

Sea Urchin Recruitment: Effect of Substrate Selection on Juvenile Distribution

R. A. Cameron¹ and S. C. Schroeter²

¹Center for Coastal Marine Studies, University of California, Santa Cruz, California 95064, USA

²Department of Biology, University of Southern California, Los Angeles, California 90007, USA

ABSTRACT: Intertidal field observations have shown that juvenile purple sea urchins *Strongylocentrotus purpuratus* are found in higher densities near adults. The same is true for subtidal populations of juvenile red sea urchins *S. franciscanus*. These distribution patterns could be influenced by any of three elements: substrate selection, early juvenile mortality or juvenile migration. Using laboratory-reared larvae, we conducted experiments designed to gauge the effect of substrate selection on juvenile distributions of these two sea urchin species. In both laboratory and field experiments, larval sea urchins showed no enhanced settlement in the presence of adults or adult-associated substrates. These results imply that early juvenile mortality or migration provide the greater influence on juvenile distributions.

INTRODUCTION

Recruitment, the appearance of the youngest age class, is a key mechanism shaping the structure of a population. This mechanism is especially important in marine benthic communities, where $\frac{2}{3}$ of the species studied possess a lengthy planktonic larval phase which is capable of dispersing great distances and recruiting into spatially separate communities (Thorson, 1961; Mileikovsky, 1971; Scheltema, 1974; Strathmann, 1974). The numbers recruiting to a population will be influenced by (1) larval availability, (2) substrate selection and metamorphosis, and (3) early juvenile mortality. The interplay of these three elements produce specific patterns of recruitment. Until patterns of larval recruitment and the factors which influence them are better documented and better understood, the generalizations underlying models of benthic communities cannot be adequately evaluated.

The Pacific coast sea urchins *Strongylocentrotus purpuratus* (purple sea urchin) and *S. franciscanus* (red sea urchin) provide good research subjects from which to draw generalizations about the interaction of the elements of recruitment and their effect on distribution. These sea urchins are conspicuous members of near-shore benthic communities and their life cycles are well described (Harvey, 1956; Hinegardner, 1969; Burke and Chia, 1978; Pearse, 1980). They are amenable to laboratory culture and their larval phase is

easily manipulated (Hinegardner, 1969; 'Marine Ecology' Volume III: Kinne, 1977).

Both purple and red urchin larvae settle on an algal and bacterial film (Hinegardner, 1969). In intertidal habitats, juvenile purple urchins are more densely distributed in areas where adults are found (Ebert, 1968; Schroeter, 1978); but in subtidal areas juveniles live in a variety of microhabitats not necessarily associated with the adults (Tegner and Dayton, 1977). In contrast, juveniles of the red sea urchin were only found near or under adults at Vancouver, British Columbia (Low, 1975) and about 80% were found near or under adults off La Jolla, California (Tegner and Dayton, 1977).

In the intertidal, purple sea urchin larvae could settle preferentially near adults; while in the subtidal they could settle indiscriminately over the entire distributional range of the adults. In contrast, red sea urchin larvae could settle preferentially near or under adults in the subtidal. These settlement patterns could result in the observed distributions of juveniles.

Preferential settlement or substrate selection occurs in response to some environmental cue (Crisp, 1974; Scheltema, 1974). In addition to adult sea urchins, a possible cue that has been suggested is encrusting coralline algae. Adult sea urchins eliminate most attached macroscopic algae in their immediate vicinity either by grazing or abrading the algae with their spines. An exception to this are the encrusting coral-

line algae which are resistant to both grazing and abrasion. As a result, substrates directly beneath urchins or frequently grazed by urchins would be expected to possess greater coverage by encrusting coralline algae than similar nearby substrates. Furthermore, encrusting coralline algae induces settlement of chiton (Barnes and Gonor, 1973), abalone (Morse et al., 1979) and sea star larvae (Barker, 1977).

On the other hand, juveniles may settle indiscriminately in both intertidal and subtidal areas and juvenile mortality or migration might produce the observed distributions. If early juvenile mortality of purple sea urchins is higher away from adults in the intertidal, the reported differences in distribution could result. Of course, no such differential in mortality need be invoked for the subtidal populations. Similarly, differential mortality could effect the juvenile distributions of the subtidal red sea urchin.

Immediately following settlement, juvenile urchins of both species also might seek microhabitats in which lower mortality occurred, and this movement could result in the observed distribution of juveniles. Obviously, a combination of all three mechanisms could be operating.

In this paper we report experiments conducted to distinguish the effect of substrate selection from early juvenile mortality and migration on the distribution patterns observed for juvenile red and purple sea urchins.

MATERIALS AND METHODS

For the experiments on purple sea urchins (*Strongylocentrotus purpuratus*), adults and substrates were obtained from Elwood Beach and Naples Reef, Santa Barbara, California (USA). Experiments with red sea urchins *S. franciscanus* were conducted with adults and substrates collected from Sand Hill Bluff, 6 miles northwest of Santa Cruz, California.

Purple sea urchin larvae were reared at 15 °C and red urchin larvae at 12 °C using the method of Cameron and Hinegardner (1974). The algal food for the larvae was *Rhodomonas lens*. Purple sea urchin larvae metamorphosed as early as 30 d after fertilization with peak metamorphosis at approximately 38 d. The earliest metamorphosis observed for red urchin larvae occurred at 40 d post-fertilization and the peak was at 50 d. In order to determine metamorphic competence for experiments, two criteria were used: (1) the appearance of a fully developed urchin rudiment which correlates in other species with the ability to undergo metamorphosis (Cameron and Hinegardner, 1974); (2) the ability of these larvae with a mature rudiment to

metamorphose on bacterial films which had developed on plastic dishes placed in the running sea water system at Santa Barbara and Santa Cruz, respectively. Ten or twenty larvae from cultures in which organisms exhibited the morphological criterion for maturity were placed in a plastic dish and scored for metamorphosis after 4 h. Only cultures exhibiting more than 80 % metamorphosis were used in subsequent studies. Depending on the number of competent larvae available, between 50–150 larvae were used in each replicate.

Tests of substrate selection were carried out with competent larvae in three ways: (1) Substrates were brought into the laboratory and incubated with competent larvae. (2) Larvae were taken in jars to an intertidal site where substrate was added. Subsequent incubation of the larvae with the substrates was carried out in the dark while the jars were being transported to the laboratory in an insulated carrier. (3) Larvae were placed in glass jars and transported by boat to a subtidal site. Substrates were collected by SCUBA and added to each jar. Incubation was carried out in insulated carriers. In all cases, the larvae were transported to the site in a minimum amount of sea water, and ambient sea water from the site was added along with the substrates. Ambient sea water alone was added to the control containers. In one experiment both an ambient sea water control and a filtered sea water control were used. The temperatures of the test containers remained very near that of the study site.

Substrates consisted of small rocks taken both from under sea urchins and from areas where no urchins were evident. Adult *Strongylocentrotus purpuratus* and *S. franciscanus* were also used as substrates. Rocks covered with encrusting coralline algae, probably *Lithothamnium* sp., which were taken from areas where urchins did not live, were also tested. In another series of experiments, pockets formed in soft subtidal rock by burrowing urchins were chipped out and used as substrate. Nearby rocks of the same composition but without urchin burrows were chipped loose and used for comparison. At Sand Hill Bluff, the soft mudstone was removed from beneath red urchins and compared with nearby cobble.

At the conclusion of the tests, formaldehyde was added to the sea water containing larvae and substrates to make a 4 % solution. The substrates were carefully washed and the combined fluids concentrated through fine nylon mesh. The retained urchin larvae were then scored under a dissecting microscope for any tissue collapse, which is the first recognizable event of metamorphosis (Cameron and Hinegardner, 1978).

The data were reduced to percent of individuals exhibiting any sign of metamorphosis. In order to

Table 1. *Strongylocentrotus purpuratus*. Experimental groups and corresponding percent metamorphosis \pm 1 standard error of the mean. In parentheses: number of replicates. Analysis of variance and Student-Newman-Keuls multiple range test (SNK) were performed on square root, arcsine transformed percents where applicable. Vertical bar: experimental groups not significantly different by SNK. Intertidal experiment performed at Elwood Beach; subtidal experiment, at Naples Reef, Santa Barbara, California. Incubation time: 4 h in all experiments

Treatment	Percent metamorphosis \pm SEM (replicates)	
(a) Laboratory experiment		
1 control	0	(2)
2 plain rock	56.0 \pm 4.0	(2)
3 rock with coralline algae	75.0 \pm 4.0	(2)
(b) Intertidal experiment		
1 control	0	(2)
2 rock from beneath urchin, but urchin removed	35.3 \pm 9.6	(2)
3 rock without urchin	48.0 \pm 6.5	(2)
(c) Subtidal experiment		
1 control	0	(3)
2 small purple urchin	3.3 \pm 0.4	(3)
3 small red urchin	4.6 \pm 1.8	(3)
4 rock with urchin pocket	26.3 \pm 12.7	(3)
5 rock without urchin pocket	50.0 \pm 7.8	(3)
6 rock largely covered with coralline algae	59.0 \pm 6.5	(3)

insure homogeneity of variance, these percentages were transformed to the arcsine of the square root of each value and analyzed by multiple analysis of variance (ANOVA) and the Student-Newman-Keuls Multiple Range Analysis (SNK) (Sokal and Rolf, 1969).

RESULTS

Substrate Selection by Purple Urchins

The percentage of urchins undergoing metamorphosis was high both in the presence of the coralline algae and the plain rock, and they are different from controls (Table 1a). When rocks from the intertidal study site at Elwood Beach were compared for their capacity to induce settlement, no difference between those from under urchins or away from urchins was seen (Table 1b). A comparison of settlement in the depressions inhabited by urchins subtidally with settlement on nearby rocky surfaces also yielded no significant differences (Table 1c). Metamorphosis in the presence of coralline algae was in the same range as that of rocky substrates. Either species of sea urchins, on the other hand, did not induce settlement to any great extent. Statistical analysis showed that settlement was significantly less with urchins than with any rock substrate, while among themselves the rock substrates did not differ.

Substrate Selection by Red Sea Urchins

In order to test the ability of a rock surface devoid of its normal bacterial films to induce settlement of red urchin larvae, boiled and washed rocks were compared to untreated rocks from the same field site (Table 2a). This test was conducted for 4 h to minimize the recolonization by microorganisms. No settlement occurred on the cleaned rocks as opposed to 73% on the untreated ones.

Another set of laboratory tests compared the ability of red and purple urchin adults, as well as rocks and ambient sea water, to induce settlement. No settlement occurred in the presence of purple urchin adults, and only 5.4% in the presence of red urchins (Table 2b). More settlement (11.9%) occurred in the presence of only ambient sea water. All these settlement values were less than on rocks collected from the field.

Substrates from a subtidal area inhabited by red sea urchins and the urchins themselves were compared (Table 2c). In this case a fraction of the larvae, 31.4%, settled in the presence of the red urchin. A larger fraction, 62.5%, settled in the presence of rocks chipped out from beneath urchins. A significantly higher percentage of the larvae settled in the presence of rock cobbles in areas distant from adult urchins.

DISCUSSION

The primary conclusion from these experiments is that both red and purple sea urchins lack specific substrate selection for either adults or substrates

Table 2. *Strongylocentrotus franciscanus*. Experimental groups opposite corresponding mean percent metamorphosis \pm 1 standard error of the mean for replicated groups. In parentheses: number of replicates. Subtidal experiment (c): analysis of variance and the Student-Newman-Keuls multiple range test (SNK) on square root, arcsine transformed percents. Vertical bar: experimental groups not different by SNK. Subtidal experiment (c) performed with substrates from Sand Hill Bluff, Santa Cruz, California

Treatment	Percent metamorphosis \pm SEM (replicates)	
(a) Laboratory experiment; incubation time: 4 h		
1 control	0.0	(1)
2 washed and boiled rocks	0.0	(1)
3 untreated rocks	73.4 \pm 3.3	(2)
(b) Laboratory experiment; incubation time: 24 h		
1 filtered sea water control	0.0	(1)
2 ambient sea water control	11.9	(1)
3 purple sea urchins	0.0	(1)
4 red sea urchins	5.4	(1)
5 untreated rocks	75.3	(1)
(c) Subtidal experiment; incubation time: 12 h		
1 ambient sea water control	0.73 \pm 0.73	(3)
2 red sea urchin	31.4 \pm 13.2	(3)
3 rocks from beneath urchin	62.5 \pm 7.3	(3)
4 rocks distant from urchin	89.9 \pm 1.7	(3)

associated with them. Intertidally, purple sea urchin larvae showed no greater specificity for rocks under adults over other rocks in the same area. Subtidally, the same picture emerges; purple urchin larvae settle equally well in the presence of rock surfaces encrusted with coralline algae, rock surfaces away from urchins and rock surfaces forming an urchin pocket. In the same tests, the larvae settled poorly in the presence of adult sea urchins. Similarly, red sea urchin larvae show no selectivity between rock substrates, provided the surface possesses a normal algal and/or bacterial film. The presence of adult sea urchins did induce some settlement of red sea urchin larvae albeit less than any rock substrate. It is curious that all three experimental groups, adult urchins, rocks away from adults and rocks from beneath adults, were significantly different in the red urchin field experiment (Table 2c). The highest settlement occurred in jars with rocks away from adult urchins rather than adults or surfaces from beneath them. If it is true that bacterial films induce settlement in these sea urchins, a long incubation time could increase the amount of settlement by permitting the establishment of an adequate film in an otherwise marginal test case. This could explain the 11.9% metamorphosis in the red urchin laboratory experiment (Table 2b), as well as the results in the field experiment (Table 2c). It is more difficult to account for the lower settlement rate in the presence of rocks from beneath urchins. Urchin grazing could reduce the bacterial film on these rocks, thereby reducing settlement. These speculations only serve to demand further experiments.

Since neither urchins nor the immediate substrate

upon which they reside is any more attractive for settlement than nearby areas or coralline algae bearing substrate from unrelated regions, we must exclude specific substrate selection as an explanation of discontinuous distribution of juveniles. The only specificity seems to be for a surface with its normal bacterial and/or algal flora. Since bacterial and algal films are ubiquitous in the sea, it seems valid to conclude that sea urchin larvae would settle on any intertidal or subtidal surface that they encountered once they become competent to undergo metamorphosis. This further suggests that larval availability to a particular area and, following settlement, juvenile mortality in that area are more important elements of the recruitment process of sea urchins than substrate selection.

The greater abundance of juvenile red sea urchins near or under adults at Vancouver Island, British Columbia (Low, 1975) and La Jolla, California (Tegner and Dayton, 1977) and of juvenile purple sea urchins near adults on intertidal sites at Sunset Bay, Oregon (Ebert, 1968) and Santa Barbara, California (Schroeter, 1978) are probably the result of differential juvenile mortality or migration in these areas. Tegner and Dayton (1977) suggested that the adults offer protection under the spine canopy thereby enhancing juvenile survival. In the case of intertidal purple urchin juveniles the adults also might maintain an environment which allows higher rates of survival for the juveniles on the substrate near them.

Our experiments do not exclude the possibility that migration is the cause of the changes in juvenile distribution. However, juvenile purple urchins maintained for 6 weeks post metamorphosis in the labora-

tory showed no inclination to leave microhabitats where active feeding occurred. The habitats used were rocks covered with encrusting coralline algae. Experiments are being conducted to determine the behavior of juvenile sea urchins in the presence of adults.

It is important to note that juvenile mortality may occur in distinctly different microhabitats and at different scales of magnitude from those of the adult. A survey of the size at metamorphosis of benthic invertebrates revealed that 65% measure 2 mm or less, placing them among the meiofauna (Thorson, 1966). Comparing the number of animals from the Oresund *Venus* community less than 2 mm with those greater in size over a short time interval, Thorson further concludes that only 1.4% survive to the larger size. If a hundred-fold reduction in numbers following settlement is the rule, then the investigator that censuses such a population even a short time after settlement would observe individuals only in particular microhabitats with high survival.

Acknowledgements. We would like to thank Dr. Henry Offen, Director, Marine Science Institute, University of California, Santa Barbara and Dr. William Doyle, Director, Center for Coastal Marine Studies, University of California, Santa Cruz, for generously providing facilities in support of this effort. Dr. E. L. Triplett, University of California, Santa Barbara, kindly provided coldroom space and supplies. Jerry Wellington and Peter Steinberg helped with the diving. We are also indebted to Drs John Pearse and Mia Tegner for thoughtful criticism of the manuscript.

LITERATURE CITED

- Barker, M. (1977). Observations on the settlement of the brachiolaria larvae of *Stichaster australis* (Verrill) and *Coscinaterias calamaria* (Gray) (Echinodermata: Asteroidea) in the laboratory and on the shore. *J. exp. mar. Biol. Ecol.* 30: 95–108
- Barnes, J., Gonor, J. (1973). The larval settling response of the lined chiton. *Tonicella lineata*. *Mar. Biol.* 20: 259–264
- Cameron, R. A., Hinegardner, R. (1974). Initiation of metamorphosis in laboratory-cultured sea urchins. *Biol. Bull. mar. biol. Lab., Woods Hole* 146: 335–342
- Cameron, R. A., Hinegardner, R. T. (1978). Early events in sea urchin metamorphosis, description and analysis. *J. Morph.* 157: 21–32
- Chia, F. S., Burke, W. (1978). Echinoderm metamorphosis: Fate of larval structures. In: Chia, F. S., Rice, M. (eds) Settlement and metamorphosis of marine invertebrate larvae. Elsevier, New York, pp. 219–234
- Chia, F. S., Rice, M. (eds) (1978). Settlement and metamorphosis of invertebrate larvae. Elsevier, New York
- Crisp, D. (1974). Factors influencing the settlement of marine invertebrate larvae. In: Grant, P., Mackie, A. (eds) Chemoreception in marine organisms. Academic Press, New York, pp. 177–265
- Ebert, T. A. (1968). Growth rates of the sea urchin. *Strongylocentrotus purpuratus* related to food availability and spine abrasion. *Ecology* 49: 1075–1091
- Harvey, E. B. (1956). The American Arbacia and other sea urchins. Princeton University Press, Princeton, New Jersey
- Hinegardner, R. T. (1969). Growth and development of the laboratory cultured sea urchin. *Biol. Bull. mar. biol. Lab., Woods Hole* 137: 465–475
- Kinne, O. (1977). Cultivation of animals: research cultivation. In: Kinne, O. (ed.) Marine ecology, Vol. III, Cultivation. Wiley, Chichester, pp. 579–1293
- Low, C. (1975). The effect of grouping of *Strongylocentrotus franciscanus*, the giant red sea urchin, on its population biology. Ph. D. thesis, University of British Columbia
- Mileikovsky, S. (1971). Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. *Mar. Biol.* 10: 193–213
- Morse, D., Tegner, M., Duncan, H., Hooker, N., Trevelyan, G., Cameron, A. (1980). Induction of settling and metamorphosis of planktonic molluscan (*Haliotis*) larvae. III. Signalling by metabolites of intact algae is dependent on contact. In: Muller-Schwarze, D. (ed.) Chemical signalling in vertebrate and aquatic animals. Plenum, New York (in press)
- Pearse, J. S. (1980). Synchronization of gametogenesis in the sea urchins *Strongylocentrotus purpuratus* and *S. franciscanus*. In: Adams, T. S., Clark, W. H. Jr. (eds) Recent advances in invertebrate reproduction. Elsevier North-Holland, Inc., Amsterdam (in press)
- Scheltema, R. S. (1974). Larval settlement of marine invertebrates. *Thalassia jugosl.* 10: 275–297
- Schroeter, S. (1978). Experimental studies of competition as a factor affecting the distribution and abundance of purple sea urchin, *Strongylocentrotus purpuratus* (Stimpson). Ph. D. thesis, Biology, University of California, Santa Barbara
- Sokal, R., Rolf, F. J. (1969). Biometry, W. H. Freeman and Co., San Francisco
- Strathmann, R. (1974). The spread of sibling larvae of sedentary marine invertebrates. *Am. Nat.* 108: 28–44
- Tegner, M., Dayton, P. (1977). Sea urchin recruitment patterns and implications of commercial fishing. *Science, N. Y.* 196: 324–326
- Thorson, G. (1961). Length of pelagic larval life in marine bottom invertebrates as related to larval transport by ocean currents: In: Sears, M. (ed.) Oceanography. *Publ. Am. Ass. Advmt Sci.* 67, pp. 455–474
- Thorson, G. (1966). Some factors influencing the recruitment and establishment of marine benthic communities. *Neth. J. Sea Res.* 3: 267–293

This paper was presented by Professor J. S. Pearse; it was accepted for printing on December 11, 1979.