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THE FOOD OF FOUR SPECIES OF PLEURONECTIFORM LARVAE IN THE EASTERN ENGLISH CHANNEL AND SOUTHERN NORTH SEA

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ABSTRACT

An examination was made of the stomach contents of the larvae of plaice, flounder, dab and sole collected in the eastern English Channel and in the Southern Bight during the winter and spring of 1971. These four species of flatfish have distinct diets and competition for food between them is largely avoided. Plaice larvae fed almost exclusively on Oikopleura; flounder larvae also ate Oikopleura but in addition a wide range of planktonic organisms including phytoplankton, polychaete larvae, lamellibranch larvae, and copepod nauplii. Dab larvae fed mainly on the nauplii and copepodite stages of a variety of copepods, but particularly of Temora. Some Temora copepodites and polychaete larvae were eaten by sole larvae, but the principal prey of these was lamellibranch larvae.

The larvae of all the species began to feed in the yolk sac stage; the initial food of all except plaice consisted of dinoflagellates, followed by tintinnids and copepod nauplii. Feeding began at dawn and the number of feeding fish and the number of food organisms in their stomachs increased throughout the day to a maximum near sunset.

There were no consistent differences between the two areas in the diets of any of the species.

INTRODUCTION

Amongst the larvae of over thirty species of fishes present in plankton samples collected from the eastern English Channel and southern North Sea (Southern Bight) during the winter and spring of 1971 were four species of Pleuronectiform fish larvae - plaice *Pleuronectes platessa* Linnaeus, 1758; flounder *Platichthys flesus* (Linnaeus, 1758); dab *Limanda limanda* (Linnaeus, 1758); and sole *Solea solea* (Linnaeus, 1758) [*Solea vulgaris*]. Although the feeding habits of the larvae of plaice are relatively well-known, both in the Southern Bight and in other areas, little has been published on the food of the other species or on possible inter-specific competition. In this paper stomach content analysis data are presented to show the food of all species and to demonstrate the relationship between them and their prey.

MATERIALS AND METHODS

The larvae came from samples collected on ten cruises from January to June 1971 by RV CORELLA using a modified Gulf III plankton sampler (Beverton and Tungate, 1967). Cruise VI, 25-28 March, Cruise VIII, 30 April-4 May and Cruise X, 2-7 June, did not include the Channel stations.

The larvae, preserved in 5% formalin, had been identified and separated from the samples before the present work began. A maximum of 35 larvae were picked at random from the preserved material for examination although at most stations fewer were available. The stations were chosen, where possible, so that a 24-hour period of feeding was covered for each species. A total of 1 308 plaice, 1 684 dab, 1 421 flounder, and 691 sole larvae were examined. Plaice larvae were available from January to April, dab from March to June, flounder from February to April, and sole in May and June.

Each larva was measured under the microscope using an eye micrometer and the stomach opened with mounted surgical needles. The food items were removed one by one, or in as small numbers as possible, identified, and removed as dissection proceeded. Only organisms from the stomach were considered as those from the lower gut were generally too digested for accurate identification, and the problem of the possibility of defaecation on capture was avoided. The term 'larvae' is taken here to include all fish up to 12 mm in length. The wet weights of the food organisms are derived from calculations given by Bogorov (1969).

RESULTS

The results are tabulated in Tables 1-4 which show the combined percentage composition of the stomach contents for all cruises.

In both the English Channel and the Southern Bight the four species have feeding regimes of two distinct types: plaice and sole larvae are specialized feeders on <u>Oikopleura dioica</u> and lamellibranch larvae respectively, while dab and flounder larvae have a more generalized diet incorporating a wide range of planktonic organisms. The findings are summarized in Figure 1 where larvae less than 5 mm in length, mainly in the yolk sac stage, and larvae greater than 5 mm are treated separately.

The mean biomass of the stomach contents of flounder, plaice, dab and sole of different size groups is shown in Figures 2(a-d). The results of all the cruises have been combined to give an overall picture of the food organisms which constitute the mass of the diet. The higher biomass of dab larvae food is partly the result of the high proportion of copepodites of Temora and other copepods in the diet; these remain in an identifiable form for longer than other types of prey. The weight of Oikopleura shown in the diets is based on the mean size of Oikopleura in the plankton samples.

Plaice larvae fed almost exclusively on Oikopleura although polychaete larvae and Pseudocalanus nauplii occurred irregularly. Oikopleura also featured in the diets of dab and particularly of flounder larvae.

Although there were food items in common, flounder larvae ate a larger proportion of soft-bodied prey and more phytoplankton than dab larvae. Green phytoplankton remains, the result of the digestion of diatoms, were frequent in the stomachs of smaller flounder larvae: the remains of Biddulphia, Nitzschia, and particularly Coscinodiscus spp. were identified. Smaller larvae also took dinoflagellates and tintinnids. After yolk sac absorption, Oikopleura and copepod nauplii were the main prey and, in addition, larvae over 5 mm in length took Temora copepodites.

Dab larvae also began feeding with dinoflagellates and tintinnids but rapidly progressed to the nauplii and later the copepodite stages of Calanoid copepods (Paracalanus parvus, Pseudocalanus minutus, Temora longicornis, and Acartia clausii). Oikopleura were taken only by some of larger larvae.

Sole larvae were present only in the May and June samples and in a smaller size range than the other species. They have relatively large mouths and began to feed in the yolk sac stage, not only on dinoflagellates, but also on small copepods, mainly Pseudocalanus nauplii, but their principal prey was lamellibranch larvae of which large numbers were eaten. Polychaete larvae were also important, particularly for the larger sole larvae, and Temora copepodites and some non-copepod Crustacea were also taken. Dinoflagellates were eaten by all sizes of larvae and probably in larger numbers than found because the delicate nature of many types of dinoflagellate would lead to their rapid breakdown in the gut leaving only the armoured dinoflagellates, particularly Peridinium spp., in identifiable form.

Size at first feeding

All four species began to feed in the yolk sac stage. The smallest larvae that had been feeding were: plaice, 4.4 mm; flounder, 2.4 mm; dab, 2.2 mm; sole, 1.8 mm. Of the plaice, 14.3% in the size range 4.0-4.9 mm (stage 1C) had been feeding, and 47.5% of dab, 35.7% of flounder, and 55.3% of sole, all between 2.0 and 2.9 mm. In general, the percentage of feeding larvae increased with growth with the largest larvae having the largest sized prey and the largest numbers of prey as well as the fewest empty stomachs.

Predator/prey size relationships

An increase in the size of prey with increasing larval size can be demonstrated most readily by examining the stages of copepodite prey. Table 5 shows the percentage of the prey of dab larvae represented by the stages of Temora in May.

Table 5 Dab larvae: Temora stages as percentage of prey

Temora stages		Length groups (mm)							
		3.0-3.9	4.0-4.9	5.0-5.9	6.0-6.9	7.0-7.9	8.0-8.9	9.0-9.9	10.0-10.9
Nauplii		18.3	35.3	25.3	30.0	15.0	12.0		0.6
Copepodite	I		3.0	5.0	31.0	5.7	7.0		
	II		3.0	3.0	7.0	8.7	14.3	7.0	3.7
	III		1.0	2.0	6.6	18.2	16.3	21.1	13.0
	IV			1.0	2.5	13.0	18.0	26.7	26.0
	V					3.3	15.0	15.0	27.0
Adults						2.5	4.3	4.3	24.0

As the larvae grew the nauplii in the diet were replaced by increasing numbers of larger stages of Temora indicating that there was selection for size for, although the smaller dab larvae were incapable of eating the larger copepodites, nauplii and smaller copepodites were available as food for the larger larvae. As larvae of a range of length groups were found in all the samples, the effect of changes in the stage composition of the copepods can be discounted. Similar trends of larger prey for larger larvae were found for other prey types of dab and flounder. It was not possible to establish definite selection of prey for size by plaice larvae whose diet consisted largely of Oikopleura which do not long survive ingestion in a measurable form, but a general increase in the size of Oikopleura faecal pellets in the plaice stomachs was at least an indication of selection.

Sole larvae were available only in small size range with no indication of selection for size except that five of the six larvae over 5 mm had been feeding on polychaete larvae, larger prey than lamellibranch larvae, the principal food of the smaller sole larvae.

Mouth size

The size of prey which can be eaten depends upon its greatest breadth and the breadth of the mouth of the fish. Copepods were found occasionally in the mouths and gullets of the fish larvae and had in each case been taken head first with the antennae and legs folded against the body. Figure 3 compares the breadth of mouth-opening with the greatest breadth of some of the principal prey organisms found in these larvae. To avoid the possibility of stretching and distorting the jaws by opening them with dissecting needles the gape measurements were taken only from fish which were preserved with the mouth wide open. In many cases the size of the prey was close to the maximum which could be taken; in those larvae preserved in the act of swallowing for example, the copepod prey completely filled the mouth. On the other hand, the size of the lamellibranch prey of sole larvae was small compared to the size of the mouth; sole larvae have mouths comparatively larger than the other larvae and which increase in size at a faster rate, perhaps indicating that at other times larger prey is taken. Most of the Oikopleura that could be measured were small with only one, from one of the larger plaice larvae, with a breadth as much as 0.5 mm, but on capture each is surrounded by its house and presents a larger target for the feeding larva.

Diurnal variations in feeding

To examine diurnal feeding rhythms, the data for each of the species from all cruises were considered together so that sufficient material was available for all times of the day. At no time of the day were all the stomachs empty, but the number of larvae with identifiable prey in their stomachs fell during the night until sunrise (dab, flounder), or shortly before sunrise (plaice), or soon after (sole) (see Figures 4a-d). During daylight hours there was in each case an increase in the number of feeding larvae and in the number of food items in their stomachs, reaching a maximum an hour or so before sunset when there was a decline in the feeding rate. At sunset, or in the case of sole approximately an hour before, feeding was resumed at an increased rate for about two hours and then stopped or declined until the morning.

Seasonal variations

There was no seasonal variation in the diet of the plaice larvae which fed principally on Oikopleura from January to April. Polychaete larvae, copepod nauplii (mainly Pseudocalanus and Paracalanus) and tintinnids were taken in late March both in the English Channel and in the Southern Bight when there was an apparent shortage of the principal prey.

Flounder larvae were abundant from late February until late April, and dab larvae from early March until June, during which time there were a number of changes in their diets, the most important of which are shown in Figures 5a and b.

Geographical variations

It was not possible to make comparisons between the Southern Bight and the English Channel for each cruise because samples were not collected from the English Channel on Cruises VI, VIII and X. Although the main food items were the same for all four species in both the English Channel and Southern Bight, there were some differences between the diets of dab and flounder larvae in the two areas.

Flounder larvae took more lamellibranch larvae in the Channel and more polychaete larvae in the Southern Bight. Similar numbers of copepod nauplii were eaten in both areas but more copepodites in the Southern Bight.

Dab larvae took lamellibranch larvae in the English Channel in April (15% of all prey) but not in the Southern Bight and rarely at other times. In April dab larvae like flounders took more Temora in the Southern Bight than in the Channel but similar numbers were taken in both areas in May and June.

Plaice larvae fed equally on Oikopleura in both areas. In April, when a shortage of these led to the larvae taking other prey, polychaete larvae were taken in both areas and Paracalanus and Pseudocalanus nauplii in the Southern Bight.

The diet of sole larvae was alike in both areas.

DISCUSSION

A comparison of the diets of the four species shows that direct competition for food is largely avoided by each specializing in a different type of food although there are prey organisms in common. A similar situation was described by Von Palsson (1973) when he compared the diets of six species of O-group fish in Icelandic waters. In both the English

Channel and the Southern Bight there may be some competition for Oikopleura between plaice and flounder larvae, but the flounder diet incorporates a number of other frequently-taken food organisms and Oikopleura may feature commonly only when in abundance; in late February when Oikopleura were scarce only two flounder larvae were found to have eaten them. Flounder larvae eat lamellibranch larvae which are the principal prey of sole larvae, but the flounders have completed their planktonic phase before the appearance of the sole. Some lamellibranch larvae are taken by dab larvae but their main food was the nauplii and copepodids of Temora.

The high percentage of larvae feeding during the day is an indication of an adequate food supply. The availability of food has frequently been considered to be a key factor in the survival of fish larvae and a shortage of suitable prey invoked to explain larval mortality. The larvae in this survey appear to have had sufficient prey available to enable them to exercise specific food preferences both in kinds of prey and in size. A possible exception occurred in late February when plaice larvae took polychaete larvae and copepod nauplii instead of their preferred diet of Oikopleura. In the laboratory plaice larvae are readily reared on Artemia nauplii but it is not probable that they would have turned to other prey in the wild had Oikopleura been available.

Larvae of all species began to feed in the yolk sac stage and Wyatt (1972) has shown that plaice larvae will survive no longer than eight days when deprived of food even though the yolk sac is not exhausted. Rosenthal (1966) recorded similar results with sole larvae.

Flagellates seem to be an important element in the diet of dab, flounder and sole larvae at first feeding, and the greenish fluid found in the stomachs of many small larvae may be derived from the breakdown of other, more delicate, forms of nanoplankton. Dinoflagellates and tintinnids occur regularly in yolk sac larvae and, although their total biomass is small, may well play some role in establishing feeding and in the well-being of the fish.

Shelbourne (1962) has shown that plaice larvae discriminate for prey size, the larger larvae taking only larger Oikopleura, and that the size of Oikopleura eaten can be estimated from the size of the faecal pellets found in the gut. I did not repeat his measurements but can confirm the absence of small pellets in the stomachs of the larger plaice larvae. Dab and flounder larvae similarly progress with growth to larger prey, although with both these species this involves taking prey of other kinds and not merely increasingly large sizes of the same prey. The effect in all cases is to reduce the catching effort and to leave the smaller prey types available to the smaller larvae. Sole larvae did not discriminate for prey size in the limited size range in which they were found. Although lamellibranch larvae were their principal prey, their relatively large mouths suggest that larger prey may be taken. A small number had eaten larger organisms including Euterpina acutifrons and Balanus nauplii both of which were recorded from sole larvae by Lebour (1918).

Some authors discuss stomach contents in terms of 'degrees of fullness' (Rudakova, 1956; Lie, 1961) but I have not found this to be a useful concept as often a distended stomach has contained nothing but fluid, while an apparently empty stomach may contain a small, tightly-packed bolus of food which will separate into many food organisms.

There are a variety of diurnal feeding rhythms for different larvae reported in the literature; all agree that the feeding rate is lowest before sunrise (Arntz, 1974; Yasunaga, 1971; Shelbourne, 1953; Bainbridge and McKay, 1968). All four species in the present survey show the same pattern of feeding, beginning at sunrise with a gradual accumulation of food during the day and reaching a maximum before sunset but with a second burst of feeding after sunset or, more probably, because of the time-lag between feeding and collection of the larvae, actually at dusk. A preliminary look at the data suggests that gadoid and other types of larvae from the same areas behave in the same way.

Although the rate at which all four species fed declined during the night, experiments by Blaxter (1969) show that sole larvae are capable of feeding in the dark from the early post-hatching stage but plaice larvae only at metamorphosis. If sole larvae detect their prey by means other than sight, and the eyes are not developed until after yolk sac resorption, their greater ability to catch the relatively non-motile lamellibranch larvae is explained because Blaxter suggests that movement perception is an important aspect of feeding and food selection among other larvae.

REFERENCES

ARNTZ, W. E., 1974. Die Nahrung juveniler Dorsche in der Kieler Bucht. Ber. dt. wiss. Kommn Meeresforsch., 23 (2), 97-120.

BAINBRIDGE, V. and McKAY, B. J., 1968. The feeding of cod and redfish larvae. ICNAF Spec. publ., 7 (1), 187-217.

BLAXTER, J. H. S., 1969. Visual thresholds and spectral sensitivity of flatfish larvae. J. exp. Biol., 51, 221-230.

BEVERTON, R. J. H. and TUNGATE, D. S., 1967. A multi-purpose plankton sampler. J. Cons. int. Explor. Mer, 31, 145-157.

BOGOROV, B. G., 1959. On the standardisation of marine plankton investigations. Int. Revue ges Hydrobiol., 44, 621-642.

LEBOUR, M. V., 1918. The food of post-larval fish. J. mar. biol. Ass. U.K., XI (4), 433-469.

LIE, U., 1961. On the growth and food of 0-group coalfish Pollachius virens (L.) in Norwegian waters. Sarsia, 3, 1-36.

von PALSSON, O. K., 1973. Nahrungsuntersuchungen an der Jugendstadien (0-Gruppen) einiger Fischarten in islandischen Gewassern. Ber. dt. wiss. Kommn Meeresforsch., 23 (1), 1-32.

PETERSEN, C. G. J., 1893. On the biology of our flat fishes and on the decrease of our flat fish fisheries. Rep. Dan. biol. Stn, IV, 146 pp.

ROSENTHAL, H., 1966. Beobactungen uber das Verhalten der Seezungenbrut. Helgoländer wiss. Meeresunters., 13 (3), 213-228.

RUDAKOVA, V. A., 1956. Materialy po pitanijii atlanticesko-skandinavskoj seljdi. Trudy PINRO, 9, 124-145.

RYLAND, J. S., 1964. The feeding of plaice and sand-eel larvae in the southern North Sea. J. mar. biol. Ass. U.K., 44, 343-364.

SHELBOURNE, J. E., 1953. The feeding habits of plaice post-larvae in the Southern Bight. J. mar. biol. Ass. U.K., 32, 149-159.

SHELBOURNE, J. E., 1962. A predator-prey relationship for plaice larvae feeding on Oikopleura. J. mar. biol. Ass. U.K., 42 (2), 243-252.

WYATT, T., 1972. Some effects of food density on the growth and behaviour of plaice larvae. Mar. Biol., 14, 210-216.

YASUNAGA, Y., 1971. Studies on the feeding habit and growth of the plaice, Paralichthys olivaceus, in the larval stage. Bull. Tokai reg. Fish. Res. Lab., 68.

Table 1 Pleuronectes platessa: percentage composition of stomach contents

Food items	Length group (mm)								Total number of food items	% of all food items
	4.0-4.9	5.0-5.9	6.0-6.9	7.0-7.9	8.0-8.9	9.0-9.9	10.0-10.9	11.0-11.9		
Coscinodiscus spp.	4	6	5						110	5.0
Paracalanus nauplii	4	2	1	1					18	0.8
Pseudocalanus nauplii	4	3	4	2					45	2.1
Other nauplii	3		1						16	0.7
Polychaete larvae		3	8	1	3				46	2.1
Oikopleura	85	79	79	94	97	100	100	100	1886	86.0
Others		10	2	2					71	3.3
% of larvae empty	82	69	35	23	22	34	21	0		
Number of food items/larva	0.2	0.8	2.4	3.2	4.7	3.6	3.4	10.0		
Number of larvae examined	78	471	464	195	51	34	12	3		

Table 2 *Platichthys flesus*: percentage composition of stomach contents

Food items	Length group (mm)								Total number of food items	% of all food items
	2.0–2.9	3.0–3.9	4.0–4.9	5.0–5.9	6.0–6.9	7.0–7.9	8.0–8.9	9.0–9.9		
Diatoms	10	7	7	2					75	3.0
Dinoflagellates	58	38	8	4	1				408	16.5
Tintinnids	20	16	12	5					395	16.0
Copepod eggs	5	9	9	2	3	1			125	5.1
Paracalanus nauplii		6	11	13	9	5	2		408	16.5
Pseudocalanus nauplii			4	5	10	8			60	2.4
Temora nauplii			5	10	5		9		195	7.9
Other nauplii		5	8	6	6	11			94	3.8
Polychaete larvae			8	16					30	1.2
Tornaria larvae		1	4	6	3				69	2.8
Lamellibranch larvae	3	8	9	8	9	5			201	8.1
Oikopleura	4	3	14	22	46	55	70	100	363	14.7
Others		7	1	1	8	15	19		49	2.0
% of larvae empty	64	43	26	13	5	0	0	0		
Number of food items/larva	0.8	4.0	4.6	5.9	4.8	2.9	8.4	2.7		
Number of larvae examined	170	555	391	273	63	27	10	3		

Table 3 *Limanda limanda*: percentage composition of stomach contents

Food items	Length group (mm)									Total number of food items	% of all food items
	2.0–2.9	3.0–3.9	4.0–4.9	5.0–5.9	6.0–6.9	7.0–7.9	8.0–8.9	9.0–9.9	10.0–10.9		
Dinoflagellates	45	16	10	3						224	4.5
Tintinnids	37	21	7							133	2.7
Oithona nauplii	14	1	2	3						17	0.3
Acartia nauplii		5	3	4	1		1			26	0.5
Paracalanus nauplii	1	10	31	32	22	19	3			1473	29.4
Pseudocalanus nauplii		6	11	10	10	6	1	1		471	9.4
Temora nauplii		11	21	19	19	19	6			1149	23.0
Other nauplii		2	2	12	15	1			2	56	1.1
Pseudocalanus copepodites				1	1	2	9	16	6	83	1.7
Temora copepodites			1	3	20	22	59	65	32	774	15.5
Other copepodites	2	4	3	4	5	6	2	6	2	221	4.4
Lamellibranch larvae		2	2	2	2	3				125	2.5
Oikopleura				2	1	15	17	6	57	21	0.4
Others		22	7	5	4	7	2	6	1	230	4.6
% larvae feeding	49	54	65	72	80	87	98	95	100		
Number of food items/larva	1.1	1.9	3.4	4.1	6.5	6.6	7.2	3.7	6.2		
Number of larvae examined	194	317	261	301	180	87	51	18	12		

Table 4 Solea solea: percentage composition of stomach contents

Food items	Length group (mm) 1.5–1.9	2.0–2.9	3.0–3.9	4.0–4.9	5.0–5.9	6.0–6.9	Total number of food items	% of all food items
Dinoflagellates		22	18	50	32		347	20.7
Tintinnids		1	2				23	1.4
Copepod eggs		12	8	6			141	8.4
Pseudocalanus nauplii	80	8	2				66	3.9
Microsetella				3	4		11	0.7
Other Crustacea	5	4	5	11			81	4.8
Polychaete larvae		1	7	9	56	100	106	6.3
Gastropod larvae		1	1				12	0.7
Lamellibranch larvae		50	53	17	7		840	50.1
Others	15	1	4	4	1		50	3.0
% larvae feeding	38	52	82	95	92	100		
Number of food items/larva	0.9	1.8	3.0	5.4	7.9	1.3		
Number of larvae examined	13	300	321	43	11	3		

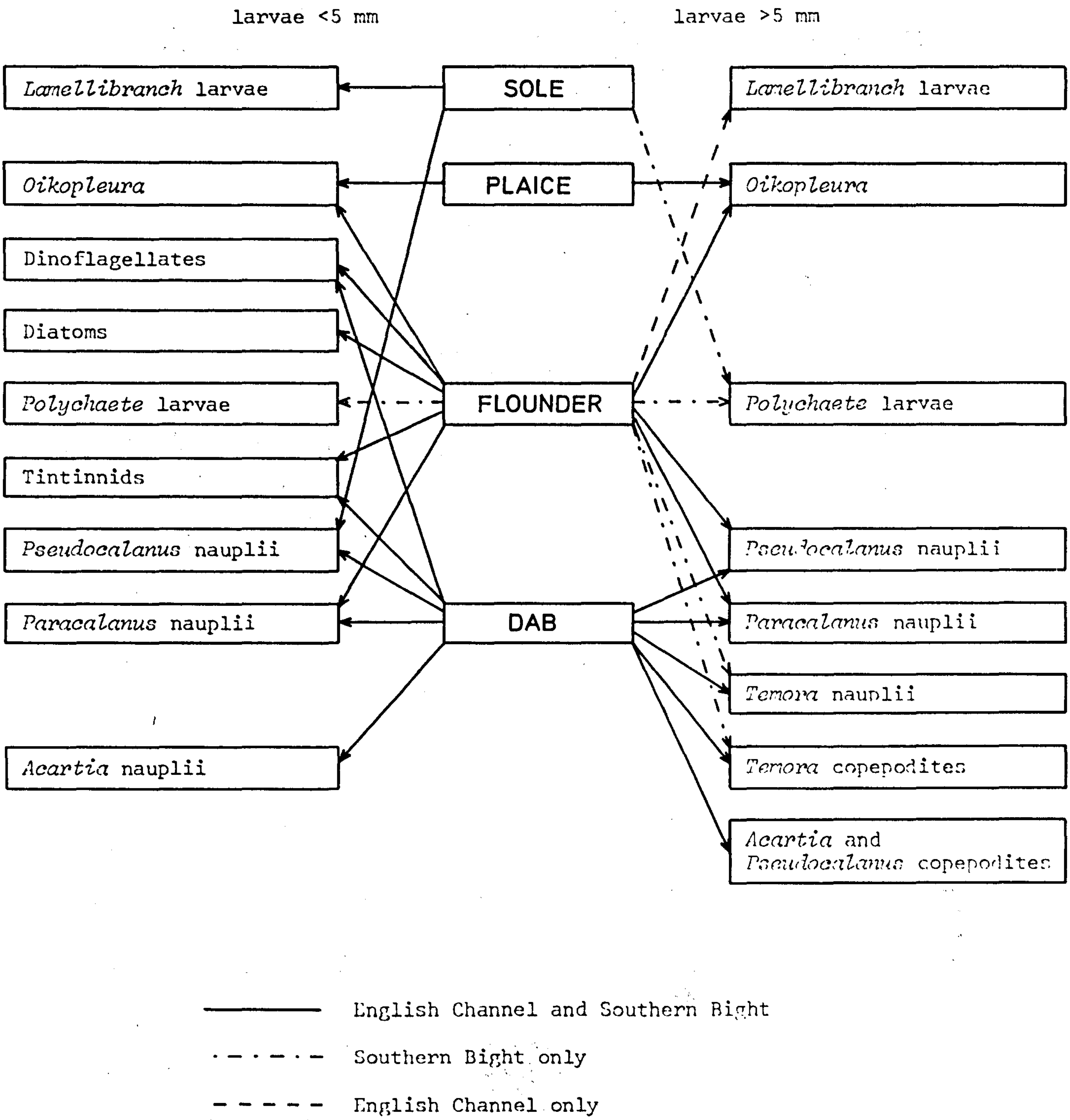


Figure 1 **Principal prey of plaice, flounder, dab and sole larvae, January to June 1971.**

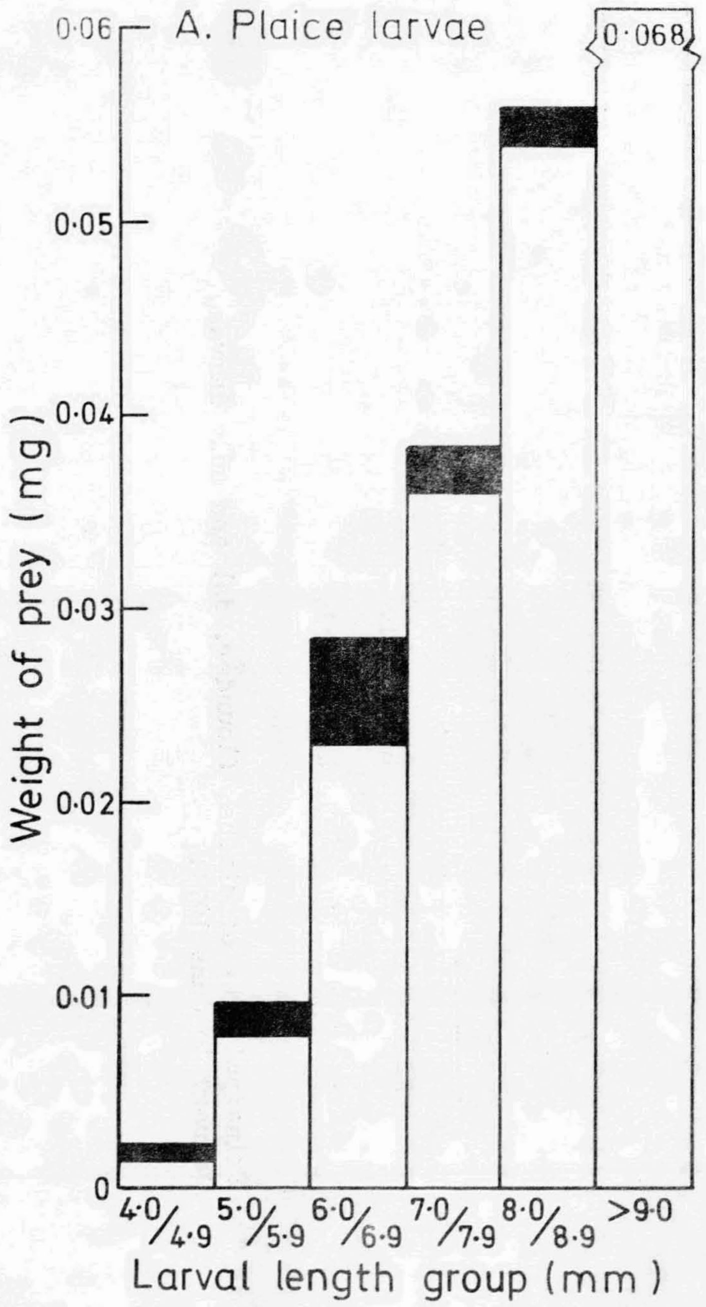


Figure 2a Pleuronectes platessa. Biomass of food organisms. Mean contents of all stomachs.

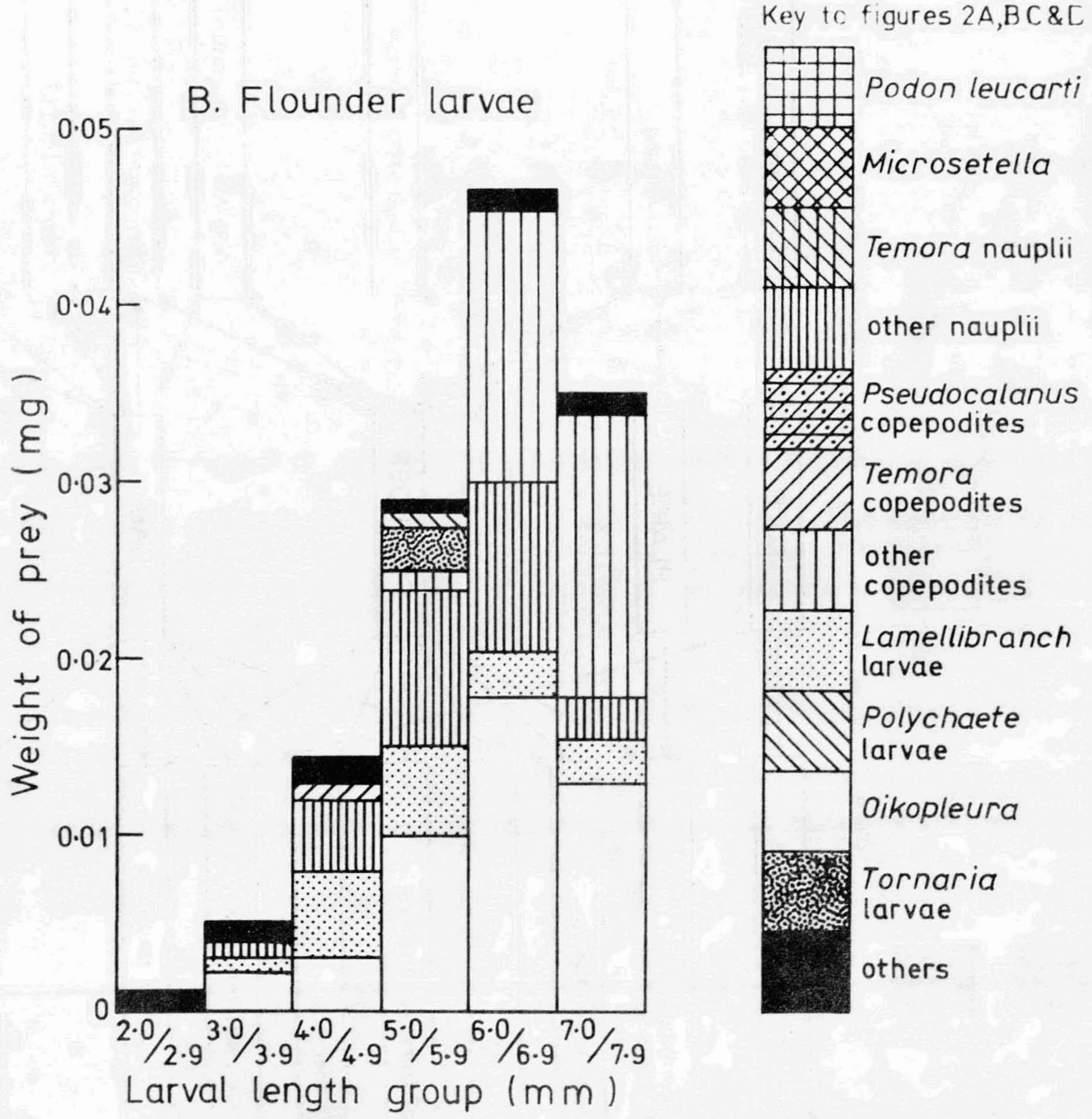


Figure 2b Platichthys flesus. Biomass of food organisms. Mean contents of all stomachs.

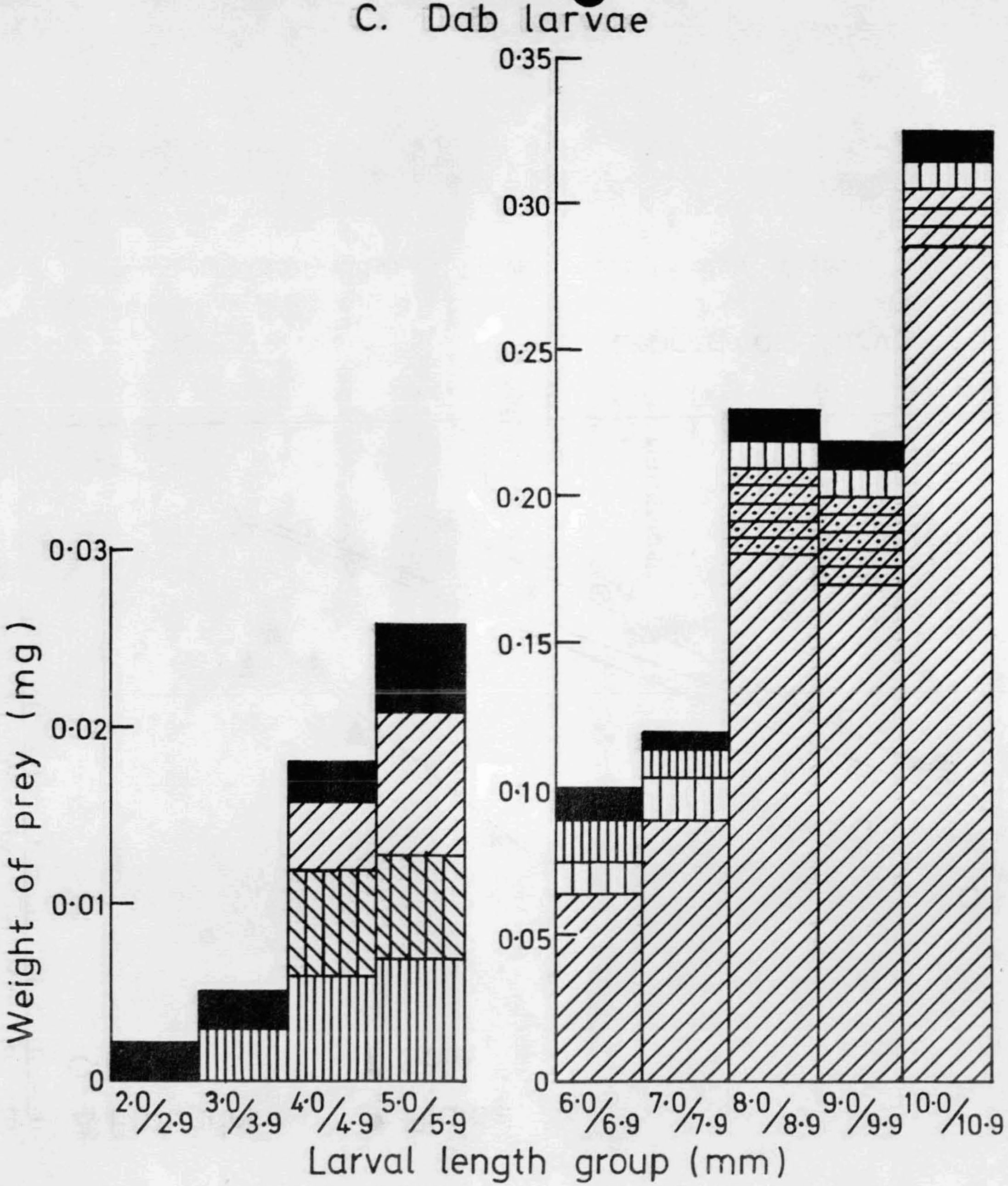


Figure 2c *Limanda limanda*. Biomass of food organisms. Mean contents of all stomachs.

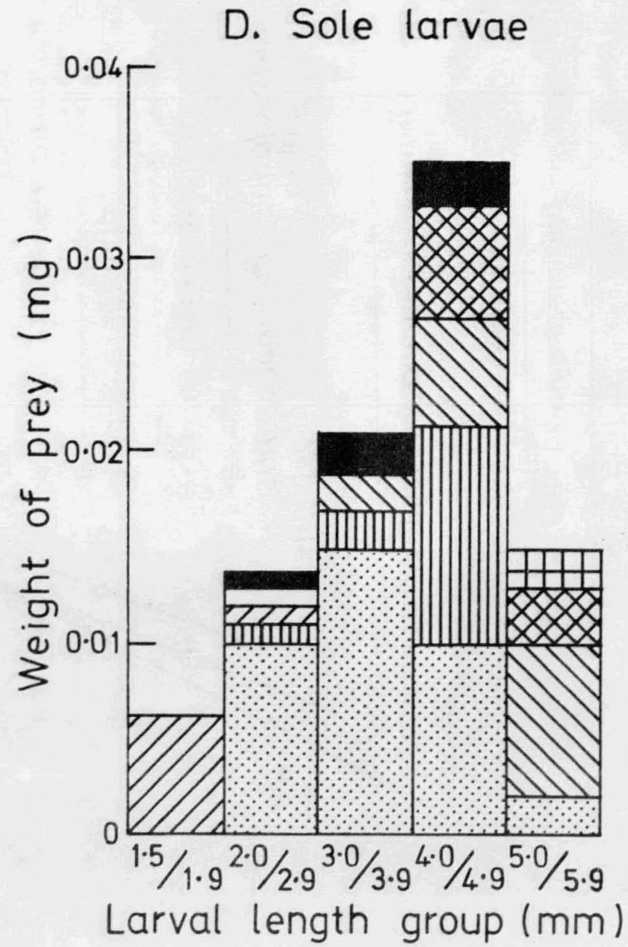


Figure 2d *Solea solea*. Biomass of food organisms. Mean contents of all stomachs.

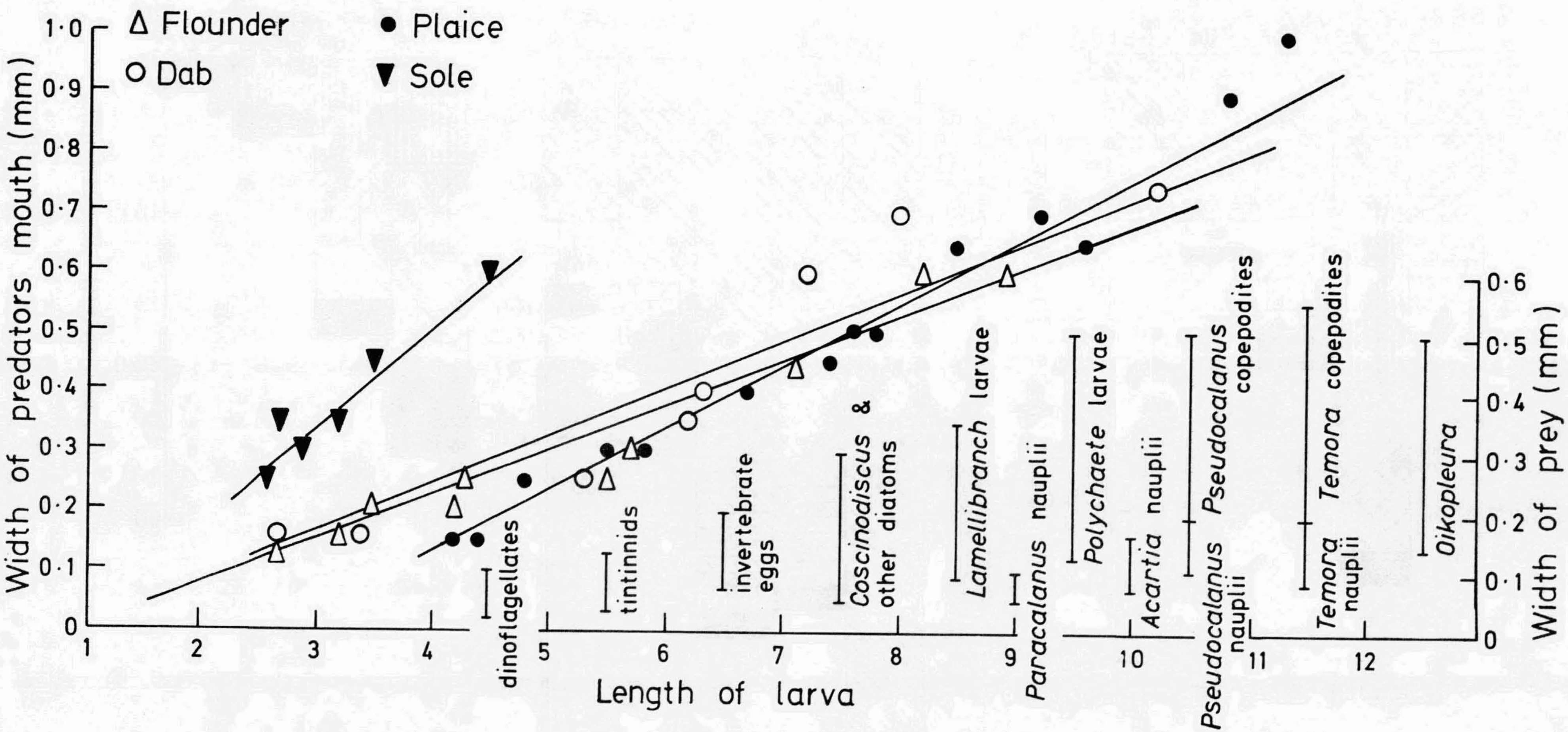


Figure 3 Relationship of width of larval mouth to size of prey.

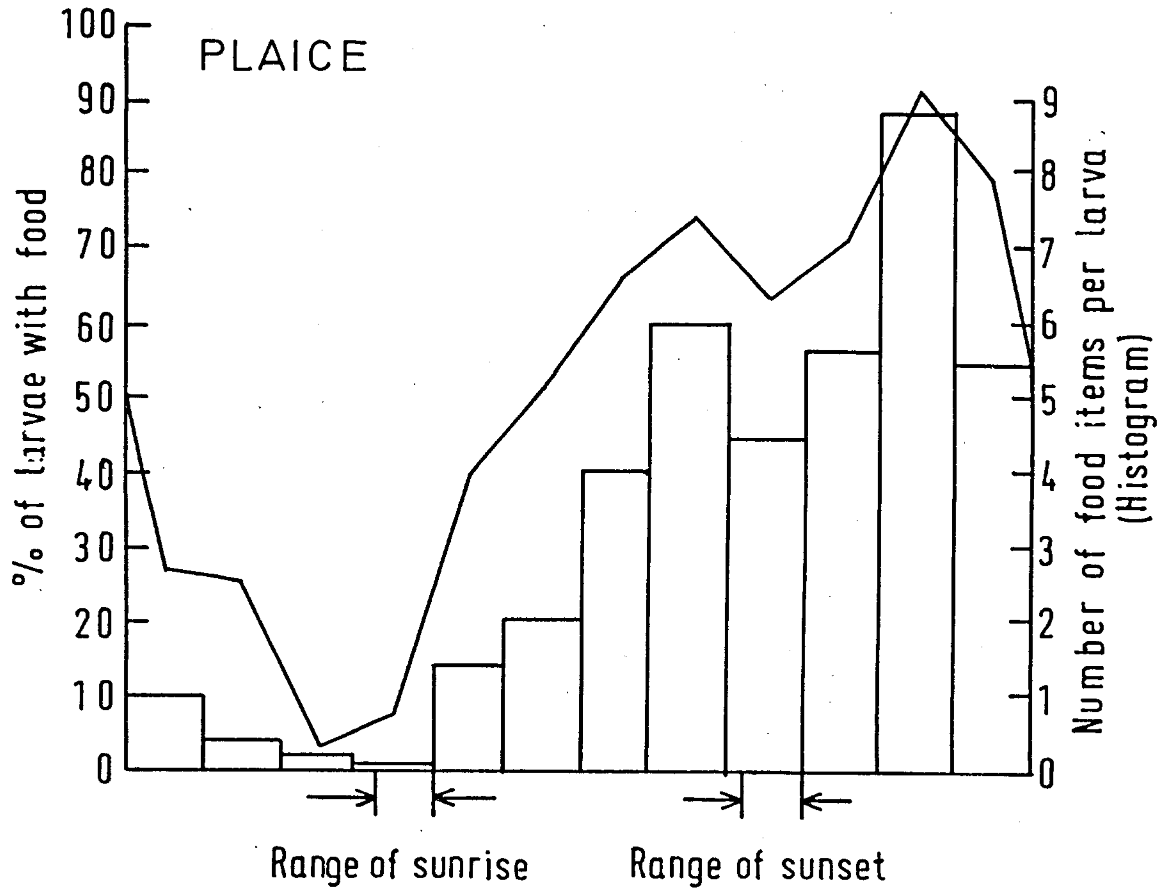


Figure 4a **Pleuronectes platessa.** Diurnal feeding periodicity, January to March.

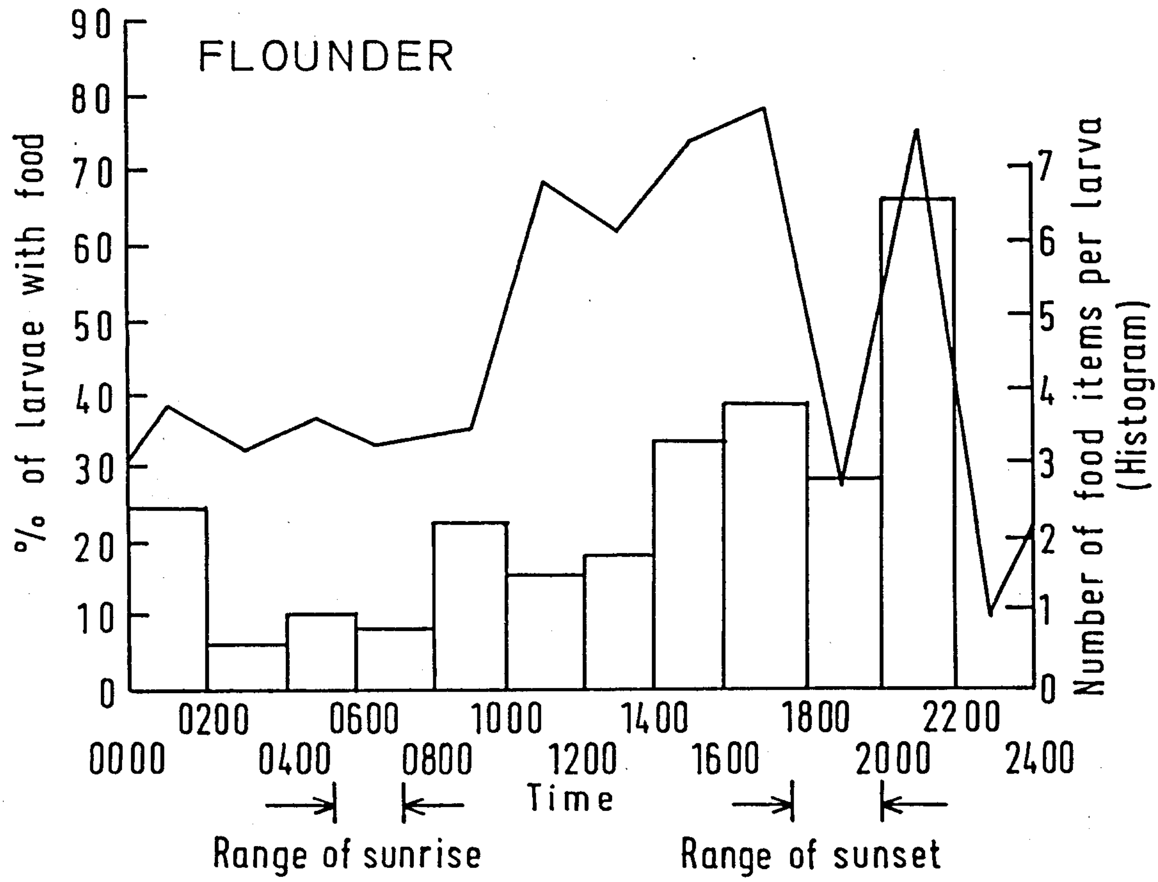
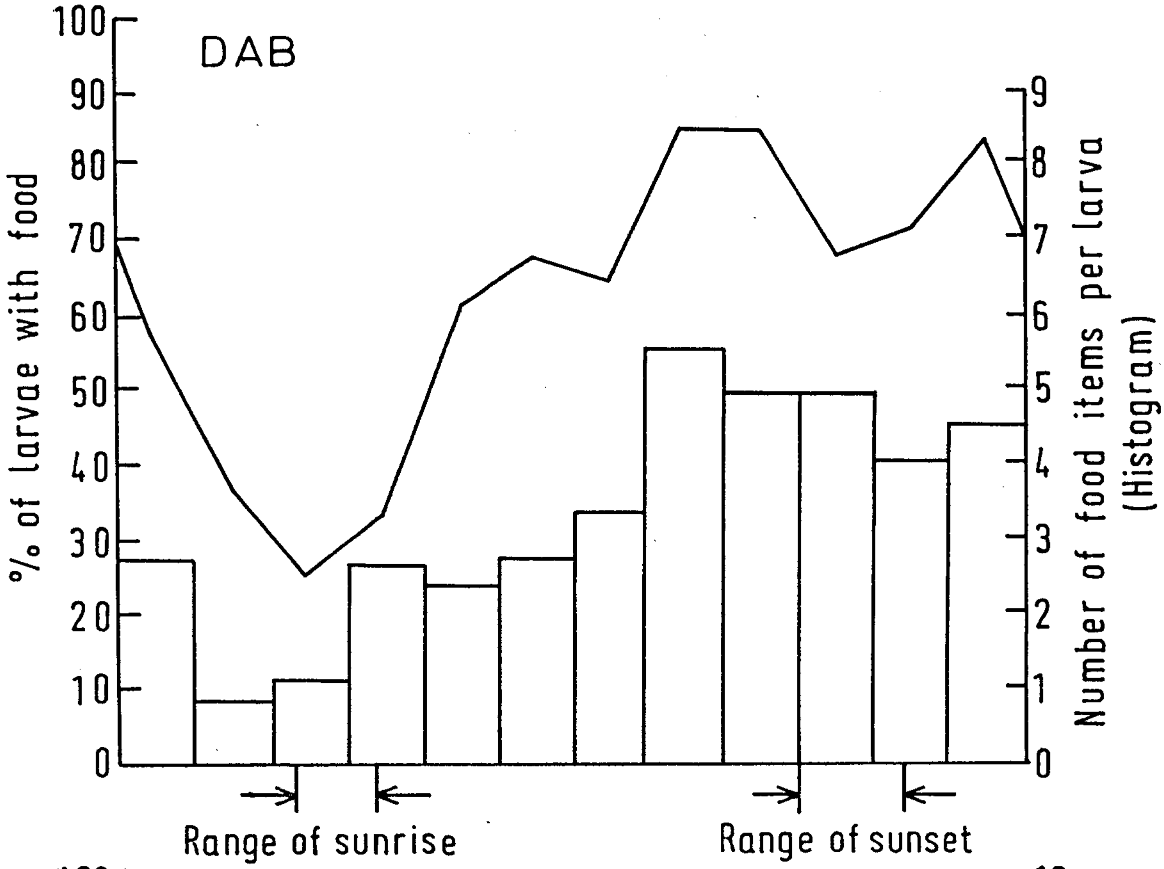


Figure 4b **Platichthys flesus.** Diurnal feeding periodicity, February to April.

Figure 4c *Limanda limanda*. Diurnal feeding periodicity, March to June.



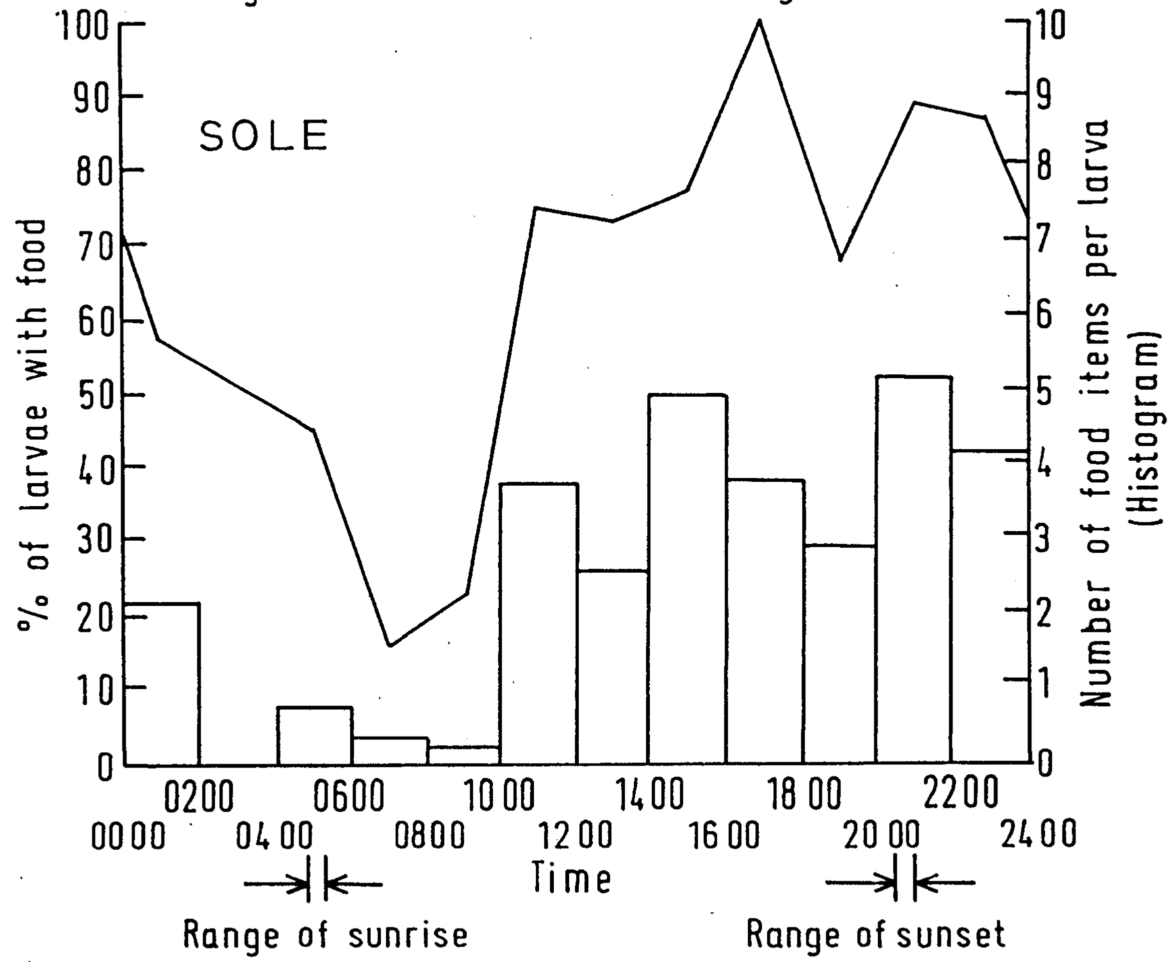


Figure 4d *Solea solea*. Diurnal feeding periodicity, May to June.

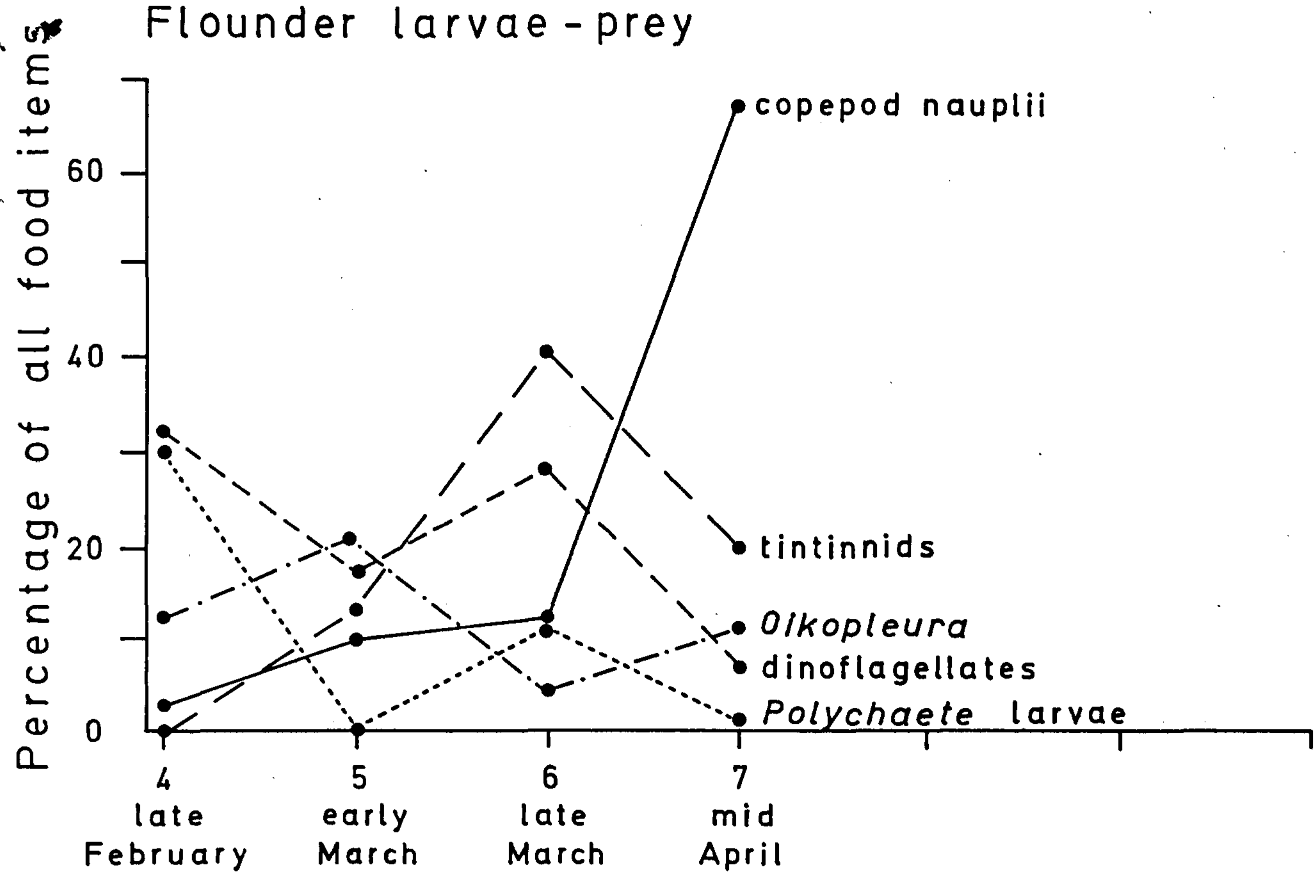


Figure 5a <u>Platichthys flesus</u>. Variations in diet, February to April, Southern Bight.

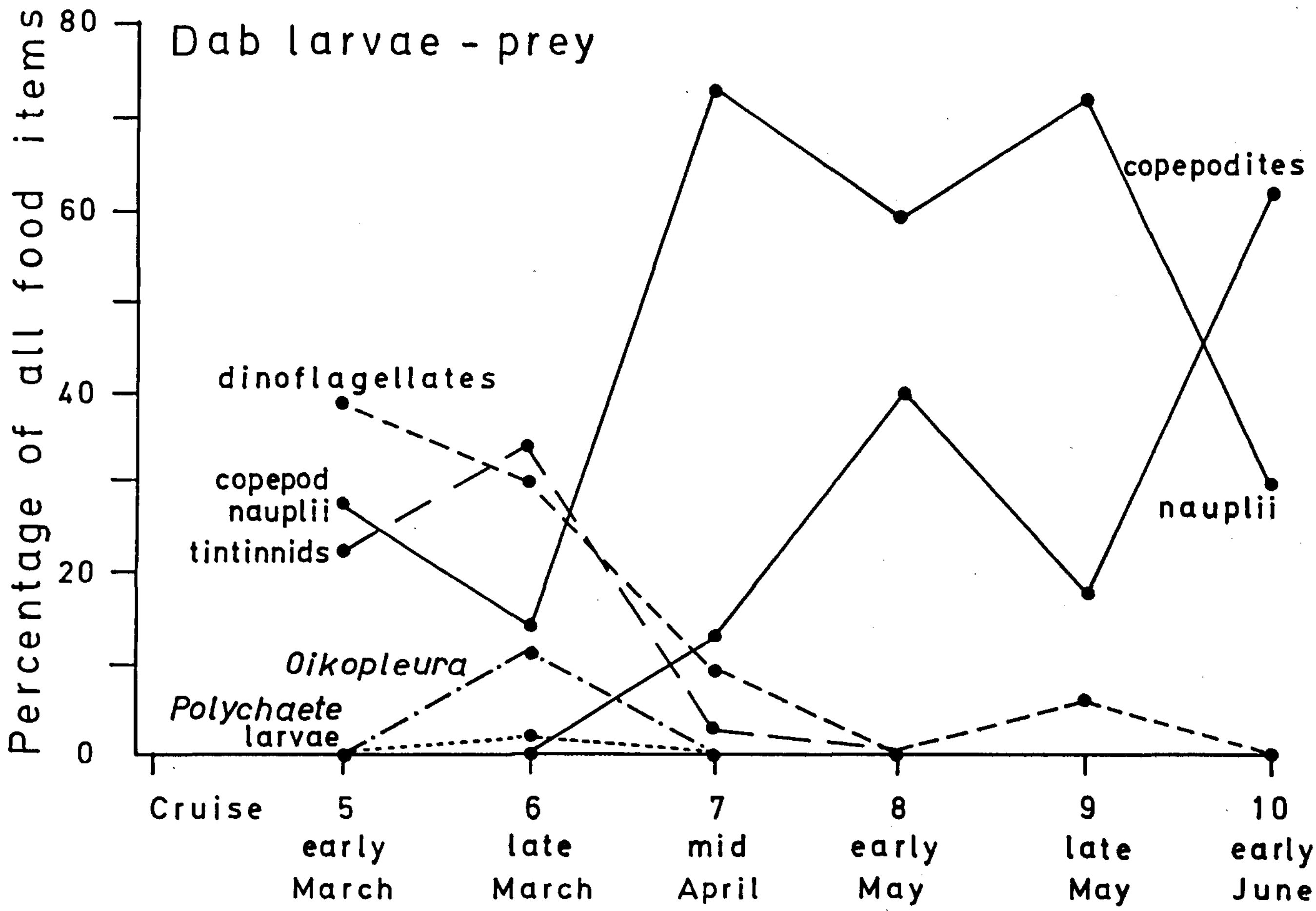


Figure 5b <u>Limanda limanda</u>. Variations in diet, March to June, Southern Bight.