Habitat selection in the tropical polychaete *Spirobranchus giganteus*

I. Distribution on corals

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Abstract

Spirobranchus giganteus (Pallas) is an obligate associate of live coral. Its distribution on corals was studied at three locations along the bank reef on the west coast of Barbados in 1986. The degree of colonisation by worms (no./surface area of coral) differed between coral species. This implies differences in larval preference at settlement and/or differences in mortality following settlement. The degree of colonisation was not correlated with total surface area nor mean coral colony size, nor with the rank of the coral in an aggression hierarchy. *Diploria strigosa*, *Porites astreoides* and *Millepora complanata* were most heavily colonised. *Montastrea annularis*, *Madracis* spp. and *Agaricia* spp. were moderately colonised and *Porites porites*, *Diploria labyrinthiformes*, *Montastrea cavernosa* and *Siderastrea siderea* were sparsely colonised. *Colpophyllia natans*, *Dendrogyra cylindricus*, *Dichocoenia stokesii*, *Eusmilia fastigata*, *Meandrina meandrites* and *Mycetophyillia* spp. were not colonised. Worm abundance differed between study sites, possibly reflecting a difference in larval availability at the three sites. Worms were significantly clustered at all sites, suggesting an attraction for conspecifics at settlement.

Introduction

A coral reef may be regarded either as a densely populated habitat where competition for space is high (Smith 1978, Anderson et al. 1981, Hunte and Côté 1989) or as a habitat in which populations are limited by the number of larvae surviving the plankton and recruiting to the reef (Doherty 1983, Victor 1984, 1986). Whether space or larval availability ultimately limits the abundance of coral-reef organisms, it is evident that coral reefs are complex ecosystems in which species diversity is high and commensal associations are common. Understanding the habitat selection processes which may underlie the distribution patterns of coral-reef

organisms, particularly the sessile commensal organisms, is an important step in understanding the complexity of coral-reef systems; but little is known about habitat selection in commensal reef organisms. Studies of sessile marine invertebrates have suggested that distribution is controlled either by larval preference at settlement (Meadows and Campbell 1972a, b, Scheltema 1974, Strathmann and Barnscomb 1979, Al-Ogilvy 1985) or by differential mortality of juveniles and young adults after settlement (Connell 1985).

Spirobranchus giganteus is a serpulid polychaete that is an obligate associate of live hermatypic coral. It is dioecious, with a planktonic larval phase of 9 to 12 d . It is found in tropical and sub-tropical seas, and has been divided by Hove (1970) into two subspecies, *S. giganteus corniculatus* in the Pacific and *S. giganteus giganteus* in the Atlantic and Caribbean.

The relationship between *Spirobranchus giganteus* and its host coral is poorly understood. The worm does not bore or excavate the coral but builds its tube on the surface of the colony. Thereafter, tubes are covered by living coral, up to the margin of the tube opening. Strathmann et al. (1984) suggested that using live coral as a substrate reduces competition between *S. giganteus* and other sedentary species for space, food and oxygen. Other serpulids occupy crevices and the underside of rocks (*Serpula vermicularis*, *Salmacina incrustans*, *Pomatoceros triqueter*), or are highly gregarious on rocky shores (*Mercierella enigmatica*, *Galeolaria caespitosa*, *Spirobranchus polycerus*). However, exposure on the coral surface may increase risk of predation (Strathmann et al. 1984). The effect of the worm on the coral is also difficult to evaluate. *S. giganteus* probably confers some structural weakness to the coral since its presence results in a hollow tube within the skeleton. However, Strathmann et al. (1984) showed that the currents created by the branchial crown of the worm draw water up from the coral surface. This may enhance water circulation and, consequently, the rate of arrival of food particles to the coral polyps. DeVantier et al. (1986) suggested that the coral–worm relationship was mutualistic, the coral providing the worm with support and

protection and the worm providing a refuge, for polyps adjacent to the tube, from the starfish predator *Acanthaster planci*.

One approach to clarifying the relationship between *Spirobranchus giganteus* and corals is to investigate habitat selection by the worm for different corals. The purpose of the present paper is to begin the study of habitat selection by investigating the distribution of the worm on corals at three locations along the bank reef on the west coast of Barbados, West Indies. Specifically, we investigate whether the degree of colonisation by worms (no./surface area of coral) differs between coral species; whether the degree of colonisation is correlated with total surface area, mean colony size or rank of the coral in an aggression hierarchy; whether the colonisation pattern differs between study sites; and whether the distribution of worms on a coral species is clustered, even, or random.

Materials and methods

Study sites

The distribution of *Spirobranchus giganteus* (Pallas) was studied at three locations along the bank reef on the west coast of Barbados in 1986 (Fig. 1). The reef extends the length of the island and varies in width from ca 30 to 100 m. It lies ca 500 to 900 m offshore and is bordered by deeper areas of sand on its landward and seaward sides. The Golden Palms study site (GP) was located 580 m offshore. The depth ranged between 10 and 16 m and the reef ridge was ca 100 m wide. The site had many sandy patches and gorgonians. The Sunset Crest study site (SC) was south of the GP site, ca 630 m offshore. Reef depth varied from 13 to 19 m. The reef ridge was 50 to 60 m wide with occasional sandy patches. The Speightstown site (SP) was the deepest and most northern site, situated ca 900 m offshore. The reef ridge had a maximum width of 30 m and sandy patches were small and infrequent. Depth ranged between 16 and 22 m.

Survey methods

Each study site was 2 500 m^2 and was marked with ropes permanently fixed along the north and south margins. The site dimensions were 50 × 50 m at GP and SC, and 25 × 100 m at SP. Forty 1 m^2 quadrats were randomly selected at each site (Zar 1984). The selected quadrats were located underwater by pairs of divers using wrist compasses and a spool of rope flagged at 1 m intervals. When a quadrat was located, it was delimited by a 1 m^2 aluminium frame. In each quadrat, corals were identified, the planar surface area of each coral-colony was quantified and the number of worms on each coral-colony counted (see Weinberg 1981 for advocacy of the quadrat-frame method over the transect). One diver measured the largest diameter of each coral head within the frame, holding the tape horizontally above the colony to get a planar view. The other diver identified the coral and both divers examined each coral
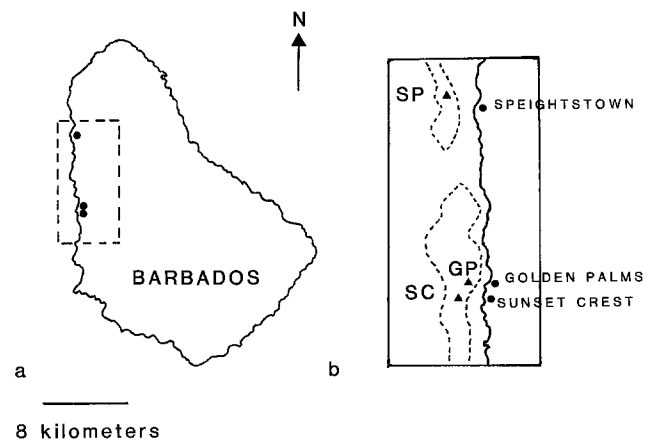

8 kilometers

Fig. 1. Barbados showing locations of the three study sites – ▲GP: Golden Palms; ▲SC: Sunset Crest; ▲SP: Speightstown

head for worms. Corals were identified to species by polyp structure (e.g. *Montastrea annularis* and *M. cavernosa*, *Diploria labyrinthiformes* and *D. strigosa*) or colony structure (e.g. *Porites astreoides* and *P. porites*) when feasible. For others (*Agaricia, Madracis, Mycetophyllia*), identification to species was considered unreliable in the field. These were identified to genus only.

Since most corals are not flat, a realistic estimation of coral-colony surface-area requires a relief factor (see Pichon 1978). Relief factors (or surface indices) for the conversion of planar surface-area into actual surface-area have been developed for British Honduras reefs (Dahl 1973) and Barbados fringing reefs (Stearn et al. 1977). Following Dahl (1973) and Stearn et al. (1977), corals in this study were divided into massive, ridge-like and branching forms, and separate conversion factors were used in surface area calculations for each category. Estimation of the surface area of massive corals was based on the assumption that colonies were roughly hemispherical, and hence that surface area $= 2 \pi r^2$ (Dahl 1973). This conversion factor was used for *Diploria strigosa, Siderastrea siderea, Montastrea cavernosa, Colpophyllia natans, Meandrina meandrites, D. labyrinthiformes, M. annularis, Porites astreoides, Dichocoenia stokesii, Dendrogyra cylindricus* and *Agaricia* spp.; all of which are roughly hemispherical on the Barbados bank reef. Dahl's (1973) conversion factor (× 5.6) for colonies in the form of plate-like ridges was used for *Millepora complanata*. The appropriate conversion factor for branching corals varies interspecifically, since the degree of branching varies. For example, Dahl (1973) used a factor of × 3 for *Acropora palmata* and Stearn et al. (1977) and Lewis (1981) used a factor of × 13 for *Porites porites* and *Madracis mirabilis*, respectively. We used a conversion factor of × 13 for both *Porites porites* and *Madracis* spp.

Statistical analysis

Coral surface-area and worm density-data were tested for normality using a Shapiro-Wilk *W*-statistics (SAS 1985). In

Table 1. Coral surface area (SA, m²/40 m²), percent coral cover (Cover) and number of colonies (n) of each coral species at three study sites

Site and species	SA	Cover	n	Site and species	SA	Cover	n	Site and species	SA	Cover	n
Golden Palms				Sunset crest				Speightstown			
Diploria strigosa	5.62	26.2	51	*M. annularis*	17.02	31.5	9	*P. porites*	23.91	24.4	53
Siderastrea siderea	3.83	17.9	51	*S. siderea*	12.33	22.8	67	*Madracis* spp.	20.49	20.9	68
Montastrea cavernosa	2.18	10.2	39	*M. cavernosa*	8.76	16.2	96	*M. annularis*	19.19	19.6	83
Porites porites	2.12	9.9	5	*D. strigosa*	4.53	8.3	18	*M. cavernosa*	8.86	9.1	81
Colpophyllia natans	1.97	9.2	5	*C. natans*	3.56	6.6	13	*C. natans*	6.02	6.2	21
Meandrina meandrites	1.59	7.4	25	*M. meandrites*	2.02	3.7	38	*S. siderea*	5.63	5.8	61
Diploria labyrinthiformes	1.37	6.4	21	*P. porites*	2.01	3.7	7	*P. astreoides*	5.52	5.6	144
Montastrea annularis	1.21	5.6	13	*D. labyrinthiformes*	1.71	3.2	22	*Agaricia* spp.	4.74	4.9	158
Porites astreoides	0.86	4.0	53	*P. astreoides*	0.97	1.8	37	*M. meandrites*	1.26	1.3	21
Dichocoenia stokesii	0.26	1.2	11	*Agaricia* spp.	0.76	1.4	38	*D. strigosa*	1.02	1.0	10
Agaricia spp.	0.25	1.2	29	*M. complanata*	0.19	0.4	19	*Mycetophyllia* spp.	0.63	0.6	11
Millepora complanata	0.18	0.8	9	*Dendrogyra cylindrus*	0.08	0.2	1	*D. labyrinthiformes*	0.32	0.3	6
				D. stokesii	0.06	0.1	3	*Eusmilia fastigata*	0.11	0.1	2
								M. complanata	0.10	0.1	11
								D. stockesii	0.03	0.03	2
Total	21.44	100	312	Total	54.0	99.9	388	Total	97.83	99.9	732

all but one case, parametric analyses were not possible as the data were not normally distributed and could not be normalised using the various transformations available (Sokal and Rohlf 1981). Total coral-surface-area values collected from the forty 1 m² quadrats at each site were normally distributed and a parametric ANOVA (analysis of variance) was used on these data to determine whether the total surface area of corals differed between sites. In all other cases, nonparametric analyses were used. Either a Kruskal-Wallis test (one-way ANOVA) or a General linear models procedure (two-way ANOVA) was used to determine: whether coral species differed in surface area within a site; whether the surface area of each coral species differed between sites; whether coral species differed in their degree of colonisation at each site; and whether the pattern of colonisation differed between sites. When ANOVA detected differences, a Tukey's studentised range test was performed to determine where the differences occurred (Zar 1984, SAS 1985). Spearman's rank correlation analyses were used to determine whether the degree of colonisation of coral species was correlated with their abundance, their mean colony size or their rank in an aggression hierarchy; and to determine which sites differed in colonisation pattern. A goodness-of-fit poisson distribution test was used to investigate the distribution of corals at each site, and the distribution of worms on a given coral species at each site.

Results

Abundance and distribution of corals

The total coral-surface-area, the surface area of each coral species, and the number of colonies of each coral species are shown for the forty 1 m² quadrats surveyed at each site in Table 1. Total coral surface area (per 40 m² of reef) at GP was 21.44 m², at SC 54.0 m², and at SP 97.83 m²; total number of coral colonies (per 40 m² reef) was 312 at GP, 388 at SC, and 732 at SP (Table 1). Note that the surface area of coral can exceed that of the reef area surveyed since the former is the actual (three-dimensional) surface area of coral and the latter is the planar surface area of reef. The numbers of coral species observed were 12 at GP, 13 at SC, and 15 at SP (Table 1). Total coral-surface-area differed significantly between sites (Table 1; parametric one-way ANOVA, $p < 0.001$), surface area at GP being significantly lower than at SC and SP in pair-wise comparisons (Tukey's test, $p < 0.001$ in both cases). Considering species separately, surface area differed significantly between sites for 11 of the 12 species (the exception was *Millepora complanata*) which occurred at more than one site, (Kruskal-Wallis test; Table 2). In pair-wise comparisons, ten species differed in surface area between GP and SP, ten between SC and SP, and six between GP and SC (Tukey's test, Table 2).

Within each study site, the surface area of coral species differed significantly (Table 1, Kruskal-Wallis test, $p < 0.001$ for each site). Most coral species were randomly distributed

at each study site (Poisson goodness-of-fit test; $p < 0.05$); the exceptions were at GP where *Montastrea cavernosa* and *Diploria labyrinthiformes* were significantly clustered (Poisson test, $p < 0.05$), and at SP where *Porites astreoides* and *Agaricia* spp. were significantly clustered (Poisson test, $p < 0.05$).

Abundance and distribution of worms

Not all coral species were colonised by *Spriobranchus giganteus* at each site, and six corals were not colonised at any site (Table 3). All corals that were colonised are subsequently referred to as colonisable corals. Worms were least abundant at SP where there was most total coral and most colonisable coral; and most abundant at GP where there was least total coral and least colonisable coral (Table 4). This suggests that worm abundance at SP was not limited by availability of colonisable coral.

The number of worms m^{-2} of coral (degree of colonisation) is shown separately for each coral species in Table 5. Corals differed significantly in their degree of colonisation at each site (Kruskal-Wallis test: GP, $p < 0.001$; SC, $p < 0.001$; SP, $p < 0.003$; Table 5). The degree of colonisation of a coral species was not correlated with its abundance rank, i.e., the more colonised corals were not the more abundant (Spearman's rank correlation coefficient: GP, $r_s = 0.10, p > 0.8$; SC, $r_s = 0.15, p > 0.7$; SP, $r_s = 0.29, p > 0.6$). Moreover, the degree of colonisation of a coral species was not correlated with its mean colony size (Spearman's rank correlation coefficient: GP, $r_s = 0.26$, $p > 0.5$; SC, $r_s = 0.64$, $p > 0.05$; SP, $r_s = 0.10$, $p > 0.5$). Finally, combining data for all sites (Table 5), the degree of colonisation of corals was not correlated with their rank by degree of aggressiveness (as determined by patterns of overgrowth on contact; Lang 1973), i.e, the more colonised corals were not the least aggressive $(r_s = 0.45$, $p > 0.2)$.

The variation in degree of colonisation of coral species at a site may be referred to as the colonisation pattern at that site. The colonisation pattern differed significantly between sites (two-way ANOVA, $p < 0.001$). Spearman's rank correlation analyses indicated a significant correlation between the colonisation patterns at GP and SC $(r_s = 0.90, p < 0.001)$ but no correlation between those at SC and SP $(r_s = 0.15$, $p > 0.7)$ or those at GP and SP $(r_s = 0.34, p > 0.3)$. This suggests that the colonisation patterns at GP and SC are similar but differ from that at SP.

In those instances where there were enough worms to permit analysis, the distribution of worms on coral species was investigated. In all cases (*Diploria strigosa* at GP and SC; *Montastrea annularis* at SC; *Porites porites* at SP),

Table 2. Probability values for Kruskal-Wallis tests (K–W) to determine which coral species differed in surface area between sites, and for Tukey's tests to identify sites at which coral species differed in surface area. Asterisk indicates coral not present at all sites. GP: Golden Palms; SC: Sunset Crest; SP: Speightstown

Coral	K-W	Tukey's test		
		GP-SC	GP-SP	SC-SP
Montastrea annularis	0.001	0.001	0.001	0.991
Siderastrea siderea	0.001	0.001	0.485	0.001
Montastrea cavernosa	0.001	0.045	0.001	0.167
Colpophyllia natans	0.002	0.045	0.001	0.001
Diploria strigosa	0.001	0.082	0.001	0.001
Porites astreoides	0.001	0.461	0.001	0.001
Diploria labyrinthiformes	0.004	0.551	0.008	0.002
Agaricia spp.	0.001	0.001	0.001	0.042
Porites porites	0.001	0.535	0.001	0.001
Meandrina, meandrites	0.019	0.148	0.176	0.005
Madracis spp.	*	*	0.001	0.001
Millepora complanata	0.085	0.442	0.156	0.029
Mycetophyllia spp.	*	*	0.001	0.001
Eusmilia fastigata	*	*	0.082	0.082
Dichocoenia stokesii	0.003	0.006	0.002	0.711
Dendrogyra cylindrus	*	0.229	*	0.229

Table 4. *Spirobranchus giganteus* Abundance at each site. GP: Golden Palms; SC: Sunset Crest; SP: Speightstown. SA: Surface Area

Abundance	GP	SC	SP
No. at site (40 m^2)	85	83	55
SA off all corals (m^2)	21.44	54.00	97.83
SA of colonisable corals (m^2)	17.52	48.27	89.46
No. m^{-2} on all corals	4.36	1.59	0.27
No. m^{-2} on colonisable corals	5.48	1.79	1.04

Table 3. Corals not colonised by *Spirobranchus giganteus,* and their abundance rank at each site. Asterisks indicate corals not colonised at any site

Golden Palms	Rank	Sunset Crest	Rank	Speigthstown	Rank
*Colpophyllia natans**	4	*Colpophyllia natans**	5	*Montastrea cavernosa*	3
*Meandrina meandrites**	5	*Meandrina meandrites**	6	*Colpophyllia natans**	4
*Dichocoenia stockesii**	9	*Porites porites*	11	*Siderastrea sidera*	5
Porites porites	11	*Dendrogyra cylindrus**	12	*Meandrina meandrites**	9
		*Dichocoenia stockesii**	13	*Diploria strigosa*	10
				Mycetophyllia spp.*	11
				Diploria labyrinthiformes	12
				Eusmilia fastigata	13
				Millepora complanata	14
				Dichocoenia stockesii	15

Table 5. *Spirobranchus giganteus*. Number of individuals per m^2 on each coral species (degree of colonization), presented separately for the three study sites and for the sites combined. GP: Golden Palm; SC: Sunset crest; SP: Speightstown

Coral	GP	Coral	SC	Coral	SP	Coral	Combined
Diploria strigosa	11.74	*P. astreoides*	7.22	*P. astreoides*	2.90	*D. strigosa*	7.61
Millepora complanata	11.11	*M. complanata*	5.26	*M. annularis*	0.83	*M. complanata*	6.38
Porites astreoides	9.30	*D. strigosa*	4.19	*P. porites*	0.71	*P. astreoides*	5.33
Agaricia spp.	3.92	*Agaricia* spp	3.95	*Agaricia* spp.	0.21	*M. annularis*	1.63
Montastrea annularis	2.48	*M. annularis*	2.47	*Madracis* spp.	0.20	*D. labyrinthiformes*	0.88
Montastrea cavernosa	1.38	*D. labyrinthiformes*	1.17			*P. porites*	0.70
Diploria labyrithiformes	0.73	*S. siderea*	0.49			*S. siderea*	0.32
Siderastrea siderea	0.26	*M. cavernosa*	0.23			*M. cavernosa*	0.25

worms were significantly clustered (Poisson goodness-of fit test, $p < 0.05$ in all cases). This clustered distribution did not result from a clustered distribution of substrate, since the corals themselves were randomly distributed (see Results, Abundance and distribution of corals).

Discussion

In this study, *Spirobranchus giganteus* was not distributed randomly among coral species. Six species of coral were never colonised at any of the study sites. Moreover, at each site, the number of worms per surface area of coral differed significantly among the coral species colonised. This colonisation pattern was similar at the GP and SC sites, but differed somewhat at SP. The number of worms present was similar at GP and SC but lower at SP (Table 4), and consequently fewer coral species were colonised at SP than GP or SC (Table 5). This may largely explain why the analyses detected a difference in colonisation pattern at SP.

The non-random distribution of worms on corals could result from preference of larvae at settlement and/or differential mortality following settlement. Post-settlement mortality was not investigated in this study. However, many sessile marine polychaetes are known to display substrate preference at settlement (Wilson 1948, 1958, 1968, 1970, Gee and Knight-Jones 1962, Williams 1964, Eckelbarger 1978, Jensen and Morse 1984, Al-Ogilvy 1985, Pawlik 1988); and planktonic larvae of *S. giganteus* in the Pacific are attracted to certain corals over others (Marsden 1987). Moreover, Marsden et al. (1990) have shown that planktonic larvae of *S. giganteus* in Barbados prefer certain coral species over others in the laboratory. The larval preference pattern closely matches the distribution pattern of worms on corals described here. This suggests that larval preference is important in generating the non-random distribution of worms on corals observed.

The factors determining the preference of *Spirobranchus giganteus* for certain species of coral are not clear. The degree of colonisation of a coral species was not affected by its relative abundance, by its mean colony size, or by its aggressiveness toward other corals. The preference pattern may therefore depend on more subtle interactions between the corals and *S. giganteus*. Hunte et al. (1990) demonstrated that body size and body proportions of *S. giganteus* differ

on different species of coral. Interestingly, worms are larger on those corals which are preferred by larvae and are most heavily colonised in the field (Hunte et al. 1990). A larger body may indicate greater gamete production and/or longer life span, i.e., the fitness of *S. giganteus* may differ on different corals.

Spirobranchus giganteus was less common at SP than at GP or SC. This did not result from a scarcity of corals, since corals were more common at SP than GP or SC. It could result from fewer larvae being available to settle and/or higher mortality following settlement. The reef at SP is deeper (16 to 22 m) than at either GP (10 to 16 m) or SC (13 to 19 m), and worm abundance is lowest at SP and highest at GP. Larvae of *S. giganteus* are photopositive during early planktonic life (Marsden 1984, 1986), those at SP must therefore descend greater distances than those at shallower sites to find suitable coral substrates. Descent to greater depth may result in reduced survival during presettlement, increased displacement by currents and less effective perception of the underlying coral; all factors that could result in fewer larvae available to settle.

The colonisation pattern of worms on coral was similar at GP and SC, but differed somewhat at SP. This may largely be an artifact of lower worm abundance at SP which results in fewer coral species being colonised (Table 5). However, differences are evident with *Diploria strigosa* and *Porites porites*. *D. strigosa* was heavily colonised at GP and SC but was not colonised at SP; *P. porites* was moderately colonised at SP but not colonised at GP or SC (Table 5). Interestingly, *D. strigosa* was rare at SP compared to GP and SC, and *P. porites* was rare at GP and SC compared to SP (Table 1). This may suggest that if a coral is relatively rare, it is undercolonised, i.e., has fewer worms per surface area of coral than expected. Undercolonisation of rare corals may be the consequence of larval attraction to corals being a chemical response in *S. giganteus* (Marsden 1987, Marsden et al. 1990). The rarer a species of coral relative to others, the weaker the signal may be, and the lower the probability of contact of larvae with the coral. If the strength of the signal decreases faster than the decrease in surface area of the coral, rarity could lead to undercolonisation, i.e., fewer worms per surface area than expected.

Spirobranchus giganteus not only prefers particular corals, but may also be attracted to conspecifics. In all cases where sufficient data were available to permit analysis, indi-

viduals of *S. giganteus* were significantly clustered. Such a distribution is common in tubiculous polychaetes and is attributed to the attraction of settling larvae to tubes of conspecific adults (Wilson 1948, 1958, 1968, 1970, Eckelbarger 1978, Jensen and Morse 1984, Pawlik 1988). A clustered distribution presumably enhances reproductive success in sessile adults with external fertilization.

Literature cited

Al-Ogilvy, S. M. (1985). Further experiments on larval behaviour of the tubiculous polychaete *Spirorbis inornatus* L. Hardy and Quivreux. J. exp. mar. Biol. Ecol. 86: 285–289

Anderson, G. R. V., Ehrlich, A. H., Ehrlich, P. R., Roughgarden, J. D, Russell, P. C., Talbot, F. H. (1981). The community structure of coral reef fishes. Am. Nat. 117: 46-495

Connell, J. H. (1985). The consequences of variation in initial settlement vs post-settlement mortality in rocky intertidal communities. J. exp. mar. Biol. Ecol. 93: 11–45

Dahl, A. L. (1973). Surface area in ecological analysis: quantification of benthic coral reef algae. Mar. Biol. 23: 239–249

DeVantier, C. M., Reichelt, R. E., Bradbury, R. H. (1986). Does *Spirobranchus giganteus* protect host *Porites* from predation by *Acanthaster planci:* predator pressure as a mechanism of evolution? Mar. Ecol. Prog. Ser. 32: 307–310

Doherty, P. J. (1983). Tropical territorial damsel fishes: is density limited by aggression or recruitment. Ecology 64: 176–190

Eckelbarger, K. J. (1978). Metamorphosis and settlement in the Sabellariidae. In: Chia, F.-S., Rice, M. E. (eds.) Settlement and metamorphosis of marine invertebrate larvae. Elsevier, New York, p. 127–144

Gee, J. M., Knight-Jones, E. W. (1962). The morphology and larval behaviour of a new species of Spirorbis (Serpulidae). J. mar. biol. Ass. U.K. 42: 641–654

Hove, H. A. ten (1970). Serpulinae (Polychaeta) from the Caribbean. 1. The genus *Spirobranchus.* Stud. Fauna Curacao 32: 1–57

Hunte, W., Côté, I. M. (1989). Recruitment in the red-lip blenny *Ophioblennius atlanticus:* is space limiting? Coral Reefs. 8: 45–50

Hunte, W., Marsden, J. R., Conlin, B. E. (1990). Habitat selection in the tropical polychaete *Spirobranchus giganteus.* III. Effects of corals on body size and body proportions. Mar. Biol. 104: 101–107

Jensen, R. A., Morse, D. E. (1984). Intraspecific facilitation of larval recruitment: gregarious settlement of the polychaete *Phragmatopoma californica* (Fewkes). J. exp. mar. Biol. Ecol. 54: 677–684

Lang, J. (1973). Interspecific aggression by scleratinian corals. 2. Why the race is not always to the swift. Bull. mar. Sci. 23: 260–279

Lewis, J. B. (1981). Estimates of secondary production of coral reefs. Proc. 4th int. Symp. coral Reef 2: 369–374 [Gomez, E. D. et al. (eds.) Marine Science Center, University of the Philippines, Quezon City]

Marsden, J. R. (1984). Swimming in response to light by larvae of the tropical serpulid *Spirobranchus giganteus.* Mar. Biol. 83: 13–16

Marsden, J. R. (1986). Response to light by trochophore larvae of *Spirobranchus giganteus.* Effects of level of irradiance, dark adaptation and spectral distribution. Mar. Biol. 93: 13–16

Marsden, J. R. (1987). Coral preference behaviour by planktonic larvae of *Spirobranchus giganteus corniculatus* (Serpulidae: Polychaeta). Coral Reefs 6: 71–74

Marsden, J. R., Conlin, B. E., Hunte, W. (1990). Habitat selection in the tropical polychaete *Spirobranchus giganteus.* 2. Larval preferences for corals. Mar. Biol. 104: 93–99

Meadows, P. S., Campbell, J. I. (1972a). Habitat selection by aquatic invertebrates. In: Russel, F. S., Young, C. M. (eds.) Advances in marine biology, Vol 10. Academic Press, London, p. 271–382

Meadows, P. S., Campbell, J. I. (1972b). Habitat selection and animal distribution in the sea: the evolution of a concept. Proc. R. Soc. Edinb. (Sect. B) 73: 145–157

Pawlik, J. R. (1988). Larval settlement and metamorphosis of sabellariid polychates, with special reference to *Phragmatoperma lapidosa,* a reef-building species, and *Sabellaria floridensis,* a nongregarious species. Bull. mar. Sci. 43: 41–60

Pichon, M. (1978). Problems of measuring and mapping coral colonies. In: Stoddart, D. R., Johannes, R. E. (eds.) research methods. UNESCO, Paris, p. 219–230

SAS (1985). SAS user's guide: statistics, version 5. SAS Institute Inc., Cary, N. C.

Scheltema, R. S. (1974). Relationship of dispersal to geographical distribution and morphological variation in the polychaete family Chaetopteridae. Thalassia jugosl. 10: 297–312

Smith, C. L. (1978). Coral reef fish communities: a compromise view. Envir. Biol. Fish 3: 107–128

Sokal, C. W., Rohlf, F. J. (1981). Biometry, 2nd edn. W. H. Freeman and Co, New York

Stearn, C. W., Scoffin, T. P., Martingdale, W. (1977). Calcium carbonate budget of a fringing reef on the west coast of Barbados, W. I. Part 1. Zonation and productivity. Bull. mar. Sci. 27: 479–510

Strathmann, R. R., Barnscom, E. S. (1979). Adequacy of clues to favourable sites used by settling larvae of two intertidal barnacles. In: Stanyk, S. E. (ed.) Reproductive ecology of marine invertebrates. University of South Carolina Press, Columbia

Strathmann, R. R., Cameron, R. A., Strathmann, M. (1984). *Spirobranchus giganteus* (Pallas) breaks a rule for suspension-feeders. J. exp. mar. Biol. Ecol. 70: 245–249

Victor, B. C. (1984). Coral reef fish larvae: patch size estimation and mixing in the plankton. Limnol. Oceanogr. 29: 1116–1119

Victor, B. C. (1986). Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. Ecol. Monogr. 56: 145–160

Weinberg, G. B. (1981). A comparison of coral reef survey methods. Bijdr. Dierk 51: 199–218

Williams, G. B. (1964). The effects of extracts of *Fucus serratus* in promoting the settlement of larvae of *Spirorbis borealis* (Polychaeta). J. mar. biol. Ass. U.K. 44: 397–414

Wilson, D. P. (1948). The relation of the substratum to the metamorphosis of *Ophelia* larvae. J. mar. biol. Ass. U.K. 27: 723–760

Wilson, D. P. (1958). Some problems in the larval ecology related to the localised distribution of bottom animals. In: Buzzati-Traverso, A. A. (ed.) Perspectives in marine biology. University of California Press, Berkely, p. 87–103

Wilson, D. P. (1968). The settlement behaviour of *Sabellaria alveolata* (L.). J. mar. biol. Ass. U.K. 48: 387–435

Wilson, D. P. (1970). The larvae of *Sabellaria spinulosa* and their settlement behaviour. J. mar. biol. Ass. U.K. 50: 33–52

Zar, J. H. (1984). Biostatistical analysis. 2nd edn. Prentice Hall Inc., Englewood Cliffs