Sponge-coral interactions on Caribbean reefs
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Chapter 4

Dynamics behind stand-off interactions between three reef sponges and the coral *Montastrea cavernosa*.

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between sponges and corals and enhances the overgrowth frequency of aggressive sponge species. On a community level, this study demonstrated that the extent to which coral overgrowth occurs depends on the competitive ability of sponges and coral cover.

I conclude that spatial competition between sponges and corals is important on reefs with high coral cover. More aggressive sponge species and hence more overgrowth interactions occur on well-developed reefs. Overgrowth success of corals by sponges depends on coral cover (irrespective of coral species) and sponge species composition.

Chapter 4

Dynamics of Exposed Stand-off Interactions Between Three Fishing Communities and the Coral Montastrea cavernosa.
ABSTRACT. Benthic organisms compete for space and stand-off interactions, i.e. interactions with no clearly observable outcome such as win or loss, are very common in marine hard substratum communities. Of all sponge/coral interactions observed in a coral reef community off Santa Marta, NE Colombia, stand-offs were more common than overgrowths. The dynamics of these stand-offs and the role played by each of the interacting organisms were examined in a series of standard observations of sponge/coral interactions involving the sponge species *Niphates erecta*, *Rhaphidophlus venosus*, *Scopalina ruetzleri* and the coral *Montastraea cavernosa*. A total of 141 interactions were photographed every two months over a period of 15 months. Changes in the number of polyps along the coral border, sponge area (cm²) and the minimum distance (mm) between sponge and coral were measured. Most sponge/coral stand-offs in this study displayed rapid changes in number of polyps along the coral border, sponge area and sponge/coral distance. Outcome of sponge/coral stand-offs depended on the life history characteristics (e.g. growth) of the sponge species. Area increase and decrease of *S. ruetzleri* and *N. erecta* were not correlated to changes in the number of polyps along the coral border. This implies a lack of direct competition between these two sponge species and *Montastraea cavernosa*. *R. venosus*, however, was often observed to take over vacant space left by the death of coral polyps (54% of interactions). To determine impact of conditional factors such as coral damage on the interaction process between *R. venosus* and *M. cavernosa*, artificial lesions were made in 43 *M. cavernosa* colonies in proximity with *R. venosus*. This resulted in a significant increase in coral polyp death in damaged compared with undamaged *M. cavernosa* colonies (22.7% versus 6.9%). This study demonstrates that 1) sponge/coral stand-offs are actually quite dynamic, 2) outcome of sponge/coral stand-offs depends on the life history characteristics of the competing sponge species, 3) actual frequency of coral overgrowth by (thinly encrusting) sponge species can only be determined by means of continuous observations, 4) coral damage on reefs may enhance deterioration of corals by increasing their susceptibility to sponge overgrowth.

INTRODUCTION

In order to survive, sessile marine organisms must acquire and successfully defend substratum. The most visible form of spatial competition occurs by direct overgrowth of organisms already occupying space. However, competition for space is not always visible, especially when chemical aggression is involved. Sponges are known to possess a wide variety of chemical substances (Faulkner 1984) which among other functions, can be used in competition for space (Aerts & van Soest submitted; Jackson & Buss 1975). Studies on sponge interactions mainly focused on the competitive mechanism employed by sponges (Sullivan et al. 1983; Porter & Targett 1988) or on the occurrence of overgrowth (Suchanek et al. 1983; Vicente 1990; Rützler & Muzik 1993; Aerts & van Soest 1997). However, the observed frequency of coral overgrowth by sponges has never been correlated to the number of stand-off interactions between the two interacting species (stand-off is defined as an interaction without a clearly observable outcome such as overgrowth). Although the
frequency of coral overgrowth by sponges can be regarded as important, the interaction categories which occur most frequently are stand-off interactions such as peripheral contact, tissue contact and non contact interactions (Aerts & van Soest 1997). It is unknown if any interactive exchange occurs in these stand-offs. There may be an apparent cessation of growth at the border of contact between the two species (Karlson 1980; Schmidt & Warner 1986) or these interactions may involve repeated reversals, by which the coral and sponge advance and retreat alternately (Chornesky 1989). Competitive abilities between species may be perfectly transitive when stand-offs are ignored (Rubin 1982; Schmidt & Warner 1986). However, in species assemblages where stand-offs are frequently encountered, they can not be ignored and should obtain a status equal to that of wins and losses when determining competitive hierarchies (Schmidt & Warner 1986; Tanaka & Nandakumar 1994).

In this study I examined the dynamics behind stand-off interactions between 3 sponge species and a coral on a Caribbean reef through continuous observations over a time period. Stand-offs are defined as contact or non contact interactions, with a sponge/coral distance of <5 cm, without a clearly observable outcome such as overgrowth. Selected sponge/coral stand-offs were followed at three reef localities, each characterised by a different sediment load. High sedimentation appeared not to enhance the frequency of coral overgrowth by sponges at a community level (Aerts & van Soest 1997) but in these observations time series of individual sponge/coral stand-offs were not included. Furthermore, I investigated if other factors such as coral damage increases the susceptibility of coral colonies to sponge competition, by inflicting lesions to corals in proximity of sponges. Since the recovery from damage leads to a decline in biological functions of corals and because energy needed to recover lesions is derived from the surrounding polyps (Meesters et al., 1994), the competitive ability of the coral may be assumed to decrease locally.

Questions I address in this study are: to what extent are sponge/coral stand-offs dynamic? Is the outcome of such encounters influenced by environmental conditions, e.g. are sponges winning more frequently in physically stressed localities? Does a conditional factor such as coral damage lead to an increasing susceptibility to sponge competition?
MATERIALS AND METHODS

Study area. Continuous observations of stand-off interactions between individuals of three sponge species and one coral species were performed along the coast of the Santa Marta area, Caribbean Colombia (11°15'N, 74°13'W; Fig. 1). On this reef 97.5% of all sponge-coral interactions were apparent stand-offs. Because sedimentation is an important environmental factor causing coral stress on reefs (Rogers, 1990), sponge/coral stand-offs were followed at three localities, each characterised by a different sedimentation load. Sedimentation data, sampled in a former study using sediment traps with a height/diameter ratio of 5:1 (see Aerts & van Soest 1997), are presented in Fig. 1. At site 3 sedimentation is significantly lower than at sites 1 and 2 (Wilcoxon signed ranks, p<0.033).

Observations of interactions. At 20 m depth (where most interactions were encountered) a total of 141 apparent sponge/coral stand-off situations were marked each with two steel nails and photographed using a NIKONOS V with a 1:3 extension tube. The
size of the photo frame was 9 by 13 cm. The sponge species *Niphates erecta* (Duchassaing and Michelotti 1864), *Scopalina ruetzleri* (Wiedenmayer 1977) and *Rhaphidophlus venosus* (Alcolado 1984) and the coral species *Montastraea cavernosa* (Linnaeus) were chosen as research subjects because they were the most common in the study area. Interactions were selected randomly. A total of 55 interactions between *S. ruetzleri* and *M. cavernosa* (n=16 site 1, n=22 site 2 and n=17 site 3), 53 interactions between *R. venosus* and *M. cavernosa* (n=16 site 1, n=19 site 2 and n=18 site 3) and 33 interactions between *N. erecta* and *M. cavernosa* (n=12 site 1, n=11 site 2 and n=10 site 3) were photographed every 2 months over a period of 15 months, between January 1994 and April 1995. Photographic sampling took place in February 1994 (one month interval), August 1994 (6 months interval), October 1994, December 1994, February 1995, April 1995. The large time lapse of the second sampling period was caused by damage to the photographic equipment.

In a series of parallel observations, the effect of coral damage on the outcome of sponge/coral stand-offs was studied. A series of additionally selected interactions of *Montastraea cavernosa* colonies and specimens of the sponge *Rhaphidophlus venosus* was monitored from February to April 1995. Coral damage was experimentally introduced through infliction of lesions of about 10 mm diameter and an average depth of 2.5 mm, into the coral tissue. These were made with a pneumatic drill powered by a scuba tank. These lesions were located approximately one polyp (= 5-10 mm) away from the outer coral tissue boundary, leaving a space of living coral tissue between the damaged part (totally devoid of live tissue), the coral boundary and the sponge tissue. This experiment was performed only with *R. venosus* because of the three sponge species observed, it appeared to react most directly to changes of the coral. The reaction of both sponge and coral species was followed by photographic sampling of each interaction after 7, 28, 56 and 77 days. Two localities with different sedimentation load (Site 1, n=10 and site 3, n=34) were compared to investigate the possible role of sedimentation stress on the outcome of the experimental interactions. At the same localities and depth undamaged *M. cavernosa* colonies interacting with *R. venosus* specimens served as controls (Site 1, n=16 and site 3, n=18).

**Interpretation of the photographs.** Because all photo frame positions were fixed, photo prints of individual interactions taken at different time periods were similar and could be compared easily. The photographic frame did not cover the whole coral and sponge colony. Observed changes in sponge specimens and coral colonies refer only to the interaction area and specimens borders within the image. Changes outside the frame were not considered. From each photograph I recorded the following features:
1) Number of polyps along the coral border within the photo frame; polyps were chosen as unit of measure because they are the basic module of a coral and because retreat or growth occurred per polyp. Length of the coral border was the same for each site and sponge species (10.5 ±1.3 cm).

2) Changes in sponge area (cm²) within the photo frame. At this scale spatial interaction is essentially two dimensional.

3) Minimum distance (mm) between sponge and coral border. If the sponge was growing parallel to the coral border the length (mm) of the contact area between sponge and coral border was measured.

4) Details of sponge/coral interactions (e.g. tissue damage, overgrowth, necrosis) which occurred during the 15 month period within the photo-frame.

5) Lesion condition (e.g regenerated, overgrown, damaged; only for interactions with experimental lesions).

Statistics. Data on the three variables (coral border changes, sponge area and sponge/coral distance) were analysed in two different ways, relative and absolute. Relative data refer to the number of interaction points displaying changes and are expressed in percentage of the total number of interaction points (table 1A). Absolute data refer to actual changes expressed as number of border polyps, cm²/year or mm/year (table 1B). To test whether the occurrence of changes of the three variables differed significantly among localities and sponge species R x C tests of independence using G-test were performed (Sokal & Rohlf 1981). The absolute values of both transformed and untransformed data of the three variables lacked a normal distribution (normality plot and Kolmogorov-Smirnov test; Sokal & Rohlf, 1981) and their variances were heteroscedastic (Barlett's test; Sokal & Rohlf 1981). As a consequence medians and ranges of the changes in sponges and corals were used (table 1B, Fig. 2) and tested among localities, species and periods with the non-parametric Kruskal-Wallis one way analysis of variance (Sokal & Rohlf 1981). Correlations between changes of polyp number and sponge area were tested with the Pearson correlation coefficient (Sokal & Rohlf 1981). Sedimentation data of the three localities (derived from Aerts & van Soest 1997) were analysed with the Wilcoxon signed ranks test (Sokal & Rohlf 1981) taking dates as blocks.
RESULTS

Dynamics of sponge/coral stand-offs

Absolute changes in number of border polyps differed among localities and were independent of sponge species. Although the occurrence of decrease, increase and no change of coral border polyps was similar for each locality (RxC independence test, p>0.05; table 1A), the magnitude of these changes was significantly different. Highest decrease in number of border polyps was found at sites 2 and 3 (Kruskal-Wallis, p<0.01; table 1B). Both occurrence and magnitude of changes in number of coral border polyps demonstrated no significant difference among sponge species. Apparently, each of the three sponge species had a similar effect on the coral border polyps.

TABLE 1. Relative values (in % occurrence; A) and absolute values (with ranges; B) of changes of the number of coral border polyps (1), sponge area (2) and sponge/coral distance (3) for each site and sponge species over 15 months. The absolute values are standardized to a per year basis. S1 = site 1, S2 = site 2, S3 = site 3, SR = Scopalina ruetzleri, NE = Niphates erecta and RV = Rhaphidophlus venosus, n = number of interactions.

<table>
<thead>
<tr>
<th></th>
<th>A</th>
<th>B</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>S1</td>
<td>S2</td>
</tr>
<tr>
<td>1) DECREASE</td>
<td>38.6</td>
<td>59.6</td>
</tr>
<tr>
<td>INCREASE</td>
<td>47.7</td>
<td>32.7</td>
</tr>
<tr>
<td>NO CHANGE</td>
<td>13.1</td>
<td>7.7</td>
</tr>
<tr>
<td>2) DECREASE</td>
<td>45.5</td>
<td>50.0</td>
</tr>
<tr>
<td>INCREASE</td>
<td>50.0</td>
<td>40.4</td>
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<tr>
<td>NO CHANGE</td>
<td>4.6</td>
<td>8.6</td>
</tr>
<tr>
<td>3) DECREASE</td>
<td>32.6</td>
<td>26.9</td>
</tr>
<tr>
<td>INCREASE</td>
<td>27.9</td>
<td>48.1</td>
</tr>
<tr>
<td>NO CHANGE</td>
<td>39.5</td>
<td>25.0</td>
</tr>
<tr>
<td>TOTAL N</td>
<td>44</td>
<td>52</td>
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</table>

Differences in frequencies of no changes, decrease and increase of sponge area and sponge/coral distance were found to depend on the identity of the sponge species. Among localities, no differences were apparent between the frequencies observed (RxC
Dynamics behind sponge/coral stand-off interactions

independence test, p>0.05). Decrease of sponge area occurred most frequently for the sponge *Scopalina ruetzleri* (RxC independence test, p<0.001; Table 1A). Of the absolute changes in sponge area, the overall sponge area decrease of *S. ruetzleri* differed significantly from the overall area increase of *R. venosus* (Kruskal-Wallis, p=0.011; table 1B). The low ranges in area decrease and increase and the average area changes of 0 cm²/year of *N. erecta* reflect its relative stability in terms of space occupancy compared with the other two sponge species (table 1B). Increase of sponge/coral distance occurred more frequently for the interaction between *Montastraea cavernosa* and *S. ruetzleri* compared to *M. cavernosa* and *R. venosus* (RxC independence test, p<0.03; table 1A). Similarly, the extent to which the sponge/coral distance increased was significantly higher for *S. ruetzleri* (Kruskal-Wallis, p=0.015; table 1B). As a result of changes in the sponge/coral distance the type of interaction between the organisms studied changed. Relatively few interactions with *R. venosus* and *N. erecta* which initially started as contact interactions (i.e. peripheral and tissue contact) ended after 15 months as non contact interactions (respectively 2.2% and 10.7%). The percentage of non contact interactions which ended as contact interactions was much higher, respectively 19.6% and 32.1%. For *S. ruetzleri*, more contact interactions ended as non contact interactions, than the reverse (resp. 25% and 20%; Fig. 2).

![Chart](image)

**FIG. 2.** Occurrence (%) of non contact interactions which ended as contact interactions (black bars) and vice versa (spotted bars) over a 15 month period for each sponge species. Total number of interactions involved is respectively 28, 46 and 40.

The dynamics of sponge/coral stand-offs mentioned above were calculated over a 15 month period. Relative and absolute changes of the three variables were also calculated at 2 month intervals to determine the impact of seasonal influences. No differences in the
occurrence of changes existed for each variable between time periods (RXC independence test, p>0.05). The majority of the selected interactions displayed no change in sponge/coral distance, decrease and increase of sponge area and decrease and no changes in number of polyps along the coral border (table 2). The absolute values of sponge area and sponge/coral distance were similar for each period (Kruskal-Wallis, p>0.05; Fig. 3B, 3C). The number of coral border polyps, however, decreased significantly more during the period February-August 1994 compared to other time periods (Kruskal-Wallis, p=0.003; Fig. 3A), probably due to the large time interval. It is remarkable that although the absolute values of each variable showed wide ranges, the median of the changes were all around zero (Fig. 3).

**TABLE 2.** Changes (in % occurrence of total number of interactions) of the number of coral border polyps, sponge area and sponge/coral distance for each time period. N = total number of interactions.

<table>
<thead>
<tr>
<th></th>
<th>Jan-Feb'94</th>
<th>Feb-Aug'94</th>
<th>Aug-Oct'94</th>
<th>Oct-Dec'94</th>
<th>Dec-Feb'95</th>
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<tr>
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<td>39.7</td>
<td>32.8</td>
<td>35.6</td>
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<tr>
<td>INCREASE</td>
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<td>19.6</td>
<td>16.9</td>
<td>27.3</td>
<td>28.6</td>
<td>23.7</td>
</tr>
<tr>
<td>NO CHANGE</td>
<td>60.7</td>
<td>22.8</td>
<td>44.1</td>
<td>33.1</td>
<td>38.7</td>
<td>40.7</td>
</tr>
<tr>
<td>N</td>
<td>61</td>
<td>92</td>
<td>118</td>
<td>121</td>
<td>119</td>
<td>116</td>
</tr>
<tr>
<td><strong>SPONGE AREA</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DECREASE</td>
<td>46.9</td>
<td>38.3</td>
<td>33.3</td>
<td>39.3</td>
<td>46.8</td>
<td>49.5</td>
</tr>
<tr>
<td>INCREASE</td>
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<td>61.7</td>
<td>61.3</td>
<td>54.7</td>
<td>41.3</td>
<td>41.4</td>
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<td>0.0</td>
<td>5.4</td>
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<td>9.0</td>
</tr>
<tr>
<td>N</td>
<td>31</td>
<td>47</td>
<td>111</td>
<td>117</td>
<td>109</td>
<td>111</td>
</tr>
<tr>
<td><strong>SPO/COR DISTANCE</strong></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>DECREASE</td>
<td>16.4</td>
<td>25.3</td>
<td>21.1</td>
<td>22.4</td>
<td>8.9</td>
<td>23.0</td>
</tr>
<tr>
<td>INCREASE</td>
<td>18.0</td>
<td>27.3</td>
<td>25.4</td>
<td>26.7</td>
<td>29.5</td>
<td>21.2</td>
</tr>
<tr>
<td>NO CHANGE</td>
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<td>50.9</td>
<td>61.6</td>
<td>55.8</td>
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<tr>
<td>N</td>
<td>61</td>
<td>99</td>
<td>114</td>
<td>116</td>
<td>112</td>
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</tr>
</tbody>
</table>

Reaction of sponges to changes in the number of coral border polyps appeared to be species specific.

1) Area changes of both *N. erecta* and *S. ruetzleri* were not correlated to the number of coral border polyps (Pearson's correlation coefficient, resp. p=0.699 and p=0.546). *N. erecta* displayed 3 cases of overtopping (9%). This means that the sponge was growing over the coral but was not attached to the coral tissue. In one case (3%) the border of the
coral showed some signs of bleaching. Neither overgrowth nor other signs of damage to the coral occurred in any of the interactions between *S. ruetzleri* and *M. cavernosa*.

![Dynamics behind sponge/coral stand-off interactions](image)

**FIG. 3.** Percentile plots of changes in A) number of coral border polyps, B) sponge area and C) sponge/coral distance for each time period. The boxes comprise 90% of all data. The vertical lines show the ranges of the data. The median of the data is displayed by the horizontal solid line.
2) Area changes of *R. venosus* were negatively correlated with changes in the number of border polyps (Pearson's correlation coefficient, *p*<0.001; Fig. 4). In contrast with the other two sponge species, *R. venosus* was often observed to take over vacant space caused by death of coral polyps (54% of the selected interactions).

**FIG. 4.** Correlation between changes in number of coral border polyps (per year) and sponge growth (cm$^2$/month) for *R. venosus*. *R* = Pearson's correlation coefficient and *p* = probability that rejection of H0 (there is no correlation) is incorrect.

**FIG. 5.** Occurrence of overgrowth (in % of total number of interactions) of the coral *M. cavernosa* by the sponge *R. venosus* for each locality. Black bars show the results of coral colonies with lesion infliction and spotted bars the control colonies. S1 = site 1, S3 = site 3, S1+S3 = average of data from S1 and S3.
Coral damage experiment

Of all interactions involving coral colonies with experimental lesions 22.7% showed overgrowth of living coral polyps by the sponge *R. venosus*. The overall occurrence of sponge overgrowth of living polyps of the control colonies was 6.9% (Fig. 5). This difference was also observed for each locality separately. At site 1 overgrowth of living polyps of damaged coral colonies by *R. venosus* was higher than overgrowth of control colonies (resp. 20% versus 0%). At site 3 these percentages were 23.5% for overgrowth of damaged corals and 13.3% for overgrowth of control coral colonies by the sponge. To determine if infliction of experimental lesions led to a higher decrease of border polyps of the coral, changes in number of border polyps of coral colonies with experimental lesions and the controls were compared. No significant differences in polyp changes could be found (Fig. 6). This means that overgrowth of experimentally damaged coral colonies by *R. venosus* is not caused by death of coral polyps.

FIG. 6. Changes of number of coral border polyps (per year) ±SE for *M. cavernosa* colonies with and without lesion infliction at each locality. Legend and abbreviation of localities as in Fig. 5.

DISCUSSION

Dynamics of sponge/coral stand-offs

Most studies on competition for space used data collected at a particular point in time (e.g. Jackson 1979; Rubin 1982; Lopez Gappa 1989; Steneck et al. 1991). If the purpose of the study is to establish competitive dominance, observations made at a single point in
time can easily lead to misjudging of interaction results, especially when stand-off interactions are involved (Tanaka & Nandakumar 1994). In a former study (Aerts & van Soest 1997) most sponge/coral interactions observed on the reef could be considered as stand-offs. The present study demonstrates that sponge/coral stand-offs were actually quite dynamic. There was no evidence of cessation of growth along adjacent edges between interacting species (as observed by Karlson 1980). In most cases, both competitors alternately lost and gained tissue and space during the 15 month interval, which conformed with the repeated reversals pattern described by Chornesky (1989) of coral-coral interactions. Coral colonies showed an overall decline in number of border polyps, which was more related to localities than to sponge species. Apparently, local environmental conditions influenced border polyp loss. High sedimentation load appeared to play no role since most polyp loss occurred at localities with less sedimentation. In some cases, especially at the locality with less sedimentation, macroalgae of the genus Dictyota were colonizing vacant space caused by recession of the sponge or coral. Partial mortality of coral colonies could be due to smothering by macroalgae (Hughes 1996) but from our photographs the possible role of algae in the loss of border polyps was not clearly observable. Variation in coral size and morphology among localities may also contribute to the observed differences in polyp loss, whereas susceptibility of corals to competition depend on their surface-perimeter ratio (Hughes 1996; Meesters et al. 1997). Decrease of number of border polyps was certainly not caused by competitive activity of neighbouring sponges because border polyp loss was similar for each sponge species.

**Sponge species strategies**

The necessity for sponges to compete with corals in order to gain space likely depends on their growth form in combination with other growth characteristics (Sebens 1986; Becerro et al., 1994). Obvious differences in the reaction of the three sponge species towards changes in the number of coral border polyps were observed. *R. venosus* with its thinly encrusting growth form and variable, fast area changes was often observed to take over vacant space due to death of coral polyps. Because the extent of polyp decrease along the coral border was similar in interactions with all three sponge species, *R. venosus* was the only one benefiting from the declining number of coral border polyps and was not causing this retreat. In general, the advance and retreat movements of *R. venosus* colonies resembled those described for encrusting colonial ascidians (Birkeland et al. 1981). *S. ruetzleri*, although also encrusting, forms thick cushions on the substratum and can therefore easily expand into height. Despite its fast and variable area changes, *S.
ruetzleri was never observed to overgrow dead coral tissue. In most cases, either S. ruetzleri or the coral border receded apparently without utilizing available space, which explains the very low frequency of overgrowth displayed by S. ruetzleri (Aerts & van Soest 1997). The same appears to apply to N. erecta. During this study N. erecta was observed to escape direct competition with the coral by growing into height (thereby overshadowing the coral colony in most cases). Probably due to its minor and relatively slow area changes, available space caused by retreated coral tissue was never observed to be taken over by N. erecta. Direct competition in terms of coral overgrowth were not observed, probably due to the elevated growth form of N. erecta. Whether sponge and coral specimens studied here redirect their growth away from the zone of interaction (Romano 1990) is difficult to determine because observations were focussed on the interacting area and did not include the whole sponge and coral colony.

In summary, stand-off interactions between sponges and corals studied here were quite dynamic. Outcome of sponge/coral stand-offs depends mainly on the ecological strategy displayed by sponge species. The necessity and/or ability of sponges to overgrow corals or take over vacant space caused by death of coral tissue appears to depend on their growth characteristics and morphology.

**Coral damage and competitive outcome**

Several field studies have revealed that regeneration of coral damage is influenced by environmental conditions (e.g. Meesters et al. 1992; Meesters & Bak 1993; Van Veghel & Bak 1994; Ward, 1995). Available energy is often limited (e.g. Bak 1983) and must be divided between several biological functions. Competition with other organisms can cause a major reduction in the physiological functioning of corals (Tanner 1995). In case of damaged corals, damage repair may locally reduce the competitive ability of the coral. Stand-off interactions between R. venosus and M. cavernosa seem to show an apparent equilibrium at the border of contact (Karlson 1980) when observed at one point in time. However, interactions between R. venosus and M. cavernosa observed over a time period showed that R. venosus often overgrows dead coral polyps at the border of contact and sporadically also living coral polyps. In case of damaged coral colonies, living coral polyps were more frequently overgrown by R. venosus. It is remarkable that overgrowth of living coral tissue of control colonies by R. venosus occurred by corals which appeared to be in a very bad condition (mean polyp decrease of 22 and 12 polyps/year). Due to the encrusting growth form of R. venosus, only observations over a time period can distinguish overgrowth activity. Very likely, a certain part of the peripheral growth
interactions observed in a former study (Aerts & van Soest 1997) were actually overgrowth interactions.

Overgrowth of living border polyps by \textit{R. venosus} was an active process, because lesion infliction did not influence decrease of the border polyps. The active role of the sponge is also demonstrated in Fig. 7 where sponge growth is directed towards the damaged area. Because bio-assays of \textit{R. venosus} extracts demonstrated biological activity (Braekman pers. comm.), this sponge may use its chemicals to compete with corals.

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure7.png}
\caption{Photographs of 2 interactions (I, II) showing the sponge \textit{R. venosus} and the coral \textit{M. cavernosa} at days 2 and 56. The corals have an experimental lesion (white spot at day 2). Growth of \textit{R. venosus} is directed towards the experimentally damaged area of the coral.}
\end{figure}

From the lesion experiment we can conclude that damage to \textit{M. cavernosa} results in a change in the interaction process with \textit{R. venosus}. Apparently, besides reducing coral growth and reproduction (Tanner 1995), damage reduces the competitive ability of the coral in such a way that sponges can benefit from it by actively overgrowing live coral tissue. This means that coral damage on reefs could enhance deterioration of corals by their increasing susceptibility to competing organisms.

Finally I can conclude that 1) competitive outcome between sponges and corals depends on the ecological strategy displayed by sponge species and 2) damaged corals are more susceptible to sponge overgrowth.