

The distribution of hydroids (Cnidaria, Hydrozoa) from micro- to macro-scale: Spatial patterns on habitat-forming algae

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Abstract

Scaling up from local, short-term experiments to larger-area and longer-term ones is crucial to address the role of scale in ecology. Few studies, however, examined large-scale spatial variability in the distribution and abundance of marine organisms, with rare attempts to directly compare spatial variation at local (centimetres–metres) vs. regional (1000's of kilometres) scale. Here, we used a hierarchical design to describe the spatial distribution of the hydroids epiphytic of the brown alga *Cystoseira amentacea*, a habitat-forming species that provides a continuous, extensive settling substrate at regional scale along the rocky coasts in the Mediterranean Sea. This continuity provides the potential to deal with scale-related variability, increasing area of investigation without adding differences deriving from habitat heterogeneity or changes in topographic complexity. Hydroids were selected for their abundance and for their life cycle features (rapid growth, small body size, early sexual or asexual reproduction and short life span), allowing rapid responses to changes in environmental conditions. The aim of this study was to analyse whether the structure of hydroid assemblages living on *C. amentacea* had a consistent pattern of variation among three portions of the algal thallus (i.e., basal, middle, and distal) across a spectrum of scales and whether having or not a pelagic stage could exert a significant influence on the distribution patterns of the species. A total of 32 species were identified. Multivariate analyses showed that hydroid colonization of *Cystoseira* occurs differently along each thallus, with patterns of variation in the structure of assemblages differing at an even smaller spatial scale than that of single plants. However, such differences varied from patch to patch. Among the 14 species identified as “important” to define the hydroid assemblage inhabiting *Cystoseira*, only one (*Clytia hemisphaerica*) has free medusae, the other species reproducing by fixed gonophores or by short-lived medusoids. Univariate analysis showed significant differences among portions of thalli in terms of spatial variability at the various scales investigated, thus suggesting that patterns of multivariate variation along the three portions of thalli might vary across scale. Overall, our results suggest that patterns of distribution of hydroids along *C. amentacea* thalli significantly vary across spatial scales but that the observed differences can be hardly interpreted on the basis of life-cycle patterns.

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1. Introduction

Quantitative studies on the variation of the distribution patterns of both single species and of species assemblages in space and time are common in ecology (e.g., Boero and Fresi, 1986; Levin, 1992; Rossi et al.,

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1992; Dutilleul, 1993; Schneider, 1994; Underwood and Chapman, 1996; Maurer, 1999; Benedetti-Cecchi, 2001; Dungan et al., 2002; Anderson et al., 2005a; van de Koppel et al., 2006). Recurrent attempts have been made at identifying *critical* scales of variability generating ecologically relevant patterns of variation across systems, and/or at understanding whether processes that occur at local scale can generate large-scale patterns (Thrush et al., 1997; Wootton, 2001; Fowler-Walker and Connell, 2002; Irving et al., 2004; Denny et al., 2004; Anderson et al., 2005b; Fraschetti et al., 2005). The detection of *critical* scales of variability, in fact, is crucial to identify the spatial extent at which different physical and biological processes are actually acting (Denny et al., 2004). Scaling up is also relevant to understand whether local variations obscure broader-scale patterns of distribution of species assemblages.

Several statistical tools are available to ecologists to measure variation from very small (centimetres–metres) to very large (>1000 km) spatial scales (Perry et al., 2002). In the marine environment, where the potential of sampling continuously at large spatial extent is rather limited, hierarchical nested designs are a powerful tool to investigate spatial (or temporal) patterns across scales. At present, most studies adopting this procedure attempted to understand the extent to which local complexity generates large-scale patterns (Åberg and Pavia, 1997; Thrush et al., 1997; Fowler-Walker and Connell, 2002; Irving et al., 2004; Kelaher et al., 2004; Anderson et al., 2005b; Fraschetti et al., 2005) and often revealed inconsistent patterns of variation in species assemblages at observation scales ranging from local to regional. Recently, biogeographic comparisons of broad morphological groups of benthic algae (Fowler-Walker and Connell, 2002; Irving et al., 2004) and of invertebrates epiphytic on kelps (Anderson et al., 2005a,b) revealed patterns that, at least in some habitats, seem inconsistent at local spatial scales but reveal similarities at wider spatial scales (Fowler-Walker et al., 2005a). Similarities of species assemblages at different spatial scales, however, can be blurred when data sets are collected at low taxonomic resolutions, potentially concealing deep ecological differences (Dauvin et al., 2003; Terlizzi et al., 2003). The necessity of high replication in experimental analyses of spatial patterns (Fraschetti et al., 2005), in fact, often led to the sacrifice of high taxonomic resolution, with potential consequences in the representativeness of data sets.

Quantification of scale-related variability in continuous habitats, such as canopy-understorey associations in shallow marine environments can help to unconfound differences deriving from habitat heterogeneity or

changing topographic complexity. The role exerted by *habitat formers* such as algae (e.g., *Ascophyllum nodosum*, *Ecklonia radiata*, *Fucus* spp., *Himantothalpus grandifolius* and *Cystoseira* spp.) and seagrasses (e.g., *Posidonia oceanica*) on the distribution of epiphytic taxa has been extensively studied worldwide (e.g., Kerneis, 1960; Boero, 1981; Jenkins et al., 1999a, b; Pavia et al., 1999; Bulleri et al., 2002; Thompson et al., 2002; Fowler-Walker and Connell, 2002; Connell, 2003a,b; Cervin et al., 2004; Irving et al., 2004; Anderson et al., 2005a,b; Fowler-Walker et al., 2005b). These *habitat-forming* species exclude and/or facilitate a suite of taxa, and their roles can be consistent in space and time (Kennelly, 1989; Bulleri et al., 2002; Irving et al., 2005), generating spatial patterns in ecological communities.

In marine rocky habitats, where space is a limiting resource for sessile organisms (Connell, 1961; Paine, 1966), *habitat-forming* species represent suitable surfaces for epibiotic settlement by increasing space availability in terms of microhabitats and providing benign environmental conditions (Russo, 1997; Morri and Bianchi, 1999). The brown algae of the genus *Cystoseira* form a rather continuous belt along the relatively pristine rocky shores of the Mediterranean Sea. Studies on their epiphytic assemblages are numerous, but no explicit quantitative study on the natural spatial scales of variation for the sessile fauna living on *Cystoseira* thalli is available to date. In this study, we tested hypotheses about the spatial scales of variation in the distribution and abundance of hydroids on *Cystoseira* (Faucci and Boero, 2000; Fraschetti et al., 2002). These sessile invertebrates are characterised by rapid growth, usually small body size, and strong seasonality (Boero et al., 1992). These features cope well with challenging substrata like algae and seagrasses, with rapid growth and turnover (Boero, 1987; Coma et al., 1992). Unlike those living on the sea-grass *P. oceanica* (Boero, 1981), the hydroids epiphytic on *Cystoseira* are not represented by a set of exclusive species (Otero-Schmitt and Perez-Cirera, 1996). The complexity of hydroid life cycles, ranging from fixed gonophores to long-lived medusae (Boero and Bouillon, 1993), could lead to the understanding of the effects of dispersal modes on distribution patterns. In the Mediterranean Sea, on hard substrates in general, hydroids are represented by two species assemblages, characterising a warm and a cold season (Boero and Fresi, 1986). The hydroid assemblage on *Cystoseira amentacea*, however, is thriving only when the alga is flourishing, i.e., in spring and summer. In the case of *C. amentacea*, thus, a single sampling session is sufficient

to cover hydroid seasonality, because the supporting alga is very reduced during the adverse season, and almost no hydroids grow on it.

Our study included 4 spatial scales, ranging from thalli (scale of centimetres) to the regional scale (scale of 100's of kilometres), with a spatial coverage of more than 800 km. Furthermore, in order to quantify potential differences in assemblage structure according to the position along the supporting alga, three portions of the thallus (scale of centimetres) were sampled.

Specifically, we tested (1) if the structure of hydroid assemblages on *C. amentacea* differed among the three portions of thalli; (2) if present, if these differences are consistent across the scales investigated, along the regional gradient; (3) if, having or not a pelagic stage could exert a significant influence on the distribution patterns of the species.

2. Methods

2.1. Study sites and experimental design

The brown algae *C. amentacea* Bory var. *stricta* Montagne, *C. compressa* (Esper) Gerloff et Nizamuddin, and *C. barbata* (Stackhouse) C. Agardh produce extensive beds in the low-shore habitats (−0.1 to 0.1 m across mean-low-level-water) of Apulia. *C. amentacea*,

in particular, is the dominant species and forms an almost continuous fringe along the regional gradient going from the Adriatic to the Ionian seas (Fraschetti et al., 2002). A survey covering almost 800 km of the Apulian coast (South Italy, from Peschici 41°57' N, 16°00' E to Taranto 40°24' N, 17°12' E) was carried out in May 1997 (Fig. 1). The coastline was divided in six adjacent sectors of unequal total length but characterised by the same span of rocky shore. For each sector, three sites, separated by at least 1 km, were selected at random. At each site, two patches, separated by at least 100 m, were also randomly selected (Fig. 1). All patches were characterised by a low-shore assemblage dominated by the presence of a dense (covering >80%) fringe of *C. amentacea*. At each patch, 30 replicate thalli of *C. amentacea* were taken haphazardly by cutting off the stipe at its base. All thalli were about 30 cm in length and were collected at about 50 cm from each other.

Samples were fixed in a 4% formaldehyde solution, sorted under a stereomicroscope for identification. To evaluate possible differences in hydroid distribution along thalli, the plants were divided into three almost equal portions (basal, middle and distal). For each patch, 10 of the 30 collected thalli were inspected basally, 10 in the middle, and 10 distally, so to ensure data independence (Fig. 1). Species abundances were estimated as ranks (Boero and Fresi, 1986) (0 = absent, 1 = present but

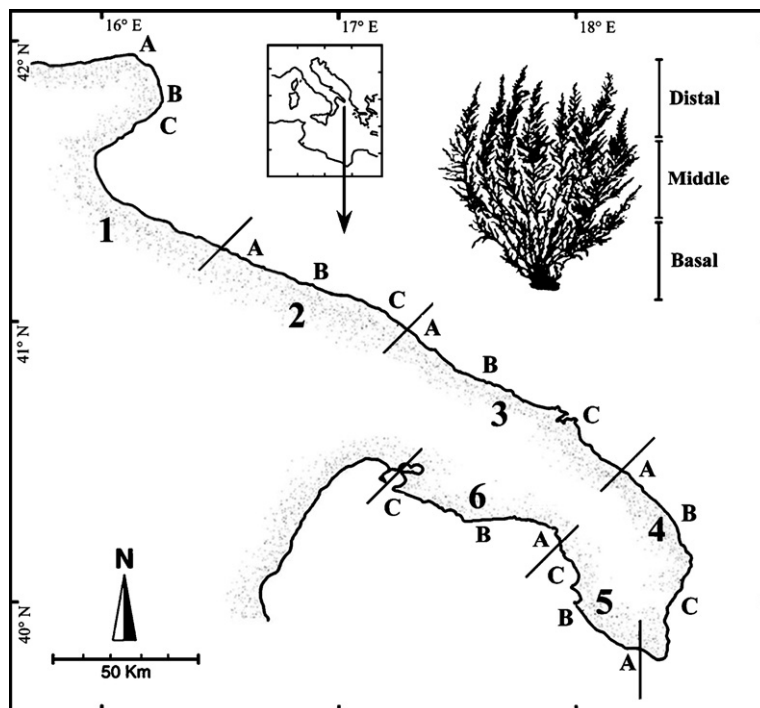


Fig. 1. Study area and its positioning in the Mediterranean Sea. Sampling sites (A, B, C) within each of the 6 sectors (1 to 6) are also shown.

rare, 2=present and fairly abundant, covering less than half of the portion, 3=abundant, covering more than half of the portion, 4=dominant, covering almost completely the portion).

2.2. Statistical analyses

The experimental design consisted of four factors: Sector (Se, 6 levels, random), Site (Si, 3 levels, random and nested in Se), Patch (Pa, 2 levels, random and nested in Site) and Portion (Po, 3 levels, Basal, Middle and Distal, fixed and crossed with all the other factors), with $n=10$, for a total of 1080 units of observation in the data set. There were 32 variables (species) included in the data set. Taxonomic details of the recorded variables are reported in Table 1.

A distance-based permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001; McArdle and Anderson, 2001) was used to analyse the multivariate data set in response to the full design. This method allows partitioning the variability in a dissimilarity matrix according to any experimental design and tests individual terms (including interactions) using permutations (Anderson and ter Braak, 2003). The analysis was based on Bray–Curtis dissimilarity (Bray and Curtis, 1957) on untransformed data. When appropriate, significant terms in the full model were analysed individually using pairwise comparison. P -values were obtained using 4999 random permutations of the appropriate units. When there were not enough possible permutation units to give a reasonable test by permutation, P -values were calculated using 4999 Monte Carlo draws from the asymptotic permutation distribution (Anderson and Robinson, 2003). The analyses were made by means of the FORTRAN-written PERMANOVA.exe program (Anderson, 2005). The multivariate pseudo-variance components for each term in the model were then calculated using direct multivariate analogues to the univariate ANOVA estimators (e.g., Searle et al., 1992).

To visualise multivariate patterns, for each of the six sectors an unconstrained non-metric multi-dimensional scaling (nMDS) plot of patch's centroid for each portion of the thalli was done on the basis of Bray–Curtis dissimilarities on untransformed data. Centroids and distances among them in Bray–Curtis space were obtained using the computer program PCO.exe (Anderson, 2003); nMDS plots of distance matrices among centroids were then generated with PRIMER v6 statistical package (Clarke and Gorley, 2001).

The average percentage procedure (SIMPER, Clarke, 1993) was used to identify, for each sector, the

Table 1

Hydroids: taxonomic list of the recorded species (m=medusa; g=fixed gonophore or short-lived medusoid)

<i>ANTHOMEDUSAE</i>	
BOUGAINVILLIIDAE	
	<i>Bougainvillia</i> sp.=m
OCEANIIDAE	
	<i>Rhizogeton nudus</i> Broch, 1909=g
HYDRACTINIIDAE	
	<i>Hydractinia fucicola</i> (M. Sars, 1857)=g
EUDENDRIIDAE	
	<i>Eudendrium capillare</i> Alder, 1856=g
	<i>Eudendrium fragile</i> Motz-Kossowska, 1905=g
	<i>Eudendrium glomeratum</i> Picard, 1952=g
	<i>Eudendrium motzkossowskiae</i> Picard, 1952=g
CORYNIDAE	
	<i>Coryne muscoides</i> (L., 1761)=g
ELEUTHERIIDAE	
	<i>Eleutheria dichotoma</i> Quatrefages, 1842=m
CLADOCORYNIDAE	
	<i>Cladocoryne floccosa</i> (Rotch, 1871)=g
<i>LEPTOMEDUSAE</i>	
PHIALELLIDAE	
	<i>Phialella quadrata</i> (Forbes, 1848)=m
HALECIIDAE	
	<i>Halecium</i> sp.=g
	<i>Halecium nanum</i> Alder, 1859=g
	<i>Halecium pusillum</i> (M. Sars, 1857)=g
	<i>Hydrodendron mirabile</i> (Hincks, 1866)=g
LAFOEIDAE	
	<i>Anthoebella parasitica</i> (Ciamician, 1880)=g
KIRCHENPAUERIIDAE	
	<i>Kirchenpaueria pinnata</i> (L., 1758)=g
AGLAOPHENIIDAE	
	<i>Aglaophenia octodonta</i> (Heller, 1868)=g
	<i>Aglaophenia pluma</i> (L., 1767)=g
	<i>Aglaophenia tubiformis</i> (Marktanner-Turneretscher, 1890)=g
PLUMULARIIDAE	
	<i>Monotheca obliqua</i> (Johnston, 1847)=g
	<i>Plumularia setacea</i> (L., 1758)=g
	<i>Ventromma halecioides</i> (Alder, 1859)=g
SERTULARIIDAE	
	<i>Dynamena disticha</i> (Bosc, 1802)=g
	<i>Sertularella gaudichaudi</i> (Lamouroux, 1824)=g
CAMPANULARIIDAE	
	<i>Campanularia</i> sp.=g
	<i>Clytia viridicans</i> (Leuckart, 1856)=m
	<i>Clytia hemisphaerica</i> (L., 1758)=m
	<i>Obelia dichotoma</i> (L., 1758)=m
	<i>Obelia geniculata</i> (L., 1758)=m
	<i>Orthopyxis crenata</i> (Hartlaub, 1842)=g
	<i>Orthopyxis integra</i> (MacGillivray, 1842)=g

percentage contribution that each species made to the measures of the Bray–Curtis similarity (calculated as 1 – Bray–Curtis dissimilarity) within portions. This analysis allowed identification of the species that were most important in characterising the assemblage across the

different portions of the thalli at each of the six sectors. Instead of using slightly higher values as is commonly done, in order to include a reasonable number of species in the output of the analysis, species were selected as “important” if they exceeded an arbitrarily chosen threshold value of percent similarity $\geq 5\%$.

In addition to the examination of potential differences among assemblages across the portions of the thalli, it was of interest to test for differences among portions of thalli in terms of spatial variability at the various scales. Calculation of components of variation from hierarchical analyses of variance allows separating sampling error from estimates of true variability associated to each spatial scale of observation (Gaston and McArdle, 1994). However, a considerable impediment in the use of variance components is that they are often calculated from a single set of data, so that a single estimate of variance components is available for each source of variation. To deal with this issue, here we rearranged the multivariate data set in order to obtain replicated, independent measures of spatial variance. First, the data were split into two halves, with $n=5$ replicates with the full experimental design for each half. Then, for each data set, the data were analysed separately using PERMANOVA for each of the three portions (basal, middle and distal) according to the full spatial hierarchical model. In this case, the multivariate pseudo-variance components were estimated for each

spatial scale (i.e., sector, site, patch and thalli), yielding two independent estimates of variability for each spatial scale at each portion. These estimates were then analysed with a two-factor analysis of variance (Scale, 4 levels, fixed and Position, 3 levels, fixed and crossed to Scale, with $n=2$ per combination of factors). This procedure allowed testing if patterns in spatial variance of hydroid assemblages were consistent or not among the different portions of the thalli.

Analysis of variance was also employed to examine spatial patterns for mean number of taxa. The model was the same described the full multi-factor design. SNK tests were employed for post-hoc multiple comparisons of the mean, when appropriate. Given the homogeneity of variances (as examined by Cochran's C test) ANOVAs were done on untransformed data.

3. Results

3.1. Composition of assemblages

The hydroids epiphytic on *Cystoseira* along the Apulian coast are represented, so far, by 41 species (Faucci and Boero, 2000; Frascchetti et al., 2002; this study). In the present study, 32 species were collected (Table 1). The nominal species *Clava multicornis*, previously recorded from Apulian *Cystoseira*, is here referred, instead, to *Rhizogeton nudus*, a species hitherto

Table 2

Permutational multivariate analysis of variance (PERMANOVA) on the basis of Bray–Curtis dissimilarity measure for abundance data from 32 variables (see Table 1)

Source	<i>df</i>	MS	<i>F</i>	$P_{(perm)}$	MS_{denom}	Perm units
Sector=Se	5	55,610.864	2.218	0.032	Si(Se)	18 Si(Se) cells
Site=Si(Se)	12	25,073.645	2.258	0.001	Pa(Si(Se))	36 Pa(Si(Se)) cells
Patch=Pa(Si(Se))	18	11,106.858	3.807	0.000	Residual	1080 raw data units
Portion=Po	2	17,045.950	0.704	0.699	Po × Se	18 Se × Po cells
Po × Se	10	24,201.994	5.117	0.000	Po × Si(Se)	54 Si(Se) × Po cells
Po × Si(Se)	24	4729.373	0.441	1.000	Po × Pa(Si(Se))	108 Pa(Si(Se)) × Po cells
Po × Pa(Si(Se))	36	10,711.026	3.671	0.000	Residual	1080 raw data units
Residual	972	2917.884				
Total	1079					

Sector	Basal vs. Middle		Basal vs. Distal		Middle vs. Distal	
	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
1	0.745	0.591	0.523	0.792	0.510	0.720
2	1.342	0.219	1.886	0.076	2.471	0.025
3	4.913	0.001	3.178	0.006	0.463	0.834
4	0.645	0.613	0.757	0.558	0.510	0.712
5	1.568	0.131	1.856	0.068	2.071	0.041
6	2.181	0.031	1.909	0.064	1.724	0.086

Each test was based on 4999 permutations of appropriate units. For each test, the term used for the denominator mean square is given in the column MS_{denom} . Multivariate pairwise comparisons among the three portions of the *Cystoseira* thalli at each of the six sector (following the significant Po × Se interaction term) are also enclosed.

unreported from the Mediterranean sea (for a description, see Schuchert, 2004). Usually, *Cystoseira* spp. are inhabited by species that thrive near the surface, being adapted to strong water movement; the hydroids recorded by the various authors are usually found also on other substrates within the same depth range. Among the 14 species that contribute to characterise the hydroid assemblage at different portions of the *Cystoseira* thalli (see Table 4), only one (*Clytia hemisphaerica*) has free medusae, the other species reproducing by fixed gonophores or by short-lived medusoids.

3.2. Multivariate patterns

The structure of hydroid assemblages significantly differed among the three portions of the *Cystoseira* thalli but differences varied from patch to patch (Table 2). Pairwise comparisons of assemblages among the

three portions of the thalli within each patch (36 sets of 3 test each) showed that in 8 cases the assemblages were significantly distinct at all portions. Significant differences in assemblages were also recorded in 15 comparisons of Basal vs. Middle portion, 9 comparisons of Middle vs. Distal and 17 comparisons of Basal vs. Distal. Only in 6 patches there were no significant differences in assemblages among the 3 portions of the thalli. Such a pattern of differences in assemblages along the thalli was fairly consistent at the larger scale of site (Table 2). Similarly to what observed at the scale of patch, differences in assemblages across thalli varied with sectors (Table 2). Pairwise comparisons of portions within each of the 6 sectors revealed significant differences in 5 out of the 18 tests (Table 2). The complex patterns of differences in hydroid assemblages across scales were portrayed by nMDS plots of patch centroids at each of the six sectors (Fig. 2). Differences

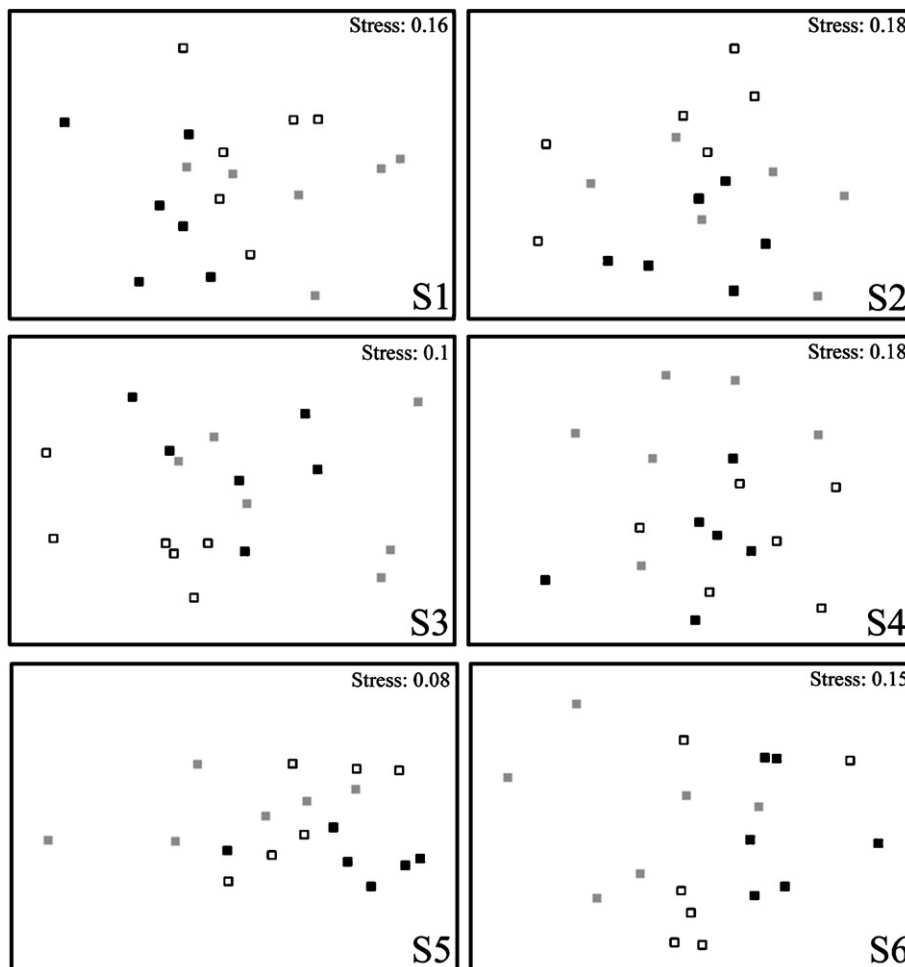


Fig. 2. Non-metric multidimensional scaling ordinations (nMDS plots) on the basis of the Bray–Curtis dissimilarity measure of patch centroids in the six sectors. Black squares=base; grey squares=median portion; white squares=distal portion.

Table 3

Contribution expressed as percentage of the species that were most important in characterising the assemblage across the different portions of the thalli at each of the six sectors

Taxon	Basal						Middle						Distal					
	S1	S2	S3	S4	S5	S6	S1	S2	S3	S4	S5	S6	S1	S2	S3	S4	S5	S6
<i>Aglaophenia pluma</i>	7.6	–	–	–	–	–	4.5	–	–	–	–	–	–	–	–	–	–	–
<i>Aglaophenia tubiformis</i>	3.8	7.9	19.9	11.5	25.4	51.0	9.1	20.1	28.6	27.4	37.9	41.0	23.9	10.6	42.0	25.1	55.6	71.6
<i>Campanularia</i> sp.	–	–	–	–	11.0	–	–	–	–	–	2.2	–	–	–	–	–	33.3	–
<i>Clytia hemisphaerica</i>	14.7	12.5	19.0	8.4	18.7	6.9	15.5	34.3	13.3	9.6	32.8	4.7	–	55.0	21.0	25.1	–	6.3
<i>Coryne muscoides</i>	–	13.6	6.8	1.5	–	–	–	4.7	13.8	–	–	–	–	13.4	14.0	–	–	–
<i>Eudendrium fragile</i>	–	8.5	1.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Halecium pusillum</i>	16.8	4.2	21.2	18.0	15.1	6.9	4.5	5.9	25.4	18.1	19.3	18.9	–	–	19.6	37.4	–	7.9
<i>Hydrodendron mirabile</i>	7.6	8.5	1.8	0.8	–	8.7	–	2.1	–	–	–	5.3	–	8.4	–	–	–	–
<i>Obelia dichotoma</i>	30.6	4.9	3.6	2.5	–	–	62.6	4.2	3.8	1.1	–	–	59.3	–	–	–	–	–
<i>Orthopyxis crenata</i>	–	–	–	–	5.3	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Orthopyxis integra</i>	5.7	6.2	14.0	25.2	–	18.2	3.7	4.2	5.5	16.5	–	20.0	16.8	–	–	12.3	–	3.1
<i>Rhizogeton nudus</i>	11.4	–	–	0.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Sertularella gaudichaudi</i>	–	–	–	27.5	17.7	4.6	–	–	–	24.5	4.3	6.8	–	–	–	–	11.1	3.2
<i>Ventromma halecioides</i>	–	26.4	8.2	–	3.4	–	–	12.7	7.7	–	3.5	3.2	–	5.6	–	–	–	7.9

The arbitrarily chosen threshold value of percent similarity was $\geq 5\%$.

across portions were clear only in a few cases while the frequent overlapping of points belonging to different portions confirmed how differences across thalli changed with scale. SIMPER selected 14 species as important in characterising the assemblages at the portions of the thalli (Table 4). Except for the basal portion in sector 1, *Aglaophenia tubiformis* was the only species that characterised the assemblages at the three portions at all sectors. *C. hemisphaerica*, *Halecium pusillum* and *Orthopyxis integra*, with few exceptions, heavily characterised the assemblages of basal and middle portions. The importance of the remaining species in characterising the assemblages across portions varied with sectors. All 14 characterising species were present on the basal portion. There were no exclusive species on basal and middle portion, regardless of sectors (Table 3).

The interaction of spatial scale and portion of thalli was significant, suggesting that patterns of multivariate variation along the three portions of thalli varied with

scale (Table 4). SNK test showed that the variability of the structure of hydroid assemblages among the three portions was always greater at the smallest scale investigated, that of thalli. In the distal portion of thalli, no extra variability was accounted for by scales larger than that of the patch, whereas in the basal and middle portions of thalli, the scales of patch and site explained most of the variability.

The SNK test compared the hydroid assemblages of the three portions of thallus (Table 4), showing that, at the scale of sector, there was no significant difference in the assemblages structure among the three portions. Significant differences were observed at the scale of patch, with the basal portion showing a greater variability than that of the medium and the distal portion. At the scale of thallus and site, no significant difference was observed between the basal and the medium portion.

The number of species in the three portions of thalli varied inconsistently at the scale of both sectors and

Table 4

Analysis of variance testing effects of spatial scale and portion of the thallus on multivariate variability

Source	df	MS	F	P	SNK			
					Scale	Portion		
Scale=S	3	0.105	1235.360		Sector	B=M=D	Basal	Se=Si<Pa<Th
Portion=Po	2	0.002	17.290		Site	B=M<D	Middle	Se=Si<Pa<Th
S×Po	6	0.001	14.720	0.000	Patch	B>M>D	Distal	Se=Si=Pa<Th
Residual	12	0.000			Thallus	B=M>D		
Total	23							

C=0.4982 (not significant)

Replicate estimates of pseudo-variance multivariate components, for each of the three portions of the thallus were obtained using MS from PERMANOVAs (see text for further details).

Table 5
ANOVA on the total number of taxa of hydroids

Source	df	MS	F	P	F-versus
Sector=Se	5	12.839	2.480	0.092	Si(Se)
Site=Si(Se)	12	5.176	1.165	0.374	Pa(Se(Si))
Patch=Pa(Si(Se))	18	4.442	4.646	0.000	Residual
Portion=Po	2	105.840	14.225	0.001	Po×Se
Po×Se	10	7.440	3.182	0.011	Po×Si(Se)
Po×Si(Se)	24	2.388	1.326	0.217	Po×Pa (Se(Si))
Po×Pa(Si(Se))	36	1.800	1.883	0.001	Residual
Residual	972	0.956			
Total	1079				

patches (Table 5). *Post-hoc* comparisons of Po×Pa(Se(Si)) interaction revealed no significant difference in number of species across portions of thalli in 16 tests out of 36. In the remaining cases, the basal portion accounted for a significantly higher number of taxa than the other two portions, and in six cases this number of species of the basal portion was comparable to that of the middle portion. The distal portion of thalli had a significantly lower number of species than that of the other two portions. *Post-hoc* comparison of significant Po×Se term showed similar patterns of higher number of species on basal portions, where differences resulted to be not significant in 2 cases out of six (i.e., at sector 2 and 6).

4. Discussion

Our results show that the patterns of hydroid distribution are significantly different on the three portions of *Cystoseira* thalli. The highest number of taxa was often recorded on the basal portion and, even though most of the selected species settled on the three portions of thalli, a suite of species was present exclusively on the base (*R. nudus*, *Eudendrium fragile*, *Orthopyxis crenata*). As a consequence, an overall pattern of distribution emerges, with decreasing epiphytes presence from basal and middle portions to the distal one, this often being less inhabited by hydroids than the other two. These differences, however, vary significantly across scales. Hydroid colonization of *Cystoseira* can occur differently along each thallus, with patterns of variation in the structure of assemblages at an even smaller spatial scale than that of single plants. Our results concur with several qualitative descriptions available in the literature for other algal substrates. Katô et al. (1961), for instance, observed that different hydroid species may occupy specific regions of algal thalli. Non-random patterns of distribution of epiphytic hydroids were also observed on other *Cystoseira* species

(Otero-Schmitt and Perez-Cirera, 1996), on the alga *Halimeda tuna* (Llobet et al., 1991), on the seagrasses *P. oceanica* (Hughes et al., 1991), and *Amphibolis griffithii* (Borowitzka et al., 1990; Watson, 1992). These Authors interpreted the differences on the basis of interspecific niche-selection enabling successful competition for space with other hydroids, algae and bryozoans. However, it has been also suggested that biological factors seem to have little influence on hydroids living on *Cystoseira*, while abiotic factors (especially wave action) could have the greatest importance in determining their distribution (Faucci and Boero, 2000). In our view, competitive interactions, patterns of recruitment, and aggregative behaviours are possibly driven by the gradient of environmental conditions and by the seasonal turnover of the supporting alga. The basal portion of the thallus, in fact, is more sheltered than the distal end, this being more subjected to disruptive wave action and to seasonal shedding of algal portions. Furthermore, the structural complexity of the algal thallus is not homogeneous: the base provides a more complex three-dimensional biogenic structure than the distal portion (Rossi et al., 2000; Chemello and Milazzo, 2002), possibly providing a higher number of potential microhabitats for epiphytes. A single thallus, thus, is not the lowest spatial scale of observation for analysing patterns of distribution of sessile epiphytes. A complex suite of factors, possibly changing in space and time, contributes to generate further differences inside each thallus.

Scale-dependent variation in hydroid assemblages has been reported (e.g., Boero, 1981, 1984; Faucci and Boero, 2000) but never explicitly quantified experimentally. The experimental design allowed a formal analysis of the interactive effect of spatial scale vs. portion of thalli on multivariate variability of hydroid distribution. In accordance with other studies, the scale of thalli had always the largest effect on the multivariate variability of the structure of hydroid assemblages on the three portions of thallus. The spatial scale of sector did not add much to the multivariate effect provided by the scale of site and, at this scale, there was no significant difference in the multivariate variability among the three portions. This is in agreement with the general recognition that, in the majority of investigated ecological systems, most variability occurs at local scale (see Frascchetti et al., 2005 for a review) and that, in some cases, variability decreases with the increase of spatial scale.

Most of the species identified in this study reproduce by fixed gonophores. The abolition of the medusa stage is very common in the hydrozoa (Boero and Bouillon, 1993): lack of a long-lived planktonic stage ensures the

permanence of a given hydroid stock at a favourable position. The trade-off for this advantage might be high rates of inbreeding and high risks of local extinction. Positive relationships between larval dispersal and geographic range of distribution have been frequently discussed and contradicted for most of invertebrates (especially for molluscs, see Scheltema, 1995) revealing that contrasting patterns have been shown for different groups of invertebrates. For hydroids, Boero and Bouillon (1993) could not find any correlations between the presence of medusae in the life cycles and the rates of endemism or cosmopolitanism of Mediterranean species. Cornelius (1992) suggested that rafting is an efficient way of dispersal for hydroids, and this should be particularly true for those living on *Cystoseira*, whose thalli fall off seasonally and are transported by currents with their epiphytic load. In this way, hydroids can remain constantly associated with their supporting algae, reducing the risk of overdispersal linked to a long-lived planktonic medusa. Johannesson (1988) predicted that, if the dispersal mode had an effect on assemblages featured by species with complex life cycles, species composition should be more variable at small spatial scales in respect to larger ones. Our results suggest that various influences on spatial distribution obscure any potential effects related on dispersal mode, leading to inconsistent patterns of variability with spatial scale. The challenge is to unravel between intrinsic processes (such as those clearly linked to organism dispersal properties) and other ecological processes likely determining complex spatial patterns of distribution of species assemblages.

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