NOTES ON STARFISH ON AN ESSEX OYSTER BED

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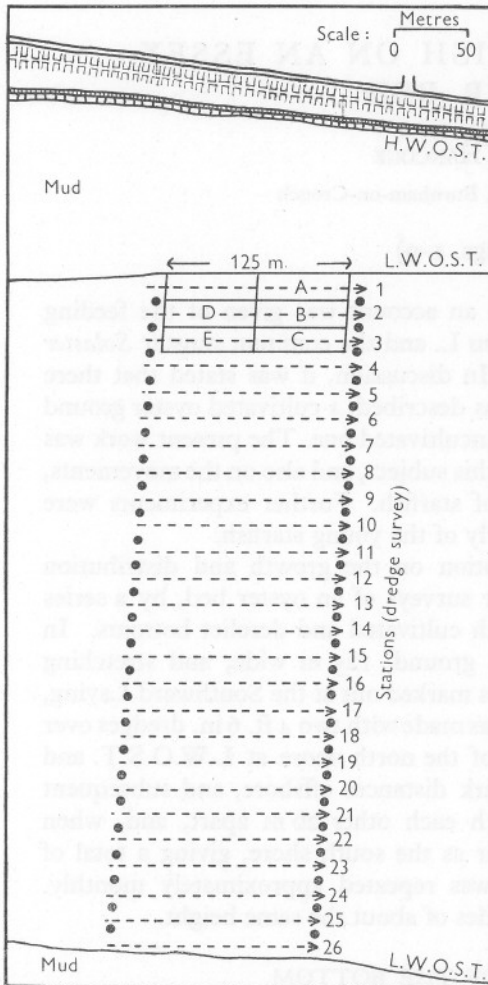
(Text-figs. 1–9)

In a previous paper (Hancock, 1955) an account was given of the feeding behaviour of the starfish *Asterias rubens* L. and the common sunstar *Solaster papposus* (L.) on Essex oyster beds. In discussion, it was stated that there was no evidence that, in the conditions described, a cultivated oyster ground provided a greater attraction than an uncultivated one. The present work was undertaken to provide information on this subject, and also on the movements, growth and ecological relationships of starfish. Further experiments were made on feeding behaviour, particularly of the young starfish.

Samples required to give information on the growth and distribution of starfish were obtained from regular surveys of an oyster bed, by a series of parallel dredge hauls covering both cultivated and derelict bottoms. In November 1954, a section of oyster ground, 125 m wide, and stretching from one bank to the other (Fig. 1), was marked out at the Southward Laying, River Crouch. The first dredge haul was made with two 4 ft. 6 in. dredges over the 125 m width, parallel to the edge of the north shore at L.W.O.S.T. and 10 m from it. Buoys were used to mark distances offshore, and subsequent dredge hauls were made parallel with each other 20 m apart, and, when time permitted, were continued as far as the south shore, giving a total of twenty-six stations. This procedure was repeated approximately monthly. The survey dates were chosen with tides of about the same height.

DESCRIPTION OF THE BOTTOM

At the Southward Laying, an area below L.W.O.S.T. is fully cultivated; most of the slipper limpets (*Crepidula*) have been removed and oysters have been relaid. Farther offshore the ground becomes semi-derelict with more *Crepidula*, and towards midstream is covered by an almost pure population of *Crepidula* (Table 1, Stations 6–11). In mid-river there is a submerged bank shallowest at Station 16 (Fig. 2) where, although little cultivation is done, tidal scour has made the bottom less muddy, and there is plenty of shell with large quantities of 'ross' or *Sabellaria*. There are some oysters, and, although *Crepidula* is present, the bottom is very much cleaner than in the deeper water over stations 6–11. The nature of the bottom at each dredge station is given in Table 1.

Scale : Metres
0   50

H.W.O.S.T.

Mud

←— 125 m. —→   L.W.O.S.T.

Stations (dredge survey) 1–26

Mud   L.W.O.S.T.

Results of grab survey
(Showing numbers of Asterias in
approx. position of grab hauls)

I. Stations A E: 10 grabs per station

				2	2	4	12	0		**A**
				4	1	11	0	0		
D	2	2	3	2	2	1	1	3	1	3	**B**
	3	0	2	1	1	4	3	3	5	3	
E	2	9	1	8	3	6	7	4	9	15	**C**
	0	5	4	5	2	6	7	8	1	0 2	

II. Stations D B (repeat): 5 grabs per station

D	5	6	3	6	2	6	11	22	1	3	**B**

Fig. 1. Map showing part of the Southward Laying, River Crouch used for dredge surveys, recapture experiment and grab sampling. Dotted lines show positions of parallel dredge hauls 1–26 between buoys (●). Enclosed rectangles (A–E) show areas surveyed by grab sampler. Areas B and D (dredge Station 2) were also used for the recapture experiment (see text). The results of the grab survey are also shown diagrammatically.

DISTRIBUTION OF ADULT STARFISH

From the results of the surveys the distribution of Asterias and Solaster was plotted (Fig. 2). Figures for bottom animals taken in dredges should be compared with caution because a dredge is not a fully reliable sampler (Shelbourne, 1957). However, the regular appearance of concentrations of

particular animals on certain sections of the river suggests that in this instance, the dredge gave a satisfactory distribution picture.

It was shown previously (Hancock, 1955) that during 1954 the largest numbers of adult *Asterias* were taken from stations 3–6 (50–110 m below L.W.O.S.T., Fig. 2). Later, during 1955 and in 1956, the main area of abundance shifted offshore, perhaps as a result of the removal by dredging

TABLE 1. SOUTHWARD LAYING, RIVER CROUCH. NATURE OF BOTTOM SHOWN BY DREDGING ON STATIONS 1–26.

Station	Nature of bottom	
	1955	1956
1	Shell, oysters, few *Crepidula*	Shell, oysters, very few *Crepidula*
2	Shell, oysters, few *Crepidula*	Shell, oysters, very few *Crepidula*
3	Shell, oysters, *Crepidula*	Shell, oysters, very few *Crepidula*
4	Shell, *Crepidula*, some oysters	Shell, oysters, few *Crepidula*
5	Shell, *Crepidula*	Shell, *Crepidula*, oysters
6	Shell, many *Crepidula*, muddy	Shell, *Crepidula*, oysters
7	Shell, many *Crepidula*, muddy	Shell, *Crepidula*, muddy
8	Shell, many *Crepidula*, muddy	Shell, *Crepidula*, muddy
9	Shell, *Crepidula*	As 1955
10	Shell, *Crepidula*	As 1955
11	Shell, *Crepidula*	As 1955
12	Shell, *Sabellaria*, *Crepidula*, some oysters	As 1955
13	Shell, *Sabellaria*, few *Crepidula* and oysters	As 1955
14	Shell, *Sabellaria*, few *Crepidula* and oysters	As 1955
15	Shell, *Sabellaria*, few *Crepidula* and oysters	As 1955
16	Shell, *Sabellaria*, few *Crepidula* and oysters	As 1955
17	Shell, *Sabellaria*, few *Crepidula* and oysters	As 1955
18	Shell, *Sabellaria*, few *Crepidula* and oysters	As 1955
19	Shell, *Sabellaria*, few *Crepidula* and oysters	As 1955
20	Shell, *Sabellaria*, few *Crepidula* and oysters	As 1955
21	Shell, *Sabellaria*, few *Crepidula* and oysters	As 1955
22	Clean shell, *Sabellaria*, few oysters	As 1955
23	Shell, *Sabellaria*, some stones	As 1955
24	Shell, *Sabellaria*, stones and mud	As 1955
25	Shell, *Sabellaria*, stones and mud	As 1955
26	Hard mud and boulders, some shell	As 1955

of large numbers of *Crepidula*, close to the cultivated ground, causing the *Asterias* to seek more abundant food farther offshore. No evidence was obtained of extensive migrations, and, particularly, there was no mass movement of adult *Asterias* to the cultivated oyster ground inshore just below L.W.O.S.T. The population was maintained just offshore in association with large numbers of *Crepidula*.

Solaster, however, had quite a different distribution and there was little overlapping between the adult populations of *Asterias* and *Solaster* (Fig. 2). The largest numbers of adult *Solaster* occurred throughout the year on grounds commencing 180 m from the north shore (Station 10 onwards) and extending to the opposite shore. They were not associated with the cultivated oyster ground near the north shore, nor with the main *Crepidula* zone (Stations 6–11). *Solaster* was mainly found on the submerged bank (Fig. 1), where
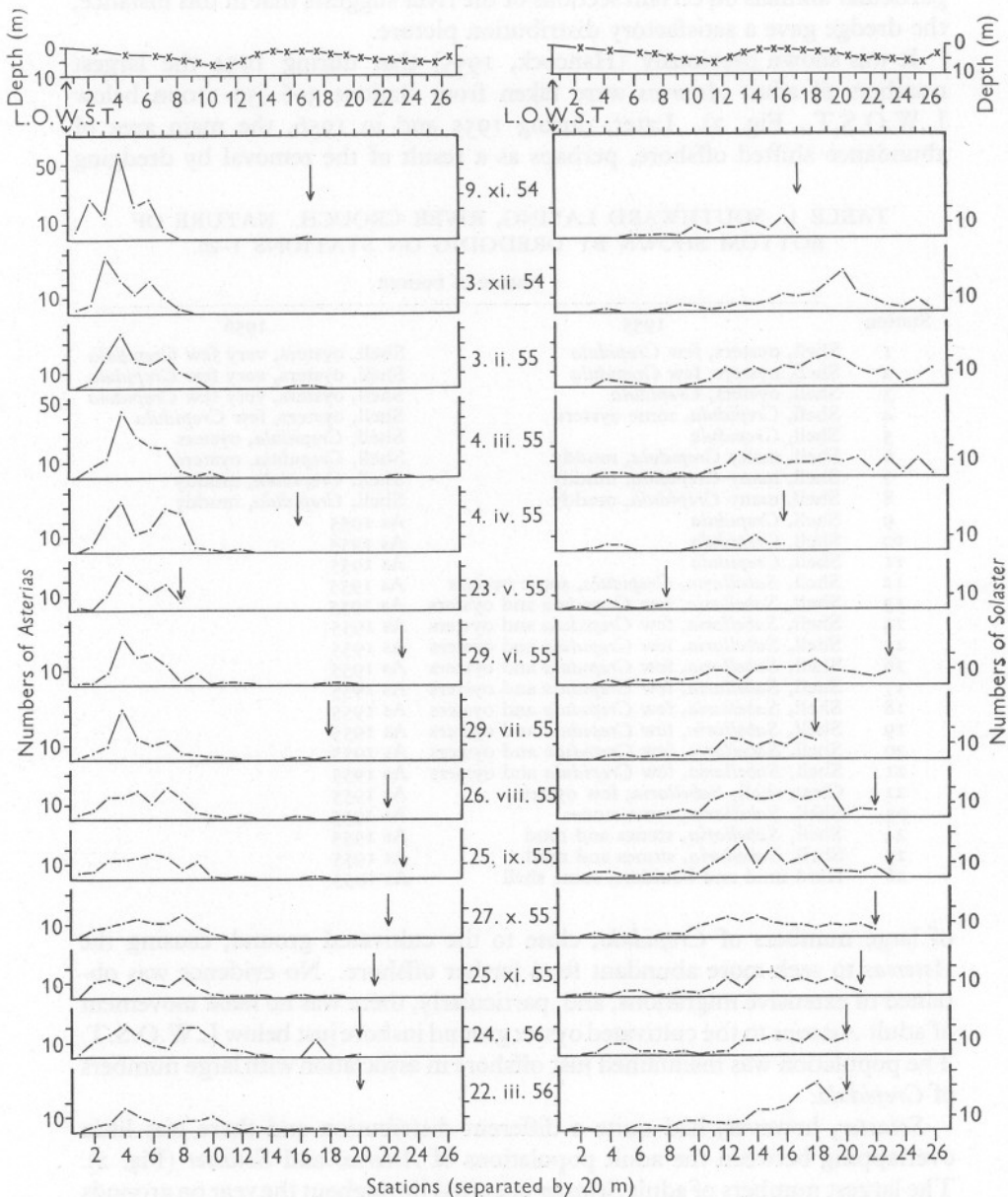
37

Fig. 2. Numbers of adult *Asterias* and *Solaster* taken using two 4 ft. 6 in. power dredges in parallel dredge hauls across the River Crouch at the Southward Laying 1954–56, commencing 10 m from L.W.O.S.T. on the north shore. Sections across the river showing mean depths are given. The final dredge station on each date is indicated by an arrow.

the bottom was of 'ross' (*Sabellaria*), some *Crepidula* and oysters, with *Alcyonidium*, *Sertularia*, *Dendrodoa* and some barnacles. The type of bottom at each station is shown in Table 1.

DISTRIBUTION AND SETTING OF YOUNG STARFISH

Juvenile *Asterias* were taken in 1955, for the first time, on 29 July, when they were 1–7 mm in maximum radius (Figs. 3, 5 and 6). By 'maximum radius' is meant the length of the largest arm from its tip to the centre of the mouth. The distribution of juveniles on the stations at the Southward Laying was compared at first by counting the population on fifty oyster shells taken at random from the dredge hauls on each station. On 29 July the largest numbers were taken on stations 2 and 3, with little settlement offshore (Fig. 3). Further settlement had occurred by 26 August when numbers had increased on all stations, but particularly offshore. When sampled on 25 November the juveniles had grown so much (Fig. 5) that they became easily detached from shells in the dredges, and the numbers on shells could no longer be used for comparison. On this and subsequent dates, the density of young starfish was estimated by subsampling the dredge contents, and calculating the numbers in two full dredges. These numbers could be compared more easily with the numbers of adult starfish (Fig. 2). Most juveniles continued to be found on inshore stations, with a fairly large settlement on Stations 12–20.

Juvenile *Solaster* appeared earlier in the year than *Asterias*, on 23 May 1955. This was expected, as in the laboratory *Solaster* spawned from 25 to 27 February 1954 at a mean temperature of 9° C, and on 16 March 1955 when the temperature was again 9° C. *Asterias*, however, did not spawn in 1954 until 29 May, when the temperature had reached 15° C. *Solaster* eggs spawned on 25 February 1954, kept under observation in the laboratory, were floating orange spheres 0·9 mm in diameter. By 2 March they had become gastrulae, which elongated in a day or two, and by 10 March had developed three larval arms (as figured by Gemmill, 1912, for *Solaster endeca*, and by Chadwick, 1914). Metamorphosed stages, less than 1 mm in diameter, with the first tube feet, were found attached to the bottom of the tank early in April. *Solaster* eggs were taken in the plankton from the River Crouch in 1956 for the first time on 26 March. The distribution of young *Solaster* at the Southward Laying was very similar to that of the adults, the greatest settlement being consistently about 250 m from the north shore (Fig. 3, Stations 11–14).

The numbers of *Asterias* settling in 1955 were much greater than those of *Solaster*. The greatest quantity taken during the year in two full dredges was 2724 on Station 2 on 23 September. The corresponding total for *Solaster* was 42 taken on Station 11 on 27 October 1955. In 1956, no settlement of *Asterias* was observed. Small numbers of *Solaster* settled, but they were not seen until 4 June, when they were considerably smaller than the previous year group was in June 1955.
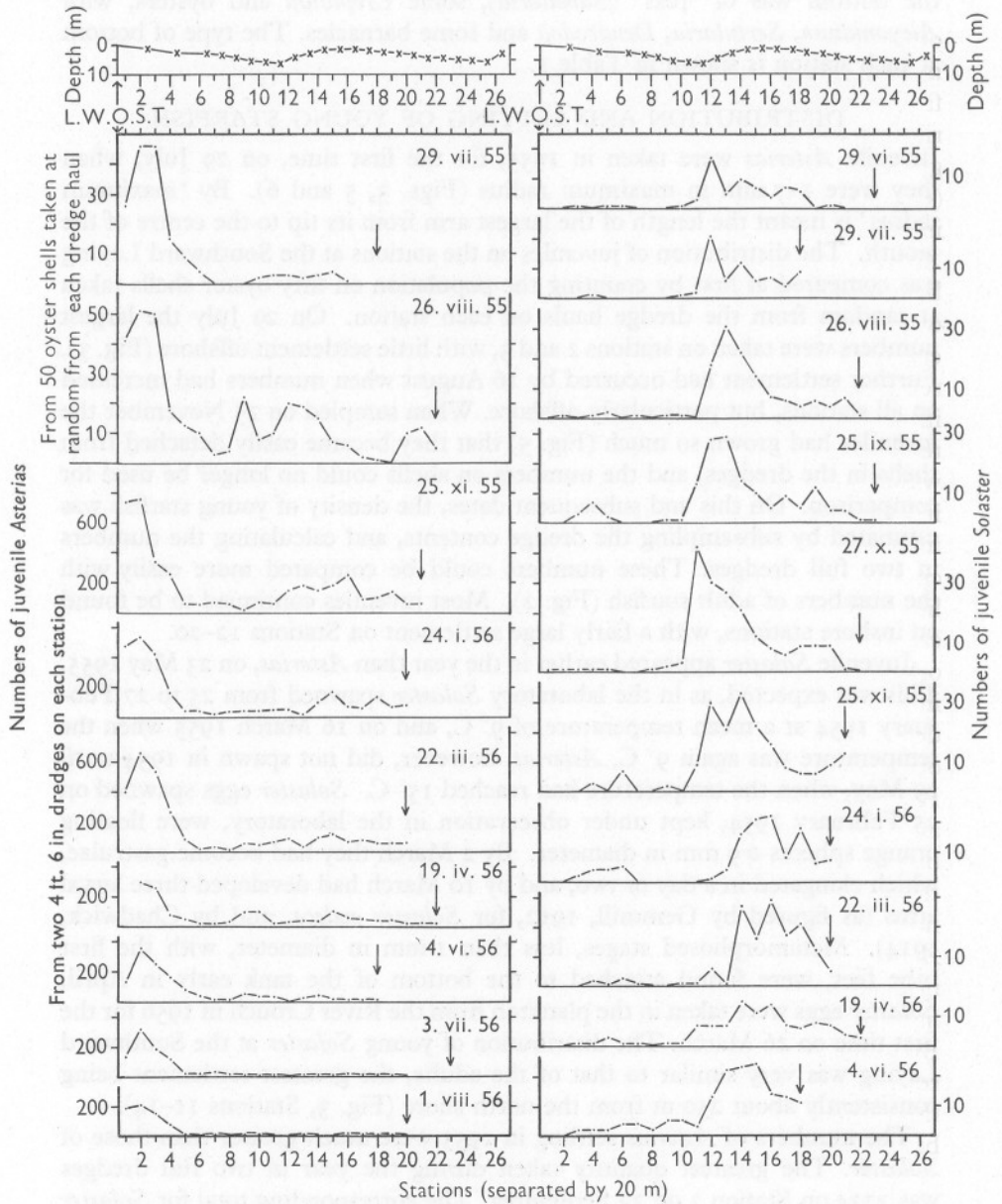
D. A. HANCOCK

Fig. 3. Numbers of juvenile *Asterias* and *Solaster* taken using two 4 ft. 6 in. power dredges in parallel dredge hauls across the River Crouch at the Southward Laying 1955–56, commencing 10 m from L.W.O.S.T. on the north shore. On 29 July and 26 August 1955 *Asterias* were counted from only 50 shells in each dredge haul. From 25 November onwards, the total number in each dredge haul has been represented. Sections across the river showing mean depths are given. The final dredge station on each date is indicated by an arrow.

There was in 1955, therefore, considerably more overlapping of the juveniles of the two starfishes than of the adult populations. Young *Asterias* settled in maximum density inshore on cultivated oyster ground, but settling also occurred farther offshore in the *Solaster* zone. Young *Solaster* settled mainly in mid-river in the region of greatest abundance of adults, suggesting perhaps a gregariousness of settling near the parents as in certain other invertebrates (Cole & Knight-Jones, 1949, in oysters; Knight-Jones & Stevenson, 1950, in *Elminius*). Both young and adult *Solaster* have been observed devouring *Asterias*, particularly juveniles, and this, coupled with the discrete settling behaviour of *Solaster*, is believed to be responsible for the no more than slight overlapping of the two adult populations. *Asterias* is capable in a lesser capacity, of devouring young *Solaster*. Although there was such an enormous settlement of *Asterias* on the Southward Laying in 1955, the numbers taken in dredge hauls decreased steadily—from over 2700 on Station 2 on 23 September 1955 to only 44 on 15 October 1956. The distribution at the Southward Laying showed that this decrease was occurring on all stations, that is, it was not due to an inshore or offshore movement. A certain amount of migration of juveniles to neighbouring grounds might have occurred, but conditions there were no different from the Southward Laying. It is believed that the great decrease in the numbers was due to a heavy mortality caused by competition and cannibalism, resulting from a prolonged shortage of natural food and predation by *Solaster*. Galtsoff & Loosanoff (1939), in America, observed that an abundant set of *Asterias forbesi* Desor, greatly decreased within 1 month after settling, and suggested that cannibalism, observed frequently between young starfish in the laboratory, was responsible. It is significant that, before the settlement of young *Asterias* in 1955, shells and oysters at the Southward Laying were densely covered by barnacles, but by the end of August 1955 it was impossible to find a live barnacle there. Until the end of 1956, although barnacle settlement was elsewhere normal, the Southward Laying was still free. It is believed that the juvenile *Asterias* devoured the barnacles, giving them no chance to grow to recognizable size. The absence of freshly settled stages of *Asterias* in 1956 may have been a direct consequence of the lack of young barnacles required as food. By mid-1956, the distribution of the young of the two species of starfish resembled that of the adult populations (Figs. 2, 3). It is interesting to note that following the reduction of the numbers of *Asterias* to a normal level, barnacles reappeared in large numbers on the Southward Laying in 1957.

POPULATION DENSITY

Two methods were employed to estimate the density of young *Asterias* on the Southward Laying. These had been used previously with some success for determining the population density of *Urosalpinx* (Hancock, in press), and

comprised (*a*) marking and recapture experiments, and (*b*) a survey using a $\frac{1}{10}$ m² van Veen grab. Loosanoff (1937, 1953) described the marking of starfishes from the Atlantic coast of America with Nile Blue Sulphate, and Vernon (1937) used Neutral Red. Feder (1955) used both these methods with success on Pacific coast starfishes, and found that plastic disc tags attached by stainless steel were useful, but very liable to cause injury or loss of the tagged arms. No doubt the proportion surviving uninjured would be useful in migration or growth studies, but the method would be less reliable for recapture data.

Employing method (*a*), an area of oyster ground 20 m wide was marked out with buoys, its inner edge being parallel to, and 20 m below, the shore at L.W.O.S.T. on the Southward Laying (Fig. 1, area D–B). Dredge hauls were made on this area on 23 September 1955, parallel to the shore, and 1000 young *Asterias* were marked and returned, to be searched for by subsequent dredging. Marking was done by diluting a stock solution of Nile Blue Sulphate about ten times with sea water. This was sufficient to dye a large number of *Asterias* immersed in it in 5–10 min. The normal reddish brown of the aboral surface became darker and bluish-green in colour. The blue coloration showed up most clearly on the parts normally white, such as the surface of spines, and the oral surface. The blue stain of Nile Blue Sulphate was retained by marked starfish until at least 10 months after marking. A series of young and old dyed *Asterias* were retained in tanks in the laboratory for several months with no significant mortality.

Young *Asterias* were capable of quite rapid movement and for this reason only an hour or two was allowed for mixing with the normal population before redredging. Dredging, marking and redredging was continued on 12 and 14 October. The first group marked on 23 September totalled 1000, and on 12 October a second group of 1450 and a final group of 2165 were dyed making a total of 4615. Bailey's (1951) modification of the 'Lincoln Index' was applied to the numbers recaptured on each date. This is: $\check{x} = a(n+1)/(r+1)$, where $\check{x}$ is the total population in the marked area, a is the number of individuals marked, n is the size of a random sample containing r marked individuals. The total number of recaptured starfish was 365, compared with 16,903 unmarked. From calculations based on marking of the three groups (Table 2), the average figure for young *Asterias* per m² over the total area of 2500 m² used for recaptures was found to be 131. Uneven distribution of marked starfish over the area may account for the large variation between 28 and 296 per m² shown in Table 2.

The sorting of several thousand small starfish from the contents of a dredge is tedious and lengthy, and it was felt that a grab survey might be more accurate and would take less time. Grabbing could not be done until a month later, on 10 November, so that the results cannot be compared strictly with those from the recapture experiment described above. An area of oyster ground below L.W.O.S.T. was divided up with buoys to include the area used in the

recapture experiment (Fig. 1). Ten grab hauls ($\frac{1}{10}$ m²) were made at random in each subarea (Fig. 1, A–E), so that their total represents the density per square metre for each station. The results showed great variation between single grab samples, from 0–15 on one station (Fig. 1, C). The bottom deposits were found to be variable, and the absence of *Asterias* could usually be related to clay or mud with no shells. A maximum of 59 per m² was found on Station C, with an average of 37 per m² for the whole area. Station D had 18, and Station B, 27 starfish per m², giving an average of 23 for the area D–B used in the recapture experiment.

The mid-level area D–B (Fig. 1) used for the recapture experiment was re-examined by a further 10 grab hauls intended to confirm the original results (Fig. 1). This time, however a total of 65 starfish per m² was obtained, compared with the previous average of 23 per m². The variation from 1 to 22 in individual grab hauls (Fig. 1) again emphasizes the patchiness of *Asterias*, and shows that a much larger number of grab hauls would be required to give more significant results.

TABLE 2. RECAPTURES OF MARKED *ASTERIAS* FROM DREDGE HAULS
OVER STATION 2 (D–B)

(Each haul with two 4 ft. 6 in. dredges.)

Date of marking	Total number marked (a)	Date of recatpure	Number of re-captures (r)	Number un-marked (n−r)	Calculated total in the area (2500 m²) $\frac{a(n+1)}{(r+1)}$	Average per m²	Average (per m²) for group
23 Sept. 55	1000	23 Sept. 55	7	2717	340,625	136	
23 Sept. 55	1000	26 Sept. 55	3	2481	621,250	249	167
23 Sept. 55	1000	12 Oct. 55	6	1997	286,286	115	
12 Oct. 55, (x)	2450	12 Oct. 55	8	1718	470,128	188	
12 Oct. 55, (x)	2450	12 Oct. 55	1	290	357,700	143	166
12 Oct. 55, (y)	4615	14 Oct. 55	30	636	99,297	40	
12 Oct. 55, (y)	4615	14 Oct. 55	126	1770	68,934	28	
12 Oct. 55, (y)	4615	14 Oct. 55	10	1754	740,498	296	95
12 Oct. 55, (y)	4615	14 Oct. 55	33	1511	209,711	84	
12 Oct. 55, (y)	4615	14 Oct. 55	141	2029	70,558	28	

Final average per 2500 m² for all recaptures = 326,499.
Average per m² for all recaptures = 131.
(x), (y): separate batches marked on the same day.

The figure of 37 per m², representing the average of the two series of grab hauls on Stations D–B, differs substantially from that of 131 obtained from recapture data from the same area, but it must be remembered that grab sampling was delayed for one month. Dredge survey results (Fig. 3) indicated that the density of young *Asterias* over the whole Southward Laying area was decreasing during this period; on 25 November 1955, for example, less than 800 were obtained per haul with two dredges on Station 2 (Fig. 1, over D–B) compared with the usual catch of nearly 2000 before the recapture

experiment. The largest number obtained in two 4 ft. 6 in. wide dredges dragged over 125 m on the same area was 2724 on 23 September 1955 on Station 2, which, when related to the area covered by the dredges, represents only 8 per m², and demonstrates the low efficiency of dredges for catching small starfish.

It is evident that, by either method, the estimation of density of a large population with such irregular distribution, even over a small area, can be based with confidence only on intensive sampling.

FEEDING

LABORATORY EXPERIMENTS

It was demonstrated in laboratory experiments (Hancock, 1955) that, although *Asterias* occasionally ate spat and adult oysters, the greater part of its food was composed of animals in competition with the oyster. The smaller sizes of *Asterias* ate large numbers of barnacles, with occasional spat of oysters and *Crepidula*. The larger ones occasionally ate oysters and oyster spat, but almost always exhibited a preference for mussels, and, in the absence of these, for *Crepidula*, and sometimes even for *Urosalpinx*.

To assess the effects of the very large number of juvenile *Asterias* which settled on the cultivated part of the oyster ground at the Southward Laying during 1955, further studies were made of the feeding behaviour of young starfish. These experiments also provided valuable information on growth.

Experiment 1

Ten *Asterias* of maximum radius 1–8 mm, were confined with an unlimited supply of barnacles, mainly *Elminius modestus* and *Balanus* spp. From 6 to 15 August 1955, 954 barnacles were devoured, representing an average of 10·6 barnacles per *Asterias* per day. The maximum feeding rate was 15·2 barnacles per day.

Experiment 2

From 9–15 August 1955, ten *Asterias* of maximum radius 1–8 mm were confined with shells bearing oyster spat, *Crepidula* spat and barnacles. During the first 3 days barnacles were eaten from all the shells, but no oyster spat, which were on the same shells, were taken. Towards the end of the experiment some oyster spat were taken, but nearly all of the barnacles had been destroyed. A total of 582 barnacles and 11 oyster spat (6 of 2 mm, 4 of 3 mm, and 1 of 7 mm average diameter), but no *Crepidula* spat, were eaten in 6 days. The *Asterias* finally measured 3·7–10·9 mm.

Experiment 3

Thirty *Asterias*, 12–13 mm max. radius, were isolated with *Crepidula* spat. In 7 days, 10–17 September 1955, only 5 *Crepidula* (7–9 mm in length) were eaten. When ten of these *Asterias* were transferred to a tank containing mussel spat, these were attacked immediately and the feeding rate greatly increased. The remaining 20 *Asterias* were retained with *Crepidula* spat, but the feeding rate continued to be low. From

10 September to 19 November 1955, only 26 *Crepidula* spat (4–13 mm in length) were eaten. The *Asterias* finally measured 8–12 mm. Only fourteen of the *Asterias* remained on 19 November 1955, the others having been the victims of cannibalism.

Experiment 4

Twenty *Asterias*, 12–13 mm, were isolated with oyster spat. Between 10 September and 2 October 1955, only 6 spat (4–8 mm diameter) were eaten. When barnacles were added on 12 October, the feeding rate increased, and, although 2566 barnacles were devoured between 12 October and 31 December 1955, no further oyster spat were taken. This experiment showed a maximum feeding rate of 5 barnacles per *Asterias* per day. The measurements of the *Asterias* were as follows:

Date (1955)	Maximum radius (mm)	Food
10 Sept.	12–13	—
12 Oct.	9–12	Oyster spat
4 Nov.	9–14	Barnacles
31 Dec.	9–19	Barnacles

Experiment 5

17 September 1955. Ten *Asterias* from Expt. 3 (12–13 mm) were confined with many mussel spat. Initially the feeding rate was high, but, as the size range of the mussel spat increased through growth, they gradually became too large for small starfish to open, and, by the beginning of December, when the mussels were all about 20 mm in length, feeding virtually ceased. When the mussels were replaced with barnacles, however, a high feeding rate was resumed.

Date (1955)	Size range of mussels (mm)	Number eaten by 10 *Asterias*	Number per *Asterias* per day
17–30 Sept.	3–10	165	1·3
1–31 Oct.	2–15	269	0·9
1–30 Nov.	3–24	84	0·3
1–7 Dec.	20–23	3	0·04
7–31 Dec.	Barnacles	480 barnacles	2 barnacles

The measurements of the starfish were as follows:

Date (1955)	Maximum radius (mm)	Food
10–17 Sept.	12–13	*Crepidula* spat
17 Sept.–12 Oct.	10–17	*Mytilus* spat
12 Oct.–14 Nov.	15–24	*Mytilus* spat
14 Nov.–31 Dec.	16–29	*Mytilus* spat and barnacles

Experiment 6

Eleven *Asterias* (all of maximum radius 20 mm) were offered equal numbers of *Crepidula* and oyster spat. Between 1 January and 29 March 1956, 32 oyster spat and 42 *Crepidula* spat were eaten. By the end of March the range of maximum radius length had decreased from 20 mm to 8–16 mm. Oyster spat eaten had a maximum diameter range of 8–25 mm and *Crepidula* 5–22 mm. The growth of these starfish is discussed below.
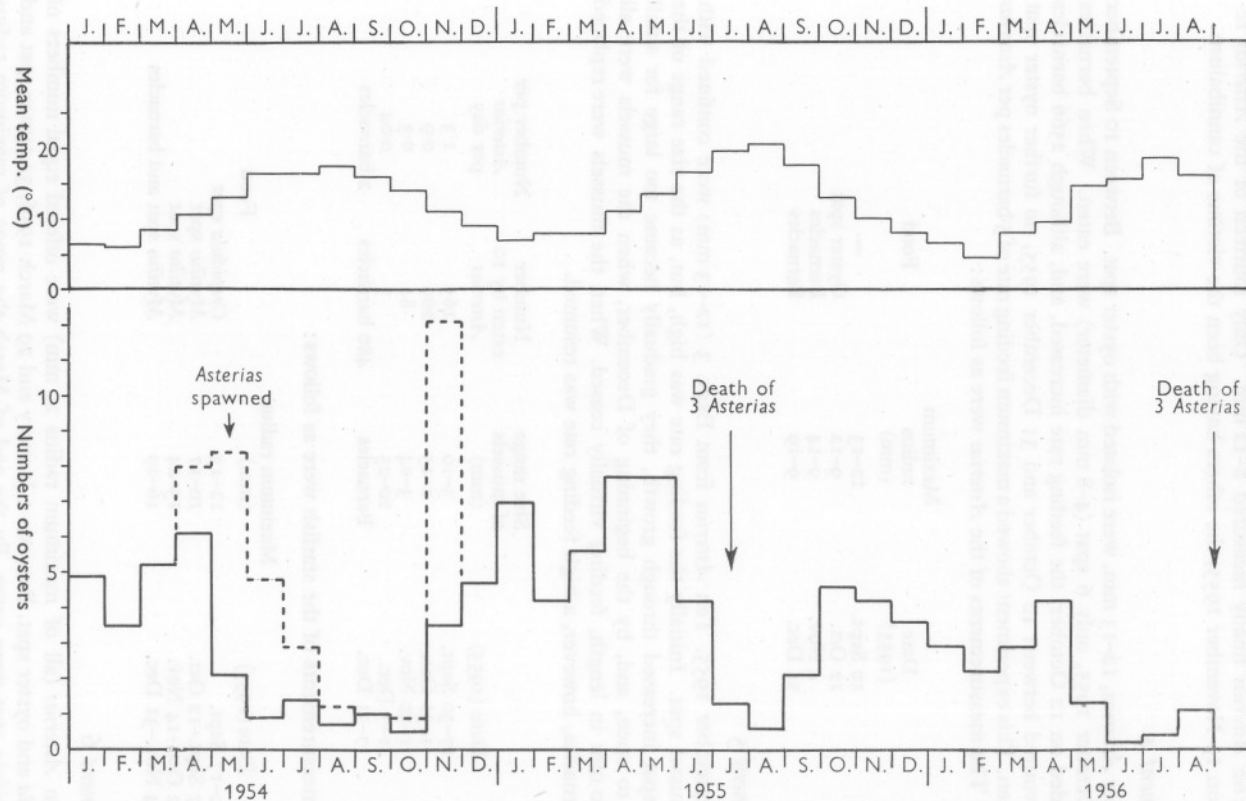
Fig. 4. Average numbers of adult oysters eaten per week by four large *Asterias* during each month from January 1954 to August 1956. From April to November 1954, *Crepidula* were offered as an alternative, and the numbers eaten in addition to oysters have been shown by a broken line. Mean monthly temperatures are also given.

Experiment 7

Five *Asterias* (maximum radius 20–30 mm) were confined with roughly equal quantities of barnacles and mussel spat. Between 26 September and 22 October 1956, 665 barnacles and 293 mussels were eaten; between 23 October and 19 November a further 262 barnacles and 636 mussels. Mussel spat occur infrequently on the Southward Laying. This experiment may provide an instance of starfish attacking, at first, familiar food, and then turning their attention to an unfamiliar alternative, which they evidently liked. Alternatively, food habits may change with growth.

Experiment 8

On 10 September 1955 a medium-sized *Solaster* (31 mm maximum radius) was confined with 20 *Asterias* (14–15 mm) and no other food. The *Solaster* needed from 10 September to 12 November 1955 to devour all the *Asterias*. During this time the size measurements of the starved *Asterias* decreased.

Experiment 9

On 10 September 1955 two small *Solaster* (maximum radius, 10–11 mm) were isolated with 20 *Asterias* (10–11 mm) and no other food. When this experiment was ended on 19 November, 12 *Asterias*. remained, though greatly decreased in size, and one *Solaster* had been eaten by the *Asterias*. The size-range of the starved *Asterias* decreased as follows: 10 September, 10–11 mm; 12 October, 8–11 mm; 14 November, 6–10 mm.

Experiment 10

The experiment described previously (Hancock, 1955, Expt. 1, p. 317), in which four large adult *Asterias* (maximum radius 140 mm) were fed on adult oysters, was continued to try to demonstrate changes in feeding rate at different times of the year. The results are shown in Fig. 4. They are slightly complicated by the addition of a number of *Crepidula* on 21 April 1954, and their removal on 13 November 1954. The numbers of *Crepidula* eaten are shown in Fig. 4, and can be seen to exceed the numbers of oysters eaten by the *Asterias*, even though the latter had been conditioned to feeding on oysters for several months. Spawning of the *Asterias* took place in the laboratory during May, and feeding reached a maximum in April–May of each year, but the rate dropped soon after spawning and reached a minimum in August during the period of highest water temperatures. Steady feeding took place throughout the winter, with a slight drop in feeding rate each February, usually corresponding with the lowest monthly average of mean daily temperatures. The optimum feeding temperature appears to be between 10 and 13° C. and occurs in April–May; above this temperature the feeding rate declines. It must be remembered, however, that the lowered feeding rate after April–May may have been associated with post-spawning effects.

Galtsoff & Loosanoff (1939) kept starfish (*Asterias forbesi*) in tanks in the United States, and found that during the pre-spawning period, from the end of May until July, at temperatures from 11·0 to 14·5° C., the majority were indifferent to food. Soon after the completion of spawning starfish became exceedingly voracious, and continued to be so until the onset of cold weather. With the vernal rise of temperature, starfish became more and more activated but ceased eating with the approach of the breeding period.

FIELD OBSERVATIONS

Throughout the surveys of the Southward Laying, records were kept of observations of feeding by *Asterias* and *Solaster*. *Asterias* was only occasionally taken when feeding, but the food of *Solaster*, which can ingest most food without pre-digesting it, was more easily recorded. *Asterias* was observed on four occasions devouring an oyster, and sixteen times eating *Crepidula*. The records of the food of *Solaster* were: *Asterias* 64, *Crepidula* 9, *Alcyonidium* 15, *Gibbula* 11, and the anemone *Diadumene* 7. The *Solaster* which were feeding on *Asterias* varied in size from 13 to 85 mm maximum radius, and it was not until late September 1955 that the incidence of feeding on *Asterias* became frequent, increasing to a maximum in March 1956. Before September *Solaster* was observed feeding mainly on other animals, this change no doubt being associated with the settlement of young *Asterias* on the offshore part of the Southward Laying inhabited by *Solaster*. Two *Solaster* (62 and 66 mm maximum radius) were found eating smaller ones of the same species. One *Solaster* of only 14 mm maximum radius was found to have enveloped a *Gibbula* of 10 mm shell diameter. Feeding on *Alcyonidium* was mostly confined to the summer months when this bryozoan was in the active phase. These results agree with the observations of Fulton (1895), who found arms of *Asterias* protruding from the mouths of many specimens of *Solaster* dredged on oyster beds in the Firth of Forth.

Adult *Asterias* taken in dredge hauls in the River Swale, Kent, in December 1956, were observed to be feeding both on adult mussels and *Crepidula* which existed together there in abundance.

PRACTICAL CONSIDERATIONS

The laboratory feeding experiments showed that young *Asterias* ate large numbers of barnacles and young mussels, on which they maintained a steady growth. Oyster spat and *Crepidula* spat were much less acceptable, and such a diet alone was inadequate for growth, with actual reduction in size often resulting. Subsequent growth of the prey under these conditions made it less liable to attack by *Asterias*. Smith (1940) found that the rate of growth of *A. vulgaris* in eastern Canada varied with the kind and abundance of food. Mussels provided a much more favourable food for growth than oysters.

The spatfall of oysters at the Southward Laying is rarely intense, and *Urosalpinx* regularly destroys nearly all those present (Hancock, 1954), so that as juveniles the starfish would normally not be a serious problem there. In fact some benefit must have resulted from the activities of the *Asterias* in keeping down the barnacles, which are the most important competitors of settling oysters for space and food (Waugh & Ansell, 1956). A study of the seasonal feeding rate of adult *Asterias* showed that the best time to inspect for damage to highly cultivated oyster grounds is in the spring of the year before

the starfish spawn. There has been no fresh evidence that *Asterias* is a serious pest of oysters under the conditions obtaining in Essex rivers, and both in the laboratory and in nature the starfish have continued to feed preferentially on competitors of the oyster.
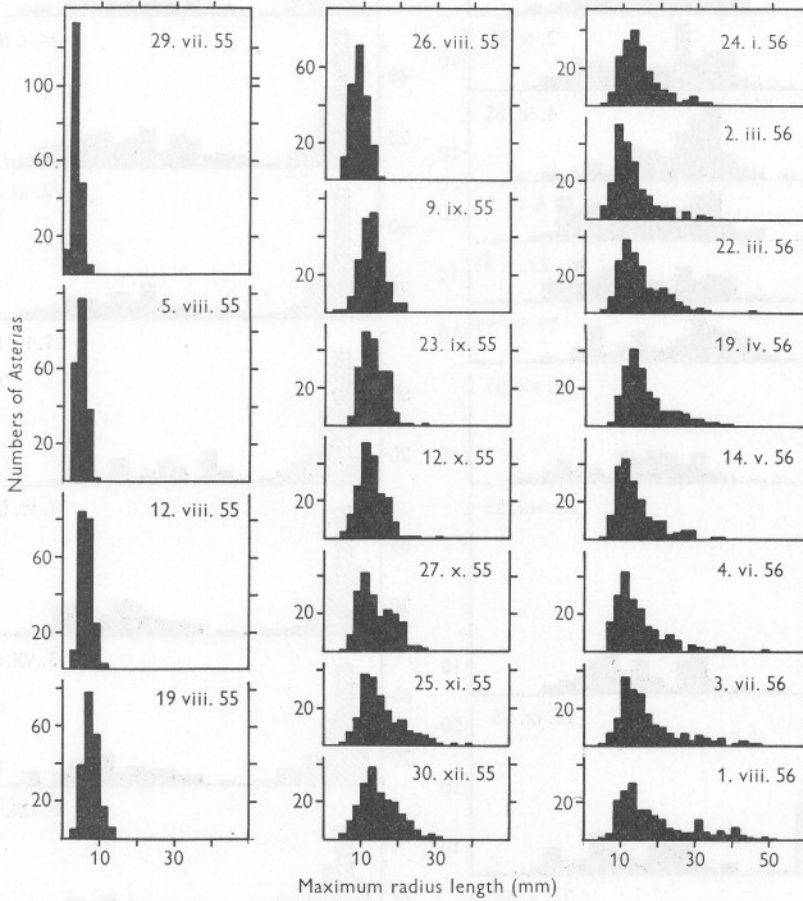

Fig. 5. Histograms showing the size distribution of young *Asterias* collected in dredge surveys from the Southward Laying 1955–56. Each sample was composed of 200 individuals. The radius lengths have been grouped at 2 mm intervals.

GROWTH

The study of population histograms does not give a clear indication of growth under natural conditions unless (1) settlement of any year group takes place over a restricted period, and (2) a large number of the form being studied settle in a particular year, so that the progress of this year group can be traced
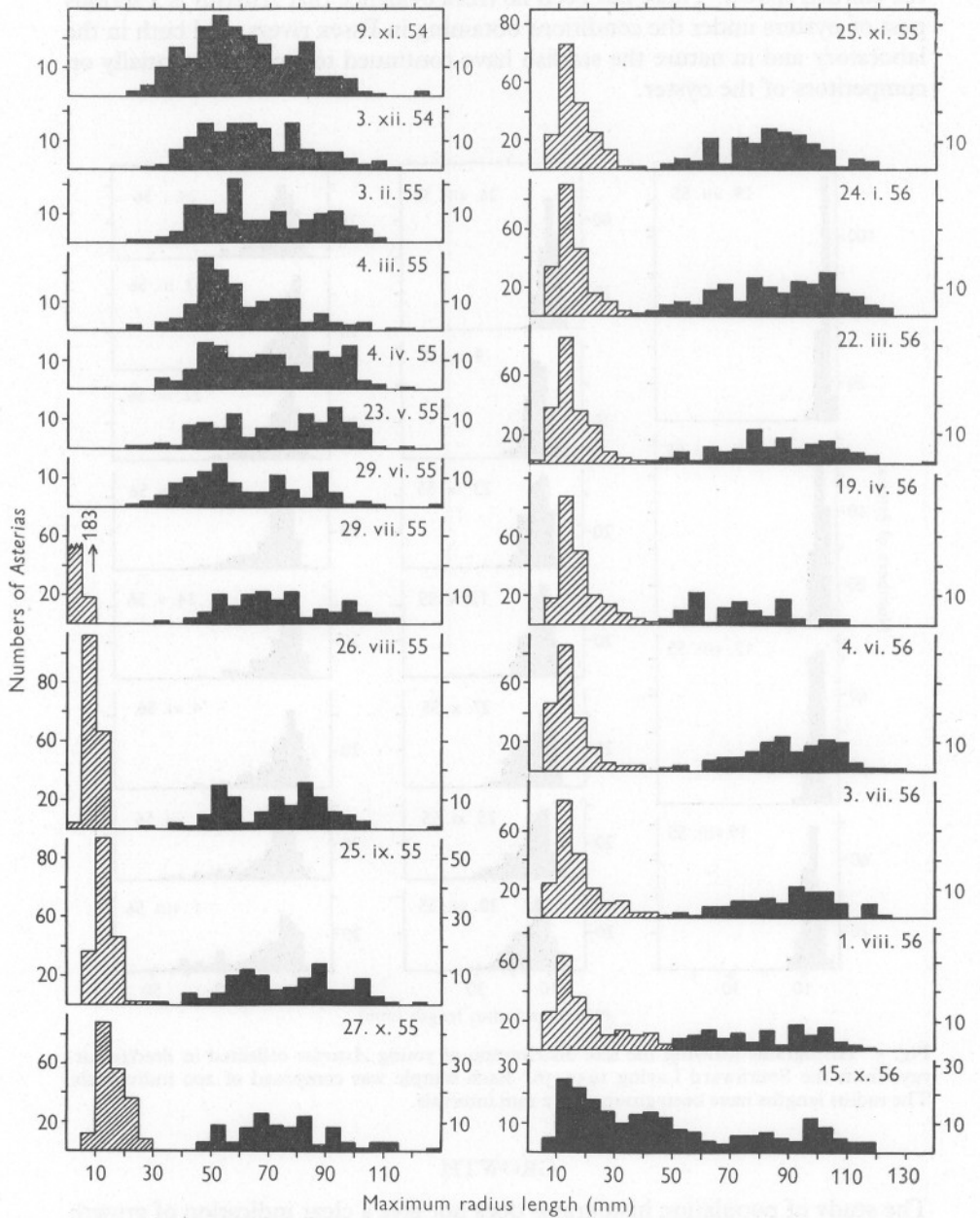
Fig. 6. Histograms showing the size distribution of young (shaded) and adult *Asterias* (blackened) collected in dredge surveys from the Southward Laying, 1954–56. Samples of 200 juveniles were measured, but all adult *Asterias* taken in the dredge surveys are shown. On 15 October 1956 all of both juveniles and adults taken were measured. The radius lengths have been grouped at 5 mm intervals, using different ordinate scales for adult and young starfish.

in consecutive histograms. It was fortunate that heavy settlements of both *Asterias* and *Solaster* occurred in 1955.

Histograms have been plotted at intervals of 2 mm for measurements of the maximum radius of arm to show the growth within the 1955 year group (Figs. 5, 7) and at 5 mm intervals to show the relationship of the year groups and their progress along the histograms (Figs. 6, 8). The *Asterias* population was sampled in two ways. First, the resident population was sampled,
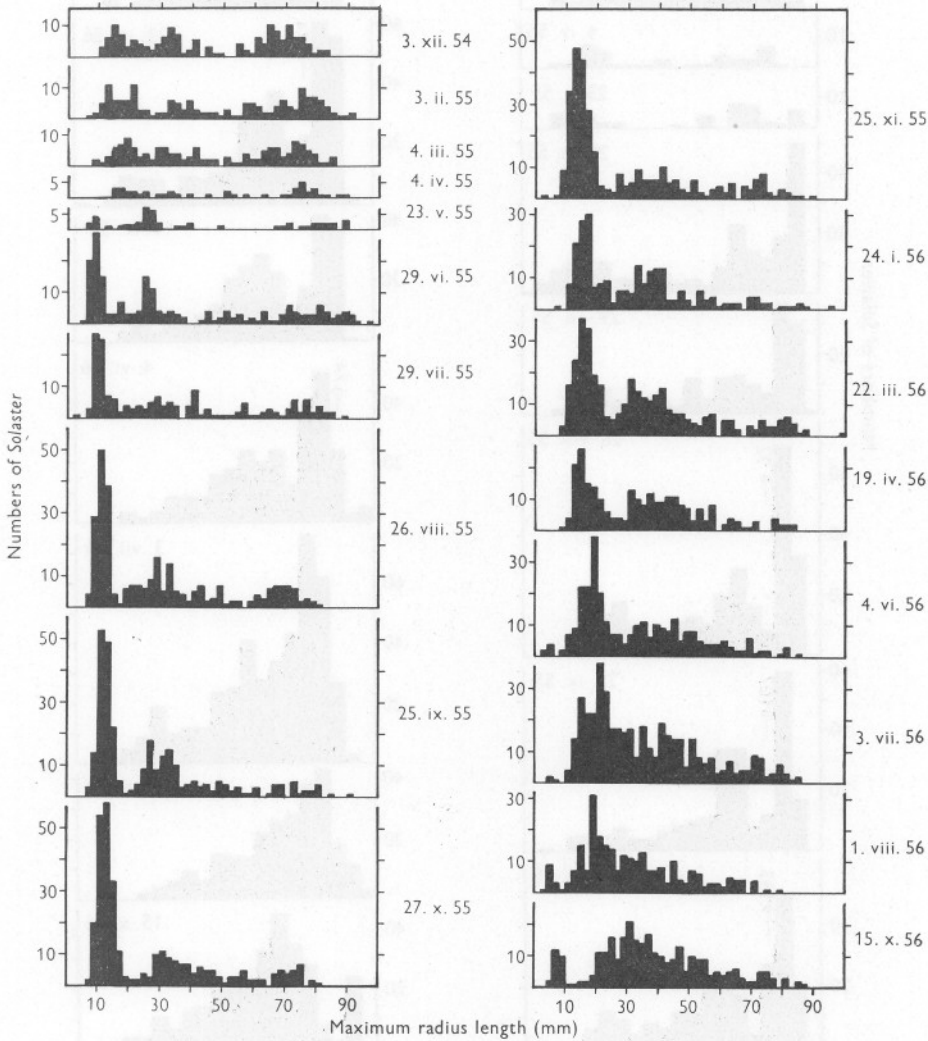

Fig. 7. Histograms showing the size distribution of *Solaster* collected in dredge surveys from the Southward Laying 1954–56. The radius lengths have been grouped at 2 mm intervals.
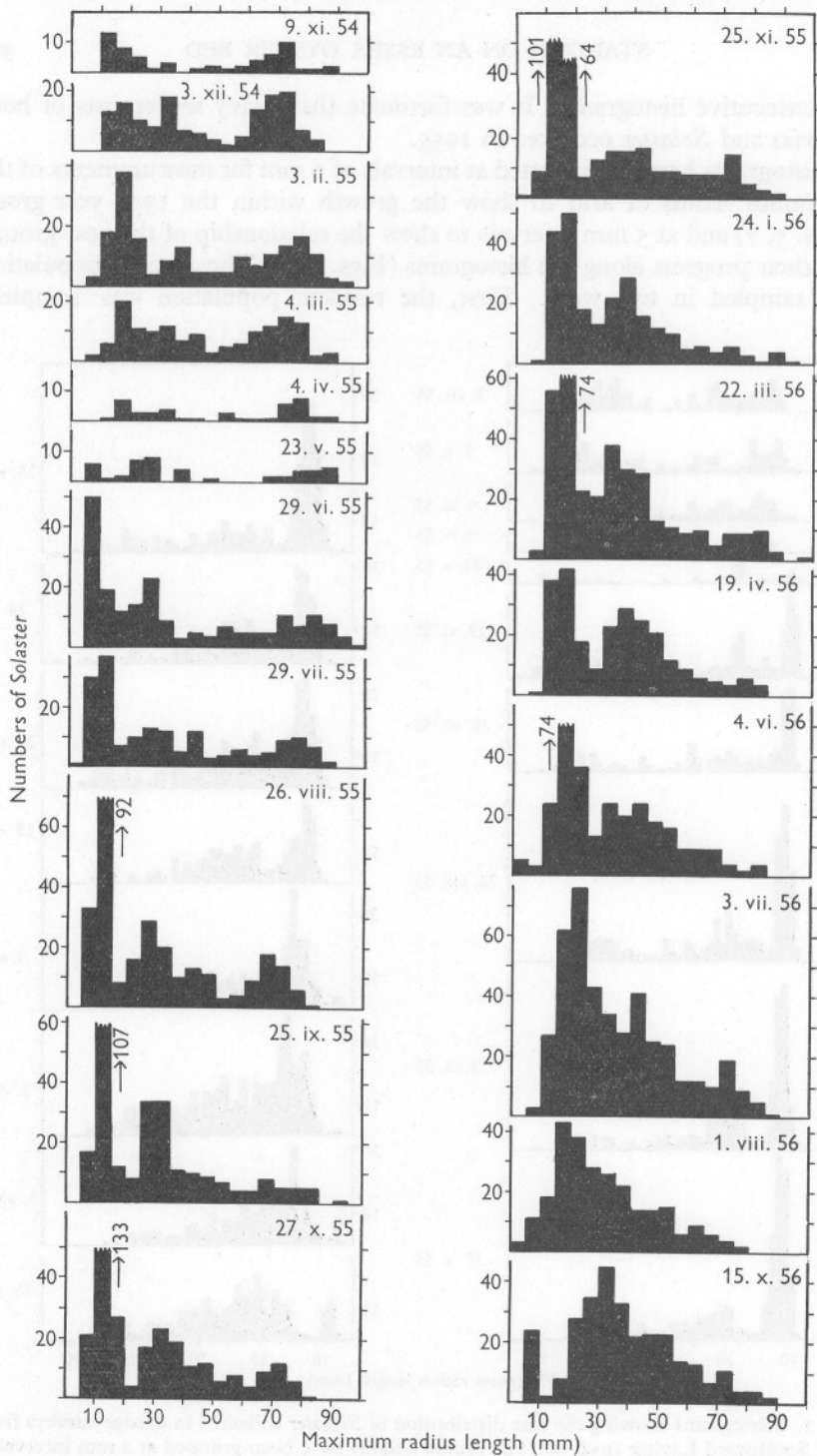
Fig. 8. Histograms showing the size distribution of *Solaster* collected in dredge surveys from the Southward Laying 1954–56. The radius lengths have been grouped at 5 mm intervals.

beginning on 9 November 1954, by measuring all *Asterias* collected in two dredge hauls over the stations examined on a particular date (Fig. 2). The settlement of 1955 0-group individuals was first noted on 29 July 1955, when the juveniles had a size range of 1–7 mm and could readily be distinguished from the older year groups in the population. Measurement of all of the enormous quantity of juveniles collected was impracticable, so that although the remainder of the population was measured as before, only a randomly selected sample of 0-group individuals from Station 2 was measured.

TABLE 3. GROWTH OF JUVENILE *ASTERIAS* AND *SOLASTER* AT SOUTHWARD LAYING, RIVER CROUCH

	Asterias			*Solaster*		
Date of collection	No. in sample	Mean length of sample (mm)	Standard error of mean	No. in sample	Mean length of sample (mm)	Standard error of mean
29. vi. 55	—	—	—	69	8·5	0·21
29. vii. 55	200	2·9	0·08	71	10·2	0·29
5. viii. 55	200	4·3	0·10	—	—	—
12. viii. 55	200	5·7	0·11	—	—	—
19. viii. 55	200	7·0	0·14	—	—	—
26. viii. 55	200	8·6	0·15	127	10·7	0·16
9. ix. 55	200	12·1	0·22	—	—	—
23. ix. 55	210	12·2	0·23	—	—	—
25. ix. 55	—	—	—	149	11·8	0·19
12. x. 55	200	12·1	0·27	—	—	—
27. x. 55	200	15·4	0·33	184	12·3	0·18
25. xi. 55	210	15·0	0·40	189	13·9	0·24
30. xii. 55	200	14·4	0·36	—	—	—
24. i. 56	246	14·2	0·34	114	15·8	0·33
2. iii. 56	241	11·8	0·32	—	—	—
22. iii. 56	473	14·3	0·26	160	15·8	0·28
19. iv. 56	278	15·9	0·38	105	16·6	0·40
14. v. 56	253	13·2	0·35	—	—	—
4. vi. 56	275	13·8	0·39	149	18·2	0·35
3. vii. 56	215	16·6	0·57	—	—	—
1. viii. 56	216	19·2	0·72	—	—	—

This sample was used to determine the standard error of the mean (Table 3). The measurements of only the first 200 individuals in each sample, however, were used for the comparative histograms (Figs. 5, 6). For this reason, in Fig. 6, the 0-group is shown on a different scale from that of the main population and is distinctly shaded. In fact, the 0-group *Asterias* represented a far larger proportion of the population than shown, and some idea of their density can be obtained by reference to Fig. 3. This method of subsampling was continued until 15 October 1956, when this year group had become so reduced that all the *Asterias* taken in the dredges could be measured. The numbers of young *Solaster* were never so great that they could not all be measured with the remainder of the population.

The mean size of each sample of 1955 0-group *Asterias* and *Solaster* (Table 3) has been plotted in fig. 9. *Solaster* showed a regular growth rate except between 24 January and 22 March 1956. The average growth between
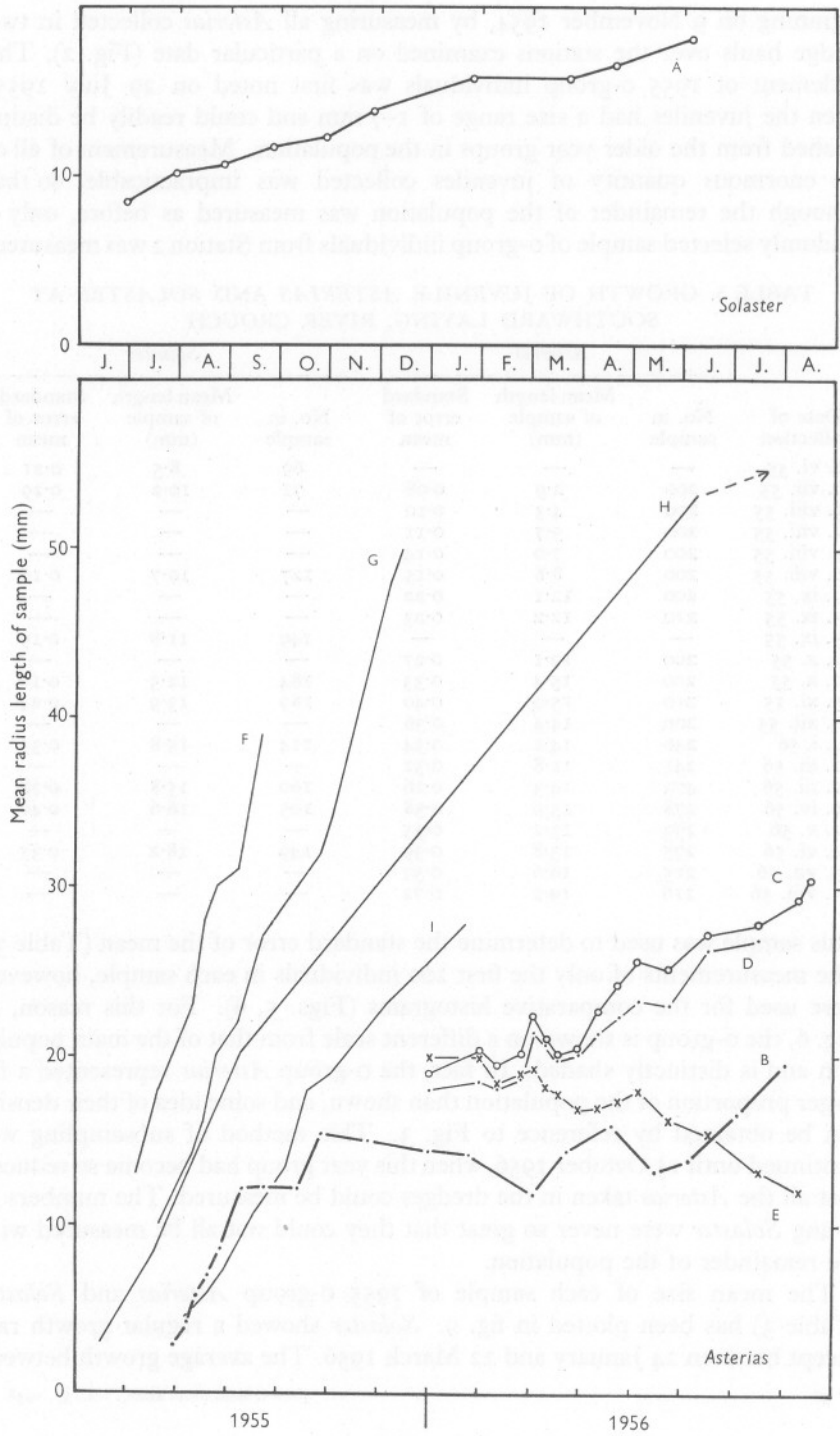
Fig. 9

29 June 1955 and 4 June 1956 has been calculated as 0·028 mm per day, with a maximum rate of 0·056 mm per day between 27 October and 25 November 1955.

A 1956 settlement of *Solaster* was first observed on 4 June, but the juveniles were less abundant than in 1955, and on 15 October 1956 their mean size was only 6·8 mm, compared with 12·3 mm for the 1955 o-group on 27 October 1955. This may have been due to a later settlement in 1956, or to the negligible crop of *Asterias* in 1956, whose young form the main food of *Solaster*. It is possible to trace the progression of the 1954 o-group *Solaster* from November 1954. A comparison of the year groups on 3 February 1955 and 24 January 1956 (Fig. 8), shows the first two modes in a similar position, indicating that in 1954 and 1955 similar conditions of growth and settlement prevailed. On 4 June, when the 1956 settlement was first observed, the 1955 set of *Solaster*, at just over 1 year old, had a mean size of 18·1 mm while the 1954 set averaged about 40 mm. From Fig. 8, it appears that in October the modes of the first few year groups are separated by regular intervals of about 20 mm; they occurred at about 10, 30–35, 50, and 70–75 mm respectively. Subsequent year groups were not clearly defined.

To state precisely the growth pattern of *Asterias* on the Southward Laying is more difficult. Newly settled juveniles were first detected in 1955 on 29 July at a mean radius of 2·9 mm. Regular rapid growth, averaging 0·22 mm per day, was recorded until 9 September (mean radius 12·1 mm), but then a check occurred. Mean size increased again between 12 and 27 October, but then decreased sharply until 2 March 1956. Reference to Fig. 5 shows that the decrease in mean size resulted from two processes; first, the range of size was increased by the slight growth of a small proportion of larger individuals, and, secondly, the mean size decreased. This is less surprising than may at first appear, in view of the shrinkage in radius length of starving *Asterias* noted in a previous section (see also Vevers, 1949). It is known that very small food organisms, e.g. barnacles, are necessary for the normal feeding and growth of young starfish. It is believed that the shortage of natural food was responsible for the enormous decline in numbers of young *Asterias* (Fig. 3) and for the reduction in the mean sizes of samples by actual shrinkage of individuals.

Growth of part of the juvenile population continued steadily from 2 March

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Legend to Fig. 9

Fig. 9. Graphs showing the growth of young *Asterias* and *Solaster*. A: mean radius lengths of samples of young *Solaster* from the Southward Laying. B: mean radius lengths of samples of young *Asterias* from the Southward Laying (see Table 3). C–E: mean radius lengths of young *Asterias* kept well fed (C, D) and starved (E) in the laboratory (see Table 4). The results of other workers are given for comparison, showing the correct calendar months for their readings. F, G: radius lengths of two typical well-fed individuals of *Asterias*, B8 and B9, kept in the laboratory by Vevers (1949). H: average radius of the arms of an *Asterias* kept in the laboratory by Bull (1934). I: mean radius lengths of samples of *Asterias* from Millport measured by Barnes & Powell (1951).

to 19 April 1956, while the mode still remained at 10–15 mm (Fig. 5). Then, after another setback in mean size, growth of juveniles continued to give the bimodal size-distribution shown for 15 October 1956 in Fig. 6. The first mode, at 10–15 mm, lies in exactly the same position as it was a year previously on 27 October 1955. Unless one knew that 1956 settlement of *Asterias* had failed, the bimodal year group shown on the October 1956 histogram might be attributed to two normal year groups, instead of to the effect of abnormal growth conditions.

Bull (1934) showed that in three *Asterias* kept in the laboratory, first spawning occurred simultaneously when two were 5 years old and the third was 6 years old. Their average size was 114 mm. It seems unlikely therefore that the checks in growth observed during the first 2 years of the present observations were associated with spawning. Galtsoff & Loosanoff (1939), however, found that in America young *Asterias forbesi* which grew rapidly were sexually mature by the end of the first year, whereas small, slowly growing animals did not mature until 2 years of age.

TABLE 4. GROWTH OF WELL-FED AND STARVED JUVENILE *ASTERIAS* IN THE LABORATORY

(12 *Asterias* in each group.)

| Date of measurement | Starved *Asterias* | | Well fed *Asterias* | |
	Mean size of group	Range	Mean size of group	Range	Mean size of group	Range
1. i. 56	20	20	19	19	18	18
1. ii. 56	20	18–22	20·3	18–26	18·5	17–20
11. ii. 56	18·3	16–21	19·5	17–25	18·2	17–20
25. ii. 56	19·0	16–22	20·2	18–25	18·8	17–23
3. iii. 56	19·3	16–21	22·4	20–25	21·5	20–24
10. iii. 56	18·2	16–20	21·0	19–24	20·8	17–23
17. iii. 56	17·8	15–19	20·1	18–24	19·8	17–22
29. iii. 56	16·8	14–19	20·4	19–22	20·2	17–23
11. iv. 56	17·0	14–19	22·7	21–24*	21·4	15–25
23. iv. 56	17·4	16–19*	24·3	22–26	22·3	19–26
5. v. 56	18·0	17–20	25·7	23–27*	23·3	18–27
23. v. 56	16·2	15–18	25·2	23–28	23·0	20–28
16. vi. 56	15·5	13–18	27·3	25–29	26·3	21–32*
16. vii. 56	13·2	11–15	27·8	23–31	26·9	21–33*
10. viii. 56	12·0	11–14	29·3	24–33	—	—
17. viii. 56	—	—	30·5	28–33	—	—

* 1 *Asterias* died.

Experiments were set up to compare the growth of regularly fed and starved starfish. On 1 January 1956, a group of twelve 20 mm *Asterias* was confined with oyster and *Crepidula* spat; from previous experience, one would regard these as having virtually starved. Separate groups of twelve 19 mm and twelve 18 mm *Asterias* were confined with an excess of live barnacles. The starfish were measured regularly, along a selected radius, until July–August 1956, when the original 20 mm group had reached 11–14 mm, the 19 mm

group 28–33 mm, and the 18 mm. group 21–33 mm (Table 4). The mean sizes of each group on the dates of measurement are shown in Fig. 9, and it is interesting to note that decreases in mean size were recorded, even for regularly fed *Asterias*, in February, March and May 1956. A sharp decrease, followed by an increase in size, was recorded in February among both the starved 20 mm *Asterias* in the laboratory and the natural population at the Southward Laying; this corresponded with the minimum water temperatures recorded in the winter of 1955–56. The May decrease in mean size of well-fed laboratory individuals was evident in the Southward Laying population, and was also shown to a certain extent by a slightly accelerated decrease in the size of starved laboratory specimens. The author is indebted to Mr S. J. Holt of F.A.O., Rome, who, from an analysis of the growth data obtained from these experiments, was able to demonstrate the general consistency between observations from the field and the laboratory. He concluded that the concurrent rearing of two groups of animals, one fed at a predetermined level and one starved, is a useful method of studying growth parameters and their relation to environmental influences. The details of this analysis will be presented in a separate paper. In the natural population it appears therefore that the gradual decrease in mean size was due to starvation, and the final increase in mean size (14 May–1 August 1956) can be related to maximum summer settlement of barnacles in the presence of greatly depleted numbers of juvenile *Asterias*.

Bull (1934) reared three specimens of *Asterias* from newly settled young to sexual maturity in laboratory tanks at Cullercoats. He recorded the average radius, from the tip of the arm to the centre of the disc, of five arms, and obtained regular growth curves. The three starfish average 42 mm in the June after settling and 114 mm at the time of first spawning. Vevers (1949) followed the growth of individual *Asterias* in the laboratory and Barnes & Powell (1951) recorded a similar and quite rapid growth rate of young *Asterias* on a barnacle-covered raft at Millport. Graphs prepared from some of their figures are included in Fig. 9 for comparison with the present observations. The growth rate shown by the Southward Laying juveniles during the period soon after their settlement, and from June to August 1956, after reduction in numbers by competition had allowed the survivors to grow normally, was very similar to earlier records. Smith (1940) found that where high population densities of *Asterias vulgaris* Verrill occurred in eastern Canada, the size of individuals tended to be smaller. The growth of well fed individuals in our laboratory approached that found by Bull (1934) and Vevers (1949), but these also had been undersized for their age when transferred to laboratory tanks on 1 January 1956. Orton & Fraser (1930) examined a population of *Asterias* on a buoy near Liverpool: Vevers (1949) converted their measurements of diameter to radius sizes, and concluded that the Mersey population had grown considerably more slowly than the individuals in his laboratory experiments.

The use of Nile Blue Sulphate for marking starfish in the field suggested an application for studying growth increments. Five *Asterias* from each group used to study growth in the laboratory were dyed with Nile Blue Sulphate. Their growth during the period 11 February–17 August 1956 was not signicantly different from that of undyed starfish, indicating that dyeing did not interfere with their normal growth processes. Eventually white undyed tips were produced on the dyed radii, but the relationship between the undyed and total increments was somewhat variable. The following typical examples showed that up to half the total increment was undyed, suggesting, not very conclusively, that intercalary and terminal growth take place in equal proportions:

Original radius length (mm)	Total increment (mm)	Undyed increment (mm)
19	12	6
19	12	3
19	10	5
18	7	3
18	6	3

It is interesting to note that the stomach pouches of *Solaster*, which had eaten dyed *Asterias*, became coloured blue, giving a useful confirmation of their feeding behaviour.

SUMMARY

Observations on the distribution of adult starfish (*Asterias rubens* L. and *Solaster papposus* (L.)) on an oyster laying in the River Crouch have revealed no marked changes in their numbers or position throughout a period of nearly two years. Slight movement of *Asterias* was recorded, not inshore on to cultivated oyster ground but offshore to more derelict ground infested by slipper limpets (*Crepidula fornicata* Say). This offshore movement may have resulted from the clearing by dredging of large quantities of slipper limpets from the inshore region, necessitating a wider search for food by *Asterias*.

Young *Asterias* settled in 1955 in maximum density inshore on cultivated oyster ground, but some settlement also occurred farther offshore in the area inhabited by *Solaster*. Young *Solaster* settled mainly in mid-river in the region of greatest abundance of adults. Both young and adult *Solaster* have been observed devouring *Asterias*, particularly juveniles, while on a lesser scale *Asterias* may eat young *Solaster*. These facts, coupled with the discrete settling behaviour of *Solaster* are believed to be responsible for the very slight overlapping of the two adult populations.

The very dense population of *Asterias* which settled in 1955 on this oyster ground in the River Crouch has decreased steadily due to the combined effects of prolonged shortage of food, cannibalism and predation by *Solaster*. The dense population of barnacles formerly present on this ground has disappeared and none were seen in 1956. There was no settlement of *Asterias* in that year.

Young *Solaster* showed a steady growth rate, but *Asterias* remained stunted until great reduction of the population allowed normal growth to be resumed. Feeding experiments showed that young *Asterias* grew well on barnacles and young mussels, which they ate readily, but young oysters and *Crepidula* were less acceptable and inadequate for normal growth.

REFERENCES

BAILEY, N. T. J., 1951. On estimating the size of mobile populations from recapture data. *Biometrika*, Vol. 38, pp. 293–306.

BARNES, H. & POWELL, H. T., 1951. The growth rate of juvenile *Asterias rubens* L. *J. mar. biol. Ass. U.K.*, Vol. 30, pp. 381–5.

BULL, H. O., 1934. Aquarium observations on the rate of growth and enemies of the Common Star-Fish, *Asterias rubens* L. *Rep. Dove mar. Lab.*, Ser. 3, No. 2, pp. 60–3.

CHADWICK, H. C., 1914. Echinoderm larvae. *Mem. Lpool mar. biol. Comm.*, No. 22.

COLE, H. A. & KNIGHT-JONES, E. W., 1949. The setting behaviour of larvae of the European flat oyster. *Fish. Invest.*, *Lond.*, Ser. 2, Vol. 17, No. 3, pp. 1–39.

FEDER, H. M. 1955. The use of vital stains in marking Pacific coast starfish. *Calif. Fish Game*, Vol. 41, No. 3, pp. 245–6.

FULTON, J. W., 1895. The past and present condition of the oyster beds in the Firth of Forth. *Rep. Fish. Scot.*, No. 14, pp. 244–75.

GALTSOFF, P. S. & LOOSANOFF, V. L., 1939. Natural history and method of controlling the starfish (*Asterias forbesi*, Desor). *Bull. U.S. Bur. Fish.*, Vol. 9, pp. 75–132.

GEMMILL, J. F., 1912. The development of the starfish *Solaster endeca* Forbes. *Trans. zool. Soc. Lond.*, Vol. 20, No. 1, pp. 1–71.

HANCOCK, D. A. 1954. The destruction of oyster spat by *Urosalpinx cinerea* (Say) on Essex oyster beds. *J. Cons. int. Explor. Mer.*, Vol. 20, pp. 186–96.

—— 1955. The feeding behaviour of starfish on Essex oyster beds. *J. mar. biol. Ass. U.K.*, Vol. 34, pp. 313–31.

—— (in press). The biology and control of the American whelk tingle, *Urosalpinx cinerea* (Say), on English oyster beds.

KNIGHT-JONES, E. W. & STEVENSON, J. P., 1950. Gregariousness during settlement in the barnacle *Elminius modestus* Darwin. *J. mar. biol. Ass. U.K.*, Vol. 29, pp. 281–97.

LOOSANOFF, V. L., 1937. Use of Nile Blue Sulphate in marking starfish. *Science*, Vol. 85, p. 412.

—— 1953. Tagging the 'Untaggable'. *Progr. Fish Cult.*, Vol. 15, No. 4, pp. 186–7.

ORTON, J. H. & FRASER, J. H., 1930. Rate of growth of the common starfish, *Asterias rubens*. *Nature, Lond.*, Vol. 126, p. 567.

SHELBOURNE, J. E., 1957. The 1951 oyster stock in the rivers Crouch and Roach, Essex, and the influence of water currents and scour on its distribution; with an account of comparative dredging experiments. *Fish. Invest., Lond.*, Ser. 2, Vol. 21, No. 2.

SMITH, G. F. M., 1940. Factors limiting distribution and size in the starfish. *J. Fish. Res. Bd Can.*, Vol. 5, pp. 84–103.

VERNON, A. A., 1937. Starfish stains. *Science*, Vol. 86, p. 64.

VEVERS, H. G., 1949. The biology of *Asterias rubens* L.; growth and reproduction. *J. mar. biol. Ass. U.K.*, Vol. 28, pp. 165–87.

WAUGH, G. D. & ANSELL, A., 1956. The effect, on oyster spatfall, of controlling barnacle settlement with D.D.T. *Ann. appl. Biol.*, Vol. 44, pp. 619–25.