# Trench warfare on the shore: interclonal aggression in sea anemones

Empirical research in behavioral ecology is dominated by studies of vertebrates and insects. The journal *Animal Behavior*, for example, during the last half of 1995 (Vol. 50), had a total of 48 papers on mammals, 43 on birds, eight on amphibians and reptiles, 17 on fishes, 33 on terrestrial invertebrates (primarily insects), and five on aquatic invertebrates (only two of which were marine). Thus, it is something of an event when a paper on social organization appears whose subject is a marine invertebrate, a brainless one to boot. Two recent papers by Ayre and Grosberg[1,2] remind us of how much behavioral biology we can learn from animals that consist of little more than a sack surrounded by tentacles.

The organism in question is the sea anemone *Anthopleura elegantissima*, a conspicuous member of the mid-intertidal rocky shore community along the west coast of the USA. Sexually produced larvae recruit onto empty space on the shore, but subsequent clonal proliferation potentially allows a single genetic individual to control substantial amounts of space. Clone-mates live cheek by jowl, but genetically distinct groups of anemones are typically separated by an anemone-free zone that calls to mind the no-man's land between the trenches of opposing forces in World War I. Like the Western Front, boundaries between clones can remain stable for years[3].

The weapons of sea anemones are specialized attack tentacles (called acrorhagi) that are filled with nematocysts – tiny spring-loaded and poison-filled harpoons. When two genetically distinct anemones are brought into contact, a characteristic aggressive response generally follows[3,4]. First, feeding tentacles are withdrawn and attack tentacles swell. Then, one or both individuals apply their attack tentacles to their opponents. The tips of the attack tentacles stick and leave behind a patch of epithelium loaded with nematocysts that cause localized tissue damage. In the case of repeated attacks without the possibility of retreat, the loser may die.

Trench warfare is a socially organized behavior, and the biology of these clonal anemones suggests a number of further analogies. First, the anemones at the 'front line' are specialized for combat, with significantly larger attack tentacles and greater numbers of attack tentacles both absolutely and especially per gram wet weight[1,2,5], as compared to more centrally located individuals. Second, when members of two clones are brought together, the loser (as assessed by withdrawal and the presence of scars) can be predicted by clone-specific differences in the propensity to attack first and the number of attack tentacles per anemone[1,2]. Anemone weight, on the other hand, is not correlated with the probability of winning a contest in pairwise interactions[1]. Repeated laboratory contact between clones leads to an initial increase in aggressive behavior, followed by an habituation that is clone-specific in its expression (that is, contact with clone A does not result in habituation to clone B)[1].

The clones studied by Ayre and Grosberg[1,2] exhibited remarkable differences in their aggressive behaviors and morphologies, as well as complex differences in behavior depending on the identity of the opponent clone. For example, some clones attack first, while others are more likely to retaliate. In some clones, front-line warriors resemble interior anemones in the number of attack tentacles, while in other clones, the front-line and interior anemones are strikingly different in morphology. For one highly aggressive clone, the speed with which it attacked varied from 11 to 95 minutes, depending on the identity of the opponent.

The long-term stability of clonal boundaries in the field suggests either that neighboring clones are not mutually aggressive, or that they are aggressive but also competitive equals. The results of Ayre and Grosberg[2] are not in a simple way consistent with either of these alternatives, however. Warriors collected from seven pairs of neighboring clones consistently fought, suggesting that they are not habituated to each other, and most neighboring clones were not competitive equals based on pairwise contests.

There appears to be two ways to accommodate this conflict between field observations and laboratory experiments. First, the habituation process that they earlier described[1] may operate in the field but not be expressed under the experimental conditions that were used (although Ayre and Grosberg[2] argue against this possibility). This would represent the clonal equivalent of the 'dear enemy' phenomenon, but it implies that the costs of aggression even to the winner outweigh the benefits to be had from acquisition of more space. In clonal organisms, however, reproductive output and clonal area are well correlated, implying that costs to the winner must be high indeed. Ayre and Grosberg[2] favor the second alternative, and argue that 'a clone could appear to consist of a team of star attackers, but not function as a winning team.' For example, less-aggressive clones may still hold their own if they invest heavily in replacement of their defeated warriors.

As Ayre and Grosberg point out, comparable patterns are found in many other unrelated organisms. In that case, why study anemones when one can study ants or antelopes, which also exhibit inter-colony or inter-individual differences in behavior and morphology related to aggression? Several features of *A. elegantissima* make it a particularly elegant system for exploring the interface between behavior and ecology. First among these is clonal reproduction. Genetically identical individuals provide the ideal material for replication, and these are available almost without limit in this species. The reaction of a specific clone to a diverse array of conditions or opponents can be tested, without worrying about the order in which they are experienced, since individual anemones can be used just once. Almost as important, they are abundant, largely stationary, and live in an accessible habitat, thus permitting long-term studies of the success of behaviorally and morphologically characterized clones under natural conditions. This aspect has not been exploited to date (no ecological records are available for the clones studied by Ayre and Grosberg), but should prove fascinating in the years to come should they or others pursue these problems. Finally, the likely critical parameters of the system are few and relatively simple to measure: attack probability, number of tentacles, reproductive output, area occupied, and genetic relatedness. While complexity emerges almost inevitably with further study, *A. elegantissima* has all the hallmarks of a classic system for unravelling the effects of genotype and environment on the expression of aggression.

While sea anemones are best known for fighting with conspecifics, their stony relatives, the corals, are famous for their interspecific contests. When corals of two species are brought into contact, the dominant species typically extrudes filaments and begins to digest what it can reach of its neighbor within 12 hours[6]. Overt aggression between members of the same species is generally delayed and less dramatic, sometimes consisting of only a suture zone separating the tissues of the two colonies[6–9]. Indeed, this difference between intra- and interspecific responses has facilitated the recognition of several cryptic species of corals[6,7,9]. All these aggressive interactions in clonal cnidarians


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depend on the ability to distinguish self from various forms of non-self, but why should conspecific non-selfs elicit strong reactions in some groups and relatively weak ones in others? This remains a polyp puzzle for the future.

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### References

1 Ayre, D.J. and Grosberg, R.K. (1995) **Aggression, habituation, and clonal coexistence in the sea anemone *Anthopleura elegantissima*,** *Am. Nat.* 146, 427–453
2 Ayre, D.J. and Grosberg, R.K. **Effects of social organization on interclonal dominance relationships in the sea anemone *Anthopleura elegantissima*,** *Anim. Behav.* (in press)
3 Francis, L. (1973) **Clone specific segregation in the sea anemone *Anthopleura elegantissima*,** *Biol. Bull.* 144, 64–72
4 Francis, L. (1973) **Intraspecific aggression and its effects on the distribution of *Anthopleura elegantissima* and some related anemones,** *Biol. Bull.* 144, 73–92
5 Francis, L. (1976) **Social organization within clones of the sea anemone *Anthopleura elegantissima*,** *Biol. Bull.* 150, 361–376
6 Lang, J. (1973) **Interspecific aggression by scleractinian corals. 2. Why the race is not only to the swift,** *Bull. Mar. Sci.* 23, 260–279
7 Lang, J. (1971) **Interspecific aggression by scleractinian corals. 1. The rediscovery of *Scolymia cubensis* (Milne, Edwards & Haime),** *Bull. Mar. Sci.* 21, 952–959
8 Neigel, J.E. and Avise, J.C. (1983) **Clonal diversity and population structure in a reef-building coral, *Acropora cervicornis*: self-recognition analysis and demographic interpretation,** *Evolution* 37, 437–453
9 Weil, E. and Knowlton, N. (1994) **A multi-character analysis of the Caribbean coral *Montastraea annularis* (Ellis and Solander, 1786) and its two sibling species, *M. faveolata* (Ellis and Solander, 1786) and *M. franksi* (Gregory, 1895),** *Bull. Mar. Sci.* 55, 151–175

# An important confluence for stream ecology

Ecology is a fascinating and curious discipline. On the one hand, ecologists commonly espouse the search for general principles and regular patterns, and profess their desire for a rigorous logical foundation. On the other hand, ecologists are often quick to acknowledge that 'the devil is in the details', that patterns are seldom scale-invariant, and that the very rules used to confirm and refute hypotheses must sometimes be bent. This ambivalence about ecology's objectives and epistemological protocols may help to explain the mixture of introspection, spirited exchange and creative thinking that accompanied a recent symposium on stream ecology (New Concepts in Stream Ecology: An Integrative Approach). The symposium was organized by J. Vaun McArthur and Peter Koetsier, and took place at the Savannah River Ecology Laboratory in New Ellenton. SC. USA last October.

adoption of new techniques (e.g. genetic tools), by a more explicit recognition of the importance of scale, and by the paradigm shift that has occurred in many areas of ecology towards a view of populations as open systems, in which dispersal can be of paramount importance. Welcome also was an increased emphasis on evolutionary perspectives, an area of stream ecology that is sorely underdeveloped. In this overview of these diverse presentations, we proceed from mechanistic studies of short-term, local-scale interactions to investigations at larger temporal and spatial scales.

The role of adaptive prey behavior in predator–prey interactions was examined by Bobbi Peckarsky (Cornell University, Ithaca, NY, USA). She presented results from extensive experimental and observational studies of interactions between grazing mayflies, predatory stoneflies and insectivorous trout. Peckarsky described tation contrasts with the more common approach in which short-term experiments are used to test equilibrium-based food web models.

Using more abstract predator–prey models, Peter Abrams (University of Maryland, College Park, USA) demonstrated how the incorporation of adaptive prey behavior and temporal variations in prey abundance could lead to quantitative and qualitative alterations of predator–prey dynamics. Given the complex behavior exhibited by these models, Abrams argued that in its current state of development, ecological theory should be used primarily to identify major areas of uncertainty about ecological interactions, rather than to make predictions in the strict sense.

LeRoy Poff (University of Maryland) focused on how local communities are assembled from a regional species pool. He proposed a methodology that emphasizes the identification of particular traits (e.g. dispersal ability, physiological tolerance) that would remove a species from the list of potential members of the system in question. Poff proposed an analytical framework for quantifying species traits and environmental filters, which led