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Recruitment in a Sea Anemone Population: Juvenile Substrate Becomes Adult Prey

Abstract. *Populations of the sea anemone* Anthopleura xanthogrammica *(Brandt) occur in tide pools and surge channels below intertidal mussel beds where they capture mussels dislodged by wave action and by sea star foraging. Dense concentrations of small juvenile anemones occur only within mussel beds and are probably the result of larval settlement or differential survival in that habitat. Areas experimentally cleared of anemones showed that recruitment was primarily by migrating juveniles and that the rate of immigration over a 2-year period was much higher in experimental removal areas near mussel beds than in those further away. Mussel beds thus function as an important juvenile habitat (refuge and nursery); juveniles later migrate downward and are then in a position to capture dislodged mussels and grow to adult size.*

Intertidal marine organisms often disperse planktonic larvae over great distances. It is thus necessary that larvae have mechanisms to locate, recognize, and settle in habitat types appropriate for juvenile growth, survival, and adult reproductive success. Specific substratum selection by invertebrate larvae has been demonstrated for species in a variety of phyla (*1*), but the process of secondary habitat selection by settled individuals has received less attention. Completely sessile species cannot change their location if it proves unsuitable, therefore the habitat selected by a larva is also that of the adult. The juvenile habitat of more mobile animals, however, can be distinct from that of adults (*2*). Sea anemones, for example, can move several centimeters per day (*3*) and thus have the option to alter location throughout their lifetime.

The anemone *Anthopleura xanthogrammica* (Brandt), a dominant member of the North American west coast intertidal community, preys primarily on mussels and other intertidal invertebrates dislodged by wave action and by sea star foraging (*4*). Anemone offspring face the problem of locating a suitable habitat for early growth and survival and later establishing themselves where dislodged mussel capture is a predictable event. Dense concentrations of small juvenile *A. xanthogrammica* (≦ 2 cm in diameter) occur only in mussel beds (*Mytilus californianus* Conrad), a physically protected microhabitat with a predictable prey resource.

At an average diameter of 3.3 ± 1.4 cm (standard deviation), juvenile anemones migrate downward from the mussel beds, thus finding sites where later mussel capture is likely. Juveniles (individuals ≦ 6.5 cm in diameter do not produce gonads) move frequently within mussel beds, around the bases of adults in tide pools, and along the sides of channels (*5*). Adult anemones (6.5 to 25 cm in basal diameter) are long-lived (several decades) and rarely move from their position in tide pools and surge channels. *Anthopleura xanthogrammica* is dioecious and reproduces by epidemic spawning of gametes followed by the development of feeding (planktotrophic) larvae that remain in the plankton for at least several weeks (*6, 7*). Larvae are difficult to culture and have not been induced to settle in the laboratory (*7*). Although larval cohorts may move together in the same water mass, their settlement site is likely to be far from the location of their parents. Unlike the sympatric congener *Anthopleura elegantissima, A. xanthogrammica* never reproduces asexually (for example, by longitudinal fission) (*8*).

The present study is part of an investigation of population dynamics, reproductive ecology, and habitat selection in *A. xanthogrammica* (*5*). Its objectives were to (i) measure rates of immigration into areas cleared of all anemones, (ii) quantify the sizes of individuals recruiting into several intertidal habitat types, and (iii) examine the role of mussel beds as juvenile habitat and as sources of recruitment into adult habitats.

Population monitoring sites were located on Tatoosh Island and at Shi Shi Beach, Washington (*5*). Both sites are on wave-exposed outer coast, the former with extensive mussel bed cover and the latter with few mussel beds. Quadrat sampling for size-frequency distributions of populations was also carried out at both sites, at Mukkaw Bay, Washington, and at several other sites along the west coast (*9*). Mapped control populations of marked individuals were established at three intertidal levels at each of the two sites and followed for 2 years (*5*) (September 1974 to October 1976). Seventeen areas were cleared of anemones (intertidal height, 0.2 to 2.2 m) above the mean lower low water between March 1973 and January 1975 and followed until June 1977. Before removal, all anemones were mapped, photographed, and measured (basal diameter) in each of the discrete tide pool or channel areas (0.3 to 0.9 m^2 per removal; 14 to 36 anemones). Anemones adjacent to the removals were marked with neutral red dye spots (*10*) as were immigrants found on subsequent visits. Sites were monitored bimonthly and all immigrants into the areas were also photographed, drawn on maps, and measured.

Anemones within mussel beds (both on mussel shells and on rock surfaces) were consistently smaller than those in tide pools and channels; at both sites the mean size increased as the intertidal height decreased (Fig. 1). Samples taken in large contiguous mussel beds at Mukkaw Bay (~ 5 km north of Shi Shi Beach) had the densest population of small individuals at any site—58 anemones in an area of 3 m^2 (diameter, 1.5 ± 0.9 cm). Another sample taken in extensive beds at Cape Arago, Oregon, had 41 anemones in a 4-m^2 area (diameter, 2.9 ± 1.5 cm). Such concentrations of small individuals were found only in mussel beds and in no other habitat type examined (Fig. 1B). Most mussel bed areas had only a few individuals per square meter, and dense concentrations were extremely patchy. A massive settlement of the congener *Anthopleura elegantissima* (Brandt) occurred on Tatoosh Island in the winter of 1972–1973 (to 600 individuals per square meter) and was monitored until 1977 (*5*), but no such obvious settlement of *A. xanthogrammica* occurred at either site between 1973 and 1977. Larval settlement of *A. xanthogrammica* is thus not a predictable annual event and is probably very patchy in time and location.

The mean diameter of anemones immigrating into all cleared areas on Tatoosh Island was 3.8 ± 2.4 cm (N = 112); that of immigrants into control areas on Ta-

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toosh Island was 3.3 ± 1.4 cm in diameter (N = 42) over the same period (*5*) while that of anemones in mussel beds was 3.2 ± 1.6 cm (N = 56). Cleared areas were thus colonized primarily by juveniles rather than by movement of adults bordering the removal area, although 15 of the 112 immigrants were adults.

Immigration rates were higher in removal areas just below the mussel beds than in areas several meters distant (Fig. 2) (correlation r = .71, $P < .001$). New arrivals usually appeared first at the lower edge of mussel beds and then migrated downward. Lateral movement was responsible for later relocation and for all immigration into areas far from the mussel beds.

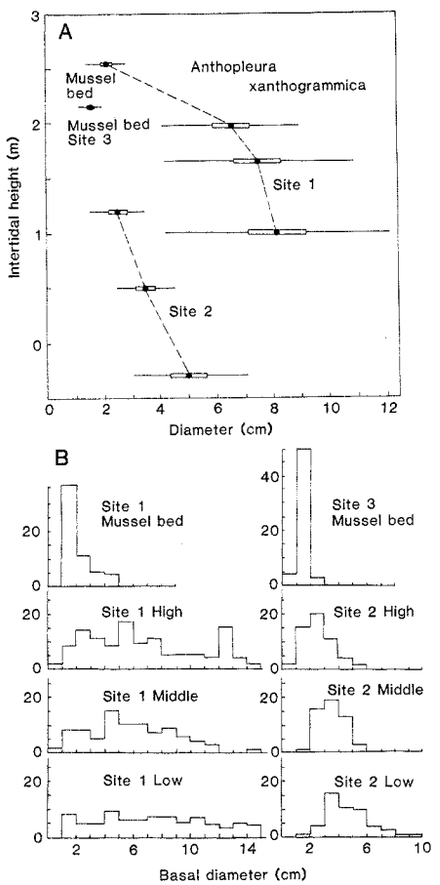

Fig. 1. (A) Size distribution of *A. xanthogrammica* in mapped populations at several intertidal heights (July 1975). The mean basal diameter is plotted with standard deviation (narrow bars) and 95 percent confidence intervals around the mean (wide bars). Site 1 is on Tatoosh Island, Washington (with extensive mussel beds), site 2 is at Shi Shi Beach on the mainland (with few mussel beds), and site 3 is at Mukkaw Bay (intermediate mussel cover) on the coast near Shi Shi Beach. Samples are from rock walls, tide pools, or channels unless marked "Mussel bed," denoting samples from within mussel beds. (B) Size-frequency distributions of *A. xanthogrammica* in each area, denoted as in (A).

The mussel bed functions as a site of juvenile growth and probably as a site of larval settlement, or at least differential survival, since this is the only place that dense concentrations of very small individuals (≦ 2 cm in diameter) were found. Beds of large mussels provide a physically protected microhabitat on exposed shores, and the interstices of such beds contain various small invertebrates (*11*) suitable as prey for small anemones. Maximum prey length taken by *A. xanthogrammica* is approximately equal to the diameter of the tentacle crown (*12*). Thus most juveniles are incapable of preying on fully grown mussels (average length, 6 cm) but can certainly feed on juvenile mussels, certain gastropods, annelids, and small crustaceans (*5*).

While mussel beds are acceptable juvenile habitat, they are also excellent settlement sites. If planktonic larvae can recruit into mussel beds, they are assured of being directly above suitable adult habitat. Larvae may be able to recognize mussels by chemical cues, but this has yet to be tested. The observed concentration of juveniles in mussel beds could alternatively result from random settlement throughout the intertidal and differential survival in mussel beds. Larval settlement directly on prey items used by both juveniles and adults occurs in several other invertebrate groups (for example, nudibranchs on pennatulids, hydroids, and corals, and abalones on coralline algae) (*13*). However, the present case is unique in that the organisms which provide the juvenile habitat or substrate (mussels) become the most important prey for the adults but such prey can only be captured from a second habitat type (pools and channels below the mussel beds).

Migration of juvenile anemones may be directed by both physical and biological characteristics of the environment. Anemones are known to direct movements in response to light (*3*), desiccation (*14*), aggression by other anemones (*15*), gravity (*16*), and current (*3*). Movement in the field has been measured for *Epiactis prolifera* (*17*), but both movement and recruitment rates have been examined only in the anemone *Actinia tenebrosa* Farqu. (*18*), which broods its young. In this species as well, adults are much more stationary than are juveniles. Recruitment, migration, and population dynamics have not been previously investigated in an anemone species with planktonic larvae.

Recruitment rates are important data for management of natural populations. Interest in *A. xanthogrammica*, and possible collecting, is likely to increase following the recent isolation of a compound with antitumor and cardiac stimulation activity (*19*). Experiments in this study lasted 2 to 4 years, and even after 4 years areas were not back to preremoval population densities. Complete recovery of areas cleared of anemones will thus take 5 years to several decades. Relatively low recruitment rates and individual growth rates (*5*) indicate that large-scale harvesting could not be supported for long.

The ability of anemones to respond to a variety of stimuli and to alter their direction of movement gives them an important capability for secondary habitat selection. Juveniles wandering to the edge of the mussel bed can then migrate downward and find sites where mussel capture is likely and where sunlight is relatively strong (for photosynthesis by the symbiotic algae). However, new recruits grew more slowly in pools with adults than in experimentally cleared areas (*5*) and thus competition for space or food probably occurs among anemones in crowded pools and channels. Juvenile mobility may also allow anemones to space themselves away from the tentacle crowns of established adults, thus reducing interference competition for prey.

This example of migration from a juvenile habitat to a distinct adult habitat illustrates that complex and highly directed habitat selection can be accomplished by organisms with fairly simple behavior. Larval selection of a juvenile habitat, and later juvenile selection of appropriate adult habitat, are necessary for specialization on dislodged intertidal mussels as prey. Although *A. xanthogrammica* can feed on a variety of prey items, there appears to be a close cou-

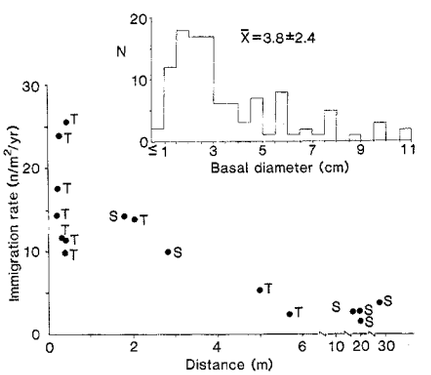

Fig. 2. Immigration rate of anemones into cleared areas over a 2-year period as the number of individuals per square meter per year, plotted against the distance from the edge of the nearest contiguous mussel bed. The size-frequency distribution of all immigrants is also shown with the mean and standard deviation for the basal diameters (inset); *T*, areas on Tatoosh Island; *S*, areas at Shi Shi Beach.

pling between the population dynamics of this anemone and the biological zonation of exposed outer coast areas with established mussel beds.

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Intracellular Recordings from Thermosensitive Preoptic Neurons

Abstract. *Intracellular recordings were made from locally thermosensitive preoptic neurons in the green sunfish,* Lepomis cyanellus. *Stable resting potentials, action potentials, and spontaneous synaptic activity were observed over approximately 4° to 5°C changes in local brain temperature. A small percentage of the warm-sensitive neurons showed exponential firing-rate responses to temperature. These cells discharged rhythmically, lacked visible synaptic input, and showed slowly depolarizing potentials leading to action potentials. Other linear and nonlinear warm-sensitive and cold-sensitive neurons showed spontaneous excitatory and inhibitory synaptic potentials giving rise to action potentials. Cells that appear to be endogenously active may be true thermodetectors, and other thermosensitive neuronal activity may be synaptically mediated.*

Neurons in the anterior brainstem of various species of endothermic vertebrates undergo changes in their activity in response to localized changes in brain temperature (*1*). Many ectotherms, both aquatic and terrestrial, actively select a preferred temperature in a thermal gradient (*2*) and, by this means, regulate their body temperature (*3*). Thermoregulatory responses, both behavioral and autonomic, are elicited by local alteration of hypothalamic temperature in ectotherms (*4*) and endotherms (*1*). On the basis of these and other findings, centrally located temperature-sensitive neurons are thought to be components of a thermoregulatory system in all vertebrates.

Extracellular single-unit studies of neurons in the anterior hypothalamus–preoptic area of endotherms (*5*) and ectotherms (*6*) have revealed the existence of temperature-sensitive and -insensitive neurons. Cells that increase their firing rate with increases in local brain temperature are classified as warm-sensitive and are thought to stimulate heat loss and inhibit heat gain mechanisms (*7*). The converse is true for cold-sensitive neurons (*7*). Thermosensitive cells exhibit both linear and nonlinear responses to temperature changes (*1*, *7*). Various models describing the central nervous control of thermoregulation are based on the discharge characteristics of warm-sensitive, cold-sensitive, and thermoinsensitive neurons (*1*, *7*, *8*). The presence of central warm and cold thermodetectors, as well as various interneuronal cell types, has been hypothesized (*1*, *4*, *8*). Other investigators suggest that only warm thermodetectors exist, from which all other neuronal responses are derived through synaptic interactions (*7*). However, this dichotomy has yet to be resolved, as has the underlying mechanism making these neurons thermosensitive. On the basis of intracellular recordings, we report that some warm-sensitive cells appear to be endogenously active and may function as thermodetectors and that other thermosensitive activity is synaptically generated.

Intracellular recordings of preoptic thermosensitive neurons were made from 22 green sunfish, *Lepomis cyanellus*, acclimated to 25° ± 1°C and approximately 8 to 10 cm long. Fish were anesthetized with MS-222 during surgery and immobilized with tubo-curare during experimentation. Gills were perfused with aerated water held at 25°C. The brain was exposed through a small hole in the skull. Local brain temperature was altered through the use of a water-perfused thermode positioned on the telencephalic surface. A fine thermocouple inserted to the level of the recording site in the contralateral preoptic region monitored brain temperature. Fine intracellular micropipettes filled with 2*M* potassium citrate were used. The most useful electrodes had d-c resistances of 30 to 50 megohms. Electrical activity was recorded according to standard intracellular techniques. An active bridge circuit in the preamplifier allowed simultaneous recording and current injection. Firing rate was recorded with a rate meter.

Spontaneously active neurons in the medial and lateral preoptic region were impaled, and there was activity monitored for several minutes with the brain temperature held constant at 25°C. Brain temperature was then altered and its effect on activity recorded. Responses were curve-fitted by computer. Several criteria were used for intracellular impalements, including a rapid ≥ 30 mV drop in d-c potential, an increase in action potential amplitude to ≥ 25 mV, often a change in the action potential waveform to monophasic positive, often the appearance of synaptic potentials and a rapid return to original d-c level after withdrawal of the microelectrode. Because of thermal expansion and compression of the brain tissue, activity could be monitored over temperature changes of 3° to 5°C. Larger changes usually resulted in loss of the impalement.

Stable recordings (15 to 50 minutes) were made from 126 preoptic neurons, of which 29 showed local thermosensitivity based on criteria established in other investigations (*7*). Cells responded in lin-

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