Sponge-coral interactions on Caribbean reefs
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Chapter 5

The role of toxicity in competition for space between sponges and corals

Lisanne Aerts & Rob van Soest

This chapter has been submitted (in adapted form) to Contributions to Zoology.
Intensities observed in a former study (Aota, J., van Soest, 1997) were actually overgrowth interactions.

Overgrowth of living border polyps by *R. venosa* was an active process. Because lesions inflicted 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 *R. venosa* extracts demonstrated biological activity (Beckman pers. comm.), this sponge may use its chemicals to compete with corals.

![Image](image-url)

**Fig. 7.** Photographs of 2 interactions: (i) showing the sponge *R. venosa* and the coral *M.* From this lesion experiment we can conclude that damage to *M. serpens* results in a change in the interaction process with *R. venosa*. Apparently, besides reducing coral growth and reproduction (Tenno, 1985), 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 sponges by increasing their susceptibility to competing organisms.

Finally, I can conclude that: 1) competitive outcomes between sponges and corals influence the growth and development of corals; 2) lesions inflicted by sponges spread and 3) damaged corals are more susceptible to sponge overgrowth.
ABSTRACT. Sponges play an important role in spatial competition. They produce a
great diversity of secondary metabolites which may play a role in interaction with other
benthic organisms. We investigated whether a relation exists between frequency of
overgrowth, toxicity and abundance of sponges. Frequency of overgrowth and
abundance of sponges were quantified over reefs in the Santa Marta area (NE
Colombia, South America). Methanol extracts and live fragments of six common sponge
species, Anthosigmella varians, Aplysina cauliformis, Desmapsamma anchorata, Irinica
felix, Niphates erecta and Scopalina ruetzleri were tested against the coral Madracis
mirabilis in laboratory conditions. Generally, there was a relation between the effect of
sponge methanol extracts and live sponge fragments. Only the sponge species N.
erecta demonstrated an extreme difference in the result of the two toxicity tests. The
relation between coral overgrowth and sponge toxicity (of methanol extracts and live
fragments) was significant, the most toxic species displayed most overgrowths. The
sponge species Desmapsamma anchorata deviated from these results by its
proportionally high frequency of overgrowth. Toxicity was also related to the number of
individuals, with the most abundant sponge species being the least toxic. This relation
was not apparent for sponge cover. In contrast, sponge cover was significantly but
inversely related to the frequency of overgrowth; the most aggressive species were least
abundant in terms of % cover. We conclude that: 1) the suggestion that toxic substances
play a role in spatial competition can not be rejected by the outcome of our results and
2) the possible role of sponge chemicals, used in spatial competition with corals, is to
maintain the position on the substratum rather than to actively gain space.

INTRODUCTION

In tropical regions more than 50% of the marine benthic species are toxic (Bakus,
1981). Among these organisms, sponges produce the greatest diversity of secondary
metabolites (Faulkner, 1984), with the most biologically active chemicals (Garson,
1994). Bioassays with sponges on antimicrobial and antifouling activity (Amade et al.,
1982, 1987; Bakus & Kawaguchi, 1984; Bakus et al., 1990; McCaffrey & Endean, 1985;
Thompson et al., 1985; Zea et al., 1986; Targett, 1988; Green et al., 1990) and
antipredation (Bakus, 1981; Green et al., 1990; Huysecom et al., 1990) have been a
common experimental approach. The problem with bioassays is the translation of
laboratory results to the ecological function of such chemical compounds in the field (La
Barre et al., 1986; Schulte & Bakus, 1992; Pawlik et al., 1995).

A function ascribed to secondary metabolites is its use in competition for space
(Jackson & Buss, 1975). This has been demonstrated in the field for some organisms
e.g. in the interaction between a reef anthozoan and filamentous algae (Bak &
Borsboom, 1984) and between a soft coral and an alga (Nys et al., 1991). Sponges play
an important role in spatial competition (Suchanek et al., 1983) and several species
were found to compete successfully with corals (Sullivan et al., 1983; Porter & Targett,
sponges lack special competitive behaviour and organs, they are supposed to use their toxic substances in interactions with other organisms to actively conquer space and maintain their positions on the substratum. Some sponges exude biologically active metabolites into their direct surrounding (Thompson, 1985; Walker et al., 1985; Schulte et al., 1991) and affect competitors even in non-contact situations (Porter & Targett, 1988). In contrast with bioassays, studies on competition for space have mostly been field studies and direct evidence for the role of secondary metabolites remains unclear. Questions, such as: is the degree of toxicity in sponges correlated to their success in competition for space, are unanswered.

The abundance of reef sponges is mainly influenced by abiotic factors, such as light, sedimentation, current strength and organic nutrients (Wilkinson & Vacelet, 1979; Wilkinson & Evans, 1989; Schubauer et al., 1990; Alcolado, 1994). In contrast, the role of biotic factors in structuring reef sponge populations is poorly understood. Predation does not seem to influence sponge abundance, since relatively few organisms feed on sponges (Randall & Hartman, 1968; Wulff, 1994) and some of the most abundant sponge species appear to be highly palatable (Pawlik et al. 1995). Also space, which is a limiting resource for all sessile organisms on coral reefs, will probably not influence sponge abundance, because sponges are often competitively dominant over other organisms (Suchanek et al., 1983). Some sponges even appeared to be more aggressive in localities where the density of competing organisms was higher (Aerts & van Soest, 1997). However, there is much contradictory data on the relation between aggression and abundance of coral reef organisms. Highly aggressive corals in the Caribbean are relatively minor components of the reef (Lang, 1973), while in the Indo-Pacific many of the most aggressive corals are dominant (Sheppard, 1979, 1982; Dai, 1990). The least aggressive coral Porites occurring in the Western Pacific can be the most dominant (Licuanan & Bakus, 1992). Data on aggression and cover of sponges are rare. Rützler and Muzik (1993) reported extreme spatial dominance and great aggression in overgrowing corals of the sponge Terpios hoshinota. If competitive dominance of sponges is related to their degree of toxicity, the most toxic sponge species may be the most abundant.

In our study, the toxicity of 6 different sponge species towards the scleractinian coral Madracis mirabilis was tested and compared with naturally occurring frequency of overgrowth. The main goal is to collect more evidence about the suggested role of toxicity in competition for space and to know if expected overgrowth capacity can be derived from toxicity experiments. To compare the effect of chemical substances present in methanol extracts with more naturally occurring sponge exudates, two toxicity tests
were performed; one with sponge methanol extracts and the other with live fragments of sponges. Together with data on sponge cover and frequency of overgrowth (overgrowth of corals), sampled in a previous study (Aerts & van Soest, 1997), the following questions were addressed:

1. Is degree of sponge toxicity correlated to success in overgrowing corals.
2. Is there a relation between degree of sponge toxicity and sponge abundance?
3. Does success in overgrowth leads to an increase in sponge abundance. In other words, are sponges actively gaining space by overgrowing corals?

**MATERIALS AND METHODS**

**Laboratory experiments.** Both sponge and coral species were sampled at the reefs of the Santa Marta area, NE Colombia (11°15'N 74°13'W). The sponge species were collected at Punta de Betin which is situated close to the institute (Aerts & van Soest, 1997). Sponge species used were *Anthosigmella varians* (Duchassaing and Michelotti, 1864), *Aplysina cauliformis* (Carter, 1882), *Desmapsamma anchorata* (Carter, 1882), *Ircinia strobilina* (Lamarck, 1816), *Niphates erecta* (Duchassaing and Michelotti, 1864) and *Scopalina rutzileri* (Wiedenmayer, 1977). These six species were chosen because of their great range in frequency of overgrowth and abundance on the reef (Aerts & van Soest, 1997). Only sponges that were free from epibions were collected in plastic bags at depths between 5m and 10m. The sponge species were collected without substratum because they were either directly (i.e. within 1 hour) put in a jar with methanol or used as sponge fragments. The coral species *Madracis mirabilis* (Duchassaing and Michelotti, 1864) was chosen as the test organism, because of its tractability and because its polyps are open during daytime. It was only present at Chengu, approximately 30 km from the institute. Corals were sampled and transported in seawater to the laboratory by boat. There, *M. mirabilis* was broken into similar-sized branches and placed in aquaria in a vertical position in pvc holders. Each aquarium contained 6 main coral branches with an average of 15 ramifications and 18 tips. They were fed *Artemia salina* and adapted to the laboratory conditions during the night (without lights). Approximately 18 hours after collection of the corals the experiments started. To ensure that all polyps were open at t=0, *M. mirabilis* was offered food half an hour before the beginning of the experiment.

**Methanol extract experiments.** Sponge specimens were cut into small fragments, preserved in 500 ml methanol and stored at a dark, cool place. After two weeks the
extracts were filtered and the filtrates concentrated by evaporation under reduced pressure (rotation evaporator). To get a maximal extraction, another 500 ml methanol was added to the sponge fragments and the procedure was repeated. After the second evaporation the sponge fragments were dried (100°C) and weighed. The final concentration of the extract (in g/ml) was calculated by dividing the dry-weight of the sponge (g) by the total amount of extract (= ml extract obtained after the first evaporation + ml extract obtained after the second evaporation). We used 6 aquaria of 3.375 liters with Madracis mirabilis branches. The seawater was continually aerated and two 100 watt daylight lamps above the aquaria maintained a stable irradiance. Four aquaria were used to test the extract and two aquaria served as controls, one to control the effect of the solvent and one without any addition. At t=0 minutes an amount of a specific sponge extract was added to the experimental aquaria and a similar amount of methanol to the solvent control aquarium. The effect of the extract and solvent on M. mirabilis was measured counting the number of ramifications and tips with open, half open and retracted polyps for each aquarium every 5 or 10 minutes and after one hour every 30 minutes. The distinction between ramification and tips was made because their polyps reacted different. The number of tips and ramifications with half open polyps was divided into halves, one halve was summed with the number of tips and ramifications with retracted polyps. This was divided by the total number of tips and ramifications present in the aquarium to obtain a percentage of retracted polyps. Depending on the initial effect, new extract was added for 6 to 8 hours, until all polyps were retracted. Every two hours the corals were offered food. The amount of extract needed to obtain 100% retraction of the polyps was designated as the lethal concentration. Each experiment was carried out twice. The lethal concentration (in g/l) was calculated by: a) multiplying the total amount of extract added (in ml) with the concentration of the sponge extract (g/ml) and b) dividing this by 3.375 liter. The measure for toxicity, used for analyses, was calculated according to the formula: toxicity = 1/lethal concentration.

Live fragments experiments. Sponge specimens were cut into small fragments and suspended in little keepers in the aquaria to imitate exudation of chemicals by damaged sponges. Four aquaria were used to test the effect of the sponge fragments and two aquaria served as controls, one to eliminate the possible effect of the keepers and one without any additional treatment. The experiment started after the cups were suspended in the aquaria (t=0 minutes). For each aquarium the number of ramifications and tips with open, half open and retracted polyps were counted every 5 or 10 minutes and after one hour every 30 minutes. Every two hours the corals were offered food. To avoid an effect due to decay of dying sponges, the duration of each experiment was limited to four hours. The same sponge volume (52 ml) was added for each species.
After the experiment sponge fragments of each aquarium were dried (100 °C) and weighed. The dry weights of 52 ml sponge volume varied between species from 2.30 to 4.46 g. The percentage of ramifications and tips with retracted polyps was calculated as for the methanol extract experiment. 50% Polyp retraction time of ramifications and tips was determined (LC50), because 100% retraction of polyps did not occur (or only for a short period of time). The measure of toxicity, used for analyses, was calculated with the formula: toxicity = 1/LC50, with LC50 expressed in hours.

Field data. Data on abundance and frequency of overgrowth of sponges were collected in the Santa Marta area, NE Colombia by means of belt transects (for further details see Aerts & van Soest, 1997). Abundance of sponge species was measured as percentage cover and number of individuals. For each species, the ability to overgrow corals was recorded as percentage of the total number of interactions for that species.

Statistics. The existence of a relationship between sponge variables (cover, overgrowth, abundance and toxicity) was computed using Simple Regression analyses. Lines were fit to linear and logarithmic models. The significance of the model was tested by means of analysis of variance (ANOVA, F-distribution) according to SYSTAT (1992).

RESULTS

Methanol extract experiments

Lethal responses of the extracts were established for 6 sponge species. Extract concentration and concentrations responsible for lethal response in Madracis mirabilis are shown in table 1. The hierarchy for toxicity was as follows (in decreasing order): Aplysina cauliformis > Anthosigmella varians > Desmapsamma anchorata > Ircinia strobilina > Niphates erecta > Scopalina ruetzleri. Addition of the extracts in lethal concentrations resulted in retraction of all polyps. These did not open again during termination of the experiment, even if the corals were offered food. Effects on the corals, percentage of coral ramifications and tips with retracted polyps, were significantly lower for the controls (solvent only and no addition). An exception was Scopalina ruetzleri; after addition of 1.13 g/l extract 60% of the coral tips and ramifications had their polyps retracted. At this concentration the water became very turbid and, because turbidity appeared to influence retraction of the polyps, no more extract was added. An exceptionally different pattern was caused by the methanol extract of Niphates erecta. The substances of N. erecta, in combination with the methanol, appeared to stimulate the corals. These exceptional results prompted us to repeat the N. erecta methanol
experiments three times. Each experiment, however, yielded the same results; after several additions of extract and solvent, the corals of the experimental aquaria were in a much better condition than the corals of the solvent control. This changed after approximately 300 minutes; the percentage of corals with retracted polyps slowly increased in the experimental aquaria and decreased in the solvent control aquarium.

| TABLE 1. Results of the toxicity experiments for each sponge species. EXTRACTS: the concentration of the extract is given in g/ml, the lethal concentration in g/l. LIVE FRAGMENTS: LC50 is expressed in hours. |
|-----------------|---------------|-------------|-------------|-------------|-------------|-------------|
| species         | methanol extract | conc. (g/ml) | ml. added | lethal conc. (g/l) | 1/lethal conc. (g/l) | FRAGMENTS |
|                 |                | extract | added |                            |                           | LC50 (hours) | 1/LC50 |
| Anthosigmella varians | 0.384 | 2.5 | 0.284 | 3.52 | 1.08 | 0.93 |
| Aplysina cauliformis | 0.340 | 1.0 | 0.101 | 9.90 | 0.71 | 1.41 |
| Desmapsamma anchorata | 0.354 | 3.0 | 0.315 | 3.17 | 3.18 | 0.31 |
| Ircinia strobilina | 0.382 | 6.0 | 0.679 | 1.47 | 1.62 | 0.62 |
| Niphates erecta | 0.111 | 40.0 | 1.316 | 0.76 | 0.12 | 8.33 |
| Scopalina ruetzleri | 0.381 | 10.0 | - | 0.00 | - | 0.00 |

Live fragments experiments

Toxicity tests were done with live fragments of sponges to imitate "natural" release of exudates by (damaged) sponges. The presence of live sponge fragments had significant effects on Madracis mirabilis colonies, but they differed from the methanol extract experiments. Not all coral ramifications and tips retracted their polyps and most polyps opened again after they were offered food. The percentage of coral ramifications and tips with retracted polyps was always significantly lower for the two controls. Thus, although sponge fragments had some effect on M. mirabilis, most corals were able to recover from it within a short period of time (approx. three hours). An exudate impact hierarchy can be established, using time at which 50% of the corals had their polyps retracted, resulting in the following sequence (in decreasing order): Niphates erecta > Aplysina cauliformis > Anthosigmella varians > Ircinia strobilina > Desmapsamma anchorata > Scopalina ruetzleri (see table 1). Here again N. erecta differed in its effect.
from the other sponge species. The polyps of the corals reacted very strongly to introduction of the sponge fragments. Within 7 minutes 50% of the corals had retracted polyps and after 180 minutes all polyps were retracted until the end of the experiment. This contrasted strongly with the effect obtained during the methanol extract experiments. The extremely different reaction of *N. erecta* makes it an outlier in the relation between the experiments with the methanol extract and the fragments, which distorts the relationship between these two toxicity tests. Excluding the *N. erecta* data point, the relation between the effect of the methanol extract and the sponge fragments was significant ($R^2=0.78$, $p=0.046$, Fig. 1).

Because of the uncertainty concerning the degree of toxicity of *N. erecta* towards corals, due to the extreme difference in effect between the two toxicity tests, analyses were performed with and without data points of *N. erecta*.

The success of *Desmapsamma anchorata* in overgrowing corals was not proportional to its degree of toxicity when compared with the other sponge species. Leaving out this outlier, together with the data points of *N. erecta*, there exists a relation between the extent of overgrowth and toxicity of sponges for both toxicity experiments (extract: $R^2=0.97$, $p=0.018$, Fig. 2A; fragments: $R^2=0.96$, $p=0.022$, Fig. 2B). If the data point of *N. erecta* is included, only the relation between overgrowth and the methanol extract experiment remains significant ($R^2=0.97$, $p=0.002$). The above mentioned relations fit the linear regression model: $Y = constant + slope \times X$. For the relation between cover and number of individuals with toxicity, regression lines fit the logarithmic model: $Y = constant + slope \times \log(X)$. For both toxicity experiments, without the data
point of *N. erecta*, no relation could be detected between sponge toxicity and cover (extract: $R^2=0.76$, $p=0.056$, Fig. 3A; fragments: $R^2=0.67$, $p=0.089$, Fig. 3B). The data point of *N. erecta* fits only into the line describing the relation between cover and toxicity of the methanol extract.

![Graph A](image1.png)

**Fig. 2.** Relation between sponge toxicity and frequency of overgrowth. The outlying datapoint of *Desmapsamma anchorata* (black triangle) and the datapoint of *Niphates erecta* (black dot) are not included in the analysis. Regression line fits the linear model $Y=a+bX$. For explanation of $R^2$ and $p$, see legend fig. 1. (A) toxicity extract, (B) toxicity live fragments.

![Graph B](image2.png)

Inclusion of this data point leads to a significant relation ($R^2=0.74$, $p=0.029$). The relation between number of individuals and sponge toxicity, without the data points of *N. erecta*, was significant for both toxicity experiments (extract: $R^2=0.94$, $p=0.006$, Fig. 4A; fragments: $R^2=0.95$, $p=0.004$, Fig. 4B). Again, the data point of *N. erecta* fits perfectly.
into the relation of number of individuals and the methanol extract experiment ($R^2=0.93$, $p=0.002$). Concerning the sponge fragment experiments, the data point of *N. erecta* distorts the relation between number of individuals and toxicity ($R^2=0.65$, $p=0.053$). From these data, we can conclude that species abundance, in terms of % cover, is not influenced by sponge toxicity. Only regarding number of individuals, sponge toxicity is correlated with species abundance.

![Image of graphs](image)

**FIG. 4.** Relation between sponge toxicity and number of individuals per square meter. The datapoint of *Niphates erecta* (black dot) is not included in the analysis. Regression line fits the logarithmic model $Y=a+b^x\log(X)$. For explanation of $R^2$ and $p$, see legend figure 1. (A) toxicity extract, (B) toxicity live fragments.

In summary, it remains unclear whether the toxicity of *N. erecta* towards corals is either low (methanol extracts) or high (sponge fragments). Excluding the data points of *N. erecta* from the analyses resulted in a significant positive relation between the two toxicity tests and between coral overgrowth and sponge toxicity. A relation also existed between number of individuals and both toxicity tests, with the most toxic species being the least abundant. No relation was present between sponge cover and toxicity. The data points of *N. erecta* always fit perfectly into the regression models concerning the methanol extract experiment, whereas it always distorted relations between sponge fragment experiments and other variables.

**Field observations**

We found 98 sponge species within 5 cm of a coral, of which 15 displayed overgrowth of corals (see Aerts & van Soest, 1997). Abundance varied between sponge species from 0.1 to 8 individuals/m$^2$ and from 0.03% to 1.12% cover. The species *Mycale laevis* was excluded from this study because of its cryptic habitat. The relation between sponge
cover and overgrowth of corals was significant and fits the regression line $Y = \text{constant} + \text{slope} \times \text{LOG}(X)$ ($R^2 = 0.73$, $p > 0.001$). Compared to other sponge species, *Desmapsamma anchorata* showed an extremely high incidence of overgrowth of corals (table 2).

**TABLE 2.** Frequency of overgrowth and sponge abundance, numerical (nr. of individuals/m$^2$) and cover (%), for each of the 15 aggressive sponge species. Percentage cover was calculated using the formula: (average size (cm$^2$) $\times$ number of individuals/m$^2$)/100.

<table>
<thead>
<tr>
<th>Species</th>
<th>overgrowth</th>
<th>nr. of ind./m$^2$</th>
<th>cover (%)</th>
<th>av. size (cm$^2$)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Agelas clathrodes</em></td>
<td>6.1</td>
<td>0.23</td>
<td>0.08</td>
<td>35.0</td>
</tr>
<tr>
<td><em>Agelas conifera</em></td>
<td>8.3</td>
<td>0.10</td>
<td>0.14</td>
<td>142.0</td>
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<td><em>Anthosigellina varians</em></td>
<td>7.0</td>
<td>0.12</td>
<td>0.51</td>
<td>419.1</td>
</tr>
<tr>
<td><em>Aplysina cauliformis</em></td>
<td>13.1</td>
<td>0.81</td>
<td>0.12</td>
<td>15.1</td>
</tr>
<tr>
<td><em>Aplysina fistularis</em></td>
<td>9.7</td>
<td>0.25</td>
<td>0.03</td>
<td>13.8</td>
</tr>
<tr>
<td><em>Callyspongia armigera</em></td>
<td>14.3</td>
<td>0.06</td>
<td>0.01</td>
<td>14.6</td>
</tr>
<tr>
<td><em>Desmapsamma anchorata</em></td>
<td>37.1</td>
<td>0.52</td>
<td>0.18</td>
<td>35.6</td>
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<tr>
<td><em>Dysidea etheria</em></td>
<td>7.2</td>
<td>1.37</td>
<td>0.03</td>
<td>2.0</td>
</tr>
<tr>
<td><em>Ircinia felix</em></td>
<td>2.7</td>
<td>1.01</td>
<td>0.29</td>
<td>29.0</td>
</tr>
<tr>
<td><em>Ircinia strobilina</em></td>
<td>4.2</td>
<td>0.23</td>
<td>0.28</td>
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<tr>
<td><em>Niphates erecta</em></td>
<td>2.5</td>
<td>2.49</td>
<td>0.27</td>
<td>10.8</td>
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<td><em>Raphidophlus venosus</em></td>
<td>0.2</td>
<td>2.20</td>
<td>1.12</td>
<td>51.0</td>
</tr>
<tr>
<td><em>Scopalina ruetzleri</em></td>
<td>0.7</td>
<td>8.02</td>
<td>0.80</td>
<td>10.0</td>
</tr>
<tr>
<td><em>Xestospongia muta</em></td>
<td>5.7</td>
<td>0.17</td>
<td>0.54</td>
<td>321.7</td>
</tr>
</tbody>
</table>

**FIG. 5.** Relation between frequency of overgrowth and cover (in %) as observed in the field for 15 sponge species. The outlying datapoint of *Desmapsamma anchorata* (black triangle) is not included in the analysis. Regression line fits the logarithmic model $Y = a + b \times \text{LOG}(X)$. For explanation of $R^2$ and $p$, see legend fig. 1.
Without the data point of this aggressive sponge species, the relation between sponge cover and overgrowth was even more obvious ($R^2=0.82$, $p>0.001$, Fig. 5). The least aggressive sponge species were the most abundant in terms of percentage cover. No relation could be found between number of individuals and overgrowth.

**DISCUSSION**

Biologically-active substances of sponges and other marine organisms have several ecological functions (Bakus et al., 1986). The determination of the ecological roles of toxic substances under laboratory conditions is often very difficult as is shown by the lack of a relation between ichthyotoxic properties of sponges and the unpalatability to reef fishes (Pawlik et al., 1995). Although methods of extraction and solvents used often contribute to differences in results of laboratory experiments (Zea et al., 1986), we found a significant relation between sponge toxicity according to methanol extracts and sponge fragments. The experiments with sponge fragments are supposed to be closer to natural conditions, although the concentration of exuded chemicals is higher in a closed seawater system and damaged sponges (in this case fragments) exude 10 to 100 times more metabolites than undamaged sponges (Walker et al., 1985). Despite these high concentrations, our experimental corals did not die and recovered after approximately three hours. Maybe the exuded chemicals are unstable and loose their activity or, alternatively, sponges release their substances only for a short period of time. Exuded toxic substances have been collected in the direct surroundings of some marine organisms (Coll et al., 1982; Walker et al., 1985; Schulte et al., 1991), but the frequency and duration of these exudations are unknown. In soft corals, some species appear to retain their toxins while others release them into the surrounding water, possibly depending on the relative roles of the compounds in anti-predatory versus anti-competitor interactions (Sammarco et al., 1985). A field experiment in which scleractinian corals were confronted with alcyonacean corals showed that affected scleractinian corals were able to recover in non-contact situations (Sammarco et al., 1985).

The sponge species *Niphates erecta* deviated extremely from the relation between the two toxicity experiments. Compared to the methanol extract, the effect on *Madracis mirabilis* polyps was much stronger and even lethal using sponge fragments. The low degree of toxicity of the methanol extract corresponds with the lack of biological activity from other bio-assays which used methanol extracts of *N. erecta* (Green et al., 1990) and with the high palatability of methanol treated pellets (Pawlik et al., 1995). Why
exudates from untreated *N. erecta* fragments induced such a strong reaction is unclear. This strong effect of *N. erecta* fragments on *Madracis mirabilis* polyps indicates that this sponge probably possesses biologically active substances, which makes the lack of a clear negative effect using methanol extract rather strange.

In our study, frequency of coral overgrowth was correlated to methanol soluble toxic substances of sponges. The same correlation was found for the sponge fragment experiments, with the exception of the extremely aggressive reaction of substances of *N. erecta*. Possibly, its active waterborne molecules are detoxified by methanol extraction. Or, this difference in reaction of *N. erecta* could be explained by the presence of more bioactive substances, which was also demonstrated for e.g. the sponge *Dysidea herbacea* (Unson & Faulkner, 1993). The only sponge species which showed a completely different pattern concerning coral overgrowth and its relation with toxicity for both methanol and sponge fragment experiments is *Desmapsamma anchorata*, the high incidence of overgrowth bears no proportion to its toxicity. The consistency of this behaviour makes it unlikely that toxic substances of *D. anchorata* play a role in spatial competition. Possibly, the extremely fast growth rate of *D. anchorata* (Sánchez, 1984) enables it to overgrow organisms. Sponge toxicity was also related to the number of individuals, with non toxic species being more abundant than toxic species. This can be a consequence of the fact that sponges may compensate lack of chemicals by directing their energy to increased growth and reproduction, instead of being used for production and storage of secondary metabolites (Chanas & Pawlik, 1995).

Competitive dominance of sponges towards scleractinian corals has been reported for several species (Sullivan et al., 1983; Suchanek et al., 1983; Porter & Targett, 1988), but the direct effect on the cover of those species has never been quantified. Only Rützler and Muzik (1993) reported the relation between the extreme abundance and aggression of the sponge *Terpios hoshinota*. In our study of the Colombian reefs, an inverse relation existed between cover of sponges and their ability to overgrow corals. The least aggressive sponges in terms of overgrowth (*Raphidophius venosus, Scopalina ruetzleri, Niphates erecta*) were the most abundant.Apparently, fast growing opportunistic species (r-strategists) will not compete actively with their neighbours, in contrast with slow growing species (k-strategists) which as a consequence need to be toxic. Also other rare long lived reef animals are known to be well protected by toxins (Endean & Cameron, 1983) and the great aggression of some corals compensated for their slow growth (Lang, 1973). According to our results, these relatively toxic slow growing species displayed most overgrowths but were not the most abundant. This implies that the function of toxic chemicals of sponges, used in spatial competition, is to maintain their positions on the substratum instead of actively gaining space. This is
supported by the fact that frequency of sponge aggression increases as the density of competing organisms increases (Aerts & van Soest, 1997).

In conclusion, the suggested role of sponge toxicity in competition for space can not be rejected by our experiments. If sponge toxicity plays a role in spatial competition between sponges and corals it is very likely a passive one, toxic chemicals of sponges are used to maintain space and not to compete actively for it.
The strong effect of *N. erata* was confirmed in both the experiments, with the exception of the extremely aggressive reaction of some specimens of *N. erata*. Possibly, the active waterborne molecules are detoxified by marine exchanges. On the basis of the materials of *N. erata*, the prevention of more aggressive interactions which was also demonstrated for *N. erata* (Scheer et al., 1983; Porter & Tappan, 1987) and the high incidence of overgrowth, a natural proportion to its density. The resistance of the behaviour makes it unlikely that toxic substances of *N. erata* can play a role in active competition. Possibly, the extremely fast growth rate of *N. erata* (Scheer et al., 1983) enables it to overgrow organisms. Sponges toxicity was also related to the number of individuals, with non toxic species being more abundant than toxic species. This may be a consequence of the fact that sponges may compensate lack of competition by directing their energy to increased growth and reproduction, instead of being used for patrolling and storage of secondary metabolites (Chartier & Piatet, 1995).

Competitive dominance of sponges towards stenothelial corals has been reported for several species (Sullivan et al., 1983; Suchanek et al., 1983; Porter & Tappan, 1986), but the direct effect on the cover of those species has never been quantified. Only Rützler and Muzik (1993) reported the relation between the extreme abundance and aggression of *Theogorgia* *terpisthela*. In our study of the Colombian reefs, an inverse relation existed between cover of sponges and their ability to overgrow corals. The least aggressive sponges in terms of overgrowth (*Raphidodictyon venosum*, *Pseudoachæna rützleri*, *R. nathans* *erata*) were the most abundant. Apparently, fast growing opportunistic species (A strategies) will not compete actively with their neighbours, in contrast with slow growing species (K-strategists) which as a consequence need to be toxic. Also other rare, long lived reef animals are known to be well protected by toxins (Gardner & Cairns, 1983) and the great aggression of some corals encouraged for their slow growth (Lamb, 1972). According to our results, these relatively long slow growing species displayed most overgrowths but were not the most aggressive. This implies that the function of some chemicals of sponges, used in active competition, is to maintain their position on the substratum instead of actively gaining space. This is