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Ascidian-associated polychaetes: ecological implications of aggregation size and tube-building chaetopterids on assemblage structure in the Southeastern Pacific Ocean

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Abstract Epifaunal polychaetes inhabit a range of habitat structures built by other organisms, such as ascidians. Here, we examine: i) the polychaete fauna inhabiting aggregations of the ascidian *Pyura chilensis* in central Chile; ii) the relationship between sample volume (aggregation size) and polychaete assemblage variables; and iii) the effect of a tube-building chaetopterid on the polychaete assemblage structure. The chaetopterid tube load on aggregations determines two ascidian morphotypes, those with a high load of chaetopterid tubes (HT morphotype) and those with a low load of chaetopterid tubes (LT morphotype). From a total of 38 aggregations studied, we found 5,524 specimens belonging to 35 species of polychaetes. Three species were the most abundant in the aggregations (*Phyllochaetopterus socialis*, *Nicolea lobulata*, and *Typosyllis magdalena*), reaching 22% of total abundance. The number of species and individuals increased with sample volume, but only the number of species number varied between morphotypes. Sample volume and the

chaetopterid tubes influenced the polychaete assemblage structure, evidencing differences between morphotypes. We suggest that both sample volume and the habitat structuring capacity of the chaetopterid tubes change the habitat complexity of the ascidian aggregations and, hence, produce differences between morphotypes related to the polychaete assemblage structure.

Keywords Habitat complexity · Ecosystem engineering · Diversity · Tube-building · Ascidians

Introduction

Epifaunal polychaetes are an important component of hard and soft bottom marine communities, capable of colonizing a variety of biogenic substrates such as algae (Fredriksen et al. 2005; Sánchez-Moyano and García-Asencio 2009), sponges (Cinar and Ergen 1998), mollusks (Thiel and Ullrich 2002; Vasconcelos et al. 2007), worm tubes (Dubois et al. 2002; Sepúlveda et al. 2003a), crustaceans (Hoberg et al. 1982; Hernández et al. 2001), echinoderms (Britayev and Zamishliak 1996) and ascidians (Fielding et al. 1994; Cerda and Castilla 2001), among others. Within these biogenic habitats, polychaetes may find food and refuge (Woodin 1978; Edgar and Aoki 1993). Moreover, some of these species such as borers, drillers or tube-builders may change the surrounding environmental conditions through perforations, excavations or simply disturbing the surface sediment, thereby affecting the other components of the fauna (Bolam and Fernández 2002; Dubois et al. 2002; Sepúlveda et al. 2003a).

Certain species of ascidians are gregarious and capable of generating complex aggregations of organisms of different sizes living in close proximity. Aggregations of this kind of organisms are called ecosystem engineers (Jones et al. 1994) because they modify the primary substrate, providing

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interstices and holes that serve as habitat for a diverse and abundant marine fauna (Guiler 1959; Cerda and Castilla 2001; Sepúlveda et al. 2003b). They also act as a biogenic substrate since the surface of the aggregation is a suitable substrate for direct settlement of many sessile organisms. Such aggregations therefore enhance local biodiversity by providing living habitats that increase complexity (Voultsiadou et al. 2010). The study of epibionts on ascidian aggregations is increasing because potential changes in the biogenic substrate resulting from disturbance or contamination will also impact the associated fauna (Roberts et al. 2008). Moreover, some ascidians are commercially collected for human consumption and their exploitation might produce cascading effects on the associated communities (Coleman and Williams 2002; Monteiro et al. 2002).

Pyura chilensis Molina, 1782, is a solitary ascidian species that forms massive aggregations and/or patches on the subtidal seafloor, made up of one or several individuals (Guiler 1959). Its geographic distribution range is between 10 and 44°S in the Southeast Pacific Ocean from the intertidal zone to a depth of 70 m (Vásquez 1983; Lancellotti and Vásquez 2000; Astorga and Ortiz 2006). Due to their high commercial value, these ascidian aggregations are locally exploited along the Chilean coast by fishermen who recognize two types of aggregations depending on harvest location, “hairy” and “bald”; these two types can occur within the same area. The difference between aggregations is due to the high or low (or absent) load of tubes built by the chaetopterid polychaete *Phyllochaetopterus socialis* Claparède, 1869, which, when occurring at high densities on some ascidian aggregations, produces the “hairy” appearance. The polychaetes tubes are of considerable size (20–40 mm) and, since they are stiff and located on the surface of the ascidian aggregation, change the external morphology as well as the effective size of the aggregations. Consequently, these tubes may change the hydrodynamics, increase the habitat complexity and oxygen demands and even produce heterogeneous habitats in a uniform environment (Callaway 2006; Van Hoey et al. 2008). These effects of tube-building polychaetes may also influence larval settlement, dispersal patterns and, therefore, produce changes in the community variables and structure (Woodin 1978; Trueblood 1991; Qian 1999; Zühlke 2001; Callaway 2006).

In this study, we examine the polychaete fauna inhabiting the aggregations of the ascidian *Pyura chilensis* in central Chile and evaluate the relationship between aggregation volume and polychaete assemblage variables (number of species and individuals) and the effect produced by the differential load of chaetopterid tubes on the polychaete assemblage structure. For this, we compared different sizes of ascidian aggregations with different load of chaetopterid tubes and we determined the effects on species richness, abundance, functional groups and polychaete assemblage structure.

Materials and methods

Study area and sample collection

A total of 38 aggregations of the ascidian *P. chilensis* were obtained in San Vicente Bay, central Chile in 2000. From aggregations analysed and studied, 21 corresponded to aggregations with high density (average 0.465 tubes/ml., “hairy” appearance, hereafter HT morphotype) and 17 to aggregations with low density (average 0.076 tubes/ml., “bald” appearance, hereafter LT morphotype) of chaetopterid tubes (i.e., the load is six times greater in the HT than in LT morphotype). The load of chaetopterid tubes displayed influences the number and size of individual ascidians, showing one to three ascidians of small size in the HT morphotype, and two to six ascidians of medium size in the LT morphotype (Sepúlveda, pers. obs.). The LT morphotype samples were collected near Roca Navia (36°44′49.71″S, 73°10′37.66″W) at a depth of approximately 5 m below MLW, while the HT morphotype samples were also collected at a depth of 5 m near playa Ramuntcho (36°45′11.99″S, 73°11′12.57″W) (Fig. 1); samples were collected by a diver equipped with “hookah” breathing gear. Samples of ascidians aggregations were removed from the rocky substrates using a spatula and metal hooks and were wrapped in situ in a 1 mm-mesh polypropylene netting to retain all associated polychaetes. The size (measured as volume) of each aggregation was determined immersing the sample in a 1,000-ml graduated cylinder and determining the volume of seawater displaced by the sample. Polychaetes from each aggregation were separated with the aid of a stereomicroscope and fixed in 10% formalin-seawater solution. Determination of total and per-sample taxonomic composition of polychaete fauna was performed to the lowest possible taxonomic level. Species abundance of all polychaetes was counted manually, and each species was assigned to trophic and locomotion functional groups of polychaetes, following Fauchald and Jumars (1979) and Jumars et al. (2014).

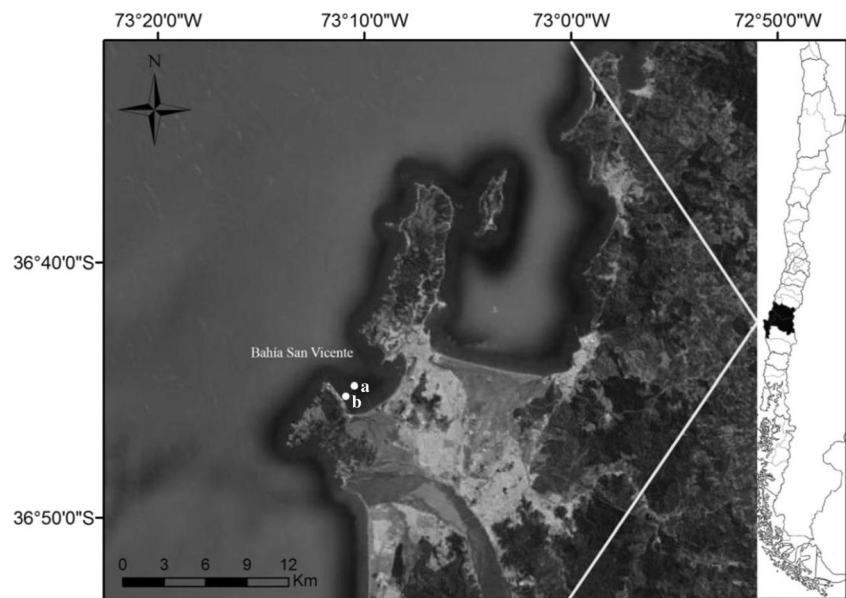
Although the results show differences between morphotypes, we assume that the variations in polychaete assemblage may be due to the collection sites, since this study does not have replicated sites. Therefore, confounding effects between sites and morphotypes are likely to affect the results of our study.

Data analysis

Relative abundances between morphotypes for feeding and locomotion functional groups were tested with contingency tables and statistical significance was evaluated through Chi-square analysis (Quinn and Keough 2002).

To assess the possible influence of sample size (aggregation volume) on the number of species and individuals of polychaetes, we utilized PERMANCOVA based on Euclidean distance matrices. Likewise, the effect of sample volume on the

Fig. 1 Sampling locations of ascidian *Pyura chilensis* aggregations in central Chile. **a** Low density of chaetopterid tubes (LT morphotype); **b** High density of chaetopterid tubes (HT morphotype)



polychaetes assemblage structure was evaluated through PERMANCOVA based on the Bray-Curtis similarity matrix after \sqrt{x} -transformed data, using morphotype as a fixed factor and volume as a covariate (Clarke 1993; Anderson 2001). Moreover, the similarity percentage (SIMPER) routine was used to determine the contribution of each species to the dissimilarity between morphotypes (Clarke and Warwick 2001). Subsequently, we standardized the raw matrix (ind./L) aimed to remove the samples size effect, and we assessed using this matrix the possible influence of the chaetopterid tubes on the polychaete assemblage structure through PERMANCOVA, using morphotype as the fixed factor and the number of tubes as a covariate (Clarke 1993; Anderson 2001).

The samples of the ascidian-associated polychaete assemblage were ordered through a multidimensional scaling (MDS) plot based on a Bray-Curtis dissimilarity matrix (Clarke and Warwick 2001). "Canonical Analysis of Principal Coordinates" (CAP) was performed to identify misclassified samples due to differences in their community (multivariate) structure within and between morphotypes. All probability values of significant fits were derived from a pseudo-F distribution calculated through 10,000 permutations from the original dataset. All analyses were performed using PERMANOVA + for the PRIMER statistical package (Clarke and Gorley 2006; Anderson et al. 2008).

Results

Taxonomic and functional composition of the polychaete assemblage

A total of 5,524 polychaetes corresponding to 21 families and 35 species were associated with the ascidian aggregations

(Table 1). More polychaetes were collected in the HT morphotype ($N=3,961$, average= 18.9 ± 148.9 SD) than in the LT morphotype ($N=1,563$, average= 92.1 ± 62.6 SD). The most abundant and frequent species in the HT morphotype were the chaetopterid *Phyllochaetopterus socialis* and the syllid *Typosyllis magdalena*, while *T. magdalena* and the terebellid *Nicolea lobulata* were most abundant in the LT morphotype (Table 1). Both morphotypes were dominated by the same pool of species (89.20% similarity), but with clear differences in species abundance between morphotypes (47.30% similarity). The species that contributed most to the average dissimilarity between morphotypes were the chaetopterid *P. socialis* (5.20%), the terebellid *N. lobulata* (3.92%) and the syllid *T. magdalena* (2.35%), reaching more than 20% of the total abundance (Table 2).

For functional groups, superficial deposit-feeders (46.95%) and carnivores (45.06%) were the most abundant in the HT morphotype, while carnivores (64.60%) were the most abundant in the LT morphotype, showing dependence between feeding functional groups and morphotypes ($\chi_5=36.054$, $P<0.001$). For locomotion functional groups, neither mobile (48.89%) nor sessile (46.90%) polychaete macrofauna showed a clear dominance pattern in the HT morphotype; however, mobile species accounted for over 80% of the polychaetes in the LT morphotype (Table 1), also showing dependence between locomotion functional groups and morphotypes ($\chi_3=27.190$, $P<0.001$).

Structure of the polychaete assemblage

In both morphotypes, the number of species as well as the number of individuals depended significantly on the sample volume (Table 3a, b and Fig. 2a, b). The scaling relationships of the covariate (volume) and number of species (Table 3a), as

Table 1 Numerical abundance (N), relative abundance ($N\%$), frequency ($F\%$) and functional group of the ascidian-associated polychaete assemblage in central-Chile (functional group: o omnivorous; c carnivorous; ff filter-feeders; sdf superficial deposit-feeders; $ssdf$ subsuperficial deposit-feeders; m mobile; dm discretely mobile; s sessile)

Species	Functional group	HT morphotype			LT morphotype		
		N	$N\%$	$F\%$	N	$N\%$	$F\%$
<i>Arabella iricolor caerulea</i> (Schmarda, 1861)	o, m	9	0.2	42.8	2	0.1	11.8
<i>Chaetopterus variopedatus</i> (Renier, 1804)	sdf, s	3	0.1	4.7	–	–	–
Cirratulidae sp.	$ssdf, m$	13	0.3	9.5	13	0.8	29.4
<i>Cirratulus tumbensis</i> (Carrasco, 1977)	$ssdf, m$	55	1.4	57.1	42	2.7	70.6
<i>Cirriiformia polytricha</i> (Schmarda, 1861)	$ssdf, m$	13	0.3	33.3	3	0.2	17.6
<i>Demonax leucaspis</i> (Kinberg, 1867)	ff, s	28	0.7	66.6	37	2.4	82.4
<i>Dipolydora socialis</i> (Schmarda, 1861)	$ff-sdf, dm$	14	0.4	33.3	2	0.1	11.8
<i>Dodecaceria gallardoii</i> (Carrasco, 1977)	sdf, s	–	–	–	4	0.3	17.6
Dorvilleidae sp. indet.	o, m	1	0.0	4.7	1	0.1	5.9
<i>Eranno bifilaris</i> (Ehlers, 1901)	c, dm	16	0.4	52.3	6	0.4	35.3
<i>Eulalia subulifera</i> (Ehlers, 1897)	c, m	110	2.8	90.4	86	5.5	88.2
<i>Halosydna</i> sp. A	c, m	6	0.2	28.5	26	1.7	70.6
<i>Halosydna</i> sp. B	c, dm	7	0.2	14.2	19	1.2	52.9
<i>Harmothoe</i> sp.	c, dm	12	0.3	23.8	–	–	–
<i>Hyboscolex oculatus</i> (Ehlers, 1901)	c, dm	29	0.7	57.1	8	0.5	29.4
<i>Lepidonotus furcillatus</i> (Ehlers, 1901)	$ssdf, m$	27	0.7	52.3	2	0.1	5.9
<i>Lysidice</i> sp.	o, m	8	0.2	28.5	2	0.1	11.8
<i>Marphysa aenea</i> (Blanchard, 1849)	o, m	10	0.3	38.1	7	0.5	29.4
<i>Naineris chilensis</i> (Carrasco, 1977)	o, m	2	0.1	9.5	–	–	–
<i>Neoamphitrite</i> sp.	$ssdf, m$	1	0.0	4.7	6	0.4	17.6
<i>Nereis callaona</i> (Grube, 1857)	sdf, s	21	0.5	47.6	36	2.3	70.6
<i>Nereis grubei</i> (Kinberg, 1866)	o, m	50	1.3	71.4	17	1.1	47.1
<i>Nicolea lobulata</i> (Hartmann-Schröder, 1965)	o, m	13	0.3	38.1	197	12.6	94.1
<i>Ophryotrocha puerilis</i> (Claparède & Mecznirow, 1869)	sdf, dm	–	–	–	2	0.1	5.9
<i>Oriopsis ehlersi</i> (Day, 1961)	c, dm	6	0.2	28.5	13	0.8	41.2
<i>Paleanotus chrysolepis</i> (Schmarda, 1861)	ff, s	4	0.1	19.0	9	0.6	47.1
<i>Pareurythoe chilensis</i> (Kinberg, 1857)	c, m	35	0.9	47.6	8	0.5	29.4
<i>Pherusa tumbensis</i> (Hartmann-Schröder, 1962)	sdf, dm	13	0.3	19.0	–	–	–
<i>Phragmatopoma virgini</i> (Kinberg, 1867)	ff, s	8	0.2	23.8	–	–	–
<i>Phyllochaetopterus socialis</i> (Claparède, 1869)	sdf, s	1,766	44.6	100	105	6.7	70.6
<i>Polycirrus chilensis</i> (Schmarda, 1861)	sdf, dm	59	1.5	80.9	33	2.1	76.5
Polynoidae sp. indet.	c, dm	6	0.2	23.8	3	0.2	17.6
<i>Protoariciella uncinata</i> (Hartmann-Schröder, 1962)	$ssdf, m$	26	0.7	61.9	11	0.7	29.4
<i>Romanchella pustulata</i> (Knight-Jones, 1978)	ff, s	30	0.8	23.8	21	1.3	47.1
<i>Typosyllis magdalena</i> (Wesenberg-Lund, 1962)	c, m	1,560	39.4	100	842	53.9	100
Total individual number per morphotype		3,961	1,563				
Total species number per morphotype		33	30				

well as on number of individuals (Table 3b), revealed that there was no interaction between sample volume and morphotype. Following adjustment for the effect of the covariate (sample volume), significant differences between morphotypes were only found for the number of species (Table 3a, b).

Moreover, in both morphotypes, the polychaete assemblage multivariate structure was dependent on the volume of the samples of *Pyura chilensis*. The scaling relationship of the covariate (volume) on the multivariate matrix structure revealed that slopes did not differ significantly between morphotypes. Following adjustment for the effect of the

Table 2 Similarity percentage (SIMPER) routine (cutoff for contributions: 75%) for species that contributed to the dissimilarity between aggregations with the high load (HT morphotype) and low load (LT morphotype) of chaetopterid tubes, indicating the average abundance per species and the average dissimilarity between morphotypes

Species	Average abundances		Average dissimilarity	Relative contribution (%)	Cumulative contribution (%)
	HT	LT			
<i>Phyllochaetopterus socialis</i>	2.76	1.14	5.20	9.87	9.87
<i>Nicolea lobulata</i>	0.43	1.69	3.92	7.44	17.32
<i>Typosyllis magdalena</i>	2.70	2.45	2.35	4.45	21.77
<i>Cirratulus tumbensis</i>	0.73	0.95	2.24	4.25	26.03
<i>Nereis callaona</i>	0.57	0.86	2.14	4.05	30.08
<i>Nereis grubei</i>	0.90	0.55	2.12	4.02	34.09
<i>Halosydna</i> sp. A	0.29	0.83	2.04	3.87	37.96
<i>Eulalia subulifera</i>	1.30	1.32	1.91	3.63	41.59
<i>Demonax leucaspis</i>	0.77	1.01	1.91	3.62	45.21
<i>Protoariciella uncinata</i>	0.71	0.35	1.90	3.60	48.81
<i>Polycirrus chilensis</i>	1.06	0.94	1.89	3.59	52.40
<i>Romanchella pustulata</i>	0.33	0.56	1.84	3.49	55.88
<i>Hyboscolex oculatus</i>	0.67	0.33	1.81	3.43	59.32
<i>Halosydna</i> sp. B	0.17	0.62	1.76	3.33	62.65
<i>Pareurythoe chilensis</i>	0.60	0.33	1.74	3.31	65.96
<i>Lepidonotus furcillatus</i>	0.63	0.07	1.72	3.26	69.22
<i>Eranno bifilaris</i>	0.56	0.35	1.56	2.95	72.17
<i>Oriopsis ehlersi</i>	0.29	0.47	1.53	2.91	75.08

samples volume, significant differences related to multivariate structure were found between samples from HT and LT morphotypes (Table 3c). The ordination analysis showed a higher assemblage structure similarity within than between morphotypes (Fig. 3); meanwhile CAP analysis showed that

94.74% of the samples (100% from the HT morphotype and 88.24% from the LT morphotype) were correctly assigned to the morphotypes according their assemblage structure (Fig. 3).

For both morphotypes, the multivariate structure of the polychaete assemblage was dependent on number of

Table 3 PERMANCOVA analyses on the number of species, the number of individuals and the polychaete assemblage structure associated with aggregations of the ascidian *Pyura chilensis*. Perms: Number of permutations performed; CV Components of variation (%)

	SS	df	MS	pseudo-F	P(perm)	CV (%)
a) Species number						
Morphotype (M)	0.186	1	0.186	12.404	0.001	22.67
Sample volume (V)	0.964	1	0.964	64.427	<0.001	48.36
M × V	0.008	1	0.008	0.562	0.457	0
Residual	0.508	34	0.015			28.97
b) Individuals number						
Morphotype (M)	0.118	1	0.118	1.764	0.190	1.64
Sample volume (V)	5.374	1	5.374	80.547	<0.001	65.56
M × V	0.113	1	0.113	1.690	0.203	1.48
Residual	2.268	34	0.067			31.32
c) Assemblage structure						
Morphotype (M)	6,598	1	6,598	8.602	<0.001	28.08
Sample volume (V)	8,764	1	8,764	11.426	<0.001	14.77
M × V	1,458	1	1,458	1.901	0.056	3.31
Residual	26,079	34	767			53.84
d) Assemblage structure (Stand.)						
Morphotype (M)	6,236	1	6,236	6.019	<0.001	28.05
Tubes number (T)	3,127	1	3,127	3.018	0.005	3.16
M × T	2,055	1	2,055	1.983	0.050	9.36
Residual	35,234	34	1,036			59.43

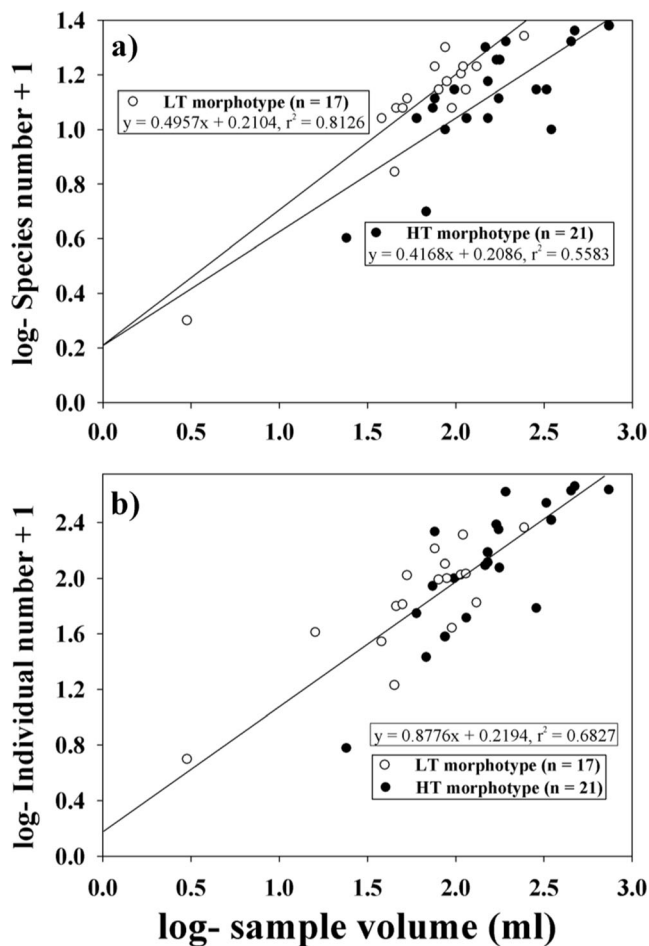


Fig. 2 Relationships between aggregation size (sample volume) and (a) number of species and (b) number of individuals for epifaunal polychaetes from *Pyura chilensis* in the LT ($n=17$) and the HT ($n=21$) morphotypes

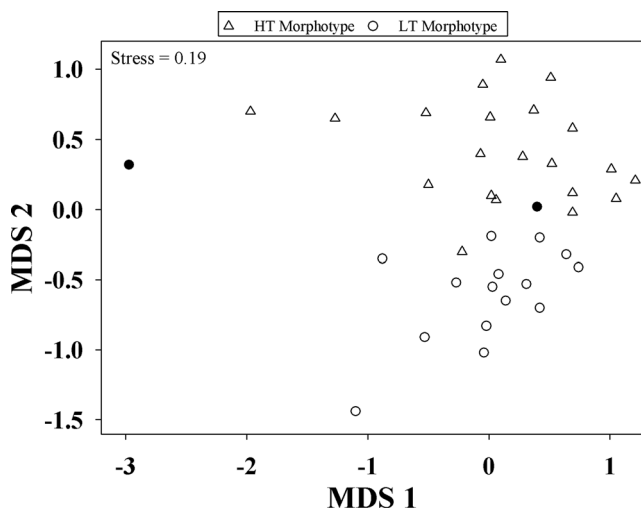


Fig. 3 Multidimensional Scaling (MDS, Bray-Curtis dissimilarity matrices) ordination plot of the ascidian-associated polychaete assemblage between HT (triangles) and LT (circles) morphotypes. Black circles correspond to misclassified samples from CAP, according to their multivariate assemblage structure

chaetopterid tubes (Table 3d). The scaling relationship of the covariate (tubes number) on the standardized multivariate matrix structure revealed the slopes did not differ significantly between morphotypes (Table 3d). Following adjustment for the effect of the number of tubes, significant differences related to the multivariate structure were found between samples from HT and LT morphotypes.

Discussion

Composition and structure of the polychaete assemblage

The present study shows that polychaete fauna associated with aggregations of the ascidian *Pyura chilensis* are highly diverse and abundant (5,524 specimens belonging to 35 species) compared with other types of biogenic substrates such as algae (Chapman et al. 2005, 17 species; Kelaher and Castilla 2005, 29 species), mollusks (Chapman et al. 2005, 15 species; Vasconcelos et al. 2007, 25 species), barnacles (Hernández et al. 2001, 19 species), cnidarians (Pérez et al. 2005, 5 species), polychaetes (Nalesso et al. 1995, 19 families; Bolam and Fernández 2002, 14 species; Sepúlveda et al. 2003a, 10 species; Albano et al. 2006, 11 species) and another ascidian species (Cerdeira and Castilla 2001, 19 species). Nevertheless, others studies have evidenced a different pattern of polychaete species richness associated with biogenic substrates, showing high diversity on others species of algae (Fraschetti et al. 2002, 58 species; Sánchez-Moyano et al. 2002, 81 species; Antoniadou et al. 2004, 79 species), seagrasses (Brito et al. 2005, 69 species) and sponges (Gherardi et al. 2001, 50 species) in comparison to bivalves, barnacles, polychaetes and ascidians.

Although the results did not show significant differences for the number of individuals between morphotypes, significant differences were found for species number. The number of individuals was higher in the HT morphotype than in the LT morphotype due to the high abundance of the tube-building chaetopterid *P. socialis*, a species that produces the “hairy” appearance in the ascidian aggregations. This, and the high raw abundance of *T. magdalena* in the LT morphotype, marked the main dominant species in ascidian aggregations. Despite this, the pattern determined that the same pool of species dominated the polychaete assemblage in both morphotypes, but with highly clear differences in their average abundances (Table 2). A similar pattern was found in studying the effects of the tube-building terebellid *Lanice conchilega* (Pallas, 1766) on the community structure of soft-bottom habitats (Van Hoey et al. 2008). This confirmed the hypothesis that the species affected by *L. conchilega* belong to the overall species pool of that habitat; this tube-building polychaete only affected the surrounding benthos in

a particular habitat, rather than forming its own community (see also Rabaut et al. 2007).

Regression analysis showed that the number of species and individuals were dependent on aggregation size, a typical situation that occurs in patchy marine microhabitats that may have temporal isolation and, therefore, have island-like features where the species and individual number increase positively with the habitat size. Some communities associated with biogenic substrates, such as holdfast-algae (Thiel and Vásquez 2000), seagrasses (Lee et al. 2001), sponges (Cinar and Ergen 1998), barnacles (Hernández et al. 2001), mytilids (Tsuchiya and Nishihira 1985), polychaetes (Sepúlveda et al. 2003a) and ascidians (Sepúlveda et al. 2003b; Voultziadou et al. 2007), generally show this pattern. This situation could be a consequence of the permanent increase of available “biogenic habitats” by animal or vegetal substrates. This means that the more space there is, the more settlement and arrival of individuals of other species there will be, thus increasing the species richness and abundance of biogenic substrates in comparison with the surrounding habitat. This increase in the number of species and individuals may be related to the “substrate’s exposition time” for newly settled polychaetes: ascidian aggregations of greater life spans favoured the formation of more interstices and holes that different types of polychaetes may inhabit. Furthermore, settling polychaetes (e.g., borers, burrowers or tube-building polychaetes) may be able to transform or alter the substrate in such a way so as to allow the entry of species that were previously unable to settle, which further increases the species richness and density within ascidian aggregations. Both feeding and locomotion functional groups showed a clear dependence pattern associated with morphotype. Many of the polychaetes found in the HT morphotype during this study were superficial or sub-superficial deposit-feeders (sensu Fauchald and Jumars 1979; Jumars et al. 2014). This type of species may possibly find food within this microhabitat, as has been proposed for filter-feeding peracarids associated with kelp holdfasts (Thiel and Vásquez 2000). Moreover, the dominance of the superficial deposit-feeders among polychaetes may be the result of a beneficial substratum provided by ascidians, where the deposit-feeders polychaetes may utilize the abundant suspended material available in their vicinity (Sepúlveda et al. 2003b).

Ecological implications of the tube-building polychaete

Some species are capable of forming three-dimensional structures on the seafloor that change the composition of benthic fauna (e.g., Diaz et al. 2003; Bomkamp et al. 2004; Castilla et al. 2004). Tube worms, for example, can create these habitats and at high densities are known to change the benthic community structure. The species of Family Sabellariidae (i.e., Genus *Phragmatopoma* and *Sabellaria*) create reefs of

rigid tubes cemented together that have diverse associated fauna (Sousa Dias and Paula 2001; Dubois et al. 2002; Sepúlveda et al. 2003a). However, even small polychaetes that barely extend above the sediment surface, such as *Pygospio elegans*, affect the composition of other fauna when they occur in dense aggregations (Bolam and Fernández 2002).

In ascidian aggregations, the presence of the tube-building chaetopterid produced positive effects on the species richness of the polychaete fauna associated with ascidians. This pattern implies that the presence of tubes contributed to higher habitat complexity in the HT morphotype aggregations. This means that the chance of encountering certain epifaunal species increases in aggregations with chaetopterid tubes. This pattern is consistent with previous studies on the effect of the tube-building terebellid *Lanice conchilega* which found that the presence of tubes in soft-bottom sediments had a positive effect on community structure, expressed as an increase in species richness and density, but contrasts with an increase in diversity of benthic invertebrates (Callaway 2003; 2006; Van Hoey et al. 2008). Certain species may even benefit from improved oxygen supply in the surrounding sediment (Callaway 2006); however the tubes may also prevent water flow over the ascidian surface. In fact, Jones et al. (1997) argued that ecosystem engineering species have both negative and positive effects on species richness and abundance on a small scale, but that the net effects are probably positive at a larger scale, encompassing engineered and non-engineered environments in ecological and evolutionary space and time.

The chaetopterid *P. socialis* generate greater incrusting of long tubes (20–40 mm) in ascidians of the HT morphotype, which are extended over the ascidian surface, modifying the structure of the primary substrate (i.e., ascidian aggregations surface) and increasing the total size of the aggregation. The creation of tubes produces more available habitats and, therefore, greater environmental heterogeneity to adherence and habitability for a wider variety of invertebrates (Luckenbach 1987; Nalesso et al. 1995; Callaway 2006; Van Hoey et al. 2008). Furthermore, tubes on the surface of aggregations may also change the external morphology and alter the size of the aggregations in comparison with the LT morphotype aggregations. Consequently, this ecosystem engineering (sensu Jones et al. 1994) may change the hydrodynamics, increase habitat complexity and may even produce heterogeneous habitats in a uniform environment (Callaway 2006; Van Hoey et al. 2008). Turbulent effects produced by tube encrustation on ascidian aggregations may influence larval settlement and dispersal patterns, sedimentation and food availability on these surfaces, producing changes in species diversity, abundance, trophic functional groups and community structure (Woodin 1978; Luckenbach 1987; Trueblood 1991; Qian 1999; Zühlke 2001; Callaway 2006; Hauser et al. 2006; Rabaut et al. 2007; Van Hoey et al. 2008), thus accentuating

the differences between morphotypes. This, along with the favourable substrate formed by ascidians for sessile organisms, which in turn form complex habitats for invertebrate fauna (Sepúlveda 2001), contributes to the maintenance of their diversity in sublittoral rocky shores (also see Ribeiro et al. 2003 with associated macrofauna to sponges).

The habitat structuring capacity of the chaetopterid *P. socialis* in the HT morphotype modifies the superficial structure of the ascidian aggregations, alters its properties and, consequently, changes the microhabitat offered by this ascidian. Both the aggregation size and tube number increase the number of species and individuals, and change the polychaete assemblage structure. We suggest that the chaetopterid tubes became abundant on ascidian aggregations that grow at sites that favour the settlement of superficial deposit- and filter-feeder species, which increases their densities within ascidian aggregations.

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