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Structure of an epiphytic hydroid community on *Cystoseira* at two sites of different wave exposure*

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SUMMARY: Epiphytism is a strategy by which opportunistic species such as hydroids, escape the intense levels of competition in marine hard bottom communities. Species of the macroalgae *Cystoseira* have a seasonal turnover of the frond, and we hypothesise that epiphytic hydroids colonising such an unstable substrate might show some degree of specialisation. Here the first systematic study on hydroid-*Cystoseira* communities is presented. In particular, the seasonal and spatial distribution of epiphytic hydroids on three species of *Cystoseira* at two sites of different wave exposure at Porto Cesareo (Ionian Sea/Italy) were investigated. Thirty-two hydroid species were recorded which are well known from other substrates and thus are not specific to *Cystoseira*; dominant species were all thecates. The influence of biological factors such as competition and the structure and abundance of the host, seem to have little influence on the hydroid community. The factors of greatest influence were mostly abiotic: sedimentation rate, nutrient levels, temperature and most especially water movement. The importance of water movement was evident in the higher colonisation of algal stems, higher hydroid frequency, larger colonies, reduced colony height, species composition, and distribution on the stems at the wave-exposed site.

Key words: epiphytic hydroids, water movement, *Cystoseira*, Mediterranean.

INTRODUCTION

The environmental factors limiting species distribution in marine benthic communities are temperature, light, water movement and substrate availability, among others. Temperature depends on water currents, depth and season, and influences nutrition, growth, life cycles and reproduction. Water movement supplies the organisms with food, nutrients and dissolved gases, prevents accumulation of sediments, and disperses waste products and larvae, but also acts as a mechanical stress factor. Many organisms have evolved morphological adaptations to withstand such stress. These structural responses are

reflected by the different distribution of families, species, or morpho-types due to differences in water movement intensity (Riedl, 1966). Among sessile organisms increasing intensity of water movement induces smaller size, lower colony height, higher population density, and a morphology that withstands high mechanical stress (Riedl, 1971; Boero, 1981b, 1984). The distribution of adults is also the result of competition and settlement behaviour, which is regulated by larval substrate choice (Hayward, 1980).

To avoid competition for space a variety of strategies have evolved. One of the most common of these strategies is epiphytism, which reduces competition because fewer species are encountered and continuous growth of the host produces new substrate for

less competitive opportunistic species (Seed, 1985). However, compared to living directly on rock, using plants as a substrate limits survival because of the turnover of host tissue and higher mechanical stress due to water movement and the flexibility of the substrate. Therefore an epiphytic life style requires specific adaptations (Seed, 1985), like fast growth to a small body size, early sexual or asexual reproduction, and a short life span (Coma *et al.,* 1992).

Hydroids are among the first colonisers of newly exposed hard substrates and often compete poorly with other sessile organisms (Gili and Hughes, 1995). Most hydroids are substrate generalists, but several species grow on a limited range of surface types. They are especially abundant on seaweeds and their distribution on these hosts is due to different preferences for various aspects of the physical environment, notably water movement and sediment deposition, and substrate choice by larvae, both between and within individual plants (Seed, 1985). The choice appears to be related to both the chemical nature and the structure and texture of the plant surface (Katô *et al.,* 1975; Seed, 1985). Compared to other sessile invertebrates, hydroids grow fast and have a short life span. Together with their, mostly, asexual method of reproduction, these characteristics make them successful epiphytes.

The different hydroid species differ in several features, like reproduction, dispersal and morphology. Thecate hydroids are able to withstand higher mechanical stress than athecates, because of their protective theca (Riedl, 1966). All hydroids have a mainly sessile polyp stage in their life cycle, but many species have a life cycle involving a free-living medusa stage, which can live for several months in the plankton before reproducing sexually. Although reproductive strategy does not seem to influence greatly the colonisation capabilities of a species (Boero, 1984), in epiphytic communities, suppression of the medusa stage and reduction in the frequency of sexual reproduction is common (Boero, 1987).

Among previous studies on epiphytic hydroids the most substantial are those on *Posidonia oceanica* (Boero, 1981a; Garcia Rubies, 1987), *Halimeda tuna* (Llobet *et al.,* 1991), *Amphibolis* (Watson, 1992), *Sargassum* (Nishihira, 1966), *Fucus serratus* (Seed *et al.,* 1981) and *Laminaria* (Schultze *et al.,* 1990). Most of these investigations have been carried out on hydroids that settle on seagrasses with two-dimensional leaves or algae with laminar fronds, which facilitate the quantification and study of the different epiphytes.

Dendroid seaweeds of the genus *Cystoseira* (Fucales, Phaeophyceae) are very abundant in the Mediterranean Sea, growing from the surface down to 100 m depth. Because species distribution depends on wave-exposure, depth and water quality, they are good descriptors of the zonation of the photophilous vegetation on hard bottom substrates (Amico *et al.,* 1985). Species of *Cystoseira* also differ in their morphology, surface characteristics of their stems and in their chemistry (Amico, 1995). As they belong to the hemiphanerophycean brown algae, they have a seasonal turnover of tissue. Their phylloids and branches of higher order are shed in the unfavourable season, usually winter, while the holdfast and primary branches persist (Cormaci, 1995). Therefore this substrate is not always available for epiphytes during the year. Epiphytic algae and other organisms on *Cystoseira* have been studied by Arrontes (1990), Otero-Schmitt and Pérez-Cirera (1996) and Russo (1997), while previous studies of hydroids on *Cystoseira* (e.g. Riedl, 1966) provide only scattered observations.

Here, the first systematic investigation of epiphytic hydroids on *Cystoseira* is presented. In particular, the seasonal and spatial distribution of epiphytic hydroids on three species, *Cystoseira amentacea* Bory, *C. barbata* (Goodenough et Woodward) and *C. compressa* (Esper), at two sites of different wave exposure on the rocky shore of Porto Cesareo (Ionian Sea/Italy) was studied. The following questions were addressed: 1) what are the characteristics of the hydroid community growing on *Cystoseira*? 2) Is there seasonality? 3) Does exposure to wave action influence the *Cystoseira*-hydroid community structure? 4) Do the characteristics of the algal species influence the hydroid communities? 5) Do differences in morphology, such as the presence or absence of a theca influence the distribution of hydroid species epiphytic on *Cystoseira*?

METHODS

The study was carried out on the rocky shore of the Ionian Sea at Porto Cesareo/Italy between July 1996 and July 1997. Algal stems were collected by SCUBA at 0.5, 2 and 3 m depth along four transects at two sites of different wave-exposure. For depth and transect, 5 stems of each of the three species of *Cystoseira* (*C. barbata, C. compressa, C. amentacea*) were collected within an area of 50x50 cm. Samples were taken monthly, weather conditions

permitting, and on each sampling date water temperature was measured. Samples were examined under a binocular.

The following data were taken for each algal stem: a) maximal stem length (cm), as a measure for the amount of substrate available and the seasonality of the algae; b) the hydroid species present; c) estimated hydroid colony size, i.e. abundance of the hydroid colonies on the stem (1: present, 2: abundant, 3: very abundant (Boero and Fresi, 1986)) where all polyps of the same species on the stem were assumed to belong to the same colony; d) distribution of the hydroid colonies on the stem (1: stipe and holdfast, 2: inner or intermediate part of the stem, 3: outer part of the stem (Arrontes, 1990)). The following diversity indices were calculated for the hydroid communities epiphytic on the stems of the three species of *Cystoseira* and from the two sites. Community diversity was measured by species number, Shannon-Wiener index of diversity (H'),

$$H' = - \sum_{i=1}^{s} p_i \ln p_i,$$

where S = number of species and p_i = proportion of total sample belonging to ith species of total algal stems, and Pielou's index of evenness (J), $J = H' / \ln S$, where H' = Shannon-Wiener index and S = number of species (Krebs, 1989). These two indices were tested for significance by a randomisation test (Solow, 1993). Species dominance was measured by Simpson's dominance index (I_{dom}) (Watson, 1992).

Ordination by Canonical Correspondence Analysis (CCA) (Ter Braak, 1986) was used to summarise the variation in species composition and frequency related to site, including their environmental variables, and season. The environmental variables were water depth (m), water temperature (°C), algal stem length (cm), number of algal stems collected, percentage of algal stems colonised, degree of algal structure (1: low structured, smooth surface; 2: high structured, smooth surface; 3: high structured, rugose surface), and dummy variables for exposed/sheltered and the three species of *Cystoseira*. As a measure of goodness of the ordination, species-environment correlations for the first two ordination axes were used. Significance levels of the ordinations were computed by a Monte Carlo permutation test. Ordination analysis and Monte Carlo permutation test were computed using the CANOCO program package developed by Ter Braak (1988).

RESULTS

Thirty-two hydroid species, twelve athecate and twenty thecate species, were recorded on the three species of *Cystoseira* (Table 1). Nine species have a free-living medusa, three have liberable eumedusoids, and twenty have fixed gonophores.

Hydroid abundance and distribution

The number of hydroid species varied from zero to seven per algal stem. Most stems from the wave-exposed site were colonised by one to three species, whereas stems from the sheltered site were mostly colonised by zero or one species. With a maximum of four species per stem, *C. compressa* was colonised by fewer species per stem than the other species of *Cystoseira*, both with maximal seven species per stem.

The percentage of stems colonised by at least one hydroid ranged during the year from 15% to 100% and was typically higher at the exposed site than at the sheltered one (Fig. 1). Colonisation was highest in autumn, but declined in winter/spring at the sheltered site, especially on *C. compressa*. This decline in colonisation correlates with the decline of algal stem length. *C. compressa* was on average less colonised than *C. barbata* and *C. amentacea*.

The abundance of the hydroid colonies on a single algal stem (Table 2a) belonged mostly to the categories 1 (present) and 2 (abundant). The difference of colony-abundance on the three species of *Cystoseira* was significant between the hydroids from the exposed site (Chi-square Test: p=0.004) and the thecates from both sites (p=0.008, p=0.003), but not between hydroids from the sheltered site or between athecates (p-value between 0.05 and 0.16). The differences between sites were always significant (Chi-square Test: p<0.0001). At the wave-exposed site more colonies belonged to category 3 (very abundant) than at the sheltered site.

The general distribution of the hydroids on the algal stem is shown in Table 2b. The central parts (category 2) of the algal stems were generally the most evenly colonised ones. The outer parts (category 3) showed the lowest colonisation, especially at the wave-exposed site. At the sheltered site the athecate hydroids were primarily distributed between the central parts of the stem and its base, whereas the thecate species were more often distributed on the central and outer parts. The differences between the sites and athecates/thecates were significant (Chi-square Test: p<0.0001).

TABLE 1. – Hydroid species recorded on *Cystoseira*. Specimens of *Aglaophenia* indet. were not identifed at species level mostly because of their small size; specimens of *Clytia* sp. belong either to *Clytia hemisphaerica* or perhaps a new species of *Clytia*. x: present, f: fertile, p: asexual propagules; g: fixed gonophores, m: medusae, mg: liberable eumedusoids or swimming gonophores; E: endemic, MA: Mediterranean Atlantic, B: boreal, TA: tropical Atlantic, IP: Indo-Pacific, CT: circumtropical, C: cosmopolitan, nc: non classifiable. (after Boero and Bouillon, 1993)

Nº species		life cycle	zoogeogr. distrib.	exposed site							sheltered site							
				July '96	September	October	February	April	June	July '97	July '96	September	December	January	February	April	May	July '97
1	*Clava multicornis* (Forskal, 1775)	g	B		x								x	x	x			
2	*Eudendrium glomeratum* Picard, 1952	g	CT?												x	x		
3	*Eudendrium motzkossowskae* Picard, 1952	g	TA	x	x	x	x	x			x	x	x	x	x	x	x	x
4	*Eudendrium ramosum* (L., 1758)	g	C									x						x
5	*Hydractinia fucicola* (M. Sars, 1857)	g	MA	x	x	x	x	x				x	x		x	x	f	x
6	*Cladonema radiatum* Dujardin, 1843	m	CT												x			
7	*Coryne muscoides* (L., 1761)	g	MA		f	f	x		f		x	f	x	x	f	x	x	x
8	*Coryne pusilla* Gaertner, 1774	g	B									x			x			
9	*Sarsia producta* (Wright, 1858)	m	TA					x										
10	*Ectopleura wrighti* Petersen, 1979	m	E									x				x		
11	*Cladocoryne floccosa* Rotch, 1871	g	CT		x							x	x	x	x	x	x	x
12	*Zanclea* sp. see Gravili *et al.*, 1996	m						x					x	x	x			
13	*Eirene viridula* (Péron and Lesueur, 1810)	m	IP					x	x							x		
14	*Mitrocoma annae* Haeckel, 1864	m	E												x			
15	*Anthohebella parasitica* (Ciamician, 1880)	mg	nc					x	x									x
16	*Halecium nanum* Alder, 1859	g	TA					x	x	x				x	x	x		x
17	*Halecium pusillum* (M. Sars, 1857)	g	TA	p	f/p	x	p	p	p	x	p	f	x	x	p		x	x
18	*Hydrodendron mirabile* (Hincks, 1868)	g	MA					x	x			x			x	x		
19	*Aglaophenia octodonta (Heller, 1868)*	g	MA		x	f	f	f	x	x	x	f	x		x	f	f	x
20	*Aglaophenia pluma* (L., 1758)	g	C					f	f	x		x				x	x	
21	*Aglaophenia tubiformis* (Marktanner-Turneretscher, 1890)	g	MA					f	f	x	x	x	x	x	x	x	x	x
22	*Aglaophenia* indet.	g		x	f	x	x	x	x	x	x	x						x
23	*Kirchenpaueria* sp.	g																x
24	*Ventromma halecioides* (Alder, 1859)	g	C	x	x	x	x	x	x	x	x	x	x	x	x	x		x
25	*Plumularia setacea* (L., 1758)	g	C	x			x	x	x	x	x				x		x	
26	*Dynamena disticha* (Bosc, 1802)	g	C						x			f						x
27	*Sertularella gaudichaudi* (Lamouroux, 1824)	g	TA		x			x	x	x	f	x	x	x	x	x		
28	*Clytia noliformis* (McCrady, 1859)	m	TA				x	x										
29	*Clytia* sp.	m		f		x	f	f	f	x	f		x	x	f	f	f	x
30	*Obelia dichotoma* (L., 1758)	m	C						f	f					x	f	x	
31	*Orthopyxis crenata* (Hartlaub, 1901)	mg	CT						x									
32	*Orthopyxis integra* (Macgillivray, 1842)	mg	C	x	f	f	x	x	x	x	x	x	x	x	x	x	x	x

TABLE 2. – Abundance and distribution of hydroid colonies on the stems of *Cystoseira*.

a) abundance on stem/colony size (% per category*)

site	*C. compressa*						*C. barbata*						*C. amentacea*			*Cystoseira tot*					
	exp.			shelt.			exp.			shelt.			exp.			exp.			shelt.		
category	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
athecata	56	44	0	87	13	0	59	18	23	61	32	7	54	46	0	**58**	**27**	**15**	**64**	**30**	**6**
thecata	46	37	17	74	22	4	32	39	29	57	35	8	37	42	21	**38**	**39**	**23**	**62**	**31**	**7**
total %	**47**	**38**	**16**	**76**	**20**	**4**	**36**	**36**	**28**	**59**	**34**	**8**	**38**	**42**	**20**	**40**	**38**	**22**	**62**	**31**	**7**

b) distribution on stem (% per category**)

site	*C. compressa*						*C. barbata*						*C. amentacea*			*Cystoseira tot*					
	exp.			shelt.			exp.			shelt.			exp.			exp.			shelt.		
category	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
athecata	80	20	0	69	19	12	70	27	3	37	49	14	70	15	15	**73**	**23**	**4**	**40**	**46**	**14**
thecata	34	50	16	15	42	43	39	56	5	17	38	45	16	70	14	**31**	**58**	**11**	**16**	**39**	**44**
total %	**37**	**48**	**15**	**22**	**39**	**39**	**42**	**53**	**5**	**23**	**42**	**35**	**19**	**67**	**14**	**35**	**55**	**10**	**23**	**41**	**36**

*1 = present, 2 = abundant, 3 = very abundant
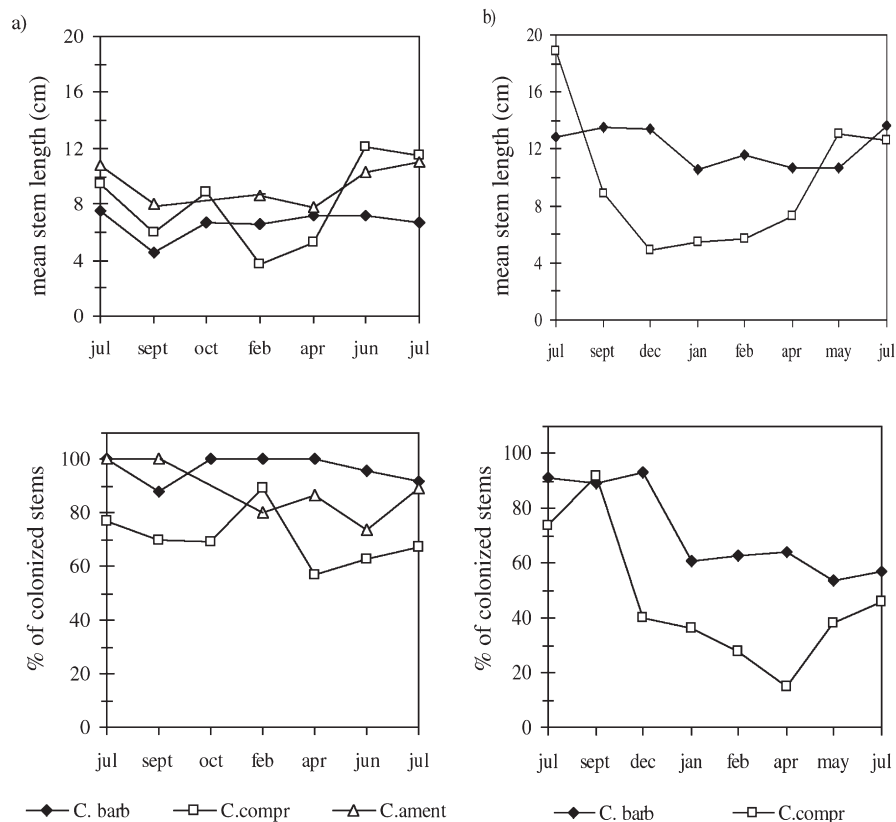**1 = stipe and holdfast, 2 = inner or intermediate part of the stem, 3 = outer part of the stem

FIG. 1. – Mean algal stem length and percentage of colonised stems of *Cystoseira* between July 1996 and July 1997 for a) sheltered and b) exposed site.

Decrease in colony height on *Cystoseira* could be observed in the arborescent species *Halecium pusillum, Ventromma halecioides, Aglaophenia* spp and *Sertularella gaudichaudi*. Colonies of the genus *Aglaophenia* had a much higher frequency at the wave-exposed than at the sheltered site.

Hydroid diversity and dominance

Of the 32 species of hydroids (Table 1) sixteen were found at both sites and on all three species of *Cystoseira*. With 27 species, the hydroids on stems of *C. barbata* from the sheltered site showed the highest species richness (Table 3). No host-specificity was found amongst the hydroids on *Cystoseira*.

The Shannon's diversity index (H') and Pielou's evenness index (J) for the hydroid communities are shown in Table 2. Differences in H' and J on the three algal species at the two sites were not significant (randomisation test: p-value between 0.074 and 0.709).

Simpson's index of dominance (I_{dom}) is shown in Table 4. The five dominant ($I_{dom}>1.0$) species were *Halecium pusillum, Aglaophenia tubiformis, Ventromma halecioides, Clytia* sp and *Orthopyxis integra*, all of which were thecate. They comprised 34-73% of the hydroid colonies found. The subdominant species with an index of dominance between 1.0 and 0.6 were *Eudendrium motzkossowskae, Hydractinia fucicola, Coryne muscoides, Cladoco-*

TABLE 3. – Percentage of algal stems colonized by at least one hydroid, total number of hydroid species recorded, Shannon-Wiener diversity index and Pielou's evenness index for the hydroid communities on the three species of *Cystoseira* at the two sites of different wave exposure.

algal substrate	*C. compressa*		*C. barbata*		*C. amentacea*
site (exposed/sheltered)	exp	shelt	exp	shelt	exp
% of colonized stems	69	43	96	67	86
mean n° of colonies/stem	1.15	0.63	2.41	1.17	1.9
total n° of hydroid species	17	19	19	27	21
H' (Diversity Index)	2.34	2.33	2.64	2.81	2.59
J (Eveness Index)	0.77	0.7	0.87	0.84	0.82

TABLE 4. – Species and order of dominance of hydroids on *Cystoseira*. Dominance index Idom = S (n/N)*10, where: n = number of colonies of species 'x', N = total colonies of all species in sample. Order = order of dominance.

No.	species	*Cystoseira compressa* exposed order	I(dom)	sheltered order	I(dom)	*Cystoseira barbata* exposed order	I(dom)	sheltered order	I(dom)	*C. amentacea* exposed order	I(dom)
	ATHECATA										
1	*Clava multicornis*	-	-	11.5	0.28		<0.01	13	0.1	16	0.01
2	*Eudendrium glomeratum*	-	-	-	-	-	-	22	0.01	-	-
3	*Eudendrium motzkossowskae*	10	0.1	13	0.16	15	0.06	7	0.75	-	-
4	*Eudendrium ramosum*	-	-	-	-	-	-	16	0.03	-	-
5	*Hydractinia fucicola*	8	0.4	7	0.71	10	0.34	10	0.23	4	0.96
6	*Cladonema radiatum*	-	-	-	-	-	-		<0.01	-	-
7	*Coryne muscoides*	15	0.03	16	0.07	12	0.21	6	0.8	11	0.11
8	*Coryne pusilla*	-	-	-	-	-	-		<0.01	-	-
9	*Sarsia producta*		<0.01	-	-	-	-	-		-	-
10	*Ectopleura wrighti*	-	-	-	-	-	-		<0.01	-	-
11	*Cladocoryne floccosa*	-	-	8	0.63	14	0.08	11	0.2	-	-
12	*Zanclea* sp.	-	-	11.5	0.28	-	-	14	0.09	16	0.01
	THECATA										
13	*Mitrocoma annae*	-	-	-	-	-	-		<0.01	-	-
14	*Eirene viridula*	-	-	-	-	-		-		-	-
15	*Anthohebella parasitica*	11.5	0.04	-	-	16	0.04		<0.01	16	0.01
16	*Halecium pusillum*	2	3	3	2.83	1	4.53	5	1.34	1	5.17
17	*Halecium nanum*	16	0.02	10	0.29		<0.01	21	0.01	12	0.07
18	*Hydrodendron mirabile*	-	-	-	-		<0.01	17	0.03	0	<0.01
19	*Aglaophenia octodonta*	7	0.41	6	0.8	4	0.91	8	0.47	9	0.18
20	*Aglaophenia pluma*	13	0.04	-	-	13	0.14	20	0.02	14	0.01
21	*Aglaophenia tubiformis*	1	4.01	2	6.92	3	1.38	1	3.61	3	1.04
22	*Aglaophenia indet.*	3	2.69	5	1.16	2	1.96	3	1.9	2	2.35
23	*Kirchenpaueria* sp.	-	-	-	-	-	-		<0.01		<0.01
24	*Ventromma halecioides*	6	0.41	4	2.75	6	0.49	4	1.45	10	0.15
25	*Plumularia setacea*	9	0.15	15	0.1	9	0.41	18.5	0.02	8	0.27
26	*Dynamena disticha*	-	-	-	-	8	0.42	18.5	0.02		<0.01
27	*Sertularella gaudichaudi*	17	0.02	-	-	5	0.64	12	0.11	6	0.42
28	*Clytia noliformis*	14	0.03	-	-		<0.01	-	-	-	-
29	*Clytia* sp.	5	0.98	1	8.02	7	0.48	2	2.5	5	0.44
30	*Obelia dichotoma*	11.5	0.04	14	0.12		<0.01	15	0.07	13	0.03
31	*Orthopyxis crenata*	-	-	-	-	-	-	-	-		<0.01
32	*Orthopyxis integra*	4	1.5	9	0.33	11	0.32	9	0.43	7	0.39

ryne floccosa, Aglaophenia octodonta and *Sertularella gaudichaudi,* which together with the dominant species comprised 55-84% of the hydroid communities.

Canonical Correspondence Analysis

The CCA ordinations were all statistically significant (P=0.01 or P<0.001), as assessed by unrestricted Monte Carlo permutation tests (overall test for the first four axes for 1000 permutations). The species-environmental correlations for the first two axes of ordination ranged from 0.72 to 0.89 and the eigenvalues for the first two axes from 0.12 to 0.2. Figure 2 summarises across both algal and hydroid species. The sites of different wave-exposure are separated by the first CCA axis in all seasons. The samples of the exposed site lie below the first axis of the plot, where colonisation is high. Most variation at the wave-exposed site is due to stem length and number of stems. Samples suggest a seasonal cycle. Samples with the lowest colonisation levels and
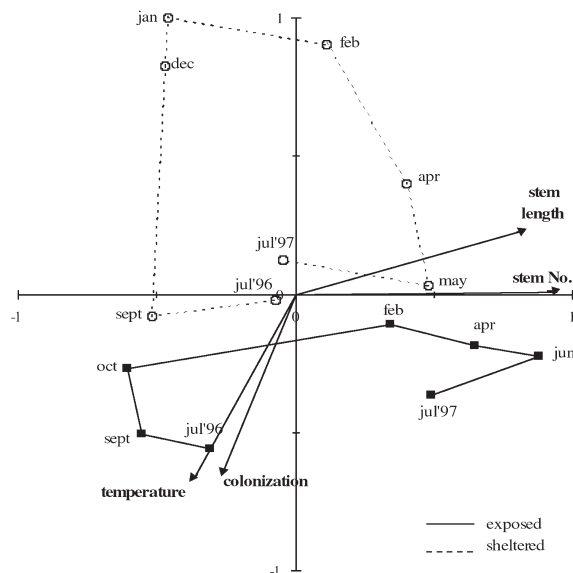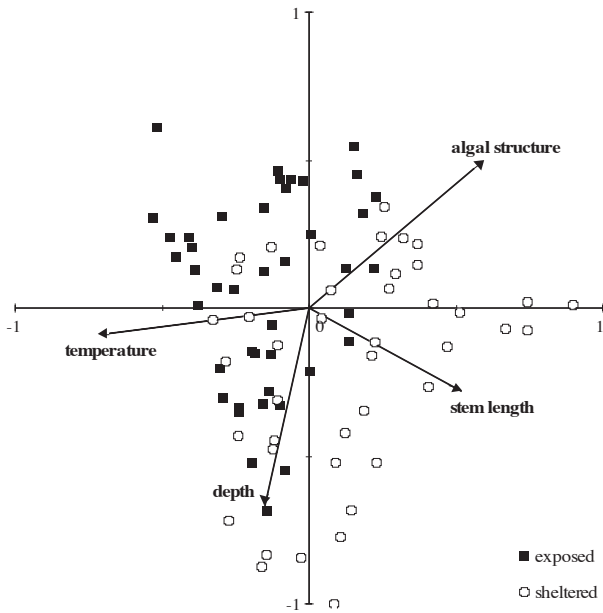

FIG. 2. – Ordination of faunal samples for exposed and sheltered sites using Analysis of Canonical Correspondence with environmental variables. x and y are the first two CCA axes. Arrows show direction and rates of variation among month in water temperature, % of colonised algal stems, algal stem length and number of sampled stems (P = 0.01).

FIG. 3. – Ordination of faunal samples for exposed and sheltered sites using Analysis of Canonical Correspondence with environmental variables. x and y are the first two CCA axes. Arrows show direction and rates of variation among sites in water temperature, water depth, algal stem length and degree of algal structure (P = 0.001).
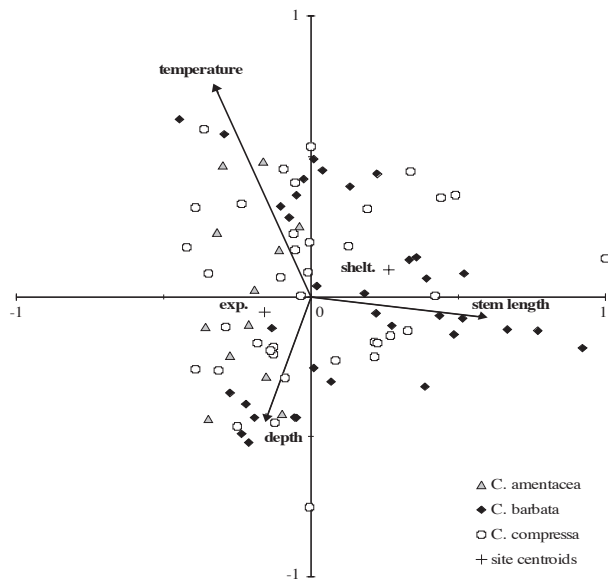

FIG. 5. – Ordination of hydroid species for athecates and thecates using Analysis of Canonical Correspondence with environmental variables. x and y are the first two CCA axes. Arrows show direction and rates of variation among samples in water temperature, water depth, algal stem length and degree of algal structure. The sheltered and exposed sites, and the three species of *Cystoseira* are shown by their centroids. Numbers indicate the hydroid species (P = 0.001).

towards the lower right of the plot. This region also represents sites where algae had long stems with high structure and where the water was colder and deeper.

Figure 4, which displays differences among the three algal species, shows that samples from *C. amentacea*, which was only found at the exposed site, lie to the left of the second CCA axis, where the centroid of the exposed site is represented. Samples for *C. barbata* show a tendency to lie along the positive region of the first CCA axis, representing sites with high stem length and shelter. Variation between the samples are influenced by water temperature, stem length and depth.

The species points in Figure 5 summarise the preferences of species for different types of sites. The athecate hydroids are separated from the thecate hydroids and lie on the plot where stem length, algal structure and shelterness is high.

FIG. 4. – Ordination of faunal samples for *Cystoseira amentacea*, *C. barbata* and *C. compressa* using Analysis of Canonical Correspondence with environmental variables. x and y are the first two CCA axes. Arrows show direction and rates of variation among samples in water temperature, water depth and algal stem length. The sheltered and exposed sites are shown by their centroids (P = 0.001).

temperature are the ones at the sheltered site during the cold season.

Figure 3, in which each point is the species composition at a particular site indicates that there is a tendency for samples at the sheltered site to lie

DISCUSSION

This study examined the seasonal and spatial distribution of epiphytic hydroids on three species of the brown algae belonging to the genus *Cystoseira*. Of the 32 epiphytic species of hydroids (Table 1) the

most abundant species are all widespread (Boero and Bouillon, 1993). The two species endemic to the Mediterranean Sea were only found occasionally. The dominant hydroid species present on *Cystoseira* are well known from habitats with a high level of stress factors (Boero, 1981b; Boero and Fresi, 1986). There are no differences in diversity and evenness among the communities of the two sites and on the three species of *Cystoseira*, but species compositions differ.

No host-specificity was found, although host-specific hydroid species are well known from other seaweeds and seagrasses (Boero, 1981a; Hughes *et al.*, 1991; Watson, 1992). All hydroid species epiphytic on *Cystoseira*, except perhaps a new species of *Clytia*, are well known from other biotic or hard bottom substrates. Twenty-three of the hydroid species found (74%) are well known from other epiphytic systems in the Mediterranean Sea (Boero 1981a; Llobet *et al.*, 1986). Substrate availability, i.e. abundance of *Cystoseira*, does not seem to strongly influence the epiphytic hydroid community. Algal substrate is generally more abundant at the sheltered site, but colonisation and number of species is higher, and colony size bigger at the wave-exposed site. Only on *C. compressa* does colonisation correlate with stem length. The high variance of stem length of *C. compressa* from the sheltered site, and therefore the high instability of substrate could have led to its low colonisation. However, the lowest monthly mean in algal stem length of *C. compressa* at the sheltered site is not lower than any mean in algal stem length at the wave-exposed site. Assuming therefore that maximal stem length is a good measure of the available space on the stems of *Cystoseira*, in the present study the amount of available substrate does not seem to be a limiting factor for the hydroid community.

This study provides evidence that hydroid communities on *Cystoseira* have a seasonal cycle. This seasonality could be dependent on substrate availability, but in this study, this factor did not seem to influence the hydroid community. As the abundance of the hydroids on *Cystoseira* coincides with those of the hydroids in the Mediterranean Sea in the cold season in general, their seasonality does not seem to be influenced by their special habitat. The occurrence of the most fertile colonies, the highest species richness and the period of highest hydroid abundance in the cold season, also supports this.

Hydroid abundance differed between the two sites experiencing different levels of wave-expo-sure. The stems of *Cystoseira* differ between sites in their length and colonisation by hydroids. At the wave-exposed site the stems of *Cystoseira* were probably shorter because of the higher mechanical stress. The higher levels of water movement could result in a higher frequency of stem breakage and so in a higher turnover rate, or in a limitation of growth to a certain length. Water movement supplies the organisms with food, nutrients and dissolved gases, prevents accumulation of sediments, and disperses waste products and larvae (Riedl, 1969). Therefore the stems were probably more frequently colonised, had a higher species frequency, a higher number of species per stem, and larger colonies. However, the tendency for hydroid colonies, especially of the fragile athecate species, to be distributed more towards the protected parts of the stems at the exposed site is likely to be a response to higher mechanical stress.

Another characteristic of epiphytic species is the reduced size or colony height, especially of arborescent species. This was observed among the hydroid species growing on *Cystoseira*. The change in morphology is also likely to be a structural response to water movement. With increasing intensity of water movement colony height decreases and population density and number of hydranths per colony increases. Because growth forms with greater hydranth density require a higher influx of nutrient particles, they tend to occupy more wave-exposed habitats (Riedl, 1971). This can be seen by examining the distribution and fertility of species with different hydranth densities. Colonies of the genus *Aglaophenia*, which have the highest hydranth density per colony, have a higher frequency and abundance at the exposed site than at the sheltered site. Species of the family Campanulariidae have the lowest hydranth density per colony. Among them, *Clytia* sp, the most frequent species colonising *Cystoseira* was clearly more abundant at the sheltered site. This is underlined by the distribution of fertile colonies among the hydroids: *Aglaophenia* spp contribute 44% to the fertile colonies at the wave-exposed site, while campanulariid species contribute only 28%. At the sheltered site the campanulariids contribute 66% and the *Aglaophenia* species only 11%.

The hydroid communities on the three species of *Cystoseira* do not differ greatly. There is, however, a trend towards decreasing colonisation, hydroid abundance and colony size from *C. barbata* to *C. amentacea* to *C. compressa*. These differences could be due to host preferences by larvae which select on

the basis of algal architecture and surface, its age or chemical substances (Nishihira, 1966; Katô *et al.,* 1975; Amico, 1995). The influence of chemical exudates seems only to be important on the same stem where the antibacterial effect prevents colonisation of young branches. This was observed mainly on *C. amentacea*, which has more complex metabolites with a much higher antibacterial action (Amico, 1995) than *C. barbata* and *C. compressa*. The most probable factor responsible for the differences in colonisation among the three species of *Cystoseira* is their morphological nature. *C. barbata* and *C. amentacea*, which are both highly branched with many micro-habitats facilitating hydroid settlement and persistence, are also more heavily colonised than *C. compressa*, which shows a simpler morphology with its flattened and smoother branches. It can be concluded, therefore, that the highest abundance of hydroids on *C. barbata* is mainly due to its highly structured morphology.

Thirty-nine percent of the epiphytic hydroid community on *Cystoseira* comprises athecate species. This is greater than that found on *Posidonia oceanica* (Boero, 1981a) or *Halimeda tuna* (Llobet *et al.*, 1991), where athecates comprise 23% and 14% of the hydroid community, respectively. In the Mediterranean Sea athecates generally comprise 48% of all hydroids (Boero and Bouillon, 1993). One reason why athecates are less common in epiphytic communities is the higher level of mechanical forces acting on them. Athecates are presumably more sensitive to these forces because they have no rigid thecae for support or for the polyp to retract into. This may also be the reason why they are more distributed on the more protected lower and inner parts of the stem. The higher frequency of athecate species on *Cystoseira* compared to other seaweeds could be due to its dendroid growth form, which offers more protected places for fragile species to withstand high mechanical stress. The dominance of thecate species among epiphytes underlines the idea that habitats with high mechanical stress are less favourable to the more fragile athecate species.

CONCLUSIONS

The hydroid species colonising *Cystoseira* may avoid the higher levels of competition found on other substrates, but only those species with features enabling them to persist in an environment of high mechanical stress survive as epiphytes. This is prob-

ably why the dominant epiphytic hydroids on stems of the brown algae *Cystoseira* from the sites of this study are thecates. The factors with the greatest influence on hydroid communities occupying sites exposed to wave action rather than more sheltered sites appear to be mostly abiotic: sedimentation rate, nutrient levels, temperature and, especially water movement. Biological factors such as the structure and surface of the host and competition seem to be secondary. The importance of water movement, which in this study seemed to have the greatest influence on the hydroid community, could be due to the shallow water depth (0.5-3 m) and high exposure to wave action of the study site.

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Note added in proof: *Clytia* sp. has been identified as *Clytia viridicans* (Leuckart, 1856) (see Pagliara *et al.*, this volume)