Chapter 6

Ecological strategy and competitive ability in the opportunistic reef sponge \textit{Desmapsamma anchorata}

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Chapter 6

Eco-geographic strategy and competitive ability in the
opportunistic reef spider Dinopelma antarctum

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ABSTRACT. The sponge species *Desmapsamma anchorata* is a very successful competitor in reefal environments. To understand its competitive success, overgrowth interactions with corals, sponges and other reef organisms were quantified and related to characteristics such as sponge growth, regeneration and predation. Reef surveys at 5 sites and depths of 5-20 m on Curaçao, showed a significant higher occurrence of *D. anchorata* in shallow waters (5 m depth). *D. anchorata* (741 specimen) appeared to be a common spatial competitor of corals (262 encounters), sponges (44 encounters), algae (44 encounters) and gorgonian species (21 encounters). Of these encounters, overgrowth by *D. anchorata* occurred more frequently with sponges, algae and gorgonians than with corals (resp. 95.5 %, 100 % and 100 % versus 80.9 %). Growth of *D. anchorata* was irregular and unpredictable (45.2 ±60.3 cm²/month, including temporal shrinkages), but potential growth rates are extremely high. Sponge/coral interaction experiments showed that such high growth rates enable *D. anchorata* to overgrow and incorporate foreign material. Experimental lesions (1 cm²) regenerated completely within 12 days, much faster than in other sponge species. The combination of fast growth and high regenerative efficiency allows for a very competitive strategy. High regenerative efficiency, enabling *D. anchorata* to re-attach very rapidly after disturbance, is compulsory for this soft-bodied shallow water organism. Experiments with fish suggest a low palatability and toxicity for *D. anchorata*. These ecological characteristics make *D. anchorata* very successful in spatial competition. The competitive dominance of *D. anchorata* and its patchy distribution mark this sponge species as a potentially disturbing factor in coral reef communities.

INTRODUCTION

Sessile benthic organisms possess a varying suite of characteristics to survive the numerous physical and biological disturbances occurring on coral reefs. These adaptations can be morphological (shape, structural enforcement), physiological (growth, regeneration, toxicity) or ecological (competition, anti-predation). Sponges are an abundant group in reef benthos. Their shape is highly variable and differs within specimens of the same species due to environmental conditions (Kaandorp, 1991; Becerro et al., 1994). Growth rate, shape and size have been recognised as ecologically important for sessile organisms in competition for space (Jackson, 1979; López Gappa, 1989; Aerts & van Soest, 1997). Similarly, a high regenerative capacity can reduce the susceptibility towards injuries from partial predation, attacks by competing neighbours or physical disturbances.

Sponges play an important role in competition for space (Suchanek et al. 1983; Nandakumar et al. 1993), but competitive mechanisms and success of sponges vary greatly among species (Aerts & van Soest, 1997; Aerts, subm.). Due to this large variation, the role of sponges in spatial competition on a reef depends highly on the sponge species composition (Aerts, subm.). Competitive ability of a sponge is not only the result of allelochemical interactions but depends also on life history characteristics such as growth rate, morphology, regeneration rate and reproductive strategy (Aerts & van
A specific combination of such features represents the survival strategy and determines the fitness and success of a species within the community. To understand the mechanisms of spatial competition displayed by sponges, and their role in coral reef communities, comparative studies of life history characteristics are needed for relevant species. The sponge species *Desmapsamma anchorata* appears to be one of the most aggressive sponge species in Caribbean reefs (Aerts & van Soest, 1997; Aerts, subm.). Spatial competition is generally visible as overgrowth, necrosis and bleaching of contact areas and in *D. anchorata* competitive activity occurs as overgrowth of interacting neighbours. *D. anchorata* is a salmon coloured sponge with a sprawling or sometimes erect growth form and series of oscular lobes. It has a smooth surface and soft consistency and is easily torn (van Soest, 1984). *D. anchorata* possesses unusual organic molecules (Carballeira & Maldonado, 1988; Carballeira & Shalabi, 1994). Laboratory experiments with extracts and pieces of *D. anchorata* showed negative effects on coral polyp activity in the coral *Madracis mirabilis*, but this does not reflect its aggressive dominance in the field (Aerts & van Soest, subm.). The successful spatial competition of *D. anchorata* must be the result of other than toxic characteristics. Toxic chemicals in sponges can also function as anti-predation mechanism (Green 1977, 1990; Pawlik 1993), as most reef sponges are preyed upon only by a few specialised vertebrate species (Meylan, 1988; Wulff, 1994). To what extent the unusual organic molecules of *D. anchorata* have a function as anti-predation needs to be studied.

To assess the status of *D. anchorata* as a competitive benthic element in coral reefs, we studied various life history characteristics such as occurrence, interactions, growth rate, regeneration and competitive success. These data are discussed in terms of spatial competition with the emphasis on the question: to what extent can *D. anchorata* be appointed as a successful competitor in coral reef environments.

**MATERIALS AND METHODS**

Experiments and observations on competition, growth, regeneration, transplantation and predation of the sponge species *Desmapsamma anchorata* were carried out on the coral reefs of Curaçao, Netherlands Antilles (Fig. 1) and interaction experiments in Santa Marta, Colombia.

**Naturally occurring interactions.** Competitive ability of *Desmapsamma anchorata* was studied by quantifying the occurrence of interaction encounters with corals, sponges and other organisms. At site 1 to 4 (see Fig. 1) belt transects were placed at three different depths (5 m, 10 m and 20 m) parallel to the coast. At site 5 belt transects were
only sampled at 5 m depth. Five transects of 10 m² were sampled at each station, resulting in a sampling area of 50 m² per depth and site.

![Map of Curaçao with the 5 sites (black dots). Site 1 is Jan Tiel, site 2 Avila Beach, site 3 Rif Marie, site 4 Daaibooibaai and site 5 Carmabi.](image)

Each *D. anchorata* specimen encountered within 5 cm from a coral, sponge or other organism was considered as interacting. Four categories of interactions were distinguished: overgrowth, peripheral growth, tissue contact and non contact interactions (for explanation see Aerts & van Soest, 1997). The number of *D. anchorata* specimens and the overall cover of corals and sponges in the belt transects were recorded.

**Interaction experiments.** Sponge specimens were confronted with the coral *Madracis mirabilis* to study interactive behaviour of the sponge. Branches of the coral were tied to 15 specimens of *D. anchorata* with plastic coated wire. The distance between the sponge and the living coral tissue was < 5 mm. The reaction of the sponge was recorded over a 27 week period (time intervals see Fig. 5). Branches of *M. mirabilis* (n=15) were tied to pieces of bare rock as a control for the effect of coral handling.

**Growth.** Growth rate of *D. anchorata* was measured at site 2 (5 m, 10 m depth), site 4 (10 m depth) and site 5 (5 m depth) (see figure 1 for sites) about every two weeks between September and December 1995. A total of 80 specimens were labeled, 20 at each depth and site. Because of the amorph, non directional growth of *D. anchorata*
sponge size changes were measured in standard surface area (cm$^2$). The maximum length of attachment to the substratum and the contour over the sponge (average of four fixed points along each sponge) were multiplied to obtain the sponge surface area in cm$^2$.

**Regeneration.** Regeneration of experimental lesions of *D. anchorata* was studied at site 5, 5 m depth. Lesions of 1 cm$^2$, 0.5 cm deep, were cut into the body wall of 20 sponge specimens using a scalpel knife and a mold. The regeneration process was observed daily during the first week and every two days during the second week.

**Transplantation.** To study whether a relation exists between the patchy occurrence of *D. anchorata* and possible variation in local growth rates, we performed transplantation experiments and growth rate measurements. A total of 80 *D. anchorata* specimens were collected at site 2 at 5 m depth and attached to PVC tubes with plastic coated wire. After three weeks of adaptation 20 specimens were translocated to site 1, 5 m depth. The remaining sponges stayed at site 2 and were transplanted to 20 m (20 specimens) and to 10 m depth (20 specimens). Twenty specimens remained at 5 m depth to serve as controls.

**Predation.** The palatability of *D. anchorata* was tested during field experiments by offering sponge pieces and bread pieces soaked in crude sponge extracts to reef fishes. Untreated bread was offered to serve as control. The toxicity of *D. anchorata* was tested during laboratory experiments with *Stegastus partitus*, a non-naturally sponge predator. The fishes (n=12) were put into separate 4 litre aquaria with running seawater. Crude extracts of *D. anchorata* (140 gram fresh-weight) were added to 6 aquaria. The remaining 6 aquaria, treated similarly with addition of seawater, served as controls. Fish behaviour, according to Schulte and Bakus (1992), was observed for one hour after addition of the sponge extract. This experiment was carried out thrice.

**RESULTS**

**Naturally occurring interactions**

A total number of 741 specimens was found in 350 m$^2$ at site 2, 4 and 5. At site 1 and 3 not a single specimen was encountered in the sampling area (=300 m$^2$). Occurrence of *D. anchorata* was depth related, with a significant higher number of specimens at 5 m depth (ANOVA p=0.005; Fig. 2). Differences among sites 2, 4 and 5 were not significant (ANOVA p=0.102). A total of 372 interaction encounters were observed between *Desmapsamma anchorata* and other reef organisms. Encounters with corals occurred most frequently (70.6 % of the total number of encounters). In most of these encounters
the sponge was overgrowing its opponents. *D. anchorata* was never overgrown by other organisms. Overgrowth activity by *D. anchorata* appeared to be higher towards sponges (95.5 %) than towards corals (80.9 %; see table 1). *D. anchorata* grew over all coral species it encountered (n=13, see Fig. 3), but the average frequency of coral overgrowth differed per species (43.4 % - 100 %).

![Graph](image)

**FIG. 2.** Occurrence of *D. anchorata* in number of specimens per m² (± SD) for each depth and site. Because of a depth related difference in occurrence, the average number of specimens per site are separated for 5 m depth (black circles) and for 10-20 m depth together (open circles).

**TABLE 1.** Total number (N) and occurrence (%) of interaction encounters and overgrowth interactions of *Desmapsamma anchorata* with reef organisms.

<table>
<thead>
<tr>
<th>SPECIES GROUP</th>
<th>TOTAL ENCOUNTERS</th>
<th>OVERGROWTH</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>%</td>
</tr>
<tr>
<td>CORALS</td>
<td>264</td>
<td>70.6</td>
</tr>
<tr>
<td>SPONGES</td>
<td>44</td>
<td>11.8</td>
</tr>
<tr>
<td>ALGAE</td>
<td>44</td>
<td>11.8</td>
</tr>
<tr>
<td>GORGONIANS</td>
<td>21</td>
<td>5.6</td>
</tr>
<tr>
<td>ANEMONES</td>
<td>1</td>
<td>0.3</td>
</tr>
<tr>
<td>N TOTAL</td>
<td>374</td>
<td>319</td>
</tr>
</tbody>
</table>
Susceptibility to sponge overgrowth was not significantly different among coral species (Kruskal-Wallis p=0.509; Fig. 3). The large variation between the two samples may be caused by an unequal rate of encounter (see table 2) or differences in local environmental circumstances.

**TABLE 2.** Total encounters (N) and overgrowth frequency (in % of number of encounters) of *D. anchorata* for each coral species. Sample 1 and 2 are independent, sampled at the same sites and depths.

<table>
<thead>
<tr>
<th>CORAL SPECIES</th>
<th>SAMPLE 1</th>
<th>SAMPLE 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>%</td>
</tr>
<tr>
<td>Agaricia agaricites (AAGA)</td>
<td>3</td>
<td>66.7</td>
</tr>
<tr>
<td>Colpophyllia natans (CNAT)</td>
<td>30</td>
<td>90.0</td>
</tr>
<tr>
<td>Dichocoria stokesi (DSTO)</td>
<td>6</td>
<td>83.3</td>
</tr>
<tr>
<td>Diploria labyrinthiformis (DLAB)</td>
<td>4</td>
<td>100</td>
</tr>
<tr>
<td>Diploria strigosa (DSTR)</td>
<td>1</td>
<td>100</td>
</tr>
<tr>
<td>Madracis decactis (MDEC)</td>
<td>4</td>
<td>100</td>
</tr>
<tr>
<td>Madracis mirabilis (MMIR)</td>
<td>45</td>
<td>93.3</td>
</tr>
<tr>
<td>Meandrina meandrites (MMEA)</td>
<td>5</td>
<td>80.0</td>
</tr>
<tr>
<td>Millepora spec. (MillSP)</td>
<td>25</td>
<td>88.0</td>
</tr>
<tr>
<td>Montastrea annularis (MANN)</td>
<td>111</td>
<td>67.6</td>
</tr>
<tr>
<td>Montastrea cavemosa (MCAV)</td>
<td>14</td>
<td>92.9</td>
</tr>
<tr>
<td>Siderastrea radians (SRAD)</td>
<td>2</td>
<td>100</td>
</tr>
<tr>
<td>Siderastrea siderea (SSID)</td>
<td>14</td>
<td>85.7</td>
</tr>
</tbody>
</table>

FIG. 3. Average frequency of overgrowth (in % of total number of encounters) ±SD of each coral species by *D. anchorata*. The average is derived from 2 independent samples (see table 2). Abbreviations of coral species are shown in table 2.
Seven sponge species were observed to interact with *D. anchorata*. No difference in susceptibility to *D. anchorata* overgrowth was apparent among sponge species as all overgrowth percentages were about 100% (Fig. 4). All encounters of *D. anchorata* with other organisms such as *Halimeda opuntia* (*n*=44), gorgonian species (*n*=21) and anemones (*n*=1) were overgrowth interactions, except for the anemone (table 1).

**FIG. 4.** Frequency of overgrowth (in % of total number of encounters) of each sponge species by *D. anchorata*. Numbers by each black dot represent the total number of encounters for each species. ACON = *Agelas conifera*, CVAG = *Callysponia vaginalis*, IFEL = *Ircinia felix*, NERE = *Niphates erecta*, NNOL = *Neofibularia nolitangere*, PANG = *Plakortis angulospiculatus* and SRUE = *Scopalina ruetzleri*.

**Interaction experiments**

Overgrowth of corals by *D. anchorata* occurred rapidly in experiments. Within 1 week 71.4% of all *Madracis mirabilis* branches were overgrown by *D. anchorata* (Fig. 5). After 4 weeks all branches were overgrown (100%). In terms of area covered, the coral branches were not immediately completely overgrown. After 1 week the mean spatial extent of overgrowth was 27.7% (Fig. 5). All coral branches but two (=96.9%) were completely overgrown 27 weeks after the experiment started.

**Growth**

Growth of *Desmapsamma anchorata* appeared to be an irregular and unpredictable phenomenon. A wide variation in growth rate was found for subsequent measurements within and among individual sponges. Besides positive growth (area increase) also
negative values (shrinkages) were measured. Both positive values (average 95.9 ±58.5 cm²/month) and negative values (average -56.5 ±40.9 cm²/month) showed large variations. The average growth rate was positive (45.2 ±60.3 cm²/month), with a maximum of 676.7 cm²/month and a minimum of -525.9 cm²/month. Growth was not correlated with depth (ANOVA, p=0.129; Fig.6). Growth of *D. anchorata* specimens at site 5 appeared to be significantly higher than at site 2 and 4 (ANOVA, p=0.001; Fig. 6).

![Graph showing overgrowth of Madracis mirabilis branches by D. anchorata](image)

**FIG. 5.** Overgrowth of *Madracis mirabilis* branches by *D. anchorata*. Black circles represent the percentage of total number of individuals which were partly or totally overgrown. Open circles represent the total coral area overgrown by *D. anchorata*.

![Graph showing mean growth rate in cm²/month (±SD) of D. anchorata specimens for each depth and site](image)

**FIG. 6.** Mean growth rate in cm²/month (±SD) of *D. anchorata* specimens for each depth and site.
Differences and similarities in absolute growth values among sites and depths were reflected by the occurrence of growth and shrinkage. At each site and depth more sponge specimens displayed growth than shrinkage (t-test \( p=0.026 \); Fig. 7). Among depths no differences were apparent between the occurrence of growth and shrinkage (ANOVA, \( p=0.306 \)). At site 5 growth occurred significantly more and shrinkage significantly less compared to sites 2 and 4 (ANOVA, \( p=0.039 \)).

![FIG. 7. Number of specimens in percentage from total number of specimens (±SE) which displayed growth (circles) and tissue loss (squares) for each depth and site.](image)

**Regeneration**

Regeneration of experimental lesions inflicted to *Desmapsamma anchorata* specimens appeared to be a very fast process. All specimens (\( n=20 \)) with artificially inflicted lesions regenerated within 12 days. The regeneration process occurred in 3 phases which were almost similar to those described for *Agelas clathrodes*, *Neofibularia nolitangere* and *Ircinia strobilina* (Hoppe, 1988). During phase 1 all sponges grew a very thin, transparent layer over the damaged surface of the lesion. In phase 2, the ectosomal layer is growing from the edges into the opening leaving only a depression in the sponge surface. The third phase consisted of filling up this depression until the lesion was completely closed. The first phase took place within one day. The second and third phases, which were sometimes difficult to separate, lasted the remaining period of about 10-11 days.
Transplantation

Good attachment of the sponges to the PVC tubes was accomplished within 2-3 days. Again, growth of the sponge pieces was irregular and highly variable. Transplantation of sponges to different depths and other localities did not influence their growth rate (ANOVA, resp. p=0.370 and p=0.562). No difference existed between growth of transplanted and non-manipulated sponges at site 2, 5 m and 10 m depth (ANOVA, resp. p=0.258 and p=0.301).

Predation

Sponge and crude extract-soaked bread pieces offered to reef fishes during field experiments were ignored by all reef fishes, whereas the control pieces were eaten. This indicates unpalatability for Desmapsamma anchorata. Fish species present during this experiment were surgeonfishes, damselfishes, wrasses, parrotfishes, a french angelfish, a filefish and a trunkfish.

Toxicity tests under laboratory conditions showed some reduced activity and balance disordering effects of the fishes during the first 25 minutes, but the fishes slowly regained their normal behaviour until they were completely recovered (t=53 minutes). The fishes in the control aquaria behaved normal during the experiment. Apparently, crude sponge extracts of D. anchorata have no toxic effects on Stegastus partitus.

DISCUSSION

The remarkably aggressive behaviour of Desmapsamma anchorata towards corals has been noticed in other studies (Aerts & van Soest, 1997; Aerts, subm.). It is interesting that the overgrowth activity of D. anchorata was even more successful towards sponges, algae and gorgonians. This phenomenon was also observed for the sponge species Niphates erecta (Aerts et al., subm.). Corals mainly defend themselves using sweeper tentacles and mesenterial filaments (Lang & Chornesky, 1990). Sponges, gorgonians and algae possibly use toxic substances in spatial competition (Sammarco et al., 1983; Nijs et al., 1991; Porter & Targett, 1988; Sullivan et al., 1983). Apparently, the defensive mechanism of corals has a greater restraining influence on overgrowth by D. anchorata than the chemical defense of sponges, gorgonians and algae. This restraining influence, however, is relative as the extent of coral overgrowth by D. anchorata is very high compared to other sponge species (Aerts & van Soest, 1997; Aerts, subm.; Aerts et al., subm.; Aerts &
Kooistra, subm.). Overgrowth success of *D. anchorata* was not mediated by chemical substances (Aerts & van Soest, subm.). The main characteristic ensuring competitive success of *D. anchorata* is its fast growth rate. Although irregular and unpredictable growth is characteristic for a wide variety of other sponge species (Hoppe, 1988; Wulff, 1990; Aerts et al., subm.; Aerts & Kooistra, subm.), growth rate of *D. anchorata* is extremely high. The direction of growth occurred in the length (over the substratum), in height and in width. Fast horizontal growth is relevant for acquisition of substratum either by seeking, or through avoidance of competition with nearby neighbours. Growth in height and width becomes important when neigbouring organisms have a growth form other than encrusting. Its fast growth rate and flexible shape enables *D. anchorata* to rapidly overgrow and completely incorporate competitors, as is shown by interaction experiments with *Madracis mirabilis* branches.

Another characteristic favouring overgrowth is the high regenerative efficiency of *D. anchorata*. Compared to other sponge species, damaged tissue was rapidly regenerated by *D. anchorata* (Hoppe, 1988; Aerts et al., subm.; Aerts & Kooistra, subm.), and this probably compensates for its soft and fragile consistency. Despite the great variety of defensive mechanisms and thus competitive ability in coral species (Lang, 1973; Lang & Chomesky, 1990), *D. anchorata* was able to overgrow all corals it encountered regardless of species. Damage to sponge tissue by coral (sweeper) tentacles may cause a lower overgrowth frequency of corals compared to sponges and other organisms, as regeneration of damaged tissue demands energy (Bak, 1983; Wahle, 1983; Meesters et al., 1994), which can result in a temporary decline in competitive activity of *D. anchorata*. Overgrowth of sponges also occurred regardless of species. Since overgrowth of sponge species, *Halimeda opuntia* and gorgonians was close to 100%, *D. anchorata* appears to be completely indifferent to any chemical defense.

Besides their function in competitive success, the characteristics of *D. anchorata* make this sponge rather insensitive to environmental disturbances. During the present study and also during fieldwork on Colombian reefs, overgrowth of *D. anchorata* by other organisms and presence of fouling organisms were never observed. In Colombia it was even the only species not overgrown by the highly toxic *Palythoa caribbeorum* (Gleibs, pers. comm.). The reason for the absence of overgrowth and fouling is not quite obvious. Extremely toxic metabolites such as phenols and alkaloids are not present in extracts of *D. anchorata*, but it possesses some unusual lipids (Carballeira & Maldonado, 1988; Carballeira & Shalabi, 1994), which may function as defensive or anti-fouling agents. Its fast growth rate allows *D. anchorata* to immediately incorporate particles attached to or organisms growing in its direct vicinity, as was observed during the interaction
experiments with *M. mirabilis* branches. When touching the soft sponge, incorporated foreign particles could often be felt within the sponge tissue (own obs.).

Predation by fishes and predation marks were never observed on *D. anchorata* individuals during field observations. Sponge mucus containing pieces offered to fishes on the reef were refused, which points to unpalatability of *D. anchorata*. The unpalatability was not caused by a toxic agent as deterrent effects to fishes were not found during the laboratory experiment. It has already been proven that toxicity and unpalatability are not necessarily related to each other (Pawlik, *et al.* 1995). Sponges can have a variety of other very species specific anti-predation strategies such as spicule density or tissue toughness (Chanas, *et al.* 1995). In *D. anchorata* spicules are hardly present and its tissue is very soft and easily torn. The mucus from damaged sponge tissue possibly accounts for the unpalatability to reef fishes. Besides that, its high regenerative efficiency allows *D. anchorata* to regenerate possible predation damage at a fast rate.

Transplantation experiments showed that both vertical (depth) and horizontal (sites) limits in distributions were unrelated to local growth rates. These experiments also demonstrated the ability of *D. anchorata* to re-attach itself rapidly to the substratum after being disturbed, as was also demonstrated in another study under laboratory conditions (Sanchez, 1984). The high abundance at 5 m depth could be the result of asexual reproduction. Strong water movements and wave action at shallow depths can easily break large *D. anchorata* specimens, which very rapidly re-attach themselves close to the original specimen, resulting in a patchy, clumped distribution. The horizontal distribution of *D. anchorata* is difficult to explain. Although *D. anchorata* was mainly found at sites with a relatively high overall sponge cover, which points to some degree of organic enrichment (Wilkinson & Cheshire, 1990; Carballo *et al.*, 1996), it remains difficult to demonstrate a direct relationship between environmental parameters and the distribution pattern of *D. anchorata*. Remarkably is the observation that *D. anchorata* specimens were often found on artificial substrata dumped by humans.

In conclusion, the ecological strategies of *D. anchorata* (rapid attachment after disturbance, high regenerative efficiency, fast growth rate, anti-predative and anti-fouling mechanisms and insensitivity towards disturbances) make this sponge species very successful in spatial competition. The competitive dominance of *D. anchorata* and its patchy distribution mark this sponge species as a potentially disturbing factor in coral reef communities.