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AGGREGATION BEHAVIOUR OF THE BRITTLE-STAR *OPHIOTHRIX FRAGILIS*

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(Text-figs. 1–2)

The role of behaviour in the formation and maintenance of dense aggregations of *Ophiothrix fragilis* has been studied by experiments carried out on the sea-bed. Individual animals were removed from extensive beds of brittle-stars with a density of 1000–2000/m^{-2} and placed nearby on the muddy gravel bottom. At current strengths of 4–8 cm/s, the brittle-stars paused for about 20 s then started walking across current. A series of walks and turns continued unless other brittle-stars were encountered. In this case the animal usually climbed on top of the others and stopped walking. Walking was not terminated if the animals encountered stones, weed, hydroids, or *Alcyonium* colonies. Large anemones and starfish were avoided. When groups of animals were placed together on the bottom, the minimum group size which survived for one day on open muddy gravel was 35 and it seemed that at least 100 were needed for the continued survival of a group. Smaller groups could survive only if protection was afforded by hydroids, *Alcyonium* or inanimate objects. The experiments demonstrate that these brittle-stars are able to recognize and respond to conspecifics and that these responses, together with responses to currents, are important in the maintenance of aggregations and hence the preservation of the optimum situation for suspension feeding.

INTRODUCTION

Dense aggregations of echinoderms on the sea bed have been described from various parts of the world. Reese (1966) considered that such an aggregation 'is a response to one or more essential environmental factors such as food or substratum, and does not reflect social behaviour *per se*'. Observations by Warner (1969, 1971) and by Brun (1969) suggested that, in aggregations of the brittle-star *Ophiothrix fragilis*, individuals may respond to conspecifics rather than solely to food or the substratum. On an apparently uniform substratum, some areas are covered with a dense bed of brittle-stars while other adjacent areas are devoid of brittle-stars. Warner (1971) pointed out that the aggregations are advantageous to the species so it seems possible that the animals might aggregate actively rather than coming to a suitable feeding area by chance. The aims in this study were to investigate the responses shown by *Ophiothrix fragilis* to its physical surroundings, to some of the other organisms living near it and, especially, to conspecifics. The animals studied are in dense aggregations off Berry Head in Southern England and all observations were made underwater in the natural habitat.

METHODS

The bed of brittle-stars studied has been described in detail by Warner (1971). It is situated at an average depth of 15 m below datum and extends in a strip at least 1 km long and 200 m wide. The bed is patchy, some areas containing no brittle-stars and other, apparently identical, areas supporting populations of 1000–2000 m^{-2}. During this study, currents of up to 20 cm/s were measured at the level of the tips of the brittle-stars' arms but all experiments were carried out when the current was within the most frequently recorded range of four to eight cm/s. At this speed the animals feed with two to three arms extended (Warner & Woodley, 1975). Dives were timed so as to avoid the brief periods when the current changes direction.

In most of the experiments a brittle-star was removed from an aggregation, placed out in the open, away from other brittle-stars, and observed. The observer swam with head 1–2 m above the experimental animal and feet downstream so that any water disturbance would not affect the animal. There were no signs of any responses to the observer from the experimental animals. The behaviour of the brittle-stars was recorded with a pencil on a roughened white perspex slate. All experiments were timed using a stopwatch and for each set of experiments the current speed and direction was measured (Warner & Woodley, 1975).

A total of 49 experiments was carried out during 14 dives. In 35 of these experiments (10 pilot experiments and 25 in which all walking by brittle-stars was measured) the following methods were used. For each experiment a site on or near the edge of a brittle-star patch was chosen and a diagram of the site drawn with the current direction shown on it. A single brittle-star was then removed from the patch as carefully as possible and placed on the muddy gravel. If an animal, when it was removed, adhered firmly to other individuals and could not immediately be separated from them, that animal was not used in the experiment. All animals used had a disc diameter of 8–12 mm. As soon as the experimental animal was placed on the substratum, the stopwatch was started and the position of the animal was marked on the diagram of the site. A note was made of the angles between (1) the source of the current, the animal, and the direction of the origin of the animal in the patch ('home'), and (2) the source of the current, the animal, and the nearest edge of the patch. The distances from the edge of the patch in the 'home' direction and from the edge of the nearest patch were also recorded. When the brittle-star started to walk the time was noted, the walk direction was estimated as an angle to the current direction, and the length of the walk was measured. At any change in direction, the time, walk direction, and walk length were recorded. The movements were marked on the diagram as well as being written down in figures. Distances were measured using scales drawn on the slate. If the brittle-star encountered an object in its walking, its response was recorded in detail. In 10 of these experiments, for each walk direction a record was kept of which arm was leading.

A further 11 experiments, the results of which were recorded in largely the same manner, involved putting a brittle-star on top of other brittle-stars, or on hydroids, or on *Alcyonium* colonies. The final experiment, which was repeated three times but was unsuccessful twice due to the activities of lobster fishermen in the area, involved laying a line on the sea bed, placing known numbers of brittle-stars alongside markers on the line and returning on the following day to see if any groups remained. The site chosen was in an area of muddy gravel, apparently identical to that occupied by the brittle-star bed 20 m away.

RESULTS

General description of behaviour of isolated brittle-star

When a brittle-star is separated from a patch and placed on the muddy gravel bottom in a current of 4–8 cm/s, it waves its arms for a few seconds, then appears to hold on to the bottom. If it touches no brittle-stars, after a pause it starts to walk. All experimental animals showed this behaviour. The median delay before walking was 20 s with upper and lower quartiles of 35 s and 10 s.

The initial walk continued for a median of 10 cm in a straight line if no other animal was touched. At the end of the walk the animal paused for a few seconds, turned, and set off in a new direction which might be at any angle from 30° to 180° to the previous direction. This sequence of actions could continue for a total distance of at least 60 cm with a median walk length of 12 cm and a gradual increase in the duration of pauses. The mean walking speed for all animals observed was 15 cm/min and the maximum speed was 45 cm/min.

The majority of animals were placed within 20 cm of a patch and regained the patch within 4 min. Ten animals walked intermittently for more than 5 min before reaching the edge of a brittle-star patch but a few did not reach a patch and were watched for 5–15 min. An example of the path taken by a brittle-star in one of these experiments is shown in Fig. 1.

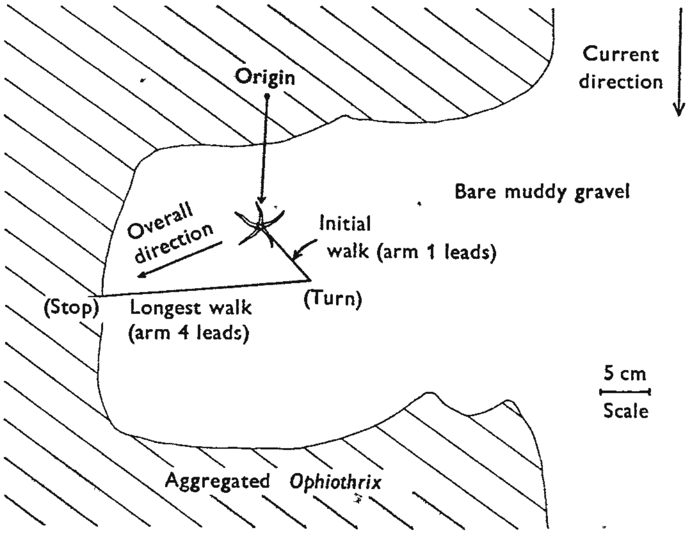

Fig. 1. Example of the route of a walking brittle-star after being removed from an aggregation and placed in isolation on muddy gravel nearby.

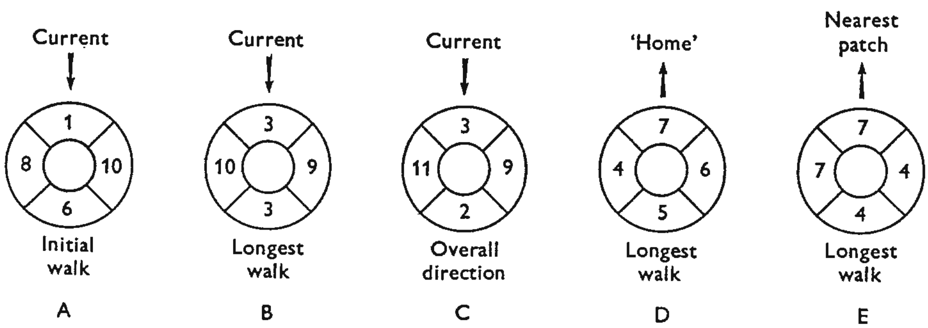

Fig. 2. Factors affecting direction of walking in *Ophiothrix*. For individuals separated from an aggregation and placed on the sea-bed, the number walking in each of the four directions is shown.

Factors affecting direction of walking

Since the direction of all walks was recorded it was possible to relate the direction of (1) the initial walk, (2) the longest walk, and (3) the overall direction from start to end of observations with (*a*) the current direction, (*b*) the direction of 'home' (the original position of the animal in the patch), and (*c*) the direction of the nearest brittle-stars (see Fig. 1). Fig. 2, A, B and C, shows that the initial walk, the longest walk, and the overall direction were most frequently across current. The possible directions are here divided into four and the number of animals which went in each of these four directions is shown.

The majority of the initial walk directions are across current and five out of the six animals classed as moving away from the current source walked at an angle of 30° or 40° to the current direction. Using a binomial t test on the data shown in Fig. 2A, it is clear that animals are more likely to walk across current than towards or away ($P < 0{\cdot}03$ 2-tailed). When the longest walk and the overall direction of movement are considered it is apparent that 80% of *Ophiothrix* walking is across current. Using the test in the same way, for Fig. 2B $P < 0{\cdot}01$ and for Fig. 2C $P < 0{\cdot}001$. The direction of home or of the nearest brittle-star patch had no effect on the direction of walking. Fig. 2D and E shows the direction of the longest walk with respect to the direction of 'home' and of the nearest brittle-star patch. These observations of longest walk and those of initial walk and overall direction show that brittle-stars move at random with respect to 'home' or the nearest brittle-star patch and thus afford no evidence for any ability to detect conspecifics which are out of reach or to orient back to their point of origin. The responses of walking brittle-stars are summarized in Table 1.

TABLE 1. SUMMARY OF RESPONSES OF WALKING *OPHIOTHRIX*

Influencing factor	Response
Current direction	Walks at 90° to current
Direction of nearest patch	Random
Direction of 'home'	Random
Encounters *Ophiothrix*	Stops walking (may climb on top)
Encounters hydroid	May pause, then continues walking
Encounters stone	Turns immediately, continues walking
Encounters *Alcyonium* or *Cerianthus*	Continues walking
Encounters large *Tealia* or *Cereus*	Turns, avoids anemone, continues walking
Encounters *Asterias*	Turns, avoids starfish, continues walking

Responses to objects or animals encountered while walking

Walking behaviour is rapidly terminated by contact with conspecifics. All experimental animals stopped within 5 cm of reaching the edge of a brittle-star patch. A few stopped immediately but most stopped briefly at contact, then climbed on top of the other animals and assumed a position from which they could hold on to the substratum as well as their neighbours. Most took longer than 10 min to start feeding. When three individuals were placed on top of a brittle-star patch and watched for 6 min, two did not walk at all and the other walked only 7 cm during this time.

During some of the experiments other animals or stones were encountered by brittle-stars but these did not terminate walking. Three animals encountered large anemones, *Tealia* or *Cereus*, and one encountered a starfish, *Asterias*. In each of these cases the brittle-star stopped and turned as soon as the other animal was touched and thus avoided it. Small anemones, *Cerianthus*, and small brittle-stars, *Ophiura albida*, were ignored by walking *Ophiothrix*. Large hydroids, *Nemertesia* or *Bougainvillia*, were encountered by nine walking *Ophiothrix*. Seven of these paused briefly, as if about to turn, and then continued walking. The other two were not observed to continue walking but one of the animals had just reached a steep slope and the other had previously been walking for 15 min and the observer was forced to leave. Two *Ophiothrix* were put down so that they were touching *Alcyonium* colonies but ignored them. Two others were placed individually within a 25 cm diameter circle of 5 cm high stones to see if they would stop when the stones were reached. Each animal was observed to turn immediately upon reaching the stones on at least three occasions (see Table 1).

It was apparent during all observations that a brittle-star could advance with one or with two arms leading and that, when it turned, another arm or arms would lead. Following this general observation, 10 animals were watched carefully to confirm it. The leading arm on the initial walk was called no. 1 and the others in clockwise direction were called 2, 3, 4 and 5. A record was kept of which arm was leading after successive turns. When an animal changed direction it was sometimes observed to rotate its disc slightly but never in such a way that the arm or arms which were previously leading could lead again. The arm or arms pointing towards the direction of movement at its onset always led (as in Fig. 1).

The final experiment was designed to find out the size of the smallest *Ophiothrix* aggregation which could survive for a day on the sea-bed and whose members were able to feed normally. When the groups of 5, 10, 20, 50 and 250 brittle-stars were placed in heaps by a line on the sea-bed, the immediate response of the animals was to start walking. Some stopped, touching others, within a minute but others became separated from the main mass and continued walking leaving behind groups somewhat smaller in numbers than the original groups. After 22 h the following numbers of animals were observed by the markers: 5 – 1 individual flattened about 20 cm away; 10 – 10 individuals 15 cm away clustered around a large *Nemertesia* colony, some were feeding but with only one arm extended into the current: 20 – 2 isolated flattened individuals; 50 – 4 together and 3 isolated individuals, none feeding; 250 – two groups of 57 and 35 individuals, mostly feeding normally. These results are in accord with the observations that, apart from occasional clusters around hydroids, *Alcyonium*, or other irregularities in the bottom such as rocks or old motor tyres, brittle-star patches are seldom smaller than 100 individuals and most patches are much larger and often continuous with one another.

DISCUSSION

It has generally been thought that aggregations of echinoderms occur due to the responses of individuals to food and to substratum rather than to one another (e.g. Reese, 1966). The results of experiments reported here show that *Ophiothrix fragilis* which live in large aggregations do respond to one another. This conclusion is supported by the observations of Warner (1969, 1971), Brun (1969), and the author that *Ophiothrix* aggregate even when adjacent areas with an apparently identical substratum are available.

Warner (1971), suggested four advantages to *Ophiothrix fragilis* of living in a dense aggregation: (*a*) individuals are less likely to be swept away by fast currents and can therefore more easily remain in a favourable feeding area, (*b*) aggregated individuals can extend more of their arms upward to feed, (*c*) the forest of arms will slow the current in their immediate vicinity thus facilitating the trapping of suspended particles, and (*d*) the efficiency of reproduction may be improved. Given these advantages, any behaviour which aids in patch formation and maintenance is of value to the species. Patch formation by undisturbed animals has not been observed but in the experiment in which groups of brittle-stars were placed on the muddy gravel and left overnight it was apparent that the smallest group which could survive and feed with nothing to anchor them was about 35. Normally, patches have to survive for longer than the duration of this experiment and the smallest undisturbed patches which were observed in the open consisted of at least 100 individuals. Warner's (1969) observation of a small patch of brittle-stars being rolled up and swept away by a faster than average current shows that very large patches are the safest. This accounts for the very high proportion of the population which live in extensive aggregations consisting of millions of animals.

If a brittle-star patch is disturbed by storms or predators, the individual animals have a mechanism for returning to a patch. The functioning of this mechanism has been shown in the experiments. Animals separated from a patch were clearly not able to detect the direction from which they had come or the animals in the nearest patch, but they were able to detect the current direction and they responded to it by walking across current. Since the bare areas between patches of brittle-stars generally take the form of long strips extending in the direction of the prevailing currents, this behaviour usually resulted in the animal regaining a patch within a few minutes. The initial direction of walking was as frequently away from the nearest patch as towards it, but animals often turned through 120°–180° and tended to walk further in the new direction so that most animals put within 20 cm of a patch reached it. The fact that experimental animals stopped walking when they encountered other brittle-stars and presumably recognized them as conspecifics was a clear result of this study. The particular characteristics of the brittle-stars which allowed recognition have not yet been elucidated but it was clear that walking behaviour was not terminated by contact with stones, plant material, hydroids, *Alcyonium*, anemones, *Asterias* or *Ophiura*.

The observation that ophiuroids have no dominant leading arm while walking has been reported by Romanes & Ewart (1881) and others listed by Binyon (1972). This study confirms that such behaviour is the same in the natural habitat of the animals.

In addition to walking across current, *Ophiothrix* responds to current direction by positioning the feeding arms so that the ambulacrum faces the current (Warner & Woodley, 1975). These brittle-stars also respond to current speed. Warner (1971) has reported that at high current speeds (25 cm/s or more) *Ophiothrix* stop feeding and crouch down, thus reducing the likelihood of being swept away. Recent observations from photographs taken at known current speeds have shown that normal feeding with two or three arms extended occurs at current speeds of up to 15 cm/s, but fewer arms are raised at 20 cm/s and none at 25 cm/s. Studies by Hannan (personal communication) in a flume with a muddy bottom showed that isolated *Ophiothrix* were swept away at 20–30 cm/s but aggregated animals were able to survive currents up to 60 cm/s. In another flume study, Castilla (1971, 1972) has reported that *Asterias* will walk upstream in currents as slow as 0·6 cm/s but that their behaviour was affected by the presence of food or noxious substances in the water. It is not surprising that this predator should show a response which is different from that of *Ophiothrix* but it is noteworthy that *Asterias* responds to such slow currents.

The location of the sense organs involved in detecting current direction is not known. Some information about the operation of this sensory system is provided by the observation that the brittle-stars remained still for a median of 20 s before walking, during which time they could have been assessing current direction.

The behaviour of *Ophiothrix fragilis* maximizes the efficiency with which the animal finds, and maintains itself in, a situation where suspension feeding is possible. The aggregation of many brittle-stars into dense patches is essential with current speeds such as those observed in the vicinity of the animals off Berry Head. The behaviour is modified at different current speeds to reduce the likelihood of animals being swept away and there is a behavioural mechanism for returning to a patch should an individual become separated. An essential part of such aggregation behaviour is that brittle-stars should recognize and respond to conspecifics and this has been demonstrated by the separation experiments.

I thank G. F. Warner for assistance while diving and for discussion of results.

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