Marine Biology (1999) 134: 491–500

O. Langmead · N. E. Chadwick-Furman

Marginal tentacles of the corallimorpharian *Rhodactis rhodostoma*. 2. Induced development and long-term effects on coral competitors

Received: 15 July 1998 / Accepted: 24 March 1999

Abstract Polyps of the corallimorpharian *Rhodactis rhodostoma* (Ehrenberg, 1934) form aggregations that monopolise patches of space on the shallow reef flats of some Red Sea coral reefs. Some of these polyps bear specialised bulbous marginal tentacles (BMTs) where they contact cnidarian competitors. BMTs differ from the normally filiform marginal tentacles (FMTs) of *R. rhodostoma*, and appear to develop from them. However, their morphogenesis and long-term impacts on spatial competition with reef corals are unknown. We experimentally induced contacts between *R. rhodostoma* polyps and colonies of the branching stony coral *Acropora eurystoma* on a shallow coral reef at Eilat, northern Red Sea. During the first 24 d of contact, the *A. eurystoma* colonies extruded mesenterial filaments that damaged the tissues of the corallimorpharian polyps. After 18 d, > 90% of *R. rhodostoma* individuals had developed BMTs, which resulted in a reversal in the direction of competitive damage. During the subsequent 1.5 years of observation, the corallimorpharians maintained well-developed BMTs, unilaterally damaged the tissues of *A. eurystoma*, and in some cases moved onto the stony coral skeletons and partially overgrew them. BMTs developed from FMTs in a series of four distinct stages, accompanied by significant changes in their morphology, cnidom, and density of nematocysts. Isolated control polyps did not develop BMTs or show any signs of damage. In contrast, corallimorpharian polyps transplanted into contact with colonies of the massive stony coral *Platygyra daedalea* began to develop sporadic BMTs, but were unilaterally and severely damaged by the corals, and started to disappear within 21 d, after the corals developed sweeper tentacles. We conclude that long-term outcomes of competition between *R. rhodostoma* and reef-building corals depend largely on the relative aggressive reach of the competitive mechanisms developed by each species. As a consequence, this corallimorpharian is an intermediate competitor in the aggressive hierarchy among Indo-Pacific reef corals. This study confirms that *R. rhodostoma* polyps may actively damage and overgrow some stony corals, leading to the formation of an almost continuous blanket of polyps in large patches of some shallow reef flats.

Communicated by R. Cattaneo-Vietti, Genova

O. Langmead
School of Ocean Sciences,
The University of Wales, Bangor,
Menai Bridge Marine Science Laboratory,
Gwynedd, LL 59 5EY, United Kingdom

N.E. Chadwick-Furman (✉)
Interuniversity Institute for Marine Science,
P.O. Box 469, Eilat, Israel, and
Faculty of Life Sciences, Bar Ilan University,
Ramat Gan, Israel

Introduction

Some cnidarians induce the morphogenesis of specialised aggressive organs during competition for space on hard marine substrata (reviewed by Lang and Chornesky 1990; Williams 1991). These include the catch tentacles of sea anemones (reviewed by Fukui 1986), and the sweeper tentacles of stony corals (reviewed by Lang and Chornesky 1990) and soft corals (Sebens and Miles 1988; Goldberg et al. 1990). Such inducible aggressive organs develop only upon contact with certain other cnidarians, and regress to normal feeding tentacles upon cessation of competitive contact (reviewed by Williams 1991). Transformation of feeding tentacles into aggressive organs increases the ability of some cnidarians to damage and overgrow their neighbours (Lang and Chornesky 1990). In some cases, their development leads to a reversal of competitive outcome over time, in which the individual developing them becomes dominant over a former aggressor (Wellington 1980; Bak et al. 1982; Chornesky 1989). Morphogenesis of aggressive structures in cnidarians is accompanied by a complete changeover of cnidom, such that relatively large nematocysts of special types, which appear to function in

aggression, almost completely replace all other cnidae, including the adhesive spirocysts (reviewed by Bigger 1988). The induced development of aggressive structures in benthic cnidarians has important effects on competitive processes on hard marine substrata, and influences the temporal dynamics of such interactions (Lang and Chornesky 1990).

Some tropical corallimorpharians of the genus *Rhodactis* (= *Discosoma*) are known to possess bulbous marginal tentacles (BMTs) that appear to function in aggression against stony coral competitors on reefs (den Hartog 1977; Miles 1991; Ridzwan 1993; Langmead and Chadwick-Furman 1999). The morphogenesis of these organs from the normally filiform marginal tentacles (FMTs), and their long-term competitive impacts, are known for only one species, *R. sanctithomae* in the Caribbean (Miles 1991). The dynamics of competition between Indo-Pacific reef-building corals and corallimorpharians are unknown, but field observations suggest that in some cases they involve the induced development of BMTs and subsequent overgrowth by the corallimorpharians of certain types of stony corals (Ridzwan 1993; Langmead and Chadwick-Furman 1999).

We describe here the morphogenesis of specialised BMTs in *Rhodactis rhodostoma* (Carlgren 1938), a common aggregating corallimorpharian that can monopolise patches of space on some Red Sea coral reef flats (Spiegel 1998; Langmead and Chadwick-Furman 1999). Through field experimental contacts with stony corals, we also demonstrate that, after a short-term reversal in competitive outcome, *R. rhodostoma* polyps actively damage, and in the long-term, partially overgrow branching stony corals. In contrast, BMTs of *R. rhodostoma* are not effective during competition against colonies of a massive stony coral that develops sweeper tentacles. We conclude that the aggressive reach and type of competitive organs developed by the members of each species determine in large part their position in the aggressive hierarchy among Indo-Pacific reef cnidarians.

Materials and methods

Field experiment

On 7 May 1996, 60 specimens of *Rhodactis rhodostoma* (Ehrenberg, 1934) were collected from the edges of aggregations at 1 m depth on the reef flat of the Coral Beach Marine Reserve, at Eilat, Israel, northern Red Sea (29°30′10″N; 34°55′15″E, site described in detail by Langmead and Chadwick-Furman 1999 and references therein). Each polyp was removed by carefully chipping away the coral rock beneath it using a hammer and chisel. The individuals varied in size, but did not contact other cnidarian species or bear obvious BMTs (as defined by Langmead and Chadwick-Furman 1999).

Following collection, the polyps were transferred to the nearby Interuniversity Institute for Marine Science (IUI) in Eilat, and maintained in outdoor running seawater aquaria at ambient sea temperature. Four polyps that exhibited handling damage were discarded, and the rock bases bearing the remaining polyps each were tagged with numbered plastic tape using an underwater adhesive. Within 2 d of collection, 18 polyps were assigned randomly to each of three field treatments: (1) contact with colonies of the branching stony coral *Acropora eurystoma* (Klunzinger, 1879) (identified according to Sheppard and Sheppard 1991), (2) contact with colonies of the massive stony coral *Platygyra daedalea* (Ellis and Solander, 1786) (identified according to Veron 1993), or (3) isolated from contact with cnidarians. The three treatments were interspersed at 2 m depth on the coral reef adjacent to the IUI, located approximately 500 m south of the collection site described above. The tagged rock base bearing each corallimorpharian was glued onto the reef using Aquamend underwater adhesive. The stony coral species were selected for contact because they were observed to be common on the shallow reef at the IUI site (though rare at the reef flat, 500 m north of this site, Loya and Slobodkin 1971), their modes of direct competition are known to genus level (Hidaka et al. 1987; Lang and Chornesky 1990), and aggressive ability appears to be similar for members of each genus (Sheppard 1979; Langmead and Chadwick Furman 1999). Six corallimorpharian polyps were placed into contact with each of three colonies of each coral type, yielding a total of 18 corallimorpharians per treatment.

The corallimorpharians were transplanted so that they barely contacted each coral during nocturnal expansion of the coral tissues, simulating the initiation of natural tissue contacts between sessile cnidarians (after Lang and Chornesky 1990). Using data from preliminary night observations, the corallimorpharian polyps were placed < 1 mm from diurnally contracted *Acropora eurystoma* colonies, and approximately 5 mm from contracted *Platygyra daedalea* colonies.

Isolated control *Rhodactis rhodostoma* polyps were glued to the reef substratum, interspersed between the experimental polyps, but not touching each other or any other cnidarians. Two polyps that detached during the first 7 d of the experiment were assumed to have suffered damage due to experimental manipulation, and were replaced.

After an acclimation period of 7 d, field observations on all transplanted polyps were made daily for the next 35 d, then monthly for 5 months, and finally at 1.5 years after transplantation. During each observation period, data were recorded on the presence of damage to either partner, defined as exposed stony skeleton on the corals, detachment of the polyp base in the corallimorpharians, or necrotic tissue or excess mucus on either (after Sebens 1976; Cope 1981; Chadwick 1991; Miles 1991). Nocturnal observations also were made each week for the first 2 months, to assess contact status between the partners, and to record behavioural interactions between nocturnally active polyps.

Laboratory analyses

Each week during the first 6 weeks of the experiment, the rock bases bearing five *Rhodactis rhodostoma* polyps in each experimental treatment were detached carefully from the reef and transported to the laboratory at the IUI for tissue sampling. Up to five marginal tentacles and part of the oral disk in the area facing coral contact were removed from each polyp. The polyps were returned to their original field treatments in exactly the same orientation within a few hours. Each polyp was sampled only once every 3 weeks to minimise potential effects of this sampling on the outcome of the field experiment.

Three types of analyses were conducted on the tissues sampled. First, changes in tentacle morphology were assessed on two marginal tentacles per polyp, by anaesthetising them in a solution of 7.5% $MgCl_2$ in distilled water 1:1 with seawater for 10 min, then mounting each tentacle separately on a glass slide in two drops of filtered seawater, and gently applying a coverslip (Size 1, 22×22 mm). Without further squashing, this preparation was examined under a Nikon Type 102 phase contrast microscope, fitted with a calibrated eyepiece reticle, and three measurements were made: (1) tentacle diameter at the tip ($= 0.5$ mm from the tip), (2) tentacle diameter at the stalk ($= 1.75$ mm from the tip), and (3) ectodermal thickness at the tentacle tip. The ratio of tip to stalk diameter was used to indicate the development of acrospheres

(swollen tentacle tips), which distinguish BMTs from FMTs (Langmead and Chadwick-Furman 1999).

Secondly, changes over time in the relative abundance of each nematocyst type were determined by further squashing the above tentacle preparations. The tip regions were examined under phase contrast at 1000× magnification, and the abundance of each nematocyst type present was estimated by examining the first 100 cnidae encountered in transects across each squashed tentacle (after Langmead and Chadwick-Furman 1999 and references therein). Folded capsules with no obvious thread were identified as developing cnidae, as confirmed by their intense staining with picrocarmine in preliminary tests. Pircrocarmine, a nuclear stain, bound to the large quantities of RNA present in the maturing cnidoblasts during protein synthesis, thus differentiated them from mature nematocysts. The capsule lengths of Type 1 holotrich nematocysts also were measured for the first ten capsules encountered, since they are known to differ significantly in size between BMTs and FMTs (Langmead and Chadwick-Furman 1999).

Finally, changes in overall nematocyst and zooxanthella densities in the marginal tentacles were assessed by removing a small portion of the oral disk in the contact region, together with three marginal tentacles, from three out of the five polyps sampled. This was done to obtain a single tissue unit bearing several tentacles in the same orientation, for examination of cross sections. The samples were immediately immersed in an anaesthetic solution for 10 min (as described above), then transferred to buffered neutral formalin for fixation. They were then prepared for histology by washing twice in distilled water, dehydrating in a graded ethanol series, clearing with toluene and embedding in paraffin (after Watson and Mariscal 1983a). Trial cross sections were cut at 6, 8 and 10 μm, revealing that the 8 μm sections were optimal. These were stained in an aqueous solution of bromophenol blue for 5 min, followed by 5 min developing time in 0.5% acetic acid in distilled water (after Mazia et al. 1953). Finally the sections were washed, dehydrated, cleared in xylene, mounted on glass slides and examined using a Dialux microscope at 400× magnification. The first several tip sections of each tentacle were discarded, until the tentacles presented a clear cross section of ectodermal cells in transverse orientation, at approximately 80 to 100 μm from the tentacle tip. In this near-tip section, the density of nematocysts in the ectoderm, and of zooxanthella cells in the endoderm, were determined in four transects of 228 μm each per tentacle, and their mean densities calculated per 100 μm of tentacle ectoderm.

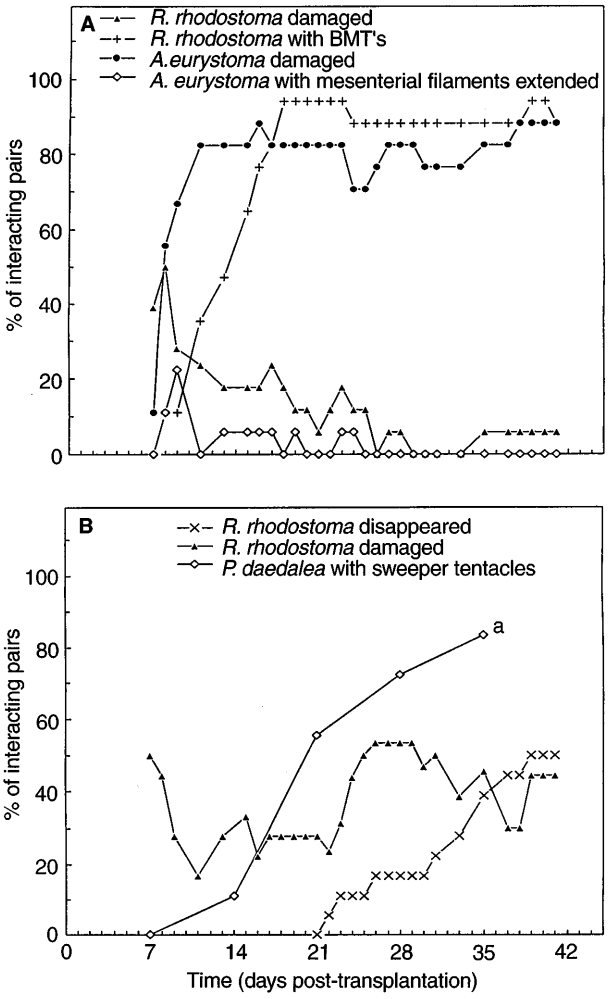

Fig. 1 *Rhodactis rhodostoma*. Outcomes of experimentally induced contacts with reef-building corals at 2 m depth on a coral reef at Eilat, northern Red Sea. $N = 18$ interacting pairs per treatment, involving: **A** the branching stony coral *Acropora eurystoma*, **B** the massive stony coral *Platygyra daedalea* (*a* indicates missing data at Week 6; all corals were contracted, thus no sweeper tentacles were recorded)

Results

Field experiment

Immediately following the initial 7 d of acclimation in the field experiment, up to 50% of the *Rhodactis rhodostoma* polyps in contact with *Acropora eurystoma* colonies exhibited damage along their polyp margins facing the corals (Fig. 1A), in the form of tissue necrosis, partially detached bases and/or excess mucus in the region of coral contact. A low percentage of polyps of *A. eurystoma* were observed extruding their mesenterial filaments onto the corallimorpharians, during both day and night dives throughout the first 24 d of contact (Fig. 1A). The percent of *R. rhodostoma* polyps damaged was higher than the percent of *A. eurystoma* polyps extruding filaments during each observation, and both processes decreased gradually throughout the experiment (Fig. 1A). In contrast, the proportion of corals with damaged tissues increased rapidly to >80% of *A. eurystoma* individuals within 10 d of contact, and remained high for the duration of the experiment (Fig. 1A). Coral damage was observed in the form of bleached or necrotic tissue, or exposed skeleton in the region of contact. In more than half the interacting pairs (56%), damage was recorded on *A. eurystoma* tissues before the adjacent *R. rhodostoma* polyps had developed visible BMTs. Almost all of the corallimorpharian polyps (94%) then developed BMTs within a few days of damaging adjacent corals (Fig. 1A). BMTs were first visible on the corallimorpharians after 8 d of contact, and by 17 d almost all *R. rhodostoma* polyps had developed these swollen, white tips on their tentacles along the margin facing coral contact (Fig. 1A). The time to develop BMTs in *R. rhodostoma* was approximately 2 weeks from initiation of coral contact (mean ± 1 SD: 13 ± 3 d). One *R. rhodostoma* polyp in this treatment detached and disappeared on Day 11.

Long-term observations up to 1.5 years indicated that 33% of the corallimorpharian polyps in the above

treatment slowly overgrew parts of the contacted corals, another 33% eventually ceased to contact the coral, and 33% were consumed by a predator (see below). Six out of the original 18 *Rhodactis rhodostoma* polyps still contacted live coral at 1.5 years after transplantation (=33%), and most of these (5/6) still possessed BMTs. All six polyps had moved off their original tagged bases and had advanced 0.3 to 2.0 cm up the skeleton of the contacted coral colony. Two of the *R. rhodostoma* polyps had moved 2 cm out of contact with the coral at 3 months, and their BMTs regressed back into normal FMTs. One polyp moved back into coral contact by 4 months, and by 5 months had redeveloped BMTs. The second *Acropora eurystoma* colony exhibited >50% mortality by 4 months after the start of the experiment, and five of the *R. rhodostoma* polyps adjacent to this dead coral lost their BMTs. The sixth polyp in contact with this coral disappeared when its base detached at 3 months. Several individuals of the predatory gastropod *Drupella* sp. were observed on the final *A. eurystoma* colony at 3 months; all six contacted *R. rhodostoma* polyps and the entire coral colony were subsequently killed by this cnidarian predator. Finally, one polyp of *R. rhodostoma* reproduced asexually via fission to produce two daughter polyps, so that 13/18 corallimorpharians remained alive at the end of the experiment in this treatment, a net decrease of 28%.

The 18 control *Rhodactis rhodostoma* polyps that were isolated from contact with corals did not develop BMTs or exhibit any signs of tissue damage during the 1.5 years of observation. One control polyp disappeared at 3 months, and two other polyps reproduced asexually by fission to produce two daughter polyps each, resulting in 19 control polyps total by the end of the experiment, an increase of 5.5%.

The outcomes of contact between the corallimorpharians and colonies of the massive stony coral *Platygyra daedalea* differed strikingly from those with the branching coral above. As above, by 7 d after initiation of contact, half of the *Rhodactis rhodostoma* polyps exhibited damage along their margins of contact with *P. daedalea* (compare Fig. 1A and B). However, in contrast to interactions with *Acropora eurystoma* corals, when the corallimorpharians contacted colonies of *P. daedalea*, they suffered massive tissue damage, resulting in complete removal of most of their marginal tentacles and even up to a third of their oral disks on the side facing contact. A relatively high percentage (20 to 50%) of *R. rhodostoma* polyps remained severely damaged throughout the first 42 d of this treatment, and by Day 21 entire corallimorpharian polyps began to disappear (Fig. 1B). The percent of disappeared polyps steadily increased to 50% by 42 d (Fig. 1B), and by 3 months (90 d) all 18 *R. rhodostoma* polyps in this treatment were gone.

During nocturnal expansion of their polyps, the massive corals contacted the tissues of adjacent corallimorpharians. In 8 to 19% of such interactions observed at 7 to 21 d after initial contact, colonies of *Platygyra daedalea* were observed to extrude mesenterial filaments onto neighbouring *Rhodactis rhodostoma* polyps. They also were observed to develop and extend sweeper tentacles up to 4 cm in length toward the corallimorpharians, beginning at 14 d after initial contact (Fig. 1B). The percent of interactions in which *P. daedalea* polyps developed sweeper tentacles increased gradually to >75% of interacting pairs by 35 d after the start of the experiment (Fig. 1B). By this time, 40% of the corallimorpharian polyps had already disappeared, and so some coral polyps developed these elongate tentacles even after their contacted corallimorpharians were gone. Some polyps of *R. rhodostoma* (19 to 33% $N=18$), began to develop BMTs at 7 to 18 d after transplantation into contact with *P. daedalea*, but this morphogenesis was interrupted by the complete removal of most marginal tentacles facing contact with the massive corals, and finally by the disappearance of all corallimorpharian polyps by 3 months.

Long-term observations indicated that the colonies of *Platygyra daedalea* did not show any signs of tissue damage throughout the 1.5 years of the experiment. The tagged rock bases of the corallimorpharian polyps in this treatment remained securely attached to the reef substratum adjacent to *P. daedalea* also for at least 1.5 years, even though the polyps originally attached to them were long gone.

Laboratory analyses

Changes in marginal tentacle micro-structure during the above experiment were examined for only two of the treatments (isolated controls and contact with *Acropora eurystoma*), because polyps in the third treatment (contact with *Platygyra daedalea*) became damaged so severely that in most cases their marginal tentacles were entirely removed by the corals (see above).

The marginal tentacles on *Rhodactis rhodostoma* polyps that faced contact with *Acropora eurystoma* corals developed significantly different morphologies than those of control polyps, at 28 d after initiation of contact (Fig. 2A, B). These changes were measurable as a significant increase in the ratio of tentacle tip to stalk diameter, indicating the formation of bulbous acrospheres at the tips of marginal tentacles that contacted corals (Pearson's correlation coefficient, $r=0.51$, $p < 0.05$). In contrast, control polyps showed no significant change in shape over time ($r=0.17$, $p>0.05$) (Fig. 2A). The tissue layer responsible for acrosphere formation was the tentacular ectoderm, which increased >100% in thickness within 28 d on the tentacle tips of polyps contacting corals ($r=0.62$, $p < 0.05$), compared with no significant increase in isolated control polyps ($r=-0.26$, $p > 0.05$) (Fig. 2B).

The nematocyst composition of marginal tentacles on the *Rhodactis rhodostoma* polyps underwent a complete changeover during the 28 d following coral contact, but did not change significantly in control polyps that were

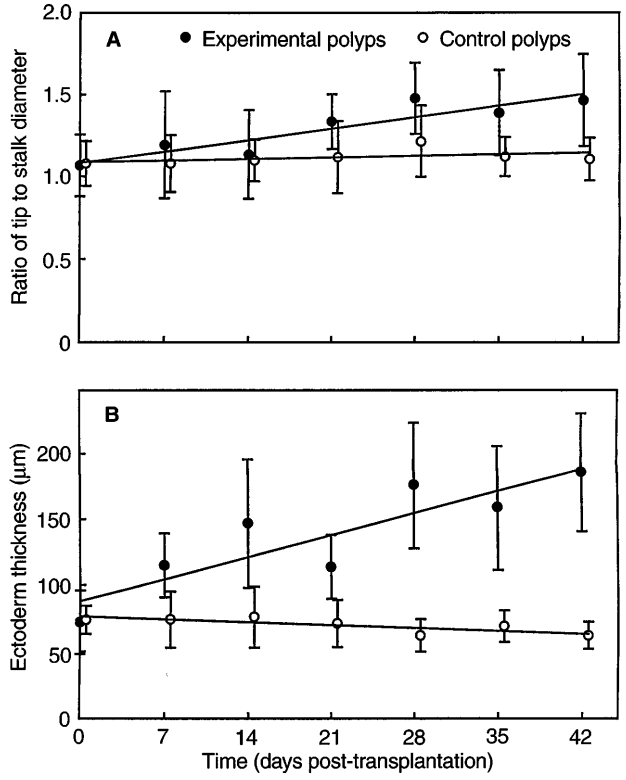

Fig. 2 *Rhodactis rhodostoma*. Changes in marginal tentacle morphology induced by contact with the branching stony coral *Acropora eurystoma* during experimental field-transplantations at 2 m depth on a coral reef at Eilat, northern Red Sea. **A** Tentacle tip to stalk diameter ratio (=acrosphere index) (mean ± 1 SD). **B** Ectoderm thickness at tip (mean ± 1 SD). $N = 10$ tentacles

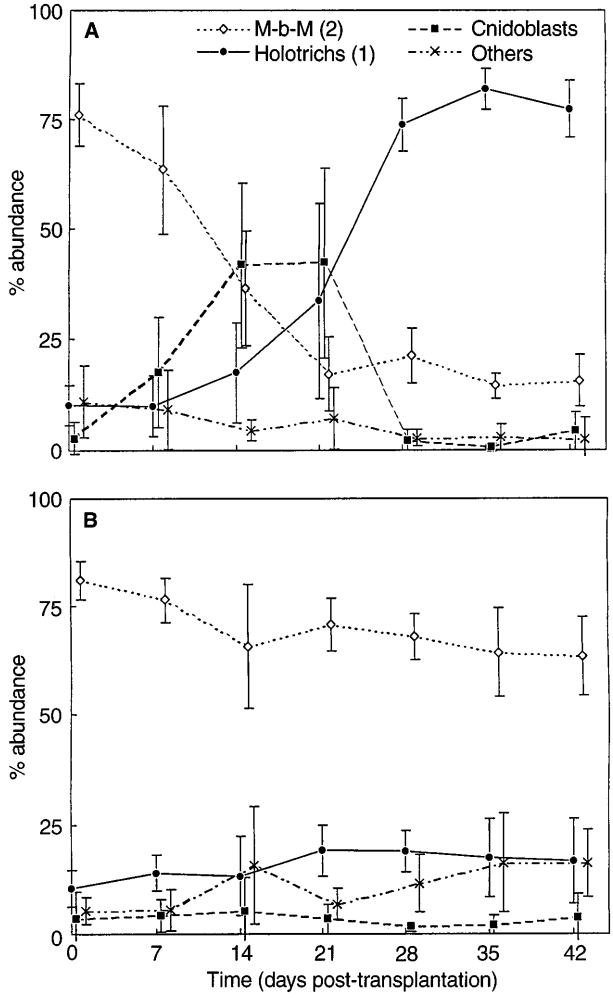

Fig. 3 *Rhodactis rhodostoma*. Changes in cnidom composition in the marginal tentacle tips of polyps experimentally transplanted at 2 m depth on a coral reef at Eilat, northern Red Sea. **A** Polyps placed in contact with colonies of the branching stony coral *Acropora eurystoma*. **B** Polyps placed on the reef substratum not in cnidarian contact (mean ± 1 SD, $N = 10$ tentacles in each treatment examined per sampling date, 100 capsules identified per tentacle) [*M-b-M*(*2*) microbasic-b-mastigophores (Type 2)]

isolated from contact (Fig. 3). This transformation of the cnidom was revealed as significant variation in the relative abundance of all four major nematocyst types in experimental versus control polyps with time, including Type 1 holotrichs ($\chi^2 = 429.69_{(6)}$, $p < 0.001$), microbasic-b-mastigophores (Type 2) ($\chi^2 = 573.15_{(6)}$, $p < 0.001$), developing cnidae ($\chi^2 = 302.34_{(6)}$, $p < 0.001$) and all other nematocysts ($\chi^2 = 252.44_{(6)}$, $p < 0.001$) (see Langmead and Chadwick-Furman 1999 for characterisation of cnidae). In the normally filiform marginal tentacles before coral contact was initiated, microbasic-b-mastigophores were the dominant nematocysts, consisting of >75% of the cnidom (Fig. 3A). A fourfold decrease occurred in microbasic-b-mastigophores from 76 ± 7% to 21 ± 6% of the cnidom, by 28 d after initial contact (Fig. 3A). By 14 to 21 d post-contact, developing cnidae became the most abundant nematocyst type (42 ± 19% and 42 ± 21% of the cnidom at 14 and 21 d, respectively), indicating a massive synthesis of new nematocyst capsules in these tentacles. After 21 d, the relative abundance of developing cnidae decreased, returning to previously low levels (2.3 ± 2.3% of the cnidom). As of 28 d post-contact, large Type 1 holotrichs had become the dominant cnidae in the transforming marginal tentacles, increasing sevenfold in relative abundance from 10 ± 4% to 74 ± 6% of the cnidom, and all other types now were present at only low levels (Fig. 3A). In comparison, microbasic-b-mastigophores remained the most common nematocyst types in the marginal tentacles of *R. rhodostoma* polyps that were not transplanted into contact with corals (Fig. 3B).

The capsules of holotrichs became significantly larger after the completion of cnidom replacement in BMTs, whereas they remained relatively small in size in the FMTs retained by non-coral-contacting polyps (Fig. 4). Over 42 d, the length of Type 1 holotrich capsules increased significantly, by 23% (Pearson's correlation coefficient, $r = 0.5_{(645)}$, $p < 0.05$). At the time of transplantation, holotrichs were 35 ± 3 µm in length (mean ± 1 SD, $N = 100$), while after 42 d they were 43 ± 5 µm. Interestingly, control polyps showed a slight but significant decrease in holotrich capsule length of 4%

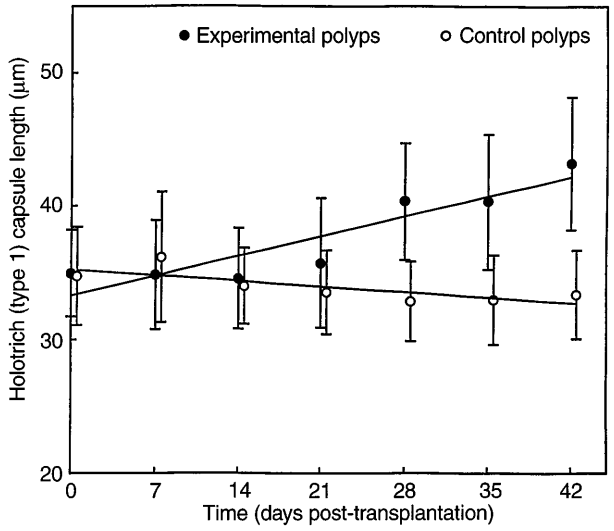

Fig. 4 *Rhodactis rhodostoma*. Changes in the capsule size of Type 1 holotrich nematocysts, in the marginal tentacle ectoderm of polyps transplanted into contact with colonies of the branching stony coral *Acropora eurystoma* (=experimental polyps), versus those transplanted onto the reef substratum but not contacting other cnidarians (=control polyps), at 2 m depth on a coral reef at Eilat, northern Red Sea (mean ± 1 SD, $N = 100$ capsules measured per sampling time in each treatment, composed of ten capsules from each of ten tentacles examined)

($r = 0.2_{(698)}$, $p < 0.05$), from 35 ± 4 μm at the time of transplantation of 33 ± 3 μm at 42 d (Fig. 4).

Finally, histological analyses of tissue sections revealed that the overall density of nematocyst capsules (count per 100 × 8 μm of ectoderm) increased 40-fold by 42 d after the start of the experiment in the marginal tentacle tips of coral-contacting polyps, whereas it remained low and constant in control, isolated polyps (Fig. 5A). Nematocysts were sparse at the start of the experiment, with only 0.4 ± 0.3 nematocysts (mean ± 1 SD) per 100 × 8 μm of ectoderm. After 42 d of interaction with the tissues of coral competitors, the ectoderm of well-developed bulbous marginal tentacles was packed with to 16 ± 3 nematocyst capsules (mean ± 1 SD) per 100 × 8 μm of ectoderm (Fig. 5A), a significant increase over time (Pearson's correlation coefficient, $r = 0.89_{(60)}$, $p < 0.05$, after $\log_{10}$ transformation of data). No such changes were seen in control polyps ($r = 0.06_{(60)}$, $p > 0.05$) (Fig. 5A). Nematocyst density remained high and constant, with large variation between individuals, in the BMTs of polyps that remained in contact with corals after 28 d (Fig. 5A). Tukey's pairwise comparison test revealed the times at which significant increases in nematocyst density occurred in the coral-contacting polyps. Three groups were extracted: (1) at Days 0, 7 and 14 post-transplantation, nematocyst densities did not differ significantly from each other; (2) nematocyst densities at 21 d were different from and intermediate to those at all other times; and (3) no significant differences in densities were found between 28, 35 and 42 d, indicating that nematocyst density had reached a high, stable level in BMTs as of Day 28.

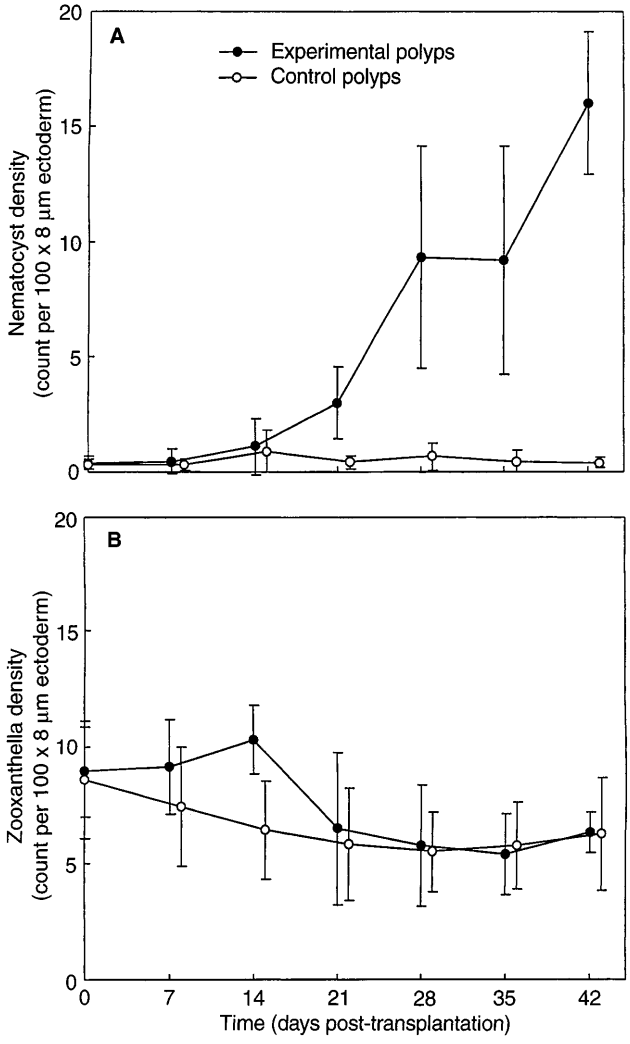

Fig. 5 *Rhodactis rhodostoma*. Changes in the density of sub-cellular components in marginal tentacle tips of polyps experimentally transplanted into contact with colonies of the stony coral *Acropora eurystoma* (=experimental polyps), versus isolated polyps transplanted onto reef substratum not in coral contact (=control polyps), at 2 m depth on a coral reef at Eilat, northern Red Sea. **A** Nematocyst density; **B** zooxanthella density (mean ± 1 SD, $N = 9$ tentacles at each sample period)

The density of zooxanthella cells in the endoderm of the above tentacles was similar to that of nematocysts in the ectoderm, at 5 to 10 cells per 100 × 8 μm of ectoderm length, and did not depend upon experimental treatment (Fig. 5B). It decreased slightly but significantly in both treatments over time (Pearson's correlation coefficients, $r = 0.539_{(61)}$, $p < 0.05$ and $r = 0.34_{(61)}$, $p < 0.05$ for experimental and control *Rhodactis rhodostoma* polyps, respectively), by about 29% in experimental polyps and 27% in control polyps (Fig. 5B).

Discussion

We demonstrate here that polyps of the tropical Indo-Pacific corallimorpharian *Rhodactis rhodostoma* develop

specialised aggressive organs along their margins during prolonged contact with some stony coral competitors. Our long-term field observations also indicate that these corallimorpharians actively damage the tissues of adjacent branching stony corals, then over >1 year slowly move onto the exposed coral skeleton, multiply via asexual reproduction, and overgrow parts of the contacted coral. These experimental results, plus previous field observations (Langmead and Chadwick-Furman 1999) may explain in part how polyps of *Rhodactis* spp. are able to monopolise patches of space on some shallow coral reefs (Ridzwan 1993; Spiegel 1998).

Our experimental manipulations confirm that the ordinarily filiform tentacles along the polyp margins of *Rhodactis rhodostoma* transform into bulbous tentacles bearing acrospheres, in response to contact with cnidarian competitors, as suggested previously (Langmead and Chadwick-Furman 1999). This is a specific response to contact with certain other cnidarians, as known for the induction of sweeper tentacles in the stony coral *Agaricia agaricites*, which takes place following contact only with several types of anthozoan competitors, and cannot be induced by artificial damage or tactile stimulation (Chornesky 1983). Nematocyst discharge by the ordinary tentacles of competitors is known to play a major role in eliciting the formation of sweeper tentacles in another stony coral, *Galaxea fascicularis* (Hidaka 1985). These studies indicate that direct tissue contact with a cnidarian competitor, potentially eliciting a histoincompatability response, is a prerequisite for such aggressive modification.

The time scale of approximately 2 weeks to first appearance (Fig. 1A) of BMTs is similar to that in the Caribbean congener *Discosoma* (=*Rhodactis*) *sanctithomae* of about 2.5 weeks (Miles 1991). This process appears to be faster than the transformation of inducible aggressive organs in some other cnidarians. The sweeper tentacles of stony corals require a few weeks to several months to develop (Lang and Chornesky 1990), and the catch tentacles of sea anemones arise over about 1 to 2 months (Purcell 1977). These time lags between initial contact with competitors and the deployment of specialised organs lead, in some cases, to a reversal in the outcome of interactions between benthic reef cnidarians (Wellington 1980; Bak et al. 1982; Chornesky 1989; Miles 1991). Among stony corals, following attack by mesenterial filament extrusion, there is a considerable time lag before the opponent counterattacks through the delayed development of sweeper tentacles (Lang and Chornesky 1990). Damage to the corallimorpharians observed here declined throughout the first month following coral contact, while damage to interacting corals increased in frequency, indicating a reversal in competitive outcome after the first 21 d of contact (Fig. 1A). Thus, the present study and that of Miles (1991) both show that short-term (less than a few weeks) outcomes of induced contacts between *Rhodactis* spp. stony corals may be the opposite of long-term results. These data support the conclusions of earlier investigators that initial competitive reactions of cnidarians are not good indicators of the final outcome of interactions between them (Bak et al. 1982; Chornesky 1989).

The morphogenesis of sweeper tentacles by the massive coral *Platygyra daedalea* observed here is the first description of the timing and induction of this process for members of this coral genus. Fully developed sweeper tentacles have been previously observed on three other species of *Platygyra* in instantaneous field observations (Hidaka et al. 1987). Thus, the ability to induce sweeper tentacles appears to be a general feature of this genus, and may largely explain the wide cnidarian-free zone that surrounds live colonies of *Platygyra* corals on reefs (Sheppard 1981; Langmead and Chadwick-Furman 1999). We show here for the first time that *P. daedalea* sweeper tentacles develop specifically in response to contact with a corallimorpharian competitor, and literally clear space around the coral by massively damaging and completely removing all corallimorpharian polyps within reach (Fig. 1B).

The aggressive reach of each benthic cnidarian species appears to largely determine its position in the hierarchy of spatial competition on reefs (Sheppard 1979, 1981). Our experimental results here confirm previous conclusions (Langmead and Chadwick-Furman 1999) that *Rhodactis rhodostoma* is dominant over stony corals that have short aggressive reaches, such as members of the family Acroporidae. The short mesenterial filaments extruded by *Acropora eurystoma* corals caused only minor damage and were ineffective once the corallimorpharians had acquired BMTs. Damage caused by BMTs appeared to increase the distance, in the form of bare coral skeleton, across which the interaction took place, potentially beyond the short reach of the *A. eurystoma* polyps (documented as <1 cm by Sheppard 1981). The damage incurred also may have affected the readiness of the coral polyps to evert mesenterial filaments, as has been suggested for other stony corals (Chornesky 1983).

In contrast, *Rhodactis rhodostoma* is subordinate to corals with relatively long aggressive reaches, such as those in the family Faviidae, including *Platygyra* spp. (Langmead and Chadwick-Furman 1999; present paper Fig. 1B). The sweeper tentacles of *Platygyra* spp. colonies appear long enough to severely damage a substantial portion of each corallimorpharian polyp, and to prevent their consistent development of BMTs. *P. daedalea* has a documented reach of 2.0 to 3.8 cm (Sheppard 1981), thus with the induction of sweeper tentacles, the coral was able to inflict damage from such a large distance that the corallimorpharian polyps could neither retaliate nor evade assault. Corallimorpharians lack basilar muscles, and thus can locomote at rates of only about 1 cm per month (Chadwick and Adams 1991), too slow to escape the long sweeper tentacles of *P. daedalea* which become fully developed in <1 month (Fig. 1B). Similarly large interactive distances occur between the polyps of *R. rhodostoma* and other faviid and mussid corals, and actinian sea anemones

(Langmead and Chadwick-Furman 1999); the latter three groups all contain species known to possess potent mechanisms of aggression (reviewed by Williams 1991). The effectiveness of specialised aggressive organs thus appears to depend mainly on their interactive reach or spatial range. The short BMTs of *R. rhodostoma* have a limited reach of < 1 cm, thus explaining the position of this species as an intermediate competitor in the aggressive hierarchy among Indo-Pacific reef-building corals (Langmead and Chadwick-Furman 1999).

Corallimorpharians in the genus *Rhodactis* appear able to dominate patches of space on some shallow coral reefs (den Hartog 1980; Ridzwan 1993; Spiegel 1998) via three complementary processes: (1) the morphogenesis of specialised aggressive organs in the form of BMTs that cause damage to a variety of contacted cnidarians (Miles 1991; Ridzwan 1993; Langmead and Chadwick-Furman 1999; present paper Fig. 1); (2) gradual movement of polyps onto the exposed skeletons of defeated coral competitors (described in "Results" above, and also for the temperate corallimorpharian *Corynactis californica* by Chadwick 1987); and (3) asexual proliferation of polyps leading to the formation of large clonal aggregations (Spiegel 1998; also documented for the congener *R. indosinensis* by Chen et al. 1995).

Our laboratory analyses revealed that complex processes at the cellular and tissue levels accompany the morphogenesis of aggressive organs in *Rhodactis rhodostoma*. These processes are similar to those known to occur during the transformation of ordinary to aggressive tentacles in other cnidarians (Purcell 1977; Watson and Mariscal 1983a; Hidaka and Yamazato 1984). We document this process for *R. rhodostoma* at three levels of organisation: in the form of increases in nematocyst density (Fig. 5A) and size (Fig. 4) at the cellular level, leading to changes in ectodermal thickness at the tissue level (Fig. 2B), and manifested at the organ level as the development of opaque, swollen acrospheres (Fig. 2A) on the tips of BMTs. In contrast to the catch tentacles of sea anemones and the sweeper tentacles of corals, which are highly extensible (den Hartog 1977; Purcell 1977; Watson and Mariscal 1983a; Hidaka and Yamazato 1984), no morphological changes take place in the marginal tentacle stalks of *R. rhodostoma* polyps to increase their length, which remains only a few millimeters. Though polyps can inflate somewhat to deploy BMTs toward target organisms, the close range nature of BMTs apparently limits the success of these corallimorpharians in competitive interactions. In previous field observations at Eilat, distances between stony corals and corallimorpharians were set by the corals, and appeared to determine the outcome of the interaction (Langmead and Chadwick-Furman 1999).

The intermediate stages observed here during transformation of BMTs from FMTs were similar to those known for developing catch tentacles in sea anemones, and sweeper tentacles in scleractinian corals (Purcell 1977; Watson and Mariscal 1983a, b; Hidaka and Yamazato 1984). At 14 d, the developing BMTs appeared visibly different from FMTs, but there was no overall increase in the density of cnidae at this stage (Fig. 5A). However, a changeover of cnida types had already begun: there was a dramatic decline in Type 2 microbasic-b-mastigophores and an accompanying increase in late stage developing cnidoblasts by 14 d (Fig. 3A). These developing nematocysts, along with precursor interstitial cells, may have migrated into the tip from the base of each tentacle. In the developing catch tentacles of the sea anemone *Halliplanella luciae*, cnidogenesis takes place in the mid and proximal (i.e. basal) regions of the tentacle, creating a cnidocyte maturity gradient along the tentacle length during transformation from an ordinary feeding tentacle (Watson and Mariscal 1983b). Once in position in the target tissue, cnidoblasts developing between the bases of ectodermal cells undergo a short vertical migration to the ectodermal surface before becoming competent cnidae (Watson and Mariscal 1983b and references therein). By 21 d, the density of cnidae had increased in BMTs (Fig. 5A), late stage cnidoblasts were still abundant, and Type 1 holotrichs had begun to increase in numbers (Fig. 3A). A similar developmental stage occurs during the morphogenesis of catch tentacles in the actinian anemone *H. luciae*, in which Stage 2 catch tentacles are characterised by the presence of many cnidoblasts, which mature eventually into holotrichs (Watson and Mariscal 1983b).

After 28 d, the development of BMTs appeared complete. The cnidom was composed of mostly Type 1 holotrichs, cnidoblasts had returned to their previously low level of abundance (Fig. 3A), and the cnidom was almost identical in nematocyst composition to BMTs previously examined from *Rhodactis rhodostoma* in natural field interactions (Langmead and Chadwick-Furman 1999). The new holotrichs in BMTs were 23% longer than those of FMTs, a characteristic also seen previously in BMTs from natural interactions (Langmead and Chadwick-Furman 1999). High abundances of holotrichs in the tissues of cnidarians are related to aggressive function (reviewed in Bigger 1988). A comparably high density of large holotrichs also occurs in the acrorhagi and catch tentacles of actinian sea anemones, and in the sweeper tentacles of scleractinians (Bigger 1988).

Interestingly, densities of zooxanthellae in the endoderm did not appear to change in response to the major re-organisation of ectoderm as FMTs transformed into BMTs (Fig. 5B). Instead, zooxanthella density decreased by up to approximately 30%, regardless of contact treatment, possibly as a result of slightly different physical conditions between the sites of collection and transplantation, which were separated by 500 m along the shore (see "Materials and methods").

All four types of developmental processes observed during the transformation of marginal tentacles occurred over the same time scale, culminating in a cessation of tissue change by 28 d after the initiation of contact (Figs. 2 to 5). This indicates that the develop-

ment of BMTs in *Rhodactis rhodostoma* is complete at all organisational levels by this time, and that this process is highly synchronised among different tissue components in the tentacles. Similar processes likely occur to create the BMTs that have been observed to occur in four congeners: *R. dawydoffi* and *R. howseii* (Ridzwan 1993), *R. indosinensis* (C.A. Chen personal communication), and *R.* (= *Discosoma*) *sanctithomae* (Miles 1991).

In summary, the marginal tentacles of *Rhodactis rhodostoma* pass through four distinct developmental stages during BMT formation: (1) recognition of certain cnidarian competitors via direct tissue contact; (2) development of visibly opaque and swollen tentacular acrospheres by 14 d post-contact, accompanied by increases in ectodermal thickness and in the proportion of developing nematocysts; (3) increased nematocyst density by 21 d after contact, as a result of the maturation and deployment of large numbers of penetrating holotrichs; and (4) the completion of tentacle transformation by 28 d, followed by continued maintenance of BMTs as long as contact with competitors persists.

Acknowledgements We thank the staff of the Interuniversity Institute for Marine Science for technical support. We also thank dive buddies A. Balderman, S. Goffredo, E. Snider and D. Torovezky for assistance during the field work, and G. Walker for help with histology. D. Glassom, R. Torres and J. Turner provided constructive criticism of the manuscript. This research was supported by a grant from the European Social Fund to OL and from Israel Science Foundation to NEC-F.

References

Bak RPM, Termaat RM, Dekker R (1982) Complexity of coral interactions: influence of time, location of interaction and epifauna. Mar Biol 69: 215–222

Bigger CH (1988) The role of nematocysts in anthozoan aggression. In: Hessinger DA, Lenhoff HM (eds) The biology of nematocysts. Academic Press, New York, pp 295–308

Chadwick NE (1987) Interspecific aggressive behaviour of the corallimorpharian *Corynactis californica* (Cnidaria: Anthozoa): effects on sympatric corals and sea anemones. Biol Bull mar biol Lab, Woods Hole 173: 110–125

Chadwick NE (1991) Spatial distribution and the effects of competition on some temperate Scleractinia and Corallimorpharia. Mar Ecol Prog Ser 70: 39–48

Chadwick NE, Adams C (1991) Locomotion, asexual reproduction, and killing of corals by the corallimorpharian *Corynactis californica*. Hydrobiologia 216/217: 263–269

Chen CA, Chen CP, Chen IM (1995) Sexual and asexual reproduction of the tropical corallimorpharian, *Rhodactis indosinensis* (Cnidaria: Anthozoa) in Taiwan. Zool Stud 34: 29–40

Chornesky EA (1983) Induced development of sweeper tentacles on the reef coral *Agaricia agaricites*: a response to direct competition. Biol Bull mar biol Lab, Woods Hole 165: 569–581

Chornesky EA (1989) Repeated reversals during spatial competition between corals. Ecology 70: 843–855

Cope M (1981) Interspecific coral interactions in Hong Kong. In: Gomez ED et al. (eds) Proc 4th int Coral Reef Symp. Vol. 2. Marine Sciences Center, University of the Philippines, Manila, pp 357–362

den Hartog JC (1977) The marginal tentacles of *Rhodactis sanctithomae* (Corallimorpharia) and the sweeper tentacles of *Montastrea cavernosa* (Scleractinia): their cnidom and possible function. In: Proc 3rd int Coral Reef Symp. Vol. 1. University of Miami Press, Miami, pp 463–469

den Hartog JC (1980) Caribbean shallow water corallimorpharia. Zool Verh, Leiden 176: 1–82

Fukui Y (1986) Catch tentacles in the sea anemone *Haliplanella luciae*: role as organs of social behaviour. Mar Biol 91: 245–251

Goldberg WM, Grange KR, Taylor GT, Zuniga AL (1990) The structure of sweeper tentacles in the black coral *Antipathes fiordensis*. Biol Bull mar biol Lab, Woods Hole 179: 96–104

Hidaka M (1985) Nematocyst discharge, histoincompatibility, and the formation of sweeper tentacles in the coral *Galaxea fascicularis*. Biol Bull mar biol Lab, Woods Hole 168: 350–358

Hidaka M, Miyazaki I, Yamazato K (1987) Nematocysts characteristic of the sweeper tentacle of the coral *Galaxea fascicularis* (Linneaus). Galaxea 6: 195–207

Hidaka M, Yamazato K (1984) Intraspecific interactions in a scleractinian coral, *Galaxea fascicularis*: induced formation of sweeper tentacles. Coral Reefs 3: 77–85

Lang JC, Chornesky EA (1990) Competition between scleractinian reef corals – a review of mechanisms and effects. In: Dubinsky D (ed) Ecosystems of the world. Vol. 25. Coral reefs. Elsevier, Amsterdam, pp 209–252

Langmead O, Chadwick-Furman NE (1999) Marginal tentacles of the corallimorpharian *Rhodactis rhodostoma*. 1. Role in competition for space. Mar Biol 134: 479–489

Loya Y, Slobodkin B (1971) The coral reefs of Eilat (Gulf of Eliat, Red Sea). Symp zool Soc Lond 28: 117–139

Mazia D, Brewer PA, Alfert M (1953) The cytochemical staining and measurement of protein with mercuric bromophenol blue. Biol Bull mar biol Lab, Woods Hole 104: 57–67

Miles JS (1991) Inducible agonistic structures in the tropical corallimorpharian, *Discosoma sanctithomae*. Biol Bull mar biol Lab, Woods Hole 180: 406–415

Purcell JE (1977) Aggressive function and induced development of catch tentacles in the sea anemone *Metridium senile* (Coelenterata, Actinaria). Biol Bull mar biol Lab, Woods Hole 153: 356–368

Ridzwan AR (1993) Recovery processes of coral communities following the crown-of-thorns starfish, *Acanthaster planci*, infestation on the east coast islands of Peninsular Malaysia. PhD thesis, University of Newcastle upon Tyne, UK

Sebens KP (1976) The ecology of Caribbean sea anemones in Panama: utilisation of space on a coral reef. In: Mackie GO (ed) Coelenterate ecology and behaviour. Plenum Press, New York, pp 67–77

Sebens KP, Miles JS (1988) Sweeper tentacles in a gorgonian octocoral: morphological modifications for interference competition. Biol Bull mar biol Lab, Woods Hole 175: 378–387

Sheppard CRC (1979) Interspecific aggression between reef corals with reference to their distribution. Mar Ecol Prog Ser 1: 237–247

Sheppard CRC (1981) "Reach" of aggressively interacting corals, and relative importance of interactions at different depths. In: Gomez ED et al. (eds) Proc 4th int Coral Reef Symp. Vol. 2. Marine Sciences Center, University of the Philippines, Manila, pp 363–368

Sheppard CRC, Sheppard ALS (1991) Corals and coral communities of Arabia. Fauna Saudi Arabia 12: 1–170

Spiegel M (1998) Sexual and asexual reproduction in the tropical corallimorpharian *Discosoma* (= *Rhodactis*) *rhodostoma* in the northern Red Sea. MSc thesis, Bar Ilan University, Ramat Gan, Israel

Veron JEN (1993) Corals of Australia and the Indo-Pacific. University of Hawaii Press, Honolulu

Watson GM, Mariscal RN (1983a) The development of a sea anemone tentacle specialised for aggression: morphogenesis

and regression of the catch tentacle of *Haliplanella luciae* (Cnidaria, Anthozoa). Biol Bull mar biol Lab, Woods Hole 164: 506–517

Watson GM, Mariscal RN (1983b) Comparative ultrastructure of catch tentacles and feeding tentacles in the sea anemone *Haliplanella*. Tissue Cell 15(6): 939–953

Wellington GM (1980) Reversal of digestive interactions between Pacific reef corals: mediation by sweeper tentacles. Oecologia 47: 340–343

Williams RB (1991) Acrorhagi, catch tentacles and sweeper tentacles: a synopsis of 'aggression' of actiniarian and scleractinian Cnidaria. Hydrobiologia 216/217: 539–545