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Substrate selection of Christmas tree worms (*Spirobranchus* spp.) in the Gulf of Eilat, Red Sea

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*Christmas tree worms (*Spirobranchus *spp.) are prominent sessile organisms inhabiting hermatypic corals in tropical and subtropical reefs. Until recently, most of the larger* Spirobranchus *species were considered to be in obligatory associations with live hermatypic corals. However, recent studies indicate that some* Spirobranchus *species can build tubes on artificial substrate as well and that others may show preferences for using specific species of corals and hydrozoans as substrates. In the present study, we conducted a survey of* Spirobranchus *spp. substrate preference in the Gulf of Eilat. We found seven morphotaxa of* Spirobranchus*, of which two may be a single new species. We show that* Spirobranchus *taxa differ not only in their morphology, but also in their substrate use. Our results demonstrate that the ecological niche of* Spirobranchus *is species-specific, and a putative innate preference exists for some substrates.*

Keywords: Polychaeta, Serpulidae, Spirobranchus, biodiversity, host specificity, Red Sea

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INTRODUCTION

Darwin (1859) may have been the first to suggest that differences between closely related species may be the result of adaptation to reducing interspecific competition via selection of different habitats. In a series of articles beginning in the 1960s MacArthur and his colleagues further developed this idea, now most often referred to as resource partitioning or, more specifically, habitat partitioning (MacArthur & Levins, 1964). Although early work primarily focused on terrestrial habitats, a recent review (Bowen *et al.*, 2013) concluded that the ecological boundaries can be important arenas for evolutionary processes in marine and other ecosystems.

Levesque *et al.* (2003) showed that resource partitioning can occur in Polychaeta. As with all members of the family Serpulidae, *Spirobranchus* Blainville, 1818 juveniles become sessile and build their own tube. The 37 *Spirobranchus* species currently recognized (Read *et al.*, 2016) are mostly distributed in subtropical and tropical zones, with *S. triqueter* (Linnaeus, 1767) even occurring in the Arctic (Pillai, 2009; Rzhavsky *et al.*, 2014). The larger species are often recorded inhabiting corals, whereas smaller representatives may occur on almost any solid substrate. A substantial amount of research has been conducted on *Spirobranchus giganteus sensu latissimo* (Marsden, 1987; Nishi & Nishihira, 1996; Petitjean & Myers, 2005; Rowley, 2008), often erroneously reported from all tropical regions as *S. giganteus* (Pallas, 1766), a species restricted to the Caribbean. The larger species of *Spirobranchus* are often named 'Christmas tree worms' for the bright colours and spiral arrangement of their radioles.

Frank & ten Hove (1992) hypothesized that morphology of branchial crowns may be correlated to different filtering strategies, which may be an indication of resource partitioning. However, despite the wide distribution and striking appearance of members of the genus, ecological processes such as habitat partitioning have not received much attention.

Most of the larger *Spirobranchus* species are associated with hermatypic corals (see below), their tubes embedded in the coral skeleton. Figure 1 shows different substrates colonized by *Spirobranchus* in the Gulf of Eilat. Growth rate and angle of the worm's tube are correlated with that of the coral in such a way that the opening of the tube will always stay on top of the surface (Nishi & Nishihira, 1999). Some taxa, such as the Caribbean *S. giganteus* and the Indo-West Pacific *S. corniculatus*, are thought to be obligate inhabitants of living corals (Hunte *et al.*, 1990a; Marsden & Meeuwig, 1990; Nishi, 1996). Members of the *Spirobranchus giganteus* complex are abundant on some coral species, rare or even absent from others. Coral preferences may differ between *Spirobranchus* taxa and thus between biogeographic regions. Dai & Yang (1995) found that in the coral reefs of Southern Taiwan, *S. corniculatus* mostly inhabit the corals *Porites lutea* Milne Edwards & Haime, 1851, *P. lobata* Dana, 1846, *P. lichen* Dana, 1846 and *Montipora informis* Bernard, 1897. In the bank reef off the West coast of Barbados the hexacoral species *Diploria strigosa* (Dana, 1846), *Porites astreoides*

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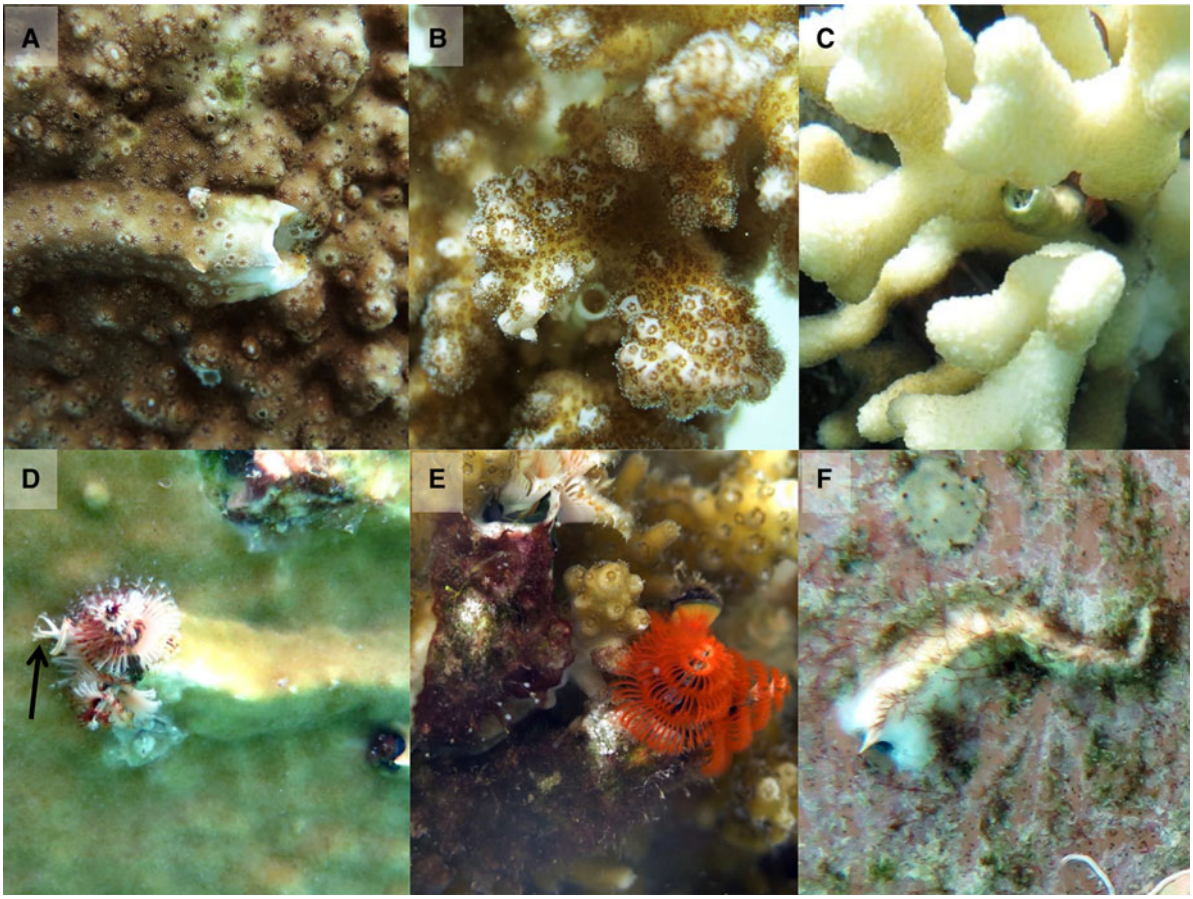

Fig. 1. Different substrates colonized by *Spirobranchus*, reef of Eilat, Israel. (A) *Spirobranchus gardineri* associated with *Cyphastrea* sp. (B) *S. gaymardi* associated with *Pocillopora* sp. (C) *Spirobranchus* sp. associated with *Stylophora* sp. (D) *S. cruciger* associated with *Millepora* sp. (E) *S. corniculatus* associated with *Acropora* sp. (F) *Spirobranchus* sp. on artificial substrate. Arrow: operculum. (A, D, F) Photos: O. Perry; (B, C, E) photos: A. Hallakoun.

Lamarck, 1816 and the hydrozoan coral *Millepora complanata* Lamarck, 1816 are most heavily colonized by *S. giganteus* while *Colpophyllia natans* (Houttuyn, 1772), *Dendrogyra cylindrus* Ehrenberg, 1834, *Dichocoenia stokesii* Milne Edwards & Haime, 1848, *Eusmilia fastigiata* (Pallas, 1766) *Meandrina meandrites* (Linnaeus, 1758) and *Mycetophyllia* spp. Milne Edwards & Haime, 1848 were not colonized (Conlin, 1988; Hunte *et al.*, 1990a). Specific searches for associated fauna in potential hosts (not only corals) may result in new association records (Hoeksema & ten Hove, 2016; Hoeksema *et al.*, 2016).

The co-occurrence of worm and coral may be of a mutualistic character. DeVantier *et al.* (1986) showed that the branchiae and especially the operculum of the worm can provide protection to the coral from predators. In some conditions the feeding behaviour may even enhance water flow close to the coral's surface (Strathmann *et al.*, 1984), which might locally prevent bleaching (Ben-Tzvi *et al.*, 2006). However, settlement of *Spirobranchus* taxa on corals is an antagonistic interaction. Corals can be aggressive towards other organisms and compete for resources using sweeper tentacles (Genin & Karp, 1994). Perhaps because of this, some of the more subordinate corals as *Porites lutea, P. lobata* and *P. lichen* were found to be most colonized by *Spirobranchus corniculatus* while the more aggressive corals such as *Mycedium elephantotus* (Pallas, 1766), *Merulina ampliata* (Ellis & Solander, 1786) and *Galaxea astreata* (Lamarck, 1816) were less colonized (Dai, 1990; Dai & Yang, 1995). Settling larvae of a species better adapted to cope with coral aggression are more likely to survive. Larval settlement preference has been demonstrated in *Spirobranchus* (Hunte *et al.*, 1990a, Marsden & Meeuwig, 1990) and may be an indicator of host-specific adaptations. An alternative view was proposed by Rowley (2008), who suggested that *S. corniculatus sensu stricto* (as *S. giganteus*) contributes to the success of its hosts in several ways and the relationship should be thought of as mutualism rather than commensalism. Regardless, Hunte *et al.* (1990a) demonstrated that substrate selection by planktonic larvae of *S. giganteus* was correlated with worm size, such that individuals located on the preferred species of coral reached a larger size. Thus, length can be a surrogate of high performance and provide evidence for adaptive host-specific interactions.

Living hermatypic corals are not the only substrate for the larger *Spirobranchus* worms. Recently, there have been records that *Spirobranchus giganteus s. str.* can also live on octocorals, rubble, and substrates such as oil buoys or pillars of a pier (Nygaard, 2008; Skinner *et al.*, 2012; Hoeksema *et al.*, 2015). Although purporting to describe *S. giganteus*, Figure 1D of Skinner *et al.* (2012) depicts *S. tetraceros* (Schmarda, 1861). Nygaard (2008) may have been studying *S. polycerus* (Schmarda, 1861), a species with spiral branchiae as well and tubes of about 5 mm across (ten Hove, 1970; Hoeksema & van Moorsel, 2016). The latter is very common

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on all kinds of hard substrates in the Antilles, including Bonaire (ten Hove, unpublished data).

The second (mainly) tropical species (but see below), *Spirobranchus tetraceros*, is an Indo-Pacific invasive in the Mediterranean (Ben-Eliahu & ten Hove, 1992), and has been reported from Turkey to inhabit artificial as well as natural hard substrata (Çinar, 2006; Çinar *et al.*, 2014). *Spirobranchus tetraceros* was also reported to inhabit artificial substrate and become an extensive fouler in the Suez Canal (Shalla & Holt, 1999; Selim *et al.*, 2005). Moreover, *S. tetraceros* seems to be an opportunistic taxon as it was reported to explosively overgrow corals immediately after a period of stress in the Persian Gulf (Samimi Namin *et al.*, 2010). In view of its exceptionally large distribution, from temperate Australia to tropical regions all over the globe, *S. tetraceros* most probably is a species-complex. Despite the body of knowledge accumulated on substrate of *Spirobranchus* spp., for some species, such as *S. gardineri* Pixell, 1913, hardly any substrate preference data are available. For the typical form (his variant types 1 and 2 in the meantime have both been named *S. richardsmithi* Pillai, 2009) the genera *Millepora* Linnaeus, 1758 spp., *Psammocora* Dana, 1846 spp. and *Stylocoeniella* Yabe & Sugiyama, 1935 spp. have been mentioned by Smith (1985: 40).

The Gulf of Eilat is the northernmost coral reef, expanding northward from the Red Sea and the Indian Ocean. Eight nominal species of *Spirobranchus* have been recorded from the Red Sea and its northern Gulf of Eilat, of which seven from both areas (Table 1). The apparent absence of the Indo-West Pacific *S. gaymardi* from the Red Sea proper while occurring in its most northern gulf is probably due to insufficient collecting effort rather than reflecting a real difference.

However, species identification remains questionable as some taxa were identified based on too few specimens; other names were regarded to be synonyms by some authors. In order to examine the potential for habitat partitioning in *Spirobranchus*, our goal was to start resolving conflicting records about which species are found in the Eilat region and what hosts they inhabit. Thus, in this study we surveyed *Spirobranchus* spp. and their distribution on different substrates in the Gulf of Eilat.

Table 1. *Spirobranchus* species reported from the Red Sea and the Gulf of Eilat.

Species	Red Sea proper	Gulf of Eilat
S. corniculatus	S	S (1)
S. coronatus	?S	?S (2)
S. corrugatus	S	U (3)
*S. cruciger**	S	S (4)
*S. gaymardi**	–	?U (5)
S. gardineri	P	P (6)
S. latiscapus	P	S (7)
S. tetraceros	P	P (8)

References: (1) Pixell (1913), Mergner (1979); (2) Gravier (1906, as *jousseaumei*), Amoureux *et al.* (1978, Figure 16); (3) Vine & Bailey-Brock (1984, Figure 5B–G), Hassan (1998); (4) Vine & Bailey-Brock (1984); (5) ten Hove, personal observation; (6) Fauvel (1933); (7) Vine & Bailey-Brock (1984); (8) Vine & Bailey-Brock (1984), Hassan (1998).
Table modified from ten Hove *et al.* (unpublished).
*Considered to be synonymous with *S. corniculatus* by Willette *et al.* (2015).
P, published, identification confirmed; S, published, but ID has since been synonymized; U, previously unpublished; ?, published, questionable (Not yet verified).

MATERIALS AND METHODS

Collecting and preservation of specimens

The research was performed on the coral reef of Eilat, Gulf of Eilat, Red Sea, 29°33′N 34°57′E, Israel. A total of 189 specimens were collected by scuba from depths of 0.5–12 m (Israel Nature-Parks Authority [INPA] permit number 2014/40533). Seven substrate types were examined for *Spirobranchus* species (Table 2). Due to INPA limitations and to prevent damage to the reef, worms were sampled mainly from branching and encrusting corals and from artificial substrates such as pillars of a pier without coral association. After taking measurements (see below), a piece of the abdomen of each specimen was preserved in 100% ethanol and stored at −20°C for molecular analysis. The rest of each specimen was fixed in 4% formaldehyde (in SW) for 24 h, rinsed in filtered seawater, transferred to ethanol 70%, and stored at 4°C.

Although we observed worms on massive coral genera such as *Porites* sp. Link, 1807 and *Dipsastraea* sp. Blainville, 1830, we did not sample them in order to minimize the damage to slow growing taxa.

Species identification

The *Spirobranchus giganteus* complex was tentatively resolved by Fiege & ten Hove (1999, Figure 4), distinguishing 12 separate species mainly on the basis of the morphology of their opercula. However, the morphospecies of the Indo-West Pacific *S. corniculatus* complex in the strict sense as distinguished by Fiege & ten Hove, *S. corniculatus* (Grube, 1862), *S. gaymardi* (Quatrefages, 1865) and *S. cruciger* (Grube, 1862), are not distinguished by DNA (Willette *et al.*, 2015).

For this study, identification of *Spirobranchus* taxa is based on the morphology of the operculum (as for instance in Willette *et al.*, 2015; however see below), which is a hard (calcareous) cover sealing the opening of the tube when the worm retracts. The morphology of the operculum can change during growth and as a result its structure in juveniles can resemble the fully grown operculum of another species (ten Hove & Ben-Eliahu, 2005). We concentrated our efforts on larger specimens, no longer subject to such ontogenetic changes. However, it is almost impossible to observe and differentiate between *Spirobranchus* taxa *in situ* because the operculum also functions as substrate for other organisms obscuring the opercular morphology (Figure 2). Overgrowth of opercula in serpulids is not uncommon, for example it was mentioned by Gambi (1986) for *Ditrupa arietina* (O. F. Müller, 1776). Because identification *in situ* is difficult, and due to confusing and changing insights in the taxonomy of the larger *Spirobranchus* taxa, many studies followed Fauvel (1953) or Day (1967) and applied their 'widespread species' concept of the nominal species *Spirobranchus giganteus* to material from Indo-West Pacific origin (Smith, 1984; DeVantier *et al.*, 1986; Nishi & Nishihira, 1999; Floros *et al.*, 2005; Ben-Tzvi *et al.*, 2006; Rowley, 2008). However, ten Hove (1970), in a first attempt to unravel the '*giganteus*' complex, drew the attention to the fact that there might be geographically more

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Table 2. Number of specimens of *Spirobranchus* spp. collected from different habitats.

Habitat	# of specimens from each species			
	S. corniculatus s. str.	***Spirobranchus* sp.**	***S. tetraceros***	***S. gardineri***
Acropora spp.	20	1	4	0
Cyphastrea spp.	0	0	0	5
Millepora spp.	32	25	0	0
Pocillopora spp.	5	0	1	0
Seriatopora spp.	2	0	4	0
Stylophora spp.	16	6	1	0
Artificial substrate	16	51	0	0

restricted taxa involved; he distinguished between two, possibly three subspecies: the Caribbean *S. giganteus* (Pallas, 1776), the Indo-West Pacific *S. corniculatus* and the Pacific Mid-American *S. incrassatus* Krøyer in Mörch, 1863. A further attempt was made by Fiege & ten Hove (1999, especially figure 4), who mentioned 12 taxa which almost all previously had been included in *Spirobranchus giganteus sensu latissimo*.

To facilitate identification, worms were collected and returned to the laboratory. We photographed each specimen using a Canon PowerShot G16 and examined each specimen using a Leica M165 FC binocular microscope and photographed it using a Leica DFC295 digital camera and LAS software. Worms' length was measured from the digital photographs, from base of radioles to end of pygidium, using image analysis ImageJ software (ver. 1.47v NIH). All specimens collected were categorized into groups (morphotypes) according to their opercular morphology, and were either compared to morphotype illustrations by Willette *et al.* (2015, figure 2 – however, in this figure two morphotypes have been switched: figure 2a, b show *Spirobranchus corniculatus*,- figure 2c, d are of *S. gaymardi*) or attributed to morphologically better defined taxa such as *S. tetraceros* and *S. gardineri*. Unfamiliar morphologies which could not be ascribed to one of the above mentioned taxa were recorded as *Spirobranchus* sp. Corals were identified to genus level by their morphology using a coral fact sheets guide (http://coral.aims.gov.au/factsheet.jsp?speciesCode=0162). It is important to note that while taxonomy of the *Spirobranchus corniculatus*-complex is still not fully resolved, this paper is focusing on ecological interactions of morphotypes with their substrate.

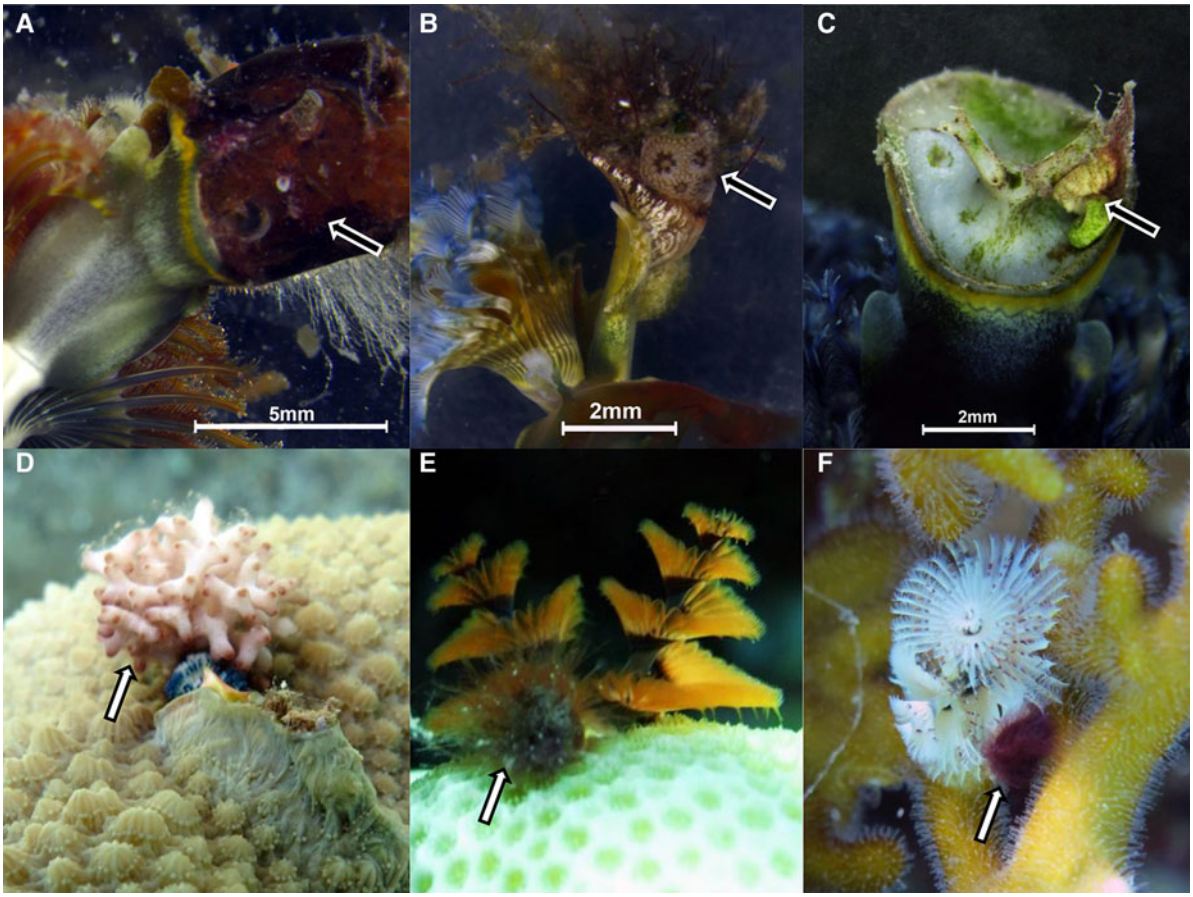

Fig. 2. Operculum as substrate: Arrows show operculum with organisms on top. (A–C) operculum under binocular, (D–F) worms *in situ*. (A) Sponge; (B) Coral; (C) *Spirorbis* tube; (D–F) Unidentified organisms. Photos: O. Perry.

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Molecular work is currently being executed on the worms collected to underpin the taxonomy of the species.

Statistical analyses

We used contingency table and χ^2 to test for association between substrate and identified morphotypes. To assess the effects of species identity and substrate type on worm length we used two-way analysis of variance. Preliminary observations revealed an apparent size difference between the two major morphotypes. Thus, in order to control for heritable differences between morphotypes, data were standardized within each species by subtracting the mean length and dividing by the standard deviation, to achieve mean of 0 and standard deviation of 1. All data analyses were carried out with R (R Development Core Team, 2012).

RESULTS

Morphological characterization

Specimens collected were divided into seven opercular morphology groups (Figure 3). Of the six species (eight nominal minus two confirmed synonyms, *Spirobranchus corniculatus* and *S. gaymardi*) reported from the Red Sea (Table 1) only five morphotypes (see below) were identified in this survey in the Gulf of Eilat. Among the 189 specimens collected, we identified the following taxa: *S. corniculatus, S. cruciger, S. gaymardi* (all three are considered part of the *S. corniculatus* complex *s. str.*, see Fiege & ten Hove, 1999, Figure 4), *S. gardineri* and *S. tetraceros*. In addition, two not previously recognized opercular morphologies were observed among the collected samples. The seven groups of opercular morphology can be defined as follows: *S. corniculatus* (Figure 3A) has an oval (more or less egg-shaped) opercular plate with two laterodorsal spines arising from a short common base. These spines each have a small dorsal tine, a secondary spinule along the bend and are forked at the tip. *Spirobranchus gaymardi* (Figure 3B) differs from *S. corniculatus* by the larger dorsal spines and a small medioventral knob to a large forked medioventral spine, all arising from a short common base. The laterodorsal spines have well developed dorsal tines, meeting mid-dorsally. In addition the dorsal spines have one or two secondary spinules along the bend of the spine and are forked at the tip. *Spirobranchus cruciger* differs from *S. gaymardi* by the dorsal tines not expanded at their tips and not meeting mid-dorsally (Figure 3C).

Spirobranchus gardineri (Figure 3D) has an oval opercular plate with one elongated almost central shaft with two dorsal and one forked midventral spines at the end, all pointing upwards. *Spirobranchus tetraceros* (Figure 3E) is recognized by an almost circular opercular plate with three pairs of antler-like spines arranged around the middle of the plate; each spine is forked at the tip (moreover, its radioles are arranged in two circles, not spirals; it is the only taxon here with anteriorly fringed peduncular wings, all others have smooth wings). *Spirobranchus* sp. two new morphotypes (Figure 3F, G) have a circular opercular plate with a pair of large dorsal antler-like spines arising from a short common base, each with a well developed dorsal tine (like those in morphotype *gaymardi*) well separated, and with two secondary spinules along the bend. There are two stout ventral spines, joined at their base, in some cases forked at their tips. A full description of this taxon is in preparation.

Species–substrate association

Nearly half of all specimens collected belong to the *Spirobranchus corniculatus* complex *s. str.* The complex was more abundantly found on corals than on artificial substrate (Table 2), but showed no preference for any particular coral species. *Spirobranchus tetraceros* and *S. gardineri* were both

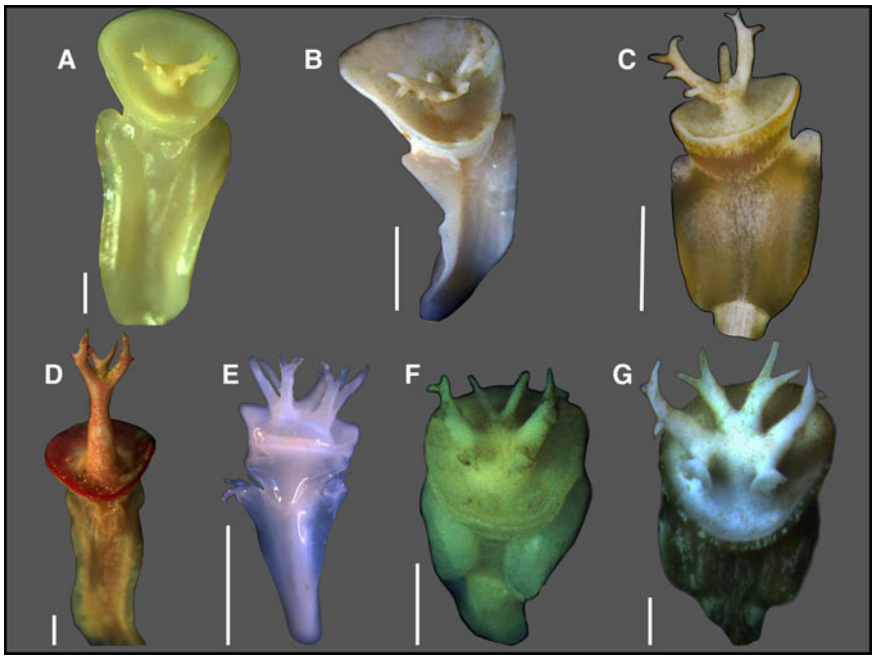

Fig. 3. Seven opercular morphology groups of *Spirobranchus* spp. from Eilat (dorsal views). (A–C) *S. corniculatus*: (A) morphotype *corniculatus s. str.*; (B) morphotype *gaymardi*; (C) morphotype *cruciger*; (D) *S. gardineri*; (E) *S. tetraceros*; (F, G) *Spirobranchus* sp. Scale bar: 1 mm. Photos: O. Perry.

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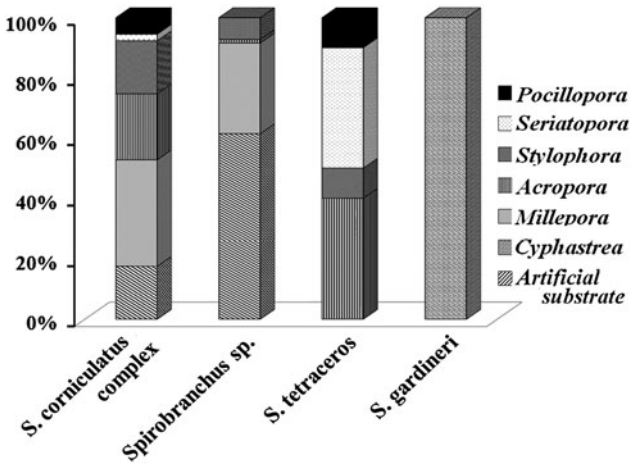

Fig. 4. Relative abundance of *Spirobranchus* spp. in different substrates.

uncommon (N = 10, 5.3% and N = 5, 2.7%, respectively) and both were found exclusively in association with corals. *Spirobranchus tetraceros* was found on *Pocillopora* Lamarck, 1816 spp., *Stylophora* Schweigger, 1820 spp., *Seriatopora* Lamarck, 1816 spp. and *Acropora* Oken, 1815 spp., whereas *S. gardineri* was found exclusively on *Cyphastrea* Milne Edwards & Haime, 1848 spp., a new record in addition to the three genera mentioned by Smith (1985). *Spirobranchus* sp. was found mainly on artificial substrate (N = 51, 61.5%). Overall, the distribution of *Spirobranchus* taxa over substrate types differed significantly ($\chi^2_{18} = 295.1$, $P < 0.001$; Figure 4). We only found sufficient numbers of the *S. corniculatus* complex and the undescribed morphotype (*Spirobranchus* sp.) for analyses of size. The average length of *Spirobranchus* sp. and *S. corniculatus* complex was 14.5 and 21 mm, respectively (Figure 5A).

Spirobranchus sp. was significantly larger when settled on artificial substrate than on corals, whereas individuals of the *S. corniculatus* complex were larger on corals and smaller on artificial substrate (Figure 5B).

DISCUSSION

Only five of the eight nominal *Spirobranchus* species previously reported from the Gulf of Eilat were found in this study. Some apparent absences can be explained by misidentification in the past, revisions in taxonomy that have occurred in the intervening years, and difference in sampling effort. *Spirobranchus latiscapus*, for instance, generally has been reported from dredged material and deeper water, not sampled by us. We cannot overrule the possibility of species disappearance from the area as a result of anthropogenic causes or climate changes (Rilov, 2016). Given the relatively limited collection efforts in this study, it is premature to interpret our results as an indication that a particular species no longer appears in the Gulf of Eilat. Data on substrates used by several of the *Spirobranchus* spp. are missing or limited.

We found five specimens of *S. gardineri* in this study, all of them associated with live *Cyphastrea*. The low abundance of *S. tetraceros* in this study is slightly surprising, having been reported to be a very abundant Lessepsian migrant in the Suez Canal and Mediterranean (Selim *et al.*, 2005). However, records from the Red Sea never mention such a massive occurrence (e.g. Ben-Eliahu & ten Hove, 2011). Another interesting difference is that the species fouls artificial substrate in the Suez Canal and Alexandria Harbour, but was only found on corals in the present study. Either it has a large ecological plasticity, which is suggested by Samimi Namin *et al.* (2010), or we are dealing with a complex of species only to be distinguished with genetics. All three morphotypes of the *Spirobranchus corniculatus* complex were identified in this study: *S. corniculatus, S. cruciger* and *S. gaymardi*. Contrary to previous records that *S. corniculatus* complex is an obligate symbiont of living corals (Nishi, 1996), this is the first record of *S. corniculatus* complex *s. str.* inhabiting an artificial substrate in addition to hermatypic corals. About 20% of these worms were found on artificial substrate in our study (Figure 4). It appears that the association with corals is not obligatory to the *S. corniculatus* complex *s. str.* in the Gulf of Eilat, all opercular morphologies belonging to the complex (thus *S. corniculatus, cruciger* and *gaymardi*) were found on corals as well as on artificial substrate. This may be attributed to differences in collecting efforts in previous studies or to differentiation in the Red Sea of the *S. corniculatus* complex. Genetic work (that has already started) may be able to shed light on this seemingly dissimilar behaviour. Two new and previously unrecognized morphologies were found which might represent a single new species. These forms showed a preference for artificial substrate, on which more than 60% had settled.

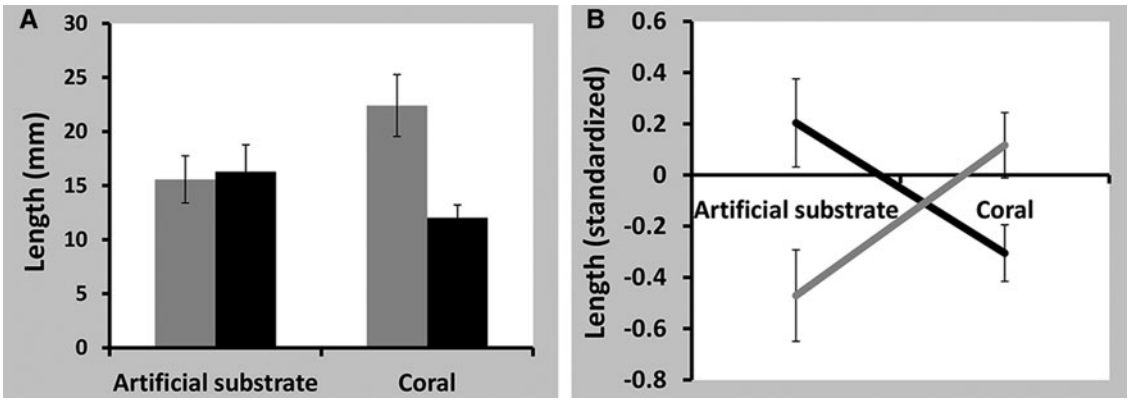

Fig. 5. The relationship between substrate and length in *Spirobranchus* associated with corals and artificial substrate. (A) Average length of *Spirobranchus corniculatus* complex (grey) and *Spirobranchus* sp. (black). (B) Standardized lengths of *Spirobranchus corniculatus* complex (grey) and *Spirobranchus* sp. (black) differed significantly as a function of substrate.

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In *S. giganteus s. str.*, the association with favourable substrate may influence fitness (Hunte *et al.*, 1990b). In a laboratory experiment, Hunte *et al.* (1990b) showed that worms that were found in their preferred habitat attained larger size. This appears to be supported by our study: worms of two species not only favoured different habitats, but they also apparently attained a larger size in their preferred habitats (*S. corniculatus* complex is more abundant and larger on corals; *Spirobranchus* sp. more abundant and larger on artificial substrate). Thus, worms of the *S. corniculatus* complex are not negatively affected by coral host defences, a finding consistent with the view that the worms may be commensal symbionts (Rowley, 2008). The opposite trend was found for *Spirobranchus* sp., preferring artificial substrates, making additional research on the relationships between different worm species and their various hosts and habitats necessary.

Spirobranchus worms sampled here showed high levels of plasticity in substrate selection. Worms were found on all six coral genera sampled, as well as on artificial substrate, though two species (*S. gardineri, S. tetraceros*) were only found on corals. The high level of plasticity in settling on a variety of substrates shown by *Spirobranchus corniculatus s.str.* as well as probably new species of *Spirobranchus* in the Gulf of Eilat may also explain the relative abundance of the genus in general.

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