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THE FEEDING HABITS OF PLAICE POST-LARVAE IN THE SOUTHERN BIGHT

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(Plate I and Text-figs. 1, 2)

INTRODUCTION

The overfishing of valuable plaice grounds in the southern North Sea, has diverted attention from the natural history of the species (*Pleuronectes platessa*) towards a better understanding of its population dynamics. The early statistical studies of Buchanan-Wollaston (1914–26) have been followed by the recent work of my colleague Mr A. C. Simpson, at the Fisheries Laboratory, Lowestoft, on egg production and survival of larvae over the plaice spawning ground in the Southern Bight.

Observations of a purely biological nature are often needed to clarify the pattern of population fluctuations derived from statistical data. For instance, efforts to assess the mortality of plaice in the Southern Bight had been somewhat impeded by gaps in our knowledge of the food and feeding behaviour of the post-larval phase. In 1950 I was given the opportunity to fill in these gaps.

A survey of literature on this subject revealed a variation in food preferences of post-larvae from different coastal areas of Great Britain. Kyle (1898), in his investigation of the Scottish plaice fishery, discovered young annelid larvae, crustacean ova, *Evadne nordmanni*, and larval molluscs in the post-larval stomachs. Lebour (1919), working at Plymouth, concluded that certain copepods and other Entomostraca formed the main food of nearly all young flatfish caught, though the plaice was poorly represented in this examination. Scott (1922), in the Irish Sea area, found harpacticoids, small copepods and algal spores to be the chief food constituents of the plaice stomachs.

As a result of the dissection of some hundreds of specimens taken in four different years the diet of plaice post-larvae from the Southern Bight is now known, in normal seasons, to be markedly different from that in the areas examined by earlier workers (Table I).

COLLECTION AND DISSECTION METHODS

In the early months of 1946 and 1947, the Hensen net was used to catch planktonic plaice post-larvae during egg-sampling cruises. The Heligoland larva net and the Agassiz trawl were introduced in 1950 and 1951, as work progressed on the post-hatching stages. Larvae and post-larvae were preserved in 2% formalin, to be later measured and classified into developmental stages 1–5. Stage 1 is the larva in which the yolk-sac is not yet resorbed. Post-larval stages 2 and 3 are planktonic and still symmetrical, whereas stage 4 covers the movement of the left eye on to the edge of the head. Stage 5, with both eyes on the right side, is thought to be the first wholely bottom stage, approaching completion of metamorphosis.

TABLE I. SUMMARY OF PLAICE POST-LARVAL FEEDING

Date of cruise	No. of post-larvae examined	Empty stomachs	Post-larvae feeding on *Oikopleura*	% feeding post-larvae containing *Oikopleura*	Other food
1946					
20–22 Jan.	158	80	65	82·5	Few copepod nauplii, significant numbers *Coscinodisus* spp., green food remains
1947					
22–28 Jan.	1	—	1	—	Nil
13–18 Feb.	35	11	—	—	Copepod nauplii, invertebrate eggs, bivalve veliger, *Coscinodiscus* frustules, green food remains
11–14 Mar.	19	7	—	—	Copepod nauplii, copepodites, small copepods, diatom debris
22–28 Mar.	6	1	—	—	*Temora longicornis* nauplii and polychaete bristles
1950					
9–12 Mar.	83	23	47	78·3	2 *Temora longicornis*, 3 copepod fragments, 1 polychaete larva, occasional diatom frustule
1951					
10–20 Feb.	32	17	12	80·0	Only few diatom frustules
27 Feb.–7 Mar.	34	14	19	95·0	1 gastropod veliger, few diatom frustules
20–31 Mar.	129	65	51	79·7	2 *Temora longicornis*, 3 fragmentary copepods, 5 with palps of *Magelona papillicornis*, occasional copepod eggs, single gastropod veliger

In 1950 and subsequent years, the gut contents were examined as follows. Specimens were placed on a black background, in order to emphasize the opaque outlines of the coiled alimentary canal. The body wall was dissected away on one side with needles; the gut severed in the anterior oesophageal and posterior anal regions, then removed into water in a watch-glass. No optical aids were needed. After disengaging liver and muscular tissue under a dissecting microscope, the gut was transferred to a drop of water on a slide and divided into three sections, by transverse cuts at the anterior and posterior stomach sphincters. These sections were laid open with needles, the lumen contents separated from gut tissue by gentle teasing, and the former examined under high power.

THE DIET IN RECENT YEARS

In February–March 1950, eighty-three undamaged post-larvae, between 5·5 and 15·5 mm. in length, were taken in the Agassiz trawl off the Dutch coast. Subsequent examination of the gut contents showed that forty-seven specimens contained black cigar-shaped pellets, always associated with transparent, indigestible matrix vesicles, arranged along the length of the gut like peas in a pod (Plate I, fig. 1). Only five specimens held the chitinous remains of copepods; in two these remains were identified as *Temora longicornis*, in the other three they were too fragmentary for identification. Twenty-three stomachs were empty. Diatoms were usually found associated with animal food remains, the principal genera being *Coscinodiscus*, *Biddulphia*, *Navicula* and *Nitzschia*. The larger thin-walled diatoms are readily taken by the yolk-sac stage larvae and the early stage-2 post-larvae. They probably represent the 'green food remains' observed in the past by a number of workers.

The black pellets and surrounding matrix vesicles were studied more closely (Pl. I, fig. 2). Pellets varied greatly in length (0·12–0·60 mm.), but their shape was more consistent. Their number varied from specimen to specimen, and their distribution within the gut was not constant. As many as sixty-two pellets were found in one gut alone, forty-two in the stomach and twenty in the intestine. As fish post-larvae are not known to produce compact faeces, these pellets were judged to be formed by a certain type of animal prey. The prey would have been soft, easily and almost completely digestible, leaving characteristically shaped pellets and a thin matrix vesicle as the only evidence of its nature. Zooplankton samples from the spawning area were examined for such an animal. *Oikopleura dioica* (Pl. I, fig. 4) fitted the description and was present at all stations where post-larvae occurred. The shape variation of pellets from the gut of *Oikopleura* and from the gut of post-larvae taken in the same locality are compared in Text-fig. 1. There is a distinct relationship. The indigestible matrix vesicles were, without doubt, the developing 'houses' of *Oikopleura* eaten by the young plaice. Lohmann (1903), in his work on the Appendicularia, noted the resistant nature of these structures. The cuticular secretions of the tunicates are now known to have a chemical composition closely allied to cellulose. The absence of cellulase from the enzymic system of the plaice post-larva would explain the indigestibility of the 'house'.

During the spring of 1951, a further series of Agassiz hauls was made over the plaice spawning grounds. A total of 195 post-larvae were caught, eleven of which bore undigested *Oikopleura* in the oesophagus (Pl. I, fig. 3), whilst a further seventy-one contained typical pellets and vesicles. Seventeen specimens held other animal food, principally *Temora longicornis*, copepod eggs and molluscan veligers. The palps of *Magelona papillicornis*, a sedentary polychaete, were found in the stomachs of a few late stage-5 post-larvae.

TABLE II. ABSTRACT OF PLANKTON ANALYSIS FOR THE SOUTHERN BIGHT, 1947

Main potential food organisms of plaice post-larvae per cubic metre. Vertical Hensen net hauls (60 meshes/1 in.).

	Station no.							
Species	1	2	3	4	5	6	7	8
Month of cruise: January								
Small copepods	N.D.	87	205	234	214	445	868	N.D.
Polychaete metatrochophores	N.D.	—	—	—	—	—	—	N.D.
Polychaete post-larvae	N.D.	—	—	—	—	—	20	N.D.
Lamellibranch post-larvae	N.D.	4	—	21	164	70	39	N.D.
Oikopleura spp.	N.D.	4	—	9	7	3	20	N.D.
Coscinodiscus concinnus	N.D.	—	—	—	33	127	296	N.D.
Biddulphia regia	N.D.	—	—	47	296	19,826	26,250	N.D.
Month of cruise: March								
Small copepods	103	56	77	77	3,796	345	329	129
Polychaete metatrochophores	4	9	—	—	56	—	16	4
Polychaete post-larvae	—	—	—	—	—	—	—	—
Lamellibranch post-larvae	—	—	22	—	422	—	41	—
Oikopleura spp.	—	—	11	—	—	—	—	—
Coscinodiscus concinnus	123	59	33	131	12,656	181	1,376	16,286
Biddulphia regia	—	2	153	1,796	1,026,563	3,055	7,904	129
Month of cruise: April								
Small copepods	1	131	112	136	129	173	94	92
Polychaete metatrochophores	—	6	13	—	—	12	23	—
Polychaete post-larvae	—	—	—	14	—	—	—	26
Lamellibranch post-larvae	—	—	—	—	—	—	—	—
Oikopleura spp.	—	—	—	—	—	—	—	—
Coscinodiscus concinnus	59	938	108	32	246	190	598	99
Biddulphia regia	—	47	15,361	289	43	138	105	59
Month of cruise: May								
Small copepods	2,918	9	11	82	195	664	1,059	N.D.
Polychaete metatrochophores	14	—	—	—	—	—	4	N.D.
Polychaete post-larvae	—	—	—	3	—	—	20	N.D.
Lamellibranch post-larvae	—	—	—	—	—	—	16	N.D.
Oikopleura spp.	—	—	—	—	—	—	—	N.D.
Coscinodiscus concinnus	879	104	203	—	3	—	4	N.D.
Biddulphia regia	8	66	53	—	25	—	—	N.D.

N.D. = no data.

Station nos. 1–8 represent a line of stations 12 miles apart stretching across the Southern Bight, from Smith's Knoll to the Hook of Holland.

TABLE III. ABSTRACT OF PLANKTON ANALYSIS FOR SOUTHERN BIGHT, EARLY MARCH 1950

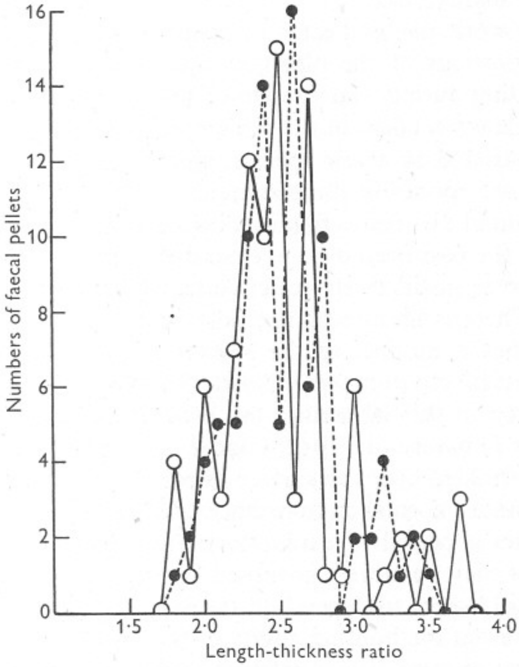
Main potential food organisms of plaice post-larvae per m.^{3}. Vertical Hensen net hauls (60 meshes/1 in.).

	Station no.									
Species	11	12	23	24	25	34	35	38	39	48
Small copepods	951	1,987	191	613	239	234	244	285	204	40
Lamellibranch post-larvae	—	—	6	5	7	—	3	—	—	2
Oikopleura spp.	82	52	181	—	83	6	54	7	41	13
Coscinodiscus concinnus	—	—	—	—	—	—	—	—	—	10
Biddulphia regia	74,320	142,629	2,694	2,885	128,892	89	7,398	152	38	31

Plankton organisms less than 0·35 mm. in length are not filtered quantitatively by the Hensen net. However, size measurements of the faecal pellets taken from plaice stomachs suggest that smaller *Oikopleura* were either relatively scarce or were not used as food by plaice post-larvae.

Ninety-six stomachs were empty. Towards the end of March 1951, fifty completely metamorphosed young plaice (15–17 mm. long), collected at stations about 25 miles west of Ijmuiden, were found to be feeding mainly on the palps of *M. papillicornis*.

Records for January 1946 show that a high proportion of feeding post-larvae of an early stage, had 'detrital pellets' in the alimentary canal. On the other hand, post-larvae caught with a Hensen net during 1947 appear to have fed on a mixed diet of large diatoms and small copepods, with an occasional molluscan veliger and polychaete larva.



Text-fig. 1. Variation in length/thickness ratio of equal numbers of pellets, from the gut of plaice post-larvae (black circles—continuous line) and of *Oikopleura dioica* (open circles—broken line).

Thus in 1946, 1950 and 1951, plaice post-larvae from the Southern Bight seem to have utilized the small population of *Oikopleura* present as a principal source of animal food during their planktonic life (Table I). Preliminary observations for 1952 give a similar picture.

The anomalous situation in early 1947, when other species assumed principal importance as food, has yet to be explained. Probably the prolonged easterly gales and icy conditions in the plaice spawning area delayed the annual increase of *Oikopleura* stocks. The organisms comprising this alternative diet are usually more abundant than *Oikopleura* in the plankton during the post-larval development period of the plaice (Tables II and III).

THE PHENOMENON OF FOOD SELECTION

There is much evidence to support the view that flat-fish post-larvae are discriminate feeders. Dannevig (1897) was of the opinion that only one food species was eaten for a time by baby plaice, though different individuals may eat different species. Petersen (1894) observed that dabs, plaice and flounders living under the same food conditions, had distinctly different food preferences. Lebour (1919) concluded that most young fish select their food from what is commonest in the plankton at the time, indiscriminate feeding seldom or never taking place.

In the present work, the food eaten by plaice post-larvae bore little relationship to the proportions of the plankton constituents. As an example, the summary of feeding during March 1950 (Table I), should be compared with the analysis of plankton taken in the same area at the same time (Table III). Feeding was restricted to a few species, and was not in proportion to the abundance of those species in the plankton.

The mechanism of diet restriction is still in doubt. The popular term 'food selection' has in the past been used to describe an effect, with the implication that fish post-larvae instinctively select certain food species when presented with a choice. There is no question of post-larvae being inherently fitted to utilize only a limited number of the species of prey normally available to them in their natural environment. North Sea plaice post-larvae have been successfully reared in this laboratory on *Artemia salina* nauplii, which they do not encounter in nature. In 1951, stage-2 post-larvae fed eagerly on dried egg fragments sprinkled over the surface of sea water in tanks.

Conceivably, under normal circumstances, young fish are able to recognize suitable food after a period of exploratory hunting activity, and the extent of this suitability may be largely governed by the vulnerability of the prey. Vulnerability would seem to depend on the size, structure and behaviour of the prey, as well as on the hunting ability of the predator.

The importance of prey size in relation to the mouth and gullet proportions of a post-larva was discussed by Lebour (1919), and elaborated recently by Wiborg (1948) for cod larvae. Observations made at sea in March 1952 revealed that stage-3 plaice post-larvae were feeding on *Oikopleura*, *Temora* nauplii, metanauplii and copepodites, which were particularly abundant, and on the large diatoms *Coscinodiscus concinnus* and *Biddulphia regia*. These organisms were occasionally found together in the same stomach. Post-larvae in earlier stages of development were eating smaller *Oikopleura*, nauplii and the usual diatoms. Advanced larval and early post-larval forms fed on diatoms only, the smallest of these food types.

Structure and behaviour play an equally important part in determining the vulnerability of prey. Lebour (1918) noticed that decapod larvae were rarely eaten by young fish, and attributed this to the spinous nature of the prey.

The number and efficiency of sense organs, conspicuousness, special escape reactions, secretion of repellents, and the swarming habit, are but a few of the factors which might well decide how far a particular prey is open to attack by a particular predator.

With the concept of vulnerability in mind, it is easy to see why the soft-bodied, slow-moving, but conspicuously vibratile *Oikopleura* should fall a ready victim to a visual feeder, as the plaice post-larva appears to be (see below).

DIURNAL FEEDING ACTIVITY

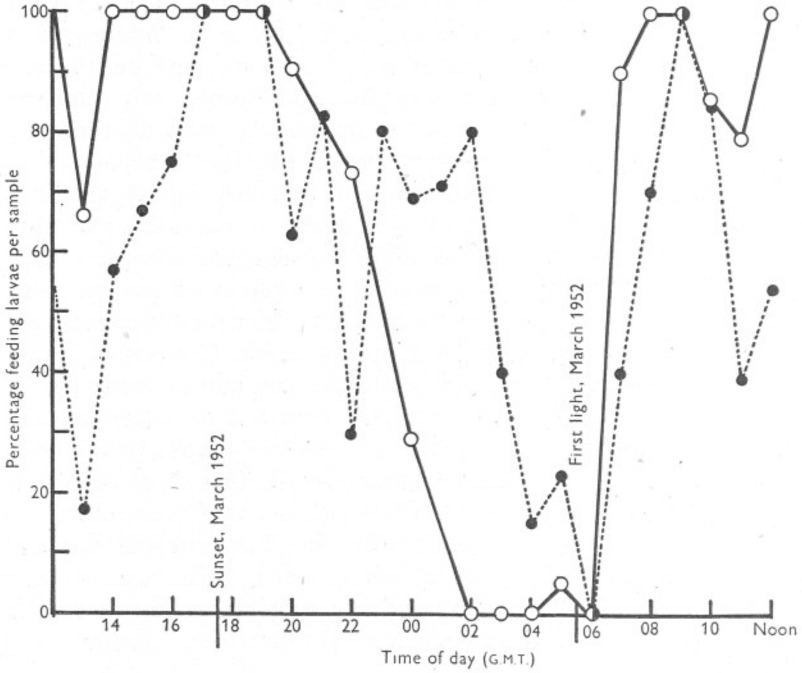
Forty-four per cent of all post-larval stomachs were empty. Other workers have referred to the lack of food traces in a high proportion of the total stomachs they investigated. Scott (1922) thought that the easy rupture of the stomachs might account for emptiness in the early planktonic forms, and that regurgitation in the net, or on addition of preservative, took place with metamorphosing and later stages. Lebour (1921) commented on the high numbers of empty stomachs encountered during work at Plymouth, and considered that infrequent feeding coupled with rapid digestion, might serve as a protective measure in young clupeoids. In these circumstances, feeding fish would only occasionally be caught.

The regurgitation theory was tested at sea in March 1952. Two vertical Heligoland larva-net hauls were made every 2 hr. in 20 fathoms of water. The plaice larvae and post-larvae of each haul were separated from other planktonic material. One catch was dissected immediately for stomach contents, and the other preserved in 2% formalin for later dissection. After 24 hr. work, no significant difference was seen in the frequency of empty stomachs between the two samples from any 2-hourly station, and the conclusion was reached that the addition of dilute formalin did not stimulate antiperistalsis. However, as the experiment progressed from day to night, a distinct falling off in the proportion of filled stomachs was noticed, followed by a sudden burst of feeding activity after first light the following morning. The experiment was continued for a further 24 hr. The pooled results for both days are represented in Fig. 6 by the continuous line. Post-larval feeding was most intense shortly after first light and for some considerable time before darkness fell, with a period of desultory feeding before and after noon. Data for the 4 years under consideration in this paper were analysed in a similar way to those of the 48 hr. station, and the results are presented in Table IV and Text-fig. 2 by the broken line. The principal gradients are not as sharply defined as for the 48 hr. station, due to differences in the extent of daylight hours between January and late March, but the first light and afternoon peaks of feeding activity are quite distinct, with a decline occurring in the early hours of the morning.

Light conditions seem to play an important part in determining the

TABLE IV. INCIDENCE OF PLAICE POST-LARVAE WITH FOOD IN THE STOMACH

	48 hr. station		Other stations	
Hour	Total larvae	No. feeding	Total larvae	No. feeding
13.00	6	4	12	2
14.00	11	11	7	4
15.00	4	4	9	6
16.00	16	16	28	21
17.00	1	1	8	8
18.00	10	10	—	—
19.00	4	4	9	9
20.00	37	34	40	25
21.00	—	—	41	34
22.00	46	35	70	21
23.00	—	—	15	12
Midnight	14	4	16	11
01.00	—	—	35	25
02.00	3	0	20	16
03.00	7	0	20	8
04.00	19	0	13	2
05.00	19	1	17	4
06.00	24	0	2	0
07.00	51	46	15	6
08.00	9	9	13	9
09.00	19	18	2	2
10.00	7	6	13	11
11.00	8	7	26	10
Noon	12	12	67	36



Text-fig. 2. Feeding periodicity of plaice post-larvae. Percentage of larvae in each sample with food in the gut, from the 48 hr. station, March 1952 (open circles—continuous line), and from other stations of recent years (black circles—dotted line).

periodicity of feeding activity in plaice post-larvae. This conclusion is reinforced by laboratory work, in which the post-larvae of plaice and plaice-flounder hybrids were subjected to changes in light conditions, other environmental factors being equal. The experiment was carried out at 9° C. using *Artemia salina* nauplii as food. On the first day of the experiment, five beakers containing batches of post-larvae were standing in tank *A*, surrounded by circulating water at 9° C., open to artificial and diffuse daylight. That same night, three of these beakers (7, 12 and 15*a*) were transferred to tank *B*, in which conditions were the same as in tank *A*, except for the complete exclusion of light. These three beakers were returned to tank *A* the following evening, whilst the remaining two beakers (11 and 15*b*) took their place in darkened tank *B*. On the evening of the third day, beakers 11 and 15*b* were transferred back to tank *A*. Observations on post-larval feeding activity were made each day at approximately 10.30, 15.00 and 18.00 hr., and the results are recorded in Table V. On no occasion were post-larvae found feeding in darkness; in lighted conditions plaice-flounder hybrids were more vigorous feeders than plaice.

TABLE V. THE FEEDING ACTIVITY OF POST-LARVAE IN RELATION TO LIGHT

1952	Time	Plaice 7	Plaice 11	Hybrid 12	Hybrid 15*a*	Hybrid 16*b*
29 Jan.	11.00	Light 1/7	Light 1/6	Light 9/9	Light 4/10	Light 1/10
	15.20	Light —	Light —	Light —	Light —	Light 7/10
	17.30	Light 2/7	Light 3/6	Light 8/9	Light 7/10	Light 7/10
30 Jan.	11.00	Dark 0/7	Light 2/6	Dark 0/9	Dark 0/10	Light —
	13.00	Dark 0/7	Light —	Dark 0/9	Dark 0/10	Light 9/10
	15.15	Dark 0/7	Light 3/6	Dark 0/9	Dark 0/10	Light 8/10
	18.00	Dark 0/7	Light 4/6	Dark 0/9	Dark 0/10	Light 8/10
31 Jan.	10.30	Light 1/7	Dark 0/6	Light 5/9	Light 6/10	Dark 0/10
	14.30	Light 5/7	Dark 0/6	Light 7/9	Light 8/10	Dark 0/10
	18.00	Light 7/7	Dark 0/6	Light 7/9	Light 8/10	Dark 0/10
1 Feb.	10.40	Light 2/7	Light 0/6	Light 4/9	Light 6/10	Light 8/10
	18.00	Light 4/7	Light 2/6	Light 7/9	Light 4/10	Light 9/10

The fractions give the number of post-larvae with food in their stomachs (numerator) and the total number of post-larvae in the beaker (denominator).

Thus there are good grounds for concluding that plaice post-larvae are visual feeders, although the possibility of an inherent daily feeding rhythm cannot be entirely overlooked. For present purposes, it is sufficient to say that a large proportion of the empty stomachs encountered during the investigation of their diet in the Southern Bight, can be accounted for by big diurnal fluctuations in feeding activity influenced by light conditions.

I am indebted to members of the staff of the Fisheries Laboratory at Lowestoft, in particular to Mr A. C. Simpson, for the experimental data on the feeding periodicity of post-larvae in tanks and for access to material from his plaice and larva surveys of 1946–52. I would also like to thank Mr J. C. Cattley for the plankton analyses and Dr H. A. Cole of the Shellfish Experimental Station, Conway, for his criticism of the manuscript.

SUMMARY

An examination was made of the stomach contents of plaice post-larvae taken from the Southern Bight spawning ground in the spring of 1950. They were found to be feeding mainly on a soft-bodied prey, which left characteristically shaped faecal pellets and an undigested matrix vesicle as the only evidence of its nature. Pellets from the post-larvae compared closely in shape with those of *Oikopleura dioica*, found in the plankton of the spawning area during the period of post-larval development.

In 1951, undigested *Oikopleura* were seen in the oesophageal regions of a few dissected specimens, in addition to typical indigestible remains in a large proportion of the total feeding post-larvae examined.

Records for 1946 suggest a similar exploitation of the *Oikopleura* population by plaice post-larvae, although the phenomenon was not repeated in 1947, when inclement weather may have interfered with the annual outburst of this prey.

The phenomenon of food selection by plaice post-larvae is discussed, with special reference to the part that vulnerability may play in limiting the number of species of prey available as food.

A feature of this and other investigations on post-larval feeding, was the occurrence of a high proportion of empty stomachs. An experiment designed to test a regurgitation hypothesis, revealed the existence of a marked diurnal pattern of feeding activity, apparently influenced by light conditions. The importance of light in feeding behaviour was confirmed by tank experiments. In this investigation a large proportion of the empty stomachs encountered can be explained by reference to diurnal fluctuations in feeding activity, supporting the view that plaice post-larvae are visual feeders.

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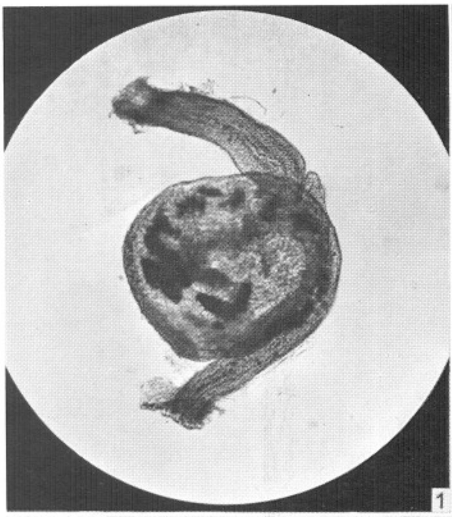
EXPLANATION OF PLATE I

Fig. 1. Complete gut of plaice post-larva, showing large pellets and matrix vesicles *in situ*; × 40.

Fig. 2. Small pellets and vesicles after removal of the gut; × 50.

Fig. 3. Undigested *Oikopleura dioica* (left centre) removed from the oesophagus (left), and matrix vesicles (right) from the stomach; × 50.

Fig. 4. Selected *Oikopleura dioica* from plankton sample. Southern Bight, February 1951; × 50.



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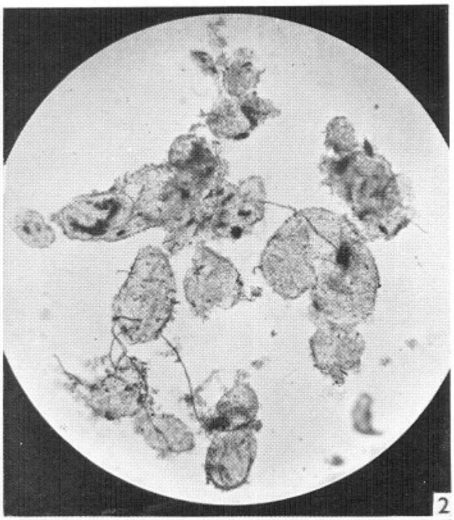

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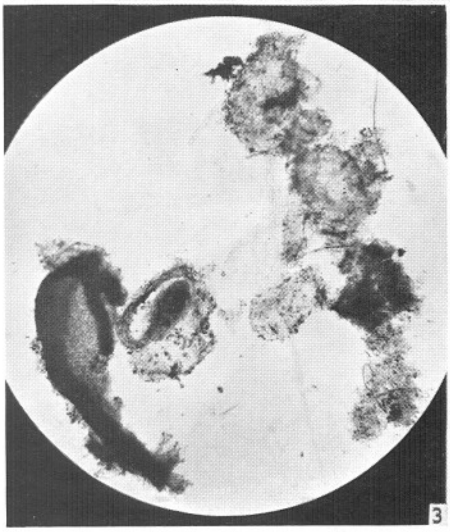

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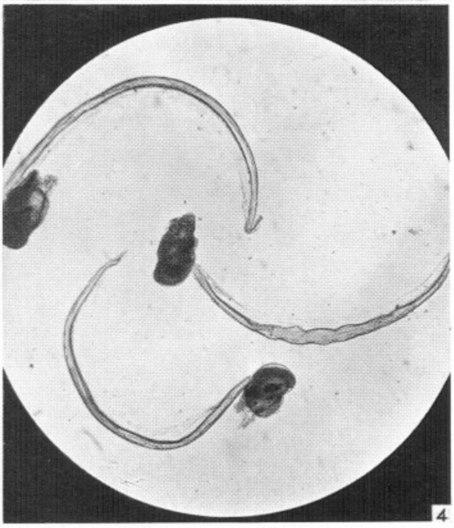

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