

Seasonal dynamics and annual production of *Cystoseira crinita* (Fucales: Ochrophyta)-dominated assemblages from the northwestern Mediterranean

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SUMMARY: Algae of the genus *Cystoseira* are the main engineering species on Mediterranean shallow rocky bottoms. *Cystoseira crinita* is an endemic species which grows in shallow and rather sheltered environments throughout the entire Mediterranean Sea. In order to investigate its role in structuring benthic assemblages and as a primary producer, three localities were sampled every two months during one year in Menorca (Balearic Islands). The total biomass of *Cystoseira crinita*-dominated assemblages showed a seasonal pattern mainly due to temporal changes in the biomass of the dominant alga. The assemblages also showed seasonality in their species richness (number of species per sample). Both total biomass and species richness peaked in summer, and their lowest values were recorded in winter. Despite these temporal patterns, *C. crinita*-dominated assemblages from Menorca showed reduced seasonality compared to *C. crinita*-dominated assemblages in other areas in the western Mediterranean, as *C. crinita* specimens kept their branches throughout the entire year. Total annual production of *Cystoseira crinita* branches and cauloids was around 1230 g dwt m⁻², which is higher than that of other *Cystoseira* species living in sheltered areas but much lower than that of *Cystoseira* species growing on exposed shores. Production was highly seasonal, and was highest in spring and null in winter and late summer.

Keywords: annual production, assemblage structure, biomass, *Cystoseira crinita*, seasonality, species richness.

RESUMEN: DINÁMICA ESTACIONAL Y PRODUCCIÓN ANUAL DE LAS COMUNIDADES DOMINADAS POR *CYSTOSEIRA CRINITA* (FUCALES: OCHROPHYTA) DEL MEDITERRÁNEO NOROCCIDENTAL. – Las algas del género *Cystoseira* son las principales especies estructuradoras de hábitat en los fondos rocosos infralitorales mediterráneos. *Cystoseira crinita* es una especie endémica que crece en fondos someros y poco expuestos al oleaje en todo el Mediterráneo. Con la intención de estudiar su papel estructurador en las comunidades bentónicas y como productor primario, se muestrearon tres localidades, cada dos meses durante un año, en Menorca, Islas Baleares. Las comunidades dominadas por *Cystoseira crinita* mostraron un ciclo anual bien establecido en su biomasa total, debido principalmente a los cambios temporales de biomasa del alga *Cystoseira crinita*. Las comunidades también mostraron cambios en su riqueza específica (número de especies por muestra). Tanto la biomasa total como la riqueza específica fueron máximas en verano, mientras sus valores mínimos se obtuvieron en invierno. A pesar de estos patrones temporales, las comunidades de *C. crinita* estudiadas mostraron una estacionalidad menor que la encontrada en otras zonas, puesto que *C. crinita* mantuvo sus ramos durante todo el año. La producción total anual de los ramos y cauloides de *Cystoseira crinita* fue de 1230 g peso seco m⁻², más elevada que la de otras especies de *Cystoseira* de modo calmo, pero muy inferior a las medidas obtenidas en especies de *Cystoseira* que crecen en lugares expuestos. La producción fue marcadamente estacional, con máximos en primavera y con valores nulos en invierno y final de verano.

Palabras clave: biomasa, *Cystoseira crinita*, estacionalidad, estructura, producción anual, riqueza específica.

INTRODUCTION

Algae in the orders Laminariales and Fucales are the main engineering species in sublittoral rocky bottoms of all temperate areas in the world (Ribera *et al.*

1992, Steneck *et al.* 2002). They are very important primary producers in coastal areas (Mann 1973) where they dominate structurally complex and diverse assemblages (Duggins 1980, Reed and Foster 1984, Graham 2004). Moreover, assemblages dominated by Fucales

serve as nursery habitats for some littoral fishes (Aburto-Oropeza *et al.* 2007, Cheminee *et al.* 2010). The majority of shallow rocky temperate coasts are occupied by Laminariales, commonly known as kelps (Dayton 1985, Steneck *et al.* 2002), while in the Mediterranean Sea these areas are occupied by algae of the genus *Cystoseira* (Fucales) (Giaccone 1973, Ballesteros 1992). The particular characteristics of the Mediterranean Sea compared to open temperate oceans, i.e. extremely reduced tides, oligotrophy, relatively high salinity and a high mean summer temperature (Ros *et al.* 1985), probably prevent the growth of kelp beds. The genus *Cystoseira* is present in the northern Atlantic Ocean and in the Mediterranean Sea (Draisma *et al.* 2010), and it is especially diverse in the Mediterranean (ca. 50 species). Different species occupy different habitats depending on depth, degree of exposure to wave action, and other environmental factors (Giaccone 1971, Ballesteros 1992, Sales and Ballesteros 2009). Most of the species of the genus *Cystoseira* are very sensitive to pollution and to other anthropogenic pressures, and they have decreased considerably during the last decades in many areas of the Mediterranean (Cormaci and Furnari 1999, Thibaut *et al.* 2005, Serio *et al.* 2006, Mangialajo *et al.* 2008). All the species of the genus *Cystoseira* except *C. compressa* are included in Annex II of the Barcelona Convention. The seasonal dynamics and annual production of *Cystoseira*-dominated assemblages have been studied by several authors (e.g. Ballesteros 1988a, 1989, 1990a,b, Pizzuto 1999), and have been found to show marked seasonality in the abundance of the dominant species and overall species composition.

Cystoseira crinita is an endemic Mediterranean species that is distributed throughout the entire Mediterranean (Ribera *et al.* 1992, Sales *et al.* 2012). It usually grows in the upper infralittoral zone on both low and intermediately exposed gently sloping rocky bottoms that are often subjected to a high degree of sedimentation (Sales and Ballesteros 2009, 2010). *Cystoseira crinita* dominates very structured assemblages that were originally described as an algal association by Molinier (1960). Historically, shallow, sheltered areas have been preferred zones for human settlements, which has profoundly altered these areas. This, together with the relatively high sensitivity of *C. crinita* to human pressures (Sales *et al.* 2011), makes this species especially vulnerable. Despite the importance of *C. crinita* in structuring assemblages, the seasonal dynamics and productivity of *C. crinita*-dominated assemblages are poorly known. The seasonality of *C. crinita*-dominated assemblages has only been studied at two sites: one in Sicily, Italy (Pizzuto 1999), and one in Catalonia, Spain (Ballesteros 1992). Almost nothing is known about its productivity. In Menorca (Balearic Islands), *C. crinita* is quite abundant in most of the coves and bays from the northern coast of the island, where it dominates complex algal assemblages (Sales and Ballesteros 2009). In terms of species composition

and structure, these assemblages are representative of the *C. crinita*-dominated assemblages from the north-western Mediterranean (Sales *et al.* 2012).

Considering the important role that *Cystoseira crinita* plays in structuring littoral assemblages (Boudouresque 1972, Ballesteros 1992, Pizzuto 1999, Sales *et al.* 2012) and its potential role as a primary producer, it is of interest to study (1) the seasonal variation in species composition and structure of the *C. crinita*-dominated assemblages, and (2) the annual production of these assemblages.

MATERIALS AND METHODS

Study sites

Three study sites were selected on the northern coast of Menorca (Balearic Islands), where assemblages dominated by *Cystoseira crinita* are frequent in shallow (0-1 m depth), rather sheltered areas (Sales and Ballesteros 2009). The selected sites were Cala Barril (40°03'N, 04°01'E), Cala Pregonda (40°03'N, 04°02'E), and Macar de Tirant (40°03'N, 04°05'E) (Fig. 1), which are north-oriented coves that are fairly sheltered and have gently sloping rocky bottoms in the first meter depth.

Environmental characterization

The temperature was measured monthly at each location during the study period (November 2006 - November 2007). Surface seawater samples (3 replicates) were collected monthly from each study location in order to determine the concentration of inorganic dissolved nutrients (phosphates, nitrates and nitrites). Analytical procedures followed Grasshoff *et al.* (1983) using an Alliance Evolution II Autoanalyzer. Two-way analysis of variance (ANOVA) was used to examine differences in inorganic nutrient concentration in seawater among study locations and dates (sampling times). Data were previously log (x+1)-transformed in order to achieve homogeneity of variances. Irradiance values for the study area were obtained from the National Meteorological Agency (AEMET).

Seasonal dynamics of assemblage structure

The species composition and species abundances of *Cystoseira crinita*-dominated assemblages were monitored from November 2006 to November 2007 at the three study locations. Three samples (replicates) were randomly collected every two months from each location, avoiding re-sampling. Each sample consisted of a square surface of 400 cm² from which the whole community (except the encrusting algae) was removed with a hammer and chisel (Boudouresque 1971). This sampling area is equal to the minimum sampling area recommended for sampling Mediterranean infralittoral assemblages (Coppejans 1980, Ballesteros 1992).

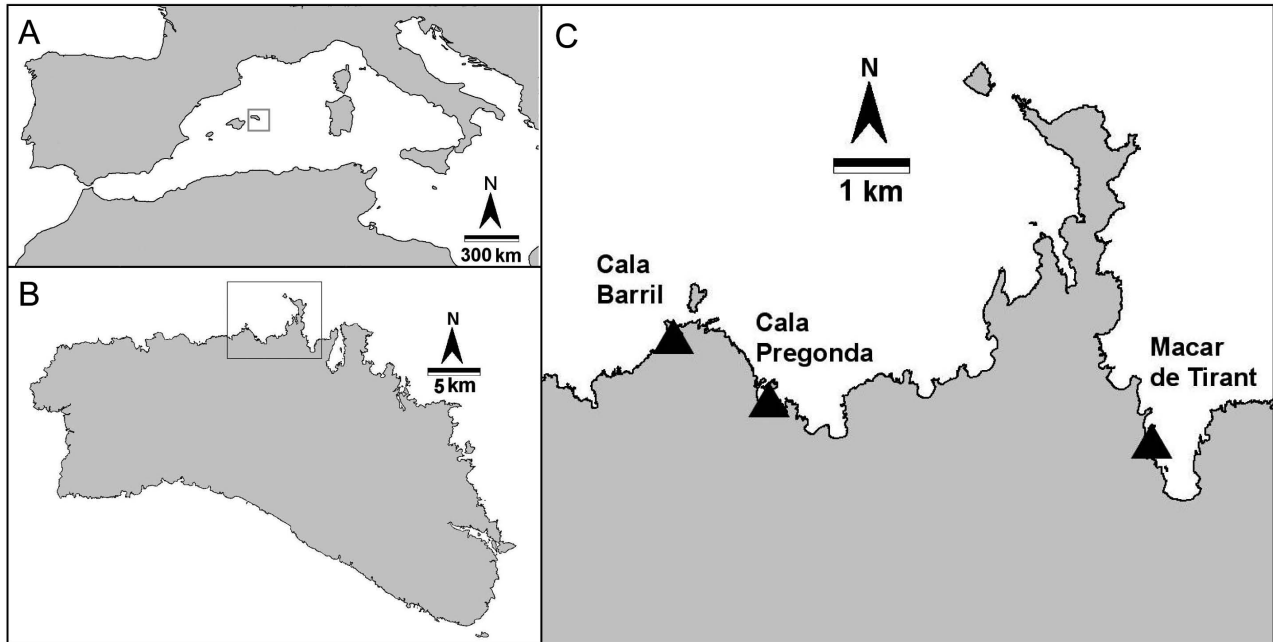


FIG. 1. – Map of the study area showing the locations of the study sites.

In the laboratory, the samples were sorted, and algal and sessile invertebrate species were identified and quantified as horizontal coverage in cm² and biomass (g dwt) following procedures described in Ballesteros (1986). Two biological data matrices were obtained: one with species abundances expressed as coverage in cm² (cover database) and one with species abundances expressed as biomass in g dwt (biomass database).

Non-metric multidimensional scaling (MDS) ordination (Kruskal and Wish 1978) was used to visualize patterns of community similarities among study locations and sampling times. Centroids (Anderson *et al.* 2008) were obtained and represented for each location and sampling time (each one was determined from three replicates). The ordination was performed on the cover database, which was previously transformed to fourth roots in order to reduce the contribution of the most abundant species, especially the dominant *Cystoseira crinita*. The Bray-Curtis similarity index (Bray and Curtis 1957) was used to construct the similarity matrix. A PERMANOVA (Anderson 2001) was also applied to the cover database to test the null hypothesis of no differences among locations and sampling times. A Relate Test against a cyclicity model matrix (Clarke and Gorley 2006) was used to test the changes in community structure according to a seasonal pattern. Two-way ANOVA was used to test for differences in total biomass (taking into account all the organisms in the assemblage), *C. crinita* biomass, and the biomass of accompanying species among study sites and sampling dates. Two-way ANOVA was also used to test for differences in species richness (number of species per sample) and Shannon Diversity indices among study sites and sampling dates (using cover data). All of these variables showed homogeneously distributed

variances and so it was not necessary to transform them in any way.

Annual production

The branch and cauloid production of *Cystoseira crinita* as well as the daily turnover ratio (r) were calculated for each location and time interval (time between each two consecutive sampling times). Branches are not perennial, and so the production of *C. crinita* was calculated by means of its annual biomass cycle using the biomass database previously mentioned. Differences in biomass were calculated for each time interval and interpreted as close estimates of production. However, *C. crinita* cauloids are perennial, and so their production was estimated by randomly choosing and tagging 100 cauloids within the assemblages at Cala Pregonda. Their lengths were monitored every four months during one year and the mean cauloid growth was calculated for each time interval. The relationship between the cauloid length and cauloid biomass was calculated from 100 *C. crinita* cauloids that were collected, measured and dried to a constant weight at 100°C during 48 hours. Growth values were converted to biomass values. The initial cauloid biomass per m² was calculated from data on the density and size structure of *C. crinita* assemblages obtained from measures taken in ten 20×20 cm quadrats randomly placed over the *C. crinita* assemblages at Cala Pregonda. To calculate the daily turnover ratio (r) of both the branches and cauloids, the following formula (Ballesteros 1992) was used:

$$r = \ln \left(\frac{P}{B_1} + 1 \right) \Delta t^{-1}$$

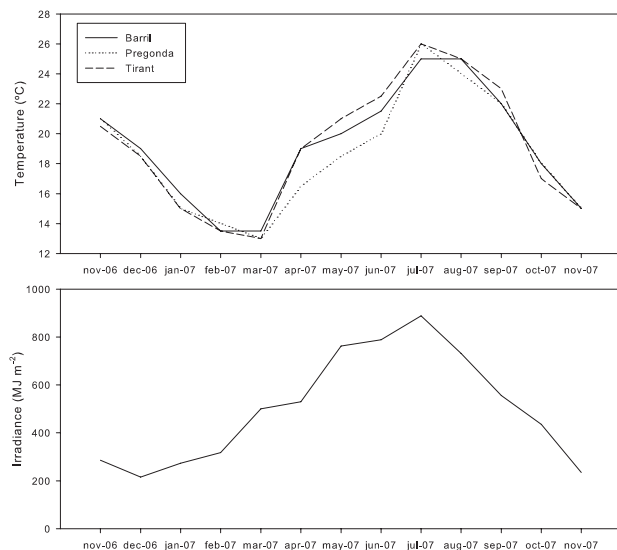


FIG. 2. – Seasonal variation of environmental parameters. Upper panel: temperature values measured monthly in situ at the three study sites during the entire study period. Lower panel: Irradiance values from the study area and for the whole study period obtained from AEMET (Spanish Meteorological Agency).

where P is the production attained during a given time interval (in g dwt), B_1 is the initial biomass (in g dwt), and Δt is the time length of the given interval (in days).

RESULTS

Environmental characterization

Seawater temperature varied between 13°C in March 2007 and 26°C in July 2007 with low variations among sampling locations (Fig. 2). The minimum surface irradiance was recorded in December 2006, with 215 MJ m⁻², and the maximum in July 2007, with 888 MJ m⁻² (Fig. 2). Nutrient concentrations were very low and did not vary significantly among locations and dates, except for the nitrate concentration, which was significantly higher in Cala Pregonda than in the other two locations studied (Table 1). The mean NO₃ concentration (\pm SE) in Cala Pregonda was 0.132 μ M (\pm 0.045), while in Cala Barril it was 0.023 μ M (\pm 0.005) and in Macar de Tirant it was 0.036 μ M (\pm 0.006). The mean PO₄ concentration values (\pm SE) were 0.061 μ M (\pm 0.004) for Cala Barril, 0.081 μ M (\pm 0.010) for Cala Pregonda, and 0.099 μ M (\pm 0.026) for Macar de Tirant. Finally, mean NO₂ concentrations (\pm SE) were 0.164 μ M (\pm 0.015) in Cala Barril, 0.246 μ M (\pm 0.182) in Cala Pregonda, and 0.210 μ M (\pm 0.025) in Cala Tirant.

Seasonal dynamics of assemblage structure

A total of 79 species were recorded from the samples, consisting of 2 cyanobacteria, 71 macroalgae (Chlorophyta, Ochrophyta, Rhodophyta) and 6 sessile invertebrates. Quantified species lists are shown in

TABLE 1. – Results of the two-way ANOVA for comparing nutrient concentrations among study locations and sampling dates. Bold: significant P values.

Effect	SS	d.f.	MS	F	P
PO₄					
Location	0.028	2	0.014	1.386	0.256
Date	0.108	12	0.009	0.897	0.554
Location×Date	0.275	24	0.011	1.144	0.320
Error	0.782	78	0.010		
NO₃					
Location	0.276	2	0.138	5.189	0.008^a
Date	0.429	12	0.036	1.348	0.210
Location×Date	0.543	24	0.023	0.852	0.661
Error	2.071	78	0.023		
NO₂					
Location	0.13	2	0.065	0.150	0.861
Date	4.47	12	0.372	0.859	0.591
Location×Date	12.01	24	0.500	1.154	0.310
Error	33.807	78	0.433		

^a Tukey test: Pregonda > Barril and Tirant ($P < 0.05$)

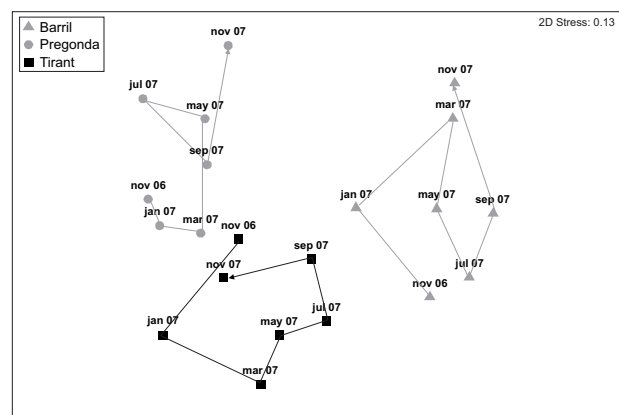


FIG. 3. – MDS ordination of the samples showing centroids for each study site and sampling time ($n = 3$). Seasonal trajectories are indicated by arrows for each study site.

Annex 1. The canopy stratum was always dominated by *Cystoseira crinita*, sometimes accompanied by a few individuals of *Cystoseira spinosa* var. *tenuior*. The most characteristic accompanying species were the coralline algae *Haliptilon virgatum* and *Jania rubens*, growing either as epiphytes of *C. crinita* or in the understory of the assemblage. Other epiphytes that were frequently found growing over *C. crinita* were the brown algae *Dictyota mediterranea* and *Sphacelaria cirrosa*, the red algae *Herposiphonia secunda* and *Dipterosiphonia rigens*, and the cyanobacteria *Calothrix confervicola* and *Symploca hydroides* (Annex 1). In the understory, the most frequent species were *Corallina elongata* and the green algae *Cladophora prolifera* and *Dasycladus vermicularis*. The assemblage was not observed to change greatly during the year. *Cystoseira crinita* kept its branches throughout the entire year; however, growth of new branches was observed during spring. Only a few accompanying species showed a clear maximum abundance in summer and autumn (e.g. *Dictyota mediterranea* and *Symploca hydroides*),

TABLE 2. – Results of PERMANOVA analysis of community structure (cover database) for the factors Location and Date (fixed factors). **Bold:** significant *P* values; **P* < 0.05.

Source of variation	df	MS	F	<i>P</i>
Location	2	9012.10	15.5130	0.0001
Date	6	1987.90	3.4219	0.0001
Location×Date	12	890.47	1.5328	0.0014
Residual	42	580.93		
Total	62			

Significant *a posteriori* comparisons for factor Date in each Location: Cala Barril: nov06-nov07 (*); Cala Pregonda: Jan07-Nov07 (*), Sep07-Nov07 (*); Macar de Tirant: Nov06-Mar07 (*), Jan07-Mar07 (*), Jan07-Jul07 (*), Jan07-Sep07 (*).

TABLE 3. – Results of two-way ANOVA tests for determining differences in total biomass, biomass of *C. crinita*, biomass of companion species, number of species per sample, and Shannon diversity, among locations and sampling times. **Bold:** significant *P* values; **P* < 0.05, ** *P* < 0.01, ****P* < 0.001. Abbreviations: BM, biomass; B, Cala Barril; P, Cala Pregonda; T, Macar de Tirant.

Source of variation	df	MS	F	<i>P</i>
Total BM				
Location	2	477	1.129	0.333
Time	6	2063	4.879	0.001^a
Location×Time	12	565	1.336	0.235
Error	42	423		

^aTukey test: Jan07 < Jul07 (***), Mar07 < Jul07 (**), Jul07 > Nov07 (**)

BM of *C. crinita*

Location	2	1634	5.639	0.007^b
Time	6	1859	6.414	0.000^c
Location×Time	12	521	1.799	0.080
Error	42	290		

^bTukey test: B>T

^cTukey test: Jan07<Jul07 (***), Mar07<Jul07 (***), Jul07>Nov07 (**)

BM companion sps.

Location	2	354.4	4.791	0.013^d
Time	6	18.8	0.254	0.955
Location×Time	12	75.9	1.025	0.444
Error	42	74.0		

^dTukey test: B<T

No. sps. per sample

Location	2	19.00	1.474	0.241
Time	6	58.62	4.548	0.001^e
Location×Time	12	20.56	1.595	0.130
Error	42	12.89		

^eTukey test: Nov06 < Sep07 (*), May07 > Nov07 (*), Sep07 > Nov07 (**)

Shannon diversity

Location	2	0.771	11.49	0.000^f
Time	6	0.057	0.85	0.538
Location×Time	12	0.075	1.12	0.369
Error	42	0.067		

^fTukey test: T>B,P

while most of the other species showed erratic changes in abundance over the year (see Annex I).

The MDS ordination (Fig. 3) separated the assemblages primarily by location and secondarily by sam-

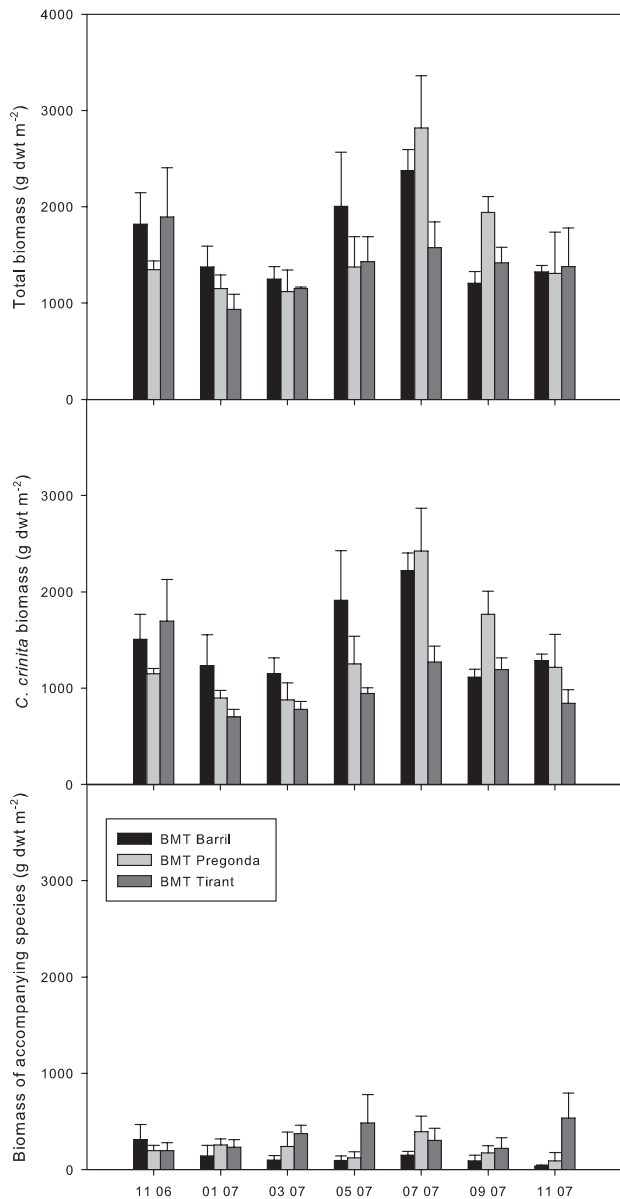


FIG. 4. – Mean biomass values (+ 1 SE) of different components of the studied assemblages for each sampling time and location.

pling time. However, both location and sampling time were significant factors in determining the composition and structure of *C. crinita* assemblages (PERMANOVA, *P*=0.0001, see Table 2). The seasonal trajectory, drawn for each location in Figure 3, indicated cyclicity only in the location Macar de Tirant (significant Relate Test: $\text{Rho}=0.387$, *P*=0.0001). The trajectories followed by the assemblages from Cala Pregonda and Cala Barril showed erratic changes tending to an upper position in the MDS from November 2006 to November 2007 (no significant Relate Tests; Cala Pregonda: $\text{Rho}=0.186$, *P*=0.097; Cala Barril: $\text{Rho}=0.112$, *P*=0.0526).

Seasonality was observed for the total biomass of the assemblage, and maximum values were found in summer (July) and minimum values at the end of win-

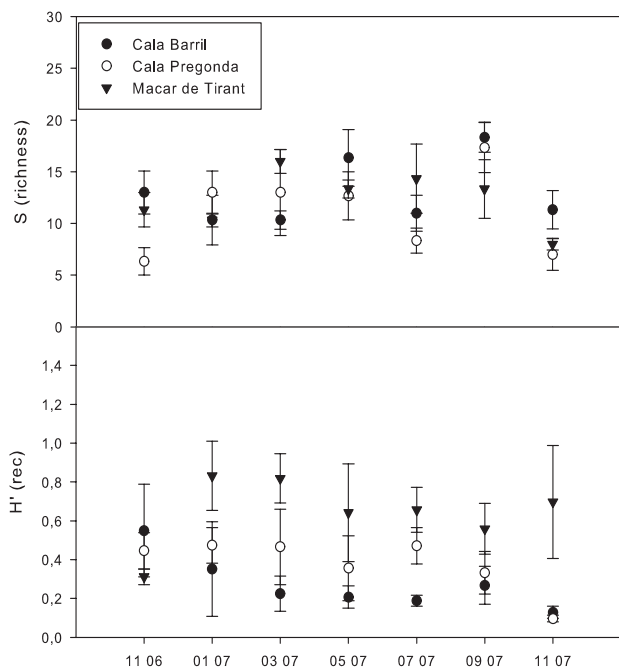


FIG. 5. – Mean richness (number of species per sample) and Shannon diversity (± 1 SE) for each sampling time and location.

ter (March) (ANOVA, $P < 0.05$; see Table 3 and Fig. 4). The biomass of the dominant species (*C. crinita*) was also significantly higher in summer than in winter; and this parameter also differed among locations with significantly higher values in Cala Barril than in Macar de Tirant (ANOVA, $P < 0.05$; see Table 3 and Fig. 4). The biomass of companion species differed significantly among locations, with higher values in Macar de Tirant than in Cala Barril, but did not differ among sampling times. ANOVA indicated significant differences in richness (number of species per sample) among sampling times, with maximum values in late summer (September) and minimum values in early winter (November) (Table 3, Fig. 5). No seasonal pattern was found for Shannon diversity, but significant differences were found for this parameter among sampling locations, with significantly higher values in Macar de Tirant than in Cala Pregonda and Cala Barril (Table 3, Fig. 5).

Annual production

The mean annual branch production of *C. crinita* was 962.1 g dwt m^{-2} , and the mean annual cauloid production of *C. crinita* was 267.6 g dwt m^{-2} (Table 4).

TABLE 4. – Annual production of *C. crinita* branches and cauloids. t: time (days), B_2 : biomass (g dwt m^{-2}) at the end of the period, B_1 : biomass at the beginning of the period, P: production (g dwt m^{-2}), r (daily biomass turnover ratio).

Location	Period	t	B_2	B_1	P	r
Branches						
Cala Barril	14 Oct 06 - 09 Jan 07	87	663.7	899.9	0.0	0.000
	10 Jan 07 - 23 Mar 07	72	774.2	663.7	110.5	0.002
	24 Mar 07 - 24 May 07	61	1348.9	774.2	574.7	0.009
	25 May 07 - 27 Jul 07	63	1434.9	1348.9	86.0	0.001
	28 Jul 07 - 21 Sep 07	55	690.4	1434.9	0.0	0.000
	22 Sep 07 - 22 Nov 07	61	802.5	690.4	112.0	0.002
	Annual production				883.3	
Cala Pregonda	10 Nov 06 - 08 Jan 07	59	402.6	630.7	0.0	0.000
	09 Jan 07 - 03 Apr 07	84	545.9	402.6	143.4	0.004
	04 Apr 07 - 22 May 07	48	922.7	545.9	376.8	0.011
	23 May 07 - 20 Jul 07	58	1737.5	922.7	814.8	0.011
	21 Jul 07 - 17 Sep 07	58	1155.0	1737.5	0.0	0.000
	18 Sep 07 - 20 Nov 07	63	713.0	1155.0	0.0	0.000
Annual production				1334.9		
Macar de Tirant	09 Nov 06 - 13 Jan 07	65	92.2	803.8	0.0	0.000
	14 Jan 07 - 04 Apr 07	80	315.5	92.2	223.3	0.015
	05 Apr 07 - 23 May 07	48	497.5	315.5	182.0	0.009
	24 May 07 - 23 Jul 07	60	760.4	497.5	263.0	0.007
	24 Jul 07 - 18 Sep 07	56	512.5	760.4	0.0	0.000
	19 Sep 07 - 14 Nov 07	56	255.4	512.5	0.0	0.000
Annual production				668.3		
Mean annual branch production				962.1		
Cauloids						
Cala Pregonda	01 May 07 - 01 Sep 07	123	790.7	672.0	118.7	0.0013
	02 Sep 07 - 01 Jan 08	121	885.7	790.7	95.0	0.0009
	02 Jan 08 - 01 Apr 08	90	915.5	885.7	29.8	0.0004
	02 Apr 08 - 02 May 08	30	939.6	915.5	24.1	0.0008
Mean annual cauloid production				267.6		

TABLE 5. – Structural parameters of different *Cystoseira*-dominated assemblages from the northwestern Mediterranean (A: sampling area in cm²; N: number of species per sample; B: biomass in g dwt m⁻²; P gdw: annual production of the dominant species in g dwt m⁻² y⁻¹; P gC: annual production of the dominant species in g C m⁻² y⁻¹).

Dominant species	A	N	B	P gdw	P gC	Reference
<i>Cystoseira crinita</i>	400	13	1532.9	1230	307.5 ^a	this study
<i>Cystoseira crinita</i>	400	62	2141.7	1127	304.9	Ballesteros (1992)
<i>Cystoseira crinita</i>	1600	31	---	---	---	Pizzuto (1999)
<i>Cystoseira caespitosa</i>	784	105	1438.8	630	233.9	Ballesteros (1990a)
<i>Cystoseira balearica</i>	250	84	---	---	---	Verlaque (1987)
<i>Cystoseira mediterranea</i>	784	51	1698.6	2600	908.9	Ballesteros (1988a)
<i>Cystoseira stricta</i>	250	36	---	---	---	Verlaque (1987)
<i>Cystoseira zosteroides</i>	1600	132	1424.9	70	24.2	Ballesteros (1990b)

^aValue estimated from the production in g dwt m⁻² multiplied by the factor 0.4 (Ballesteros 1989).

Branch production was highly seasonal with maximum values in spring, and null values in winter and at the end of summer. The daily turnover ratio was highest in late winter and spring.

DISCUSSION

Seasonal dynamics of assemblage structure

Although the assemblages dominated by *C. crinita* are highly structured (Molinier 1960, Boudouresque 1972, Ballesteros 1992, Pizzuto 1999), they seem to be less rich in species than assemblages dominated by other *Cystoseira* species from the NW Mediterranean (Table 5). This could be related to the particular places where these assemblages occur, which are usually exposed to a high degree of sediment abrasion.

A seasonal pattern was found in the structure of the *C. crinita*-dominated assemblages, mainly related to seasonal variation in *C. crinita* biomass, in close coincidence with seasonal temperature variation (minimum values in March and maximum values in July). Seasonality was also detected in species richness, which had a minimum peak in January, coinciding with minimum values of irradiance, and a maximum peak in September when the water is still warm but *C. crinita* biomass has decreased. Indeed, light intensity and temperature are usually the most important factors determining the seasonal patterns of growth and primary production of seaweeds (Chesire *et al.* 1996). The seasonal patterns found in this study agree with those described for other phytobenthic Mediterranean assemblages (Ballesteros 1990a), with the maximum biomass in late spring and the maximum species richness in autumn. Compared to *C. crinita*-dominated assemblages from other areas in the Mediterranean, *C. crinita*-dominated assemblages from Menorca show reduced seasonality as *C. crinita* plants keep their branches throughout the entire year, similarly to what Pizzuto (1997, 1999) found in assemblages from Sicily. In contrast, Sauvageau (1912) and Ballesteros (1992) described almost complete loss of branches in winter for *C. crinita* from Catalonia and the Albères coast (France). Populations from Mallorca (Balearic islands) and Algiers (southern Mediterranean) seem to display a marked seasonality, and cauloids are al-

most devoid of branches from April to August, with the highest development of branches at the end of winter (Sauvageau 1912, Gómez *et al.* 1982). These differences in seasonality may be due to environmental differences already described between the northern Mediterranean and the central and southern Mediterranean areas (e.g. differences in temperature and trophic regime; Sales *et al.* 2012) or to local environmental conditions.

Although seasonality was found for some structural parameters of the assemblage, location was an even more important factor in determining community structure, as evidenced by the MDS plot. Important variations in local factors, like exposure degree, morphology of the coast and nutrient concentration, could explain this pattern. The *C. crinita*-dominated assemblages from Cala Pregonda and Cala Barril showed erratic temporal trajectories in the MDS plot, tending to an upper position from November 2006 to November 2007. This pattern closely agrees with the model presented by Ballesteros (1990c), suggesting that the assemblages tend to a different state with multiple intermediate stable points. In contrast, in Macar de Tirant the temporal trajectory described by the assemblages was circular and returned back to the original state after one year. In this location, assemblages were greatly desiccated in January 2007 due to high atmospheric pressure that affected the sea water level at the study locations. This suggests that the assemblage was able to recover from this natural disturbance in just one year.

Annual production

The annual production of the studied *C. crinita*-dominated assemblages was lower than that estimated for assemblages dominated by *Cystoseira mediterranea* that grow in exposed areas, but considerably higher than that of assemblages dominated by *Cystoseira caespitosa* (growing in sheltered areas) and assemblages dominated by *Cystoseira zosteroides* (from deeper areas; Table 5). This pattern is probably due to the influence of hydrodynamism, which usually increases primary production (Leight *et al.* 1987). Compared to other abundant and well-known Mediterranean macrophytes, such as the seagrasses

Posidonia oceanica (estimated production of 238-714 g dwt m⁻² y⁻¹; Pergent *et al.* 1994) and *Cymodocea nodosa* (usually 160-820 g dwt m⁻² y⁻¹ but up to 2470 g dwt m⁻² y⁻¹; Agostini *et al.* 2003), or other algae such as *Rissoella verruculosa* (1241 g dwt m⁻² y⁻¹; Ballesteros 1991a), *Halimeda tuna* (680 g dwt m⁻² y⁻¹; Ballesteros 1991b) and *Codium vermilara* (295 g dwt m⁻² y⁻¹; Ballesteros 1988b), the primary production values estimated for *C. crinita*-dominated assemblages in this study (1230 g dwt m⁻² y⁻¹) are amongst the highest. Moreover, it should be considered that the results on annual production presented in this paper are an underestimation, as biomass losses due, for example, to herbivory and storms have not been taken into account (Golléty *et al.* 2008).

The annual production values estimated for *Cystoseira*-dominated assemblages are comparable to other marine systems around the world that are considered very productive, as for example kelp beds and seagrasses (Mann 1973 and references therein). However, while the role of *Cystoseira* in structuring ecosystems is well recognized (e.g. Bulleri *et al.* 2002), much less attention has been paid to its role in ecosystem carbon budgets. We know of only one study in which *Cystoseira balearica* is demonstrated to be a source of carbon for species inhabiting adjoining ecosystems (Cardona *et al.* 2007).

Conclusion

In conclusion, we found a seasonal pattern for the structural and functional parameters of *Cystoseira crinita*-dominated assemblages. The seasonality is mainly due to the change in biomass of the dominant species— with minimum values between January and March and maximum values in July —and to the variation in species richness— with minimum values in November and a secondary minimum peak in July, and maximum values in September. Variation in *C. crinita* biomass coincides with seasonal temperature variation, while fluctuations in species richness agree with the seasonal pattern in irradiance combined with a negative effect of *C. crinita* biomass in July. Although the mean annual production values of the assemblages dominated by *C. crinita* are lower than those of assemblages dominated by *Cystoseira* species growing in exposed zones, they are still comparable to some of the most productive marine systems.

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ANNEX 1 (cont.). – Mean species cover (in horizontal cm²) at each locality and sampling time.

	Cala Barril			Cala Pregonda			Macar de Tirant						
	Nov	Jan	Mar	May	Jul	Sep	Nov	Jan	Mar	May	Jul	Sep	Nov
<i>Jania rubens</i> v. <i>comiculata</i> (Linnaeus) Yendo				0.3									
<i>Laurencia</i> cf. <i>chondrioides</i> Boergesen						0.1							
<i>Laurencia</i> cf. <i>minuta</i> Vandermeulen et al.						0.1							
<i>Laurencia minuta</i> subsp. <i>scammacciae</i> Furnari & Cormaci			0.1										
<i>Laurencia</i> sp.											0.1		
<i>Lophosiphonia cristata</i> Falkenberg													
<i>Monosporus pedicellatus</i> (Smith) Solier							0.1						
<i>Nitophyllum micropunctatum</i> Funk										0.2			
<i>Padina pavonica</i> (Linnaeus) Thivy	3.4			0.4	0.6	0.2					0.3	0.5	
<i>Peyssonnelia harveyana</i> Crouan & Crouan ex C. Agardh	0.1												
<i>Peyssonnelia rubra</i> (Greville) J. Agardh				0.1		0.1							
<i>Peyssonnelia</i> sp.						3.3							0.2
<i>Peyssonnelia squamaria</i> (Gmelin) Decaisne													
<i>Phyllophora crispa</i> (Hudson) Dixon			0.3										
<i>Polysiphonia furcellata</i> (C. Agardh) Harvey											0.1		
<i>Polysiphonia opaca</i> (C. Agardh) Morris & De Notaris													
<i>Polysiphonia scopulorum</i> Harvey		0.1											
<i>Polysiphonia subulifera</i> (C. Agardh) Harvey													
<i>Rhodophyllis divaricata</i> (Stackhouse) Papenfuss							0.2						
<i>Rytiphlaea tinctoria</i> (Clemente) C. Agardh				0.9		0.7							
<i>Spermothamnion repens</i> (Dillwyn) Rosenvinge												0.1	
<i>Sphaelaria cirrosa</i> (Roth) C. Agardh		0.1		0.7	0.1	0.2						2.4	
<i>Taonia atomaria</i> (Woodward) J. Agardh				2.2	0.3								
<i>Ulva clathrata</i> (Roth) C. Agardh							0.1						
<i>Ulva compressa</i> Linnaeus													
<i>Valonia utricularis</i> (Roth) C. Agardh	1.8	0.8	0.1	0.1	1.5	3.7	3.0						
<i>Womersleyella setacea</i> (Hollenberg) R.E. Norris						1.4							
<i>Wuermannia miniata</i> (Sprengel) J. Feldmann & Hamel													
Sessile macroinvertebrates													
<i>Amathia lendigera</i> (Linnaeus, 1758)													3.2
<i>Arca noae</i> (Linnaeus, 1758)													0.4
<i>Campanularia</i> sp.		0.1											
<i>Caryophyllia inornata</i> (Duncan, 1878)													
Hydroids													
<i>Mytilus galloprovincialis</i> (Lamarck, 1819)	0.1		0.1	0.1			0.1				0.1	0.3	0.1
<i>Turbicellepora magnicostata</i> (Barroso, 1919)													