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Notes on the swarming behaviour and population density of *Asterias rubens* L. (Echinodermata: Asteroidea) feeding on the mussel, *Mytilus edulis* L.

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Dense and extensive aggregations (swarms) of *Asterias rubens* invaded subtidal and low intertidal beds of young *Mytilus edulis* at Morecambe Bay, Irish Sea, in certain summers (March–September) during 1968 to 1976. The largest intertidal swarm occupied about 2·5 ha (1600 × 15 m) at its peak, and contained at least $2 \cdot 4 \times 10^6$ starfish of 6 cm mean arm radius. Feeding concentrations within swarms commonly attained 300 to 400 starfish per m^2, representing a wet weight biomass of around 12 to 16 kg/m^2. In 3 months (June–August), the largest swarm systematically cleared mussels from 50 ha, which otherwise should have held at least 3500 tonnes of 20 mm seed by September. The frontal boundary of large swarms sometimes advanced 150 to 200 m per month, or 5 to 7 m daily. Swarms retreated rapidly to deeper water in early autumn and apparently overwintered outside the bay. Movements and navigation of swarms towards mussel beds are discussed in relation to the olfactory sense and positive rheotaxis demonstrated recently in *A. rubens*.

Introduction

The starfish *Asterias rubens* L. (syn. *A. vulgaris,* Verrill) is probably the most destructive predator of natural and cultivated stocks of the mussel *Mytilus edulis* in northern Europe (Seed, 1969; Korringa, 1976) and of oysters in eastern Canada (Smith, 1940). In Britain, it is feared widely by mussel cultivators, especially in North Wales and the Wash, but it is only an occasional pest of *Ostrea edulis* L. (Hancock, 1969). *A. rubens* is generally confined to the subtidal zone in waters of high salinity (> 30 ‰) but in summer it sometimes occurs in the low intertidal zone.

Much effort has been devoted to finding methods for removing *A. rubens,* and also *A. forbesi,* Desor in North America, from oyster and mussel beds (Galtsoff and Loosanoff, 1939; Smith, 1940; Korringa, 1976). Few direct measurements of population density and biomass have been reported for *Asterias,* however. For *A. rubens,* Hancock (1958) used mark-recapture methods to estimate densities of young starfish on beds of *O. edulis* in southeast England; Brun (1968) measured directly (by diving) adult densities on a bed of *Chlamys islandica* (O. F. Müller) in Norway, while Gulliksen and Skjæveland (1973) assessed from diver-collected samples the dry biomass of *A. rubens* feeding on the ascidian *Ciona intestinalis* (L.) in Borgenfjorden. In the western Baltic Sea, Anger et al. (1977) and Nauen (1978) estimated biomass on different substrates from samples taken by divers and dredges.

Large aggregations or swarms of *A. rubens* were encountered at very high densities and feeding on beds of young mussels situated just above and below Extreme Low Water Mark of Spring Tides (ELWMST) at Morecambe Bay, northwest England (Dare, 1973; 1976). Wherever time permitted, observations were made on density and movements of swarms. This paper presents all the data collected from 1968 to 1976 at one particular group of mussel beds in Morecambe Bay. Observations by divers on a subtidal aggregation of *A. rubens* elsewhere in Morecambe Bay during the summer of 1976 are reported by Sloan and Aldridge (1981).

Methods

Observations were made on a 120 ha mussel-bearing ground situated 4 km offshore on the northern side of the 16 km wide entrance to Morecambe Bay, in the Irish Sea (Fig. 1). This ground, known locally as 'South America' skear[1], is an almost level expanse of firmly packed pebbles upon which large settlements of mussel spat occur almost every winter and early spring (Dare, 1973; 1976). The mussel bed at 'South America' is totally uncovered only on the largest spring tides and then

[1]A local term for an intertidal area of stable, pebble, or boulder ground upon which mussel beds often develop; probably derived by coastal erosion of glacially formed drumlins.

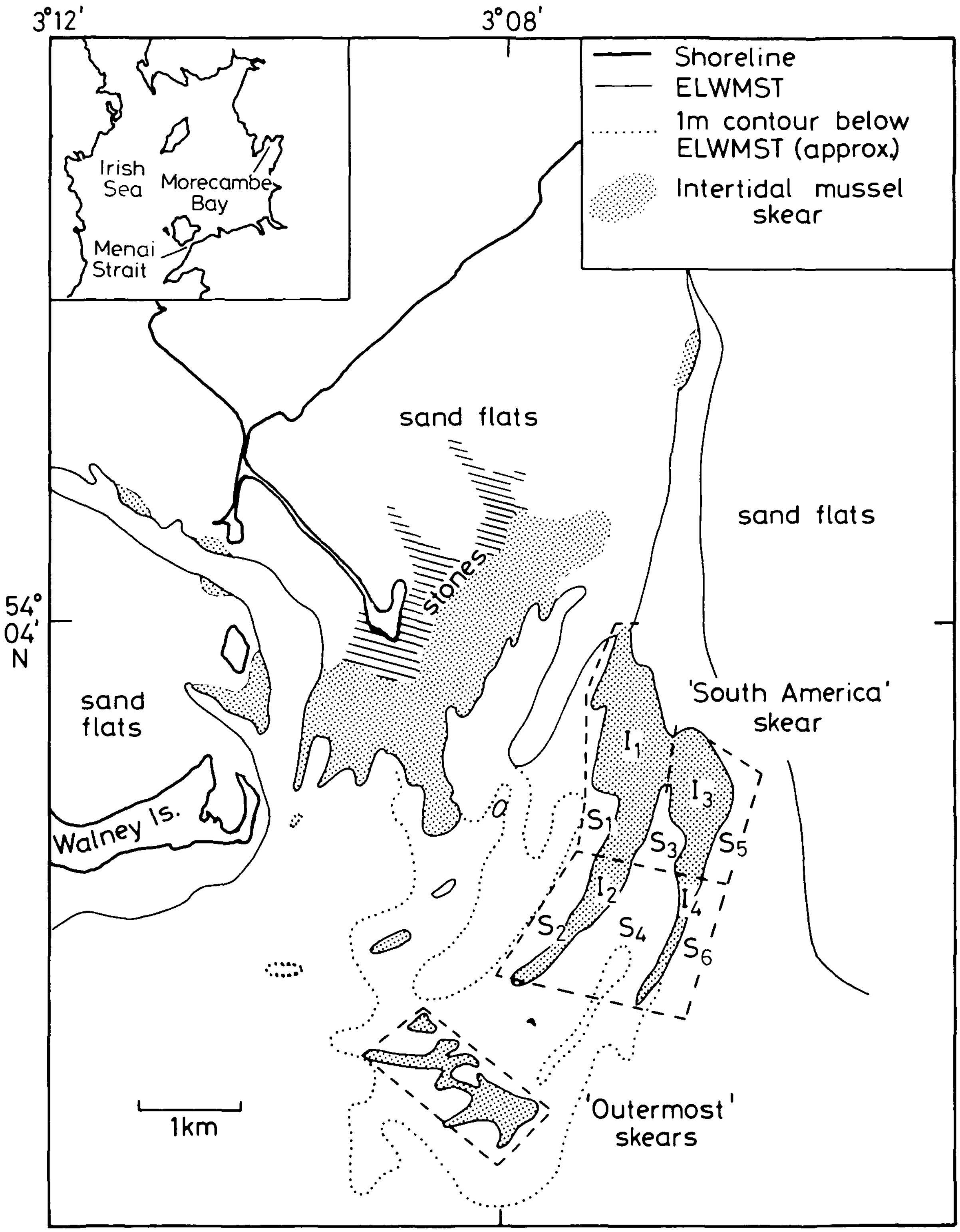

Figure 1. The study area in Morecambe Bay, showing the location of 'South America' skear and adjacent mussel beds, and the starfish recording areas (enclosed by dashed lines). (Based on Admiralty Chart 2010, 1968 edition). Extreme Low Water Mark of Spring Tides (ELWMST) is indicated.

for a maximum duration of 4 h at its inshore end; the highest point is about one m above extreme low water mark. To seaward, there is a broad shallow region of stony and sandy bottom upon which mussel settlements also occur frequently, notably on the broad flat 'Outermost' skears which emerge for 1 to 2 h at low water of large spring tides. These skears form a shelf between 'South America' skear and the deeper (5–10 m) water in the northern entrance of the bay.

Starfish distribution was plotted on a survey map of the 'South America' bed usually at monthly intervals from spring until autumn during 1968 to 1976. For recording purposes, this mussel bed was subdivided into four intertidal sectors, I_1 to I_4, and six subtidal sectors, S_1 to S_6 (Fig. 1). In years when large invasions occurred, samples of starfish were collected; body size was measured as the maximum arm radius taken from the tip of the longest arm to the mouth (Hancock, 1958). Swarm density was estimated in one year (1972) by counting starfish collected by hand within $0 \cdot 1$ m^2 quadrat samples (n = 25). Biomass was estimated crudely by weighing starfish after they had drained for one hour.

The observations, incidental to the main field work on *Mytilus,* were restricted further by the remoteness of the starfish infestation areas and by the brief time available for sampling at this very low shore level. When weather conditions permitted, brief inspections of the 'Outermost' skears mussel beds were made in five of the summers in order to supplement the more regular observations further inshore.

Results

Incidence of swarms

The incidence and distribution of starfish in the study area is summarized in Table 1. Annual abundance and distribution varied widely. Starfish were very scarce throughout the entire area in only one year (1974) and at 'South America' in three years (1968, 1970, 1974). An unusually large and widespread invasion at 'South America' in 1969 was followed by smaller and much more localized influxes in five of the next seven years. Further offshore, at 'Outermost' skears, starfish swarms appeared almost annually, being observed in four of the five summers when visits were made to these grounds.

Influxes at 'South America' were confined to spring and summer, March–September; only occasional individuals were seen in other months. In the major invasion years (1969, 1972, 1976) the main swarms did not reach 'South America' until May–June and they disappeared during September at about the time of onset of autumnal westerly gales. In the Wash, North Sea coast, intertidal swarms of *A. rubens* were once observed as late as November–December (G. Davies, personal communication), though others disappeared in October (J. M. Bray, personal communication).

Starfish were most prevalent in the shallow subtidal zones at 'South America', especially around the seaward and eastern edges of the skear. Movements into the intertidal zones occurred mostly at 'Outermost' skears and on the narrowest parts (I_3, I_4) of 'South America' less than $0 \cdot 5$ m above ELWMST. The wider and more exposed sectors were invaded only in 1969 when starfish moved 300 m beyond and up to about $0 \cdot 75$ m above ELWMST, and experienced some 3 h of aerial exposure on each spring tide ebb during early mornings and evenings. In the Wash, intertidal starfish swarms have been observed on mussel beds 100 m beyond and up to $0 \cdot 5$ m above ELWMST (G. Davies, personal communication).

Size and behaviour of swarms

The extent and monthly movements of the largest (1969) starfish swarm recorded at 'South America' are

Table 1. The incidence of starfish on mussel beds in the Morecambe Bay study area during 1968 to 1976.

Year	'South America' mussel bed: Intertidal sectors I_1	I_2	I_3	I_4	Subtidal sectors S_1	S_2	S_3	S_4	S_5	S_6	'Outermost' skears mussel bed
1968	0	0	0	–	0	–	0	–	–	–	–
1969	4	4	2	–	4	4	3	2	0	–	–
1970	0	0	0	0	1	1	1	1	1	1	2
1971	0	0	2	0	0	0	0	0	2	–	2
1972	1	0	2	2	0	0	3	4	0	2	3
1973	1	1	0	0	2	2	0	0	0	0	–
1974	0	0	0	0	1	1	1	1	1	1	1
1975	0	0	2	3	1	1	0	0	2	3	–
1976	0	0	0	2	0	1	0	4	0	1	4

Starfish abundance rankings:
0, absent or rare (less than 1 per 500 m^2); 1, many widely scattered individuals (less than 1 per 10 m^2); 2, dense swarm; small area and localized; 3, dense swarm; invasion over wide area; 4, dense swarm; large scale invasion over very wide area; –, no observations.

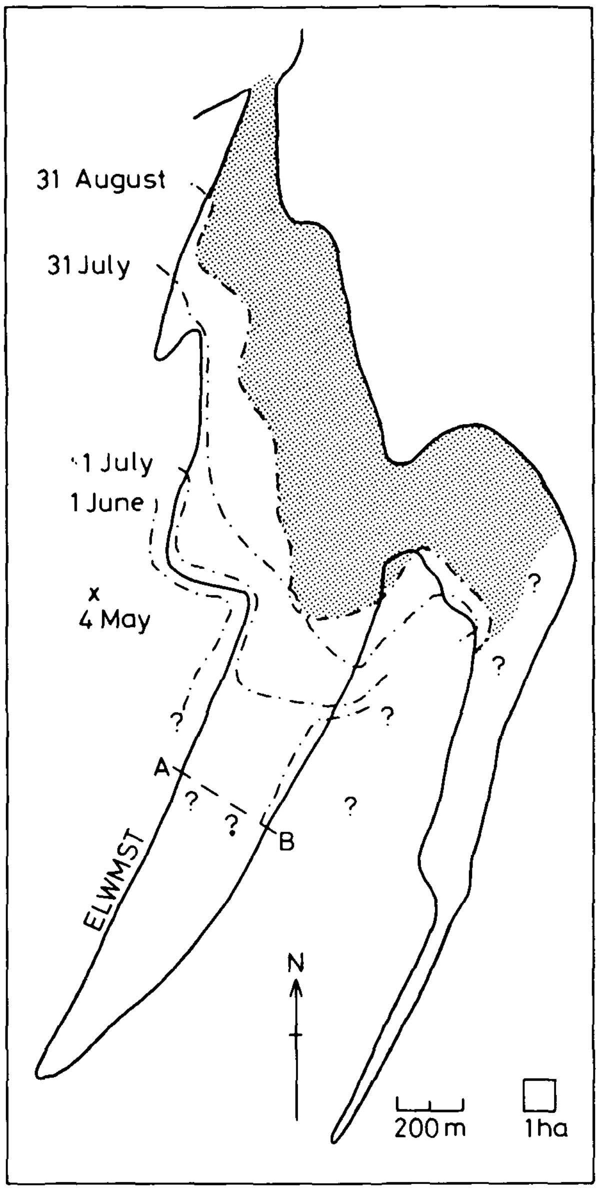

Figure 2. Map of the 'South America' mussel bed, showing the monthly progress of the starfish swarm above Extreme Low Water Mark of Spring Tides (ELWMST) during the May–August 1969 invasion. The stippled area denotes mussel bed still intact at 31 August and 12 October. Starfish removed all mussels from the intertidal ground between line A–B and the swarm's front line at 31 August. Positions of the front are indicated —·— on given dates; x = first sighting. Areas not inspected are marked ??

shown in Figure 2. The densely aggregated starfish moved in a highly coherent manner from southwest to northeast across the intertidal mussel bed. They formed a long, narrow band which at its peak in August was about 1600 m long and 15 m average width, and thus occupied about 2·5 ha of ground. The swarm travelled up to 300 m intertidally in two months, 1 July to 31 August, and left a completely devastated zone in its wake containing empty mussel shells and a few starfish stragglers. Upon the rapid disappearance of the swarm in autumn, a sharply marked boundary between the predated and untouched sectors of the mussel bed was readily apparent. Approximately 50 ha of ground had been cleared totally of seed mussels (0- and 1-groups). The two age groups had mean lengths of 9 mm and 25 mm respectively on 1 July; on 31 August the 0-group mean length was 20 mm (1-group did not survive). A survey of the surviving sector of the mussel bed in October showed that the cleared zone could then have contained 3500 to 4500 tonnes of mussels.

The 1972 invasion, by contrast, remained just below ELWMST (at S_3 and S_4, Fig. 1) where the starfish attacked 1-group mussels of mean lengths between 27 mm (May) and 37 mm (August). The swarm moved into the bay between the two 'arms' of 'South America' in an inverted U-shaped formation. From mid-May, the apex of the arc travelled about 200 m in one month and 700 m in three months. The swarm cleared numerous scattered mounds of mussels from a 35 to 40 ha area by mid-August. At its maximum, the starfish band was at least 1000 m long but only 15 to 25 m wide.

Further offshore, towards and around the 'Outermost' skears, swarms were either dense but irregular in shape, or were diffused over a very extensive area.

Density and biomass of swarms

During major invasions starfish generally aggregated into a dense, smothering layer so that the young mussels beneath were scarcely visible. At maximum feeding density, the individuals formed a single layer with arms overlapping, as illustrated by Brun (1968). Data collected in 1969 and 1972 at 'South America' are given in Table 2, and compared with information available from other areas.

Densities of starfish at 'South America' in 1972 commonly reached 300 to 400 animals per m² on the mussel mounds, with a crude wet biomass averaging around 13·6 kg/m². The overall density of the entire swarm would have been less, though not less than 100 animals per m², because many starfish were thinly spread on bare mud between the mussel patches. Assuming an overall mean density of 100 starfish per m² and swarm dimensions of 1000 × 15 m gives a minimum population estimate of $1 \cdot 5 \times 10^6$ starfish (60 tonnes) in this particular swarm. A similar density in the feeding patches was noted in 1969. Although no samples were taken, a photograph of 0·5 m² of a representative aggregation contained at least 195 starfish. At a minimum of 100 per m² overall, the 1969 swarm would have comprised at least $2 \cdot 4 \times 10^6$ starfish (96 tonnes) in August. In both years, the August swarms consisted of small- to medium-sized starfish of 6 cm mean

Table 2. Dimensions of starfish swarms at Morecambe Bay and elsewhere.

Region		Tidal level	Prey[1]	Swarm dimensions Length (m)	Width(m)
1	Morecambe Bay, Aug 1969	intertidal	*M*	1 600	15
2	Morecambe Bay, Aug 1972	subtidal	*M*	>1 000	15–25
3	Morecambe Bay, Jul–Aug 1976	subtidal	*M*	525[4]	30[4]
4	Menai Strait, May 1971	subtidal	*M*	435	35
5	Norway, Jun 1967	subtidal	*C*	> 100	10
6	Norway, 1969–1970	subtidal	*Ci*	–	–
	Crouch estuary,				
7	(a) Sep 1955	subtidal	*B*	>2 500 m^2	
8	(b) Oct 1955	subtidal			
9	Canada	subtidal	*O*	–	–
10	Western Baltic Sea, Jun–Aug 1976	subtidal	*M*	–	–
11	Western Baltic Sea, Jun–Aug 1976	subtidal	*H*	–	–

Region	Swarm density n/m^2 (±95%)	Biomass kg/m^2 (wet wt)	Mean arm radius in cm $\bar{r}$	range	Source
1	300 –400[3]	12–16[3]	6·0	2·5– 8·5	This study
2	340 ± 26·5[3]	13·6[3]	6·0	1·0– 8·5	This study
3	44 ± 22[4]	about 5·5	9·4	5·0–14·0	Sloan & Aldridge (1981)
4	17·4± 7·4	2·5±1·3	>10·0		McCreadie et al. (unpubl. rep.)
5	(a) 48 ± 12·8 (edge)	about 14[2]	13·2	6·9–16·0	Brun (1968)
5	(b) 97 ± 10·9 (centre)	about 29[2]	13·2	6·9–16·0	
6	–	0·38 (max. dry wt)	–	–	Gulliksen & Skjæveland (1973)
7	(a) 167	–	1·2	0·5– 3·2	Hancock (1958)
8	(b) 115	–	1·2	0·5– 3·2	
9	15	–	(3·5 modal diam.)		Smith (1940)
10	809 ± 85 (s.e.)	0·40	1·1	0·5– 3·0	Anger et al. (1977)
11	31·2± 2·8 (s.e.)	0·04	1·5	1·0– 4·0	

[1]Prey: *M* = *Mytilus edulis*, *C* = *Chlamys islandica*, *O* = oysters (*Crassostrea virginica* presumably), *B* = barnacles (*Balanus* sp., and *Elminius modestus*) on oyster bed, *Ci* ≈ *Ciona intestinalis*, *H* = *Hydrobia ulvae*.
[2]Biomass estimated by author from stated mean body size and Morecambe Bay arm radius: wet body weight data.
[3]Feeding concentrations on mussel patches.
[4]Estimated from authors' Figures 2 and 4 for the swarm area.
All data obtained from direct sampling (divers or on foot) except those for Crouch Estuary (dredging mark-recapture exercise) and Canada (removal by mopping).

maximum radius (range: 1·0–8·5 cm). The mean showed little monthly variation and the population appeared to be mainly homogeneous (one year class) throughout the summer. Larger starfish were seen in shallow water offshore in other years.

Starfish were preyed upon at every opportunity (15–20% of tides each month) by thousands of large gulls (*Larus argentatus*, mainly) from the breeding colonies on nearby Walney Island. Bird predation was so restricted to low spring tides, however, that it had little evident impact on the numbers of starfish.

Discussion

The extensive swarms of *A. rubens* at Morecambe Bay in 1969 and 1972 were numerically denser than any previously reported for the observed size range (Table 2).

The subtidal aggregation in Morecambe Bay studied in July 1976 by Sloan and Aldridge (1981) was 2 km west of the present study area and in 3 to 6 m depth. It was composed of starfish larger than those usually found at 'South America' though the density was much lower, with a maximum of $89/m^2$ (Table 2). From these authors' data, it is estimated that the concentrated leading zone of their swarm covered about 1·5 ha of mussels and contained at least 700 000 starfish (90 tonnes live weight) at an average density of 5·5 kg/m^2. This swarm behaved similarly to those at 'South America' skear.

The dense aggregation attacking *Chlamys islandica* (Brun, 1968) was composed of much bigger individuals, however; its biomass could have attained about 29 kg/m² at the centre. In the Wash, G. Davies (personal communication) recorded 3·2 cm radius starfish at densities of 304 to 836/m² on an intertidal bed, while J. M. Bray (personal communication) recorded 3 to 5 cm radius starfish at densities up to 470/m² on another bed. Over an area of about 2750 km² of Kiel Bay, Nauen (1978) estimated a mean biomass (wet weight) of only 0·12 kg/m² but this represented a standing stock of 32 000 tonnes of starfish. Nearby, in Lübeck Bay, young *A. rubens* of about 1·1 cm mean radius attained maximum densities of 324 to 809/m² (0·2–0·4 kg/m² biomass wet weight) when feeding on dense settlements of 1 to 2 mm *Mytilus* spat attached to mobile algal carpets drifting over the sandy bottom; much lower densities occurred on the fine sand itself (Anger et al., 1977).

Large, dense aggregations of *A. rubens* are clearly highly efficient predators and can have a major, even catastrophic, impact on local prey populations (Seed, 1969). At Morecambe Bay, starfish consumed hundreds of tonnes of young mussels during summer invasions, and similar mortalities of cultivated mussel crops have occurred in the Wash (G. Davies, personal communication). A small swarm in the Menai Strait (Table 2), estimated at about 150 000 starfish, with a biomass of 20·8 tonnes, was estimated to have consumed 70 tonnes live weight of marketable mussels (57 mm mean length) (McCreadie et al., unpublished report). The starfish population of Kiel Bay is calculated to require annually 120 000 tonnes of food, drawn mainly from the *Abra alba* community (Nauen, 1978).

Starfish swarms feeding on mussels and scallops all adopted the form of long, narrow bands – only 10 to 35 m wide but from 10 to 100 times as long (Table 2) – and sometimes comprised millions of individuals. The conformation of Morecambe Bay aggregations seemed to reflect largely the initial direction of contact with a densely populated mussel bed. Where mussels occurred as widely scattered clumps, as in the offshore shallows, starfish were dispersed rather thinly (less than 20/m²) over a wide area. However, as individuals moved inshore and contacted a discrete mussel bed those in the front apparently stopped to feed, enabling those in the rear progressively to catch up and thus accumulate into a dense but narrow zone of feeding starfish which gradually spread laterally along the near edge of the mussel bed. The shape of the swarm thus tended to follow closely the outline of the mussels, as it also did in the Menai Strait (McCreadie et al., unpublished report).

The rate of frontal advance across the 'South America' mussel bed in 1969 and 1972 averaged generally about 150 to 200 m per month, or 5 to 7 m per day. The rate may be expected to vary according to size and dispersion of the prey, tidal level, temperature, and starfish density or 'population pressure'. The subtidal band at Morecambe Bay observed by Sloan and Aldridge (1981) advanced inshore about 300 m in 18 days at 16 to 18°C sea temperature, i.e. a rate of approximately 16 m per day (estimated from Sloan and Aldridge, 1981, Fig. 2). In Canada, 4 cm diameter subtidal starfish moved directly toward food (oysters), from a range of at least 12 m, at a speed of 6 m per day (Smith, 1940).

The origin of the Morecambe Bay swarms was not investigated. Recently settled starfish, such as those recorded by Hancock (1958) on oyster beds, were seen rarely (small numbers in one summer only). Instead, observations indicated that starfish entered the bay from deeper water close by, where, after presumably having settled in the previous summer, they then overwintered. Although beds of adult mussels were scarce in the deeper water, this region attracts spat settlements on hydroid colonies (Dare, 1976). A mechanism by which *A. rubens* can locate and move towards food has been demonstrated recently, from Y-maze and other behavioural experiments, by Castilla and Crisp (1970; 1973) and Castilla (1972) who showed that this species has a well-developed olfactory sense with adaptive preferences and avoidances. It will move towards the scent of living mussels and other preys but laboratory starfish showed seasonal food-seeking behaviour, being attracted towards mussels in winter and spring (November–May) but not responding to prey attractants during June–October. Starfish also display positive rheotaxis and move upstream in the presence of water currents as weak as 0·15 cm/s (Castilla and Crisp, 1973). The observed spring immigrations of starfish at Morecambe Bay are explicable on such a behavioural basis if the individuals used ebb tide currents to detect and move towards the mussel populations, first at 'Outermost' skears and later at 'South America' skear. In invasion years, swarms had already reached the mussel beds by June when, according to Castilla (1972), food-seeking behaviour should cease. However, food consumption was apparently maximal during the summer at Morecambe Bay.

The rapid and total disappearance of starfish from the mussel beds in early autumn occurred when food was still abundant and seawater temperatures (13–15°C) were higher than during the spring immigration. The cause of the departure is uncertain. Castilla and Crisp (1973) identified various physical and biological factors, indicative of possibly harmful or dangerous conditions, which would induce negative or reversed rheotaxis in *A. rubens* in the laboratory. These stimuli included reduced salinity (below 25‰), lowered oxygen tension, effluents from damaged and spawning lamellibranchs, and extracts and mixtures of certain amino acids. Of this range, only products from damaged and decomposing mussels (and perhaps from the underlaying biodeposits accumulated during summer) seem likely to have been operative at Morecambe Bay. On the other hand, starfish might have responded to the onset of rough weather in September when, in some years, the 'South America' mussel bed is liable to be extensively destroyed by wave action (Dare, 1976). Such a response would have survival value by reducing the risk of a swarm being swept far upshore onto the sandflats where destruction by desiccation and gull predation would ensue.

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