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AGGRESSION, HABITUATION, AND CLONAL COEXISTENCE IN THE SEA ANEMONE *ANTHOPLEURA ELEGANTISSIMA*

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Abstract.—Interclonal encounters between sessile cnidarians, including the sea anemone *Anthopleura elegantissima*, often elicit the deployment of specialized structures such as acrorhagi (modified tentacles) used for aggression. Fighting ability appears to be an important determinant of the outcomes of interclonal competition for space. Consequently, all else being equal, populations should come to be dominated by a small number of the most aggressive clones. Nevertheless, this and previous studies show that clonal diversity is very high in local populations of *A. elegantissima*. Such high levels of diversity could persist if (1) extant clones differed little in their fighting abilities, (2) rates of resource renewal were high enough to prevent the population from reaching competitive equilibrium and there were trade-offs between investment in aggression and other traits (such as sexual reproduction) associated with the acquisition of free space, or (3) clones were not mutually aggressive. This study first characterizes agonistic interactions among replicated pairings of the polyps of seven clones of *A. elegantissima*. We found a transitive dominance hierarchy, underlain by clone-specific variation in both agonistic behavior and in the numbers of acrorhagi per polyp. Clones consistently differed in their propensity to attack and to retaliate, and in their responses to different clones. Repeated stimulation by an alternate clone also modified the expression of agonistic behavior. These modifications, which involved both enhancement and habituation, represented responses to the stimulating clone, rather than nonspecific modification of agonistic behavior. Taken together, the results show that the outcomes of intraspecific competition for space among *A. elegantissima* clones may be decided by a combination of intrinsic behavioral and morphological attributes of competing clones, as well as prior histories of interactions with other clones. Because clones differ widely in their fighting abilities, clonal coexistence in *A. elegantissima* likely involves an interaction among the complexities of agonistic behavior, opportunities for colonization, and trade-offs between aggression and sexual reproduction.

For many sessile and sedentary organisms, habitable space is often the single resource that limits the potential for growth, and ultimately the reproductive output and survival, of individual genotypes. The extrinsic constraints on fitness imposed by the availability of favorable substratum, and consequently the importance of competition for space, will be particularly great among sessile, clonal organisms, with their potentially unlimited capacity for genotypic expansion (Williams 1957; Hamilton 1966; Francis 1973*a*, 1973*b*; Jackson 1977, 1985; Janzen 1977; Caswell 1985; Cook 1985; reviewed in Harvell and Grosberg 1989; Hughes

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1989). Indeed, numerous studies of overgrowth in epibenthic marine algae and clonal animals (reviewed in Jackson 1977, 1985; Buss 1986, 1990; Sebens 1986; Paine 1990) and interspecific interactions in terrestrial, clonal plants (see, e.g., Turkington and Harper 1979; Pentecost 1980; reviewed in Harper 1985; Silander 1985; Eriksson 1993) chronicle the impacts of spatial competition on correlates of individual reproductive success.

Sessile, clonal species often differ widely in their interspecific competitive abilities (reviewed in Silander 1985; Buss 1986, 1990; Sebens 1986; Lang and Chornesky 1990). These differences can often be explained in terms of species-specific variation in morphology (Jackson 1979; Harper 1985); the ability to produce allelochemicals (Jackson and Buss 1975; Buss 1976; Lovett et al. 1989; Storey 1991); tolerance of shading (Dayton 1975; Harper 1985), overgrowth (Sebens 1986), predation, and disturbance (Paine 1984); and the potential to initiate highly specific agonistic behaviors (Lang 1973; Wahle 1980; Wellington 1980; Buss et al. 1984; Grosberg 1988). In turn, these differences commonly lead to predictable interspecific dominance hierarchies (Lang 1973; Jackson 1977, 1983; Osman 1977; Russ 1980; Buss 1981, 1986, 1990; Grosberg 1981; Greene and Schoener 1982; Chornesky 1983). Nevertheless, competitive relationships between sessile, clonal species can be reversible, with outcomes being influenced by variation in a spectrum of factors, including illumination, nutrient availability, levels of physical disturbance, surface contour and angle, intensity of parasitism and predation, presence of symbionts, density, relative sizes of competitors, and inducible morphological changes (Buss 1979*a*, 1979*b*, 1990; Karlson 1980, 1983; Osman and Haugness 1981; Russ 1982; Karlson and Shenk 1983; Paine 1984; Sebens 1986; Harvell 1990; Lang and Chornesky 1990). Such reversals, along with competitive standoffs in which neither contestant wins an interaction, can slow or prevent competitive exclusion, and enhance the maintenance of species diversity (Karlson 1980, 1981, 1985; Silander 1985; Sebens 1986, 1987).

The same demographic characteristics of sessile, clonal species that promote high levels of interspecific competition for space also potentially generate intense interclonal competition (Ayre 1984; Harper 1985; Buss 1990; Schmid 1990; Kroon et al. 1992; Eriksson 1993). In contrast to our understanding of interspecific competitive relationships, variation in those relationships, and the processes that lead to interspecific coexistence, there are comparatively few studies of interclonal dominance relationships and coexistence among conspecific clones of sessile plants (Turkington and Harper 1979; Ellstrand and Roose 1987; Kroon et al. 1992) and animals (Ivker 1972; Bigger 1980; Buss et al. 1984; Willis and Ayre 1985; Buss and Grosberg 1990; Ellison and Harvell 1991; Yund 1991). Just as the outcomes of interspecific contests may be influenced by species-specific differences in size, morphology, growth rate, and armament, interclonal variation in the expression of the same traits may affect interclonal dominance relationships (see, e.g., Turkington and Harper 1979; Buss and Grosberg 1990). Furthermore, the nature and outcomes of interclonal interactions can be strongly influenced by the genetic identities per se (i.e., allotypes) of competing clones. For example, interclonal interactions among sessile, clonal cnidarians often involve aggression, which entails the deployment of specialized structures (e.g., acrorhagi, catch tentacles,

digestive filaments, or stoloniferous extensions of the gastrovascular system; reviewed in Buss et al. 1984; Williams 1991) that are heavily armed with batteries of penetrant, toxic nematocysts. Agonistic behavior is generally restricted to interactions between individuals belonging to different clones (i.e., allogeneic interactions); contacts between clonemates (i.e., isogeneic interactions) generally do not elicit aggression (reviewed in Grosberg 1988).

If interclonal aggression in cnidarians determines the outcome of intraspecific competition for space, then in the absence of substantial disturbance in a space-limited habitat, populations should come to be dominated by a small number of the most aggressive, evenly matched, clones (Karlson 1980; Sebens and Thorne 1985). Similarly, all else being equal, interclonal spatial competition in terrestrial plants should lead to local dominance by one of a few competitively dominant clones (Silander 1985). Nevertheless, studies of the population genetics of several species of clonal plants (reviewed in Ellstrand and Roose 1987; Hamrick and Godt 1989) and aggressive, clonal cnidarians (see, e.g., Shick et al. 1979; Ayre 1983; Neigel and Avise 1983; Heyward and Stoddart 1985; Hunter 1985; Hoffmann 1986; Ayre and Willis 1988) show that levels of clonal diversity are high, even on very local scales (i.e., square centimeters to square meters).

There are at least three scenarios that could reconcile the apparent discrepancy between the ecological prediction that clonal diversity should be low and the genetic observation that clonal diversity is often high. First, in a manner analogous to the maintenance of species diversity in space-limited communities (see, e.g., Armstrong 1976; Hastings 1980), if rates of disturbance and resource renewal are high enough to prevent the population from reaching competitive equilibrium (sensu Levin and Paine 1974), then trade-offs between investment in aggression and other characters associated with the acquisition of space (or other resources), such as rates of asexual propagation and sexual reproduction, could allow coexistence (Hebert and Crease 1980; Sebens and Thorne 1985; Eriksson 1993). Under these circumstances, clones could differ in their fighting ability, as long as clones that are subordinate competitors in terms of fighting ability are superior at acquiring uncolonized space (Armstrong 1976; Soane and Watkinson 1979; Sebens 1987; Yund 1991). Second, competitive reversals (sensu Russ 1982; Sebens 1986) or standoffs (sensu Karlson 1980) between specific pairs of clones may be so frequent that competitive exclusion rarely occurs. Third, competing clones may not be mutually aggressive (see, e.g., Karlson 1981), either because they lack sufficient allogeneic disparity to evoke agonistic behavior (reviewed in Grosberg 1988) or because protracted interactions may lead to habituation (Purcell and Kitting 1982; Kaplan 1983; Sebens 1984; Sauer et al. 1986; Brace and Santer 1991).

Along exposed rocky shores of the west coast of North America, the sea anemone *Anthopleura elegantissima* forms dense clonal aggregations in the midintertidal zone. The process of clonal establishment begins with the recruitment of a planktonic, sexually produced larva. Subsequent asexual fission of adults leads to clonal expansion (Sebens 1982*a*, 1982*b*). *Anthopleura elegantissima* lives only on rocky substrata; thus, local topography and other physical features of the habitat proximally constrain the size, shape, and continuity of aggregations (Sebens 1982*b*). However, even on apparently favorable surfaces that are densely

colonized, there can be persistent (up to 4 yr), anemone-free regions, up to 5 cm across, that separate groups of anemones (Äbel 1954; Francis 1973*a*). These polyp-free zones are also known in the acontiate anemones *Metridium senile* (Purcell 1977) and *Sagartia elegans* (Shaw 1991) and in hydroids such as *Hydractinia symbiolongicarpus* (Yund 1991).

For many years, the origin of these anemone-free zones was unclear; however, in a series of laboratory studies on *A. elegantissima*, Francis (1973*a*, 1973*b*) showed that when the tentacles (or other parts) of two polyps from distinct aggregations come (or are brought) into contact, a stereotypical set of agonistic behaviors ensues. This repertoire of behaviors, which occurs in one or both allogeneic individuals, begins with the retraction of the feeding tentacles and the dilation of a distinctive set of nonfeeding tentacles, the acrorhagi. When the acrorhagi are fully inflated, one or both contestants apply their inflated acrorhagi to the other individual. As the distal tip of an acrorhagus touches an allogeneic individual, the nematocyst-laden acrorhagial epithelium detaches and adheres to the opponent (for a complete description, see Francis 1973*b*). This sequence may be repeated, sometimes reciprocally, in a given contest; eventually, one of the anemones withdraws both its acrorhagi and feeding tentacles, and retreats, if possible. If retreat is impossible, the attacked anemone may eventually die from its injuries. On the basis of these observations, Francis (1973*a*, 1973*b*) argued that, at least in *A. elegantissima*, interclonal aggression plays an important role in competition for space.

As with many other species of clonal plants and benthic, clonal invertebrates, levels of intraspecific competition for space appear to be high in *A. elegantissima* (Sebens 1982*a*, 1982*b*), as do levels of clonal diversity (Francis 1973*a*, 1973*b*; Sebens 1982*b*; Smith and Potts 1987). Nevertheless, it is still not known whether clones differ in their fighting abilities, much less how interclonal differences in morphology, agonistic behavior, and allotypic identity influence dominance relationships. In this study, we first characterize dominance relationships and underlying patterns of behavioral and morphological variation among clones of *A. elegantissima*. Using clonal replicates of each genotype, we determine whether the propensity to initiate an acrorhagial response toward nonclonemates varies among clones and in different interclonal combinations, whether the propensity to attack or retaliate is related to the final outcome of an encounter, and how morphological attributes such as size and numbers of acrorhagi affect the outcomes of interclonal contests. We then experimentally test whether the agonistic response can be modified—either in the form of habituation (tolerance) or a heightened response—by repeated encounters with members of different clones. Finally, we consider how fixed and inducible interclonal differences in agonistic behavior and outcomes can influence the maintenance of clonal diversity in *A. elegantissima*.

METHODS

Collection and Maintenance of Animals

We sampled anemones from the centers of 10 aggregations (clones A–J), seven of which were known to be male (A–G), within a large local population at Doran

Rocks, approximately 4 km south of the Bodega Marine Laboratory, Bodega Bay, California (31°18′ N, 123°03′ W). The Doran Rocks site stretches along nearly 800 m of shore, with variously sized intertidal boulders separated from one another by uninhabitable substrata consisting of small cobbles or sand.

We collected individual anemones by gently levering them from the rock surface, using a small spatula or screwdriver. We then scraped their pedal disks clean of algae and other foreign material before transporting them to the lab in 4-L plastic bags, one-third filled with seawater. We discarded any anemones with damaged disks or columns, placed all other anemones in recirculating seawater aquaria (13°–14°C with a 12L:12D schedule), and gave them 24 h to attach to small (≈2–4 cm in diameter), flat pebbles. During subsequent experiments, we maintained animals under these conditions for up to 14 d without feeding.

Electrophoretic analyses of *Anthopleura elegantissima* at this and other sites reveal that populations consist of many hundreds of clones (Sebens 1982*b;* Smith and Potts 1987; R. K. Grosberg and D. J. Ayre, unpublished results). Clones are typically confined to spatially discrete boulders or are separated by an interclonal boundary (sensu Francis 1973*a*, 1973*b*) when in contact on the same rock.

Aggregations A–G each inhabited a different boulder, separated from other boulders by sand. At least 20 m of shoreline intervened between each of the sampled aggregations. We selected these aggregations because they contained central polyps (i.e., more than two anemone diameters from any border) of approximately the same size. We chose to use these central polyps because, unlike the peripheral "warrior" polyps described by Francis (1976), they were unlikely to have recently encountered nonclonemates. This should minimize the chance for morphological and behavioral modifications elicited by prior contact with nonclonemates.

Genetic Identities of Aggregations

We used horizontal starch gel electrophoresis to confirm that each aggregation was genetically distinct from all of the others included in this study and to ensure that members of each aggregation were clonemates. At the conclusion of the experiments described below, we prepared tissue extracts from six anemones from each putative clone, as described by Black and Johnson (1979). To prepare and stain the gels, we followed the general protocols of Harris and Hopkinson (1976); we used buffer recipes from Selander et al. (1971) and followed their numbering system. We screened the anemones for 10 enzyme systems and a total of 11 variable enzyme-encoding loci. (We numbered loci, and lettered alleles in order of decreasing electrophoretic mobility.) Four of the variable loci—malate dehydrogenase (*Mdh-1* and *Mdh-2;* EC 1.1.1.37), octopine dehydrogenase (*Odh;* EC 1.5.1.11), and 6-phosphogluconate dehydrogenase (*6-Pgd;* EC 1.1.1.44)—gave the clearest bands on buffer system 5. Buffer system 6 gave the best results for three additional variable loci—xanthine oxidase (*Xo;* EC 1.2.3.2), leucine aminopeptidase (*Lap-2;* EC 3.4.11), and leucyl alanine peptidase (*Pep La;* EC 3.4.11). The remaining three variable loci—glucosephosphate isomerase (*Gpi-1* and *Gpi-2;* EC 5.3.1.9), phosphoglucomutase (*Pgm;* EC 2.7.5.1), and mannose phosphate isomerase (*Mpi;* EC 5.3.1.8)—were assayed on buffer system 9.

TABLE 1

GENOTYPES OF 10 CLONES OF *ANTHOPLEURA ELEGANTISSIMA* BASED ON ELECTROPHORETIC ANALYSIS FOR 11 VARIABLE ENZYME-ENCODING LOCI

Clone	*Mdh-1*	*Mdh-2*	*6-Pgd*	*Pep La*	*Lap-2*	*Mpi*	*Pgm*	*Gpi-1*	*Gpi-2*	*Xo*	*Odh*
A	bb	aa	ab	aa	bb	ab	bb	aa	aa	ab	bb
B	bb	aa	aa	bb	ab	bb	bb	aa	aa	bb	bb
C	aa	aa	bb	ab	aa	bc	ab	ab	ab	bb	bb
D	bb	ab	bb	aa	aa	bc	bb	aa	aa	ab	bb
E	bb	aa	ab	aa	bb	ab	bb	aa	aa	bb	bb
F	bb	aa	bb	bb	bb	ab	aa	aa	aa	bb	bb
G	bb	ab	bb	aa	aa	bc	ab	aa	aa	ab	bb
H	bb	aa	bb	aa	bb	bc	bc	ab	ab	aa	ab
I	bb	ab	bb	bb	aa	bc	ac	bc	bd	aa	. . .*
J	bb	aa	aa	ab	bb	bc	bc	bb	cc	aa	. . .*

NOTE.—We assayed six individual polyps of each clone. With the exception of one individual of clone E (which displayed a genotype identical to that of clone D), all replicates were identical.

* No activity.

Electromorph banding patterns for most of the variable loci fit the descriptions of Smith and Potts (1987). Under our assay conditions, however, each allelic band at the *Mdh-2* locus was accompanied by two apparent satellite bands (as described in other anemones [Hunt and Ayre 1989]). Unlike Smith and Potts (1987), who report variation at the xanthine dehydrogenase locus, we failed to detect activity for this enzyme.

All of the 10 aggregations (putative clones) differed electrophoretically for at least one enzyme locus, and, with a single exception, all of the replicates from within each aggregation were genetically identical (table 1). In addition, each of the clones differed in its pattern of color markings (Francis 1973*a*). We therefore considered each of the aggregations to represent a separate clone. The exception was a single individual from aggregation E, which displayed a multilocus electrophoretic profile identical to that characteristic of aggregation D. These anemones were frozen at the conclusion of the dominance hierarchy experiment (see below); up until that time, members of clones D and E had been completely separated. Consequently, we assume that we incorrectly labeled this animal when preparing it for electrophoretic analysis.

Experimental Designs

Interclonal dominance trials.—To determine the dominance ranks of clones collected from the field and the consistencies of such rankings, we paired anemones from each of seven clones (A–G) in all possible combinations. We also examined whether clonal characteristics such as the mass of individual polyps and number of acrorhagi affected the outcomes of pairwise interactions.

We initially collected at least 250 anemones from each clone and placed the anemones from different clones in separate aquaria prior to the start of the experiment. During this period, the anemones in each aquarium lived at naturally high densities and hence contacted the tentacles of at least one other clonemate at all times. Although we noted some apparently spontaneous acrorhagial inflation (also

reported by Francis [1973*a*]), no actual fighting occurred that resulted in ectodermal peeling and scarring.

After 10 d in the aquaria, in what amounts to a round-robin tournament, we paired single anemones from each of the seven clones with members of the other six clones. For each possible interclonal combination (21 in all), we initiated eight replicate contests, for a total of 168 pairings involving 336 anemones. No anemone was used in more than a single contest. We haphazardly assigned anemones from each clone to each of six possible interclonal combinations. For each clone, the mean weights of the six groups of eight anemones did not significantly differ (single-factor ANOVAs; all P's $> .05$).

We allowed the pairs to remain in contact for 24 h, or until one anemone attacked and defeated its opponent. We observed these contests at 1-min intervals for the first 2 h of contact, and less frequently after that. At each observation we recorded whether one or both individuals behaved aggressively, whether an acrorhagial peel occurred (i.e., a completed attack), and whether one or both anemones moved out of the range of attack. At the end of each trial, we judged an anemone to have won its contest if its opponent was both scarred and had moved away onto the floor of the aquarium (the most common outcome), or if the opponent was both scarred and had moved out of tentacular reach of the aggressor by changing its posture. We scored three classes of interaction as "unresolved": cases in which animals remained in contact for the duration of the trial, cases in which both anemones moved apart, and cases in which one animal moved away but showed no signs of acrorhagial scarring.

We used two methods to construct a dominance hierarchy from the round-robin tournament. In the first procedure, which is basically analogous to match play in golf, the winner of a "match" (i.e., the eight replicate contests that constitute a match, or combination) is the clone that wins the most pairwise contests in the match. Our match scoring approach weighted each interclonal combination (six for each of the seven clones) equally by assigning an entire clone a win (a score of one) or loss (a score of zero) based on whether a clone won or lost more of the eight replicate contests in a combination (i.e., a match) than its counterpart. At the extreme, a clone could receive a score of one both if it won a single one of eight replicate contests (but lost none) and if it won all eight replicate contests. When neither clone won more replicate contests than the other, both clones received a score of 0.5. When neither clone responded to the other in all replicate contests in a combination, we once again assigned a score of 0.5 to each clone. Scores could thus range from zero to six. To construct an overall ranking, we summed the scores for each clone and ranked the clones from highest to lowest total score. This scoring approach emphasizes the overall outcome of a multicontest match and ignores the fact that an outcome scored as an overall victory (or loss) could involve very different ratios of wins to losses in each interclonal combination. For example, an outcome scored as a victory could be accompanied by no losses, or as many as three losses.

An alternative to the match play scoring approach is "medal play." Medal play assigned equal weight to all replicate contests of a combination, giving a score of one to a clone for each contest in which it was victorious and a score of zero

for each loss. Unresolved individual contests received a score of 0.5. Thus, clonal scores could range between zero and 48 (six unique interclonal combinations per clone times eight replicate contests). In contrast to the match play approach, medal play emphasizes overall win/loss records for all contests in all combinations. In so doing, this scoring approach gives greater weight to combinations in which the win/loss differential is largest.

At the end of the 24-h trial, we dissected the anemones to expose their coelenterons, blotted off any excess water, and weighed them. We also checked for the presence of acrorhagial scarring. We froze six additional (i.e., not used in the trials) individuals from each clone pending electrophoretic determination of their genotype (see *Genetic Identities of Aggregations*) and relaxed 10 more polyps in 10% $MgSO_4$ for several hours to allow counts of their acrorhagi.

Effects of repeated stimulation on agonistic behavior.—This experiment characterized clone-specific patterns of response to initial and repeated contacts with other clones and hence tested for the existence of clone-specific memory and tolerance in the acrorhagial response. We examined the responses of six (A–F) of the seven clones (A–G) used in the dominance hierarchy study described previously.

Four days after the field collection of the 250 central individuals from clones A–G, we haphazardly selected anemones from clones A–F and initially assigned five or six anemones in each clone to each of four treatments (fig. 1):

1. The specific memory treatment assayed the effects of daily stimulation by members of a single counterpart clone on the acrorhagial response of six members of a given clone. We paired clones (A with B, C with D, and E with F) and stimulated each individual by contact with tissue from the alternative clone for up to 10 min per day, for 5 consecutive days. On days 1–4, stimulation involved placing each anemone in tentacular contact with an intact individual from the specific memory group of the alternative clone. We ensured that no anemone from a given clone contacted the same member of the alternative clone more than once during this period of initial stimulation. The pairing of intact individuals typically elicits an acrorhagial response from only one member of the pair. On days 1, 2, and 4, we recorded the time taken for the first individual of each pair to complete a successful acrorhagial peel onto its nonclonemate partner. At that time, we separated the contestants. If neither individual in a contest completed an acrorhagial peel, we separated the contestants after 10 min of contact. In both cases, we discontinued stimulation until the next day.

On day 5, we stimulated each of the six anemones, using an excised segment of column and tentacular tissue from a previously unused member of the alternate clone rather than an intact anemone. We used this method of stimulation on day 5 in this treatment, and all others, to allow scoring of the acrorhagial response of the stimulated clone independently of the behavior of the clone used to stimulate it. This final stimulation involved 10 s of contact, at 1-min intervals, for 10 min, or until the stimulated anemone completed an acrorhagial response onto the piece of stimulating tissue.

2. In the specific memory control treatment, to assess whether repeated stimulation altered the rate of acrorhagial response, control groups of five anemones

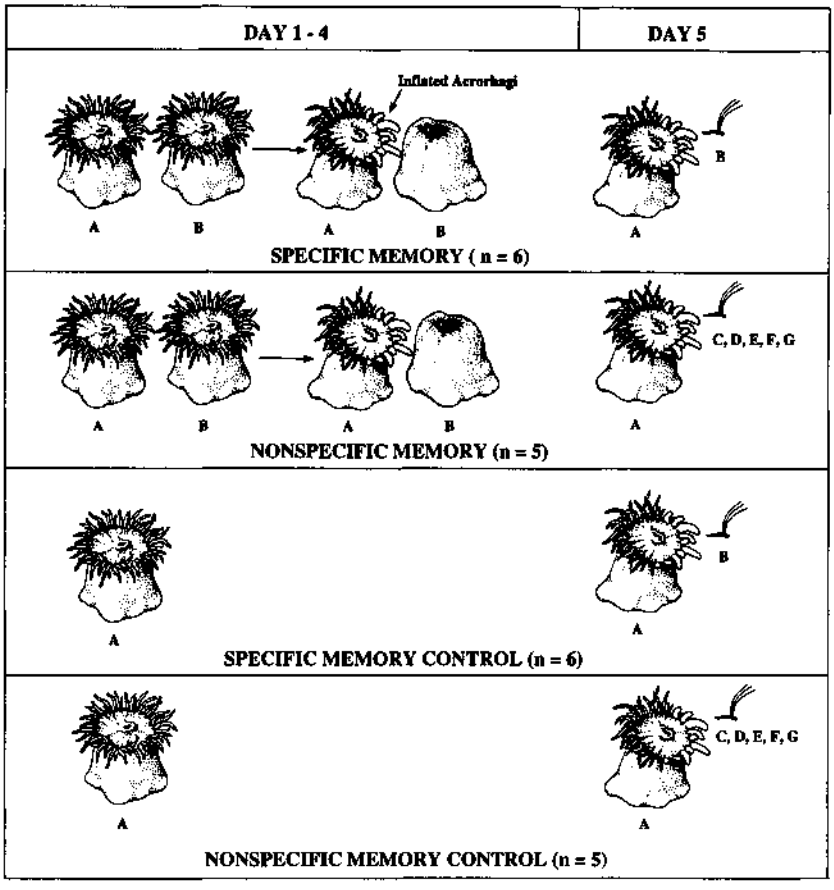

FIG. 1.—Protocol for the repeated stimulation experiment. For each of six clones (A–F), we allocated randomly selected groups of polyps to four treatments. This figure shows the protocol for clone A only, with letters below polyps (and forceps) identifying clones. In both the specific memory and nonspecific memory treatments, we stimulated polyps of clone A with an intact individual of its alternate clone, B, on days 1–4 for 10 min on each day. We did not stimulate polyps in the specific memory control or nonspecific memory control treatments during the first 4 d. On day 5, we stimulated polyps of clone A for 10 min with excised tentacular tissue from clone B polyps (specific memory and specific memory control treatments) or excised tentacular tissue of polyps from one of five other clones (nonspecific memory and nonspecific memory control treatments).

from each clone received no stimulation until day 5, when they were exposed to excised tissue of their respective alternate clones. As in the previous treatment, we observed whether members of the stimulated clone mounted an acrorhagial response, and, if so, how long it took for a full response.

To determine whether the acrorhagial responses measured in each of the stimulated clones in the specific memory and specific memory control treatments were indeed specific to their alternate clones or were simply generalized effects that could have been elicited by any nonclonemate, we used two further treatments:

3. In the nonspecific memory treatment, we stimulated five anemones on days 1–4 by exposing them to intact individuals of their alternate clones (as in the specific memory treatment). On day 5, we stimulated each of these individuals by exposure to one of the five remaining clones (including clone G) that was not an alternate clone used in the initial 4 d of stimulation. As before, we determined whether there was an acrorhagial response, and, if so, how long it took for the stimulated individual to complete an attack.

4. In the nonspecific memory control treatment, as in treatment 2, we stimulated the control group only on day 5 (using five clones, including clone G), and only with excised tissue taken from nonclonemates that had been isolated until that time.

Immediately following the conclusion of this experiment, we measured wet weights of all polyps using the methods described above under *Interclonal dominance trials*. At this time, we also examined under a dissecting microscope the ripe gonads of each anemone to determine gender.

RESULTS

Interclonal Dominance Trials

Overall frequencies of agonistic behavior.—Most of the interclonal combinations (19 of 21) produced an agonistic response in at least some of the replicate contests, and most of the replicate contests within each interclonal combination elicited agonistic behavior, judged by the presence of acrorhagial scars on one, or both, contestants (fig. 2). Two combinations—A versus E and D versus G—did not elicit an agonistic response from either clone (see *Interclonal variation in agonistic behavior*, below). All told, 149 of 168 contests (89%) showed aggression, and all clones—in at least some combinations with other clones—displayed the full repertoire of agonistic behavior. Seventy-seven percent ($n = 129$) of the 168 contests yielded clear victories after 24 h (fig. 2). Of those contests with a unilateral victor, 71 of 129 (55%) gave decisive outcomes within the first hour of contact. The victor usually was the only anemone that attacked. However, both anemones attacked and scarred their opponents in 47 (28%) contests; in 23 of these 47 (49%) contests that involved retaliatory attacks, a draw ensued. In 10 of the remaining 24 cases that involved bilateral attacks, the anemone that responded second eventually won the encounter.

Dominance rankings.—Clones differed dramatically in their fighting abilities, as reflected in the dominance hierarchies shown in figure 2, and regardless of the scoring method used to construct the hierarchy. For example, the rankings of the most dominant (B and F) and subordinate (C and D) clones did not vary with the ranking method (fig. 2). The ranks of the three intermediate clones—A, E, and G—varied slightly according to the method used to construct the hierarchy. For instance, clone E ranked third on the basis of medal play, whereas it tied for fourth (with clone G) on the basis of the match method (fig. 2).

The extent to which overall dominance rankings can be used to predict the outcomes of specific interclonal combinations will be influenced by both the frequency of intransitive dominance relationships among clones (i.e., A > B, B >

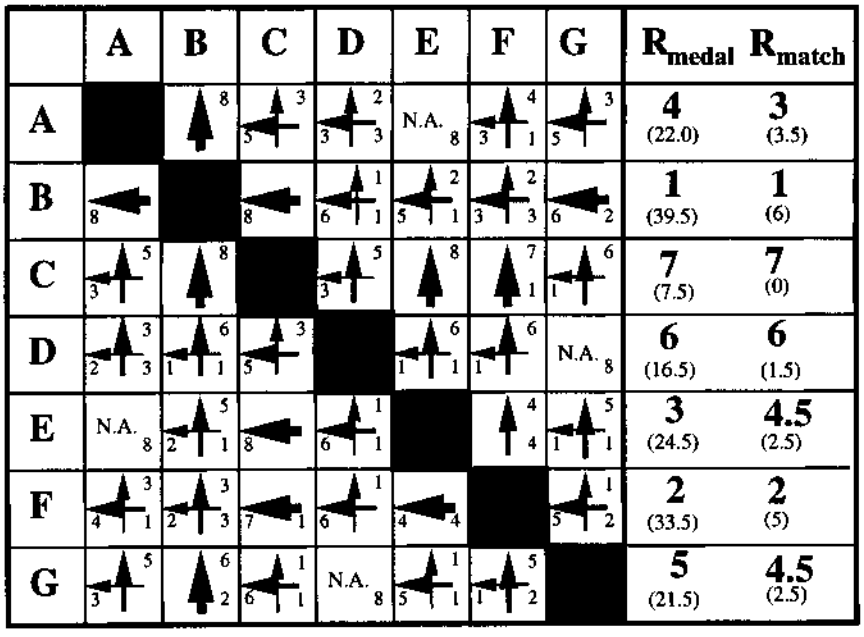

FIG. 2.—Interclonal dominance hierarchy for clones A–G of the anemone *Anthopleura elegantissima*. For each interclonal combination, arrows indicate the victors in 24-h contests between eight randomly selected pairs of polyps. The sizes of the arrows are proportional to the numbers of victories. The values in the top right, bottom left, and bottom right of each cell correspond, respectively, to the number of contests won by the clone indicated in the column, the number of contests by the clone indicated in the row, and the number of unresolved contests between the two clones. We ranked clones on the basis of success across all interclonal pairings (R_{medal}) and all interclonal combinations (R_{match}). We show the complete matrix to simplify interpretation of the performance of individual clones.

C, but C > A) and the consistency of dominance relationships among the replicate contests in an interclonal combination. If relationships are primarily transitive and the outcomes of replicate contests are consistent, then overall rankings should be reliable predictors of the outcomes of interclonal contests. On the other hand, if there are numerous intransitivities, or outcomes among replicate contests vary, then predictions of specific pairwise outcomes will be less reliable. At the level of interclonal combinations, the match and medal ranking procedures revealed no intransitivities (fig. 2). In 18 of the 21 possible combinations, the rankings correctly predict the outcome of each combination (fig. 2). With the exception of combinations involving identically ranked clones, or combinations that do not elicit aggression, overall rankings reliably predict the outcomes of all interclonal combinations for which predictions can be made.

Interclonal variation in agonistic behavior.—The use of a simple hierarchy to characterize dominance relationships reflects only the outcomes of agonistic encounters and therefore masks many aspects of behavioral variation underlying differences in outcome. As we report below, there are distinctive behavioral

patterns that characterize several clones, especially with respect to the sequence of, and propensity for, acrorhagial deployment. Nevertheless, the expression of some aspects of a clone's agonistic behavior can vary with the clonal identity of an opponent.

The highest-ranked clones, B and F, display the most striking and consistent contrasts in clone-specific behaviors. Clone B attacked its opponent in 46 of 48 contests and was the first to attack in 41 of the 44 cases in which we could determine the order of attack. Like clone B, second-ranked clone F attacked its opponent in 44 of 47 scorable contests; however, in contrast to clone B, clone F attacked second (i.e., retaliated) in a significantly greater proportion of cases (at least 16 of 44 attacks; $\chi^2 = 9.6$, df = 1, $P < .005$, with Yates's correction). All told, of the 47 retaliatory attacks we documented, 24 involved clone F, significantly more than involved any other clone ($\chi^2 = 10.8$, $P < .005$). The remaining clones tended to attack much less frequently than the top-ranked clones; notably, clone C, the lowest-ranked clone, attacked in only 12 of 48 contests (cf. 46 and 44 for clones B and F, respectively; χ^2 for clone B = 47.4, $P < .001$; χ^2 for clone F = 41.2; $P < .001$).

A more detailed analysis of behavioral variation at the level of specific interclonal combinations reveals three additional noteworthy patterns. First, as mentioned earlier, there are two interclonal combinations (A vs. E and D vs. G) in which neither clone responded agonistically, despite the fact both clones behaved agonistically in other interclonal combinations. However, the nature of contests between clones A and E, and between clones D and G, differed substantially. Contests between clones A and E resembled an interaction between clonemates, with anemones remaining in tentacular contact (often with their tentacles fully expanded) for up to 24 h with no detectable acrorhagial inflation. Eighteen days later, we repeated this interclonal combination with previously untested members of clones A and E. In this case, five of six pairs remained passively in contact for 24 h, but one member of clone E attacked its partner from clone A 25 min after first contact. In contrast, all contests between clones D and G produced a series of tentacular contacts and withdrawals, followed by each anemone crawling out of tentacular reach of the other.

Second, the incidence of retaliatory attacks (or counterattacks) varies substantially among interclonal combinations. For example, seven of eight pairings between the top-ranked clones, B and F, elicited retaliatory attacks. Likewise, six of eight pairings between clones E and F led to retaliation and scarring of both contestants. Indeed, of the 47 contests that featured retaliation, 18 occurred in only three of the 21 interclonal combinations, all of which involved clone F. In each of the other 18 interclonal combinations, retaliation occurred in a maximum of three contests in each combination.

Third, the time to deploy acrorhagi varied markedly for a given clone, depending on the clonal identity of its opponent. Although this pattern appears in most clones, it is easiest to analyze for clone B, both because this clone showed the highest incidence of agonistic response, and, in virtually all cases, it initiated an attack. For clone B, the mean time to deployment of acrorhagi differed significantly among interclonal combinations (single-factor ANOVA: $F = 270.495$, df

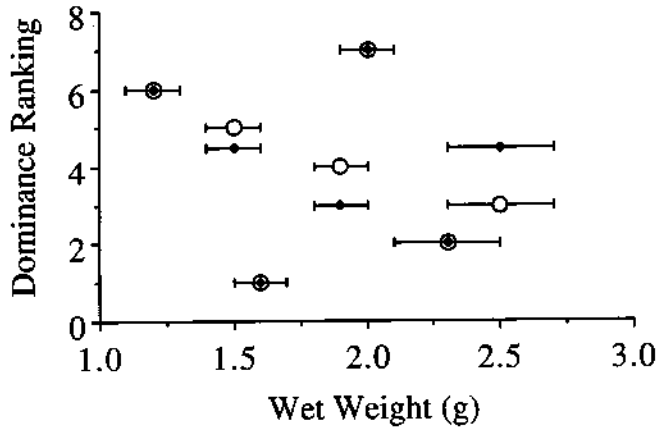

FIG. 3.—Mean wet weight (± SE) vs. dominance ranking for clones A–F of the sea anemone *Anthopleura elegantissima*. We ranked clones on the basis of success across all interclonal pairings (R_{medal}; *open circles*) and all interclonal combinations (R_{match}; *closed diamonds*).

= 5,35, $P < .0001$), ranging from 11.5 ± 2.9 min ($\bar{X}$ ± SE) against clone A to 95.2 ± 3.0 against clone D.

Effects of Polyp Weight and Acrorhagial Numbers on Dominance Rankings and Response Times

The mean weights of individual anemones differed significantly among the seven clones used to construct the dominance hierarchy (single-factor ANOVA: $F = 13.652$, df = 6, 329, $P < .0001$; fig. 3). Dominance rankings, however, did not predictably vary with anemone weight (medal ranking: Spearman rank correlation, $r_s = -0.321$, $P = .431$; match ranking: $r_s = -0.126$, $P = .757$). Polyps from the dominant clone B were, on the average, smaller (1.6 ± 0.1 g) than those of each of four subordinate clones, including the seventh-ranked clone C (2.0 ± 0.1 g). Furthermore, across all contests that had a clear victor (n = 129), the smaller anemone won in 54 cases. In contests that involved retaliation and bilateral scarring, the larger anemone of the pair won in 18 cases, but lost in nine. Nevertheless, this difference was not significant (binomial test: Z [two-tailed] = 1.63, $P > .1$).

On the basis of random samples of 10 polyps taken from each of the seven clones, the mean number of acrorhagi varied significantly among the clones (single-factor ANOVA: $F = 7.298$, df = 6,63, $P < .0001$). Despite the fact that the middle-ranked clone E had the greatest number of acrorhagi (Scheffe's F-test: $P < .05$), higher-ranked clones typically had more acrorhagi than lower-ranked ones (fig. 4). If medal ranking is used to produce the dominance hierarchy and clone E is included, $r_s = 0.88$ ($P = .031$); without clone E, $r_s = 0.99$ ($P = .028$). If match ranking is used and clone E is included, $r_s = 0.70$ ($P = .086$); excluding clone E from this analysis gives $r_s = 0.99$ ($P = .028$). Including only those responses in which an individual polyp was the first to attack in the pairing, we

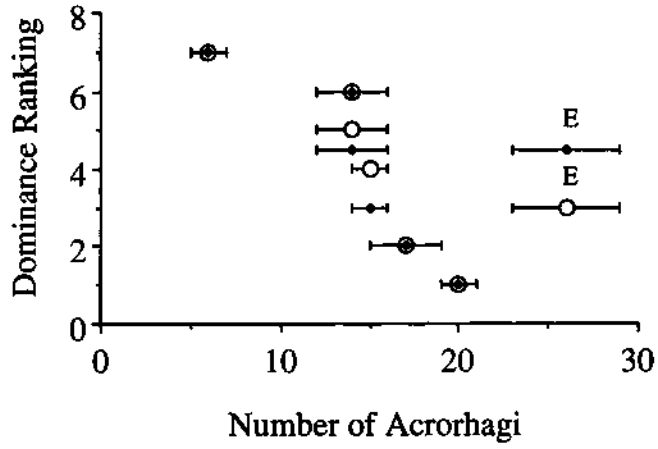

FIG. 4.—Mean number of acrorhagi (± SE) vs. dominance ranking for seven clones (A–F) of the sea anemone *Anthopleura elegantissima*. We ranked clones on the basis of success across all interclonal pairings (R_{medal}; *open circles*) and all interclonal combinations (R_{match}; *closed diamonds*).

found no evidence in any of the clones for a relationship between individual polyp weight and the measured time to a first attack (all $r^2 < 0.1$; all $P > .5$).

Effects of Repeated Stimulation on the Expression of Agonistic Behavior

Specific memory and nonspecific memory treatments: days 1–4.—For these two treatments, we stimulated polyps on 4 consecutive days (for up to 10 min daily) by placing them in tentacular contact with intact polyps of their alternate clone in each of three interclonal pairings (A vs. B; C vs. D; E vs. F). We found substantial interclonal variation in the proportion of individuals in the three interclonal pairings that responded aggressively to both initial and repeated contact with an intact nonclonemate (fig. 5). By the fourth day of stimulation, the proportion of polyps in clones B, C, E, and F that completed an aggressive response had increased over that on the first day (fig. 5). For example, in the contests between clones A and B, clone B responded aggressively on the first day of stimulation in three of 10 scorable pairings. On the second and fourth days of stimulation, clone B reacted agonistically toward clone A in nine of 10 scorable pairings.

All treatments: day 5.—We continued the experiment using groups of five or six replicate polyps from the four clones (B, C, E, and F) in which at least some individuals had completed an aggressive response in the first 4 d. We assessed the responsiveness of previously stimulated members of each clone by again stimulating individual polyps with excised tissue of their alternate clone (specific memory treatment) or a novel clone (nonspecific memory treatment). We also measured the responses of polyps in two control groups of previously unstimulated polyps, which we stimulated with tissue from their alternate clone (specific memory control treatment) and tissue from a novel clone (nonspecific memory

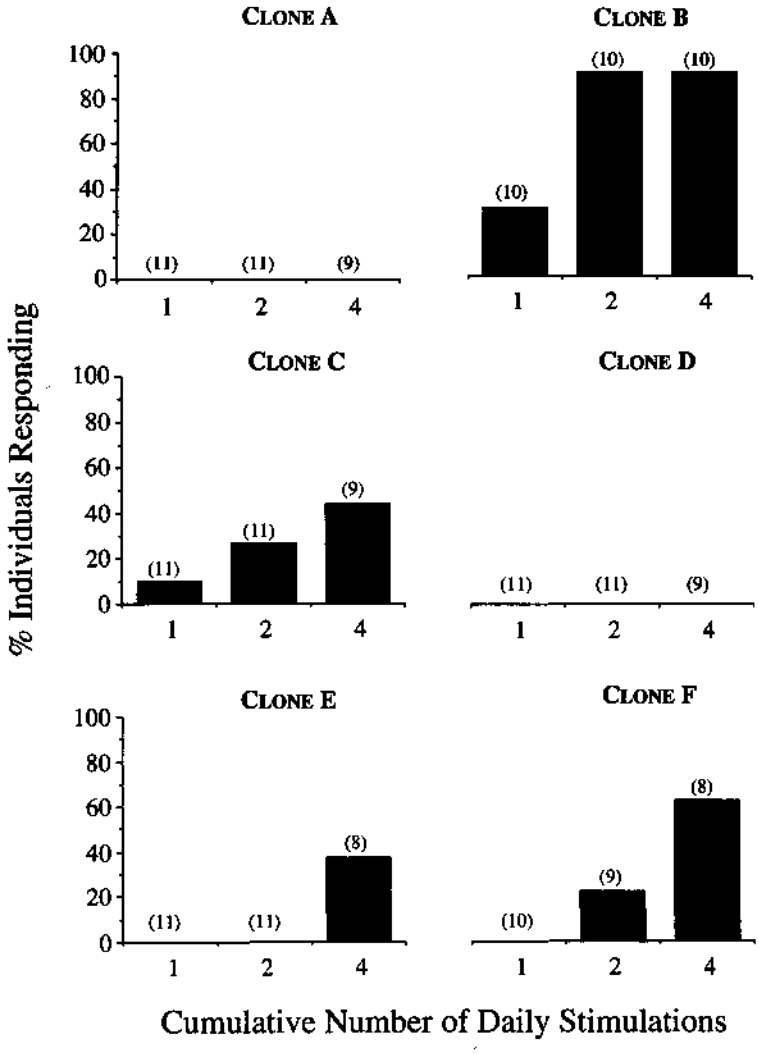

FIG. 5.—The percentage of individual polyps in each of the six clones (A–F) that completed an acrorhagial response within the 10-min period of stimulation by an intact polyp from their alternate clones, on the first, second, and fourth days of stimulation. Sample sizes (in parentheses) denote the number of polyps that remained expanded for the full 10 min of stimulation. The stimulated polyps were from the specific memory and nonspecific memory treatments described in fig. 1.

control treatment). In no case did excised isoclonal tissue elicit an acrorhagial response (unreported data).

To determine whether the responsiveness of each of these four clones varied across treatments, we used a Kruskal-Wallis nonparametric ANOVA based on ranked time to respond. We measured responsiveness as the time necessary to complete an agonistic response. Polyps that did not complete a response within

TABLE 2

NUMBER OF *ANTHOPLEURA ELEGANTISSIMA* POLYPS THAT COMPLETED AN ACRORHAGIAL ATTACK IN FOUR DIFFERENT ALLOGENEIC STIMULATION TREATMENTS

		TREATMENT			
TEST CLONE	ALTERNATE CLONE	Specific Memory (n = 6)	Specific Memory Control (n = 5)	Nonspecific Memory (n = 6)	Nonspecific Memory Control (n = 5)
B	A	1 (305)	5 (491)	5 (320)	2 (405)
C	D	2 (386)	4 (387)	2 (396)	1 (303)
E	F*	5 (456)	0	2 (407)	1 (521)
F	E*	4 (367)	0	2 (435)	0

NOTE.—We measured the responses of groups of five or six polyps of each of four test clones (B, C, E, F) during 10 min of exposure to the excised tissue of their alternate clone (specific memory and specific memory control treatments) or one of five other clones (nonspecific memory and nonspecific memory control treatments). Figures in parentheses are the mean time (s) to complete attacks for those polyps responding within the 10-min period of stimulation.

* Responsivenesses of the four treatment groups were significantly heterogeneous ($P < .05$) as judged by Kruskal-Wallis nonparametric ANOVA.

10 min received a time of 10 min plus 1 s, and so all share the highest rank in the analysis. In terms of the total number of polyps that responded across all four treatments, clones E and F were the least responsive clones. However, they were also the only clones to show statistically significant heterogeneity in time to respond (Kruskal-Wallis ANOVA, $P < .05$; table 2). Nonparametric multiple comparisons tests (Siegel and Castellan 1988, pp. 213–214) for these two clones failed to reveal which pairs of treatments differed significantly. Nevertheless, both clones exhibited the greatest responsiveness in the specific memory treatments. For each of these two clones, repeated stimulation by their alternate clone (specific memory treatment) produced the greatest number of definitive responses on day 5 (i.e., five of six pairings for clone E and four of six pairings for clone F). Exposure of previously stimulated individuals to the tissue of a novel nonclonemate (i.e., the nonspecific memory treatment) produced the next greatest number of responses (two of four in both clones E and F), but only one of 22 tested animals in both clones responded aggressively in either of the control treatments (table 2). Clone C was the second most responsive clone (11 of 22 animals tested, with at least one animal responding in each of the four treatments). However, in contrast to clones E and F, the times to respond were quite similar across treatments (Kruskal-Wallis ANOVA: $P > .5$; table 2).

Clone B, as in the earlier phase of the experiment, was the most responsive clone on day 5, with a total of 13 of 22 polyps producing an acrorhagial response (table 2). However, only one of six clone B anemones responded to repeated stimulation by clone A (i.e., the specific memory treatment). This overall lack of response to members of clone A contrasts with the results on day 4, when nine of 10 of such continuously stimulated anemones attacked their clone A opponents. Furthermore, in both the specific memory control and nonspecific memory treatments, 10 of 11 pairings elicited an acrorhagial response from clone B.

TABLE 3

NUMBER OF CLONE B POLYPS THAT COMPLETED AN ACRORHAGIAL ATTACK IN THE SECOND ALLOGENEIC STIMULATION EXPERIMENT

DAYS OF STIMULATION	TREATMENT			
	Specific Memory	Specific Memory Control	Nonspecific Memory	Nonspecific Memory Control
3	6 (383)	0*		
5	2[a] (155)	0[a]	5[b] (645)	0[a,†]

NOTE.—We measured the responses of groups of eight clone B polyps during 10 min of exposure to the excised tissue of clone A polyps (specific memory and specific memory control treatments) or one of eight other clones (C–J; nonspecific memory and nonspecific memory control treatments). On day 3 we used only the specific memory and specific memory control treatments. Figures in parentheses are the mean time (s) to complete attacks for those polyps responding within the 10-min period of stimulation. Shared superscript letters indicate treatments that were judged not significantly different ($P > .05$) by Tukey-type nonparametric multiple comparisons test.

* Treatments significantly heterogeneous as judged by Mann-Whitney U-test ($P < .005$).

† Treatments significantly heterogeneous as judged by Kruskal-Wallis nonparametric ANOVA ($P < .02$).

The results of the specific memory treatment in the context of the other treatments imply that the response of clone B to clone A had been enhanced up to day 4 by repeated exposure, but by day 5, clone B had developed a specific loss of responsiveness (i.e., tolerance) to clone B. Nevertheless, there was, at best, marginally significant variation in responsiveness among the four treatments (Kruskal-Wallis ANOVA: $P = .063$; table 2). Consequently, we repeated the experiment 10 d later, using a slightly modified experimental design. In this trial, we increased the number of anemones per treatment to eight, and polyps from clones C–J provided nonspecific stimulation. We also assigned two additional groups of eight clone B anemones to specific memory and specific memory control treatments, and we tested these individuals against excised tissue on day 3 rather than day 5.

This repeat trial for clone B once again demonstrated initial enhancement, relative to controls, of aggressive behavior directed toward clone A, and the later onset of clone-specific tolerance toward clone A (table 3). During the enhancement phase, six of eight anemones responded on the third day of repeated stimulation by clone A, whereas none of the eight control anemones responded (Mann-Whitney test: $P < .005$; table 3). After 5 d of repeated stimulation by clone A, there was significant overall heterogeneity among treatments (Kruskal-Wallis ANOVA: $P < .02$). However, in contrast to the apparent enhancement of response after the first 3 d of stimulation, by day 5, the pattern changed, with only two of eight anemones responding in the specific memory treatment. This lack of response after 5 d appears to reflect the development of tolerance, rather than a general decrease in responsiveness, because the nonspecific memory treatment group was the most responsive (nonparametric Tukey-type multiple comparison [Zar 1984, p. 199]: $P < .05$; table 3).

DISCUSSION

If the outcomes of interclonal agonistic encounters in benthic cnidarians are the primary determinants of clonal fitness, then at competitive equilibrium the maintenance of locally high levels of clonal diversity requires either that coexisting clones exhibit comparable fighting ability, or—to a greater or lesser degree—not be mutually aggressive. The interclonal dominance trials suggest that the first explanation alone is not generally plausible in *Anthopleura elegantissima*, because allogeneically naive polyps taken from the centers of clones differ dramatically in their fighting ability. The results of the dominance trials reveal a transitive hierarchy of competitive relationships among the seven tested clones, underlain by repeatable variation in clone-specific agonistic behaviors. This variation minimally encompasses fixed, clone-specific variation in the tendency both to initiate an agonistic attack and to retaliate against a first attack by an opponent. For instance, the two most aggressive (both as first attackers and retaliators) clones, B and F, were overall the top-ranked clones. This facet of the study also shows that the expression of differences in agonistic behavior often depends on the clonal identity of an opponent; in some interclonal combinations, naive polyps do not fight; and standoffs and reversals in outcomes occur in numerous pairings. For example, although one clone won the majority of contests in 15 of the 19 interclonal combinations, only five of the 15 were significant majorities. In behavioral terms, our study indicates that reversals and standoffs, along with clone-dependent expression of aggression, interact with fixed patterns of agonism to determine dominance rankings among naive polyps under laboratory conditions.

Other studies suggest that morphological traits, such as size or weight (see, e.g., Brace et al. 1979), differences in growth form (Hauenschild 1954; Ivker 1972; Francis 1976; Buss et al. 1984; Willis and Ayre 1985; Buss and Grosberg 1990; Yund 1991), and numbers of acrorhagi (Francis 1976), can also affect outcomes of intraspecific agonistic contests and dominance rankings. As in *Anthopleura krebsi* (Bigger 1980) and *Actinia tenebrosa* (Ayre 1982), our study of *A. elegantissima* failed to show any statistically significant effects of weight on time to response, outcome of contests, and overall dominance ranking. However, the dominance rankings of clones did correlate strongly with mean number of acrorhagi in naive (i.e., previously unstimulated) polyps. Thus, interclonal variation in morphology—specifically, numbers of acrorhagi—together with interclonal differences in innate behavior, can account for the pattern of completely transitive interclonal dominance shown by both the match and medal rankings.

Beyond the influence of fixed behavioral and morphological differences among clones on outcomes of agonistic encounters, our study further shows that repeated stimulation by another clone can specifically modify the agonistic response of individual polyps, but only toward that clone. These patterns of acquired behavioral change demonstrate clone-specific memory in the form of habituation (clone B vs. clone A) and strongly suggest that enhancement also occurs (clone E vs. clone F and clone F vs. clone E). Other studies on cnidarians, including the scleractinian coral *Montipora verrucosa* (Hildemann et al. 1977, 1980), the gorgonian *Swiftia exserta* (Salter-Cid and Bigger 1991), and three other anemo-

nes—*Metridium senile* (Purcell and Kitting 1982), *Anemonia sulcata* (Sauer et al. 1986), and *Actinia equina* (Brace and Santer 1991)—indicate that prior interactions with nonclonemates can either reduce or intensify agonistic behavior, but all leave open the question of whether there is specific memory or merely a nonspecific enhancement or diminution of response.

Taken together, our data show that simple conditional aggression, as first described by Francis (1973*a*, 1973*b*), fails to capture the complexity of agonistic behavior in *A. elegantissima*, and perhaps in cnidarians in general. In particular, the design of our study allowed us to distinguish three factors that explain interclonal and individual variation in the expression of aggression: innate morphological and behavioral variation among clones, behavioral variation intrinsic to particular interclonal combinations, and inducible behavioral variation among individual members of a clone. Although the results of previous studies on agonistic behavior in cnidarians suggest that several of these aspects of behavior and morphology can influence the outcomes of agonistic encounters, for the following reasons, these studies cannot reveal the scope of interclonal and individual variation in these, and other, aspects of agonistic behavior:

1. A uniform and unambiguous method of scoring must be used to characterize both the occurrence of aggression and the outcomes of interactions. In this study, we scored a positive agonistic response only when the full repertoire of agonistic behavior, through to peeling of the distal epithelium, was completed. Furthermore, we scored outcomes as decisive victories only when an opponent both was scarred and had moved away from its attacker. Several studies use incomplete acrorhagial responses (i.e., mere inflation of acrorhagi) as evidence of agonistic behavior (e.g., Brace et al. 1979; Brace 1981; Brace and Santer 1991); yet acrorhagial inflation need not lead to a full attack (D. J. Ayre and R. K. Grosberg, personal observation). Moreover, many previous studies score only the occurrence of an attack, and not the outcome (e.g., Bigger 1980; Brace and Santer 1991). In so doing, these studies—at the very least—do not allow for the possibility of retaliatory attacks. Our data show that retaliation can be a common behavior of certain clones (e.g., clone F) and interclonal combinations (clone B vs. clone F). Finally, some studies fail to distinguish between unilateral and bilateral responses (Hildemann et al. 1977; Purcell and Kitting 1982; Brace and Santer 1991).

2. Of comparable importance is the need to ensure that all putative clones are genotypically distinct. Our electrophoretic analysis showed that all of the clones used in this study differed genetically. In contrast, most previous studies of cnidarian agonistic behavior infer genotypic identity from either the coaggregation of individuals (e.g., Francis 1973*a;* Bigger 1980; Hildemann et al. 1980; Sauer et al. 1986; Brace and Santer 1991) or shared morphological characteristics (e.g., Francis 1973*a;* Bigger 1980; Purcell and Kitting 1982). Because members of different clones can be associated in natural populations (see, e.g., Purcell and Kitting 1982), and morphological variation in characters used to distinguish putative clones may not be genetically based (see, e.g., Heyward and Stoddart 1985), indirect inferences of clonal identities are suspect.

3. To distinguish between inter- and intraclonal sources of variation minimally

requires replication within interclonal combinations, as well as the use of different individuals for every replicate. To establish the dominance relationships, we used eight independent replicate pairs in all of the interclonal combinations (see also Bigger 1980; Willis and Ayre 1985). All other studies that report intraspecific variation in cnidarian agonistic behavior fail to replicate interclonal combinations (Sauer et al. 1986), use the same individuals repeatedly to "replicate" a particular interclonal combination (Brace 1981; Purcell and Kitting 1982), or use the same individuals in a series of different interclonal combinations (Bigger 1980).

4. To characterize the spectrum of behavioral repertoires, it may be necessary to examine a range of clones in a variety of interclonal combinations. When we conducted the dominance trials, we documented the behaviors of seven clones in all pairwise combinations. Some of these combinations revealed unique aspects of behavioral variation. For example, four of the clones in this study failed to behave agonistically toward one other clone but responded aggressively in the five other interclonal combinations. This shows that the absence of a response toward other clones is a relatively common phenomenon that is a normal aspect of interclonal interaction (cf. Francis 1973*a*).

5. An experimental design that can determine whether repeated stimulation by a nonclonemate modifies agonistic behavior, and—more important—whether such modifications represent specific memory, must include treatments that allow contrasts both between the effects of single and multiple stimulations and between specific (i.e., modified response toward a single alternate genotype) and nonspecific (i.e., modified response toward any alternate clone) stimulation. Several articles claiming to document modification of behaviors by repeated stimulation (e.g., Hildemann et al. 1980; Sauer et al. 1986) do compare responses of stimulated and unstimulated individuals; however, they fail to contrast the effects of specific and nonspecific stimulation. Moreover, given that there can be daily changes in the responsiveness of unstimulated individuals (Francis 1973*b*), it is essential to control for temporal variation in responsiveness that is independent of the treatment effects. In addition to the results of our study on *A. elegantissima*, only Salter-Cid and Bigger (1991) include such controls. Other studies (Hildemann et al. 1977; Sauer et al. 1986; Brace and Santer 1991) compare responses after repeated stimulations to initial responses of naive individuals; consequently, it is impossible to distinguish the effects of repeated stimulation from day-to-day changes in responsiveness that are independent of the treatments. Finally, the treatments should be replicated sufficiently (such that treatment effects can be statistically distinguished), and each replicate of each treatment must be truly causally independent. For example, if the same individual is used both to stimulate another clone and to assess responsiveness, then—to the extent that behaviors can be reciprocally modified by prior contact—the replicates of that treatment are not independent (see, e.g., Purcell and Kitting 1982; Sauer et al. 1986; Brace and Santer 1991).

From an evolutionary and ecological perspective, the question remains, as in many systems involving intraspecific competition in clonal plants (reviewed in Ellstrand and Roose 1987; Hamrick and Godt 1989), How, in both *A. elegantissima* and hydrozoans in the genus *Hydractinia* (Ivker 1972; Buss et al. 1984;

Yund et al. 1987; Yund and Parker 1989; Buss and Grosberg 1990; Yund 1991), is so much variation in so many aspects of agonistic behavior (and presumably interference competitive ability) maintained within a population of clones competing for an apparently simple resource such as space? Part of the explanation must lie in the complex and long-term dynamics of clonal establishment and expansion. Although individual polyps of *A. elegantissima* are relatively short-lived (a few years, according to Sebens 1982*b*), clones may be extremely long-lived and the time necessary to reach equilibrium so great that competitive exclusion would be difficult to observe (if it were ever achieved). Most studies, including our own, focus on relatively short-term interactions between individual polyps, whereas a more realistic analysis would include the entire ontogeny of a clone. Clonal development, and ultimately interclonal interactions, begin with the settlement of a sexually produced planula larva (Ford 1954) into one of several distinct kinds of habitat. Where and when colonizable space is rare, most successful larvae likely settle into mussel beds (Sebens 1982*b;* D. J. Ayre and R. K. Grosberg, personal observations) or other structurally complex habitats such as dense stands of barnacles (D. J. Ayre and R. K. Grosberg, personal observations), where they may be repelled by other genotypes (Sebens 1982*b*). Recruits asexually proliferate by fission, and eventually compete for space with other clones (Sebens 1982*b*). Successful clones appear to escape the bounds of the mussel or barnacle beds and can form extensive (i.e., >10 m^2; Sebens 1982*a*), contiguous clonal aggregations. Under this scenario, the process of acquiring space involves clones moving from a structurally complex habitat where interactions with numerous other clones are likely to be common (Sebens 1982*a*) to a structurally simpler one where clonal diversity per unit area is considerably lower (Sebens 1982*a;* D. J. Ayre and R. K. Grosberg, personal observations). Alternatively, if habitat disturbance (sensu Dayton 1971) regularly opens space, then larvae may settle and initiate the process of clonal expansion before interclonal contacts occur (Sebens 1982*b*). At the extreme, a clone could dominate a discrete habitat patch (such as a boulder) without encountering another clone.

The different pathways by which clones of *A. elegantissima* can acquire space suggest that trade-offs among clonal investment in aggression (including the production and maintenance of acrorhagi and other functionally specialized weapons, as well as repairing damage sustained in agonistic contests), sexual reproduction, and asexual proliferation lead to the persistence of interclonal variation in behavior and morphology. The functional and morphological differentiation within clones of so-called warrior polyps (with relatively large numbers of acrorhagi and relatively small gonads) at interclonal borders from more central polyps (that devote a greater fraction of their resources to the production of gonads) is consistent with the existence of such trade-offs, at least at the level of individual polyps. Under these circumstances, larger clones may enjoy an agonistic competitive advantage over smaller clones, because larger clones (both absolutely and proportionately) have more central individuals available to replace damaged or dead peripheral warriors (Sebens 1986; Francis 1988). Although comparable "social organization" (sensu Francis 1976) is not known in other clonal anemones, similar morphological specialization of individual units to reproductive and defensive

functions does occur in a variety of colonial hydrozoans, anthozoans, and bryozoans, as well as social insects (reviewed in Harvell 1994).

From a behavioral perspective, what remains to be determined is whether clone-specific differences in the interference competitive abilities of individual nonwarrior polyps extend to peripheral warrior polyps along interclonal borders, and whether behaviors at the level of individual polyps reflect differences in interference competitive abilities at the level of entire clones in a natural setting. To the extent that clones do actually differ in their interference competitive abilities, the occurrence of clone-specific habituation and enhancement of the agonistic response, along with the potential for clones to modify their investment in warrior versus nonwarrior polyps, implies that these differences may change through time.

Our study, in concert with the results of other studies of interference competition in clonal invertebrates (reviewed in Buss 1990) and plants (reviewed in Harper 1985; Silander 1985; Ellstrand and Roose 1987), confirms that cooccurring clones often differ in numerous selectively important traits. Consequently, a simple balance between input of new clones by recruitment and mutation and extinction of clones by drift cannot alone generally account for standing levels of clonal diversity in natural populations. The processes that maintain clonal diversity are likely to be similar to those maintaining species diversity (Sebens and Thorne 1985). Under some conditions (e.g., low intensity of disturbance), interspecific competition can slow the rate at which species (and perhaps clonal) diversity declines, particularly when competitive relationships are intransitive (sensu Buss and Jackson 1979; Karlson and Jackson 1981; Russ 1982). However, we found little evidence for such intransitivities, at least in terms of outcomes of agonistic interactions. In contrast, the high frequencies of both standoffs (in which neither contestant in a pairing decisively wins) and reversals (where members of subordinate clones win at least some pairings with members of dominant clones) suggest that these outcomes may be just as influential in the maintenance of clonal diversity as they appear to be in the maintenance of species diversity (reviewed in Karlson 1980; Sebens 1986, 1987).

This study on interclonal aggression in *A. elegantissima* highlights two other selective processes that can influence the likelihood of clonal coexistence. First, because some interclonal combinations elicited aggression, whereas others did not, frequency-dependent selection could act either to stabilize clonal diversity or reduce it, depending on the frequencies of contact between mutually aggressive and mutually nonaggressive clones. Second, recurrent encounters between the peripheral polyps of a given pair of agonistic clones can lead to highly specific habituation or enhancement of aggressive behavior. Consequently, the maintenance of clonal diversity can depend not only on clone-specific differences in aggressive behavior, but also on the capacity for, and persistence of, modifications in both patterns of behavior (e.g., habituation and enhancement) and investment in functionally specialized polyps.

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