

YALE PEABODY MUSEUM

P.O. BOX 208118 | NEW HAVEN CT 06520-8118 USA | PEABODY.YALE.EDU

JOURNAL OF MARINE RESEARCH

The *Journal of Marine Research*, one of the oldest journals in American marine science, published important peer-reviewed original research on a broad array of topics in physical, biological, and chemical oceanography vital to the academic oceanographic community in the long and rich tradition of the Sears Foundation for Marine Research at Yale University.

An archive of all issues from 1937 to 2021 (Volume 1–79) are available through EliScholar, a digital platform for scholarly publishing provided by Yale University Library at <https://elischolar.library.yale.edu/>.

Requests for permission to clear rights for use of this content should be directed to the authors, their estates, or other representatives. The *Journal of Marine Research* has no contact information beyond the affiliations listed in the published articles. We ask that you provide attribution to the *Journal of Marine Research*.

Yale University provides access to these materials for educational and research purposes only. Copyright or other proprietary rights to content contained in this document may be held by individuals or entities other than, or in addition to, Yale University. You are solely responsible for determining the ownership of the copyright, and for obtaining permission for your intended use. Yale University makes no warranty that your distribution, reproduction, or other use of these materials will not infringe the rights of third parties.



This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License.
<https://creativecommons.org/licenses/by-nc-sa/4.0/>



Relationship of water motion to the shallow water distribution and morphology of two species of sea urchins

by Andrew L. Lissner^{1,2}

ABSTRACT

A 13-month field and laboratory study was conducted at Santa Catalina Island, California, USA to determine some of the effects of water motion on the shallow water distribution of the sea urchin *Centrostephanus coronatus* Verrill. The depth distribution of another sea urchin species, *Strongylocentrotus franciscanus* (A. Agassiz), includes shallow areas of strong water motion (<2 m depth) from which *C. coronatus* is absent. Differences in attachment strength and morphology of the two species were investigated as possible mechanisms affecting the differences in depth distribution.

Density of *C. coronatus* along subtidal transects generally increased with increased depth, ranging from 0 individuals at depths less than 2 m to 1.7/m² at 16 m depth; the majority of the population occurred deeper than 4.2 m. Measurements of relative water motion, using clod cards, made near the shallowest depths of occurrence of *C. coronatus* indicate that these depths are characterized by high levels or sharp increases in water motion. Laboratory wave channel experiments conducted at Scripps Institution of Oceanography, La Jolla, California, indicate that *C. coronatus* are dislodged at lower wave amplitudes when exposed to sharp increases in amplitude, than when exposed to more gradual increases. These results suggest that areas of strong water motion such as noted along the field transects may directly or indirectly limit the distribution of *C. coronatus*. Evidence suggesting that the effects of water motion on *C. coronatus* are relatively direct was obtained from field experiments in which *C. coronatus* were transplanted to deep (13 m) and shallow (3 m) quadrats, and changes in the number of individuals were determined following exposure to calm (\leq Sea State 2; $n = 2$) as compared to rough ($>$ Sea State 2; $n = 6$) conditions. The majority (7 to 9 out of 10) of the animals remained in the deep quadrats following calm and rough conditions, with 5 or 6 remaining in shallow quadrats following calm conditions. In contrast, 0 to 2 individuals remained in shallow quadrats following exposure to rough conditions.

Additional results of wave channel experiments indicate that *C. coronatus* are dislodged at lower wave amplitudes than are *S. franciscanus*. The ability of *C. coronatus* to withstand dislodgement during exposure to strong water motion was estimated indirectly by comparing the number of podia used in attachment by *C. coronatus* and *S. franciscanus*. *Strongylocentrotus franciscanus* had significantly more ($p < .001$) podia/animal than did *C. coronatus* for the animals tested, ranging from 56 to 100 podia per pore pair row for *C. coronatus* ($n = 15$), and from 146 to 214 for *S. franciscanus* ($n = 16$). Differences in the number of podia used in

1. Catalina Marine Science Center, University of Southern California, Avalon, California, 90704, U.S.A.

2. Present address: Ocean Sciences Department, Interstate Electronics Corporation, 10231 Maikai Drive, Huntington Beach, California, 92646, U.S.A.

attachment were not significant, however results suggest that *S. franciscanus* uses at least 3 to 4 times more attachment podia (32 to 51 per pore pair row; $n = 9$) than does *C. coronatus* (2 to 8 per pore pair row; $n = 10$).

Although other factors such as differential predation may contribute to the observed field distributions, results of the present study strongly suggest that *C. coronatus* is not well adapted to conditions of strong water motion, and that limitations in attachment strength, relative to *S. franciscanus*, probably limit the shallow water distribution of this species.

1. Introduction

Water motion can be an important factor affecting the behavior, morphology, and abundance of many types of marine organisms including sea anemones (Koehl, 1977), sponges (deLaubenfels, 1947; Watson, 1976), crinoids (Meyer, 1969; Macurda, 1973), mussels (Harger, 1970; Price, 1982), gastropods (Dethier, 1982; Menge, 1978), algae (Choat and Schiel, 1982; DePaula and Oliveira, 1982), crabs (Hines, 1982) and sea urchins (Russo, 1977; Cowen *et al.*, 1982; Ebert, 1982). For some sea urchin species, grazing activity is apparently limited by exposure to strong water motion such as high waves and surge (Himmelman and Steele, 1971; Mann and Breen, 1972; Mann, 1973; Ogden *et al.*, 1973; Abbott *et al.*, 1974; Lissner, 1980; Choat and Schiel, 1982; Cowen *et al.*, 1982). Ebert (1982) provides extensive data indicating that water motion (exposure to surf) can have a significant effect on the annual survival rates and body wall size of many sea urchin species; relatively exposed areas may be inhabited by different species having different adaptations (e.g., thicker tests) than species associated with protected habitats.

Numerous studies including those by Kitching and Ebling (1961), Leighton *et al.* (1965), Paine and Vadas (1969), North and Pearse (1970), North (1971), Ebert (1977), Nelson and Vance (1979), Pearse and Hines (1979), Duggins (1980), Carpenter (1981), and Sammarco (1982) have shown that grazing by sea urchins can significantly affect the local distribution and abundance of many organisms comprising rocky subtidal and intertidal communities. Mediation of grazing activity, or exclusion from some areas as a result of strong water motion or other factors such as predation (*sensu* Nelson and Vance, 1979), may therefore have a significant effect on benthic communities by creating a refuge of relatively reduced grazing. The present study assessed the mechanism(s) that might produce such a refuge as related to limitations by strong water motion of the shallow water depth distribution of the sea urchin *Centrostephanus coronatus*.

Centrostephanus coronatus Verrill occurs in many rocky subtidal areas from Santa Cruz Island, California (pers. obs.) to Ecuador (Clark, 1948), and can be an important grazer on benthic communities (Nelson and Vance, 1979). The species depth range is from 5 m (Mortensen, 1940) to at least 66 m depth (Given, pers. comm.), although in some areas of the Gulf of California it may occur intertidally (R. Brusca, pers. comm.). Qualitative observations by Lissner (1978) at Santa Catalina, Santa Cruz, and San Clemente Islands, California, suggest that in relatively exposed areas such as rocky

headlands and the windward side of the islands, the shallowest depth at which *C. coronatus* occurs is >12 m as compared to ≥ 5 m in more protected areas. Lissner (1980) demonstrated that activity (emergence from shelter holes), and presumably grazing by *Centrostephanus coronatus* was significantly reduced during periods of strong water motion (storm waves and surge) at shallow (5 m) as compared to deep depths (15 m), and suggested that strong water motion may limit the shallow depth distribution of this species. The present study tested this assumption by conducting (1) SCUBA surveys along fixed transects to determine the depth distribution of *C. coronatus*, and to measure relative water motion associated with the shallowest depths at which the species occurred, (2) field transplants of *C. coronatus* to shallow (3 m) and deep (13 m) areas to determine the number of transplanted individuals remaining in these areas following exposure to calm versus rough conditions, and (3) laboratory wave channel experiments and morphological comparisons to assess the potential attachment strength of *C. coronatus* relative to another sea urchin species, *Strongylocentrotus franciscanus* (A. Agassiz). *Strongylocentrotus franciscanus* exhibits a broader potential depth range (intertidal to at least 110 m) than *C. coronatus*, including shallow areas characterized by strong waves and surge, from which *C. coronatus* is absent (pers. obs.). The results of this study are used to assess some of the differences in depth distribution, morphology and behavior of the two species as related to apparent differences in the levels of water motion to which they may be exposed.

2. Methods

a. Study sites

The laboratory portion of the study was conducted at the Catalina Marine Science Center (CMSC) and the Scripps Institution of Oceanography Hydraulics Laboratory, Santa Catalina Island and La Jolla, California, USA, respectively. The field study was conducted using SCUBA at five sites located offshore from CMSC (site locations presented in Lissner, 1980): Bird Rock North and South (BRN and BRS), Sea Water Intake East and West (SWE and SWW) and Sea Water Intake/Blue Cavern (SW/BC).

Species composition of biological communities at the study sites is typical of southern California kelp bed communities (*Macrocystis pyrifera* and *Eisenia arboorea*) described by Given and Lees (1967).

Transects at BRN and BRS were located near the southeast side of Bird Rock in an area of nearly vertical rock cliffs; the transects ranged from 0 to 16 m depth MLLW and were 17 and 18 m long, respectively. Transects at SWE, SWW, and SW/BC were located between Big Fisherman's Cove and Blue Cavern Point in an area of rock reefs from 0 to 12 m depth MLLW and were 46, 50, and 14 m long, respectively. Shallow segments of the transects, from approximately 0 to 5 m depth, were located inshore from *Macrocystis* beds, while the deeper segments (>5 m depth) traversed through the

beds. Water motion at the study sites includes waves and surge (oscillatory flow) and tidal currents (relatively steady flow); however, for the purposes of the study, potential differences in the effect(s) of these flow regimes were not considered since all are common, potentially overlapping features in the study area.

b. Distribution and abundance

Distribution and abundance of *C. coronatus* was determined at monthly intervals from September 1976 to September 1977 along five transects (BRN, BRS, SWE, SWW, SW/BC). Transects were marked using a nylon line attached to 2 cm diameter reinforcing bar stakes which were hammered approximately 10 m apart into the substratum. Counts of the number of *C. coronatus* present were made during daylight hours by a diver swimming the length of one side of the transect, counting all of the sea urchins within arm's reach (2 m); this procedure was repeated on the other side of the transect, thereby completing a census of a 4 m wide band. Although *C. coronatus* are withdrawn into crevices or holes during daylight hours, their spines protrude from the shelter opening, thus making it possible to census the animals accurately without making night dives.

Data from the transect counts were used to determine the shallowest depths below which 95% of the *C. coronatus* population occurred. Measurements of relative water motion near these depths (hereafter referred to as shallow occurrence depths) were then made to assess the relationship between water motion and the upper bathymetric limit of the species. Since the deepest depths of occurrence can range to at least 66 m, the transects representing the shallow part of the total range, these shallow depths actually represent the upper bathymetric limit for more than 95% of the population. The use of 95% instead of 100% of the transect population provided a more consistent estimate of the pattern of distribution since small numbers (<5) of *C. coronatus* sometimes occurred in shallow transect areas (2 m to 4 m depth) during calm conditions, however, they were absent or reduced in number following episodes of strong wave and surge conditions. Adult *C. coronatus* normally exhibit a high degree of fidelity in homing to shelter holes (Vance, 1979); this tendency should result in relatively stable numbers of individuals within local populations except in marginal habitats (e.g., areas of strong water motion) where greater changes in abundance might be expected.

c. Measurements of water motion

Relative water motion along subtidal transects was measured using calcium sulfate cubes glued to plastic cards (clod cards; Doty, 1971; Doty and Doty, 1973; Lissner, 1978). Differences in dissolution rates of the cubes may result from several factors in addition to water motion including the shape and size of the cubes, and the mixture and type of calcium sulfate used (Doty, 1971). To control for potential differences in the size, weight and shape of the cubes, each cube was made from the same brand and

Table 1. Summary of Sea State conditions used to designate field trials at the Santa Catalina study sites as calm (\leq Sea State 2) or rough ($>$ Sea State 2).

Sea State	Description	Wind velocity range (knots)	Average wave height (m)
0	Calm, light breeze	0-6	0-0.05
1	Gentle breeze	7-10	0.06-0.27
2	Moderate breeze	11-16	0.27-0.88
3-4	Fresh breeze	17-21	0.88-1.50

mixture of calcium sulfate and sea water, and cast in identical, round-bottomed ice cube trays. Weights of the cubes were adjusted to within ± 0.1 g of each other (approximately 30 g initial weight) by flat filing the sides to be glued to the card. Dissolution rates also may vary slightly with temperature and salinity, however these differences usually are not significant (Doty, 1971). To allow for comparison of results from different clod card lots, a diffusion index (DF) was calculated based on the weight lost by each clod card placed in the field divided by the weight lost by control clod cards maintained in still water in the laboratory (Doty, 1971).

During the study, three clod cards were placed by divers at each of the five depths along the transects (BRN, BRS, SWE, SWW, SW/BC), and retrieved after 24 hours exposure. The shallow occurrence depths, below which 95% of the populations occurred along each transect, were used as the center locations for clod card placement; additional locations were established 1.5 and 3.0 m shallower and 1.5 and 3.0 m deeper than the center location. One trial was conducted along the transects each month in January, February, March, July and August, 1977. An important assumption of this method is that the relative water motion along each transect was generally constant from day to day due to unchanging conditions of bottom topography and depth (standardized to MLLW), even though the absolute level of water motion may change daily or seasonally. Mean DF's (± 1 SD; $n = 15$) were calculated for each of the five depths along each transect and converted to a percentage of the largest mean DF from any transect. This conversion standardized the DF's among the depths and transects to provide a measure of relative water motion. These data were then plotted against depth for each transect to provide a visual representation of areas of large change in water motion with depth.

d. Field transplants

Individuals of *C. coronatus* were transplanted from Bird Rock and Habitat Reef to an area near the SW/BC transect to determine (1) if the animals remained in transplant areas during calm sea conditions, and (2) if the number of transplanted animals decreased significantly during rough conditions. Calm conditions were defined as \leq Sea State 2, and rough conditions as $>$ Sea State 2 (Table 1 and Lissner, 1980). Four transplant areas were established: two at 3 m depth and two directly downslope at

13 m depth. The 3 m depth areas correspond to a depth that is shallower than *C. coronatus* normally occurs at Catalina; the 13 m depth areas are well within the normal depth range. One 3 m × 3 m quadrat was located in each area using steel reinforcing bar stakes to mark the corners. All sea urchins (*C. coronatus* and/or *S. franciscanus*) were removed from within the quadrats and for a distance of 1 m surrounding each quadrat.

Each experiment consisted of transplanting 10 tagged *C. coronatus* to one quadrat at each depth. Tagged individuals were used so that any immigrants moving into the quadrats would not accidentally be counted. Animals were transplanted alternately between the two quadrats at each depth during successive trials; the "empty" quadrat for one trial was used as the transplant quadrat for the next trial. Each transplanted animal was placed by hand into a burrow or crevice judged to be of the same type normally occupied by *C. coronatus*. The number of sea urchins in the transplant quadrats was counted after 14 days; empty quadrats also were censused to determine if any movement of animals into these areas had occurred. Daily conditions were classified as calm or rough using direct observations (Sea State) and weather reports. A transplant trial was classified as rough if at least one day out of 14 was rough, and calm if none of the 14 days was rough. Eight trials were performed. Differences between the number of *C. coronatus* remaining in shallow versus deep quadrats after exposure to calm or rough conditions was compared using a Kruskal-Wallis test with tied ranks (Zar, 1974).

e. Method of tagging

Various techniques for tagging sea urchins have been attempted with some success (Ebert, 1965; Lees, 1968; Ogden *et al.*, 1973; Mattison *et al.*, 1977), however the brittleness of the spines and test of *C. coronatus* made these previous methods inappropriate for use in the present study. Nelson and Vance (1979) described a successful technique for tagging *C. coronatus*, however I judged this method to be too time consuming and expensive for use in the present study, and consequently developed a new method. Individual tags were constructed by threading a piece of monofilament through the eye of a No. 12 barbed fishhook and a section of colored plastic insulator (for use in identification), and then tying the monofilament in a loop. The circumference of the loop was adjusted so that it was less than one-half the length of the primary spines of the animal; this was to reduce tag loss due to fish grazing. The tag was applied to the animal by holding the fishhook with a hemostat and inserting it on the aboral surface at the junction of the periproct and genital plates. Tags can be applied underwater in the field or in the laboratory. Tagged and untagged individuals were successfully maintained in aquaria for periods up to three months with no apparent differences in behavior (e.g., activity and feeding) or survival between the groups, as judged by haphazard observations during the tests.

f. Laboratory dislodgement experiments

Several laboratory experiments were performed using the wave channel at the Hydraulics Laboratory of the Scripps Institution of Oceanography to determine the relative wave amplitude(s) necessary to dislodge (1) *C. coronatus* as compared to *S. franciscanus* and (2) *C. coronatus* sheltered in artificial burrows (plastic tubes) as compared to unsheltered *C. coronatus*. These experiments examined relative differences between attachment strength of the two species when exposed to waves, and as such may not be directly comparable with the field data which probably result from a combination of waves and surge (oscillatory flow), and tidal currents (relatively steady flow). However, the overall results (e.g., the relative ability of each species to withstand conditions of strong water motion) should be in agreement.

The wave channel is 33 m long \times 0.5 m wide, with a maximum water depth of 0.5 m. Wave amplitude and frequency is controlled using a hydraulic paddle. Based upon initial experimentation, wave frequency for the present study was set at one wave per second and the amplitude was varied between 0.5 and 9.0 (approximately 5 cm to 15 cm wave height) on a relative scale. Wave velocity over the range of amplitudes tested was approximately 4 to 12 cm/sec based on information provided by the Scripps Institution staff.

Ten *C. coronatus* (average test diameter 60 mm) and 10 *S. franciscanus* (average test diameter 95 mm) were tested; the animals represented haphazardly selected adult urchins collected near the Catalina study sites. Four animals (4 *C. coronatus* or 2 *C. coronatus* and 2 *S. franciscanus*) were placed in the channel for each trial. At the beginning of a trial the animals were placed in the channel for 10 minutes and then picked-up by hand and repositioned in a line at right angles to the direction of wave propagation. Behavior of the animals was noted during the trials.

Exposure to single waves. Two *C. coronatus* and two *S. franciscanus* were exposed to a single wave of 0.5 amplitude followed by a five-minute calm period. The amplitude then was increased by 0.5 and another wave generated followed by a five-minute calm period. This procedure was repeated until dislodgement occurred; five trials were performed using 10 individuals of each species.

Exposure to repeated waves. Two *C. coronatus* and two *S. franciscanus* were exposed to repeated waves of 0.5 amplitude for five minutes. The amplitude then was increased by 0.5 and waves generated for five additional minutes; no intervening calm period was allowed. This procedure was repeated as described above.

Exposure with and without shelter. Two 10 cm diameter \times 12 cm long opaque plastic tubes were attached to a plywood board to provide shelter for *C. coronatus* exposed to single and repeated waves as described above. The tubes were open at both ends and

orientated horizontally with the openings in line with the direction of wave propagation. Four *C. coronatus* were tested during each trial; two animals were unsheltered in line with the openings to the tubes, and two were placed (sheltered) in the tubes. Starting amplitudes were set at 1.0 below the levels which resulted in dislodgement during the single and repeated wave exposures described above. Amplitudes were increased until both individuals of one of the test groups (sheltered or unsheltered) were dislodged. Three trials were performed using different combinations of 10 individuals.

g. Morphological comparisons

Potential differences in the relative attachment strength of *C. coronatus* as compared to *S. franciscanus* were studied by comparing (1) total number of podia, and (2) number of podia used during attachment to a flat surface. On rugose surfaces characterized by holes and crevices, both spines and podia can be used effectively in bracing and attachment; use of spines is reduced on relatively flat surfaces, and podia are the primary method of attachment. Exposure on flat surfaces probably approximates field conditions of exposure while the urchins are foraging outside of shelter holes or crevices. Animals used for these comparisons were adult urchins haphazardly selected near Bird Rock and Sea Water Intake. Estimates of the total number of podia per animal were made by counting pore pairs on cleaned, dried tests of 15 *C. coronatus* and 16 *S. franciscanus*. Tests were cleaned in a 1:10 solution of commercial bleach (5% sodium hypochlorite) and water. Both species characteristically have five double rows of pore pairs (ambulacra) per individual, with each pore pair corresponding to the location of one podium. One row of pore pairs was counted for each ambulacrum. Test diameter (mm) was measured using dial calipers.

Data presented by Ebert (1982) suggest that for many sea urchin species there is a more or less linear increase in some parameters (e.g., jaw length) with increased test diameter. Data from the present study were analyzed using regression analysis (Zar, 1974) to determine whether a linear relationship existed between the number of podia and the test diameter of different sized adults of *S. franciscanus* and *C. coronatus*. An analysis of covariance (Zar, 1974) was then performed to test for interspecies differences between the slopes and y -intercepts of the regression equations, and consequently differences in the number of podia potentially used in attachment.

The number of podia used during attachment to a flat surface was determined by taking photographic slides of the oral surface of 10 *C. coronatus* and 9 *S. franciscanus* while they were attached to the side of a glass aquarium. Test animals were grasped by hand and gently rocked using a horizontal motion to stimulate firm attachment to the glass. Podia were then counted in projected slide transparencies to determine the number of attached podia for each animal. Attached podia were visible as round discs corresponding to the distal sucker of each podium. Test diameters were measured and the data were analyzed as described above.

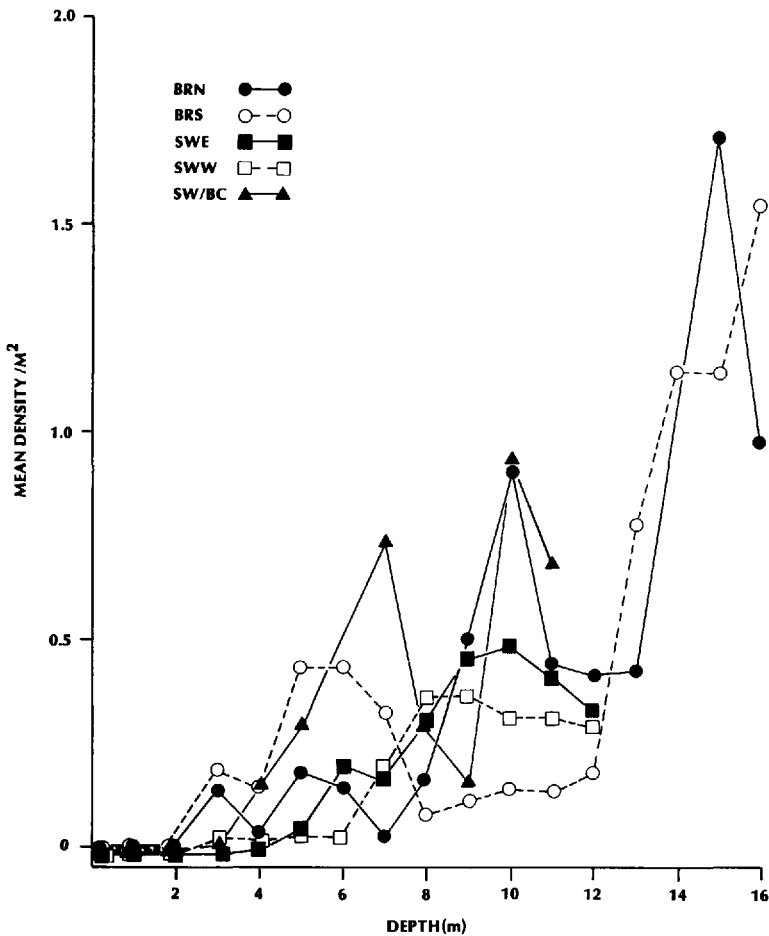


Figure 1. Mean density of *C. coronatus* along five transects at Santa Catalina Island ($n = 13$ months).

3. Results

a. Distribution of *C. coronatus* in relation to water motion

Density of *C. coronatus* along five subtidal transects (BRN, BRS, SWE, SWW and SW/BC) generally increased with increased depth during the 13-month study (Fig. 1). No individuals were observed at depths less than 2 m. Densities ranged from 0 to 0.2/m² from 2 to 4 m depth. From 4 m to 10 m depth most values were within the range of 0.3 to 0.4/m², and were highest (to 1.7/m²) from 10 m to 16 m depth (Fig. 1). Numbers of *C. coronatus* varied only slightly during the study (Lissner, 1978), probably as a result of the high degree of fidelity in homing exhibited by adults of this

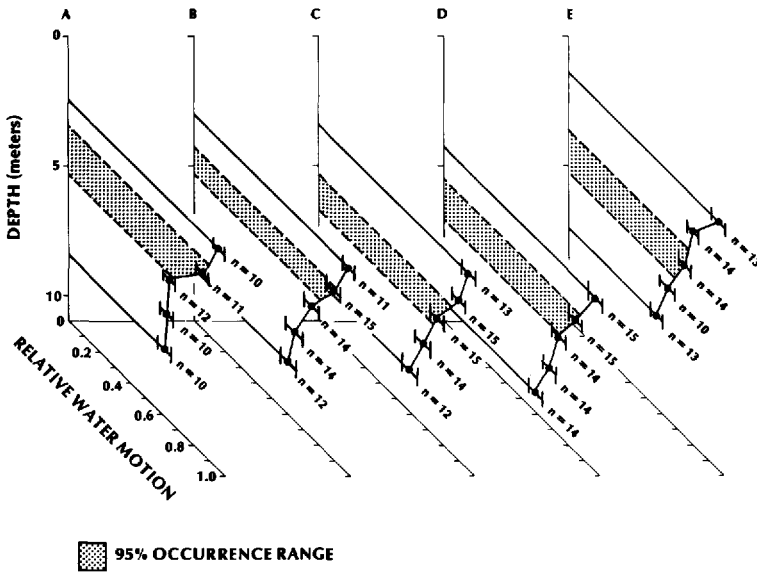


Figure 2. Relative water motion and range of shallow occurrence depths (upper bathymetric limits) of *C. coronatus* along BRN, BRS, SWE, SWW and SW/BC transects (A–E, respectively). Horizontal bars show ± 1 SD; n = total number of clod cards for each depth.

species (Vance, 1979). Means ($X \pm 1$ SD; $n = 13$ months) of the shallowest depths of occurrence of *C. coronatus* along each transect were $4.2 \text{ m} \pm 0.7$ (BRN), $4.6 \text{ m} \pm 0.4$ (BRS), $6.3 \text{ m} \pm 0.5$ (SWE), $6.1 \text{ m} \pm 0.4$ (SWW), and $4.4 \text{ m} \pm 0.5$ (SW/BC). Relative levels of water motion measured near these depths, using clod cards, increased with decreased depth along each transect; however, the increases were not linear and each transect had a region characterized by relatively sharp increases in water motion (Fig. 2). Comparison of these data with the range of shallow occurrence depths for *C. coronatus* indicates that the regions of sharp increase in water motion coincide with or are shallower than the shallow occurrence depths for this species (Fig. 2). These results suggest a limit to the shallow depth distribution of *C. coronatus* that may be directly or indirectly related to conditions of strong water motion.

Relative water motion at each of the five depths along the transects was relatively constant from month to month during the study as indicated by the low standard deviations exhibited by these data (Fig. 2). These results suggest that the regions of sharp increase in water motion are a relatively constant feature of each transect, even though absolute levels of water motion may change daily or seasonally, and may have little or no effect on *C. coronatus* during calm periods.

b. Wave channel experiments

Results of exposure to single waves (sharp increases in water motion) and repeated waves (gradual increases in water motion) in the laboratory wave channel indicate that

Table 2. Numbers of transplanted *C. coronatus* remaining in shallow and deep quadrats after 14 days exposure to rough as compared to calm conditions; 10 *C. coronatus* were transplanted to each depth for each trial. A Kruskal-Wallis test with tied ranks was used to test for differences between the four groups of data. *R* = rough; *C* = calm; rank is indicated in parentheses.

Deep ^R	Deep ^C	Shallow ^R	Shallow ^C
8(4*)	9(1.5*)	2(12*)	6(9)
8(4*)	9(1.5*)	2(12*)	5(10)
8(4*)		2(12*)	
7(7*)		1(14)	
7(7*)		0(15.5*)	
7(7*)		0(15.5*)	
*Tied ranks			
$n_1=6$	$n_2=2$	$n_3=6$	$n_4=2$
$R_1=33$	$R_2=3$	$R_3=81$	$R_4=19$
$N = 16$	$m = 5$	$v = 3$	
$H=13.412$	$C = 0.979$	$H/C = 13.694 = P < .01$	
$\chi^2_{0.05, 3} = 7.815$			

S. franciscanus were not dislodged during any of the trials at amplitudes up to 9.0, while *C. coronatus* were dislodged at relatively low wave amplitudes (2.5 to 5.0). *Centrostephanus coronatus* also were dislodged at lower amplitudes (2.5 to 3.0) during exposure to sharp increases as compared to gradual increases in water motion (3.5 to 5.0). In contrast, *C. coronatus* sheltered in plastic tubes were not dislodged during any of the trials at amplitudes up to 9.0.

Observations made during the experiments indicated that unsheltered *C. coronatus* initially were attached to the bottom of the wave channel using their podia, with primary and secondary spines extended radially. As the wave amplitude was increased, spines were lowered with the primary spines pointing away from the direction of wave propagation. Finally, the number of podia used in attachment were reduced until dislodgement occurred. Once an animal was dislodged, it was unable to reattach until the waves were discontinued. The lowered spine orientation was similar to the behavior of shallow (5 m depth) populations of *C. coronatus* observed during night dives under Sea State 1 and 2 conditions.

Strongylocentrotus franciscanus also were attached to the wave channel by podia during the exposure trials, but lowered spine orientation similar to that exhibited by *C. coronatus* was not observed.

c. Field transplants

Rough conditions occurred during six of the transplantation trials, while calm conditions occurred during two trials. Data on the number of *C. coronatus* remaining in the quadrats were grouped into four categories based on quadrat depth (shallow

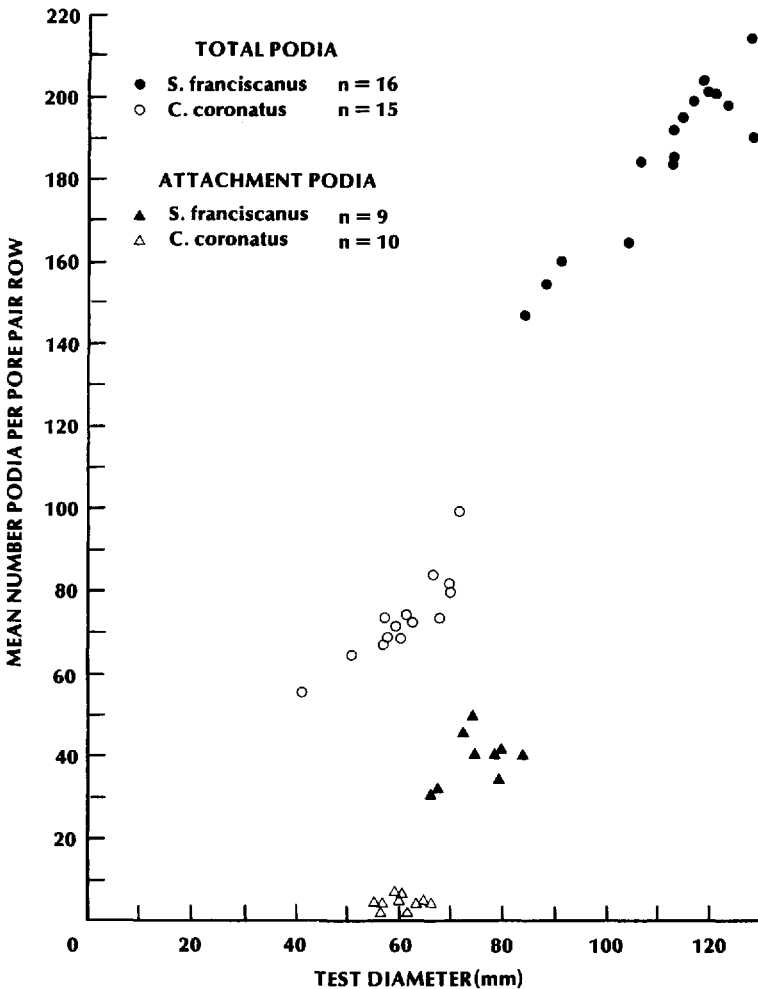


Figure 3. Mean number of podia and attachment podia per pore pair row versus test diameter (mm) of *C. coronatus* and *S. franciscanus* collected at Santa Catalina Island.

versus deep) and exposure (rough versus calm). Results of a Kruskal-Wallis test on these data indicate that a significant difference ($p < .01$) exists between the four groups (Table 2). The majority (5 to 9 out of 10) of the transplanted individuals remained in the deep quadrats following exposure to calm or rough conditions and in the shallow quadrats following exposure to calm conditions (Table 2). In contrast, 0 to 2 *C. coronatus* remained in the shallow quadrats following exposure to rough conditions (Table 2), suggesting that the distribution of *C. coronatus* in some shallow areas may be directly limited by exposure to rough conditions relative to deeper depths.

Table 3. Comparison of the average number of podia versus test diameter (mm) for *C. coronatus* and *S. franciscanus*.

Linear Regression

C. coronatus $y_i = 8.51 + 1.06x$

S. franciscanus $y_i = 35.24 + 1.36x$

ANOVA ($H_0: b = 0$)

	<i>C. coronatus</i>	<i>S. franciscanus</i>
<i>n</i>	15	16
<i>b</i>	1.06	1.36
Σx^2	853.08	85322.69
Σy^2	1485.73	5714.94
Σxy	904.17	115185.63
<i>F</i>	23.64*	85.76*

*Indicates $p < .01$ ANCOVA ($H_0: b_1 = b_2$)

$b_1 = 1.06 \quad b_2 = 1.36$

$(S^2 y \cdot x) p = 41.82$

$t = 1.30 \quad t_{(2),27} = 2.052$

$.50 < t < .10$

ANCOVA ($H_0: a_1 = a_2$)

$a_1 = 8.51 \quad a_2 = 35.24$

$b_c = 1.35$

$t = 14.22* \quad t_{(2), 18} = 1.048$

*Indicates $t < .001$.*d. Morphological comparisons*

The number of podia per animal and the number of podia used in attachment by *C. coronatus* and *S. franciscanus* are presented in Figure 3. Mean numbers of podia per pore pair row ranged from 56 to 100 for *C. coronatus*, and from 146 to 214 for *S. franciscanus*; corresponding test diameters ranged from 41 to 71 mm and from 84 to 128 mm, respectively (Fig. 3). Regression analysis of these data indicates a linear relationship between the number of podia and test diameter for both species (Table 3). Comparison of the slopes (*b*) and *y* intercepts (*a*) of these regressions using ANCOVA indicates that the slopes are not significantly different ($.50 < t < .10$), but that the *y* intercepts are significantly different ($t < .001$). These results suggest that *C. coronatus* has significantly fewer podia per individual than does *S. franciscanus*.

Mean numbers of attachment podia per pore pair row ranged from 2 to 8 for *C. coronatus* and from 32 to 51 for *S. franciscanus*; corresponding test diameters ranged from 54 to 66 mm and from 65 to 85 mm, respectively (Fig. 3). Results of the regression analyses testing the linearity of the relationship between test diameter and number of attachment podia were not significant ($p > .05$) for *C. coronatus* ($F = 0.009$) or *S. franciscanus* ($F = 0.996$). However, inspection of the data presented in

Figure 3 does suggest that during the study *S. franciscanus* used at least 3 to 4 times more attachment podia than did *C. coronatus*.

4. Discussion

Water motion can be a significant factor directly or indirectly affecting the abundance, behavior and morphology of benthic organisms (Lewis, 1968; Reidl, 1971). Direct effects include factors such as dislodgement of organisms as a result of exposure to strong waves and surge (Shelton and Robertson, 1981; Barton and Carter, 1982; Cowen *et al.*, 1982). Indirect effects include mediation of the grazing to which a community may be subjected as a result of reduced activity of important grazers during periods of strong water motion (Lissner, 1980; Choat and Schiel, 1982; Cowen *et al.*, 1982; Dethier, 1982).

The present study focused on the direct effects of water motion on the shallow water distribution of the sea urchin *Centrostephanus coronatus*. Results of field surveys indicate that the majority of the *C. coronatus* population along 5 transects occurred below 3.4 m depth, with occurrence along two transects (SWE and SWW) restricted to depths below 5.5 m (Figs. 1 and 2). Transect areas near these depths were generally characterized by relatively high levels or sharp increases in water motion as indicated by the results of the clod card study (Fig. 2). Results of the wave channel experiments suggest that these regions of strong water motion may represent zones of increased potential for dislodgement of *C. coronatus*, thereby limiting the distribution of the species. No *C. coronatus* were observed at depths shallower than 2 m. The number of individuals occurring between 2 to 4 m depth was highly variable between surveys, particularly after storms, while those occurring deeper than 4 m exhibited relatively stable numbers. These results would be expected if depths less than 4 m correspond to areas of marginal habitat for *C. coronatus*, while depths greater than 4 m represent preferred habitat (*sensu* Krebs, 1978). Stability of the populations within preferred habitat probably is maintained by the high degree of fidelity in homing exhibited by this species (Vance, 1979).

Results of transplantation experiments (Table 2) provide the most direct evidence that strong water motion may limit the shallow water distribution of *C. coronatus*. Water motion typically decreases with increased depth (e.g., Fig. 2). During conditions of strong water motion, the greatest effects on an organism should be observable at shallow depths, with few if any effects noted for deeper populations. Exposure of *C. coronatus* to rough sea conditions resulted in larger decreases in the number of individuals transplanted to shallow (3 m) as compared to deep (13 m) depths (Table 2). In contrast, only slight decreases occurred in shallow and deep populations during calm conditions (Table 2). A similar relationship was observed by Lissner (1980) for the effect of water motion on activity (emergence from shelter holes) of *C. coronatus*; activity of deep populations was nearly 100% during calm and rough conditions

however activity of shallow populations was significantly reduced during rough conditions.

Koehl (1977) noted that sea anemones can reduce the drag to which they are subjected from strong water motion by reducing their height (posturing) during periods of increased flow. Drag studies of *C. coronatus* have not been conducted, however the spine lowering response observed during the wave channel experiments and during exposures to strong surge in the field also may serve to decrease the risk of dislodgement by reducing the surface area exposed to water motion. Increases in substrate rugosity, including protection afforded by shelter holes, may significantly reduce the potential for dislodgement of *C. coronatus* since both spines and podia can be used to brace against the walls of the shelter. Hines (1982) noted that some crab species do not appear to seek shelter during storms and as a consequence many individuals may be lost (swept away) from local populations. The effectiveness of shelter holes in reducing dislodgement is demonstrated by the results of the wave channel experiments in which *C. coronatus* placed in artificial shelters were not dislodged at any of the amplitudes tested. Use of shelter holes or behavioral mechanisms such as reduced activity during conditions of strong water motion may serve to extend the bathymetric range of *C. coronatus* into shallow areas from which the species might otherwise be excluded.

The ability of an organism to withstand conditions of strong water motion is related to several factors including shape (drag and turbulence relationships), behavior (orientation and activity) and attachment strength (Reidl, 1971). Mechanisms such as spine lowering, the use of shelter holes, and modified activity patterns all probably increase the ability of *C. coronatus* to withstand strong water motion. However, limitations in attachment strength may be a primary factor making these adaptations necessary. Greatest attachment strength apparently is achieved by the use of both spines and podia for bracing and attachment, such as can occur in shelter holes or crevices. During foraging outside of shelters, the use of spines in bracing is necessarily reduced, thus making podia the primary mechanism of attachment.

Attachment strength was not determined directly during the study, however counts of podia were used to provide an indirect indication. Results of podia counts of *C. coronatus* and *S. franciscanus* predict greater attachment strength for *S. franciscanus* (Fig. 3, Table 3) corresponding to the results of wave channel experiments in which unsheltered *C. coronatus* were dislodged at lower wave amplitudes than where *S. franciscanus*. Morphological comparisons as described in this paper are potentially useful in making predictions about population distributions and behavior of other species of sea urchins relative to conditions of water motion. Ricklefs *et al.* (1981) caution against making assumptions about the ecology of an organism based solely on morphological data, but they conclude that this approach can provide valuable insight, particularly for between species comparisons, when applied with supportive ecological data.

Although the present study focused on the effects of water motion, numerous other factors including predation and competitive interactions can be important in structuring benthic communities (Dayton, 1971; Krebs, 1978; Menge, 1979; Paine and Levin, 1981; Choat, 1982). Common predators of *C. coronatus* at Santa Catalina Island include the wrasses *Semicossyphus pulcher* and *Halichoeres semicinctus* (Nelson and Vance, 1979); however, since these species are common throughout the depth ranges in the study areas (pers. obs.) it seems unlikely that the patterns of depth distribution observed for *C. coronatus* can be explained solely on the basis of differential predation.

Lissner (1978) assessed the potential for competitive exclusion of *C. coronatus* from shallow areas by *S. franciscanus*; removal of *S. franciscanus* from depths less than 3 m did not result in any significant change (increase) in the number of adjacent *C. coronatus* populations or migration of *C. coronatus* into the removal areas during the 12-month study. No obvious aggressive encounters (e.g., bulldozing) between the two species were observed during the study, and individuals of both species were commonly observed in close proximity to one another, sometimes with their spines touching, in the field and when placed together in laboratory aquaria. These results suggest that interference competition (sensu Park, 1954) by *S. franciscanus* is not a significant factor limiting the shallow depth distribution of *C. coronatus*. Other potential types of biological interactions, such as exploitation competition by *S. franciscanus* or competition from other species were not addressed by the present study.

The effects of water motion on *C. coronatus* probably range from insignificant effects in some protected areas, to large effects in exposed locations, such as the windward side of Santa Catalina Island, with populations occurring only at deeper depths (>12 m). Results from this study probably represent average conditions in the study area since measurements of water motion and the depth distribution and abundance of *C. coronatus* were made at several sites over a seasonal cycle which included storms and calm periods. A recent study by Cowen *et al.* (1982) indicates that storms can be a significant factor affecting local abundances of sea urchins (*S. franciscanus*), and emphasizes the importance of conducting studies concerned with the distribution and abundance of shallow water organisms during a range of seasonal events which include storms as well as calm periods. Episodic events such as large storms may be the most significant factors affecting many benthic communities (Rogers *et al.*, 1983).

Acknowledgments. This study was completed as part of a doctoral dissertation at the University of Southern California, and represents contribution number 65 from the Catalina Marine Science Center (CMSC). I gratefully acknowledge the assistance of the staff, faculty and students of CMSC during the field portion of the study. Special thanks to R. Brusca, R. Chew, J. Dorsey, R. Douglas, K. Fauchald, R. Given, K. Green and J. Kastendiek for their constructive comments. An earlier version of the paper was greatly improved based on comments by T. Ebert and two anonymous reviewers. Additional thanks to L. Lissner for typing and reviewing the manuscript, and to J. Dorsey for help in preparation of the figures.

REFERENCES

- Abbott, D. P., J. C. Ogden and I. A. Abbott (eds.). 1974. Studies on the activity pattern, behavior, and food of the echinoid *Echinometra lucunter* (Linnaeus) on beachrock and algal reefs at St. Croix, U.S. Virgin Islands. Special Publication 4, West Indies Laboratory, Farleigh Dickinson University, 111 pp.
- Barton, D. R. and J. C. H. Carter. 1982. Shallow-water epilithic invertebrate communities of eastern Georgian Bay, Ontario, in relation to exposure to wave action. *Canadian J. Zool.*, *60*, 984-993.
- Carpenter, R. C. 1981. Grazing by *Diadema antillarum* (Philippi) and its effects on the benthic algal community. *J. Mar. Res.*, *39*, 749-765.
- Choat, J. H. 1982. Fish feeding and the structure of benthic communities in temperate waters. *Ann. Rev. Ecol. Syst.*, *13*, 423-429.
- Choat, J. H. and D. R. Schiel. 1982. Patterns of distribution and abundance of large brown algae and invertebrate herbivores in subtidal regions of northern New Zealand. *J. Exp. Mar. Biol. Ecol.*, *60*, 129-162.
- Clark, H. L. 1948. A report on the echini of the warmer eastern Pacific, based on the collections of the VELERO III. Allan Hancock Pac. Exped., *8*, 351 pp.
- Cowen, R. K., C. R. Agegian and M. S. Foster. 1982. The maintenance of community structure in a central California kelp forest. *J. Exp. Mar. Biol. Ecol.*, *64*, 189-201.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.*, *41*, 351-389.
- deLaubenfels, M. W. 1947. Ecology of the sponges of a brackish water environment at Beaufort, North Carolina. *Ecol. Monogr.*, *17*, 31-46.
- DePaula, E. J. and E. C. Oliveira. 1982. Wave exposure and ecotypical differentiation in *Sargassum cymosum* (Phaeophyta-Fucales). *Phycol.*, *21*, 145-153.
- Dethier, M. N. 1982. Pattern and process in tidepool algae: factors influencing seasonality and distribution. *Botanica Mar.*, *25*, 55-66.
- Doty, M. S. 1971. Measurement of water movement in reference to benthic algal growth. *Botanica Mar.*, *14*, 32-35.
- Doty, M. S. and J. E. Doty. 1973. Abrasion in the measurement of water motion and the clod-card technique. *Bull. So. Cal. Acad. Sci.*, *72*, 40-41.
- Duggins, D. 1980. Kelp beds and sea otters: an experimental approach. *Ecology*, *61*, 447-453.
- Ebert, T. A. 1965. A technique for the individual marking of sea urchins. *Ecology*, *46*, 193-194.
- 1977. An experimental analysis of sea urchin dynamics and community interactions on a rocky jetty. *J. Exp. Mar. Biol. Ecol.*, *27*, 1-22.
- 1982. Longevity, life history, and relative body wall size in sea urchins. *Ecol. Monogr.*, *52*, 353-394.
- Given, R. R. and D. C. Lees. 1967. Santa Catalina Island biological survey. Survey report No. 1, University of Southern California Press, Los Angeles, California, 124 pp.
- Harger, J. R. E. 1970. The effect of wave impact on some aspects of the biology of sea mussels. *Veliger*, *12*, 401-414.
- Himmelman, J. H. and D. H. Steele. 1971. Food and predators of the green sea urchin *Strongylocentrotus droebachiensis* in Newfoundland waters. *Mar. Biol. (Berlin)*, *9*, 315-322.
- Hines, A. H. 1982. Coexistence in a kelp forest: size, population dynamics, and resource partitioning in a guild of spider crabs (Brachyura, Majidae). *Ecol. Monogr.*, *52*, 179-198.
- Kitching, J. A. and F. J. Ebling. 1961. The ecology of Lough Ine, XI. The control of algae by *Paracentrotus lividus* (Echinoidea). *J. Anim. Ecol.*, *30*, 373-383.

- Koehl, M. A. R. 1977. Effects of sea anemones on the flow forces they encounter. *J. Exp. Biol.*, *69*, 87–105.
- Krebs, C. J. 1978. *Ecology: The Experimental Analysis of Distribution and Abundance*, Harper and Row Publishers, New York, NY, 678 pp.
- Lees, D. C. 1968. Tagging subtidal echinoderms. *Underwater Naturalist*, *5*, 16–19.
- Leighton, D. L., L. G. Jones and W. J. North. 1965. Ecological relationships between giant kelp and sea urchins in southern California. *Proc. 5th Int. Seaweed Symp.*, Pergamon Press, New York, NY, 141–153.
- Lewis, J. R. 1968. Water movements and their role in rocky shore ecology. *Sarsia*, *34*, 13–36.
- Lissner, A. L. 1978. Factors affecting the distribution and abundance of the sea urchin *Centrostephanus coronatus* Verrill at Santa Catalina Island. University of Southern California dissertation, Los Angeles, CA, 168 pp.
- 1980. Some effects of turbulence on the activity of the sea urchin *Centrostephanus coronatus* Verrill. *J. Exp. Mar. Biol. Ecol.*, *48*, 185–193.
- Macurda, D. B. 1973. Ecology of commatulid crinoids at Grand Bahama Island. *Hydro-Lab*, *2*, 9–24.
- Mann, K. H. 1973. Seaweeds: their productivity and strategy for growth. *Science*, *182*, 975–981.
- Mann, K. H. and P. A. Breen. 1972. The relation between lobster abundance, sea urchins, and kelp beds. *J. Fish. Res. Bd. Canada*, *29*, 603–605.
- Mattison, J. E., J. D. Trent, A. L. Shanks, T. B. Akin and J. S. Pearse. 1977. Movement and feeding activity of red sea urchins (*Strongylocentrotus franciscanus*) adjacent to a kelp forest. *Mar. Biol.*, *39*, 25–30.
- Menge, B. A. 1978. Predation intensity in a rocky intertidal community. Effect of an algal canopy, wave action and desiccation on predator feeding rates. *Oecologia* (Berlin), *34*, 17–35.
- 1979. Coexistence between the sea stars *Asterias vulgaris* and *A. forbesi* in a heterogeneous environment: a non-equilibrium explanation. *Oecologia*, *41*, 245–272.
- Meyer, D. L. 1969. Functional morphology and living habits of shallow unstalked crinoids of the Caribbean Sea. *Geol. Soc. Am. Abstr. Progr.*, Pt. 7, 150–151.
- Mortensen, T. 1940. A monograph of the Echinoidea, Volume III-1. C.A. Reitzel, Copenhagen, Denmark, 510 pp.
- Nelson, B. V. and R. R. Vance. 1979. Diel foraging patterns of the sea urchin, *Centrostephanus coronatus* as a predator avoidance strategy. *Mar. Biol.*, *51*, 251–258.
- North, W. J. (ed.). 1971. The biology of giant kelp beds (*Macrocystis*) in California. *Beihefte zur Nova Hedwigia*, *32*, 1–600.
- North, W. J. and J. S. Pearse. 1970. Sea urchin population explosion in southern California coastal waters. *Science*, *167*, 209.
- Ogden, J. C., D. P. Abbott and I. Abbott (eds.). 1973. Studies on the activity and food of the echinoid *Diadema antillarum* Philippi on a West Indian patch reef. Special Publication 2, West Indies Laboratory, Fairleigh Dickinson University, 96 pp.
- Paine, R. T. and R. L. Vadas. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp. on benthic algal populations. *Limnol. Oceanogr.*, *14*, 710–719.
- Paine, R. T. and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monogr.*, *51*, 145–178.
- Park, T. 1954. Experimental studies of interspecific competition in two species of *Tribolium*. *Physiol. Zool.*, *27*, 177–238.
- Pearse, J. S. and A. H. Hines. 1979. Expansion of a central California kelp forest following the mass mortality of sea urchins. *Mar. Biol.*, *51*, 83–92.

- Price, H. A. 1982. An analysis of factors determining seasonal variation in the byssal attachment strength of *Mytilus edulis*. J. Mar. Biol. Assoc., U.K., 62, 147–155.
- Reidl, R. 1971. Water movement: animals, in Marine Ecology Vol. 1, Pt. 1, O. Kinne, ed., Wiley, New York, NY, 1123–1156.
- Ricklefs, R. E., D. Cochran and E. R. Pianka. 1981. A morphological analysis of the structure of communities of lizards in desert habitats. Ecology, 62, 1474–1483.
- Rogers, C. S., M. Gilnack and H. C. Fitz. 1983. Monitoring of coral reefs with linear transects: a study of storm damage. J. Exp. Mar. Biol. Ecol., 66, 285–300.
- Russo, A. R. 1977. Water flow and the distribution and abundance of echinoids (Genus *Echinometra*) on an Hawaiian Reef. Aust. J. Mar. Freshwater Res., 28, 693–702.
- Sammarco, P. W. 1982. Echinoid grazing as a structuring force in coral communities: whole reef manipulations. J. Exp. Mar. Biol. Ecol., 61, 31–55.
- Shelton, C. R. and P. B. Robertson. 1981. Community structure of intertidal macrofauna on two surf-exposed Texas sandy beaches. Bull. Mar. Sci., 31, 833–842.
- Vance, R. R., 1979. Effects of grazing by the sea urchin *Centrostephanus coronatus* on prey community composition. Ecology, 60, 537–546.
- Watson, A. L. 1976. Preliminary observations on the influence of water movement on population structure in the sponge *Ancorina corticata* (Carter) (Choristida: Demospongiae). Proc. New Zealand Ecol. Soc., 23, 45–50.
- Zar, J. H. 1974. Biostatistical Analysis, Prentice-Hall Inc., New Jersey, 620 pp.

