

AGONISTIC BEHAVIOR IN THE INTERTIDAL SEA ANEMONE *ANTHOPLEURA XANTHOGRAMMICA*

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ABSTRACT

The large intertidal sea anemone *Anthopleura xanthogrammica* (Brandt) forms aggregations of genetically distinct individuals at exposed sites along the west coast of North America. Individuals are often in close tentacle contact and remain that way for several years. However, this species displays the same agonistic behavior, inflation, and application of acrorhagi, as does its smaller clone-forming congener *Anthopleura elegantissima*. The behavior is frequent and more common among large individuals than small ones. Field transplants were used to show that non-neighbor anemones elicit the full acrorhagial response but that neighbors in close contact fail to behave agonistically towards each other. Microscopic examination of tissue samples revealed that conflicts between opposite sex anemones were as common as those between same sex anemones and that neighbors found in close contact were also as likely to be the same sex as the opposite.

Field anemone removal experiments in crowded pools and channels were used to compare subsequent movement of anemones released from crowding to movement of anemones never crowded and of those continuously crowded. Newly released anemones do move away from their neighbors but generally do not move out of tentacle contact. These results support the hypothesis that the application of acrorhagi serves more of a communication function than one of severe intraspecific competition. An anemone that has been attacked receives information on the size and position of its neighbor and can then move or not depending on available space. If movement is not possible, the agonistic behavior of its neighbor probably decreases or disappears altogether as a result of habituation.

INTRODUCTION

The existence of agonistic behavior among sea anemones was one of the most surprising additions to our knowledge of coelenterate behavior. Certain anemones use acrorhagi, vesicular extrusions at the margin of the column, to damage anemones of other species and even anemones of different genotypes within the same species (Abel, 1954; Bonnin, 1964; Francis, 1973a, b, 1976; Bigger, 1976, 1980; Brace and Pavey, 1978; Sebens and Paine, 1978; Ottaway, 1978; Williams, 1978, 1980; Brace *et al.* 1979; Brace, 1981; Ayre, 1982; Sebens, 1982b). Other anemones employ elongate (catch) tentacles as aggressive organs (Williams, 1975; Purcell, 1977; Kaplan, 1983) or use their feeding tentacles to damage other anemones and corals (Sebens, 1976). Similar sweeper tentacles also occur in another anthozoan group, the scleractinian corals (den Hartog, 1977; Richardson *et al.*, 1979; Wellington 1980) and are used agonistically as a mechanism distinct from the extrusion of mesenterial filaments and extracoelenteric digestion of neighboring corals (Lang, 1971, 1973; Connell 1976;

Wellington, 1980). Anemones are not known to extrude mesenterial filaments as an agonistic behavior. If anemones evolved from coral ancestors as suggested by Hand (1966), it appears that the extracoelenteric digestion behavior was lost and that acrorhagi evolved as new organs associated with agonistic behavior. Acrorhagus-like organs are also found in at least one corallimorpharian, a group morphologically intermediate between corals and anemones (den Hartog, 1977).

All anemone species bearing acrorhagi use them agonistically (Bigger, 1980), both interspecifically and intraspecifically, although anemones that reproduce asexually do not attack members of the same clone (Francis, 1973b, 1976, Bigger, 1976, 1980; Ayre, 1982; Sebens, 1982b). A possible exception to this observation was the large intertidal anemone *Anthopleura xanthogrammica* from the Pacific coast of North America. Although its acrorhagi are well developed, agonistic behavior was either never observed (Francis, 1973b) or observed only once in many hours of observation (Lindberg, 1976; Bigger, 1980; Sebens, 1983; Koehl, pers. comm.). Francis (1973b) suggested that acrorhagi were vestigial in this species, which forms dense aggregations of unrelated individuals in close contact (Batchelder and Gonor, 1981; Sebens, 1981a, b, d, 1982a, 1983). These anemones do not maintain a wide and regular spacing between individuals (as in *Actinia equina*, Brace *et al.*, 1979; *Phymactis clematis*, Sebens and Paine, 1978; Brace, 1981, or the solitary form of *Anthopleura elegantissima*, Francis, 1979; Sebens, 1983). *A. xanthogrammica* does not reproduce asexually; it reproduces sexually by broadcast spawning followed by external fertilization and a lengthy planktonic development (Seibert, 1974). The present study was initiated to determine the importance of acrorhagi to *A. xanthogrammica* under field conditions.

Recent studies have shown that another anemone, *Metridium senile*, forms mixed-genotype aggregations in the field and habituates to non-clonemate anemones, reducing the frequency of agonistic behavior with time (Purcell and Kitting, 1982). Kaplan (1983) suggested that agonistic behavior does not occur between *Metridium* clones of opposite sex and that individuals of opposite sex will comele on artificial substrata in the field. The possibilities that *A. xanthogrammica* in contact in the field have 'habituated' to each other, or that opposite sex contacts are more frequent than same sex contacts, were also investigated.

MATERIALS AND METHODS

Field studies were begun during September 1982 and continued during September 1983 at Tatoosh Island, Washington (48°27'N; 122°57'W), a very exposed open coast location at the northwest tip of the Olympic Peninsula. Laboratory observations on several hundred *Anthopleura xanthogrammica* and extensive field observations at low tide (1973–1977) failed to show agonistic behavior between individuals in close contact although one aggressive encounter by an *Anthopleura elegantissima* in an aquarium was followed by acrorhagi inflation and application by a large *A. xanthogrammica* (10 cm diameter). A single instance of agonistic behavior was observed in the field during a SCUBA dive at Tatoosh Island (1–2 m depth) in which two adjacent individuals (12–14 cm diameter) were observed with acrorhagi inflated. One raised the acrorhagi and brought them down onto the other individual. Given these observations and the two single observations reported in the literature (Lindberg, 1976; Bigger, 1980) it appeared that anemones kept in the laboratory were not behaving normally and that extensive field observations, when anemones were submerged, might be required to investigate the behavior. *A. xanthogrammica* lives in low intertidal habitats with extreme wave action and specimens in flowing sea water aquaria rarely expand to the degree seen in the field; they will often refuse suitable food and are thus not

behaving normally. Anemones observed in tide pools and rock crevices at low tide are often wholly or partly contracted. Those that are expanded are in quiescent water and their tentacles are thus not being brought into contact with neighbors even a few centimeters away.

During September 1982 observations of anemones were made just after mid-tide for 2–4 h by snorkeling (at areas 3, 7, 9, and M-3 in Fig. 3, Sebens, 1983). This area receives moderate wave action but is just protected enough to allow snorkeling (diving); it includes approximately 300 anemones. Anemones are generally less crowded here than in more exposed pools and crevices but some pools can be found where most of the available space is occupied and anemones are in close contact. Even where sparse, a few anemones can be found in pairs or triplets with obvious contact between tentacles. Inflation and application of acrorhagi were observed several times during this period. Positions of the anemones were mapped and the basal diameters of each anemone involved in an interaction were measured and recorded on the next low tide.

Experimental encounters were also effected during this period. Anemones (7–12 cm diameter) were carefully removed from the rock and transplanted into contact with one or two other anemones at locations > 2 m from their initial site of attachment. The transplanted anemones were enclosed in wide mesh (chicken-wire) enclosures sealed at the bottom so that each anemone was tightly enclosed but the tentacles and parts of the column protruded through the wide mesh. These enclosures were then attached to masonry nails driven into cracks or holes in the rock using nylon cable ties. This method kept the transplanted anemone in contact with resident (subject) anemones and prevented movement of the enclosure during wave surge. Eighteen transplants were set up during morning low tides and monitored by snorkeling as the tide rose in the afternoon. Yellow plastic flagging tape was attached to one of the nails to facilitate recognition of the experiments under water. Basal diameters of all individuals in the transplants were measured, and thus the sizes of all anemones that either did or did not inflate the acrorhagi were known. Ten additional transplants were effected in which a large (3 cm) *A. elegantissima* was moved into contact with one or two *A. xanthogrammica*.

The same protocol was used during September 1983. Twenty-two transplants of individuals separated by 2 m or more were effected. In addition, 27 anemones which were originally in close contact with at least one other (≤ 1 cm between basal disc edges) were each transplanted to the opposite side of their original neighbors. Given their slow rates of movement, anemones in such close contact must have been in contact for at least several days and probably much longer. Therefore, the potential for habituation existed and, if this had occurred, such pairs should have shown little or no agonistic behavior toward each other.

Anthopleura xanthogrammica has maximum gonad development and is fully mature in September and spawns in October or slightly later (Sebens, 1981d). All anemones used in experiments or observed in agonistic encounters were sampled for later sex determination. Another 24 pairs in close tentacle contact were also sampled for sex determination. Wedges of the anemones were cut out with a razor blade (20–50% of the anemone), placed into numbered plastic bags, and preserved with 7.5% formalin in sea water. In October 1983 all anemone samples were hand-sectioned at several levels of the column and the 1–3 mm thick sections were examined at 20–40 $\times$ under a dissecting microscope. When gonads were found, pieces were removed, pressed gently below a coverslip, and examined at 100 $\times$ with a compound microscope. Oocytes, mature ova, and testis tubules were evident in these preparations.

Anemone movement was investigated by mapping anemones in photographs

taken during 1974–1976. Clearings had been made in tide pools and channels to follow the rate of immigration of new anemones (Sebens, 1981a, b). For the present study, all anemones bordering the removal areas were mapped from projections of the photographs. The positions of anemones were re-mapped five times during the following 12–15 months. Movement was slow enough that individuals could easily be identified based on their relative size and orientation. In a few cases a new small individual appeared and previously one tens of centimeters away had disappeared. If no other major rearrangement occurred, it was assumed that this represented the same individual. The shortest possible path of each anemone was diagrammed for each interval and the total linear movement was summed at 3–4 and 12–15 months. This represents the least possible movement between sampling visits that could produce the new pattern.

Bordering individuals were separated into groups: those surrounded by other anemones and/or pool and channel walls (crowded), those released from crowding on one side by the experimental removal of their neighbors, and those that were initially uncrowded. An adjacent unmanipulated area (control M-3, Sebens, 1983) was also mapped by the same technique to measure the movement of initially uncrowded anemones. Any anemone in contact with one or no others was considered uncrowded. Measurements on anemones experimentally released from crowding should indicate whether the presence of neighbors causes anemones to move away if there is suitable space available. The adjacent space is known to be suitable because of its prior occupation by crowded adult anemones.

RESULTS

Agonistic behavior in the field

Thirty-four natural agonistic encounters were observed during this study. An agonistic encounter between two *Anthopleura xanthogrammica* is identical in sequence and postures to that described for *A. elegantissima* (Francis, 1973b). After initial contact by the tentacles or column of a neighboring individual, the first anemone to initiate the behavior (termed “aggressor”) pulls the tentacles back and up from the region of contact, bends away, then inflates the acrorhagi which are translucent green with pale green to white tips. The acrorhagi are held almost perpendicular or at least at an angle of 45° to the substratum at this point. The acrorhagi are then brought down on the other anemone in a sweeping motion by the contraction of the column on the side with the inflated acrorhagi. The tentacles are usually bent away from the acrorhagi or even partially deflated (Fig. 1). The sweep continues downward and causes the acrorhagi to contact the tentacles and then most of the column of the other (termed “attacked”) anemone, leaving patches of light-colored dehiscent ectoderm from the acrorhagi (peeling) on the dark column of the attacked anemone. Ectoderm also adheres to the tentacles of the attacked anemone but is less readily seen because of the lack of color contrast and the fact that the tentacles are rapidly contracted. The downward sweep stops at the base of the attacked anemone and the aggressor’s acrorhagi are often deflated before it again assumes its erect posture. After this sequence the aggressor either returns to its normal expanded posture with no acrorhagi visible or, in fewer cases, contracts and retracts the tentacles. The entire sequence from inflation of the acrorhagi to the return to normal posture lasted nine minutes in one timed episode, but was sometimes even more rapid. The attacked anemone almost invariably contracts, retracts the tentacles, and remains in this posture for minutes to hours. Only in two cases did the attacked anemone inflate acrorhagi during the observation and thus continue the agonistic encounter.

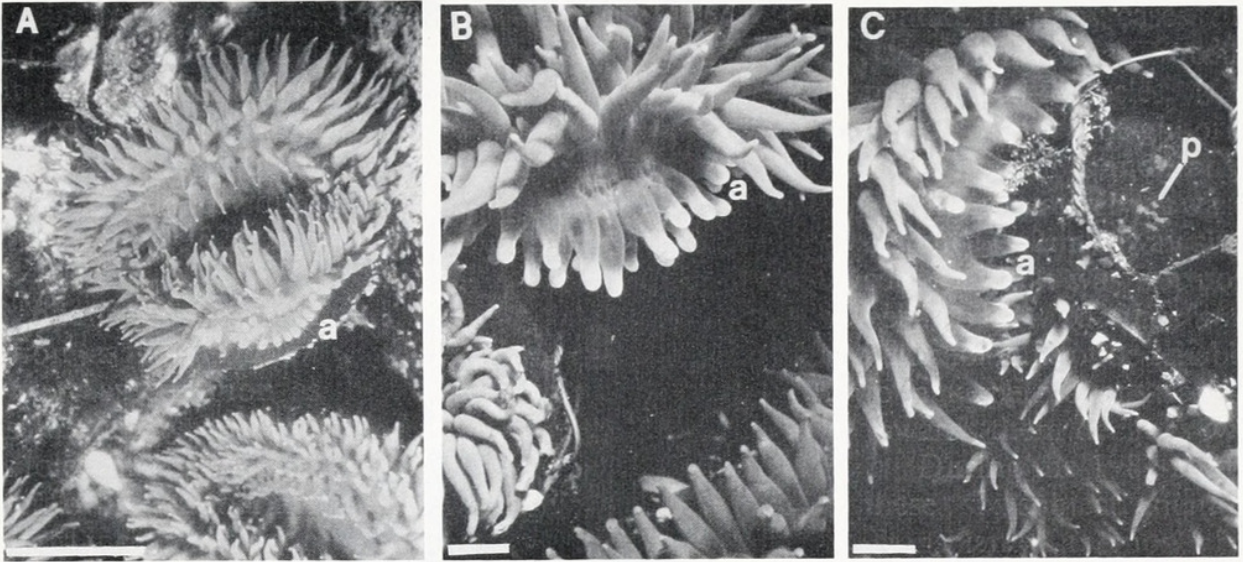


FIGURE 1. A. *Anthopleura xanthogrammica* agonistic encounter, Tatoosh Island, Washington. The individual at the top has its acrorhagi (a) inflated on the side facing its neighbor. Scale bar = 5 cm. B. Acrorhagi of a subject anemone prior to contact with an experimentally transplanted anemone in a wire enclosure. Scale bar = 1 cm. C. Acrorhagi tip ectoderm (light patches (p)) adhering to the column of a transplanted anemone (peeling). Scale bar = 1 cm.

The short duration of the behavior and the color similarity between tentacles and acrorhagi make this behavior easy to miss even during many hours of field observation. Also, it appears that water movement is the most common means by which anemones come into contact, as noted by Francis (1973b) for *Anthopleura elegantissima*. Anemones in tide pools or aquaria are thus much less likely to show the behavior. I have seen only two agonistic encounters in tidepools and one of these occurred as I stirred the water by reaching into the pool to measure anemones. My impression from snorkeling observations is that the behavior occurs most frequently during wave action. It takes only 10–15 minutes for the anemones to fully expand when the tide comes in. When the water is a half meter or less deep even small waves knock the anemones into each other. Of all the agonistic behavior observed, most was between anemones 4–6 cm apart (10 pairs) although there were cases where the anemones were 0–3 cm apart (6 pairs). The mean distance between fighting anemones was $3.0 \text{ cm} \pm 2.3 \text{ cm S.D.}$ ($n = 16$).

The entire study area contained 283 *Anthopleura xanthogrammica* of which 168 were in close contact ($\leq 4 \text{ cm}$ between bases) with at least one other individual of the same species. During the 1982 study twelve incidents of intraspecific agonistic behavior were observed (out of 98 anemones in potential contact) and 6 incidents of such behavior between *A. xanthogrammica* and *A. elegantissima*. During the 1983 study period 18 intraspecific agonistic incidents were observed in the same area (out of 77 anemones in potential contact) and 3 instances of agonistic behavior with *A. elegantissima*. Anemones were observed for a total of 16 out of 84 hours during which the anemones were submerged, which was 19% of the total time when agonistic behavior could have been observed. The average frequency of intraspecific agonistic behavior in 1982 was thus .25 incidents per adult anemone in contact with others per day and .26 incidents in 1983. Accordingly, an anemone would experience one agonistic encounter every four days on average.

However, not all anemones are equally likely to participate in agonistic interactions (Fig. 2). Anemones with $\leq 7 \text{ cm}$ basal diameters displayed agonistic behavior in only three cases, out of 36 anemones (8%) during the study. Anemones with $\leq 6.5 \text{ cm}$

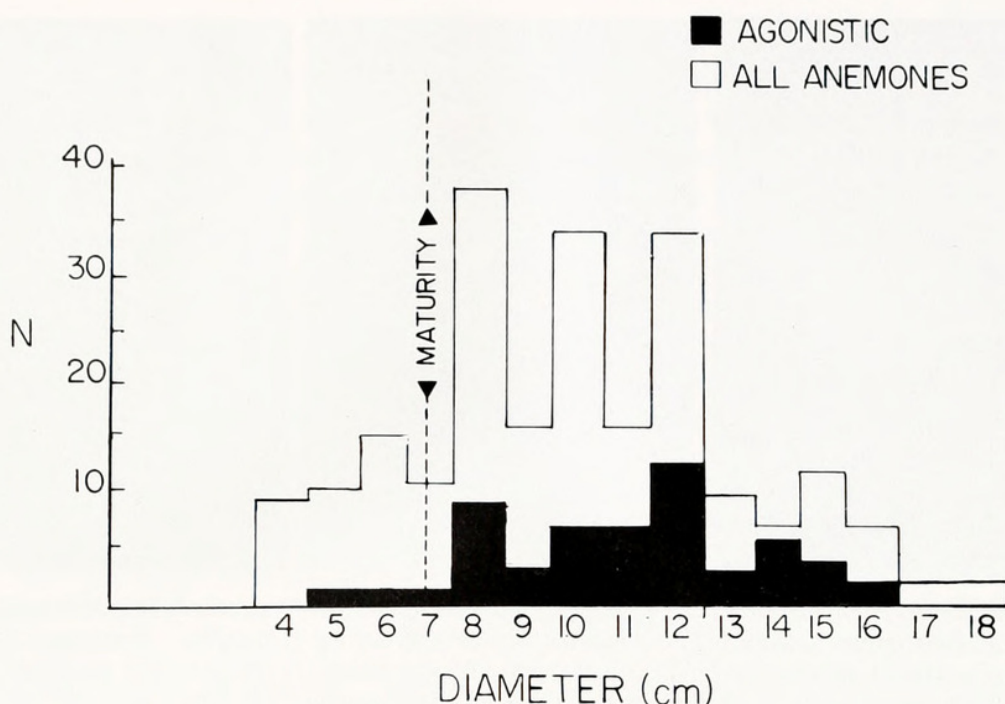


FIGURE 2. Sizes of *Anthopleura xanthogrammica* that displayed agonistic behavior (acrorhagal inflation) compared to the size distribution of all anemones mapped during the study.

basal diameters were found to be immature (juveniles) in this and an earlier study (Sebens, 1981d) while most individuals above that size had obvious male or female gonads. Anemones with 7.5–10 cm basal diameters displayed 19 agonistic behaviors out of 88 anemones observed (22%) and anemones > 10 cm displayed 35 such encounters out of 90 anemones (38%). Clearly juveniles are unlikely to participate in agonistic encounters either as aggressor or as defender, while adults do so frequently. A chi-squared test was performed on juvenile and adult categories assuming as the null hypothesis that agonistic behavior would be observed equally in both groups. The hypothesis must be rejected ($\chi^2 = 13.7$, $P < 0.005$) and the frequency of such behavior is thus significantly lower among juveniles. There was no significant difference between large (>10 cm) and small (≤ 10 cm) adults. One hypothesis for the low incidence of agonistic behavior in juveniles results from their small size and perimeter: the probability of contacting other anemones would be lower among smaller individuals compared to larger individuals. However, small anemones move more frequently (Sebens, 1981b, this study) and could experience even more contacts per unit time than do the adults.

For all natural agonistic interactions, the size of the aggressor was plotted against that of the anemone that had been attacked (Fig. 3). In some cases the initiation of aggression could have been missed and only the response seen. However, most observation periods began soon after the tide covered the anemones and continued for several hours. In only two cases was there a responding inflation and application of acrorhagi by the attacked anemone. Others may have done so after the period of observation, meaning a lag time of up to several hours between stimulus and response. For 21 of 28 anemones in Figure 3 the aggressor was larger than the attacked anemone; for 6 of 32 they were equal; and for 2 of the 28 the aggressor was smaller. A chi-squared test on the data in Figure 3, assuming equal frequencies of aggression by the larger and by the smaller member of a pair as the null hypothesis, shows that the opposite was true ($\chi^2 = 12.9$, $P < 0.005$); the aggressor was significantly larger. In

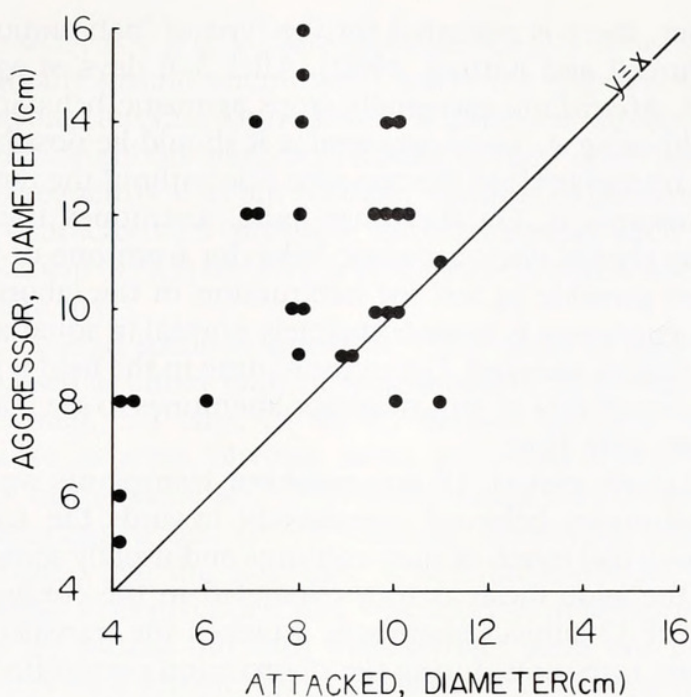


FIGURE 3. Sizes of anemones in pairwise natural agonistic encounters. The first or only anemone seen to inflate the acrorhagi is termed the "aggressor."

general, larger anemones appear to be both more aggressive and more likely to attack individuals smaller than themselves.

For the adult anemones, the frequency of agonistic behavior was 30% of all anemones observed in potential contact (in 19% of the time submerged, 1983). From these data, the estimate of the frequency of agonistic behavior becomes .34 incidents per anemone per day in the study area. This estimate establishes that agonistic behavior in *A. xanthogrammica* is very common in natural populations.

During the same study period nine incidents of agonistic behavior were observed between *Anthopleura xanthogrammica* and *A. elegantissima*. In six of those incidents only *A. elegantissima* inflated the acrorhagi and in two incidents only *A. xanthogrammica* did so. In one case an *A. elegantissima* inflated the acrorhagi after being attacked by an *A. xanthogrammica*. In no case was there a response by *A. xanthogrammica* to a previous aggression by *A. elegantissima*. The only other anemone occurring with *A. xanthogrammica* in this study was *Tealia coriacea* (eight individuals observed), but no agonistic encounters were observed between *A. xanthogrammica* and this species. In 1982, 11 *A. elegantissima* transplants were placed in contact with *A. xanthogrammica*; of these only 2 (18%) elicited acrorhagi inflation by *A. xanthogrammica*. However, the small size of *A. elegantissima* may have precluded contact in some cases.

On the most exposed points of Tatoosh Island, *Anthopleura xanthogrammica* often carpets the floors of tidepools and channels, sometimes so densely that another adult anemone could not be added easily (Sebens, 1981b, 1983). There were several smaller pools that had a similar dense packing of anemones in the area used for this study. Even where space was obviously available and anemones were not crowded it was easy to find pairs or greater numbers of anemones clearly in contact with each other. *A. xanthogrammica* does not reproduce asexually, and its planula larvae develop in the plankton and spend at least several weeks before settling (Siebert, 1974). It is, therefore, extremely unlikely that neighboring anemones are any more closely related than those not in contact. Since the anemones fight frequently yet tolerate close

contact in many cases, there is potential for the type of 'habituation' that occurs in *Metridium senile* (Purcell and Kitting, 1982). After 3–6 days of agonistic behavior, using catch-tentacles, *Metridium* essentially stops agonistic behavior. If this had occurred between neighboring *A. xanthogrammica* it should be possible to remove one of the neighbors and transplant it to the opposite side without the remaining anemone acting aggressively towards it. On the other hand, anemones transplanted from a distance (≥ 2 m) away should elicit agonistic behavior from one or both members of such pairs. It was not possible to test for habituation in the laboratory because the behavior of *A. xanthogrammica* is never completely normal in aquaria and the agonistic behavior cannot be reliably induced. Given more time in the field it would be possible to make permanent transplants of non-neighbor anemones to see if agonistic behavior towards them declines with time.

During the 1982 study period, 18 non-neighbor transplants were carried out. Of these, six subject anemones behaved aggressively towards the transplant (Fig. 4). Transplanted anemones had much of their columns and usually some of their tentacles protruding through the wide mesh as they expanded in the confined space. During the 1983 period, six of 32 subject anemones attacked the transplants, for a total of 24% showing agonistic responses during the observation period (in 19% of total submerged time). This translates to a maximum of 1.3 such behaviors per subject anemone per day, much higher than the .34 interactions in the population at large. Twenty seven transplants of anemones originally in close contact were carried out during the 1983 study period. Only one (3.7%) of the subject anemones showed agonistic behavior (Fig. 4), which would give a maximum estimate of .20 agonistic encounters per neighboring anemone per day. A chi-squared test was performed, assuming equal frequency of agonistic behavior in each group as the null hypothesis. The hypothesis

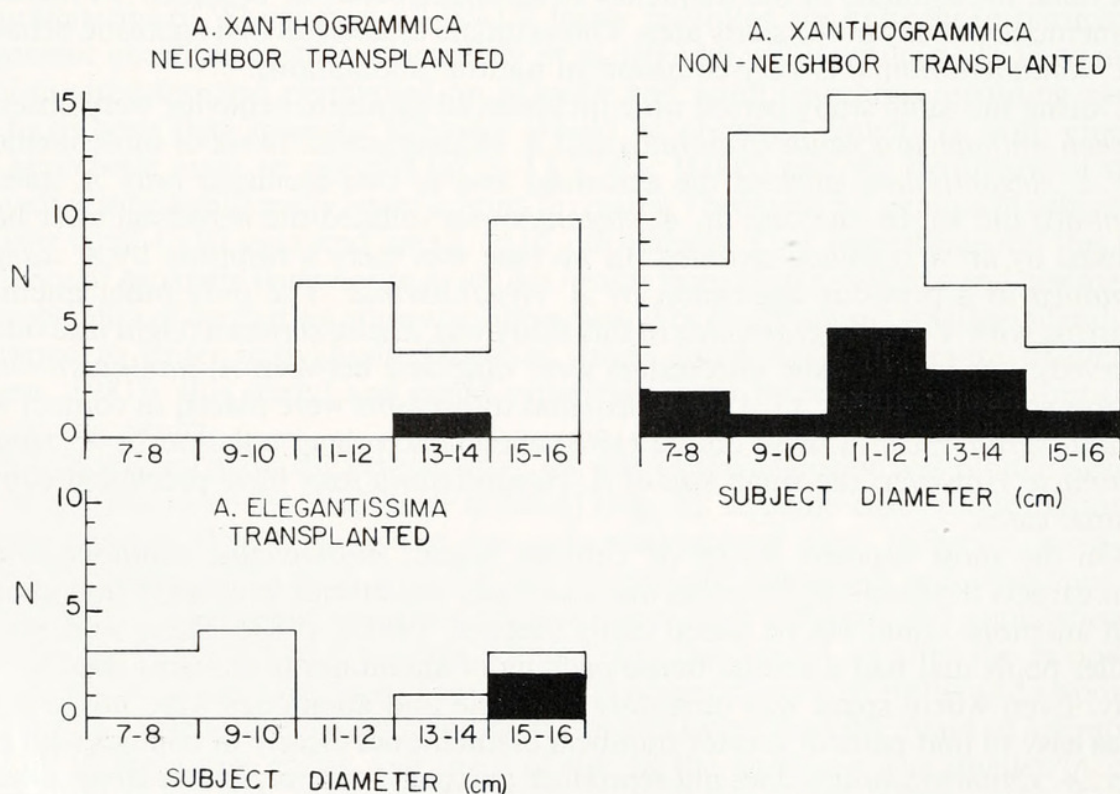


FIGURE 4. Sizes of anemones that did or did not display agonistic behavior (acrorhagal inflation) during transplant experiments. Light bars include all subject anemones, dark bars only those that showed agonistic behavior.

was rejected ($\chi^2 = 4.25$, $P < 0.05$); there was significantly more such behavior in the transplants of originally distant anemones. Clearly the response to contact with non-neighbors is very strong, but that for neighbors is almost nonexistent. One explanation for this result is that neighbors have habituated to each other and that the agonistic behavior occurs infrequently if at all. Another possible explanation is that neighbors have some special characteristics (probably not relatedness), such as the sexual sorting out suggested by Kaplan (1983) for *Metridium senile* in which anemones fail to attack those of the opposite sex.

The analysis of gonad sections from the 1983 study is summarized in Table I. Anemones were classed as either male or female adults, juveniles (≤ 7 cm), or without gonad ('not determined,' > 7 cm). Of the 15 natural agonistic encounters observed and sampled, 4 were between obvious adult male and female anemones, 4 were between anemones of the same sex, 2 involved adults and juveniles and 5 involved anemones of undetermined sex. Of 19 naturally occurring neighboring anemones (≤ 2 cm between bases) that did not fight, 4 were male-female pairs, 5 were of the same sex, 3 were adults with juveniles, and 7 were between anemones of undetermined sex. There is thus no sorting out into male-female pairs nor is agonistic behavior limited to encounters with anemones of the same sex. Among the transplanted and subject anemones the same result held; neighbors included both same sex (7) and opposite sex (5) pairs. Non-neighbor transplants that fought included opposite (2) as well as same sex (2) pairs and those that did not fight also included opposite (9) and same sex (13) pairs. Based on these findings, sex does not appear to influence agonistic behavior nor does the reproductive state of the adults; adult individuals without gonads engaged in several agonistic encounters as did those with gonads.

Movement in response to neighbors

Anemones bordering experimental anemone removal areas were classed as adults or juveniles by their size and were also categorized as to their initial situation: (1) uncrowded, (2) crowded, and (3) crowded then released from crowding, on one side, by the experimental removal of neighbors. The removal experiments were originally

TABLE I

Sex categories of anemone pairs used in experiments, found in close contact, or displaying agonistic behavior (136 anemones dissected and examined)

	Total Pairs	Male/ Male	Female/ Female	Male/ Female	Male/ Juv.	Female/ Juv.	Male/ Neut.	Female/ Neut.	Neut/ Neut.
Natural agonistic encounters	15	1	3	4	1	1	3	2	0
Pairs in close contact	19	4	1	4	1	2	1	5	1
Transplants: close contact	20 (1)	3	4	5	2	0	2 (1)	4	0
Transplants: originally distant	34 (6)	4 (1)	7 (1)	9 (2)	1	0	3	7 (1)	3 (1)
Total agonistic encounters	22	2	4	6	1	1	3	3	1

Numbers in parentheses in the transplant groups are those that did behave agonistically.

Juv. = juvenile, Neut. = unable to determine sex.

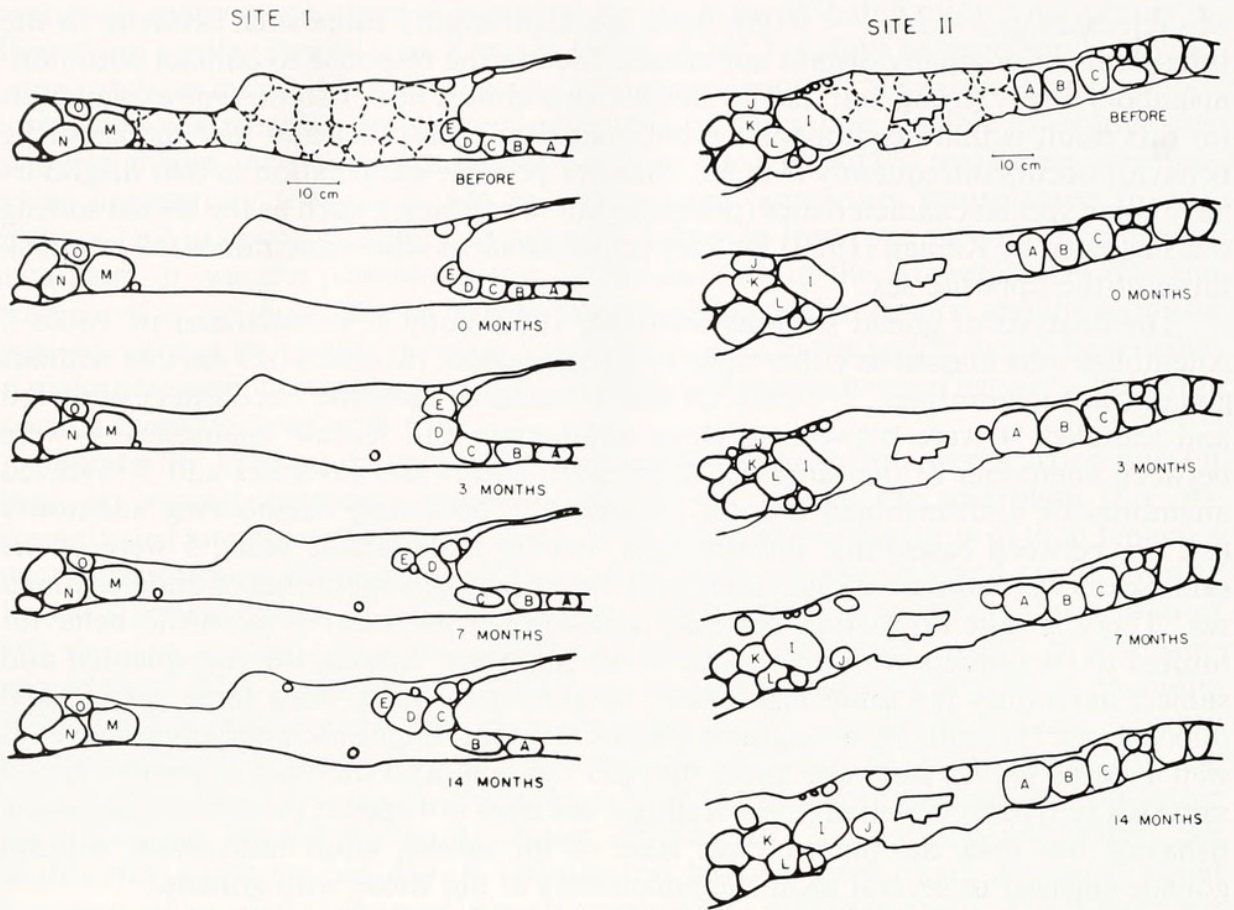


FIGURE 5. Two experimental anemone removal areas on Tatoosh Island. Dashed circles represent anemones removed from the channels, solid circles represent those that remained. Adult anemones close to the removal areas are identified by letters. Note that individuals A-E at site I moved substantially but each remained in contact with one or more neighbors. Only anemones A and J and a few juveniles moved measurably at site II.

conducted to measure the rate of immigration and the sizes of immigrating anemones (Sebens, 1981a, b), not to measure movement as a function of initial position. Only the removal areas within approximately 30 m or less of the 1982–1983 study areas were analyzed in this study.

Movement was greatest among both adult (≥ 7 cm diameter) and juvenile (< 7 cm) anemones newly released from crowding (Figs. 5, 6). Solitary anemones and continuously crowded anemones moved much shorter distances, if at all. Analysis of Variance (ANOVA), followed by a Student-Newman-Keuls multiple comparisons test (SNK), was used to test for differences in total summed linear displacement after 3–4 months, and after 12–15 months (Sokal and Rohlf, 1968). After 3–4 months, the released adults had moved farther than either the crowded or solitary adults (ANOVA, $F_s = 24.8$, d.f. = 2,70, $P < 0.001$), but there was no difference between either of the latter groups (SNK). The same was true after 12–15 months ($F_s = 35.5$, d.f. = 2, 69, $P < 0.001$). Among the juveniles, the released group differed only from the solitary ones after 3–4 months ($F_s = 2.7$, d.f. = 2,31, $P < 0.05$) and only from the crowded ones after 12–15 months ($F_s = 3.2$, d.f. = 2,31, $P < 0.05$). Juvenile movement was significantly greater than adult movement only after 12–15 months in the solitary group ($F_s = 5.9$, d.f. = 1,48, $P < 0.05$) and not among crowded or newly released anemones (Fig. 6).

These results suggest that adult movement is extremely slow, only tens of centimeters in a year, and that juvenile movement is only about twice as rapid. However,

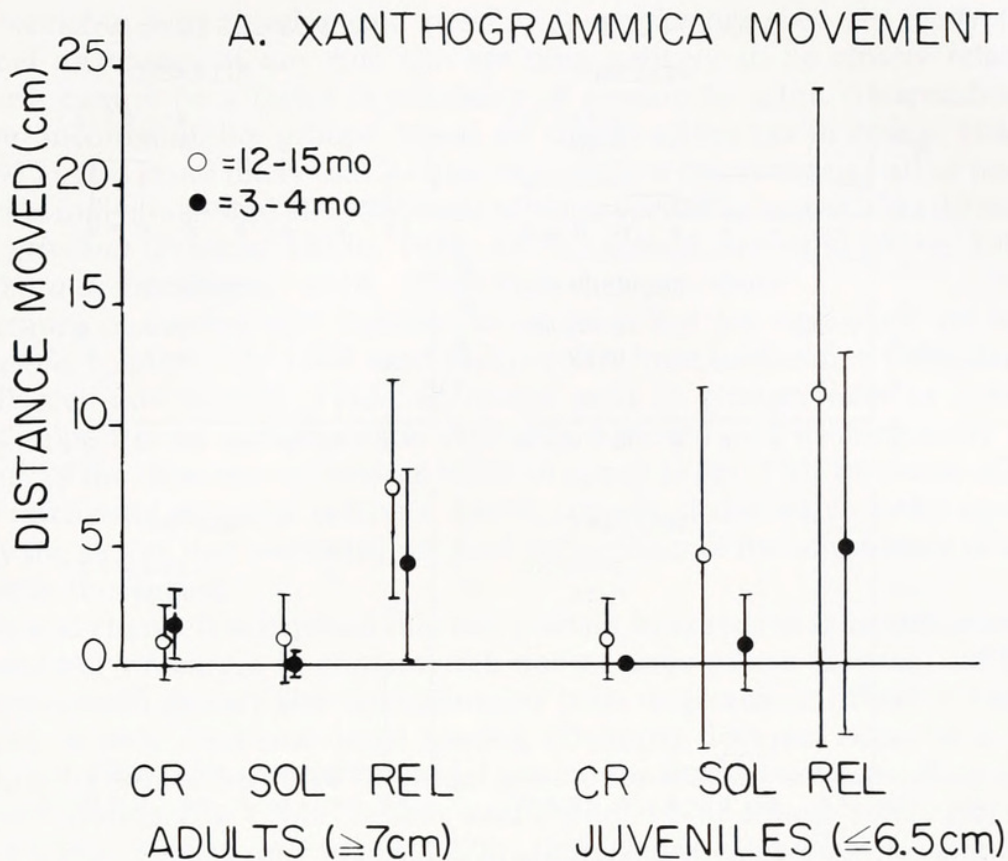


FIGURE 6. Distances moved by all anemones bordering the experimental anemone removal areas. CR = continuously crowded anemones, SOL = solitary anemones, REL = anemones released from crowding by the experimental removal of their neighbors.

far more juveniles than adults moved into all experimental removal areas during 1973–1977 (Sebens, 1981a, b, 1982a, b). Many of these juveniles came from >0.5 m away because they did not appear in the map from the previous sampling period. The rates of juvenile movement in this study omit all juveniles not present at initiation and may thus greatly underestimate juvenile mobility.

It is clear that continuously crowded adults and adults with abundant available space adjacent to them hardly moved at all (Fig. 7). Anemones crowded before the experiment, then given free space, moved into it but did not separate themselves from neighboring anemones by any great distance, usually remaining close enough for tentacle contact. The mean distance between nearest neighbor basal discs of newly released anemones after 12–15 months was $0.9 \text{ cm} \pm 1.9 \text{ cm S.D.}$ ($n = 20$) as opposed to $0.2 \text{ cm} \pm 0.5 \text{ cm S.D.}$ ($n = 20$) before removal. These means are not significantly different. From this experiment it appears that *A. xantho grammica* will move away from conspecifics if space is available but that they do not maintain a wide spacing between neighbors as do other large non-cloning anemones (*Solitary Anthopleura elegantissima*, *Phymactis clematis*, *Phymanthea pluvia*) which behave agonistically (Sebens and Paine, 1978; Francis, 1979; Brace, 1981) and maintain at least one body diameter between neighbors.

DISCUSSION

The large intertidal anemone *Anthopleura xantho grammica* displays an acrorhagal agonistic behavior almost identical to that of its sympatric congener *A. elegantissima* (Francis, 1973b, 1976). The behavior increases in frequency with anemone size in

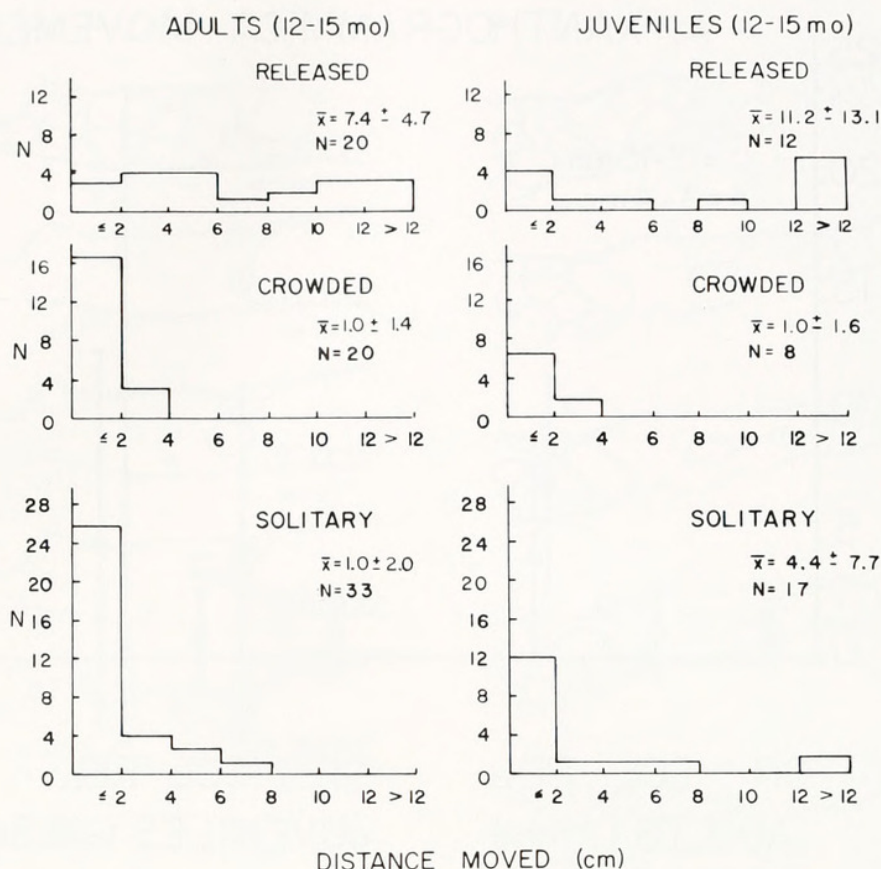


FIGURE 7. Distribution of distances moved by juvenile and adult anemones bordering the experimental anemone removal areas. "Crowded" anemones were those continuously crowded, both before and after the removal. "Solitary" anemones were in contact with one or no other anemones before and after the removal. "Released" anemones were released from crowding by the experimental removal of their neighbors. $\bar{x} \pm S.D.$ are given as cm moved.

the field and, among large anemones, may occur as frequently as once per day. Individuals found in contact, and which have probably been in contact for long time periods, are far less likely to behave agonistically toward each other than are widely separated anemones. This tolerance for contact with genetically dissimilar adults led Francis (1973b) to postulate that the acrorhagi were possibly vestigial in this species. Bigger (1980) and Lindberg (1976) reported single cases of acrorhagal inflation and agonistic behavior in tidepool and aquarium situations respectively. Prior to this study I saw only one intraspecific agonistic episode in the field and one between *A. xanthogrammica* and *A. elegantissima* in a flowing sea water aquarium. The present field observations and experiments suggest that agonistic behavior is frequent and important in natural populations of *A. xanthogrammica*. *Anthopleura elegantissima* recognizes genetically identical clonemates and confines agonistic behavior to encounters with non-clonemates and to other anemone species (Francis, 1973b, 1976; Sebens, 1982b). Recognition of non-clonemates is based on intact tissue surfaces (Lubbock, 1980) and may be related to 'immunoincompatibility' as suggested for corals (Hildemann *et al.*, 1975, 1977, 1979; Bigger and Runyan, 1979; Bigger, 1980). However, surface mucus will elicit nematocyst discharge in interspecific encounters of several anemone species (Lubbock, 1979; Ertman and Davenport, 1981) and may be the general basis for recognition of other anemone species, sometimes followed by initiation of agonistic behavior. *A. xanthogrammica* does not reproduce asexually (Hand, 1955; Sebens, 1983) and reproduces sexually by spawning gametes into the sea water where fertilization and subsequent development occur (Siebert, 1974). Planula larvae require

several weeks to fully develop and possibly longer before they are ready to settle. Individual anemones at any one site are thus unlikely to be closely related, and relatedness cannot be a factor in tolerance of contact by adult conspecifics, unless there are 'incompatibility groups' based on shared alleles (as in corals, Hildemann *et al.*, 1977). It is more likely that *A. xanthogrammica* can recognize all or most other conspecific individuals and all individuals of other species as 'not-self' as do individual *A. elegantissima* (Francis, 1973b, 1976, 1979), *Actinia tenebrosa* (Ayre, 1982), and *Anthopleura krebsi* (Bigger, 1976, 1980) from distinct clones.

Tolerance of contact with conspecific adults is not sex dependant (as suggested for *M. senile*, Kaplan, 1983) and most likely results from habituation (as in *Metridium senile*, Purcell and Kitting, 1982). Same-sex pairs in contact were as common as those of opposite sex and agonistic behavior occurred just as frequently between anemones of the same sex as between those of opposite sex. This tolerance of contact, and the infrequent agonistic behavior during periods of still water, or in aquaria, are probably the factors that prevented previous recognition of the importance of agonistic behavior in this species.

Pools and channels at exposed sites can contain hundreds of individuals per square meter, most of which are in contact with one to three others (Sebens, 1983). Areas with lower overall density also contain many pairs or greater numbers of individuals in contact. A wide inter-individual spacing obviously does not occur as a result of agonistic behavior. Other large intertidal anemones that do not reproduce asexually (*Phymactis clematis* in Chile, Sebens and Paine, 1978; Brace, 1981; *Phymanthea pluvia* in Chile, Sebens and Paine, 1978; *Anthopleura elegantissima* solitary form, Francis, 1979) usually maintain spaces of one or more individual diameters between individuals by bending the column far over and reaching out with the tentacles and then with the acrorhagi. *Actinia equina* (Brace *et al.*, 1979), *A. tenebrosa* (Ottaway, 1978; Ayre, 1982), *Bunodactis cavernata* (Bigger, 1980), and *Anemonia sargassensis* (Bigger, 1980) are also reported to maintain a distance between individuals as a result of agonistic behavior.

Crowded adult *Anthopleura xanthogrammica* that were experimentally provided with suitable space on one side moved significantly more than did either continuously crowded or uncrowded anemones in this study. Although they did not establish a wide spacing between individuals, they did move away from the crowded areas of pools and channels; they also increased the distance between themselves and their neighbors, although usually not by enough to prevent frequent tentacle contact. Therefore, these anemones do move in response to crowding, although slowly. Agonistic behavior may thus be a form of information transfer, communicating the position of neighbors to any one anemone. If suitable space is available, the anemone bordering that space could then move into it and away from its neighbor.

Excessive crowding probably causes the anemones' tentacle crowns to interfere with each other. This could reduce the probability of prey capture [dislodged mussels, barnacles, and other invertebrates (Sebens, 1981c)] by reducing the total surface area of the tentacle crown; shading by other anemones could also reduce the photosynthetic rate of symbiotic algae. In fact, crowded anemones grew less rapidly than did those experimentally released from crowding in a previous study (Sebens, 1983). This effect was most obvious in the intermediate (6–10 cm diameter) size range. Anemones ≤ 6.5 cm diameter were highly mobile; they appeared and disappeared from study areas frequently and accounted for most of the recruitment into cleared areas (Sebens, 1981a, b, 1983). Reduced crowding, even though it may still involve tentacle contact, could thus be advantageous to all anemones concerned.

The extremely wave-exposed habitats occupied by *Anthopleura xanthogrammica*

may impose a constraint on wide spacing. Koehl (1977) has noted that the relatively even surface formed by closely adjacent tentacle crowns of this species could reduce the shear forces tending to deform or detach the anemones. Instead of impinging on the side of each anemone, the rapidly flowing water during wave surge goes over their oral discs. In fact, solitary *A. xanthogrammica* are found more commonly in habitats with less exposure and in deep crevices at the exposed sites. Koehl (1977) also found that this species changes its shape, increasing the height to diameter ratio from the most exposed areas to those with less wave action. This suggests that forces imposed by water motion are indeed important. Biomechanical properties would thus select against a behavior that provides a very wide spacing away from all neighbors.

There are two other possible functions for intraspecific agonistic behavior in *A. xanthogrammica*. The first is competition for space within crowded pools and channels. The largest anemones often inhabit the centers of pools and channels and the smallest ones are limited to the sloping sides or are found between the large adults, overshadowed by their tentacle crowns (Sebens, 1981b, 1983). The small movements of the large anemones over months to years may represent a 'jockeying for position' within the pool. Even if most space is taken, there are still better and worse places to be. The central horizontal floor of pools and channels may well receive the most dislodged prey during periods of heavy wave action, and the least shading by surrounding rock, which would reduce photosynthesis by the symbiotic algae. The second possible function is defense of space from potential immigrants. Small anemones migrate into pools and channels at rates of several individuals per square meter per year (Sebens, 1981a, b). Without agonistic behavior by the residents, such anemones might crowd the area to the maximum. As it is, they are given information that parts of the area are already crowded and are thus encouraged to leave.

Anthopleura xanthogrammica also behaves aggressively towards *A. elegantissima* and may do so towards other species as well. At the sites examined, intraspecific contact was by far the most common but close proximity of *A. xanthogrammica* and *A. elegantissima* was probably the next most common situation. *A. elegantissima* individuals are generally ≤ 3 cm diameter at Tatoosh Island but can be very large at other sites (to 6 cm diameter) and even larger individuals of the solitary form are common in California (Francis, 1979). Therefore, agonistic behavior between these two species is probably common and may be an important mechanism of interspecific competition for space.

The influence of anemone size on agonistic behavior has been demonstrated for *Actinia equina* (Brace and Pavey, 1978; Brace *et al.*, 1979) and for *Phymactis clematis* (Brace, 1981). Large anemones have a lower threshold (less time from stimulus to response) for initiation of agonistic behavior and they tend to win contests with smaller individuals. However, *Actinia tenebrosa* does not fit this pattern; large anemones often lose to smaller ones (Ayre, 1982) and it appears that the resident anemone has a great advantage, winning most contests independent of size (Ottaway, 1978). Size is also important for *Anthopleura xanthogrammica* where larger individuals are more frequently the aggressors. The final outcome of each encounter is unknown because the anemones never moved perceptibly in the period available for study, but the attacked anemone often remained closed for hours. It is therefore most likely that the largest anemones are the dominant competitors in this species as well. Brace (1981) has suggested that the decrease in time to initiate agonistic behavior (after initial contact) as a function of anemone size serves a specific function; it prevents small anemones from starting or continuing fights that they can't win. The rapidity with which an anemone begins aggression following initial contact of two individuals conveys information on the probable size of that individual. If it aggresses first, it is

probably larger. This may explain why so few of the attacked anemones in this study fought back. Once the size information is conveyed, the attacked individual need not continue the bout. Instead it remains contracted, avoiding further damage, and may slowly move away.

The acrorhagal agonistic behavior of *Anthopleura xanthogrammica* may well be an important means of competition for space, as it seems to be in the clonal species *A. elegantissima* (Francis, 1973b, 1976). Extensive damage to an attacked anemone was observed only once in this study, suggesting that the agonistic behavior serves more frequently as communication rather than as absolute aggression or defense. This idea is supported by the species' ability to reduce or eliminate the agonistic behavior after prolonged contact. An anemone that stands its ground may eventually be accepted by its neighbors, but it is to the intruder's advantage to move away if suitable space is available, thus avoiding severe overcrowding.

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