2008

A critical evaluation of the symbiotic association between tropical tube-dwelling Polychaetes and their Hermatypic coral hosts, with a focus on Spirobranchus giganteus (Pallas, 1766)

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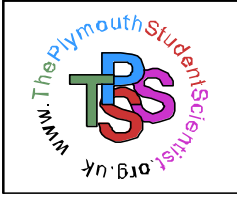
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2008

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Abstract

Coral reefs are high in species diversity with a low effective population size for most species and a high incidence of specific co-evolved relationships. Hermatypic corals are associated with, and attract a variety of, symbionts and commensals which helps to maintain coral reef biodiversity. However, little is known about such associations. Tropical tube-dwelling polychaetes provide an interesting surrogate in the enhancement of current understanding of such associations posing the question: what is the nature of the symbiotic association between tropical tube-dwelling polychaetes and their hermatypic coral hosts? This question is addressed by reviewing the life history and ecology of the conspicuous serpulid *Spirobranchus giganteus* (Pallas, 1766), an obligate associate of living hermatypic corals showing host species specificity. The distribution, life history and behavioural patterns of this taxon are suggestive of more than the currently perceived commensal association between its coral hosts. Most notably, recent studies have suggested the up regulation of *Spirobranchus giganteus* symbiotic association from commensalism to mutualism, with *Spirobranchus giganteus* protecting the coral host from predation, and increased water circulation to adjacent polyps facilitating coral recovery in algal dominated coral colonies. Such recent evidence illustrates the importance of associate organisms on coral reefs.

Key Words: *Spirobranchus giganteus*; symbiotic; association; polychaetes; coral; tube-dwelling

Introduction

Coral reef communities are renowned for their ecological complexity, exemplified by a level of coevolution among interacting species (DeVantier *et al*, 1986). Understanding such interactions and subsequent associations helps understand coral reef biodiversity, trophic structure and biochemical cycling, therefore assisting in making informed decisions on coral reef conservation. Hermatypic (reef building) corals deposit a structural $CaCO_3$ framework contributing up to 97% of the gross carbonate budget (GCP) of a coral reef (Mallela & Perry, 2007). Corals provide secondary space to other organisms (Todd, pers.comm., 2007), attracting a variety of symbionts and commensals such as sponges, polychaetes, pyrgomatid barnacles, vermetid gastropods, bivalves, tunicates, and hydroids (Scott, 1987; Scott & Risk, 1988; Kleemann, 2001; Tapanila, 2004; Floros *et al*. 2005; Scraps & Denis, 2007).

The term symbiosis is 'the living together of unlike organisms (symbionts)' (Bary, 1879 in Moran, 2006). For the purpose of this review the following definitions are of significance: parasitism, where one party gains considerably at the expense of the host (Dales, 1957); commensalism, where one party (the commensal) benefits whilst the host suffers no deleterious effect; and mutualism, where two (or more) species reciprocally benefit from the presence of the other species (Martin & Britayev, 1998).

It has been suggested that the species composition of associated polychaetes is a reflection of the surrounding environment (Bailey-Brock, 1976; Low *et al*. 1995). Polychaete tube-dwelling associates either bore into the coral matrix as bioeroders, or build a calcareous tube on the coral surface (Dai & Yang, 1995), contributing towards the reef's GCP as secondary carbonate producers (Bailey-Brock, 1976; Mallela & Perry, 2007). For example the composition of the polychaete boring community was seen to change with the increased degradation of *Porites* colonies (Pey-Clausade *et al*. 1992). Conversely sites with elevated sediment input have little, or no, serpulids (Perry & Smithers, 2006) due to the physical impairment of settlement, feeding, reproduction, and growth (Mallela & Perry, 2007).

Little is known of the life cycles of commensal polychaetes (Nishi, 1996; Martin & Britayev, 1998; Kleemann, 2001), however what is known is based largely on the tube-dwelling serpulid *Spirobranchus giganteus* (Pallas, 1766), an obligate associate of living hermatypic corals found in tropical and subtropical waters (Smith, 1984a; Strathmann *et al*. 1984;

DeVantier *et al*. 1986; Marsden, 1984, 1986, 1987; Marsden & Meeuwig, 1990; Marsden *et al*. 1990; Hunte *et al*. 1990a, b; Dai & Yang, 1995; Martin & Britayev, 1998; Qian, 1999; Floros *et al*. 2005; Lewis, 2006). *S. giganteus* is a dioecious filter feeding heterotroph, with a planktonic larval phase of 9-12 days (Smith, 1984a; Marsden, 1987; Marsden *et al*. 1990) and an estimated adult life span of over 30 years, one of the longest among marine annelids (Nishi & Nishihira, 1999). Its calcareous tube can be up to 20 cm in length and is usually deeply embedded in the coral skeleton (Nishi & Nishihira, 1999), which has often led to the misinterpretation that *S. giganteus* is a boring species (White, 1976; Nishi, 1996; Borger, 2006; Scaps & Denis, 2007). However Smith (1984a) reported that larvae settle on exposed coral skeleton and extend their tubes towards the living tissue, which subsequently obscures the tube.

The non-random distribution of *Spirobranchus giganteus* on specific coral species has been well documented (Bailey-Brock, 1976; Smith, 1984a; Scott, 1987; Marsden, 1987; Hunte *et al*. 1990a; Pey-Clausade *et al*. 1992; Dai & Yang, 1995; Nishi, 1996; Floros *et al*. 2005) and could be a consequence of larval preference at settlement or differential mortality following settlement (Connell, 1985; Hunte *et al*. 1990a). Much work therefore, has been done on the life history and ecology of *Spirobranchus giganteus* (Ten Hove, 1970; White, 1976; Strathmann *et al*. 1984; Smith, 1984a, b, 1991; DeVantier *et al*. 1986; Marsden, 1984, 1986, 1987; Marsden *et al*. 1990; Marsden & Meeuwig, 1990; Hunte *et al*. 1990a, b; Dai & Yang, 1995; Nishi & Nishihara, 1999; Floros *et al*. 2005), yet the relationship with its coral host is still unclear. Strathmann *et al*. (1984) and DeVantier *et al*. (1986) suggest that the coral-worm relationship is mutualistic, the coral providing the worm with support, nutrition and protection from predation by fish and Crustacea, and the worm enhancing water circulation for coral feeding and providing a refuge for polyps adjacent to the tube from predation and algal growth (Dai & Yang, 1995; Ben-Tzvi *et al*. 2006). *S. giganteus* also appears to have unique factors within its ontogeny endearing it more suitable to tube-dwelling and a symbiotic existence than its Sabellid counterparts; a calcareous tube and thoracic membranes being the synapomorphic characters (Ten Hove, 1984; Smith, 1991), as well as reduced regenerative abilities (accept for the operculum) and increased specialization of the branchial crown (Smith, 1991).

There are two currently recognized subspecies for *Spirobranchus giganteus* primarily based on operculum morphology (Ten Hove, 1970; Nishi, 1996): *Spirobranchus giganteus*

giganteus (Pallas, 1766) (Atlantic and Caribbean) with operculum spines emerging separately and highly variable; and *Spirobranchus giganteus corniculatus* (Grube, 1862) (Red Sea to Central Pacific) with operculum spines joined at a common base, being less variable. However, operculum variability observed within this taxon has caused much confusion (Ten Hove, 1970; Nishi, 1996). Therefore for the purpose of this review the two subspecies will be referred to collectively as *S. giganteus* unless specified otherwise.

The aim of this review is to determine the symbiotic association between tropical tube-dwelling polychaetes and their hermatypic coral host, through a critical evaluation of the life history and ecology of the conspicuous serpulid *Spirobranchus giganteus* (Pallas, 1766).

Distribution

The non-random distribution of *Spirobranchus giganteus*, on specific coral taxa, has been well documented even though the coral species colonized differ geographically (Bailey-Brock, 1976; Smith, 1984a; Scott, 1987; Marsden, 1987; Hunte *et al.* 1990a; Pey-Clausade *et al.* 1992; Dai & Yang, 1995; Nishi, 1996; Marsden & Meeuwig, 1999; Floros *et al.* 2005). Dai & Yang (1995) suggest that *S. giganteus* may be morphologically selective of coral species; tabulate *Acropora* spp. provide an elevated platform which reduces sedimentation risk (Floros *et al.* 2005), foliaceous and branching forms often experience a higher rate of mortality than the massive form during natural disturbances. Coral species frequently colonized by *S. giganteus*, in both the Caribbean (Hunte *et al.* 1990a) and the Pacific are of massive form and occur in prominent positions (Strathmann *et al.* 1984; Hunte *et al.* 1990b; Martindale, 1992; Dai & Yang, 1995). Massive corals usually have a longer life span, for example: a colony of the frequently colonized host coral *Porites lutea* was estimated at being over 500 yrs (Dai & Yang, 1995), therefore worms inhabiting such corals might have higher fitness (Hunte *et al.* 1990b). There is no information in longevity of *S. giganteus* on different coral species (Hunte *et al.* 1990b); however Smith (1984b) and Nishi & Nishihira (1999) suggested a life span of over 30 yrs. Nishi & Nishihira (1999) further suggested that host corals are likely selected with a similar growth rate to that of the worm. *S. giganteus* regulates the growth rate of its tube by changing the wall thickness, yet settlement on rapidly growing species weakens the tubes, and settlement on slow growing corals resulting in stunted tubes. Hunte *et al.* (1990b) showed that spatial constraints did not appear to limit worm body size as coral species with the largest

worms were the most heavily colonized in the field, and were also preferred by worm larvae in the laboratory. They concluded that the non-random distribution of *S. giganteus* on corals results primarily from active habitat selection by planktonic larvae, and that habitat selection displayed by the larvae is probably adaptive (Hunte *et al*. 1990b).

Both corallite (skeletal structure of a single polyp) size and morphology have been related to coral associate distribution (Scott, 1987; Dai & Yang, 1995; Wielgus *et al*. 2006a; Scaps & Denis, 2007). Wielgus *et al*. (2006a) showed that boring spionid worms generally infested plocoid (corallites with their own walls) coral species with small polyps. Such species have a high coenosteum to corallite ratio; which may facilitate infestation by providing a sufficient surface area. Similarly the boring bivalve *Pedum spondyloideum* has been shown to favour corals with small corallites such as *Montipora*, *Porites* and *Cyphastrea* (Kleemann, 2001; Scaps & Denis, 2007). The same can be said for *Spirobranchus giganteus* as illustrated in Figure 1a and Table 1, where the majority of coral species with small corallite size were significantly ($F_{13}=2.55$, $P<0.005$) inhabited by *S. giganteus*. Such corals are predominantly plocoid (Figure 1b & Table 1) and species such as *Porites lutea* and *Porites lobata* are

(a)   (b)
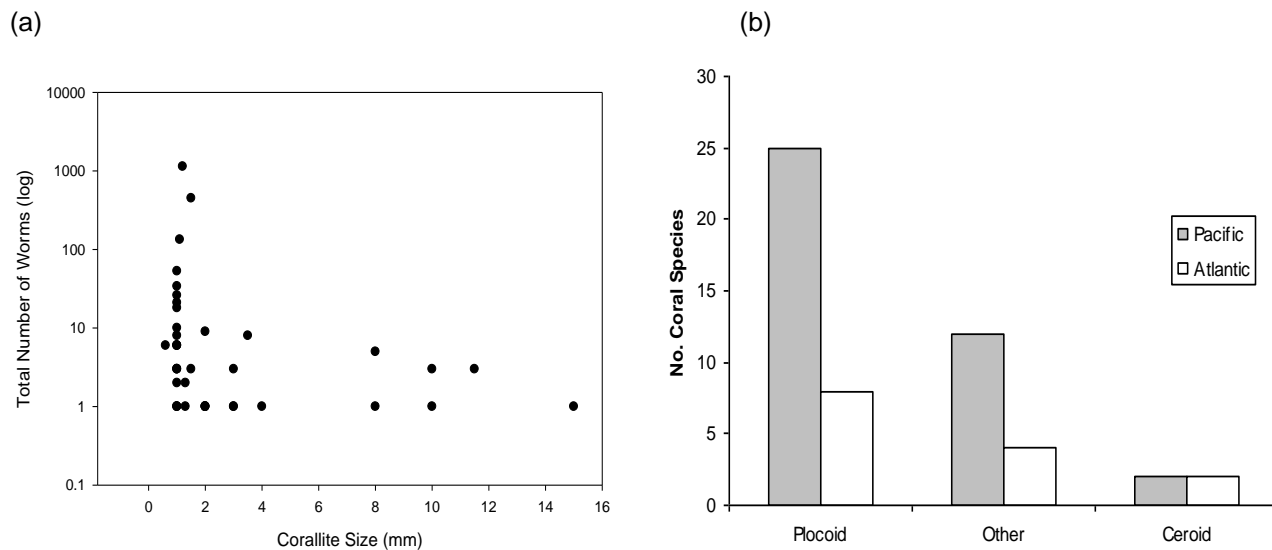
Figure 1: (a) Total number of worms vs corallite size of host coral colonies. 1-Way ANOVA; data square root transformed, $F_{13}=2.55$, $P<0.005$ (Data from: Dai & Yang, 1995). (b) Colony morphology of host corals from the Pacific and Atlantic. Plocoid: Corallites with own walls; Ceroid: Corallites with shaired walls (Veron, 2000; Data from: Bailey-Brock, 1976; Marsden & Meeuwig, 1990; Hunte *et al*. 1990; Dai & Yang, 1995; Beaver *et al*. 2004).

extremely robust in terms of colony morphology as well as photochemistry (Henniger *et al*. in press). However Smith (1984a) observed that *S. giganteus* larvae successfully settled on the non-living edge of live corals and that larvae which did settle on the live coral tissue fell off after several days, unable to make a sufficient attachment. Juveniles found on live tissue away from the coral boundaries were suggested to be as a consequence of recent damage e.g. from scarid grazing scars (Smith, 1984a).

The distribution and abundance of *Spirobranchus giganteus*, in different reef areas is likely affected by environmental factors and the availability of colonized substrate (Dai & Yang, 1995). *S. giganteus* abundance has been shown to be highest between 6-18 m depth (Dai & Yang, 1995; Floros *et al*. 2005), yet mean worm density on individual coral species was found to be independent of the abundance, distribution and competitive dominance of available coral by Hunte *et al*. (1990a) and Marsden & Meeuwig (1990). Conversely, Dai & Yang (1995) found that coral species in Taiwan frequently colonized by the worms such as *Porites lutea*, *Porites lobata*, *Porites lichen*, *Montipora informis*, are competitively subordinate in terms of aggression (Dai, 1990). Very few species with high aggressiveness such as *Mycedium elephantotus*
, *Merulina ampliata* and *Galaxea astreata* were successfully colonized by the worms (Table 1). These facts indicate that planktonic larvae of *S. giganteus* may be susceptible to the nematocysts of aggressive corals (Dai & Yang, 1995). However Smith (1984a) observed that searching larvae (from the Great Barrier Reef) appeared immune from the polyps' nematocyst discharge. There appears to be disparity between the different coral species colonized relative to the two subspecies, thus geographic location. It is possible that *Spirobranchus giganteus giganteus* is more robust in terms of nematocyst defense and colonization selection than *Spirobranchus giganteus corniculatus*. Further data are necessary in order to observe any notable trends between the two regions. The *Spirobranchus* genus does confer a degree of immunity to nematocyst discharge (as observed by Smith, 1984a) as both subspecies are known to inhabit the aggressive hydrocoral *Millepora* spp. (Hunte *et al*. 1990a; Dai & Yang, 1995; Lewis, 2006; Ben-Tzvi *et al*. 2006). This may, however be consequential, unlike *Spirobranchus polycerus* (Schmarda**)** which is constrained by adaptation through hermaphroditism, to a commensal existence primarily on *Millepora complanata* (Marsden, 1993; Lewis, 2006). Interestingly larvae of the Caribbean boring bivalve *Lithophagia bisulcata*

Table 1: Coral species, corallite size, number of colonized colonies by *Spirobranchus giganteus*, total number of worms and colony morphology (Data in Taiwan, taken from Dai & Yang, 1995; Corallite size and Morphology from Veron, 2000). *Aggressive corals (Dai, 1990).

Coral Species	Corallite (mm)	No. Colonized Colonies	Total Worm No.	Colony Morph
Porites lutea	1.2	40	1138	Plocoid
Porites lobata	1.5	35	450	Plocoid
Montipora informis	1	33	53	Plocoid
Porites lichen	1.1	21	134	Plocoid
Montipora spongodes	1	7	26	Plocoid
Montipora spumosa	1	6	21	Plocoid
Montipora monasteriata	1	7	10	Plocoid
Montipora venosa	1	3	6	Plocoid
Favia speciosa	10	3	3	Plocoid
Cyphastrea serailia	3	3	3	Plocoid
Favites abdita	11.5	3	3	Plocoid
Montipora foveolata	1	4	34	Plocoid
Montipora tuberculosa	1	2	8	Plocoid
Montipora grisea	1	4	18	Plocoid
Montipora aequituberculata	1	2	3	Plocoid
Montipora foliosa	1	2	2	Plocoid
Millepora platyphylla	1	5	6	Plocoid
Acropora loripes	2	1	9	Other
*Galaxea astreata	3.5	1	8	Other
Porites rus	0.6	1	6	Plocoid
Favia pallida	8	1	5	Plocoid
Seriatopora hystrix	1	1	3	Other
Stylocoeniella armata	1.5	1	3	Other
Montipora verrucosa	1	1	1	Plocoid
Acropora digitifera	2	1	1	Other
Porites annae	1.3	1	1	Plocoid
Cyphastrea microphthalma	3	1	1	Plocoid
Astreopora cucullata	2	1	1	Conical
Barabatoia amicorum	10	1	1	Other
*Mycedium elephantotus	15	1	1	Excert
*Merulina ampliata	1	1	1	Valleys
Stylophora pistillata	1	1	1	Conical
Montipora undata	1	2	6	Plocoid
Porites nigrescens	1.3	1	2	Plocoid
Millepora tenera	1	1	3	Other
Cyphastrea chalcidicum	3	1	1	Plocoid
Acropora humilis	2	1	1	Other
Acropora hyacinthus	2	1	1	Other
Coeloseris mayeri	4	1	1	Ceroid
Favites pentagona	8	1	1	Ceroid

(d'Orbigny) are immune to its preferred host coral *Stephanocoenia michelini* nematocysts, yet stung by those rarely inhabited (Scott, 1988).

The distribution of *Spirobranchus giganteus* therefore, is host specific, due to differential mortality following settlement or pre-settlement larval preference, which has been found to respond positively to water-borne exudates of corals commonly colonized by *S. giganteus* (Marsden, 1987; Marsden *et al*. 1990; Marsden & Meeuwig, 1990). Interestingly, larvae may also be attracted to conspecifics as adults cluster on some *Porites* colonies for example, while adjacent colonies may be devoid of worms (Smith, 1984a). A reproductive strategy that infers maximum gamete fertilization and overall survival on the reef (Dai & Yang, 1995, Rodriguez *et al*. 1993, Pawlik, 1991).

Larval Settlement & Development

Resettlement preferences are reflected in adult distribution (Hunte *et al*. 1990b). During the planktonic stage, larval responses to biological factors: conspecifics, sympatric species, biofilms, prey species, and environmental factors such as water flow, light intensity, chemical cues and properties of the substrate may have a great influence on larval dispersion and settlement (Pawlik *et al*. 1991; Rodriguez *et al*. 1993; Qian, 1999). Larval settlement of the polychaete *Capitella* sp *I*, for example, was significantly enhanced by sulphide enriched sediments (Cuomo, 2005). *Spirobranchus giganteus* larvae exhibit active preference in the laboratory for the coral species most heavily colonized in the field (Marsden, 1987; Marsden *et al*. 1990; Marsden & Meeuwig, 1990).

Smith (1984a, b, 1991) and Marsden (1984, 1986, 1987) in a series of studies on the larvae of *Spirobranchus giganteus*, attributed various developmental and behavioural characteristics to the association between *S. giganteus* and its host coral. *S. giganteus* is dioecious with a 9-12 day planktotrophic larval phase (Smith, 1984a; Marsden, 1987; Marsden *et al*. 1990). Within the first 24 hrs the first larval ocelli (compound eyes) develop (Smith, 1984a, b) facilitating positive phototaxis to visible light of wavelengths shorter than 590nm (Marsden, 1984). Smith (1984b) found that simple cerebral ocelli photoreceptor cells display a close structural and functional relationship between ciliary rootlets and specialized mitochondria that exhibit a level of structural advancement only otherwise seen in the lancelet *Branchiostoma*. Olsson (1962) proposed that they were trapping energy produced by the

mitochondria as a role in receptor conformation. Furthermore, gradual development of the light response reflects stages in ocelli photoreceptor development (Smith, 1984a, b) and the establishment of functional neural connections developing in 24-48 hrs larvae (Iacalli, 1984). Interestingly, the activity patterns within the nervous systems of the nudibranch larvae *Phestilla sibogae* changed in response to their coral prey exudates (Leise & Hadfield, 2000). Marsden (1987) found that the 1-4 day trochophore larvae of *S. giganteus* showed significant chemical preference to host coral, indicating chemosensory behaviour.

The early development of such structures in the trochophore larvae may, therefore, confer to the attraction towards conspecific or coral exudates, mucus or a combination of these cues. Wild *et al*. (2004) reported that up to 80% of released mucus is dissolved, thus illustrating that mucus derived chemicals habituate the water column. Moreover simultaneous positive photo and chemotaxis during the planktonic stage might have the net effect of maintaining larvae below the surface waters over the coral reef, suggesting that the role of this stage in the life history of the worm is more than one of passive dispersal (Marsden, 1987).

The exact role, if any, of ocelli receptors for chemosensory behaviour is unresolved. What is clear is *Spirobranchus giganteus* larvae respond to biophysical cues from adults or adult sites (Hunte *et al*. 1990b). Such cues mask the photoresponse at the demersal stage, immediately prior to metamorphosis which is not completed until after settlement (Smith, 1984a; Marsden, 1984, 1986). Smith (1984a) observed that larvae enter a searching phase, swim over the substrate, pause and flex the abdomen from side to side across the substratum. Marsden (1986) suggest such behaviour maybe concerned with the development of coral species recognition. Settlement eventually takes place even in the absence of a suitable substratum, triggering the final phase of metamorphosis. Development must proceed therefore, according to a genetic programming (Smith, 1984a), unlike the *Phestilla sibogae* larvae which metamorphose only in response to a natural exudate from its prey *Porites compressa* (Leise & Hadfield, 2000). *S. giganteus* larvae forced to settle on a glass surface completed metamorphosis with no further development and died after two days (Smith, 1984a), indicating that survival of *S. giganteus* in dependent on its live coral host. Thus a number of sensory modalities are probably employed by the settling larvae, especially chemo-, thigmo-, and photosensation (Smith, 1984b).

On settlement *Spirobranchus giganteus* secrete a mucus tube, the basis for rapid carbonate (calcite or aragonite; Smith, 1985; Rouse & Pleijel, 2001) deposition towards and across the living coral surface (Smith, 1984a). The coral surrounds the tube and incorporates it within its skeleton. The settled worms rapidly grow and initially put down at least a body length of tube (0.5-1 mm) per day (Smith, 1984a). Palps soon develop and keep the tube opening smooth and moist preventing the overgrowth of host coenosteum tissue (Lewis, 2006). Larval ocelli are retained throughout metamorphosis and are initially responsible for the withdrawal response within 24 hours of tube construction, until the development of branchial photoreceptors and the operculum within 1-2 weeks (Smith, 1984b). The paired branchial eyes of *S. giganteus* represent the most complex photoreceptor organs yet described in the Sabellida and are probably the closest rivals to the compound eyes of arthropods (Smith, 1984b). Such an advanced adaptation to tube-dwelling existence is considered of phylogenetic significance (Smith, 1984b).

Spawning

Natural spawning of *Spirobranchus giganteus* has seldom been observed (Smith, 1984a). However, mass spawning events have recently been documented from the Gulf of Mexio (Beaver *et al.* 2004; Hickson, 2007). In both cases simultaneous spawning of male and female *S. giganteus* and host corals (*Montastraea annularis, M. aveolata, M. cavernosa, M. franksi, Diploria strigosa*), occurred in the evening during slack neap tides with nominal wind and wave action (Beaver *et al.* 2004; Hickson, 2007). Such conditions minimize gamete distribution by water turbulence and wave action, increasing the chances of fertilization. Simultaneous spawning may increase the likelihood of successful settlement, potentially due to coral exudates remaining in the adjacent water column. Such reproductive strategies have been shown to be successful in predation swamping (Gladstone, 2007); however this may also result in gamete dilution and sperm limitation. Interestingly, Biermann (1998) demonstrated positive selection for interspecific divergence in the gamete recognition proteins in six species of the sea urchin genus *Strongylocentrotus*. Variations in receptor proteins occurred due to an excess of and divergence in non-synonymous changes in DNA sequences between the six urchin species, facilitating successful fertilization without hybridization in urchins which have

overlapping ranges and spawning (Biermann, 1998). Biermanns work, however, could potentially illustrate what might be occurring between *S. giganteus* and its varying operculum types. It would be intriguing to see if variations in operculum morphology were host coral specific and clustered in distribution, thus intra specific divergence.

The drag produced by winds blowing over the sea surface, and water flowing over a stationary bottom, creates strong vertical gradients in both magnitude and direction of horizontal flow (Eckman, 1996) which disperse pre-competent larvae (larval development before settlement) and water-borne exudates. The timing of spawning events and a preference by young *Spirobranchus giganteus* larvae for a substance diffusing from coral &/or conspecifics, acting together with a known positive phototaxis, may be adaptive helping to maintain larvae in surface waters over the reef in the vicinity of a specific coral until competency (Marsden, 1987).

Trophic Interactions

Spirobranchus giganteus like most coral associates, is a filter feeding heterotroph creating aboral (bottom up) feeding currents due to laterofrontal cilia but depends on ambient currents to prevent multiple re-filtration of its own excurrent stream through its branchial crown (Strathmann *et al*. 1984). Strathmann *et al*. (1984) demonstrated that currents created by the branchial crown draw water up from the coral surface. This may enhance water circulation and consequentially, the arrival rate of food particles to the coral polyps (Floros *et al*. 2005; Dai & Yang, 1995; Hunte *et al*. 1990), as well as providing nutrition for the worm.

Improved water circulation close to the coral surface would decrease susceptibility to bleaching (Nakamura *et al*. 2003), improve dispersal of waste products of the coral host, and increase nutrient availability from waste materials excreted by the associated fauna (Mokady *et al*. 1998). The boring bivalve *Lithiphaga simplex* has been shown to produce considerable amounts of ammonium as nitrogenous waste products which are recycled by the coral host and may account for a significant portion of the coral/zooxanthellae nitrogen requirements (Mokady *et al*. 1998). Mokady *et al*. (1998) further considered that the symbiotic association between the bivalve and host coral to be mutualistic, however *Lithophaga* also colonizes dead coral substrata (Kleemann, 2001). Interestingly Rotjan & Lewis (2006) found that selective

Figure 2: *S. giganteus* with coral mucus (arrowed) in tentacle whorls (© Sonia Rowley).

grazing by scaridae fish favoured colonies with high densities of associates. They further revealed that coral tissue associated with *Spirobranchus giganteus* had significantly higher nitrogen content compared to grazed and intact massive *Porites* colonies (Rotjan & Lewis, 2006). Yet Kicklighter and Hay (2006) demonstrated that due to retraction and conspicuous branchial colouration, predation risk on *S. giganteus* was significantly reduced regardless of being significantly more palatable than other polychaetes.

Biological systems that conserve or recycle nitrogenous materials are an advantage in oligotrophic waters typical of coral reef environments (Mokady *et al*. 1998). Fitt (1985) found that the zooxanthellae *Symbiodinium microadriaticum* were only attracted to nitrogenous compounds ~1 cm from source. He further noted that *S. microadriaticum* strains varied in chemosensory ability inferring preservation in strain selection between the host and dinoflagellate. Also Grover *et al*. (2006) using ^{15}N-urea showed that urea uptake was at least 4x higher in the coral than zooxanthellae, and 5x higher in the light, demonstrating the involvement of nitrogenous substances in the calcification process. Thus elevated nitrogen evident of coral associates such as *Spirobranchus giganteus* may assist in zooxanthellae

acquisition and calcification.

Coral mucus is an important carrier of energy and nutrients with high concentrations of Ca^{2+} (Marshall & Wright, 1998; Clode & Marshall, 2002). Clode and Marshall (2002) suggested that coral mucus maintains a Donnan equilibrium (medium which separates an unequal distribution of diffusible ions between two ionic solutions) at the oral-sea-water interface facilitating Ca^{2+} uptake. *Spirobranchus giganteus* precipitates $CaCO_3$ from glands adjacent to the coral surface, therefore it is possible that Ca^{2+} present in the mucus is taken up and used by the worm. Furthermore Wild *et al.* (2004) noted that up to 50% of photosynthate was lost to coral mucus. Coral mucus uptake (as illustrated by Strathmann *et al.* 1984; Figure 2) and utilization by *S. giganteus*, resulting in nitrogen secretion, subsequent use by the host coral and zooxanthellae with a possible increase in mucus Ca^{2+} concentration further utilized by the worm may be occuring. To test this hypothesis, the use of ^{45}Ca and ^{14}C (as used by Marshall & Wright, 1998) and ^{15}N (as used by Gresty & Quarmby, 1991) may ascertain any trophic recycling &/or niche partitioning (Tapanila, 2004) occurring between *S. giganteus*, host coral and its zooxanthellae.

The microbial composition of coral mucus has also been well documented (see Brown & Bythell, 2005). Comparative analyses of the microbial content of coral mucus, worm gut content and exhalent using *rpo* PCR, DGGE, sequencing and clone library techniques (Bourne & Munn, 2005) may indicate if any microbes are being utilized by the worm with a potential view to pathogen removal.

Therefore, the relationship between *Spirobranchus giganteus* and coral host may benefit from niche partitioning strategies including differing dietary requirements and vertical tiering (Tapanila, 2004). No alteration in corallite size or polyp density is also suggestive of a reduction in spatial competition between *S. giganteus* and its coral host, with its branchial whorls sufficiently above the substratum (Tapanila, 2004; Martin & Britayev, 1998). This is unlike boring spionids, which are shown to have marked decrease in polyp density immediately adjacent to their tubes (Wielgus *et al.* 2006a).

Several associates benefit the hosts by preying upon the larvae of boring animals, by removing detritus and coral mucus, and even by attacking potential predators of the corals (Nogueira, 2003; DeVantier *et al.* 1986). DeVantier *et al.* (1986) suggested that a predator-

induced selection may be operating as an ecological mechanism in the development of the interaction from the *Spirobranchus giganteus* commensalism into facultative mutualism. Predation by *Acanthaster planci* on a colonized *Porites* colony induced retraction followed by immediate reappearance of *S. giganteus*. The operculum and branchial crown pushed against the tube feet and arms of the star fish, causing the predator to rapidly move away (DeVantier *et al.* 1986). Observations two years after this predation event revealed areas of living polyps beneath the worm's branchial crowns showing evidence of regrowth above the surrounding algal covered skeleton, with asexual budding occurring in the outermost polyps (DeVantier *et al.* 1986). Polyp recovery has also been documented on the faviid coral *Cyphastrea chalcidicum* which was covered in turf algae, apart from three small areas of living tissue surrounding *S. giganteus* tubes (Ben-Tzvi *et al.* 2006). After one year the coral tissue had rapidly grown, a phenomenon also observed in bleached *Favia favus* and predated *Favia laxa* colonies (Ben-Tzvi *et al.* 2006). Conversely, Borger (2005) stated that all Dark Spot Syndrome (DSS) Type III blemishes were caused by irritation of the coral surface from *S. giganteus* and horseshoe worms. Recent work by Renegar *et al.* (2007), suggest that DSS is likely a stress response instead of a true disease although *S. giganteus* was not specified. The consequence of DSS is of serious consideration as it has been shown to progress the more destructive Black Band Disease and White Plague (Rosenberg & Loya, 2004; Borger, 2005).

Conclusion

On reflection of the empirical evidence presented in this review there are clear adaptive responses to both a tube-dwelling and symbiotic existence expressed by the serpulid *Spirobranchus giganteus*. The nature of its symbiotic association with its coral host still remains to be seen. However, there are strong implications as to why this may be more than just a commensal association as is commonly perceived, probably a reflection of the current lack of knowledge in this area (Martin & Britayev, 1998).

Spirobranchus giganteus shows a non-random distribution on specific coral hosts (Bailey-Brock, 1976; Smith, 1984a; Scott, 1987; Marsden, 1987; Hunte *et al.* 1990a; Pey-Clausade *et al.* 1992; Dai & Yang, 1995; Nishi, 1996; Floros *et al.* 2005), clustering within specific colonies. Such ecology has been shown to relate to coral morphology (Floros *et al.*

2005), aggressiveness (Dai, 1990), corallite size (Dai & Yang, 1995) and conspecifics (Smith, 1984a). *S. giganteus* is uniquely adapted to tube-dwelling life possessing a specialized branchial crown and photoreceptors (Smith, 1991), spawning synchronicity (Beaver *et al*

Figure 3: Clustering: Mutualism, commensalism or parasitism? (© Sonia Rowley**).**

. 2004; Hickson, 2007), trophic interactions, predator defense and polyp growth (DeVantier *et al*. 1986; Ben-Tzvi *et al*. 2006). Yet such interpretations should be treated with caution, as the important issue is not the presence or absence of benefits and damages to each of the participants, but the balance between them (Mokady *et al*. 1998). Therefore evolutionary trends may exist within the term 'symbiosis' between *S. giganteus* and its coral host (Figure 3).

Acknowledgements

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