SCI. MAR., 55(3): 475-481 1991

Ecology of *Chondrus crispus* Stackhouse (Rhodophyta) in the Northern coast of Spain. I Seasonal patterns*.

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SUMMARY: The seasonal aspects of two *Chondrus crispus* populations growing along the central coast of Asturias (northern Spain) were studied and compared with other regions. Biomass seems to show a seasonal pattern determined by seawater temperature and irradiance. Density and size-development classes seem not to be correlated with these environmental factors. Ploidy composition show a slight predominance of tetrasporophytes, and some causal factors are discussed.

Key words: Chondrus, seasonal patterns, Asturias, N. Spain.

RESUMEN: ECOLOGÍA DE *Chondrus crispus* STACKHOUSE (RHODOPHYTA) EN LA COSTA NORTE DE ESPAÑA. I. PAUTAS ESTACIONALES. — Se estudia la variación estacional de *Chondrus crispus* en dos localidades de la costa central de Asturias. La variación de biomasa se relaciona con la irradiancia y con la temperatura del agua, mientras que el número de frondes y clases de desarrollo no parecen relacionarse con los parámetros físico-químicos analizados. La composición haploide-diploide muestra una ligera dominancia de los tetrasporofitos. Se comparan estos resultados con los de poblaciones de otras latitudes y se discuten algunos factores causales de estas pautas estacionales.

Palabras clave: Chondrus, pautas estacionales, Asturias, N. de España.

INTRODUCTION

Along the north coast of Spain, *Chondrus crispus* Stackh. characterizes a community in the intertidal zone between 0.4 and 0.8 m above the Lowest Astronomical Tides (L.A.T.). Dense stands appear along the west part of this coast but from the Nalon's mouth only marginal populations can be found. Finally, the community disappear due to the "meridional" influence of the Bay of Biscay (ANADÓN, 1983; MENÉNDEZ and FERNÁNDEZ, 1990).

C. crispus is, after *Gelidium sesquipedale,* the most important seaweed resource in Spain for carrageenan extraction. It has been studied in other latitudes (for a review, see PRINGLE and MATHIESON, 1986) and temporal patterns can be distinguished, but few population studies have been done.

The present work describes the seasonal variations of biomass, number of fronds, size distribution, net production and ploidy composition as well as correlations with some abiotic factors throughout the year.

MATERIALS AND METHODS

Field work was carried out at two unexploited sites on the coast of Asturias (northern Spain), be-

*Received December 19, 1990. Accepted May 15, 1991.

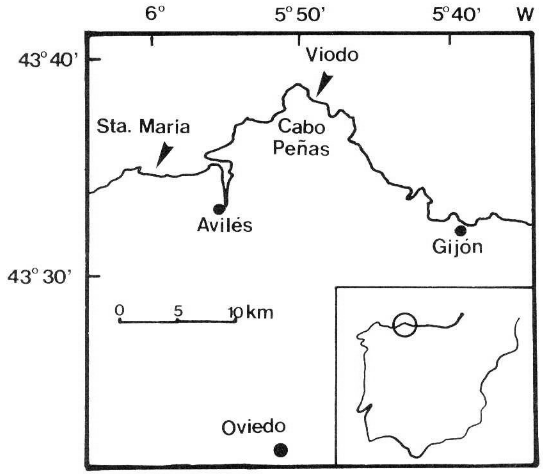

FIG. 1. — Map showing study sites.

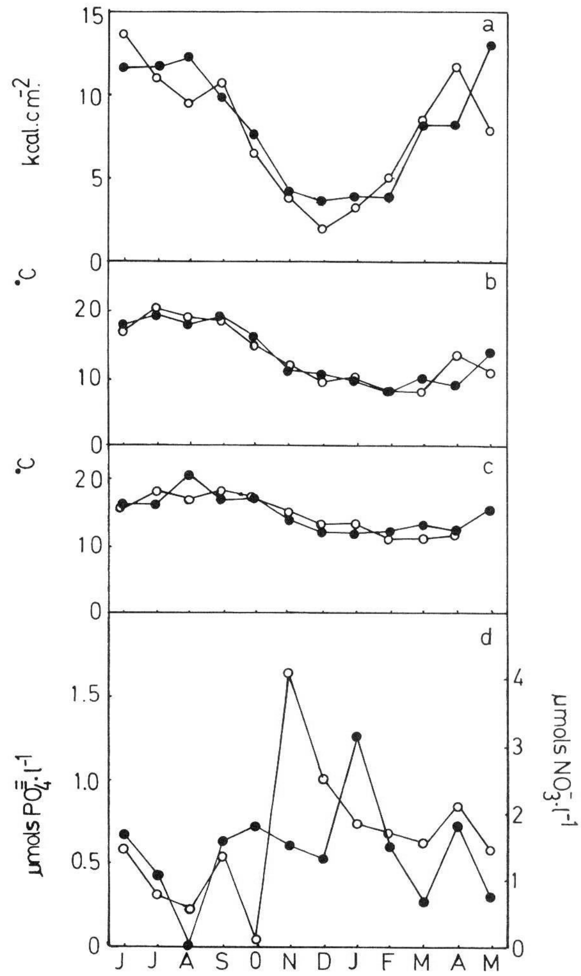

FIG. 2. — Seasonal variations in mean monthly values of total incident energy (a), air temperature (b), superficial seawater temperature (c); open circles —Santa María, closed circles— Viodo. Seasonal variations in nutrients in Viodo (d); open circles-nitrates, closed circles-phosphates.

tween June 1983 and June 1984 at Santa María and between June 1984 and June 1985 at Viodo (Fig. 1).

As the samples were located in homogeneous intertidal areas with a weak slope and a cover of *Chondrus crispus* of about 80 %, one sample per month of 3000 cm^2 —60 × 50 cm—, was collected randomly. This area satisfied the homogeneity values for biomass, number of fronds and size-development classes (estimated on the basis of values of the coefficient of variation and chi-square for heterogeneity, MENÉNDEZ, 1985).

All fronds were classified into three size-development classes on the basis of TAYLOR (1970, 1971) modified by MCLACHLAN *et al.* (1988). Class I: fronds without dichotomies, Class II: fronds with one or two dichotomies, and Class III ("adults"): fronds with more than two dichotomies and able to be fertile.

Biomass was expressed as dry weight after 48 h. at 60 °C. Net production was estimated by monthly increases in biomass (WESTLAKE, 1974). Algal epiphytes growing on *C. crispus* were observed monthly at Viodo using an arbitrary scale of abundance, cited in Table I. Frond length was measured to within 1 mm.

The determination of vegetative tetrasporophytes and gametophytes was carried out at Viodo by the resorcinol-acetal test (CRAIGIE and LEIGH, 1978). The ploidy composition of the Santa María population was obtained from a random sample of 50 plants, collected in October 1985.

On the days chosen for sampling, the surface temperature was measured and water samples were collected to determine the nitrate and phosphate content with a Technicon autoanalyzer. Air temperature data was supplied by the weather stations of Avilés and Gijón and total incident radiation by the weather station of Oviedo.

RESULTS AND COMPARISON WITH OTHER REGIONS

Environmental factors

Figure 2 shows the variations of environmental parameters throughout the period under study. Incident radiation shows a seasonal cycle with minimum values from November to March and increasing values from March to August; from this month on there is a gradual decrease (Fig. 2a). Air and seawater temperature (Figs. 2b and 2c) show quite similar values in

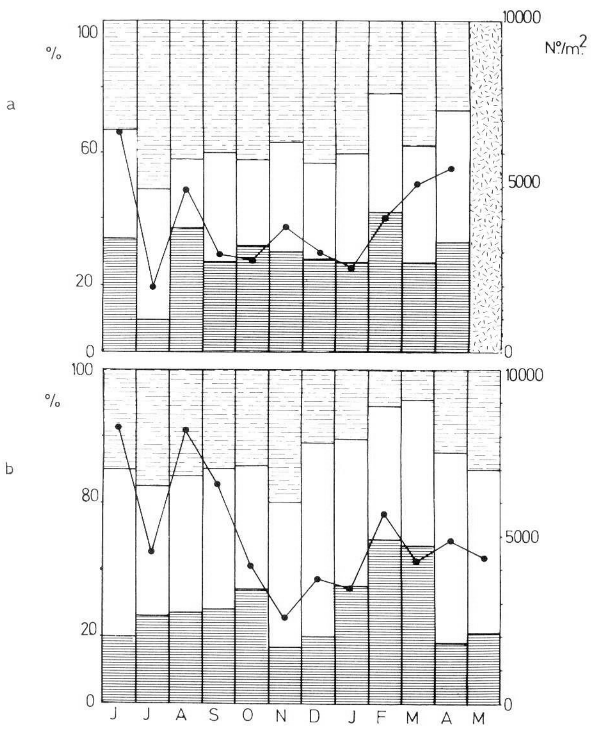

FIG. 3. — Seasonal changes in number of fronds and percentage of the three development-size classes. (a) Viodo (b) Santa María. ▤ Class I ☐ Class II ▤ Class III. No data for May in Viodo

winter; they gradually increase from April until August and, from this month on, they slowly decrease. Nutrients (Fig. 2d) reach maximum value in autumn (nitrate) and winter (phosphate), decreasing after April and reaching minimum values during the summer.

Annual variation of number of fronds

Total number of fronds (Fig. 3) show three maximum values which are specially noteworthy in June (Viodo), as well as June and August (Santa María del Mar). Minimum densities occur in July (Viodo) and November (Santa María). This pattern is due to the fronds belonging to development classes I and II and is stronger in Santa María, especially during the winter months (Fig. 3b). Viodo gives quite similar percentages throughout the year (Fig. 3a). There is a continuous recruitment from the holdfast throughout the year, in accordance with the observations of PYBUS (1977). Seasonal variation affects all development classes in contrast with Pybus's observations. This is evident in Santa María, with few adults from December to April, coinciding with the maximum

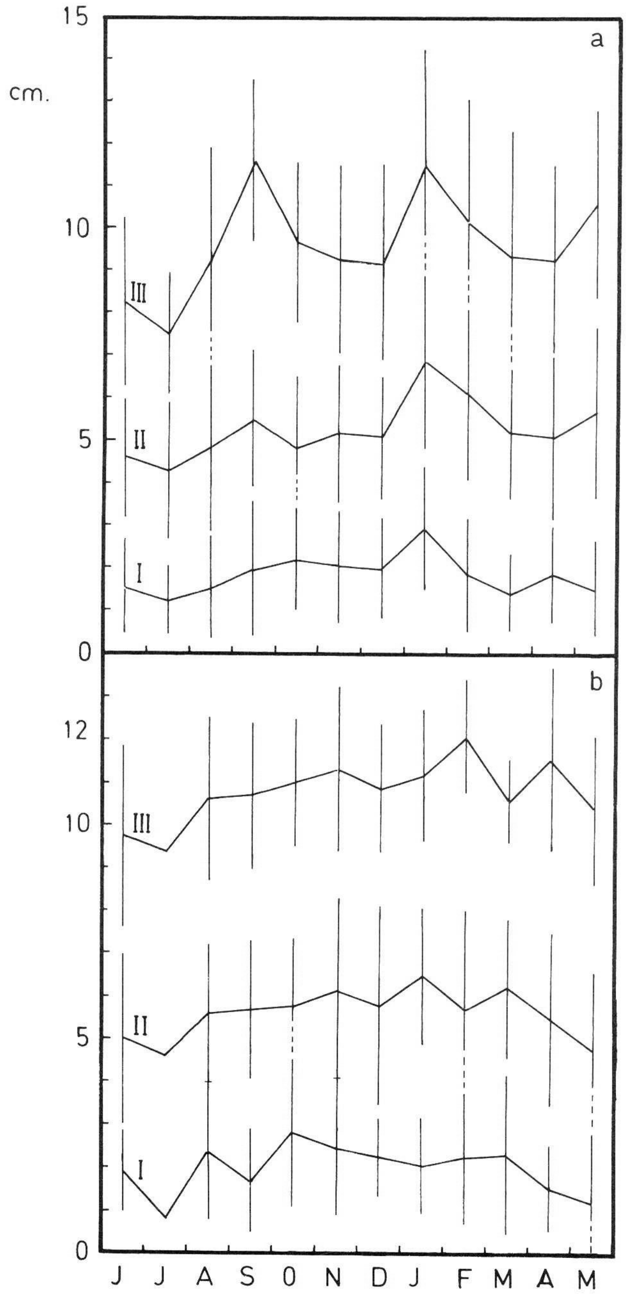

FIG. 4. — Mean seasonal changes in size of the three development-size classes. (a) Viodo (b) Santa María. Vertical bars = Standard deviation × 2.

values of class I. This is a situation where the disappearance of adults favours the expansion of juvenile fronds (PYBUS, 1977).

Annual variation of average size

This is a good parameter for classes I and II but with larger fronds is poor because the growth is lat-

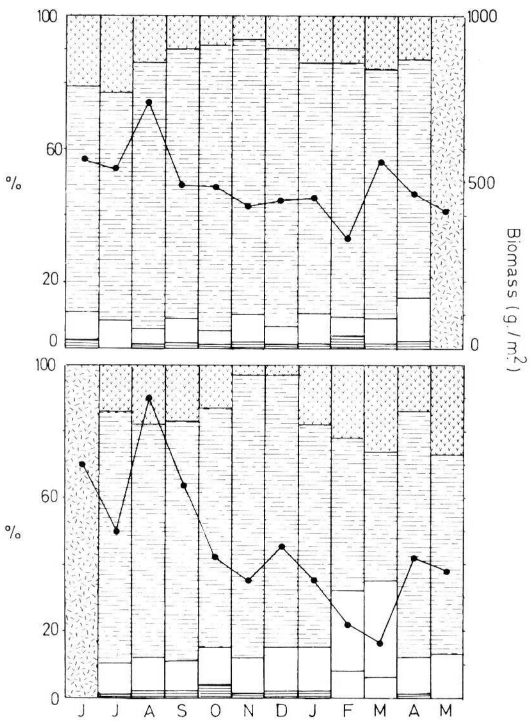

FIG. 5. — Seasonal changes in biomass and percentage of the three development-size classes. (a) Viodo (b) Santa María. ▤ Torn pieces ▤ Class I ▭ Class II ▤ Class III. No data for May in Viodo

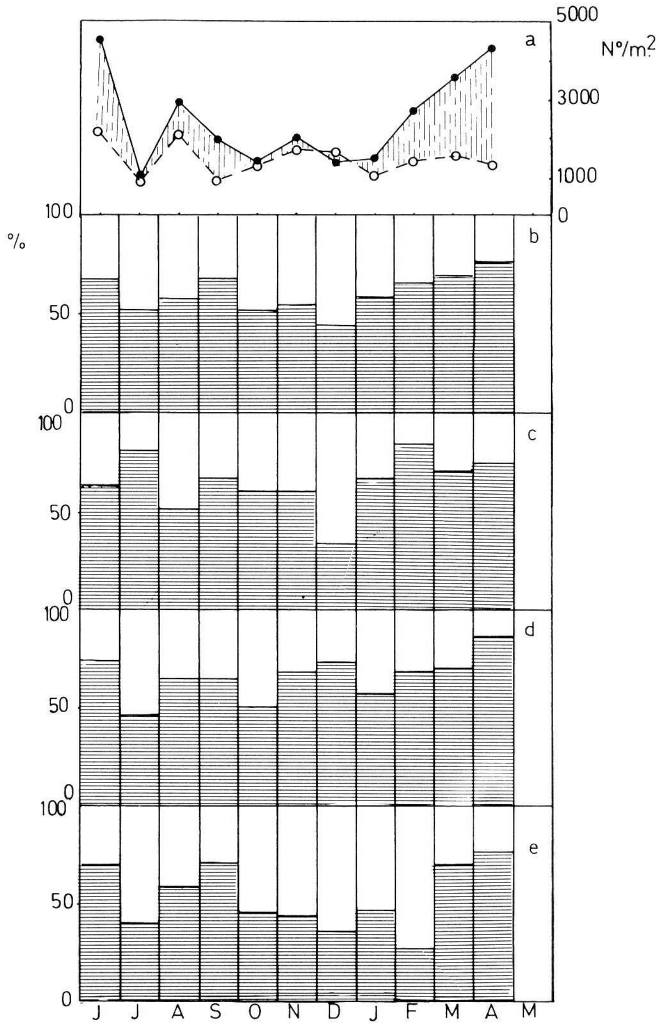

FIG. 6. — (a) Seasonal changes in number of gametophytic (open circles) and sporophytic fronds (closed circles) in Viodo. (b) Percentage of gametophytes ▭ and sporophytes ▤ in the global sample, (c) in class I, (d) in class II and, (e) in class III. No data in May.

eral (McLACHLAN *et al.*, 1988). At any rate, little seasonal variation is shown (Fig. 4) because of the great variability for all the size-development classes. The values are much higher than those found by MATHIESON and BURNS, 1975, 5.5-6.0 and 3.6-4.0 cm).

Biomass and Production

Biomass reaches three maxima, the most outstanding in August (Fig. 5). Minimum values occur in February (Viodo) and March (Santa María). There is a sharp decrease of biomass in August and November. Maximum biomass is 905 g/m^2 in Santa María and 744 g/m^2 in Viodo. The contribution of development class III is important in both cases, accounting for 60 % of total biomass according the observations of SHARP (1987) and McLACHLAN *et al.* (1988). The contribution of juvenile classes is less, although in February and March, they make up 30 % of the total in Santa María (Fig. 5b).

Dry weight values per m^2 are similar to those reported from Canada and the U.S.A. (TAYLOR, 1970; 1972; MATHIESON and BURNS, 1975; PRINGLE, 1979) and much higher than those of Ireland (PYBUS, 1977).

Annual net productivity was estimated to be to 1095 g/m^2 in Santa María and 623 g/m^2 in Viodo. Periods of production occur in spring and summer and the periods of losses take place at the end of the summer and autumn.

Gametophyte/Tetrasporophyte ratio

Observations of this ratio were carried out at Viodo and occasionally at Santa María. We found a predominance of tetrasporophytes throughout the year (62 % diploids and 38 % haploids), except for autumn when the densities of both were quite similar (Fig. 6a and b). According to development classes

TABLE 1. — Epiphytic flora on *Chondrus* fronds. Seasonal changes. Presence (+) Scarce (1) Abundant (3)

	June	*July*	*August*	*September*	*October*	*November*	*December*	*January*	*February*	*March*	*April*	*May*
Gelidium latifolium	+	+			+	+	+			+	+	1
Gelidium pusillum			+	+		+	+		+			
Calliblepharis jubata		+		+		+	+			+	+	
Caulacanthus ustulatus							+					1
Mesophyllum lichenoides												+
Champia parvula			+		+					+		1
Lomentaria articulata												+
Chylocladia verticillata												+
Callithamnion hookeri		+										+
Ceramium diaphanum		+										
Ceramium rubrum	1	+	+	2	+							+
Cryptopleura ramosa			+	+	+	+				+	+	+
Polysiphonia denudata		+	+	2	+	+	+					
Pterosiphonia complanata					+	+						
Ectocarpaceae unidentified		+								+		
Sphacelaria fusca												1
Dictyota dichotoma			+	+		+						
Enteromorpha compressa		+										
Enteromorpha ramulosa		2	2		+							
Ulva rigida	+	1	+									

(Fig. 6c, d, e) the general predominance of tetrasporophytes is noteworthy during the entire year; only class III shows a slight dominance of gametophytes in autumn and winter. Ploidy composition in Santa María was similar (55 % of diploids and 45 % of haploids).

Algal epiphytes

They are very scarce or even lacking during the winter and start to appear in spring becoming very abundant on adult fronds during the summer (Table 1). Their abundance decreases during autumn, although the high degree of epiphytism is striking in November, especially on fertile tetrasporophytes with broken tips, which seem to favour the attachment of epiphytes. The most representative species are seasonal and the most outstanding are *Enteromorpha ramulosa*, which can reach lengths of 50 cm, *Ulva rigida, Polysiphonia denudata, Ceramium rubrum, Sphacelaria fusca* and *Champia parvula*.

Chondrus crispus is not a good species for the development of algal epiphytes and, thus, they develop on the adult distal portions —with large foliar surface— and especially in the dichotomies (McLachlan *et al.*, 1989) and on broken portions. These observations coincide with those of Pybus (1977), although the periods of most abundance of algal epiphytes are restricted to the end of spring and the summer. The presence of epiphytes during the rest of the year is limited to mature fronds which are partially broken or torn.

DISCUSSION

The numerous of studies of *Chondrus cripus*, see Pringle and Mathieson (1986), indicate a seasonal growth for both biomass and lenght, each of which reaches a maximum during late spring or summer and a minimum in winter. These pattern are seen in our data but some variations were observed. The great difference between number of fronds of subtidal Canadian populations and intertidal populations growing on our coast could be due to harvesting. This activity, with removal of larger fronds, increases both the number of juveniles as well as production (McLachlan et al., 1989).

The relationship between the seasonality of environmental factors and the phenology of seaweeds is well known in temperate regions. Several of these factors are held responsible for growth. Among them are irradiance, water temperature, nutrients and, in intertidal species, the variables related with the aerial environment, such as temperature, humidity and rainfall; all these are closely related to time of emersion.

There seems to be no agreement as to what factors are responsible for this seasonal pattern. Neish and Fox (1971) state that irradiance is the main factor, Mathieson and Burns (1975) that nutrients are involved and, Prince and Kingsbury (1973a, b) that temperature is the main variable. If, in additiion, we bear in mind that *Chondrus* has a very high tolerance to variations in temperature, salinity and irradiance (MATHIESON and BURNS, 1975; MATHIESON and PRINCE, 1973) the situation becomes even more difficult to interprete. This paper suggests that the growth observed from April on is directly correlated with increases of water temperature, above 15 °C, which are within the optimum range (PRINCE and KINGSBURY, 1973b), as well as the incident energy, while the level of nutrients gives an inverse relationship. The maximum in biomass coincides with levels of nitrates and phosphates close to zero. Taking into account that the response of seaweeds to variation of nutrients is not immediate (CHAPMAN and CRAIGIE, 1977) and that they can use ammonia excretions of animals and bacteria as a nitrogen source (MANN, 1982), it seems unlikely that only nutrient depletion is the cause of discolored thalli and the large losses at the end of summer. Other authors (NIELL, 1976; PYBUS, 1977) support the opinion that the aerial conditions of summer at times of emersion could be responsible for these phenomena. Unfortunately, up to now there is no clear evidence and no new information is supplied by our data.

Finally, regarding the ploidy composition, the populations of *Chondrus crispus* present a great variability ranging from dominance of gametophytes or tetrasporophytes to a wide variety of intermediate situations. Many explanations have been given to justify the predominance of one phase or another (CRAIGIE and PRINGLE, 1978; BATTACHARYA, 1985; MAY, 1986; LAZO *et al.*, 1989). In our study area there is a slight predominance of tetrasporophytes in contrast with the observations of BATTACHARYA (1985) on the coast of Canada, that supports the hypothesis that diploids may be less competitive in the intertidal zone. BARILOTTI (1971) theorized that diploids are always favoured except if the environment select for recessive homozygosity. We don't know what environmental factors could be favouring diploids, because space is not limited (the percentage cover was less than 100 %), the substrate is stable (solid rock) and we assume that there were no differences between mortality at the first stages of development of both diploids and haploids (BATTACHARYA, 1985). Information on a long term basis is needed, as pointed out by MAY (1986) as the holdfast lasts many years, longer than time of study.

ACKNOWLEDGEMENTS

This work was supported by the Spanish Ministry of Science and Education (C.A.I.C.Y.T. Project N.° 2636-83). We are grateful to Dr. J. McLachlan and Dr. J. D. Pringle for helpful suggestions.

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