The Aggregation Behavior of *Diadema* (Echinodermata, Echinoidea)

J. S. PEARSE and S. W. ARCH

Environmental Health Engineering, California Institute of Technology; Department of Biology, The University of Chicago

Many species of echinoids occur together in aggregations of both single and multiple species composition. Some short term aggregations may be associated with reproductive activities, but in most cases the aggregations seem to be responses to localized environmental factors and involve little "social" interaction among the different individuals (Reese, 1966). Populations of tropical diademid echinoids, however, may form aggregations involving true social behavior. Large "flocks," "families." "colonies" or "social clusters" of *Diadema setosum* or *D. savignyi* have been noted on the Great Barrier Reef (Saville-Kent, 1893; Stephenson, *et al.*, 1931; H. L. Clark, 1921, 1946; Roughley, 1951; Dakin & Bennett, 1963), at Suez (Fox, 1926) and off central Japan (Onada, 1936). Similar aggregations have been observed of *D. antillarum* and *Astropyga magnifica* in the Caribbean (Randall, *et al.*, 1964; Kier and Grant, 1965) and *D. mexicanum* in the Eastern Tropical Pacific (Pearse, 1968a). Such aggregations do not seem to be simple passive responses to environmental limitations because adjacent areas of apparently identical substratum and feeding conditions are not occupied.

We were able to make intermittent observations of populations of *D. setosum* and *D. savignyi* while snorkel diving off Singapore, northeast Borneo (Darvel Bay), New Britain (Rabaul), Bougainville (Kieta), Guadacanal (Honiara), the New Hebrides (Port Vila) and New Caledonia (Noumea). Scattered solitary individuals were found hidden in the reefs of all these areas. Small aggregations of 20 to 30 animals, similar to those described by Magnus (1967) in the Red Sea, were seen around crevices in the reefs and rocks at Rabaul (dock area) and Honiara. Aggregations of up to several hundred animals on open reef flats occurred at Rabaul (Dawapia Rocks), Kieta and Port Vila. Observations made over a period of two days at Rabaul and seven days at Kieta provided data on the stability and social nature of the aggregations.

Composition and Stability of the Aggregations

H. L. Clark (1921) and Mortensen (1940) believed that *D. setosum* and *D. savignyi* tended to form separate species specific aggregations. Most of the aggregations we observed, however, contained both species. We had little difficulty

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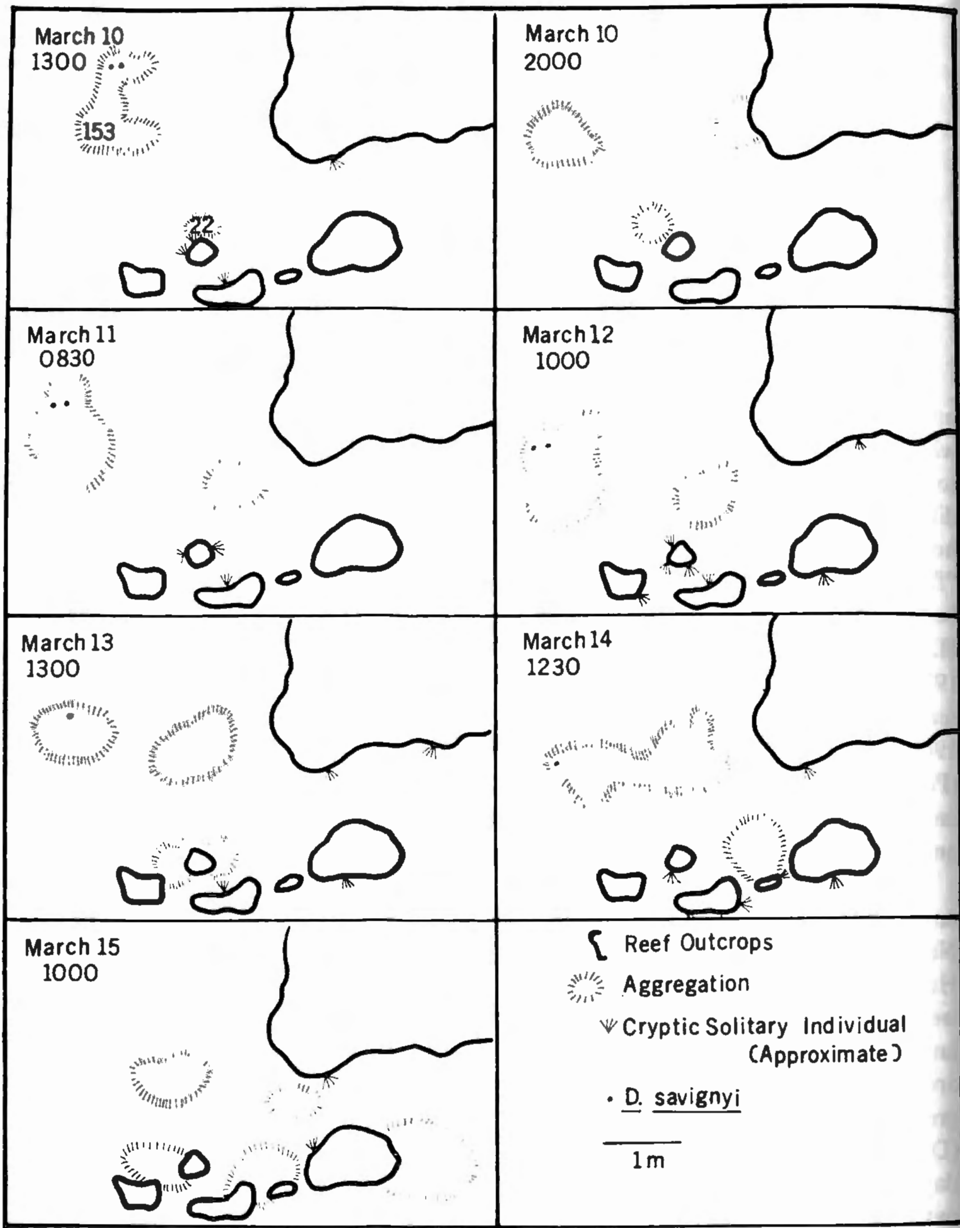

Fig. 1. Changes in several aggregations of *Diadema* at 2–3 m depth on the reef flat next to the pier at Kieta, Bougainville Island, Solomon Islands. The reef outcrops were mainly masses of dead coral. The area with the aggregations was fine silt and coral rubble which sloped gently toward the bottom of the figures. The dates and times of each observation are given in the upper left-hand corner of each figure. The total number of individuals in the aggregations at 1300 hours, March 10, 1965, was counted and is given; no further counts were made to minimize disturbance. All the individuals in the aggregations were *D. setosum* except for the two individuals of *D. savignyi* marked by dots. The March 10 observation at 2000 was made during a night dive when the species could not be distinguished.

distinguishing the two forms despite A. M. Clark & Owen's (1965) doubts that they are distinct species. Individuals of *D. setosum* were distinguished from those of *D. savignyi* by their longer spines, blue spots rather than blue lines, an orange ring around the anal cone, and especially the five interradial white spots (Mortensen, 1940). (These characters are not very constant, however, in the Gulf of Suez (Pearse, in pless).) At Rabaul the ratio of *D. setosum* to *D. savignyi* was about 3:1 in both the aggregations in the open and in the animals scattered cryptically among the rocks and reefs. A ratio of about 1:1 was found in the population at Honiara, but at Kieta many less *D. savignyi* were present and the ratio was less than 100:1.

Stephenson, *et al.* (1931) reported that aggregations of *D. setosum* on the Great Barrier Reef remained "in approximately the same situation for months at a time." We made daily measurements with a meter stick of several aggregations at Kieta for a period of six days. As shown in Figure 1, the aggregations did remain in the same region, but there was a great deal of change in their shape and position, as they broke into smaller units and fused into larger units.

The occurrence of two easily distinguished forms of *Diadema* allowed us to follow changes in individual composition of the aggregations. Individuals of *D. savignyi* served as "tags" within aggregations otherwise composed of *D. setosum*. At the beginning of our observations at Kieta, two specimens of *D. savignyi* were found within the aggregations. The relative positions of the specimens of *D. savignyi* changed daily (Fig. 1), and on the fourth day one had left the aggregates. Neither specimen could be found on the sixth day, even though extensive search was made of the entire area. Apparently, individual animals wander into and out of the aggregations from the surrounding reefs.

These observations indicate that aggregations of *Diadema* are not stable in either size, shape, position or individual composition. Individuals of *Diadema* are probably omnivorous scavengers that feed on silt, detritus and algae scraped off rocks (Mortensen, 1940; Randall, *et al.*, 1964; Lewis, 1964; Pearse, in press). It seems reasonable to assume that the movements and changes in the aggregations are at least partly due to grazing activities in the area.

Social Behavior and Aggregating Mechanisms

The aggregations that were watched closely at both Rabaul and Kieta seemed to behave as single "social" units. When undisturbed, the individuals within the aggregates waved their spines slowly about, touching and crossing the spines of neighboring animals. The shorter secondary spines were especially active in this interplay between individuals. When one individual on the edge of an aggregate was gently prodded with an iron bar, it immediately waved its spines about rapidly (although not pointing its spines toward the disturbing stimulus as solitary individuals tended to do). This increased activity stimulated neighboring animals to wave their spines faster, striking and stimulating other animals, so that a "wave of excitation" passed through the aggregate. When the initial stimulus was gentle and singular, the "wave of excitation" passed through only a few animals before dissipating. When stronger and more persistent prods were given, the excitation passed through the whole aggregation, and all the animals excitedly waved their spines about. The analogy between this behavior and the operation of a simple nerve net system was both obvious and striking.

With continued strong prodding, the entire aggregation moved away from the point of irritation as a unit. Finally, very strong stimulation caused the animals nearest the stimulus to climb over neighboring animals so that the moving unit was several animals high.

When individuals of *Diadema* were removed from an aggregate and placed next to the same or another aggregate so that their primary spines just touched the primary spines of individuals within the aggregation, they *always* immediately joined the aggregate. Once within the aggregate, an interplay of the secondary spines ensued for a short period before the new entry "settled" into place. If the animal was placed further from the aggregate so that there was no contact between the primary spines, a different behavior occurred. At first the individual did not move from where it had been placed, but it simply waved its spines about vigorously. The animal then began to move about slowly. Six of nine animals removed so that their spines were 1 to 10 cm from the spines of the aggregated individuals moved slowly but steadily toward the aggregation. When spine contact with individuals on the periphery of the aggregate was made, the displaced individual quickly moved into the aggregate. The remaining three animals so removed from the aggregates moved slowly toward a reef outcrop about 30 cm away and nestled under ledges.

Although more quantitative data are needed, these observations suggest that the aggregations are formed and maintained through scototaxic (dark attracted) and thigmotaxic responses. By being attracted to dark areas, the animals would approach either an already established aggregation or a dark crevice or ledge in a reef outcrop. Magnus (1967) also believed that individuals of *Diadema* are attracted to "dark contrasting horizons." Species of *Diadema* are among the most light sensitive of the echinoids; they have very well developed shadow responses (Yoshida, 1966) and marked diurnal activity (Thornton, 1956; Magnus, 1967). Such light sensitivity further suggests that scototaxic responses could be important. Once within an aggregate or crevice, however, position might be maintained by the interplay of the spines with other individuals or with the solid substratum.

The one night observation made at Kieta suggests that thigmotaxic responses may be the principal factor maintaining the aggregates. As shown in Fig. 1, the aggregations were fully formed even at night and not dispersed as would be expected if aggregation was simply a scototaxic response. Moreover, the solitary individuals that were cryptic by day were seen by us to forage out into the open at night (under the pier flood lights at Rabaul) as well as by Thornton (1956) and Magnus (1967) in the Red Sea. It therefore appears that thigmotaxis between individuals within an aggregation is in some way different from that between solitary individuals and a rock or coral substratum.This difference may be related to a chemotaxis among the different individuals similar to that suggested by Dix (1969) for the echinoid *Evechinus chloroticus.*

Adaptive Significance of Aggregating Behavior

It seems unlikely that aggregation in *Diadema* is related to reproduction. Gonadal samples were taken between January and March, 1965, both from aggregated populations at Rabaul, Kieta and Port Vila, and unaggregated populations at Singapore, northeast Borneo and Noumea. Histologic examination revealed that all the animals in all the samples contained mature or nearly mature gametes (Pearse, 1968b). Moreover, aggregation was not observed at any time during the reproductive cycle of *D. setosum* in the Gulf of Suez (Pearse, in press).

Rather, the aggregations probably have a protective function. An aggregation of these long spined urchins at least appears much more formidable than single animals in the open, and single animals, in fact, are rarely found in the open during the day. Although Randall, *et al.* (1964) list a large number of predators (mostly fish) on *D. antillarum*, they also believe that the aggregating behavior is mainly for "mutual protection."

Because solitary cryptic individuals and small partially sheltered aggregations occurred wherever large aggregations were found, large aggregations in the open probably result whenever the population size greatly exceeds the number of suitable hiding places in the reefs. Magnus (1967) suggests that competition for hiding places among crevices in the reefs may force individuals out into the open where they form aggregations. The fact that the animals either hide in the reefs or crowd together in aggregations further suggests that the aggregating behavior has a protective function.

Summary

Our observations suggest the following about the aggregating behavior of *Diadema*:

1. Although the aggregations are persistent, they are constantly changing in shape, size, position and individual composition.
2. Scototaxic responses may be important in the formation of the aggregations.
3. Maintenance of the aggregations probably depends on a thigmotaxic interplay of the spines between different individuals. This is not a simple thigmotaxic response, however, because solitary individuals that are cryptic in the reefs by day leave their crevices to forage at night while aggregations do not break up at night.
4. The aggregations probably function as protective social units. When disturbed several to the animals wave their formidable spines about, and with intense stimuli, the entire aggregation moves away as a unit.
5. The aggregations probably form when the populations are so large that

many individuals are more likely to contact each other rather than hiding places within the reef.

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