Petersen, K.

A REVIEW OF INTRA- AND INTERSPECIFIC AGGRESSION AMONG SEA ANEMONES

by

KRISTINE K. PETERSEN

A CRITICAL ESSAY

Presented to the Department of Biology
of the University of Oregon
in partial fulfillment of the requirements
for the degree of

Master of Science

March 1989

Approved: [redacted] ________

ACKNOWLEDGMENTS

The author expresses sincere appreciation to Dr. Jan Hodder and Dr. James Carlton for their guidance throughout my graduate career. I also thank my good friends John Megahan, Gina and Eduardo Gomez-Cornejo and Brenda Thomas for their unending encouragement. Special thanks to Dr. Robert Terwilliger for his part in the completion of this paper. Through his death I have learned a lot about life.

TABLE OF CONTENTS

Chapter Page

I. INTRODUCTION 1

II. MORPHOLOGY 3

Organs of Aggression 3

III. BEHAVIOR 9

Actiniid Sea Anemones 9

Acontiarian Sea Anemones 13

IV. RECOGNITION 15

Mucus Antigenicity 15

Surface Bound Receptors 18

Pheromones 19

V. POPULATION DYNAMICS 20

Dominance 20

Reproductive Strategy 23

Competition for Space 24

VI. FUTURE RESEARCH 28

REFERENCES 30

LIST OF TABLES

Table Page

1. Sea anemones that display aggressive behavior 2

2. Types of nematocysts found in Anthozoans 4

INTRODUCTION

This paper reviews the current knowledge of aggressive behavior in sea anemones (Anthozoa), considering the type of organs used in aggression and the lifestyles of the sea anemones involved. The mechanisms involved in the recognition of related anemones and the role of aggression in structuring populations are also addressed.

Lifestyles of sea anemones vary from living within large colonies of genetically indentical individuals such as *Anthopleura elegantissima*, to solitary individuals living out of contact with any other anemones, as does *Anthopleura xanthogrammica*. *Metridium senile* commonly lives in aggregations of genetically dissimilar animals. The role of intra- and interspecific aggressive interaction may differ according to the lifestyle of the species. The species that have been reported exhibiting aggressive behavior are listed in Table 1.

Table 1: Sea Anemones that display aggressive behavior

a) ENDOMYARIA

Actinia equina
Anemonia sargassensis
Anthopleura elegantissima
Anthopleura xanthogrammica
Anthopleura artemisia
Phymactis clematis
Actinia tenebrosa
Anemonia sulcata
Anthopleura krebsi
Anthopleura balli
Bunodosoma cavernata

b) ACONTIARIA

Cereus pedunculatus
Diadumene leucolena
Diadumene kameruniensis
Diadumene lineata
Habrosanthus bathanae
Sagartia elegans
Sagartia erthrochila
Sagartiomorphe carlgreni
Diadumene schilleriana
Diadumene neozelanica
Diadumene cincta
Flosmaris bathamae
Metridium senile
Sagartia troglodytes
Sagartiogeton undatus
Verrillactis paguri

MORPHOLOGY

Organs of Aggression

Behavioral experiments demonstrating that sea anemones are capable of complex behavioral responses to external stimuli began in the early 1900's (Jennings, 1905, Hargitt, 1907). In 1954 Abel first noted aggressive behavior in sea anemones (Williams, 1978). Since then, the presence of certain specialized organs, such as acrorhagi and catch tentacles, has been shown to add to the aggressive behavioral repertoire of some sea anemones.

Acrorhagi

Acrorhagi are distinct organs found only in members of the family Actiniidae. Not all actiniid anemones possess acrorhagi but all species with acrorhagi have been observed in aggressive encounters with other anthozoans. These organs, located in a groove just below the tentacles, are morphologically more similar to tentacles than to verrucae, the adhesive organs found on the column of sea anemones (Bigger, 1982). Internally, acrorhagi are continuous with the coelenteron.

To further understand acrorhagi it is helpful to examine their morphology more closely. This involves examination of the special cells, cnidocytes, found in all coelenterates. The type, proportion and arrangement of these specialized cells constitute the cnidom of each organ in the sea anemone. They are round or oval cells embedded within the epidermis that contain an encapsulated organelle called a cnida. One end of the cnidocyte has a tripartite series of apical flaps that open when stimulated. Stimulation can be either chemical or mechanical. Hydrostatic pressure then causes the capsule to explode and evert the cnida (Barnes, 1980).

Classification of the cnidocytes is based on the structure of the cnidae (Mariscal, 1974). Nematocysts are one type of cnidocyte found in sea anemones. The base of the cnida thread is typically enlarged and referred to as the shaft portion of the thread. The shaft may have spines in different sizes and configurations. The thread may differ considerably in diameter, occurrence of spines, and length. Several types of nematocysts are found in anthozoans (Table 2).

Table 2: Types of nematocysts found in Anthozoans (Mariscal, 1974; Bigger, 1982; Watson and Mariscal, 1983).

Holotrichous isorhiza - Thread has uniform diameter from base to tip. Spines are found along the total thread length.

Basitrichous isorhiza - Thread has uniform diameter from base to tip. Spines located only at the thread base.

Atrichous isorhiza - Uniform diameter along thread with no spines on shaft or thread.

Microbasic amastigophore - Large diameter thread with spines found along the total thread length.

Microbasic mastigophore - Well developed shaft that taper abruptly into threads. Spines along total thread length.

Another type of cnidocyte commonly found in sea anemones are spirocysts. These adhesive cells are found in tentacles and verrucae. The capsule walls of spirocysts are very thin. The long spineless threads are covered with adhesive tubules (Watson and Mariscal, 1983).

Comparision of the cnidom, the nematocysts and spirocyst, of tentacles and acrorhagi was done for *Anthopleura krebsi* (Bigger, 1976). Tentacles possess basitrichous isorhazi nematocysts and spirocysts in roughly equal proportions. The cnidom of acrorhagi is made up of atrichous isorhazi nematocysts and large spirocysts. Nematocysts outnumber the spirocysts in acrorhagi. The stem of the acrorhagi contains many secretory cells and few nematocysts. The cnidom of other actiniid species is similar (Hand, 1955; Mariscal, 1974; Williams, 1978; Bigger, 1976). Ciliary cones are often found in association with nematocysts (Barnes, 1980). Ciliary cone complexes are found in conjuction with nematocysts in both acrorhagi and tentacles. The function of these cones is not completely understood. It is thought that they act as mechanical receptors and play a role in nematocyst discharge.

The number, size and color of acrorhagi vary among and within species. For example, A. elegantissima individuals located on the edge of a colony have more and larger acrorhagi than those individuals in the center of the colony (Francis, 1973b). Acrorhagi are used exclusively for aggression towards other anthozoans. They remain flaccid and inconspicuous when the anemone is not involved in an aggressive conflict. At the onset of an aggressive encounter the acrorhagi nearest the region of stimulation become swollen and extend toward the opponent.

Catch Tentacles

Anemones from several different families of the subtribe Acontiaria possess catch tentacles. Catch tentacles are modified feeding tentacles capable of enormous enlargement in terms of both diameter and length (Purcell, 1977). The change from feeding tentacle to catch tentacle in Diadumene lineata has been described in three stages (Watson and Mariscal, 1983a).

> Stage 1. intermediate catch tentacle, histolgically similiar to feeding tentacles, but with swollen bulb-like regions along the length of the tentacle.
> Stage 2. tentacles tapered normally and then begin to constrict near the tip, cnidom begins to show changes.
> Stage 3. additional small holotrichs and many large holotrichs begin to appear.

The cnidom of catch tentacles is radically different than that of feeding tentacles (William, 1975). Catch tentacles have holotrichs, atrich and microbasic amastigophores while feeding tentacles have mostly spirocysts, and microbasic mastigophores, with a few basitrichs at the tentacle-oral disk interface (Purcell, 1977; Williams, 1975).

The presence of catch tentacles is not consistent within species. Populations of M. senile from the west coast of North America that have been examined show developed catch tentacles consistently (Kaplan, 1983). Metridium senile from the east coast of North America, however, do not show catch tentacle development consistently. Metridium senile north of the Shark River, New Jersey, have catch tentacles, whereas those south of the Shark River have never been reported to have them. To explain this phenomenon it is hypothesized that the southern population is a monoclonal population or that genetic diversity is very low. Thus the population does not show aggressive behavior and does not need catch tentacles. Electrophoretic examinations of fifty-one individuals from the southern population revealed that there were thirty-three distinct genotypes, thus the low diversity hypothesis was not supported (Kaplan, 1983).

Ambient temperature affects the development of catch tentacles. Metridium senile individuals from California bearing catch tentacle were maintained in the laboratory at 21 degrees centigrade. At temperatures above 20 degrees centigrade catch tentacles atrophied due to the increased metabolic demands of animals living at higher temperatures (Kaplan, 1983). Temperature may influence the occurrence of catch tentacles in North American populations south of the Shark River. Further experimentation is needed to fully understand the reason populations in southern North America lack catch tentacles.

Unlike the acrorhagi of actiniid sea anemones which are found deflated on all individuals and may be utilized in aggression immediately after initial contact with another anemones, catch tentacles are modified feeding tentacles and take several weeks to form. Metridium senile forms complete catch tentacles in nine weeks in the laboratory (Purcell, 1977). This time delay in the occurence of aggressive behavior may enable acontiarian anemones to live in non-clonal aggregations. In these large groups contact between individuals may occur infrequently and therefore no catch tentacles develop and co-habitation is possible. A more plausible explaination of the grouping seen in some acontiarian sea anemones is a a limited ability to habituate to non-clonal contact. Anemones that do develop catch tentacle use them as long 'sweepers'. When an unwanted neighbor is encountered the catch tentacle reacts as described above.

BEHAVIOR

The aggressive behavior sequence of actiniid anemones is different from that of acontiarian by virtue of the different organs involved, necessitating the examination of the behavior of each group separately.

Actiniid Sea Anemones

Actiniid anemones frequently live in large clonal aggregations, and also commonly occur as solitary individuals; rarely are they found in non-clonal aggregations. Individuals from one colony are assumed to be of indentical genetic make-up, whereas individuals from colonies well spaced in the intertidal or with slight differences in coloring or stripe patterns are assumed to be genetically dissimilar.

All species possessing acrorhagi have been observed participating in aggressive contests (Bigger, 1980). When clonal individuals are brought into contact no reactions ensue. The tentacles intermingle freely and no attempt to avoid contact is made by either anemone. A review of the literature on intra- and interspecific aggression in acrorhagial sea anemones led to a synthesized description of the behavior of unrelated individual sea anemones when in contact into three general responses (Bigger, 1980):

1) after several tentacular withdrawls, the tentacles of the two anemones interlaced and each animal treated the other as an inert object;

2) one or both anemones avoided contact with the other individual;

3) the acrorhagial response was initiated by one or both anemones.

The first possible response rarely occurs. In cases where no aggressive reaction occur the individuals may have similar genetic markers and may not be able to identify the other anemone as a non-clonmate. The second response is common in only two species, *Anemonia sargassensis* and *Anemonia sulcata*.

The acrorhagial response in Actiniid anemones involves a series of behaviors. This response is similar in all actiniid species (Bigger, 1976; Brace *et al*. 1979; Brace, 1981; Ottaway, 1978). The following is a description of the five phases that constitute the acrorhagial response (Francis, 1973b).

> (1) STIMULATION (or initiation), during which the tentacles of the two anemones repeatedly come into contact and withdraw from contact,
> (2) INFLATION, during which the acrorhagi commence to become turgid,
> (3) APPLICATION, during which the inflated acrorhagi are pushed toward the source of stimulation,
> (4) ECTODERMAL PEEL, during which damage is inflicted on another anemone,
> (5) RECOVERY, during which the anemone returns to its normal posture.

Contact of two anemones usually involves the movement of one individual into contact with another. The initiation of the acrorhagial response depends on the recognition or lack of recognition of one anemone to another. Observations of the behavior following an aggressive encounter differs between and within species.

Commonly, on completion of the acrorhagial attack the loser of the encounter moves away from the other anemone (Ottaway, 1978). Another possible reaction of the losing anemone is avoidance without pedal locomotion. An anemone may remain closed or bend away from the winner thus avoiding further contact. This response occurs in three species, the clonal form of A. elegantissima, Actinia equina, and Phymactis clematis (Francis, 1973a,b; Brace et al., 1979; Brace, 1981).

The completion of the initial acrorhagial response may intitiate a retaliatory acrorhagial response by the victim. Encounters of this type have been observed between Actinia equina, Actinia tenebrosa and Phymactis clematis (Brace et al., 1979; Ottoway, 1978; Brace, 1981). After the retaliation, the initial aggressor may respond with a third acrorhagial attack. Usually following the third response one anemone avoids further contact by bending away or moving out of range from tentacular contact. Occasionally a 'stalemate' results where both anemones remain open. A few instances of possible habituation have been reported for Anthopleura balli and A. xanthogrammica

(Brace *et al.*, 1979). Some experiments have suggested that the acrorhagial response in *A. krebsi* can be influenced by prior experience (Bigger, 1980). This suggestion opposes the earlier findings of Ottoway (1978) in which no evidence of a learned avoidance due to repetitive contact with a particular individual occurred in *Actinia tenebrosa*.

Aggressive encounters in the laboratory can result in the complete detachment of the losing individual. This has been shown with *Phymactis clematis* (Brace, 1981). Similar results have been obtained with *A. equina* (Brace *et al.*, 1979). The occurrence and importance of detachment in natural populations are virtually impossible to assess.

Some anemones show unique responses to attack. For example, *P. clematis* exhibits a 'full attack' (Brace, 1981). This consists of the retraction of all tentacles, inflation and pulling together of all acrorhagi. *Phymactis clematis* then bends towards the opponent and strikes with all of the acrorhagi simultaneously. In some species this complete acrorhagial response is not exhibited. For example, *Anemonia sargassensis* and *A. sulcata* do not complete the acrorhagial attack. After stimulatory contact *A. sulcata* avoids further contact by bending its column away or moving via pedal locomotion out of tentacular contact from the opposer (Dorsett and Turner, 1986). The acrorhagi of *A. sargassensis* inflate following contact but no application behavior has been observed. Interestingly, laboratory manipulation with tentacles from *A. krebsi* or *Bunodosoma cavernata* when brought into contact with a turgid *A. sargassensis* acrorhagus will elicite an ectodermal peel. Most often *A. sulcata* and *A. sargassensis* repond to stimulation by bending away or moving out of contact with the other anemone.

Acontiarian Sea Anemones

The first observations of catch tentacles led investigators to believe that they might aid in feeding (Williams, 1975), although no studies were conducted to show this to be the case. Later it was discovered that the main role of these tentacles is in intra- and interspecific aggression (Williams, 1975; Williams, 1978).

Observations of an assemblage of anemones of three different species, *M. senile*, *Sagartia troglodytes* and *Diadumene lineata* (*Haliplanella luciae*) confirmed the role of catch tentacles in interspecific aggression (Williams, 1980). Individuals located together on one rock were transported by excavating the entire rock and reloacting the rock to a laoboratory tank for observation. On the seventy-eighth day of observation, one catch tentacle of a *D. lineata* was observed touching the tentacles of a *M. senile*. After two seconds the *M. senile* tentacles grasped the *D. lineata* catch tentacle as if it were prey. Ten seconds later the *M. senile* contracted swallowing the catch tentacle with its own tentacles still visible. The D. lineata catch tentacle slowly contracted and broke off the tip about one minute later; at this time the M. senile tentacles writhed vigorously. Fifteen minutes later two other catch tentacles of D. lineata became active and repeated the sequence. During this second sequence it took approximately six minutes before the catch tentacle severed in the contracted M. senile (Williams, 1980). This is the first observation of the use of catch tentacles in interspecific aggression. More work is needed to substantial the impact of interspecific aggression on a larger scale.

The general aggressive behavior of acontiarian sea anemones consists of catch tentacles 'patroling' the area surrounding the anemone. When contact is made with an unfamiliar anemone the catch tentacle tip sticks to the neighboring anemone. The 'victim' of the attack pulls away sharply. The adherence of the catch tentacle tip and the reaction of the victim anemone are indications of nematocyst discharge. The catch tentacle tip is severed and remains attached to the 'victim' anemone. Within hours of the encounter an area of necrosis appears where the injury occurred.

RECOGNITION

The recognition capabilities of sea anemones are quite remarkable. These organisms are able to determine how genetically similar another individual is to itself with just a few seconds of contact. The mechanisms involved in this acute recognition system are not understood. However several theories have been explored.

Mucus Antigenicity

One possible mechanisms is a component or components of the mucus secreted by each sea anemone (Lubbock, 1979a). It is expected that the composition of the mucus would vary from species to species and seems likely that some components would vary among genetically dissimilar individuals. The role of mucus antigenicity in the recognition within and among species was explored using three species of sea anemones: Gyrostoma hertwigi, Stoichactis haddoni (Stichodactyla haddoni), and Radianthus ritteri. Mucus composition is different among these species but rather similar within species (Lubbock, 1979a). Work with A. elegantissima aimed at locating the causal substance in clonal recognition demonstrated that mucus does not provide the necessary information about genetic relationships. Mucus from non-clonemate conspecifics did not elicit nematocysts discharge; however, the tentacles were withdrawn. The withdrawal of tentacles indicates that the anemones recognize the mucus as non-clonal. Whether or not the anemones can recognize it as conspecific mucus rather than some other foreign stimuli is not known. Nematocyst discharge did occur when tissue contact was made. A particularly interesting response was generated between A. elegantissima and A. xanthogrammica. Mucus from A. xanthogrammica was applied to A. elegantissima. A slight nematocyst discharge resulted. In contrast, mucus from A. elgantissima caused heavy nematocyst discharge in A. xanthogrammica. The reason for A. elegantissima accepting A. xanthogrammica mucus and not visa versa is unknown. It is suggested that A. elegantissima is buffered against the causal substance in the A. xanthogrammica mucus while A. xanthogrammica lacks this buffering capability (Ertman and Davenport, 1981). The conclusion that mucus is not a causal substance in recognition among sea anemones has been repeatably demonstrated (Bigger, 1976; Lubbock, 1979a,b, 1980; Ertman and Davenport, 1981).

Recent experiments involving manipulated samples of mucus did not confirm the results of earlier studies (Sauer et al., 1986). This study was aimed at identifying an immunological recognition system within the mucus of sea anemones. For a system to be considered immunological three criteria (outlined by Hildemann et al. as cited by

Sauer et al. 1986) must be met. These criteria are: (1) The existence of antagonistic reactions (2) specific reactivity and (3) selectively altered reactivity upon renewed contact (inducible memory). This study suggested that the substances capable of triggering the acrorhagial response were free components of the mucus (Sauer et al. 1986). One of the treatments led to the conclusion that the effector molecules must be proteins, while another treatment suggested that the effector molecules are glycoproteins. While isolated glycoprotein can trigger an acrorhagial response, it does not trigger the ectodermal peel phase of the behavior. They suggest that there may be several effector components involved in the culmination of the complete behavior. One concern with Sauer et al.'s study is that the methods used to prepare the mucus solutions before presenting it to a sea anemone were designed to separate the mucus into components. This consisted of excising tentacles and then freezing them in liquid nitrogen. After thawing and centrifuging to remove tissue the resulting liquid was assumed to be pure mucus. It is possible that centrifuging the tentacle tissue with the mucus might cause some tentacular cells to burst, and the cellular fluid would contaminate the mucus. They also report that after repeated contacts the response time is shortened.

Overall, Lubbock (1979a), Ertman and Davenport (1981), and Sauer *et al*. (1986), suggest that mucus might aid in recognition of individuals at the interspecific level. Yet, mucus is not the causal substance in the intraspecific recognition of sea anemones.

Surface Bound Receptors

Another possible recognition mechanism is that of a surface bound substance. This theory suggests that the effectors and receptors are integrated in the tissue rather than being suspended in the mucus. This would necessitate actual contact between individuals to invoke a reponse. Work with *A. krebsi* and *A. elegantissima* suggested that clonal recognition depends upon genetically determined chemical markers in the surface membrane of the epithilial cells (Bigger, 1976; Lubbock, 1980). These markers are assumed to differ between clones except in rare cases where non-clones may have similar markers.

Observations and experiments focusing on the components, receptors and eliciting factor(s) of the acrorhagial response in *A. krebsi* were performed with naturally occurring groups of individuals (whose genetical relatedness was unknown). Contests with clonal anemones yielded no acrorhagial responses. In 98% of the trials involving non-clones an aggressive encounter ensued

(Bigger, 1976). This implies that the effectors and receptors are part of the tissue.

Pheromones

The chemical structure of what was termed an alarm pheromone of A. elegantissima has been isolated (Howe and Sheikh, 1975). The pheromone was discovered when anemones of a single clone were held in the laboratory in an arrangement such that six individuals were held in each of twenty-four bowls and the bowls were stacked four high. Sea water flowed into the top bowl and then drained down to the lower bowls. When one anemone in a top bowl was damaged the other anemones in the bowl reacted in a series of one to four rapid convulsive radially symmetrical flexures of the tentacles toward the base of the column. A few seconds later the anemones in bowls below the injured anemone acted in the same way. Isolated samples of the pheromone did not evoke the typical acrorhagial response of aggressive behavior and its role if any in aggressive encounters has not yet been determined.

POPULATION DYNAMICS

Dominance

The characteristics which allow one individual to dominate over another are not yet clear. Several studies have explored possible characteristics, including color and individual size, to explain this phenomenon of dominance.

Color

Several species exhibit distinct color varieties. Actiniid sea anemones such as *Actinia equina* and *Phymactis clematis* are found in at least two distinguishable color morphs. The pedal disks of *A. equina* are found ranging in color from dark red to pink in upper and middle intertidal regions, and with a grey to green color in the lower intertidal zone. This color variation is due to allelic differences at two enzyme loci (Donoghue *et al*. 1985). The acrorhagi of individuals within each color morph varies from lightly colored to prominently colored. The sea anemones with dark red pedal disks dominate over individuals with light red-pink pedal disks; however, it is difficult to accurately separate dark red and red-pink anemones visually in the field. Therefore, they are considered one color morph. Aggressive encounters between individuals from the red-pink morph and the grey-green morph indicate that the red-pink morph is dominant (Brace et al., 1979; Donoghue et al., 1985). While the segregation of color morphs in the intertidal may be the result of this dominance heirarchy this has not been explicitly explored.

The three color morphs of P. clematis from Chile are categorized as red/brown, green and blue. Phymactis clematis has a similar littoral distribution of color morphs as A. equina. Red/brown and green anemones live in the upper-middle region of the intertidal and the blue morph is found in the lower zone. This similarity suggests that a difference in aggressiveness is present among the color morphs. Surprisingly, this is not the case. The three color morphs of P. clematis are equally aggressive (Brace, 1981). The different distributions of these color morphs have not been explained.

A unique response occurs in Anemonia sulcata which has two color morphs. Segregation of the brown and green color morphs occurs in the laboratory if nonclonal anemones are placed together in a group (Dorsett and Turner, 1986). This segregation consists of a 'distancing' response whereupon the anemone moves at an average speed of 7-11 cm an hour resulting in separation of up to 64 cm. A group of non-clonal individuals with similar color move out of tentacular contact at an average speed of 1-3 cm an hour. This spacing behavior of the two color morphs occurs without the completion of the acrorhagial response described earlier. In this species the green color morph is dominant. Actinia sulcata occupies a limited intertidal zone and does not display the vertical zonation found in Actinia equina and Phymactis clematis (Dorsett and Turner, 1986; Brace et al., 1979; Brace, 1981, Brace and Quick, 1985).

These studies have shown that a dominance heirarchy based on color morphology does exists in three of the four species examined. This is not the only factor contributing to the intertidal distribution of individuals but may account for the vertical zonation of the color morphs of Actinia equina.

Size Related Aggression

The color variety experiments also suggest that anemone size is a key factor in dominance (Brace and Pavey, 1978; Brace et al., 1979; Brace, 1981; Donoghue et al., 1985). During the color variety experiments of A. equina reviewed above, larger individuals attacked before smaller opponents and subsequently won encounters (Brace et. al., 1979). Brace and Pavey (1978) concluded that during the initial contact the anemones are able to 'size-up' each other. The mechanism(s) by which this occurs have not been discovered.

Subsequent experiments by Brace (1981) led to the re-evaluation of the previous conclusions. He found that anemones do not 'size-up' their opponent, but react by means of a physiological response. This aggressive response is dependent on a lowering of reaction threshold with an increase in anemone size. The outcome of encounters are completely size dependent (Brace, 1981). Larger individuals have a lower reaction threshold, hence, initiate attack and win the encounter.

Reproductive Strategy

Kaplan (1983) explored the relationship between intraspecific aggression and reproductive strategy. An anemone's position relative to members of the opposite sex effects its ability to reproduce successfully. The extent of information acquired through tentacular contact between two sea anemones is not known. Kaplan states it may be possible for Metridium senile to identify members of the opposite sex. Experiments were conducted with catch tentacle bearing M. senile from Monterey, California. Aggression between anemones was observed only between non-clonal individuals of the same sex.

The use of aggression as a reproductive strategy in the actiniid sea anemone Anthopeura xanthogrammica has been dismissed as a possible motive for associations of genetically distinct individuals (Sebens, 1984).

Competition for Space

In many marine environments suitable space is almost always limited. The chief cause for aggressive behavior in sea anemones is competition for space (Francis, 1976; Sauer, *et al.*, 1986; Ayre, 1983; Brace and Quick, 1985; Jackson, 1977; Ottaway, 1978; Purcell and Kitting, 1982; Russo, 1984; Sebens, 1982). The role that inter- and intraspecific aggression plays in population dynamics has been studied extensively in actiniid sea anemones. Relatively few papers have discussed how it effects acontiarian population dynamics.

Acontiarian Sea Anemones

Metridium senile is one of two acontiarian species in which the role of inter- and intraspecific aggression in population dynamics has been investigated (Purcell and Kitting, 1982; Purcell, 1977; Fukui, 1986).

The subtidal population distribution of *M. senile* was examined by Purcell (1977). She found aggregations of clonal individuals with marked separations between colonies. The individuals on the colony edges possess catch tentacles. Aggregations of nonclones were also observed but in this cases all anemones had catch tentacles. Populations of *M. senile* colonies bordered by colonies of Anthopleura elegantissima were observed in which no anemone-free zone existed but the M. senile had catch tentacles. Contact with nonclonal conspecifics usually resulted in an aggressive response. Contact with A. elegantissima always led to a violent response on the part of M. senile (Purcell, 1977).

Subsequent studies of similar populations were done to determine if population distribution in Metridium senile is stable (Purcell and Kitting, 1982). Sites with groups of genetically identical animals, two or more clones intermingling and two or more clones in close proximity but not touching were followed. As expected the colonies consisting of one clone did persist. The other configurations also persisted. This was attributed to habituation to nonclonemated contact. This is the first report of habituation between non-clonemates.

A single study of the role of catch tentacles in population dynamics was done with the species Diadumene lineata (= Haliplanella luciae) (Fukui, 1986). The results concure with those of early M. senile studies (Purcell, 1977), but they do not suggest habituation to non-clonemates.

Actiniid Sea Anemones

The majority of work exploring inter- and intraspecific aggressionn among sea anemones has been done with actiniid sea anemones. However, most work on inter- and intraspecific aggression concerns relatively few species. The population dynamics of *Anthopleura elegantissima* and *Actinia tenebrosa* have been investigated particularly thoroughly (Francis a,b 1973, 1976, 1979; Ottaway, 1978; Ayre, 1982, 1983, 1984, 1987).

Colonies of *Anthopleura elegantissima* occupy large areas in the middle intertidal zone. Intraspecific aggression enables A. *elegantissima* to maintain anemone-free zones between colonies (Francis a,b, 1973, 1976). *Anthopleura elegantissima* is sometimes found living out of contact with other individuals. This solitary lifestyle produces larger anemones. The vertical range of solitary *A. elegantissima* is narrower and overlaps the range of the colonial form. It has been suggested that these two forms are sibling species (Frances, 1979). The congener, *A. xanthogrammica*, is found throughout the range of *A. elegantissima*. Examination of the intertidal locations of each species suggests that the two species compete for space (Frances, 1979). *Anthopleura xanthogrammica* is a large, solitary species. Intraspecific competition in this species is rare (Russo, 1984).

The solitary anemone *Actinia tenebrosa* reproduces both asexually and sexually. Asexual reproduction is via brooded young (Ayre, 1984). As the clonal young mature, they move out of contact with the parent; thus do not form colonies. Renewed contact between an adult and its brooded young does not produce the aggressive response. Contact with a non-clone does initiate an aggressive response. The dispersal of brooded young creates a pattern of fine scale clumping of genetically identical anemones (Ayre, 1987). The fine scale spacing of clonal anemones interferes with the settlement of genotypically unique sexually produced recruits (Ayre, 1982, 1983, 1984). The pedal locomotion of A. tenebrosa is associated in part with intraspecific aggression (Ottoway, 1978). Individuals move in relation to environmental gradients as well as in response to contact with a conspecific.

In summary, some species exhibit dominance with respect to different color varieties. The dominance of one color variety over another may contribute to the intertidal distribution of each color type. In general, larger anemones are dominant over smaller conspecifics. The use of intraspecific aggression as a reproductive strategy has not been investigated adequately. Colonies of genetically identical individuals maintain anemone-free zones between genotypically unique colonies. Solitary sea anemones exist out of tentacular contact from other individuals. Competition for space is the driving force for aggression among these animals.

FUTURE RESEARCH

Extensive research of intraspecific aggression has shown that anemones do compete for resources. One area that has not been thoroughly investigated is the role of interspecific aggression. The distribution of some species in the intertidal and the subtidal might be the result of interspecific aggression. The spatial range in which each species is found also may be affected by competition among species.

Conclusions drawn in two studies with Metridium senile are not in aggreement (Purcell and Kitting, 1982; Kaplan, 1983). Although their conclusions may not be mutually exclusive, questions concerning how they fit together still exist. Purcell and Kitting's study concluded that the longevity of aggregations of non-clonal individuals is due to habituation of anemones in frequent contact. Isolation of individuals followed by re-introduction to former groupmates results in aggressive interaction thereby maintaining aggressive tendencies in the species. The possibility of the anemones actively segregating into groups based on sex or color morph is not addressed (Purcell and Kitting, 1982). Kaplan's study concludes that individuals segregate themselves by sex. Males remain in placid contact with females, but are aggressive toward other males (Kaplan, 1983). Comprehensive studies examining the role of habituation and/or active segregation in this species need to be performed to thoroughly understand aggression in this species.

The most aggressive color variety of Actinia equina and Phymatis clematis live in the high intertidal zone. This distribution of color varieties suggests that this might be the most suitable habitat for sea anemones in the intertidal (Brace and Quick, 1985, 1986). The hypothesis that the most aggressive color variety occupies the most suitible habitat is testable by examining parameters such as food supply and predation in the upper, middle and lower intertidal zones.

How these animals differentiate between clonal and non-clonal neighbors and between conspecifics and different species is not understood. Studies of surface bound receptors need to be continued. An electrophysiological approach has been suggested by Brace (1981). The ciliary cones found at the tips of acrorhagi need to be examined more closely to determine their role in the recognition of neighboring anemones.

REFERENCES

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

AYRE, D.J. 1983. The effects of asexual reproduction and inter-genotypic aggression on the genotypic structure of populations of the sea anemone *Actinia tenebrosa*. *Oecologia* (Berlin) *57*:158-165.

AYRE, D.J. 1984. Effects of environmental and population density on the sea anemone *Actinia tenebrosa*. *Aust. J. Mar. Freshw. Rev.* *35*:735-746.

AYRE, D.J. 1987. The formation of clonal territories in experimental populations of the sea anemone *Actinia tenebrosa*. *Biol. Bull.* *172*:178-187.

BARNES, R.D. 1980. The Cnidarian and Ctenophores. Pages 150-170 in *Invertebrate Zoology*. Saunders College, Philadelphia.

BIGGER, C.H. 1976. The acrorhagial response in *Anthopleura krebsi*: intraspecific and interspecific recognition. Pages 127-136 in G. O. Mackie, ed., *Coelenterate ecology and behavior*. Plenum Press, New York.

BIGGER, C.H. 1980. Interspecific and intraspecific acrorhagial aggressive behavior among sea anemones: a recognition of self and non-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.

BRACE, R.C. AND J. PAVEY. 1978. Size-dependent dominance hierarchy in the anemone *Actinia equina*. *Nature* *273*:752-753.

BRACE, R.C., J. PAVEY, and D.L.J. QUICKE. 1979. Interspecific aggression in the color morphs of the anemone *Actinia equina*: the 'convention' governing dominance ranking. *Anim. Behav.* *27*:553-561.

BRACE, R.C. 1981. Intraspecific aggression in the color morphs of the anemone *Phymactis clematis* from Chile. *Mar. Biol.* 64:85-93.

BRACE, R.C. AND D.L.J. QUICK. 1985. Further analysis of individual spacing within aggregations of the anemone *Actinia equina*. *J. Mar. Biol. Assoc. U.K.* *65*:35-53.

BRACE, R.C. AND D.L.J. QUICK. 1986b. Seasonal changes in dispersion within an aggregation of the anemone *Actinia equina*, with a reappraisal of the role of intraspecific aggression. *J. Mar. Biol. Assoc. U.K.* *66*:49-70.

DONOGHUE, A.M. AND D.L.J. QUICKE AND R.C. BRACE. 1985. Biochemical-genetic and acrorhagial characteristics of pedal disc colour phenotypes of *Actinia equina*. *J. Mar. Biol. Assoc. U.K.* *65*:21-33.

DORSETT D.A. AND R. TURNER. 1986. Colour-morph dominance and avoidance responses of *Anemonia sulcata*. *Mar. Behav. Physiol.* *12*:115-123.

ERTMAN, S.C. and D. DAVENPORT. 1981. Tentacular nematocyte discharge and "self-recognition" in *Anthopleura elegantissima* Brandt. *Biol. Bull.* *161*:366-370.

FRANCIS, L. 1973a. Clone specific segregation in the sea anemone *Anthopleura elegantissima*. *Biol. Bull.* *144*:64 -72.

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

FRANCIS, L. 1976. Social organization within clones of the sea anemone *Anthopleura elegantissima*. *Biol. Bull.* *150*:361-376.

FRANCIS, L. 1979. Contrast between solitary and clonal lifestyles in the sea anemone *Anthopleura elegantissima*. *Amer. Zool.* *19*:669-681.

FUKUI, Y. 1986. Catch tentacles in the sea anemone *Haliplanella luciae*: role as organs of social behavior. *Marine Biology* *91*:245-251.

HAND, C. 1955. The sea anemones of central California, Part II. The Endomyarian and mesomyarian anemones. *Wasman J. Biol.* *13*:37-99.

HARGITT, C.W. 1907. Notes on the behavior of sea anemones. *Biol. Bull.* (Woods Hole, Mass) *12*:274-284.

HOWE, N.R., AND Y.M. SHEIKH, 1975. Anthopleurine: a sea anemone alarm pheromone. *Science* *189*:386-388.

JACKSON, J.B.C. 1977. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. *Am. Nat.* *141*:743-767.

JENNINGS, J.S. 1905. Modifiability in behavior I. Behavior of sea anemones. J. Exp. Zool. 2:447-473.

KAPLAN, S. 1983. Intrasexual aggression in Metridium senile. Biol. Bull. 165:416-418.

LUBBOCK, R. 1979a. Mucus antigenicity in sea anemones and corals. Hydrobiologia 66:3-6.

LUBBOCK, R. 1979b. Chemical recognition and nematocyst excitation in a sea anemone. J. Exp. Biol. 83:283 -292.

LUBBOCK, R. 1980. Clone-specific cellular recognition in a sea anemone. Proc. Natl. Acad. Sci. 77:6667-6669.

MARISCAL, R.N. 1974. Nematocysts. In: Coelenterate Biology: Reviews and New Perspectives (eds Muscatine, L. and Lenhoff, H.M.). pp 129-178. Academic Press, London.

OTTAWAY, J.R. 1978. Population ecology of the intertidal anemone Actinia tenebrosa I. Pedal locomotion and intraspecific aggression. Aust. J. Mar. Freshwater Res. 29:787-802.

PURCELL, J.E. 1977. Aggresive function and induced development of catch tentacles in the sea anemone Metridium senile (Coelenterata, Actinaria). Biol. Bull. 152:355-368.

PURCELL, J.E. and C.L. KITTING. 1982. Intraspecific aggression and population distributions of the sea anemone Metridium senile. Biol. Bull. 162:345-356.

RUSSO, A.R. 1984. Space partitioning within populations of sea anemones (genus: Anthopleura) in the California rocky intertidal zone. Internationale Revue der Gesamten Hydrobiologie (Berlin) 69(4):521-528.

SAUER, K.P., M. MULLER and M. WEBER. 1986. Alloimmune memory for glycoprotein recognition molecules in sea anemones competing for space. Marine Biology 92:73-79.

SEBENS, K.P. 1982. Asexual reproduction in Anthopleura elegantissima (Anthozoa: actinaria): seasonality and spatial extent of clones. Ecology 63(2):434-444.

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

WATSON, G.M. and R.N. MARISCAL. 1983a. The development of sea anemone tentacles specialized for aggression: Morphogenesis and regression of the catch tentacle of *Haliplanella luciae* (Cnidaria, Anthozoa) *Biol. Bull.* *164*:506-517.

WATSON, G.M. and R.N. MARISCAL. 1983b. Comparative ultrastructure of catch tentacles and feeding tentacles in the sea anemone *Haliplanella*. *Tissue and Cell*. *15*(6):939-953.

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*(2):84-86.