8 m depth, however differing from March to May (fall). The general seasonal pattern is similar with the maxima of all type of plants at the beginning and the end of the year, although at the beginning of the year the maximum biomass of each reproductive phase was observed at different depths.

Bathymetric and seasonal variation of total density and density of reproductive plants

The total density of plants (Fig. 4A) remained constant throughout the year at 8 and 10 m depth (50 - 60 and 20 - 40 algal units m^{-2} respectively). The seasonal maxima showed by this parameter at 4 and 6 m depth are the opposite than that observed with biomass (Fig. 4A). This indicates that while at 4 m depth plants are large at the beginning of the year (high biomass and low density), the maximum in density at 6 m is represented by small plants. On the other hand, at the end of the year, plants are small at 4 m and large at 6 m. Lower and more uniform densities throughout the year were detected at 8 and 10 m of depth.

The density of reproductive plants (Figs. 4B, 4C) had the same seasonal pattern as the total density for both tetrasporic and cystocarpic plants, with a significant displace ($P<0.01$) from January to March in the maximum at 6 m depth. In general, cystocarpic plants were less numerous than tetrasporic plants. Samples taken at 8 and 10 m depth (Figs. 4B, 4C) showed

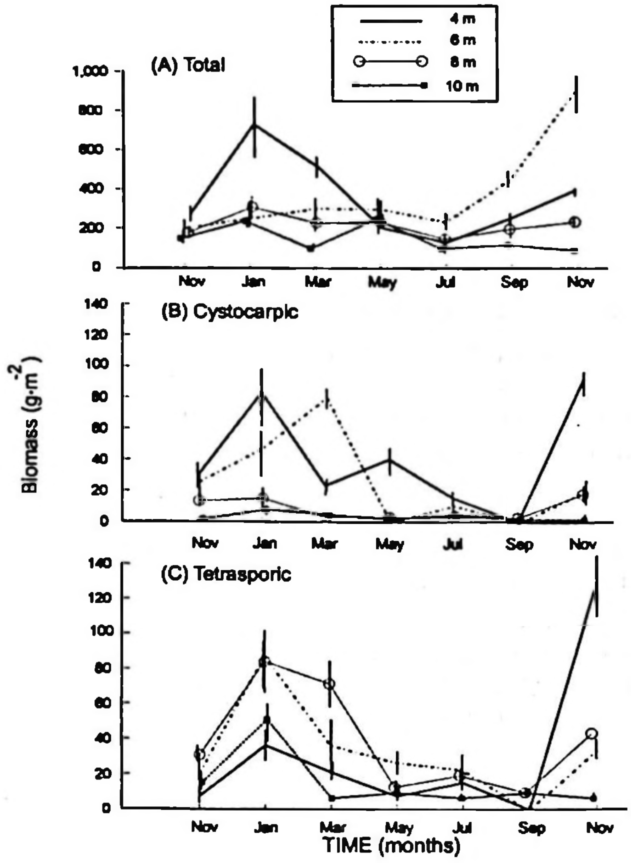

Figure 3. Bathymetric variations in seasonal biomass of *C. chamissoi*. (A)total, (B) cystocarpic and (C) tetrasporic fronds. Bar= 2 standard errors.

Variaciones batimétricas en biomasa estacional de *C. chamissoi*. (A) Frondas totales, (B) cistocárpicas y (C) tetraspóricas, Barra = 2 errores estándar.

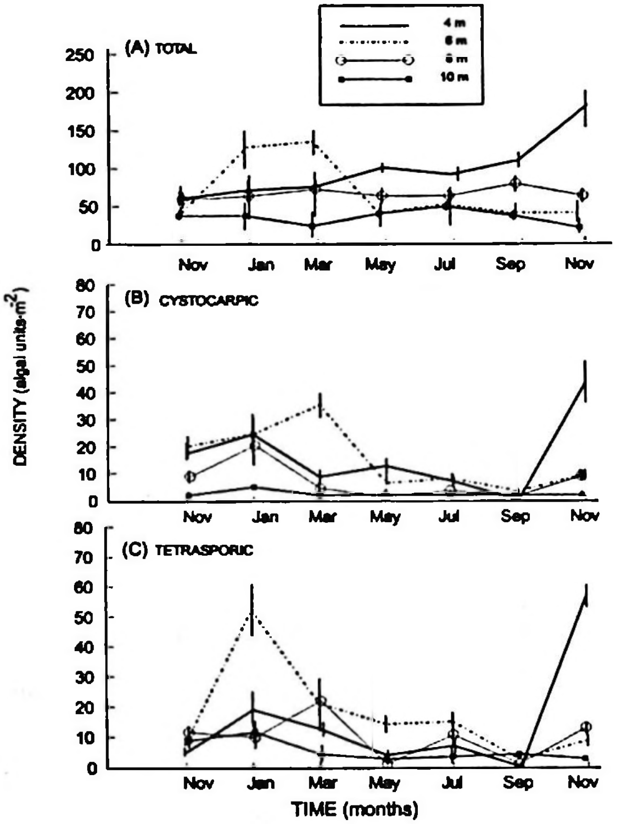

Figure 4. **Bathymetric variations in seasonal density of *C. chamissoi*. (A)total, (B) cystocarpic and (C) tetrasporic fronds. Bar= 2 standard errors.**

Variaciones batimétricas en densidad estacional de *C. chamissoi*. (A) Frondas totales, (B) cistocárpicas y (C) tetraspóricas, Barra = 2 errores estándar.

that cystocarpic as well as tetrasporic density displayed a detectable increase in January.

Seasonal and spatial frequency distribution of frond length for total and reproductive plants

The frequency of longer fronds, considering all fronds sampled independently from depth, was significantly greater ($P<0.05$) during summer months (Fig. 5) than winter months. Fronds over 8 cm long had the highest percentage in January and November 1992, with fronds smaller than 4 cm increasing in proportion towards wintertime representing 40% of the population by July.

Reproductive fronds of each phase followed a similar pattern in frond length frequency distribution as total fronds (Figs. 5B, 5C), nevertheless, they were always larger-sized than plants with no reproductive structures ($P<0.05$). Reproductive fronds were usually over 4 cm long and this fact became more evident between May and November. During most of the year cystocarpic fronds showed a greater proportion of longer fronds than tetrasporic ones, except in July ($P<0.05$) when there were no significant differences in size between phases. Figure 6 shows the frequency distribution of frond length in relation to depth depicting the increase in proportion of shorter fronds with increasing depth, with fronds less than 8 cm being more frequent at lower depths (Fig. 6). Frequency distribution of frond length of reproductive plants had a similar trend, although with differences between phases. At 10 m of depth (Fig. 6B), cystocarpic fronds were less than 8 cm long.

Gametophyte/sporophyte ratio of fertile and sterile plants

Gametophytes throughout the year represented 60% of the population with no significant variation in time (Fig. 7A). This ratio did not change with depth (Fig. 7B).

DISCUSSION

C. chamissoi has been characterized by this study as an alga with seasonal behavior in abundance as well as having clearly restricted bathymetric limits. The bulk of the population grows between 4 and 6 m of depth with a noticeable increase in biomass during the summer months (November through February). The low abundance recorded during November of the first year, compared to the same month on the second year (Fig. 2A) could be explained by the exploitation of this resource by the nearby fishermen village during the previous year or simply because the summer arrived earlier. Since plant density per unit area remains uniformly constant throughout the year (Fig. 2B), the significant increase in biomass in January and November of the same year can be explained by the growth of individual plants.

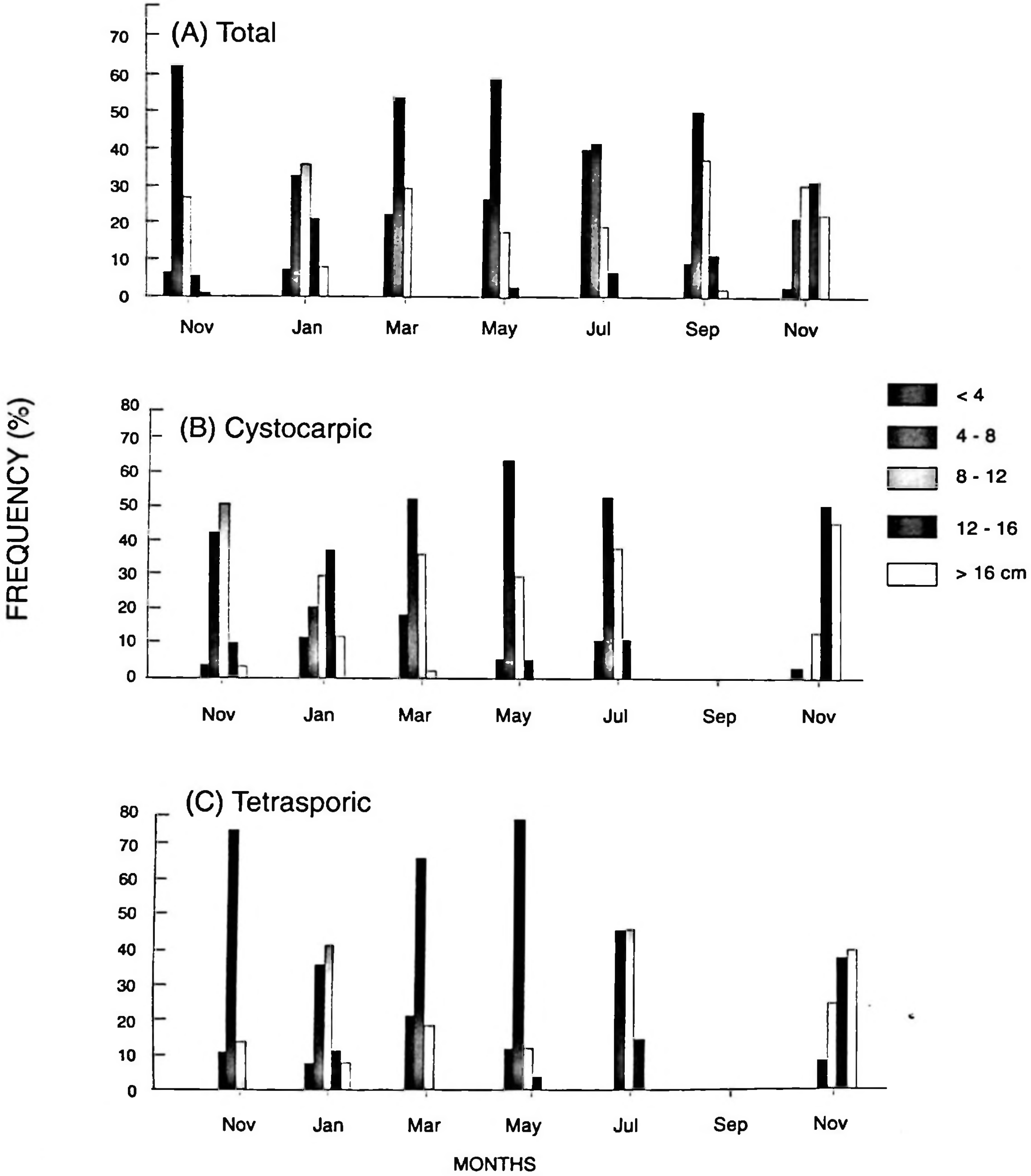

Figure 5. Seasonal variation of total fronds (A), cystocarpic fronds (B) and tetrasporic fronds (C) length.

Variación estacional en longitud de frondas totales (A), frondas cistocárpicas (B) y frondas tetraspóricas (C).

This fact is supported by the increase in frequency of longer fronds during these months (Fig. 6). Similar results have been observed in *Iridaea cordata* (Turn.) Bory (Hansen & Doyle, 1976). The occurrence of basal discs that remain attached to the sustrate long periods of time (> 1 year) developing new fronds each growing season is common in Chondracanthusceae (Hansen, 1977; Taylor *et al.*, 1981; Foster, 1982; May, 1986; Sousa, 1986). Likewise, after the

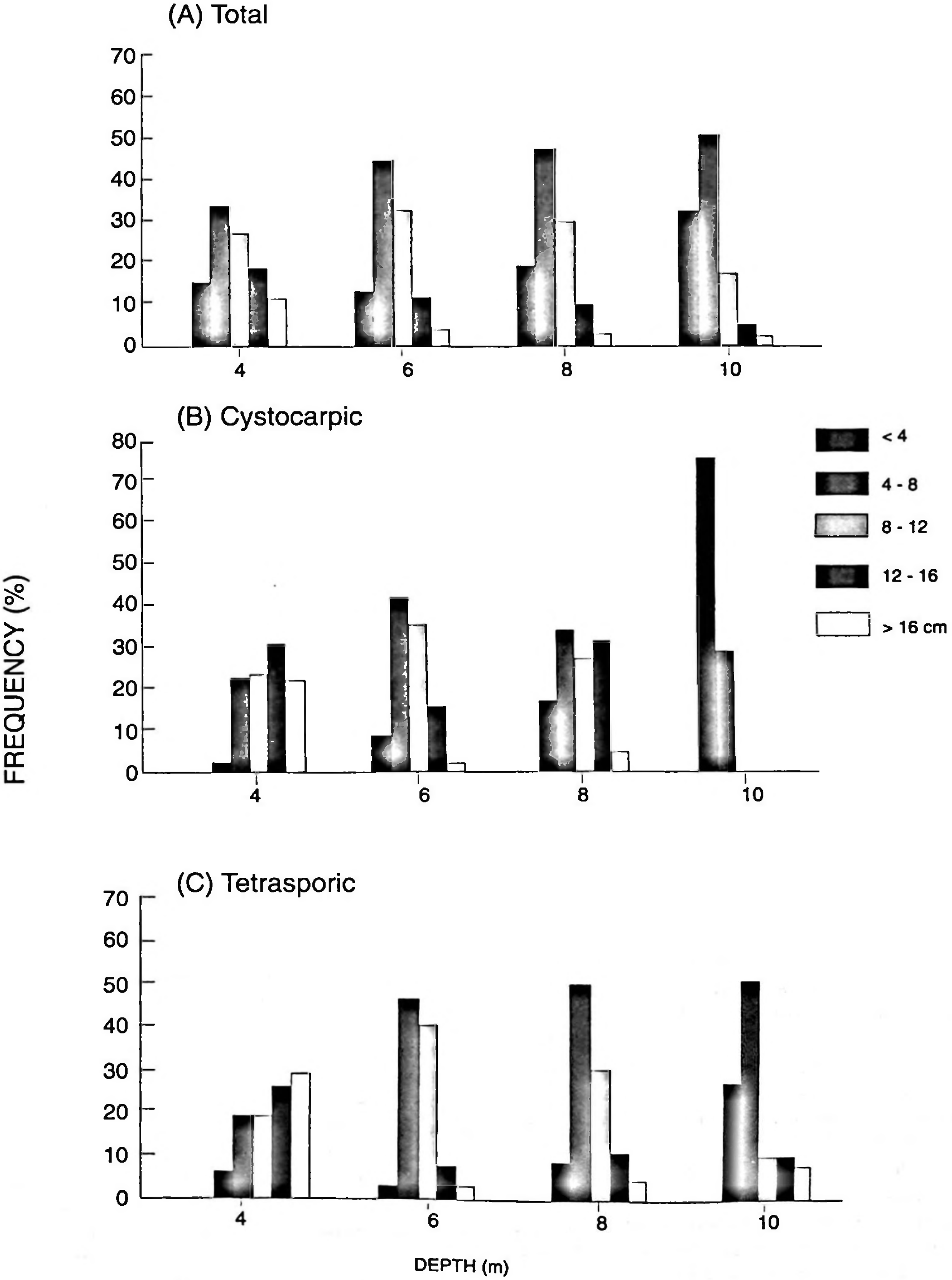

Figure 6. **Bathymetric variation of total fronds (A), cystocarpic fronds (B) and tetrasporic fronds (C) length.**

Variación batimétrica en longitud de frondas totales (A), frondas cistocárpicas (B), y frondas tetraspóricas (C).

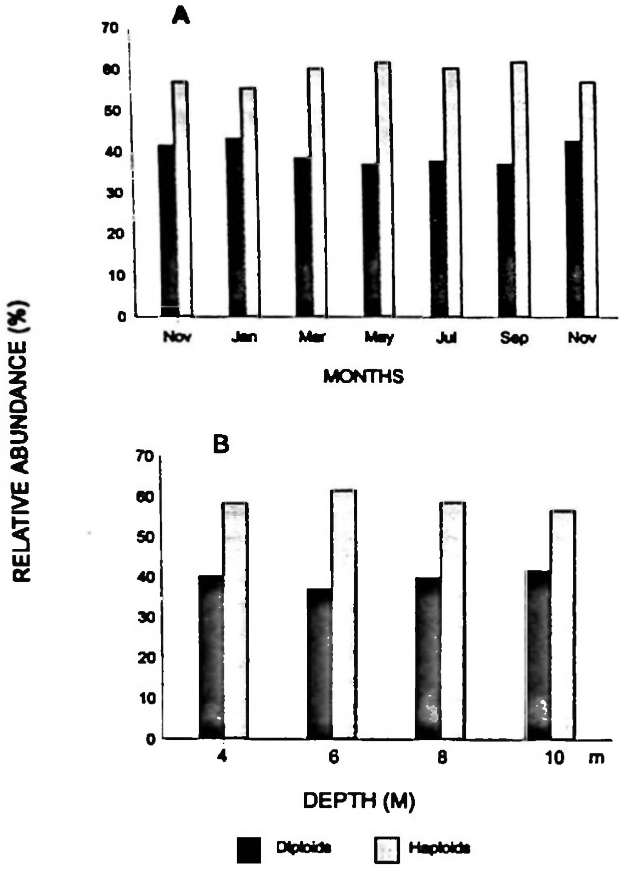

Figure 7. **Relative abundance of haploid and diploid thalli in *C. chamissoi* population. Variations in time (A) and depth (B) including sterile and reproductive thalli.**

Abundancia relativa de talos haploides y diploides en la población de *C. chamissoi*. Variaciones en tiempo (A) y profundidad (B) incluyendo talos estériles y reproductivos.

maximum observed in January, biomass decreases drastically in autumn with no significant variations in the number of plants present per area unit (Fig. 2B). This is probably due to the loss of plant material as indicated by the low frequency of fronds longer than 12 cm recorded in the winter period (Fig. 6). At the same time, a replacement by smaller fronds seems to be occurring during winter.

Bathymetrically, the maximum density of plants occurred at 6 m during the first growing season whereas it was detected at 4 m during the second one. In addition, biomass measurements indicated that, during the first growing season, plants were not only more abundant at 6 m but also smaller than at 4 m of depth. The situation is similar during the second growing season when plants, more abundant at 4 m this time, are also smaller than at 6 m depth. Somehow, this fact can be related to the displacement in seasonal plant abundance. Since during the second growing season the summer is delayed, plants that grow closer to the surface receive higher levels of irradiance and temperature than plants inhabiting at lower depths by the time the sampling was made. Once the full development of the season arrived (later than in the first year) the optimal conditions for growth could be displaced to lower subtidal areas (6 m) as could have happened in the first growing season.

C. chamissoi, as well as several other seaweeds (DeWreede & Klinger, 1988) has a maximum growth that coincides with the maximum fertility (in terms of abundance of reproductive plants, Fig. 2A), although the contribution of reproductive plants to the total population is small (30%). Since this increment in biomass is mainly due to the growth in frond length which, in turn, are those that develop reproductive structures, this correlation is not surprising. Nevertheless, when the growing season is suposedly delayed for increment in biomass, it is not so for the occurrence of reproductive structures suggesting a more complex interaction between the environment and the endogenous factors that trigger their formation.

Reproductively mature sporophytes are always more abundant in the population although, the analysis of sterile specimens (Fig. 7), demonstrates a clear dominance of the haploid over the diploid stage. This disparity in the phase ratio, in particular the sporophytic dominance, for an isomorphic alga has been mentioned for several other Chondracanthusceae (Hansen & Doyle, 1976; May, 1986; Lazo *et al.*, 1989). This fact has been attributed either to random events that affect just by chance one or other phase settlement or to differences in the reproductive and / or physiological characteristics of each phase (May, 1986). This lack of variation throughout time in the phase ratio of *C. chamissoi* is probably due to the permanence of their basal discs which would regenerate upright fronds seasonally. Nevertheless, a different possibility in this case can be argued, that is, the occurrence of a greater vegetative propagation of one phase than the other by means of drifting fronds that are able to reattach to the sustratum and regenerate entire new plants, an event that is commonly seen in this species growing in tanks. Abundant drifting fronds are especially observed in certain periods of the year and quick and simple experiments have been set up to demonstrate the capacity of loose fronds to re-attach to the sustratum (unpublished data). This feature can be particularly important for the maintenance of the population in view of the small proportion of reproductive plants found.

Seasonal differences between the maxima of reproductive tetrasporophytic and gametophytic density and biomass have been reported for other Chondracanthusceae (Prince & Kingsbury, 1973; Mathieson & Burns, 1975; Abbott, 1980; Hannach & Santelices, 1985; Westermeier *et al.*, 1987; Poblete *et al.*, 1987); it is presumed that the maturation of both phases respond to different environmental conditions. Interestingly, the differential phase ratio remains throughout time and depth, whereas the reproductive individuals of both phases show a distinct seasonal and spatial pattern. Differences in spatial distribution patterns, i.e. decrease in abundance of cystocarpic plants with depth, versus a uniform abundance of tetrasporic plants (at least until 8 m of depth), have been detected for various other species of algae (Barilotti, 1971; Prince & Kingsbury, 1973; Edwards, 1973; Mathieson & Burns, 1975; Mathieson & Norall, 1975; Craigie & Pringle, 1978; Norall *et al.*, 1981; Hannach & Santelices, 1985). The number of gametophytes that become reproductive is less than the number of tetrasporophytes that do so, indicating that gametophytic reproduction is being inhibited by depth. The specific factors involved in reproduction of *C. chamissoi* are still unknown and could be either environmental or endogenous like in other species (West, 1968; Edwards, 1971; Guiry, 1984; McLachlan *et al.*, 1988). Studies upon aspects such as differences in the performance of early stages of development (González & Meneses, 1996) resulted in higher rates of settlement and germination for tetraspores which could explain the higher ratio of haploid plants in the field. However, once sporophytes germinate, they display faster growth than gametophytes. Since plants with reproductive structures are those with longer fronds, the sporophytic growth rate could partially explain the higher frequency of tetrasporic plants found in Puerto Aldea.

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