Hydrobiologia **216/217**: 539–545, 1991.
R. B. Williams, P. F. S. Cornelius, R. G. Hughes & E. A. Robson (eds),
Coelenterate Biology: Recent Research on Cnidaria and Ctenophora.

Acrorhagi, catch tentacles and sweeper tentacles: a synopsis of 'aggression' of actiniarian and scleractinian Cnidaria

R.B. Williams
Norfolk House, Western Road, Tring, Herts. HP23 4BN, UK

Key words: Zoantharia, aggression, evolution, acrorhagi, allogeneic recognition, catch tentacles, sweeper tentacles, competition, nematocysts

Abstract

Three types of organ (acrorhagi and catch tentacles in sea anemones, and sweeper tentacles in corals) are described with regard to both morphology and 'aggressive' function. Species known to possess such organs are listed. Research on the functions of these particular organs is reviewed and some exceptions to their usual behaviour patterns are highlighted. Further research on allogeneic recognition might shed more light on the phylogeny of anemones and corals.

Introduction

All free-living organisms require space in which to live, and animals and plants have evolved a great variety of means by which they can maintain or expand it. Amongst Cnidaria, for instance, the hydroid *Hydractinia echinata* (Fleming) has evolved a size refuge from competition, whereby a colony may grow too large to be overgrown subsequently by a superior spatial competitor such as *Podocoryne carnea* (Sars), another hydroid (McFadden, 1986). A sea anemone may simply swallow another as if it were prey, or organs such as acrorhagi or catch tentacles may be used to sting, incapacitate or kill a competitor (Williams, 1975). Scleractinian corals exhibit an even wider range of options, including the simple overgrowth of colonies, extracoelenteric digestion by mesenterial filaments (Lang, 1971, 1973), contact avoidance through tissue withdrawal or secretion of a cementum wall to separate soft tissue, i.e., xenogeneic incompatibility (Hildemann *et al.*, 1975), and the use of sweeper tentacles to sting competitors (den Hartog, 1977).

These interactions may involve individuals or colonies of other cnidarians. Whether they should be variously described as aggression, defence or feeding behaviour is unclear, but generally the net result is to keep individuals or colonies separate from each other by some means. This review deals only with those forms of behaviour, usually termed 'aggressive', involving the use of one of 3 kinds of organ, viz., acrorhagi and catch tentacles which occur in 2 infraorders of anemones, and sweeper tentacles which occur in 4 suborders of hard corals. The questions arise: what differences and similarities occur in their structure and use; what are the physiological bases of their use; what selection pressures affect them; and what does study of them contribute to our knowledge of the phylogeny of the Actiniaria and Scleractinia?

Organs of 'aggression'

Organs of 'aggression' occurring in the infraorders Endomyaria and Acontiaria of the order Actiniaria (anemones) and in the order Scleractinia (corals) are usually used in interactions with other hexacorallians, and only rarely in those with members of other classes of cnidarian (Bigger, 1980).

Acrorhagi

Acrorhagi have been reported only from certain genera of anemones in the family Actiniidae (Endomyaria). When present, they occur in a circlet below the tentacle crown (Stephenson, 1928). The potential to develop them is considered a generic character, but occasional individuals of a species may still lack them. Acrorhagi are hollow sacs, their cavities continuous with the coelenteron. They can be dilated and, by movements of the column (overtopping), brought into contact with an encroaching anemone. After contact, pieces of acrorhagial ectoderm of the 'aggressor' adhere to the body of the victim whilst discharging into it the large holotrichous nematocysts ('atrichs' in the older literature) characteristic of acrorhagi (Äbel, 1954). The victim may then move away from the 'aggressor' or even detach completely from the substrate. Within a few days necrosis may ensue, sometimes causing death (Williams, 1978; Brace, 1981). The behavioural sequence usually occurs only following repeated tentacular contact with a genotypically distinct anemone: mere proximity has been held not usually to initiate the response (Francis, 1973).

The following 13 species of 5 actiniid genera have been shown to exhibit this so-called aggressive behaviour with the use of acrorhagi: *Actinia equina* (L.) (see Äbel, 1954); *Actinia tenebrosa* Farquhar (see Ottaway, 1978); *Anemonia sargassensis* Hargitt (see Bigger, 1980); *Anemonia sulcata* (Pennant) (see Sauer *et al.*, 1986); *Anthopleura elegantissima* (Brandt) (see Francis, 1973); *Anthopleura artemisia* (Pickering) (see Francis, 1973); *Anthopleura ballii* (Cocks) (see Williams, 1978); *Anthopleura xanthogrammica* (Brandt) (see Bigger, 1980); *Anthopleura krebsi* Duchassaing & Michelotti (see Bigger, 1976); *Anthopleura asiatica* Uchida & Muramatsu (see Fujii, 1987); *Bunodosoma cavernata* (*sensu* Verrill, *non* Bosc) (see Bigger, 1980); *Bunodosoma biscayensis* (Fischer) (see den Hartog, 1987); and *Phymactis clematis* (Drayton) (see Brace, 1981).

Catch tentacles

These organs occur only in the Acontiaria (Actiniaria), in certain genera of several families. They occur usually in the primary (inner) cycle of the feeding tentacles and sometimes also in the secondary and tertiary cycles. They can usually be recognized by their thick, blunt appearance when contracted, their peculiar 'searching' movements during which they extend to many times the length of the feeding tentacles, and microscopically by their holotrich nematocysts (Williams, 1975). Catch tentacles do not occur on every individual of those species known to possess them.

If a catch tentacle touches a feeding tentacle or the column of a neighbouring anemone, the tip often becomes stuck fast to it. The catch tentacle slowly retracts until a constriction appears where it breaks, just behind the tip. The victim usually contracts, retaining the detached tip of the 'aggressor's' catch tentacle, and may retreat from the 'aggressor'. Necrosis of tissue around the adhering tip may occur a day or so later, sometimes resulting in death (Williams, 1975). Catch tentacles have been recognized so far in the following 16 species, belonging to 10 genera: *Cereus pedunculatus* (Pennant) (see Gosse, 1858–59); *Diadumene schilleriana* (Stoliczka) (see Stoliczka, 1869); *Diadumene leucolena* (Verrill) (see Verrill, 1866); *Diadumene neozelanica* Carlgren (see Carlgren, 1929); *Diadumene kameruniensis* Carlgren (see Carlgren, 1929); *Diadumene cincta* Stephenson (see Stephenson, 1925); *Flosmaris bathamae* Hand (see Hand, 1961); *Habrosanthus bathamae* Cutress (see Cutress, 1961); *Haliplanella luciae* Verrill (see Williams, 1975); *Metridium senile* (L.) (see Portielje, 1933); *Sagartia elegans* (Dalyell) (see Gosse, 1858–59); *Sagartia troglodytes* (Price) (see Dalyell, 1848); *Sagartia ornata* (Holdsworth) (den Hartog, pers. comm.); *Sagartiomorphe carlgreni* Kwietniewski (see Carlgren, 1940); *Tricnidactis errans* Pires (see Pires, 1988); and *Verrillactis paguri* England (see England, 1971). These 10 genera are assigned to 6 families: *Diadumene* – Diadumenidae; *Haliplanella* and *Tricnidactis* – Haliplanellidae; *Sagartia*, *Cereus*, *Habrosanthus* and *Verrillactis* – Sagartiidae; *Metridium* – Metridiidae; *Flosmaris* – Isophelliidae; *Sagartiomorphe* – Sagartiomorphidae.

Sweeper tentacles

Sweeper tentacles occur only in the Scleractinia (hard corals). They are similar in form and general behaviour to the catch tentacles of the Acontiaria, although detachment of the tentacle tip after contact with another coral polyp does not seem to have been recorded. As with catch tentacles, sweeper tentacles do not occur on every polyp (or colony) of those coral species known to possess them. Sweeper tentacles have been observed in 13 species referred to 11 genera: *Agaricia agaricites* (L.) (see Lewis & Price, 1975); *Dichocoenia stokesi* Edwards & Haime (see Bak & Elgershuizen, 1976); *Euphyllia ancora* Veron & Pichon (see Sheppard, 1982); *Galaxea fascicularis* (L.) (see Fujita, 1983); *Madracis mirabilis* (Duchassaing & Michelotti) (see Bak *et al.*, 1982); *Madracis decactis* (Lyman) (see Chornesky, 1983); *Merulina ampliata* (Ellis & Solander) (see van Moorsel, *in* Ates, 1988); *Montastrea cavernosa* (L.) (see Lewis & Price, 1975); *Plerogyra sinuosa* (Dana) (see van Leeuwen, *in* Ates, 1988); *Pocillopora damicornis* (L.) (see Wellington, 1980); *Pocillopora robusta* Verrill (see Wellington, 1980); *Porites andrewsi* Vaughan (see Sammarco *et al.*, 1982); and *Stephanocoenia michelinii* Edwards & Haime (see Bak & Elgershuizen, 1976). The 11 genera are referred to 9 families: *Euphyllia* and *Plerogyra* – Caryophylliidae; *Merulina* – Merulinidae; *Montastrea* – Faviidae; *Galaxea* – Oculinidae; *Dichocoenia* – Meandrinidae; *Agaricia* – Agariciidae; *Pocillopora* and *Madracis* – Pocilloporidae; *Stephanocoenia* – Astrocoenidae; *Porites* – Poritidae. These families fall into 4 suborders: Astrocoeniidae and Pocilloporidae – Astrocoeniina; Faviidae, Merulinidae, Meandrinidae and Oculinidae – Faviina; Poritidae and Agariciidae – Fungiina; Caryophylliidae – Caryophylliina.

Recent research

Acrorhagi

Following Äbel's elucidation in 1954 of the function of acrorhagi in *Actinia equina*, little interest was stimulated, and Bonnin confirmed these results only in 1964. A further delay ensued until the work of Francis (1973) on *Anthopleura elegantissima*. However, this was soon followed by a succession of papers demonstrating similar behaviour in further species (Bigger, 1976, 1980; Ottaway, 1978; Williams, 1978; Brace, 1981; Sauer *et al.*, 1986). Meanwhile, studies were being carried out which showed that the so-called aggressive behaviour of anemones enables them to compete for space. This is true both of groups of clonal species such as *Anthopleura elegantissima* (see Francis, 1973) and of solitary species such as *Actinia equina* (see Brace & Quicke, 1986). Although 'aggression' usually follows contact between two genetically distinct anemones, it may occasionally occur spontaneously in *Anthopleura elegantissima* (see Francis, 1973) and *Actinia equina* (see Williams, 1978); or maybe not at all after contact, for example between *Anthopleura ballii* and *Anemonia sulcata* (see Williams, 1978), and between genetically dissimilar individuals of *Actinia tenebrosa* (see Ayre, 1982) or *Anthopleura krebsi* (see Bigger, 1980). Conspecific habituation has been demonstrated for *Anthopleura xanthogrammica* by Sebens (1984) and *Actinia equina* by Brace & Santer (1991).

Actinia equina has been used to test for waterborne compounds which might cause apparently spontaneous behaviour (R.B. Williams, unpubl.). Twenty anemones living at least 2 m apart on a beach were each collected into separate polythene bags, carefully avoiding any cross-contamination by mucus. They were subsequently each kept alone in dishes of 100 ml of artificial seawater for

24 h and then the water from each of 10 random dishes was exchanged with the water of one of the 10 remaining dishes. No resulting acrorhagial response was observed over the ensuing 3 h. Attempts were then made to evoke responses by placing fresh mucus from the 10 originally selected anemones amongst the tentacles of the 10 remaining individuals. Again, this was unsuccesful: Bigger (1976) obtained a similar result with *Anthopleura krebsi*. In *Anemonia sulcata*, however, a glycoprotein in the mucus stimulates the acrorhagial response and an alloimmune memory has been demonstrated (Sauer *et al.*, 1986).

Catch tentacles

After more than a century of chance observation on catch tentacles by various workers, P.R.G. Tranter and R.B. Williams showed that they are used in apparently 'aggressive' behaviour by *Cereus pedunculatus*, *Sagartia elegans*, *Sagartia troglodytes* and *Diadumene cincta* against other species of anemone or against genetic variants of their own species (see Williams, 1975). It was soon suggested that, by analogy with the acrorhagi of clone-forming actiniids, catch tentacles of *Metridium senile* are used to maintain interclonal segregation (Purcell, 1977). Further studies on the mixing of clones indicated that the frequency of use of catch tentacles by some individuals may decrease through ensuing habituation (Purcell & Kitting, 1982). It has also been shown that physical contact between anemones is required for catch tentacles to develop from feeding tentacles and that once they develop, unless occasional contact is maintained, they will regress. In fact, they transform from feeding tentacles and back again with concomitant changes in the nematocyst complement (Purcell, 1977; Watson & Mariscal, 1983). An attempt (R.B. Williams, unpubl.) to demonstrate the induction of catch tentacle development by water-borne compounds, by keeping 20 *Diadumene cincta* from 4 different sites individually in glass tubes closed at each end with gauze all in one 10 l tank for 20 days, was unsuccessful.

As with acrorhagial responses, further work has revealed inconsistencies in what at first seemed clear-cut behaviour of catch tentacles. Kaplan (1983) showed that in *Metridium senile* catch tentacles may not be deployed against some non-clonemates, those of the opposite sex not being attacked: indeed the non-response may increase the likelihood of successful fertilization by increasing the proximity of males to females. However, in *Haliplanella luciae*, Fukui (1986) observed no differences between catch tentacle interactions between the sexes. Furthermore, she observed that the individual deploying a catch tentacle against another is consistently the one which eventually moves away. However, Williams (1980) reported for the same species that the 'aggressor' may not move at all. A characteristic of *Haliplanella luciae* seems to be that its catch tentacles do not cause necrosis (Williams, 1980; Fukui, 1986). These recent observations show that the term 'fighting tentacle' coined by Purcell (1977) is not appropriate for all anemones.

Sweeper tentacles

Sweeper tentacles were discovered quite recently (Lewis & Price, 1975). Following den Hartog's (1977) suggestion that they might have an 'aggressive' function, Richardson *et al.* (1979) ascribed to them a defensive role in reversing scleractinian interactions involving extracoelenteric digestion. Clearly, colonial coral polyps cannot move away in response to an aggressor. Sweeper tentacles develop apparently in response to contact with digestively superior species of coral or with other Anthozoa (Chornesky & Williams, 1983; Wellington, 1980; Chornesky, 1983; Bak *et al.*, 1982; Fujita, 1983; Hidaka & Yamazato, 1984). Like most catch tentacles, sweeper tentacles of some corals cause necrosis (Chornesky, 1983; Wellington, 1980) but according to Bak & Elgershuizen (1976) they appear to impart no particular aggressive advantages to *Stephanocoenia michelinii* and *Dichocoenia stokesi* at least. Sweeper tentacles arise by transformation of feeding tentacles (Wellington, 1980), as do catch tentacles.

Discussion

Throughout the relevant literature, behaviour in which acrorhagi, catch tentacles or sweeper tentacles are used is referred to as aggressive, and indeed, most of the behavioural sequences seem to fit Carthy & Ebling's (1964) definition of aggression, although there are exceptions with all these 3 kinds of organ. However, phrases such as 'attempt to inflict damage' or 'threaten to inflict damage' (Carthy & Ebling, 1964) seem to be examples of anthropomorphism. 'Definable physiological changes' have been demonstrated in the form of changed electrical activity following cellular recognition of allogeneic protein by the acrorhagi of *Anthopleura elegantissima* (see Lubbock & Shelton, 1981). There have been some other attempts, all on actiniids, to elucidate the mechanisms of self and non-self recognition (Lubbock, 1980; Bigger, 1980; Ertman & Davenport, 1981; Sauer *et al.*, 1986) but it is not yet possible to propose a general hypothesis to explain all recorded observations. Recognition seems to be more akin to an immune response to tissue-bound antigens (see Hildemann *et al.*, 1979), perhaps involving alloimmune memory (Sauer *et al.*, 1986), than to repetitive detection of soluble free molecules as with feeding response activators (see above: unpubl. results of R.B. Williams).

Despite the structural similarity of acrorhagi and verrucae (Stephenson, 1928), Bigger (1982) considered the former to be homologues of tentacles. Catch tentacles are clearly tentacle homologues and so, if Bigger's view is accepted, acrorhagi and catch tentacles must be regarded as homologous. However, Williams (1975) considered that acrorhagi and catch tentacles are analogous and constitute a case of convergent evolution. Catch tentacles and sweeper tentacles, since they develop from feeding tentacles, are here considered to be homologous. Comparisons of the cnidomes of acrorhagi, catch tentacles and sweeper tentacles were made by Williams (1975), den Hartog (1977), and Bigger (1988) who has also reviewed the role of the nematocysts in these organs.

Future studies might profitably be directed at attempts to define any physiological changes, particularly of an electrophysiological nature, in 'aggressive' episodes, and to confirm whether allogens generally reside in surface-bound proteins or in free mucus. The latter would establish whether the broadly similar behaviours of all 3 kinds of organ have similar underlying mechanisms. The results might shed more light on the phylogeny of anemones and corals (see Hand, 1966; Schmidt, 1974).

Acknowledgements

I thank R.C. Brace, J.C. den Hartog and P.F.S. Cornelius for helpful comments on the typescript, and J.C. den Hartog for permission to use his unpublished observations.

References

Äbel, E. F., 1954. Ein Beitrag zur Giftwirkung der Aktinien und Funktion der Randsäckchen. Zool. Anz. 153: 259–268.

Ates, R. M. L., 1988. Verlengde tentakels bij tropische koralen. Zee-Aquarium 38: 4–7.

Ayre, D. J., 1982. Inter-genotype aggression in the solitary sea anemone *Actinia tenebrosa*. Mar. Biol. 68: 199–205.

Bak, R. P. M. & J. H. B. W. Elgershuizen, 1976. Patterns of oil-sediment rejection in corals. Mar. Biol. 37: 105–113.

Bak, R. P. M., R. M. Termaat & R. Dekker, 1982. Complexity of coral interactions: influence of time, location of interaction and epifauna. Mar. Biol. 69: 215–222.

Bigger, C. H., 1976. The acrorhagial response in *Anthopleura krebsi*: intraspecific and interspecific recognition. In G. O. Mackie (ed.), Coelenterate Ecology and Behavior. Plenum Press, N.Y.: 127–136.

Bigger, C. H., 1980. Interspecific and intraspecific acrorhagial aggressive behavior among sea anemones: a recognition of self and not-self. Biol. Bull. 159: 117–134.

Bigger, C. H., 1982. The cellular basis of the aggressive acrorhagial response of sea anemones. J. Morph. 173: 259–278.

Bigger, C. H., 1988. The role of nematocysts in anthozoan aggression. In D. A. Hessinger & H. M. Lenhoff (eds), The Biology of Nematocysts. Academic Press, London: 295–308.

Bonnin, J.-P., 1964. Recherches sur la 'réaction d'aggression' et sur le fonctionnement des acrorrhages d'*Actinia equina* L. Bull. biol. Fr. Belg. 98: 225–250.

Brace, R. C., 1981. Intraspecific aggression in the colour morphs of the anemone *Phymactis clematis* from Chile. Mar. Biol. 64: 85–93.

Brace, R. C. & D. L. J. Quicke, 1986. Seasonal changes in dispersion within an aggregation of the anemone *Actinia equina*, with a reappraisal of the role of intraspecific aggression. J. mar. biol. Ass. U.K. 66: 49–70.

Brace, R. C. & S.-J. Santer, 1991. Experimental habituation of aggression in the sea anemone *Actinia equina*. Hydrobiologia 216/217: 533–537.

Carlgren, O., 1929. Über eine Actiniariengattung mit besonderen Fangtentakeln. Zool. Anz. 81: 109–113.

Carlgren, O., 1940. A contribution to the knowledge of the cnidom in the Anthozoa. Acta Univ. lund. (New Ser.) 36 (3): 1–62.

Carthy, J. D. & F. J. Ebling, 1964. The natural history of aggression. Academic Press, N.Y., 449 pp.

Chornesky, E. A., 1983. Induced development of sweeper tentacles on the reef coral *Agaricia agaricites*: a response to direct competition. Biol. Bull. 165: 569–581.

Chornesky, E. A. & S. L. Williams, 1983. Distribution of sweeper tentacles on *Montastraea cavernosa*. In M. L. Reaka (ed.), The Ecology of Deep and Shallow Coral Reefs. National Office of Undersea Research, Rockville: 61–67.

Cutress, C. E., 1961. *Habrosanthus bathamae*, n. gen., n. sp. (Actiniaria: Sagartiidae) from New Zealand. Trans. r. Soc. N.Z. 1: 95–101.

Dalyell, J. G., 1848. Rare and remarkable animals of Scotland, 2. Van Voorst, London, 322 pp.

Den Hartog, J. C., 1977. The marginal tentacles of *Rhodactis sanctithomae* (Corallimorpharia) and the sweeper tentacles of *Montastrea cavernosa* (Scleractinia); their cnidom and possible function. Proc. 3rd int. Coral Reef Symp. 1: 463–479.

Den Hartog, J. C., 1987. A redescription of the sea anemone *Bunodosoma biscayensis* (Fischer, 1874) (Actiniaria, Actiniidae). Zool. Meded., Leiden 61: 533–559.

England, K. W., 1971. Actiniaria from Mururoa Atoll, Tuamoto, Polynesia. Cah. pacif. 15: 23–40.

Ertman, S. C. & D. Davenport, 1981. Tentacular nematocyte discharge and 'self-recognition' in *Anthopleura elegantissima* Brandt. Biol. Bull. 161: 366–370.

Francis, L., 1973. Intraspecific aggression and its effect on the distribution of *Anthopleura elegantissima* and some related sea anemones. Biol. Bull. 144: 73–92.

Fujii, H., 1987. The predominance of clones in populations of the sea anemone *Anthopleura asiatica* (Uchida). Biol. Bull. 172: 202–211.

Fujita, H., 1983. Induced formation and behavior of the sweeper tentacles of a scleractinian coral *Galaxea fascicularis*. Galaxea 2: 78–79.

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

Gosse, P. H., 1858–59. Actinologia Britannica. Van Voorst, London, 362 pp.

Hand, C., 1961. Two new acontiate New Zealand sea anemones. Trans. r. Soc. N.Z. 1: 75–89.

Hand, C., 1966. On the evolution of the Actiniaria. In W. J. Rees (ed.), The Cnidaria and their Evolution. Academic Press, London; N.Y.: 135–146.

Hidaka, M. & K. Yamazato, 1984. Intraspecific interactions in a scleractinian coral *Galaxea fascicularis*: induced formation of sweeper tentacles. Coral Reefs 3: 77–86.

Hildemann, W. H., C. H. Bigger & I. S. Johnston, 1979. Histoincompatibility reactions and allogeneic polymorphism among invertebrates. Transplant. Proc. 11: 1136–1141.

Hildemann, W. H., D. S. Linthicum & D. C. Vann, 1975. Transplantation and immunoincompatibility reactions among reef-building corals. Immunogenetics 2: 269–284.

Kaplan, S. W., 1983. Intrasexual aggression in *Metridium senile*. Biol. Bull. 165: 416–418.

Lang, J. C., 1971. Interspecific aggression by scleractinian corals. I. The rediscovery of *Scolymia cubensis* (Milne Edwards and Haime). Bull. mar. Sci. 21: 952–959.

Lang, J. C., 1973. Interspecific aggression by scleractinian corals. II. Why the race is not only to the swift. Bull. mar. Sci. 23: 260–279.

Lewis, J. B. & W. S. Price, 1975. Feeding mechanisms and feeding strategies of Atlantic reef corals. J. Zool., Lond. 176: 527–544.

Lubbock, R., 1980. Clone-specific cellular recognition in a sea anemone. Proc. natn. Acad. Sci. U.S.A. 77: 6667–6669.

Lubbock, R. & G. A. B. Shelton, 1981. Electrical activity following cellular recognition of self and non-self in a sea anemone. Nature, Lond. 289: 59–60.

McFadden, C. S., 1986. Laboratory evidence for a size refuge in competitive interactions between the hydroids *Hydractinia echinata* (Flemming) and *Podocoryne carnea* (Sars). Biol. Bull. 171: 161–174.

Ottaway, J. R., 1978. Population ecology of the intertidal anemone *Actinia tenebrosa*. I. Pedal locomotion and intraspecific aggression. Aust. J. mar. freshwat. Res. 29: 787–802.

Pires, D. de O., 1988. *Tricnidactis errans* n. gen., n. sp. (Cnidaria, Actiniaria, Haliplanellidae) from Guanabara Bay, Rio de Janeiro, Brazil. Revta bras. Biol. 48: 507–516.

Portielje, A. F. J., 1933. On a remarkable and purposive feeding behaviour in the sea-anemone *Diadumene cincta* Stephenson, a short note on *Metridium senile* var. *pallidum* (Holdsworth) and *Anthopleura thallia* (Gosse), also until now unknown on the Dutch shore, and a list of Dutch Actiniaria. Tijdschr. ned. dierk. Vereen. (Ser. 3) 3: 132–144.

Purcell, J. E., 1977. Aggressive function and induced development of catch tentacles in the sea anemone *Metridium senile* (Coelenterata, Actiniaria). Biol. Bull. 153: 355–368.

Purcell, J. E. & C. L. Kitting, 1982. Intraspecific aggression and population distributions of the sea anemone *Metridium senile*. Biol. Bull. 162: 345–349.

Richardson, C. A., P. Dustan & J. C. Lang, 1979. Maintenance of living space by sweeper tentacles of *Montastrea* *cavernosa*, a Caribbean reef coral. Mar. Biol. 55: 181–186.

Sammarco, P. W., J. C. Coll & S. La Barre, 1982. Competition between soft corals (Octocorallia) and scleractinian corals: species-specific allelopathy. Aust. mar. Sci. Bull. 79: 21.

Sauer, K. P., M. Müller & M. Weber, 1986. Alloimmune memory for glycoproteid recognition molecules in sea anemones competing for space. Mar. Biol. 92: 73–79.

Schmidt, H., 1974. On evolution in the Anthozoa. Proc. 2nd int. Coral Reef Symp. 1: 533–600.

Sebens, K. P., 1984. Agonistic behavior in the intertidal sea anemone *Anthopleura xanthogrammica*. Biol. Bull. 166: 457–472.

Sheppard, C. R. C., 1982. Coral populations on reef slopes and their major controls. Mar. Ecol. Prog. Ser. 7: 83–115.

Stephenson, T. A., 1925. On a new British sea anemone. J. mar. biol. Ass. U.K. 13: 880–890.

Stephenson, T. A., 1928. The British sea anemones, 1. Ray Society, London, 148 pp.

Stoliczka, F., 1869. On the anatomy of *Sagartia schilleriana* and *Membranipora bengalensis*, a new coral and a bryozoan living in brackish water at Port Canning. J. Asiat. Soc. Bengal 38: 28–63.

Verrill, A. E., 1866. On the polyps and echinoderms of New England with descriptions of new species. Proc. Boston Soc. nat. Hist. 10: 333–357.

Watson, G. M. & R. N. Mariscal, 1983. The development of a sea anemone tentacle specialized for aggression: morphogenesis and regression of the catch tentacle of *Haliplanella luciae* (Cnidaria, Anthozoa). Biol. Bull. 164: 506–517.

Wellington, G. M., 1980. Reversal of digestive interactions between Pacific reef corals: mediation by sweeper tentacles. Oecologia 47: 340–343.

Williams, R. B., 1975. Catch-tentacles in sea anemones: occurrence in *Haliplanella luciae* (Verrill) and a review of current knowledge. J. nat. Hist. 9: 241–248.

Williams, R. B., 1978. Some recent observations on the acrorhagi of sea anemones. J. mar. biol. Ass. U.K. 58: 787–788.

Williams, R. B., 1980. A further note on catch-tentacles in sea anemones. Trans. Norfolk Norwich Nat. Soc. 25: 84–86.