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ORIGINAL ARTICLE

Epibiont community variation on two morphologically different hydroid colonies: *Amphisbetia operculata* and *Plumularia setacea* (Cnidaria, Hydrozoa)

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Abstract

Information on differential fouling abundance and seasonal variation of hydroid colonies is scant. These biological structures seem to be relevant for recruitment of other taxa. In this sense, the present study provides information about vagile and sessile organisms on two morphologically different hydroid colonies, *Amphisbetia operculata* and *Plumularia setacea*, during all four seasons. Both species are frequent components of the benthic rocky outcrop community of Mar del Plata (Argentina). A total of 49 epizoites on *A. operculata* and 44 on *P. setacea*, belonging to 12 divisions/phyla were identified. The main groups found on both colonies were bryozoans, crustaceans and molluscs. In both basibiont hydroids, epibiont species coverage, richness and composition changed between the studied seasons, but total colony height did not influence total coverage. Morphological differences between the two hydroid colonies determined coverage differences at two colony heights and the type of attached organisms that could be found on these colonies. Algae and filamentous invertebrates are very scarce in the studied community, and thus *A. operculata* and *P. setacea* appear as the unique and frequent arborescent structures multiplying the available substrata in the analysed outcrops. Thus, hydroid colonies might play an important role providing habitats for epibionts. Furthermore, the morphological differences between both hydroids may determine coverage difference and the kind of attached organisms found on these colonies.

Key words: Benthic communities, epibiosis, hydroid colonies, southwestern Atlantic

Introduction

Epibiosis is a general and broad term that refers to a non-symbiotic, facultative relationship between two species. It is the spatial association between an organism acting as substrate (basibiont) and a sessile organism (epibiont) attached to the basibiont's outer surface (Wahl 2009). In fact, many benthic groups (e.g. ascidians, bryozoans, sponges, molluscs, crustaceans, cnidarians) may act as basibiont and/or epibiont (Davis & White 1994; Wahl & Mark 1999). In marine ecosystems epibiosis is a common phenomenon, more frequently found on hard substrata where competition for space may be strong (Wahl 1989; Wahl & Mark 1999).

Hydroids appear as frequent substrate-generalist epibionts, because due to their small size they can colonize several biological substrates (Boero 1984; Gili & Hughes 1995; Oliveira & Marques 2007; Genzano et al. 2009). They also colonize stems of hydroid colonies of conspecifics (autoepizoism, see Millard 1975) as well as other hydroid species (Genzano et al. 2009; Jaubet & Genzano 2011).

On the other hand, large hydroid colonies can potentially play an important role as a basibiont for many organisms. Their fast growth by means of asexual reproduction enables them to increase their biomass quickly, multiplying the substrate available for organisms that can attach to them (Round et al. 1961; Hughes 1975; Boero 1984; Gili & Hughes

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1995; Di Camillo et al. 2005; Zintzen et al. 2008). Hydroid colonies present a filamentous structure that rises several centimetres from the sea floor. Thus, they influence different physical factors, particularly current velocity and sediment deposition and the distribution of epizoites on them (Hughes 1975; Harvey & Bourget 1997; Bourget & Harvey 1998).

On sublittoral outcrops off Mar del Plata (Argentina), two hydroid species may play an important role as basibionts: *Amphisbetia operculata* (Linnaeus, 1758) (Hydrozoa, Sertulariidae) and *Plumularia*

setacea (Linnaeus, 1758) (Hydrozoa, Plumulariidae) (Figure 1). Both species are very abundant throughout the year, forming dense clumps which can reach several centimetres in height. In addition, these hydroid colonies appear as the unique filamentous structure in the area (Genzano et al. 2011), as algae are scarce and markedly seasonal. Consequently, their presence represents available substrata for the attachment of other organisms. However, information on the specific richness and seasonal epibiont abundances together with the influence of colony morphology over epibiont coverage is scant.

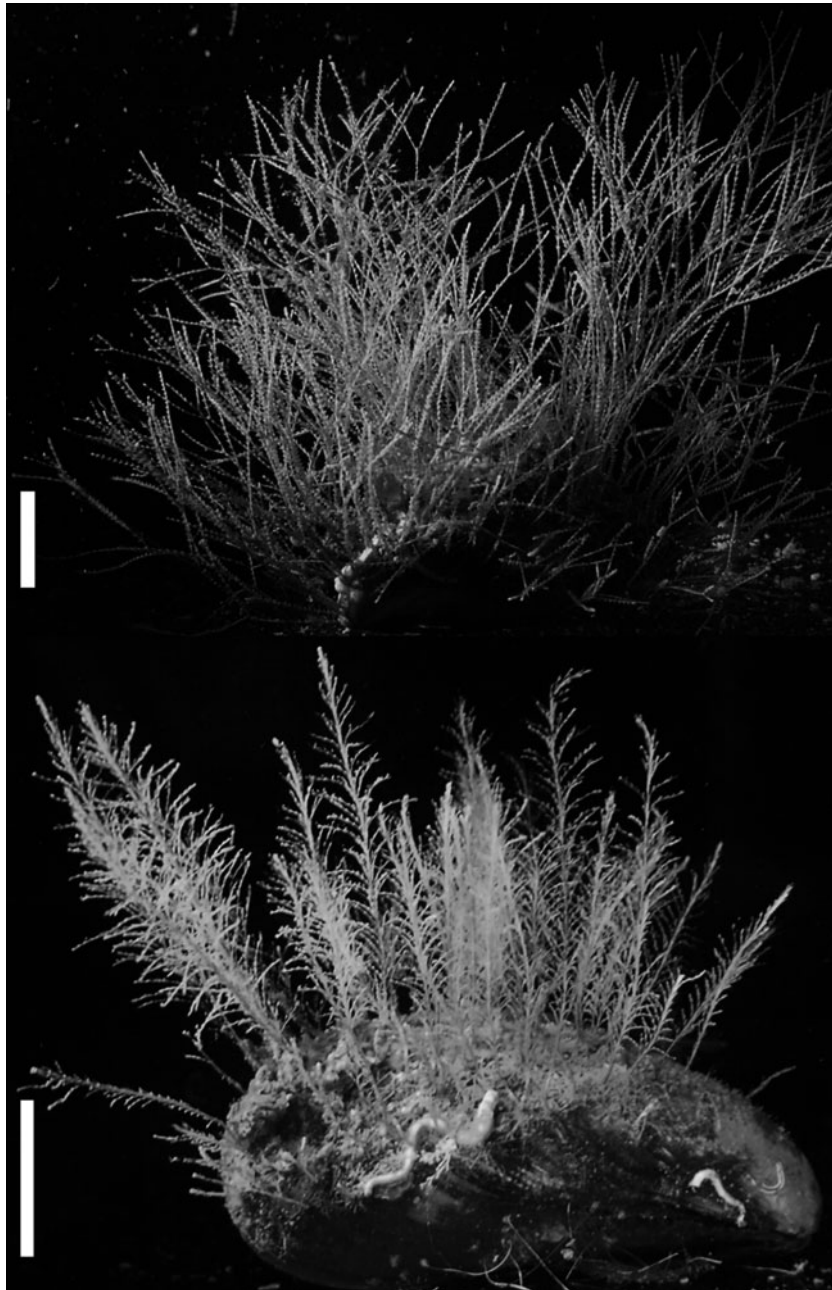


Figure 1. *Amphisbetia operculata* (upper panel) and *Plumularia setacea* (lower panel) colonies on *Mytilus edulis*. Scale bars: 1 cm.

Therefore, the main aim of this study was to analyse and compare the epibionts attached to *A. operculata* and *P. setacea* from sublittoral rocky outcrops off Mar del Plata. Seasonal changes and variations in epizoite coverage at different heights on basibionts were evaluated. Characters of basibionts influencing or determining epibiont coverage are also discussed.

Materials and methods

Amphisbetia operculata and *Plumularia setacea* colonies were randomly collected every month between November 2000 and September 2001. Sampling was performed on the rocky outcrop named Banco del Medio (38°10'S–57°28'W, 18–20 m depth), Mar del Plata (Argentina), by means of SCUBA diving. This outcrop consists of large fragmented quartzite boulders, with a small slope, so depth is relatively constant. The sublittoral rocky area constitutes the largest hard substrate in the zone. The area is affected by a littoral current (south to north), semi-diurnal tidal currents and high-energy waves; storms and winds from the SE are frequent, mainly in autumn and winter (Lanfredi et al. 1992). Storms and winds, particularly, produce sediment resuspension. Consequently, diving is usually undertaken under dangerous conditions, with water visibility ranging between 0.5 and 6 m, average 3 m. Water temperature is variable through the year; maximum summer values reach 18–19°C and minimum winter values of 7–8°C were recorded (see Genzano et al. 2011 for more details).

During the SCUBA sampling, hydroid colonies were collected by hand and placed in plastic bags. Colonies were immediately preserved in a 5% formaldehyde seawater solution (42 and 55 colonies of *A. operculata* and *P. setacea*, respectively). Large colonies of *A. operculata* and *P. setacea* are important to organisms which live attached to their stems, as well as for different mobile species. Unfortunately, as diving conditions were treacherous, during each underwater sampling colonies from the same hydroid species were stored together, i.e. all *A. operculata* colonies collected during a sampling month were kept in the same bag but separately from *P. setacea* colonies. This procedure only allowed us to perform an inventory list of all mobile fauna found on each hydroid species as epibionts could move from one colony to another. Under a stereomicroscope all mobile and attached organisms were identified at the lowest possible taxonomic level. Data were grouped according to the seasons of the year.

In order to standardize the measurement of the abundance of solitary and colonial attached organisms, the percentage of coverage for each epibiont

species was calculated. To accomplish that, each colony of both species was extended and branches carefully separated over a Petri dish previously marked with 200 points at random. All the points that coincided with stems of the colony and those that coincided with some particular sessile organism were counted, estimating their coverage over the colony as percentage. Also, the frequency of occurrence of all epibiont groups was calculated as the number of hydroid colonies with a particular epibiont attached over the total of colonies analysed. Thus, differences between the studied seasons in epibiont coverage, richness and frequency of occurrence were measured. Total colony heights (from the hydrorhizae to the top of the colonies) of all analysed colonies were also measured.

To analyse epibiont coverage variation we assessed whether total coverage (dependent variable) varied with the explanatory variables of colony height (basibiont size effect), period of the year (studied seasons) and among basibiont species (differences between *A. operculata* and *P. setacea*). To accomplish that, generalized linear models (GLM) were built. These models have a binomial distribution and their canonical link was specified (Crawley 2005; Zuur et al. 2009). Additionally, similar GLMs were built to determine the influence of colony height, season of the year and basibiont species (explanatory variables) on total richness (dependent variable). These models have a Poisson distribution and the canonical link was specified (Crawley 2005; Zuur et al. 2009). Model selection was performed using information theoretic procedures (IT; Crawley 2005; Symonds & Moussalli 2011). During the comparison procedure, we first constructed a global model (i.e. with all independent variables) so that we had a reference point. Then, models with different numbers and combinations of the explanatory variables and a model without any of the independent variables (i.e. null model) were fitted. Thus, models with all possible combinations of variables were considered. Model comparisons were made with the Akaike information criterion for small samples (AICc), differences in AICc (Δi) and AIC weights (w_i) (Johnson & Omland 2004; Symonds & Moussalli 2011). When several models presented a good fit ($\Delta i < 2$), model averaging was performed between them. To supplement parameter likelihood evidence, 95% confidence intervals were also calculated for all estimated parameters in each selected model.

Furthermore, a similarity percentages routine (SIMPER) was used to identify those species which contributed most to dissimilarities among hydroid basibiont species and the studied seasons (groups). This analysis calculates the contribution of each species to the overall dissimilarity between the

groups considered (average dissimilarity) and the overall average dissimilarity between pairs of groups was considered (Clarke & Warwick 2001).

The percentage of epizoic organisms over different heights of both basibionts was also evaluated. To accomplish that, hydroid colonies were divided at their proximal zone (the first 3 cm from hydrorhizae) and their distal zone (from the upper proximal zone to the top of the colonies). Coverage variations in different zones were analysed using a Wilcoxon test.

All statistical analyses were performed with the Open Access Software R (R Development Core Team 2011). Model selection and averaging were calculated with the *MuMIn* package (Barton 2009) that has a range of functions to automate an IT-AIC approach. A SIMPER analysis was performed with the *vegan* package (Oksanen et al. 2013).

Results

Sessile and mobile macrobenthic species found on colonies of both hydrozoans are listed in Table I. A total of 49 epizoites on *Amphisbetia operculata* and 45 on *Plumularia setacea* were identified. Arthropods, hydrozoans and bryozoans were the most represented groups in number of species. Only 14 epibiont species were found exclusively on *A. operculata* while 10 species were exclusive on *P. setacea*. Information on mean coverage and frequency of occurrence of all the species attached over the colonies of both

hydrozoan basibionts are presented in Tables II and III.

The GLM analyses of total coverage variation indicated that two models had presented the highest weighted AICc and better fit, including the explanatory variables, season and basibiont species. These models account for 92% of the variation in total coverage throughout the year (Table IV). Because both models presented $\Delta i < 2$, an average model was obtained. Season was the most important variable explaining total coverage variation over both hydroid species. Furthermore, there was no difference in total coverage between basibiont species (confidence intervals including zero) (Table IV). The relative abundance of epibionts on *A. operculata* was high during summer and autumn (54.4% and 55.8%, respectively), decreasing during winter (16.5%). Likewise, *P. setacea* total coverage varied between a minimum during winter and a maximum during summer (37.5% and 65% coverage, respectively) (Tables II, III; Figure 2). Because colony height was excluded from model analyses, this variable did not influence total epibiont coverage, at least for the range of colony sizes analysed in this study. It is noteworthy that some of the studied colonies of both hydroid species were almost completely or completely covered with epibionts throughout the year.

In the same way, the GLM analyses of richness variation indicated that three models had presented the highest weighted AICc and better fit, including the explanatory variables season, basibiont height

Table I. List of the taxa observed on *Amphisbetia operculata* and *Plumularia setacea* clumps at the sublittoral outcrop of Mar del Plata. (*) taxa used in quantitative analysis; (Ao) epizoites found only on *A. operculata* clumps; (Ps) epizoites found only on *P. setacea* clumps; (Ec) ecto-parasitic organisms.

Algae	<i>Rhodymenia</i> sp.(*) ; <i>Pterisiphonia</i> sp.(*) ; <i>Polysiphonia</i> sp. ^(Ps) ; <i>Ceramium</i> sp. ^(Ps) ; <i>Ulva lactuca</i> (L.) ; Chlorophyta genus et species indet (*)
Porifera	<i>Tedania</i> sp. ^(Ao) ; <i>Callyspongia</i> sp. ^(Ao) ; Genus et species indet.(*)
Cnidaria	<i>Filicellum</i> sp. (*) ; <i>Sertularella mediterranea</i> Hartlaub, 1901 ^(Ps) ; <i>Sertularella striata</i> Stechow, 1923 (*) ^(Ps) ; <i>Clytia gracilis</i> (Sars, 1850)(*) ; <i>Obelia dichotoma</i> (Linnaeus, 1758) (*) ; <i>Campanularia agas</i> Cornelius, 1982(*) ; caulus indet.(*) ; <i>Ectopleura crocea</i> (Agassiz, 1862) ^(Ps) ; <i>Halecium beanii</i> (Johnston, 1838) ^(Ao) ; <i>Halecium delicatum</i> Coughtrey, 1876 ^(Ao) ; <i>Anthothoe chilensis</i> (Lesson, 1830) ^(Ao)
Platyhelminthes	<i>Notoplana</i> sp.
Nematoda	Genus et species indet. ^(Ao) ; <i>Deontostoma conicum</i> Pastor de Ward, 1995 ^(Ps)
Bryozoa	<i>Aetea anguina</i> (Linnaeus, 1758)(*) ; <i>Bugula</i> sp.(*) ; <i>Bicellarella</i> sp.(*) ^(Ps) ; <i>Celleporella</i> sp.(*) ; <i>Osthimosia</i> sp.(*) , <i>Membranipora</i> sp.(*)
Annelida	<i>Halosydnella australis</i> (Kinberg, 1856) ; Polynoidae genus et species indet. ^(Ao) ; <i>Alitta succinea</i> (Leuckart, 1847) ; Nereididae genus et species indet. ; <i>Syllis gracilis</i> Grube, 1840 ; <i>Syllis prolixa</i> Ehlers, 1901 ; <i>Procerastea halleziana</i> Mallaquin, 1893(*) ^(Ec) ; <i>Diopatra viridis</i> Kinberg, 1865 ; Serpulidae genus et species indet.
Mollusca	Oviposition indet. ; <i>Chaetopleura</i> sp. ^(Ps) ; <i>Crepidula</i> sp. ; <i>Costoanachis sertulariarum</i> (d'Orbigny, 1839) ; <i>Mytilus edulis</i> Linnaeus, 1758(*)
Arthropoda	Tubes of Gammaridea(*) ; Pycnogonida genus et species indet. ^(Ao) ; <i>Achelina assimilis</i> (Haswell, 1885) ^(Ao) ; <i>Tanystylum orbiculare</i> (Wilson, 1878) ^(Ao) ; protonymphon larvae ^{(Ps)(Ec)} ; <i>Monocorophium insidiosum</i> (Crawford, 1937) ; <i>Jassa falcata</i> (Montagu, 1808) ; <i>Caprella eximia</i> Mayer, 1890 ; <i>Idotea balthica</i> (Pallas, 1772) ; Tanaidacea genus et species indet. ^(Ps) ; <i>Pleoticus muelleri</i> (Spence Bate, 1888) ^(Ao) ; <i>Pachycheles laevidactylus</i> Ortman, 1982 ^(Ao) ; <i>Platyxanthus crenulatus</i> A. Milne-Edwards, 1879 ^(Ao) ; <i>Leucippa pentagona</i> H. Milne Edwards, 1834 ^(Ao)
Echinodermata	<i>Ophioplocus januarii</i> (Lütken, 1856)
Chordata	<i>Molgula</i> sp.

Table II. Mean coverage (% \pm SEM) and frequency of occurrence (in parentheses, %) of epizoitic taxa on the basibiont *Amphisbetia operculata*. Su, summer; A, autumn; W, winter; Sp, spring.

Epizoites	Su	A	W	Sp
Richness	9	7	9	3
Colonies analysed	13	6	13	10
Division Rhodophyta				
<i>Pterosiphonia</i> sp.	1.9 \pm 1.1(23.1)	–	–	–
Division Chlorophyta				
Genus et species indet.	0.5 \pm 1.1(7.7)	–	0.5 \pm 1.1(7.7)	–
Phylum Porifera				
Genus et species indet.	–	–	1.4 \pm 0.7(30.8)	–
Phylum Cnidaria				
<i>Clytia gracilis</i>	5.3 \pm 2.4(53.9)	3.8 \pm 2.5(33.3)	–	–
Phylum Bryozoa	18.4 \pm 4.5(92.3)	23.8 \pm 6.9(83.3)	72 \pm 2.5(69.2)	1 \pm 0.7(20)
<i>Aetea anguina</i>	3.8 \pm 2.3(23.1)	5.3 \pm 3.4(33.3)	2.1 \pm 2.1(7.7)	–
<i>Bugula</i> sp.	–	0.7 \pm 0.7(16.7)	0.3 \pm 0.3(7.7)	–
<i>Celleporella</i> sp.	5.3 \pm 1.9(46.2)	2.4 \pm 2.4(16.7)	0.9 \pm 0.6(15.4)	1 \pm 0.7(20)
<i>Osthimosia</i> sp.	9.3 \pm 4.8(46.2)	15.5 \pm 7.7(50)	3.9 \pm 1.4(46.2)	–
Phylum Annelida				
Tubes of <i>Procerastea halleziana</i>	0.3 \pm 0.3(7.7)	–	2.8 \pm 1.5(23.1)	16.7 \pm 3.7(100)
Phylum Mollusca				
<i>Mytilus edulis</i>	15.9 \pm 3.3(92.3)	8.0 \pm 3.5(83.3)	1.7 \pm 1(23.1)	23.3 \pm 23.3(100)
Phylum Arthropoda				
Tubes of Gammaridea	12.1 \pm 3.8(69.2)	20.1 \pm 8.2(83.3)	3.0 \pm 1.3(38.5)	–
Total abundance	54.4 \pm 6.3	55.8 \pm 14.4	16.5 \pm 4.2	41 \pm 5.7

Table III. Mean coverage (% \pm SEM) and frequency of occurrence (in parentheses, %) of epizoitic taxa on the basibiont *Plumularia setacea*. Su, summer; A, autumn; W, winter; Sp, spring.

Epizoites	Su	A	W	Sp
Richness	14	7	3	12
Colonies analysed	12	15	7	21
Division Rhodophyta				
<i>Rhodymenia</i> sp.	2.8 \pm 1.1(28)	1.7 \pm 1.7(6.7)	–	0.8 \pm 0.8(4.8)
<i>Pterosiphonia</i> sp.	2.1 \pm 1.1(25)	1.7 \pm 1.7(6.7)	–	0.8 \pm 0.8(4.8)
<i>Pterosiphonia</i> sp.	0.7 \pm 0.7(8.3)	–	–	–
Division Chlorophyta				
Genus et species indet.	3.7 \pm 2.3(33.3)	1.8 \pm 1.3(13.3)	–	8.1 \pm 2.6(47.6)
Phylum Cnidaria	8.7 \pm 3.8(41.7)	–	3.1 \pm 2.2(28.6)	4.3 \pm 1.8(33.3)
<i>Clytia gracilis</i>	1.0 \pm 1.0(8.3)	–	–	1.1 \pm 0.5(19.1)
<i>Obelia dichotoma</i>	–	–	3.1 \pm 2.2(28.6)	–
<i>Campamularia agas</i>	0.5 \pm 0.5(8.3)	–	–	–
<i>Sertularella striata</i>	0.3 \pm 0.3(33.3)	–	–	1.0 \pm 0.6(14.3)
<i>Filellum</i> sp.	6.8 \pm 3.1(33.3)	–	–	–
Caulus indet.	–	–	–	2.2 \pm 1.6(14.3)
Phylum Bryozoa	22.4 \pm 6.0(75)	2.9 \pm 1.9(20)	5.9 \pm 3.9(42.9)	13.2 \pm 4.1(52.4)
<i>Aetea anguina</i>	8.5 \pm 2.8(58.3)	–	5.9 \pm 3.9(42.9)	9.6 \pm 3.1(42.9)
<i>Bugula</i> sp.	9.2 \pm 3.2(50)	0.9 \pm 0.7(13.3)	–	2.3 \pm 1.4(14.3)
<i>Bicellariella</i> sp.	2.7 \pm 1.3(16.7)	–	–	–
<i>Celleporella</i> sp.	–	1.3 \pm 1.1(13.3)	–	0.3 \pm 0.3(4.8)
<i>Osthimosia</i> sp.	1.9 \pm 1.4(16.67)	0.7 \pm 0.7(6.7)	–	–
<i>Membranipora</i> sp.	–	–	–	1.0 \pm 0.8(9.5)
Phylum Annelida				
Tubes of <i>Procerastea halleziana</i>	–	–	–	3.5 \pm 1.5(28.6)
Genus et species indet.	1.7 \pm 1.4(16.7)	–	–	–
Phylum Mollusca				
<i>Mytilus edulis</i>	12.9 \pm 4.7(50)	1.5 \pm 1.2(13.3)	–	8.4 \pm 3.3(52.4)
Phylum Arthropoda				
Tubes of Gammaridea	13.7 \pm 3.9(58.3)	31.3 \pm 4.0(93.3)	28.5 \pm 8.8(100)	11.8 \pm 2.8(61.9)
Total abundance	65 \pm 11.7	39.3 \pm 4.6	37.5 \pm 3.9	50.1 \pm 8.1

Table IV. Generalized linear models explaining variation in total coverage (A) and total richness (B) on *Amphisbetia operculata* and *Plumularia setacea* (Ps) clumps due to the basibiont high (H), seasons (S) and among basibiont species (Bs). The null model, global model and models with a support up to $\Delta i < 2$ are provided. Models are listed in decreasing order of importance. Additionally, parameter estimate (\pm SE), confidence interval and relative importance of each variable is given after model averaging. Parameter estimates are weighted averages (using model AICc weights) from models with $\Delta i < 2$. k , number of model parameters; AICc, Akaike information criterion for small samples; Δi , AICc differences; w_i , normalized weights of AICc; CI, Confidence intervals. The variable season is relative to summer. The variable epibiont is relative to *A. operculata*.

Models	k	AICc	Δi	w_i	Explanatory variable	Relative importance	Parameter estimate \pm SE	CI	
								Lower	Upper
(A) Total coverage $n = 97$									
S	1	867.2	0	0.50	Intercept		1.16 (0.29)	0.41	1.79
S + Bs	2	867.5	0.34	0.42	S-<i>autumn</i>	0.92	-1.06 (0.15)	-1.35	-0.76
S + Bs + H	3	870.9	3.68	0.08	S-<i>winter</i>		-1.75 (0.18)	-2.10	-1.36
Null	0	988.0	120.88	0.00	S-<i>spring</i>		-0.97 (0.13)	-1.23	-0.71
					Bs - Ps	0.42	0.18 (0.13)	-0.08	0.45
(B) Total richness $n = 97$									
S	1	360.6	0	0.51	Intercept		1.33 (0.16)	1.02	1.64
S + H	2	362.3	1.70	0.22	H	0.22	0.02 (0.02)	-0.03	0.07
S + Bs	2	362.6	2.00	0.19	S-<i>autumn</i>	0.92	-0.56 (0.18)	-0.92	-0.20
S + Bs + H	3	364.6	3.98	0.07	S-<i>winter</i>		-0.58 (0.19)	-0.95	-0.22
Null	0	369.8	9.20	0.01	S- <i>spring</i>		-0.29 (0.15)	-0.59	0.001
					Bs - Ps	0.19	-0.06 (0.13)	-0.31	0.19

and basibiont species. These models account for 92% of the variation in total richness throughout the year (Table IV). As models presented $\Delta i < 2$, an average model was obtained. Season was the most important variable explaining richness variation over both hydroid species. Colony height and basibiont species did not influence total epibiont richness (confidence intervals including zero; Table IV). Epibiont richness presented a similar pattern to the abundance variation throughout the studied seasons. Although this pattern is not obvious in *A. operculata*, this relationship is more evident in *P. setacea* (Tables II, III). In the latter, higher values were found during summer and decreased during winter (reaching 14 and three species, respectively; Figure 2).

The overall epibiont coverage dissimilarity and the epibiont group's contributions to dissimilarities

between basibionts and seasons for both hydroid species are shown in Table V. According to SIMPER analysis, there are differences in the coverage and kind of attached organisms found on both colonies. The overall epibiont coverage dissimilarity between both basibiont species was 78.11%. The epibiont groups with the highest percentage of contribution to this dissimilarity were crustaceans, which contributed to the greatest dissimilarity (26.13%) between *A. operculata* and *P. setacea*, while molluscs and bryozoans contributed 16.49% and 16.37%, respectively. The remaining epibiont groups made a minor contribution to dissimilarity between both basibiont species (Table V).

Species with the highest percentage contribution to coverage dissimilarity between seasons in *A. operculata* were bryozoans, crustaceans and molluscs,

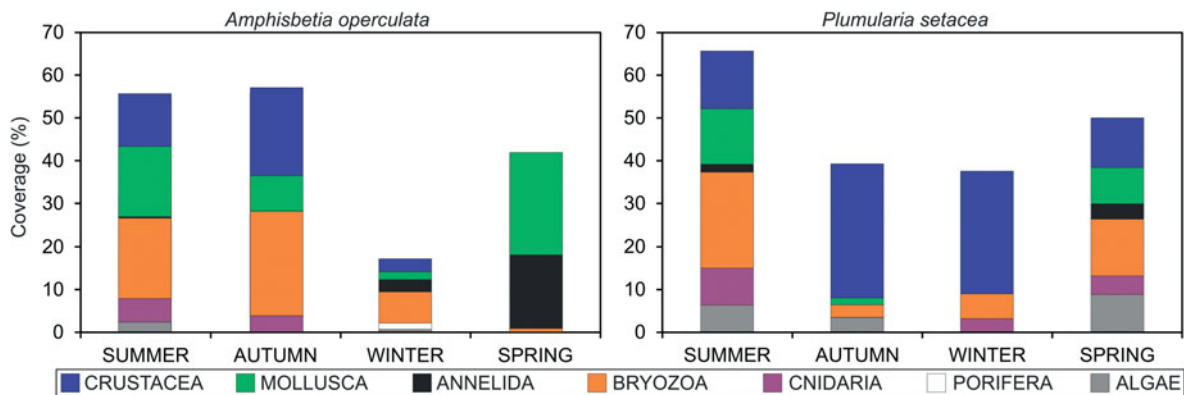


Figure 2. Cumulative percentage of coverage of each taxonomic group on the basibionts *Amphisbetia operculata* and *Plumularia setacea* colonies throughout seasons.

Table V. Percentage of contribution (SIMPER) of epibiont groups in the coverage dissimilarity between both hydroid basibionts (A) and between the sampled seasons for each hydroid basibiont species (B). Ao, *Amphisbetia operculata*; Ps, *Plumularia setacea*; Al, Algae; An, Annelida; Br, Bryozoa; Cn, Cnidaria; Cr, Crustacea; Mo, Mollusca; Po, Porifera; OAD, Overall average dissimilarity.

Comparisons groups	Epibiont groups							
	Br	Cr	Mo	An	Cn	Al	Po	OAD
(A) Ao – Ps	26.13	16.49	16.37	6.91	5.84	5.32	1.05	78.11
(B) Su – Au	18.48	16.14	12.17	0.40	5.80	3.61	0	56.59
Ao Su – Wi	22.05	13.86	20	3.72	6.67	7.52	3.23	77.05
Su – Sp	18.8	11.12	14.61	16.76	5.13	3.45	0	69.85
Au – Wi	27.33	21.36	10.01	3.58	3.31	7.88	3.61	77.07
Au – Sp	22.29	17.9	20.14	17.79	2.80	3.27	0	84.19
Wi – Sp	9.02	5.82	35.66	23.59	0	7.81	3.75	85.65
Ps Su – Au	18.39	29.56	10.82	0	8.93	3.92	–	71.63
Su – Wi	21.56	22.7	11.9	0	11.46	3.48	–	71.09
Su – Sp	19.25	18.74	12.64	1.29	10.86	6.27	–	69.05
Au – Wi	8.39	31.58	0.42	0	3.62	1.55	–	45.55
Au – Sp	8.44	25.02	6.05	1.41	4.43	5.30	–	50.65
Wi – Sp	10.7	24.06	6.86	1.57	7.50	4.64	–	55.33

changing their contribution values between pairs of seasons considered (Table V). A notable difference between the analysed seasons was due to the tubiculous annelid *Procerastea halleziana* Mallaquin, 1893 which exhibited the highest coverage during spring (16.7%). The blue mussels (*Mytilus edulis* Linnaeus, 1758) were more abundant during spring and summer (23.3% and 15.9%, respectively). Tubes of gammarids reach maximal coverage values during summer and autumn (12.1% and 20.1%, respectively), and colonies of the hydroid *Clytia gracilis* (Sars, 1850) are present only during these seasons. Instead, bryozoans, mainly *Celleporella* sp., *Osthimosia* sp. and *Aetea anguina* (Linnaeus, 1758), reach their highest coverage only during autumn (23.8%) (Table II, Figure 2).

As with *A. operculata*, there are differences in epibiont coverage during the studied seasons for *P. setacea* (Table III, Figure 2). Species making the highest percentage contribution to this dissimilarity were crustaceans, bryozoans, molluscs and cnidarians, changing their contribution percentages between the pairs of seasons considered (Table V). The more remarkable differences are mainly due to

tubes of gammarids, which dominate during autumn and winter (31.3% and 28.5% coverage, respectively). However, blue mussels and bryozoans (mainly *A. anguina* and *Bugula* sp.) were the most abundant during spring–summer (8.4–12.1% and 13.2–22.4%, respectively; Table III, Figure 2).

The remaining species on both hydroid basibionts presented low coverage and frequency of occurrence (Tables II, III) and represented a minor contribution to dissimilarity between the analysed seasons (Table V). Therefore, they were considered as occasional associates.

The analysis of coverage variation on different zones of the hydrocaulus indicated that, for *A. operculata* colonies, the proximal zone was the most colonized by epizoites (Wilcoxon test, $T = 803$, $P < 0.0001$, Figure 3). The main groups found here were bryozoans and mytilids, although annelids, crustaceans, bryozoans and mytilids were found on both the proximal and distal zones. Contrarily, *P. setacea* colonies were practically colonized only at their proximal zone for all epizoite groups (Wilcoxon test, $T = 1804$, $P < 0.0001$, Figure 3).

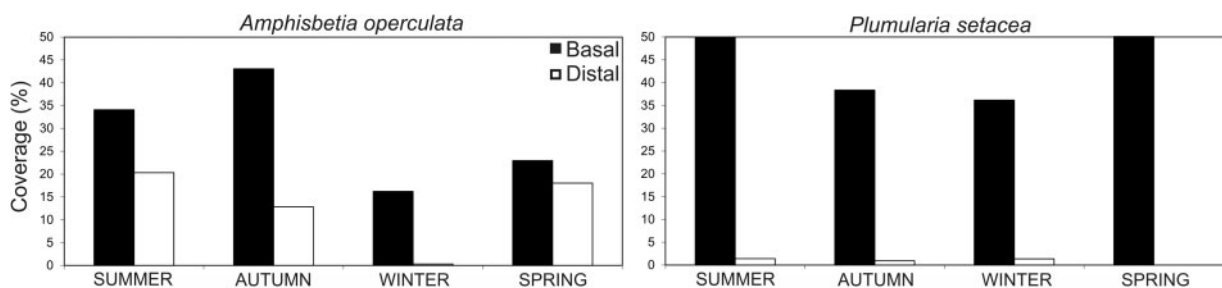


Figure 3. Percentage of coverage of all epizoites found on the basibionts *Amphisbetia operculata* and *Plumularia setacea* throughout seasons in the proximal and distal zones of the colonies.

Discussion

The present study is the first step in understanding the epibiont dynamic over two morphologically different and abundant hydroid colonies, *Amphisbetia operculata* and *Plumularia setacea*. According to Harvey & Bourget (1997) and Bourget & Harvey (1998), filamentous structures could passively influence the settlement of spats. Several organisms attached to primary filamentous structures that rise above the seafloor will allow a high survivorship of larvae during early stages of development, avoiding predation (Moreno 1995). Therefore, filamentous organisms, such as large hydroid colonies, are important physical and biological factors influencing the settlement phase and regulating the abundance and biodiversity of the organisms attached to them. As hard substrata are limited, the basibiont provides the epibiont with this valuable resource and allows them to reach all the required resources that water transports. The numerous vagile and attached epizoites found on both hydroid colonies (Table I) underscore the importance of this phenomenon in the study area. Because the presence of algae or other filamentous invertebrates in the area are scarce and markedly seasonal, *A. operculata* and *P. setacea* appear as the unique and frequent arborescent structures (Genzano et al. 2003; Genzano et al. 2011). They can reach several centimetres in height and form dense clumps, which are present throughout the year in high frequencies and abundances (Genzano et al. 2002), multiplying the available substrata on the analysed outcrops. Furthermore, in this study we found that both colonies present high epibiont coverage and richness values throughout the year. These morphological and ecological characteristics favour epizoism. Thus, *A. operculata* and *P. setacea* might play an important role in generating habitats.

Round et al. (1961) reported a larger number of species (99 macro-epibionts) associated with *A. operculata* colonies in Codium Bay (England). Although their work was performed in a different area and they found more species (richness), most of the groups observed by them were also represented in our study. To our knowledge, the present study is the first one analysing the macro-organisms associated with *P. setacea* colonies, as previous works investigated the presence of epibiotic bacteria on this species (Stabili et al. 2008).

The highest richness and coverage values of the attached organisms on colonies of both hydroid species were found during summer. This could be the result of a combination of the epibiont's reproductive period and an increase in the growth rate of the majority of organisms during that season, which

is more pronounced in cold-temperate waters (Gili & Hughes 1995; Kaiser et al. 2005). Even though epibiont coverage on *P. setacea* changes very little throughout the year, species found during each season do change, pointing out an epibiont coverage species composition variation between the studied seasons. This pattern is also observed in *A. operculata* colonies. Furthermore, it is in summer when the highest coverage, frequency of occurrence and heights of hydroid substrate are registered (Genzano et al. 2002). It should be noted that from GLM analyses it was found that total colony height did not influence the level of epibiont coverage and richness in both *A. operculata* and *P. setacea* colonies, at least for the range of colony sizes analysed here.

As previously stated, structures of certain heterogeneity attract mobile fauna, probably as a result of adaptive behaviour. However, such structures are also subjected to settlement by larvae and algal spores and to recruitment by migrating mobile fauna. Also, basibionts may offer both a number and size of spaces that protect an individual from predation and access to the available food. Whether the epibiont-basibiont interactions are specific or not, epizootic organisms obtain different types of benefit by colonizing these hydroid colonies. A taller substrate above the seabed would provide access to currents that offer better resources (van Duren 2007) and avoid the harmful effects of sedimentation. An example of this is that many hydroid species that act as epibionts are more frequently found than other types of substrate (Genzano et al. 2009; Jaubet & Genzano 2011).

Moreover, the hydroid basibionts studied here exhibit morphological differences. In *P. setacea*, as in many Plumulariidae, the type of branching is pinnate, and the main stem (or hydrocaulus) is erect. It is plume-like, i.e. the hydrocaulus is divided into side branches (hydrocladia) which are unbranched and alternate and present numerous nematothecae (defensive structures) containing nematophores full of batteries of nematocysts. By contrast, hydroids of *A. operculata* (Sertulariidae) exhibit a slender and flexible three-dimensionally arranged colony, branching and re-branching dichotomously to form bushy tufts and lack nematothecae (Figure 1) (see Millard 1975 for full morphological description of colonies).

The morphological differences between both hydroids may determine coverage disparities at the proximal and distal zones and the kind of attached organisms that could be found on these colonies. Due to the presence of numerous defensive structures in *P. setacea*, most fouling organisms on these colonies are micro-crustaceans (Gammaridea) and species that build and live in tubes made of various substrates that are cemented together. The chitinous

exoskeleton and the tubes protect them from the action of the nematocysts. This would explain the fact that most organisms are present only on the proximal zone of the plumulariid colonies, as these areas usually lack branches and represent portions of stems without nematothecae (see Figure 1).

Harvey & Bourget (1997) and Bourget & Harvey (1998) showed that the density of recruits of invertebrates that are set in arborescent substrates depends on the diameter and heterogeneity of its ramifications. This determines the abundance and biodiversity (in terms of species richness) of the attached organisms. Thus, it may be assumed that the more complex the basibiont structure is, the greater number of niches it will have. Thereby, they offer a high degree of structural complexity and many niche sizes, which are advantageous for both small and juvenile organisms (Taylor 1998). Bushy colonies of *A. operculata* (Figure 1) would provide refuge and habitats for recruits of other species of invertebrates (e.g. crab juveniles, small shrimp, pycnogonids, mussel spat). This idea was also suggested by Roux et al. (1995), who indicated that sertulariid colonies (unidentified species) could be a refuge for juvenile shrimp in the Gulf San Jorge (Argentina) and Bremec et al. (2008) who noted the importance of *Symplectoscyphus subdichotomus* (Kirchenpauer, 1884) as primary substrate of scallops in the Argentinean shelf break frontal area. In addition, Genzano et al. (2002) remarked on the use of *A. operculata* colonies as a substrate for blue mussel spat, thereby avoiding predation from sea urchins (Genzano et al. 2003).

Nevertheless, for many of the epibionts found on both hydroid colonies both basibionts provided no more than a substrate to cling to, being considered as just 'fouling surfaces'. This is particularly true for vagile species. Thus, most organisms found over both hydroid colonies represent a facultative epizoidal association. However, a more complex inter-specific relationship is present in some organisms. The tubiculous polychaetes *Procerastea halleziana* Malaquin, 1893 and protonymphon pycnogonid larvae are ectoparasites on the colonies and are able to feed by piercing the wall of the hydranths (Genzano 2002; Genzano & San Martín 2002). On the other hand, caprellids are ordinary clepto-commensalids which snatch the food previously caught by the polyps (Bavestrello et al. 1996; Genzano 2002).

Hydroid colonies increase the number of available habitats for organisms. Dynamics of the diverse and profuse assemblage of epibionts indicate that the studied basibiont hydroid species are important components of the benthic communities, providing a substrate for different organisms throughout the

year. This importance is illustrated by the fact that many species that are abundant on these basibionts are rare or absent in the surrounding area (Genzano et al. 2011). Hydroid colonies play a role as substrate-multiplier species generating habitats for many associated organisms. Thereby, they modify the environmental conditions with their own physical structures. To fully understand the effect of these basibiont species over the benthic community, species abundance and diversity should be simultaneously sampled in both hydroid colonies and in the surrounding environment.

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