

The daily food intake of 0-group plaice (*Pleuronectes platessa* L.) under natural conditions: changes with size and season

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Samples of 0-group plaice collected in Filey Bay, Yorkshire, during July and September–October 1969 were analysed to estimate their daily food intake by 5 mm length groups. In July there was a linear relationship between daily food intake and body weight, equivalent to 10 % whole body weight per day over the size range 18 mm to 49 mm. In the autumn when the fish examined were 40 mm to 80 mm, the relative food intake fell to 1.5 % body weight per day, but it is not certain that the relation between daily food intake and body weight was linear.

The change in diet of 0-group plaice is described in relation to the size of the fish. It is concluded that diet changes to maintain an optimal prey size between 0.5 % and 10 % of the predators' weight. This change in diet keeps to a minimum the number of prey organisms required each day and, due to the falling relative feeding rate with increase in mean size, explains why larger fish in the population are more likely to have empty stomachs than small fish.

Metamorphosing plaice larvae are shown to cease feeding for more than 24 to 36 hours. This may be due either to fewer attacks, or fewer successful attacks resulting from a changing eye–mouth configuration.

Introduction

Between 1968 and 1973 a detailed study was made of the population dynamics of 0-group plaice (*Pleuronectes platessa* L.) populations in Filey Bay (54°12'N 00°16'W), Yorkshire (Lockwood, 1972, 1974 a, b; 1980 a, b; Bannister, Harding, and Lockwood, 1974; A qualitative and quantitative investigation of feeding behaviour formed part of these studies.

The mean daily food intake per fish in the population during July 1969 was equivalent to 8–11 % of the whole body weight per day, but by September–October this was reduced to 1–3 % per day (Lockwood, 1980 b). As there was a slight increase in sea temperature from 12.6°C to 13.2°C between the time that the summer and the autumn samples were taken, it was concluded that the temperature difference could not account for the difference in the feeding levels. Alternative explanations for these differences might be that the reduction in feeding level was related either to the fishes' size, or to a change in diet, possibly resulting from a change in prey abundance. These possibilities are considered in this paper.

The data, previously used to estimate the mean daily food intake per fish in the population during summer and autumn (Lockwood, 1980 b) are re-analysed to examine the relationship between daily food intake and size of fish. In addition to the quantitative analysis of daily food intake, a semi-quantitative assessment of the fishes' diet is made with particular attention to the change in prey size.

Materials and methods

Estimation of daily food intake

As a detailed description of the materials and methods has already been given (Lockwood, 1980 b), only a brief summary will be given here.

The 0-group plaice were sampled on eight occasions, twice on spring tides (series a and b) and also on neap tides (series c and d) in July 1969, and similarly during September–October 1969 (series e–h). The fish were caught with a young flatfish beam trawl (Riley and Corlett, 1966) at 3 h intervals over a period of 24 h. Each catch of 0-group plaice was divided into two approximately equal parts, *A* and *B*. All *A* samples were anaesthetized and preserved at the time (*t*) of capture. All *B* samples were kept without food for 3 h in a deck tank of sea water at ambient temperature. Three hours after capture (*t* + 3) these fish were anaesthetized and preserved, and a new catch was made and divided into samples *A* and *B*. At the end of the 24 h period this procedure gave eight pairs of samples the collection and pairing of which are summarized in Figure 1.

Analysis was carried out in the laboratory. The fish were measured and divided into 5 mm length groups. The stomach contents were removed from each fish, sorted into one of seven main food groups: *Lanice* tentacles; other polychaetes; harpacticoid copepods; mollusc siphons; amphipods; cumaceans, and 'others'. Each food group was combined with the same food group from other fish in the same length group from that

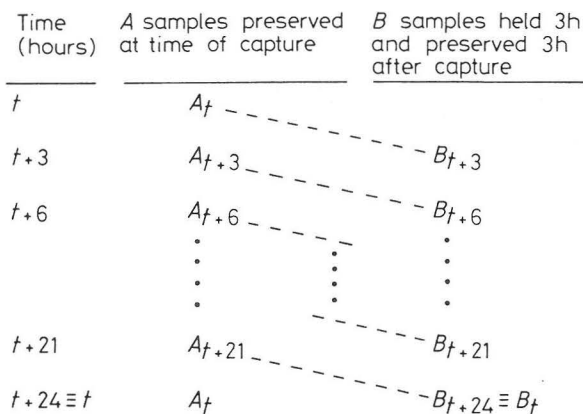


Figure 1. A summary of the sampling procedure followed to measure daily food intake. The broken lines link the samples taken from the same trawl haul, while the subscripts signify the time of preservation. It was assumed that sample A_t was equivalent to sample A_{t+24} , and sample B_{t+24} was equivalent to sample B_t .

sample. All fish were weighed wet and then the fish, and the stomach contents, were dried to constant weight at 60°C, and weighed to 0.02 mg. The mean weight of fish and the mean weight of food per 5 mm length group were calculated for each A and B sample. These weights of food, expressed as mg dry weight food/g fish whole dry weight, were used to estimate the daily food intake by 5 mm length groups.

When estimating the daily food intake, a number of assumptions were made (Lockwood, 1980 b) which are summarized here. It was assumed that: sample A_t was truly representative of the population at the time of capture and preservation, t ; the B sample caught at time t , but held without food for 3 h before being preserved as sample B_{t+3} , was representative of the population at time $t+3$, except that fish in the sample had only digested food, not fed; the difference in mean stomach contents between samples A_{t+x} and B_{t+x} equalled the average quantity of food eaten by each fish in the free population during the 3 h period prior to time $t+x$; when feeding ceased, $A_{t+x} - B_{t+x} = 0$.

When estimating the mean daily food intake for all fish in the population, it was found that this final assumption was not valid due to retarded digestion¹ (Lockwood, 1980 b), i.e. the mean stomach contents of sample B_{t+x} were greater than those of sample A_{t+x} resulting in a negative estimate of food ingested. These negative estimates were used to estimate the amount by which the observed daily food intake should be increased to account for retarded digestion (i.e. 8 × the mean of the negative estimates). Separate corrections were calculated for each 5 mm length group in summer and autumn.

The change in diet

The changes in diet with increase in size of fish, and by

months, were investigated by two methods. The first was by the percentage occurrence method (Hynes, 1950). Samples of 0-group plaice were taken along 5 standard transects from 2 to 12 m depth in Filey Bay during each month from May to October 1968 (Lockwood, 1974 b). From each month's sample 2 fish were taken from every 10 fish, or less, in each 5 mm length group. The stomach contents were removed and identified. The number of stomachs containing a particular food item were expressed as a percentage of the number of stomachs in the sample which contained food. The results were prepared by 10 mm length groups all months combined, and by months all length groups combined.

The second method of analysing the diet utilized the samples collected in 1969 for estimating the daily food intake. The change in relative importance of the seven major food groups from summer to autumn, expressed as a percentage of the total weight of food removed from the stomachs, has already been described (Lockwood, 1980 b). This change was examined further by expressing the mean weight of prey organisms as a percentage of the mean weight of the predator by 5 mm length groups.

Results

Fish length:weight relationships

The live weights of 0-group plaice were estimated from the measured lengths of preserved fish by the expression \ln live weight (mg) = $-5.03 + 3.10 \ln L$ (mm) (Lockwood and Daly, 1975). From these estimates, and the dry weight measurements taken during the preparation of samples for estimating daily food intake, it was found that whole body dry weight was 20.5 % of the live weight.

Estimation of daily food intake

A total of 128 A and B samples was collected. Four samples were unsuitable for use due to inadequate preservation; values were interpolated for these samples by taking the mean of the preceding and following sample in the series. From the 124 remaining samples, 38 estimates of daily food intake were made for fish in nine 5 mm length groups. The distribution of these length groups by season, and the number of fish from which each estimate is made are summarized in Table 1. As the 40 to 44 mm length group was common to both seasons, data for this length group are presented in detail in Table 2 to demonstrate the method of estimating daily food intake. The results for this length group are also shown in Figure 2 alongside the comparable data from the whole population analysis (Lockwood,

¹Throughout this paper digestion refers to gastric digestion, the passage of food through the stomach.

Table 1. The sampling dates in 1969, sample sizes, and length ranges used to estimate the daily food intake of 0-group plaice by 5 mm length groups.

Series	Date	Length group (mm)								
		< 25	25-29	30-34	35-39	40-44	45-49	50-54	55-59	≥ 60
a	19-20 Jul	89	230	244	138	171	0	-	-	-
b	30-31 Jul	0	110	192	228	0	100	-	-	-
c	24-25 Jul	117	174	224	151	58	0	-	-	-
d	26-27 Jul	96	146	207	166	89	0	-	-	-
e	26-27 Sep	-	-	-	-	149	184	154	152	0
f	30 Sep-1 Oct.	-	-	-	-	145	173	203	143	117
g	3-4 Oct	-	-	-	-	98	165	195	136	112
h	7-8 Oct	-	-	-	-	98	175	155	107	85

Table 2. Measured daily food intake from the stomach contents of paired samples of 0-group plaice taken at 3 h intervals. Mean A_t , mean dry weight of food in stomachs, mg food/g fish, at time of capture; mean B_t , mean dry weight of food in the stomach, mg food/g fish, 3 h after capture; $A_t - B_t$, dry weight of food eaten, mg food/g fish, in the 3 h period prior to death. (-), sample missing from series due to inadequate preservation. The numerical value for the mean stomach contents of missing samples is the arithmetic mean of preceding and following samples.

	Time of death GMT	Sample size A	A_t mean weight	Sample size B	B_t mean weight	$A_t - B_t$
Series a. Incomplete series of observations						
19-20 Jul						
Series b. Mean dry wt of fish 0.1468 g						
30-31 Jul	0845	10	5.23	11	0.25	4.98
	1145	11	11.65	11	6.55	5.10
	1445	7	7.08	12	4.77	2.31
	1745	9	11.79	16	1.76	10.03
	2045	12	19.49	10	3.40	16.09
	2345	7	22.72	15	14.31	8.41
	0245	11	6.88	6	10.75	-3.87
	0545	11	2.32	12	2.90	-0.58
Total		78		93		42.47
Series c. Mean dry wt of fish 0.1484 g						
24-25 Jul	0845	5	9.13	0	(4.20)	4.93
	1145	0	(22.10)	6	4.22	17.88
	1445	5	35.08	0	(21.99)	13.09
	1745	3	12.54	8	39.75	-27.21
	2045	4	34.66	3	3.74	30.92
	2345	5	19.30	2	33.54	-14.24
	0245	10	22.89	(-)	(18.86)	4.03
Total		34		24		37.77
Series d. Mean dry wt of fish 0.1537 g						
26-27 Jul	0750	2	4.85	(-)	(6.05)	-1.02
	1050	10	0.58	4	2.41	7.17
	1350	10	3.53	0	(4.74)	-1.21
	1650	8	19.22	6	7.08	12.14
	1950	7	28.50	6	10.38	18.12
	2250	4	25.61	10	15.71	9.90
	0150	6	12.05	0	(12.70)	-0.65
	0450	8	4.00	8	9.69	-5.69
Total		55		34		38.76

Cont'd

Table 2 cont'd

	Time of death GMT	Sample size A	A_t mean weight	Sample size B	B_t mean weight	$A_t - B_t$
Series e. Mean dry wt of fish 0.1659 g						
26-27 Sep	0715	7	3.89	7	1.10	2.79
	1015	7	9.60	11	4.71	4.89
	1315	7	8.11	6	10.66	-2.55
	1615	10	2.42	10	3.47	-1.05
	1915	12	0	4	0.13	-0.13
	2215	12	0	15	0	0
	0115	14	1.67	12	0	1.67
	0415	5	2.34	10	0.13	2.21
Total		74		75		7.83
Series f. Mean dry wt of fish 0.1626 g						
30 Sep-1 Oct	0915	10	0	6	0.70	-0.70
	1215	16	0	11	0	0
	1515	0	(0.27)	10	0.33	-0.06
	1815	9	0.53	13	0.29	0.24
	2115	11	0.61	10	0.12	0.49
	0015	5	0.17	7	1.17	-1.00
	0315	10	0.07	10	0	0.07
	0615	13	0.23	4	0	0.17
Total		74		71		-0.79
Series g. Mean dry wt of fish 0.1551 g						
3-4 Oct	0825	3	0.26	8	0	0.26
	1125	8	0.80	4	0.34	0.46
	1425	10	0.54	8	0.02	0.52
	1725	(-)	(0.60)	8	0.13	0.47
	2025	6	0.67	0	(0.08)	0.59
	2325	8	0.06	0	(0.04)	0.02
	0225	10	0.07	10	0	0.07
	0525	9	0.38	6	0.05	0.33
Total		54		44		2.72
Series h. Mean dry wt of fish 0.1456 g						
7-8 Oct	0915	14	0.31	10	1.28	-0.97
	1215	5	1.78	10	0.96	0.82
	1515	4	1.11	0	(2.38)	-1.27
	1815	5	7.06	2	3.79	3.27
	2115	8	13.58	3	1.49	12.09
	0015	6	4.00	3	6.37	-2.37
	0315	4	4.35	8	6.99	-2.49
	0615	8	2.87	8	3.13	-0.26
Total		54		44		8.82

1980 b). During July, both the feeding level and periodicity of the 40 to 44 mm length group were very similar to the levels and periodicity of all fish combined. In the autumn, this particular 5 mm length group appears to feed more during the night than does the population as a whole, but the feeding level was still similar.

The full set of 38 estimates of daily food intake by 5 mm length groups, including the 40-44 mm length group, are given in Table 3. The relationship between daily food intake and whole body dry weight is shown in Figure 3. Despite the previous assessment showing that the fish in July ate more food than the larger fish in the autumn, it is quite clear that in any given series the larger fish in the population ate more food than the

smaller fish in the population. In July the relationship between daily food intake and body weight was linear, but while larger fish continued to eat more than small fish in September-October, the exact form of the body size to food intake relationship is less certain.

The eight estimates of mean daily food intake (all lengths combined) made previously (Lockwood, 1980 b) are given in Table 4. From these estimates a single mean daily food intake and mean body weight were calculated for the summer (series a-d) and for the autumn (series e-h). In the summer the daily food intake was equivalent to 10 % whole body weight per day and in the autumn to 1.5 % whole body weight per day. These average estimates are represented by the

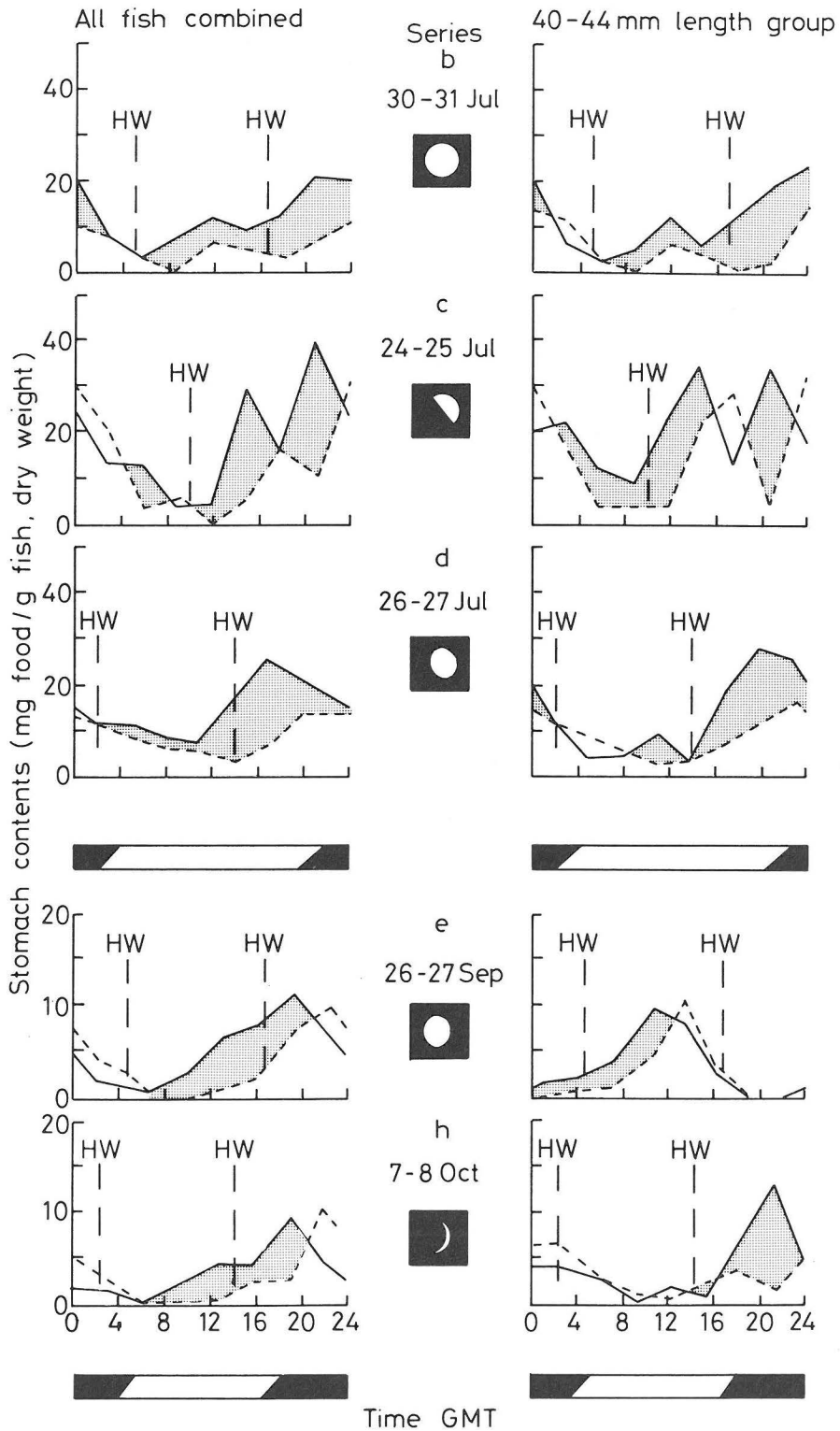


Figure 2. The daily feeding activity of 0-group plaice on five of eight occasions sampled. On the left the results from all fish combined (Lockwood, 1980 b), and on the right, the results for the 40 to 44 mm length group only. The solid line shows the mean stomach contents at the time of capture, the broken lines show the mean stomach contents 3 h after capture. The shaded area represents the period of feeding activity. The phase of the moon is shown for each sampling period and the hours of darkness by the day-night bars. The time of high water (HW) is also shown.

Table 3. Estimates of mean daily food intake per 0-group plaice by 5 mm length groups.

Series	Length group (mm)	Total sample size	Daily food intake			Mean dry weight of fish (g)	Estimated mean daily food intake per length group (mg dry weight)
			mg food/g fish (dry weights)		% whole body weight		
			measured	corrected			
a	< 25	89	2.92	77.45	8.84	0.0222	1.96
c	< 25	117	-44.17	41.36	4.14	0.0227	0.94
d	< 25	96	14.27	99.80	9.98	0.0252	2.52
a	25-29	230	-19.98	80.59	8.06	0.0403	3.25
b	25-29	110	49.87	110.48	11.05	0.0410	4.53
c	25-29	174	56.47	117.08	11.71	0.0420	4.92
d	25-29	146	61.94	122.55	12.26	0.0422	5.17
a	30-34	244	50.20	84.82	8.48	0.0648	5.50
b	30-34	192	64.81	99.43	9.94	0.0664	6.60
c	30-34	224	48.58	83.20	8.32	0.0657	5.47
d	30-34	207	63.83	98.45	9.84	0.0745	7.33
a	35-39	138	44.45	105.49	10.55	0.0978	10.32
b	35-39	228	57.15	118.19	11.82	0.1003	11.85
c	35-39	151	40.27	101.31	10.13	0.1009	10.22
d	35-39	166	65.27	126.04	12.60	0.1065	13.45
b	40-44	171	42.47	96.94	9.69	0.1468	14.23
c	40-44	58	37.77	92.24	9.22	0.1484	13.69
d	40-44	89	38.76	93.23	9.32	0.1537	14.33
b	45-49	100	42.33	102.33	10.23	0.2050	20.98
e	40-44	149	7.83	17.14	1.71	0.1659	2.84
f	40-44	145	-0.79	8.52	0.85	0.1626	1.39
g	40-44	98	2.72	12.03	1.20	0.1551	1.87
h	40-44	98	8.82	18.13	1.81	0.1456	2.64
e	45-49	184	4.65	14.81	1.48	0.2228	3.30
f	45-49	173	-0.12	10.04	1.00	0.2147	2.16
g	45-49	165	0.41	10.57	1.06	0.2123	2.24
h	45-49	175	2.16	12.32	1.23	0.2056	2.53
e	50-54	154	13.63	24.66	2.47	0.3132	7.72
f	50-54	203	-1.02	10.01	1.01	0.2940	2.94
g	50-54	195	-0.26	10.77	1.08	0.2839	3.06
h	50-54	155	-4.72	6.31	0.06	0.2781	1.75
e	55-59	152	7.64	10.18	1.02	0.3916	3.99
f	55-59	143	-2.14	21.40	2.14	0.3898	8.34
g	55-59	136	-1.19	22.35	2.24	0.3782	8.45
h	55-59	107	1.83	25.37	2.54	0.3705	9.40
f	≥ 60	117	-5.77	13.58	1.36	0.5684	7.85
g	≥ 60	112	-0.40	19.18	1.92	0.5454	10.46
h	≥ 60	85	17.34	36.92	3.69	0.5234	19.32

straight lines, drawn through the origin, shown in Figure 3. Linear regressions fitted to the summer and to the autumn data do not differ significantly from the lines drawn through the origin. From these observations it is concluded that the daily food intake of the 0-group plaice in a sample is directly proportional to body weight. This is a time-independent relationship. The time-dependent relationships resulting from an increase in mean size or seasonal change are less clear. The mean daily food intakes (mg food/fish) of the population in summer and autumn are shown (+) in Figure 3. These estimates show a decrease in food intake with increase in population mean size. This may be a function of

growth, or it may be a seasonal effect, resulting from changing availability of food.

Changes in diet

The results from the qualitative analysis of stomach contents from May to October 1968 are given in Tables 5 and 6. The changes in relative importance of certain major food items between May and October, and the changes with increase in size of fish, are shown in Figure 4. The tentacles of the sedentary polychaete worm *Lanice conchilega* (Pallas) formed a major part of the 0-group plaice diet at the time of settlement (May to

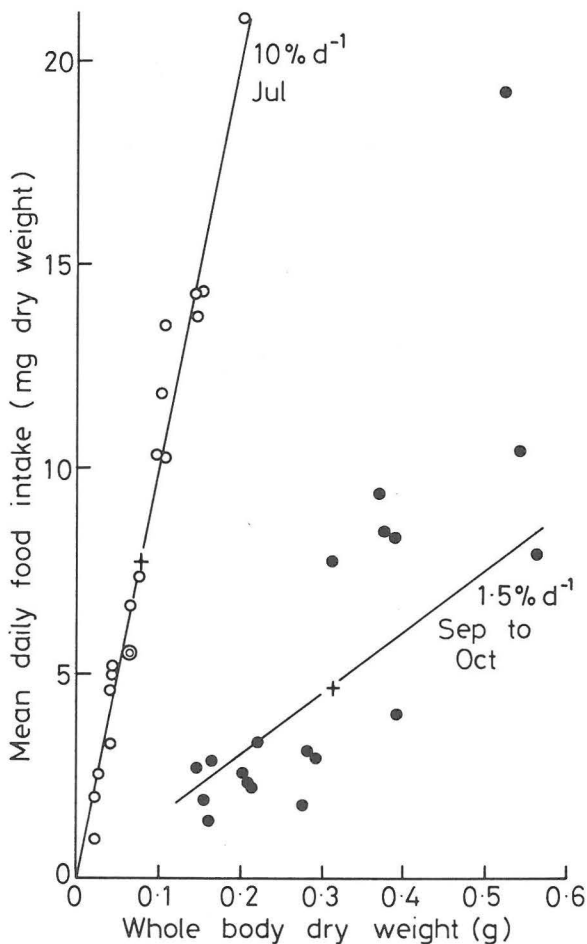


Figure 3. The daily food intake of 0-group plaice by 5 mm length groups. Samples taken in July are shown by open circles, the closed circles show the samples taken in September–October. The straight lines are drawn through the population mean estimate of daily food intake (+) and the origin. These lines do not differ significantly from linear regressions fitted to the observations.

June, when they are 10 to 30 mm). The importance of this item in the diet then decreased as the fish increased in size. Similarly, harpacticoid copepods formed part of the diet of small 0-group plaice, but as the fish increased in size they turned their attention to larger errant prey organisms, notably amphipods and cumaceans. At first sight this change appears to follow the changing seasons, but there is a discernible pattern in the size of the prey in relation to the size of the predator.

The mean dry weight of major food items are tabulated against the mean dry weight of 0-group plaice by 5 mm length groups in Table 7. The size of the prey organisms is expressed as a percentage of the predators' weight. As the prey organisms are ranked according to size there is a diagonal band of values running across the matrix, between the bold lines, where the relative size of the prey falls between 0.5 and 10 % of the 0-group

plaice body weight. If this band of observations is compared with the changes in diet illustrated in Figure 4 there appears to be a correlation between diet and the prey:predator ratios within this band. The implication is that 0-group plaice will not attack a prey organism larger than 10 % of its own body weight. Conversely the importance of a prey organism in the diet decreases rapidly once its relative size falls below 0.5–1 % of the plaice body weight.

Samples taken between May and the end of July indicate that as many as 20 % of the 0-group plaice population may not be feeding. This is shown in Figure 4 by the occurrence of fish with both gut and stomach empty. The diurnal periodicity shown in Figure 2 can account for the observation of either empty stomachs, or of empty guts, which are seen in most months and length groups, but it cannot account for both empty stomach and gut together. The diurnal period without feeding (generally the hours of darkness) is not long enough to enable all food to pass right through the gut and leave a completely empty system. Thus, the late larval stages and small 0-group fish, which were found without food, probably had not fed for at least 24 h.

Discussion

Sample size and feeding periodicity

The initial analysis of daily feeding periodicity and estimates of daily food intake (Lockwood, 1980 b) derived some statistical stability, and hence validity, from the large sample size. Nominally this was 50 fish per *A* and *B* sample, a total of 800 fish per series. By breaking these samples down into 5 mm length groups this advantage might have been lost, and the validity of the method undermined. Of the 38 separate estimates of daily food intake given in Table 3, 31 are based on the analysis of 100 fish or more. Of the 7 which are based on fewer than 100 fish, 4 are in the 40 to 44 mm length group which is analysed in detail, and compared with the population mean results. The weighted mean feeding rate of this length group in July, 9.2 % whole body weight per day, is very close to the population mean of 9.9 % whole body weight per day. In the autumn the feeding rates were even closer, 1.4 % whole body weight per day for the 40 to 44 mm length group and 1.5 % whole body weight per day for the population. Similarly, the feeding periodicity of the 40 to 44 mm length group is much the same as for the population as a whole (Fig. 2). Feeding was most intense during the hours of daylight, but did not always cease at sunset, particularly if the moon was full. The greatest difference between the results for the 40 to 44 mm length group and for the whole population is seen in series h. While on average, the population fed through the hours of daylight, the 40 to 44 mm length group appears to have fed only at night. However, the estimated daily feeding rate in this series (1.8 % whole body weight, Table 3) was very

Table 4. Estimates of the mean daily food intake per 0-group plaice, Filey Bay, 1969. The measured daily food intake is corrected for retarded digestion by the addition of a value equal to the mean of the negative estimates of 3 h food intake. The values for these corrections are: July series 533.77 mg food/g fish; September–October series 11.24 mg food/g fish (from Lockwood, 1980 b). The estimates made by Bregnballe (1961) in Kysing Fjord, Denmark are also given for comparison.

Series	Total sample size <i>N</i>	Measured daily food intake (mg food/g fish)	Corrected daily food intake (mg food/g fish)	% whole body weight	Mean dry weight of fish (g)	Estimated mean daily food intake (mg dry weight)
Jul						
a	736	27.66	81.43	8.1	0.0617	5.00
b	799	50.78	104.55	10.4	0.0997	10.42
c	727	52.01	105.78	10.6	0.0713	7.54
d	736	51.81	105.58	10.6	0.0796	8.44
Total	2 998	Population mean		9.9	0.0785	7.80
Sep/Oct						
e	742	10.85	22.09	2.2	0.3350	7.40
f	790	-0.63	10.31	1.0	0.3245	3.39
g	734	-0.37	10.87	1.1	0.3094	3.36
h	650	3.83	15.07	1.5	0.2869	4.32
Total	2 916	Population mean		1.5	0.3150	4.57
May/June (Bregnballe, 1961)						
1	—	—	—	53	0.0257	13.6
2	—	—	—	54	0.0291	15.7
3	—	—	—	53	0.0313	16.6
4	—	—	—	56	0.0425	23.8

Table 5. The diet of 0-group plaice in Filey Bay. Analysis of stomach contents by percentage occurrence (Hynes, 1950) from May to October 1968 and December 1967.

	May		Jun		Jul		Aug		Sep		Oct		Dec 1967	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
No. of fish examined	31		98		53		55		47		55		66	
Stomach only empty	2	6.4	18	18.4	16	30.2	2	3.6	2	4.2	5	9.1	60	90.0
Gut only empty	1	3.2	9	9.2	13	24.5	0	—	0	—	0	—	60	90.0
Stomach and gut empty	1	3.2	9	9.2	9	17.0	0	—	0	—	0	—	60	90.0
Stomachs holding food	29		80		37		53		45		50		6	
<i>Lanice</i> tentacles	28	96.6	68	85.0	18	48.6	37	69.8	11	24.4	21	42.0	2	33.3
Polychaetes	0	—	0	—	3	8.1	9	17.0	13	28.9	10	20.0	6	100.0
Harpacticoid copepods	1	3.4	5	6.3	19	51.4	8	15.2	7	15.6	5	10.0	3	50.0
Mollusc siphons	0	—	0	—	8	21.6	5	9.4	18	40.0	8	16.0	0	—
Amphipods	0	—	1	1.3	0	—	16	30.2	23	51.1	17	34.0	1	16.7
Cumaceans	0	—	0	—	0	—	15	28.3	1	2.2	12	24.0	2	33.3
Other	0	—	2	2.5	2	5.4	2	3.8	2	4.4	4	8.0	0	—

Daily food intake in relation to size of fish

close to the population mean feeding rate (1.5 % whole body weight; Lockwood, 1980 b) in the same series. The general view of the data given in Table 3 and shown in Figure 2 suggests that these reduced sample sizes do not invalidate the method, even for the 40 to 44 mm length group, which utilized fewer than the average number of fish.

As noted earlier, the relation between body size and daily food intake was clear, and simple, in the July series. The large fish ate more each day than the smaller fish, and there was very little deviation from a straight line (Fig. 3). This low variability is probably the result of sampling during a period of fine sea conditions (Lockwood, 1980 b). The autumn series of samples were taken during a period which coincided with equi-

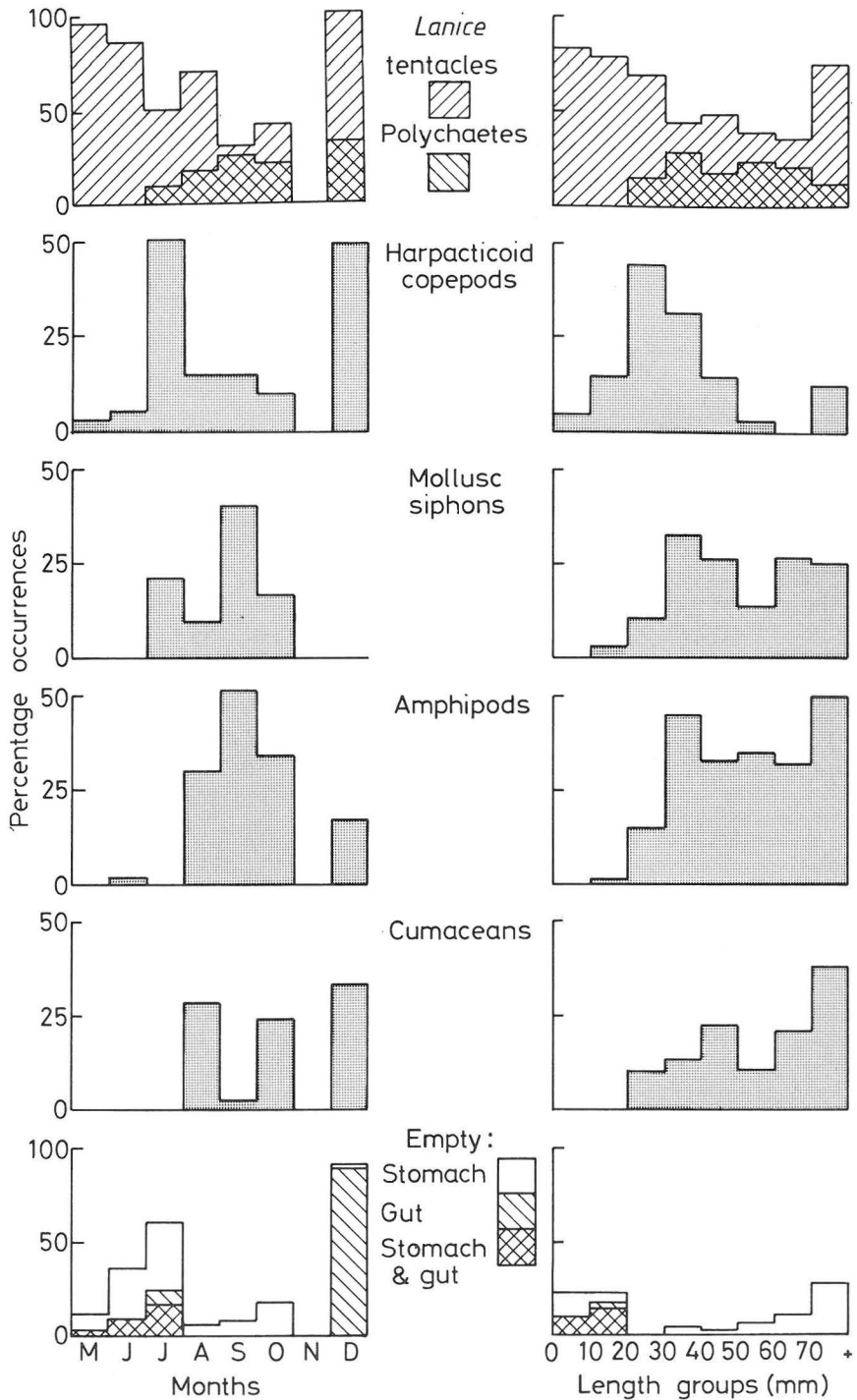


Figure 4. The diet of 0-group plaice. The change in relative importance of major food groups by months on the left, and by 5 mm length groups on the right.

nocturnal gales and extreme tidal ranges. As plaice are principally visual feeders (de Groot, 1971) these disturbed environmental conditions probably contributed to the greater variability in the estimates of daily food

intake compared with the summer series. Nevertheless, it is still true to say that in the autumn, the larger fish ate more than the smaller fish. This observation on the relation between daily food intake and size of fish is a

Table 6. The diet of 0-group plaice in Filey Bay. Analysis of stomach contents by percentage occurrence for 10 mm length groups from May to October 1968.

	Total length (mm)															
	< 11		11-20		21-30		31-40		41-50		51-60		61-70		> 70	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
No. of fish examined	23		141		20		32		52		39		21		11	
Stomach empty	5	21.7	31	22.0	0	-	1	3.1	1	1.9	2	5.1	2	9.5	3	27.3
Gut empty	2	8.7	21	14.9	0	-	0	-	0	-	0	-	0	-	0	-
Stomach and gut empty	2	8.7	17	12.1	0	-	0	-	0	-	0	-	0	-	0	-
Stomachs holding food	18		110		20		31		51		37		19		8	
<i>Lanice</i> tentacles	15	83.3	87	79.1	14	70.0	14	45.2	25	49.0	15	40.5	7	36.8	6	75.0
Polychaetes	0	-	-	-	3	15.0	9	29.0	9	17.7	9	24.3	4	21.1	1	12.5
Harpacticoid copepods	1	5.6	16	14.6	9	45.0	10	32.2	8	15.7	1	2.7	0	-	1	12.5
Mollusc siphons	0	-	2	1.8	2	10.0	10	32.2	13	25.5	5	13.5	5	26.3	2	25.0
Amphipods	0	-	1	0.9	3	15.0	14	45.2	17	33.3	13	35.1	6	31.6	4	50.0
Cumaceans	0	-	0	-	2	10.0	4	12.9	11	21.6	4	10.8	4	21.1	3	37.5
Other	5	4.5	0	-	0	-	1	3.2	1	2.0	1	2.7	0	-	1	12.5

truism, which should be received without surprise. However, there are aspects of these data which may be unexpected. On the basis of field work and laboratory experiments with 0-group turbot (*Scophthalmus maximus* L.), Jones (1973) states (p. 379): ". . . in absolute terms larger fish eat more than smaller fish, in relative terms (i.e. food as a percentage of body weight) the reverse is true". Bromley (1974) found that the same was true for 0-group sole (*Solea solea* L.) in the laboratory. Jones's first observation is in accord with the data given here, but not the second. The daily food intake, as a percentage of body weight, was constant over the size ranges studied in the summer, and more or less so in the autumn. If the relative daily food intake (as a percentage of body weight) is to decrease with increase in size of fish, the regression lines drawn through the estimates

in Figure 3 need to have a positive intercept on the y-axis, or to describe an asymptotic curve. In neither summer nor autumn series of data is there a hint of an asymptotic curve, and regression lines fitted to the data do not differ significantly from the lines drawn through the origin.

A similar series of feeding estimates for recently metamorphosed plaice, taken in Kysing Fjord, Denmark, was made by Bregnballe (1961). He gave his results in wet weights, but for comparability with the results described above they may be converted to dry weight by the factor 0.205. Not only is this the conversion ratio for 0-group plaice given above, but also it is the average conversion ratio for nine species of annelids and four species of epibenthic crustaceans similar to those eaten by 0-group plaice (Brawn, Peer, and Bentley, 1968).

Table 7. The change in relative size of major prey organisms in the diet of 0-group plaice. Prey size is expressed as a percentage of plaice whole body dry weight. Prey organisms most frequently occur in the plaice diet when their relative size falls between the two bold lines, > 0.5 %, < 10 %.

Prey	Mean dry weight (mg)	Predator										
		Length groups (mm)										
		10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	61-64
		3	9	19	37	62	97	144	204	280	372	482
Harpacticoid copepods	0.1	3.3	1.1	0.5	0.3	0.2	0.1	0.1	0.1	+	+	+
<i>Lanice</i> tentacles	0.2	6.6	2.2	1.0	0.5	0.3	0.2	0.1	0.1	0.1	0.1	+
Mollusc siphons	1.0	33.3	11.1	5.3	2.7	1.6	1.0	0.7	0.5	0.4	0.3	0.2
Cumaceans	2.7	89.7	29.9	14.2	7.3	4.3	2.8	1.9	1.3	1.0	0.7	0.6
Molluscs	3.5	117.0	39.0	18.5	9.5	5.7	3.6	2.4	1.7	1.2	0.9	0.7
Sedentary polychaetes	3.7	123.3	41.1	19.5	10.0	6.0	3.8	2.6	1.8	1.3	1.0	0.8
Errant polychaetes	6.1	204.7	68.2	32.3	16.6	9.9	6.3	4.3	3.0	2.2	1.6	1.3
Amphipods	7.3	244.0	81.3	38.5	19.8	11.8	7.6	5.1	3.6	2.6	2.0	1.5

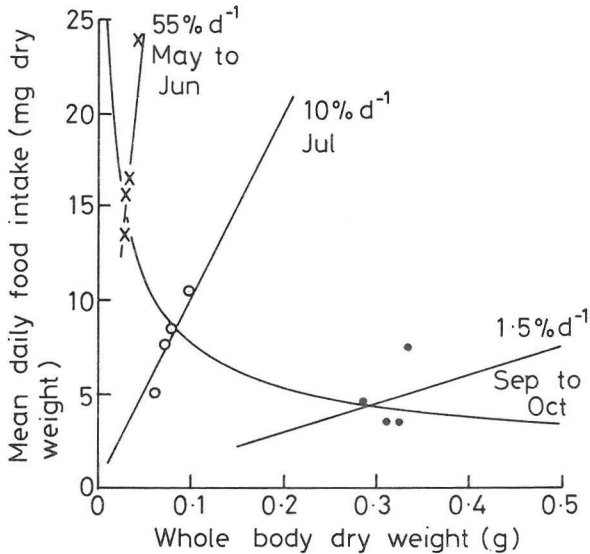


Figure 5. The estimated daily food intake of 0-group plaice with increase in mean size of the population. The curve is fitted to the 12 populations' mean estimates of daily food intake. Four are from Kysing Fjord, May 1957 (x) (Bregnballe, 1961), 8 are from Filey Bay in July (o), and September–October (•) 1969. The straight lines cover the size range of fish sampled, and show the relationship between food intake and body size at the time of sampling (Fig. 3).

The dry weight equivalents of Bregnballe's estimates are given in Table 4 and are shown as daily food intake against body weight in Figure 5. Here too the larger fish eat more than the smaller fish in absolute terms (mg food per fish), but the line drawn from the origin through the mean of the four population estimates suggests that the relative food intake is constant at about 55% of the body weight per day.

From the results described above, and with the support of Bregnballe's data, it is concluded that, over the limited size range present in a sample of 0-group plaice, the large fish eat more each day than small fish, but as a percentage of body weight the daily food intake is constant.

Daily food intake in relation to growth and season

Between July and September–October, the mean dry weight of fish in the samples increased from about 0.1 g to about 0.3 g (Fig. 3). On the basis of laboratory experiments we should expect the daily food intake to increase with increase in mean weight of fish (Jones, 1973; Bromley, 1974), but it has already been shown that the mean daily food intake fell (Lockwood, 1980 b). A comparison between the smallest fish in the population in July (about 0.02 g dry weight) and the smallest fish in September–October (about 0.15 g dry weight) shows (Fig. 3) that this group maintain, or possibly increase, their absolute food intake (mg food per fish).

In contrast, a comparison between the largest fish in the population shows that their absolute daily food intake was approximately halved between summer and autumn, but this decrease is not so great as when comparing fish of the same size. Fish which were 40 to 44 mm in July consumed about 14 mg food per day in July but only about 2 mg food per day in September–October (Table 3). These observations are so at variance with what laboratory data predict that some explanation must be sought which is not simply related to increase in mean size.

It is well established in the laboratory that, within their normal environmental temperature range, fish will eat more, both absolutely and relatively, at higher temperatures (Brett, 1979). The possibility of temperature influencing these results has already been discounted as the temperature in July was less than 1°C different from what it was in September–October (Lockwood, 1980 b). Also, Bregnballe (1961) recorded a wider temperature range in Kysing Fjord (13°–17°C) than was recorded at Filey Bay (12°–13°C) but could not demonstrate any temperature effect on food consumption. If the decrease in food consumption is not a function of temperature, it has been suggested (above and Lockwood, 1980 b) that the disturbed environmental condition in the autumn may have inhibited feeding sufficiently to restrict the daily food intake. A comparison between Bregnballe's results, which were collected in fine, settled conditions, with the July results, when conditions were also fine, does not support this simple environmental hypothesis. Nor can the change be accounted for simply by a reduction in the abundance of prey. The mean standing stock of benthic prey organisms in Filey Bay, June to December 1968, was more or less constant (Lockwood, 1972).

To analyse these changes further the mean population estimates of daily food intake are compared with those made by Bregnballe (1961). These data are summarized in Table 4 and shown in Figure 5. The straight lines drawn in Figure 5 extend over the total size range of fish sampled in May (Bregnballe, 1961), July, and September–October, with their slopes equivalent to the relative feeding rates on each occasion (see above and Fig. 3). Although environmental conditions were not dissimilar, there is a fall in both absolute and relative feeding rates between Bregnballe's samples of metamorphosing plaice, and the July samples from Filey Bay. This comparison calls into question the idea that the decreasing daily food intake is a response to deteriorating environmental conditions and raises the possibility once more that the change is a function of increase in mean size. The distribution of the 12 populations' mean feeding estimates shown in Figure 5 suggests that the change in daily food intake with growth follows some form of negative curve. Because Bregnballe's methods were not identical with those used at Filey Bay his results are not strictly comparable, and therefore no firm conclusions may be reached about the

shape of this curve. The curve drawn in Figure 5 is a power curve of the form:

$$\text{Daily food intake (mg dry weight)} = 89.93 \bar{w}^{-0.53}$$

where \bar{w} is the mean dry weight (mg) per fish.

It is not suggested that this is the definitive relationship between daily food intake and growth; the curve is fitted just to illustrate the time-dependent relationship, compared with the time-independent relationships illustrated by the straight lines.

Change in diet

Changing diet and prey size are factors which are not normally incorporated in laboratory experiments, and this may be one of the reasons why laboratory results are not always in accord with field observations. The results presented here, and those of other similar studies (Bregnballe, 1961; Macer, 1967; Edwards and Steele, 1968; Thijssen, Lever, and Lever, 1974) show that 0-group plaice have a very mixed diet. This may vary from area to area, and even from year to year (Macer, 1967), but certain key features are common to all areas. In Filey Bay, tentacles of the sedentary polychaete *Lanice conchilega* were the dominant prey organism in the stomachs at the time of settlement. Polychaete tentacles were also dominant in Red Wharf Bay (Macer, 1967), but small whole polychaetes were important in Kysing Fjord (Bregnballe, 1961) and the Wadden Sea (Thijssen et al., 1974). In Firemore Bay the siphons of bivalve molluscs were the dominant food item at this stage (Edwards and Steele, 1968). While these food items differ in detail, they are all similar in that they are small, soft, abundant, and presumably, easily grazed. Later in the year the similarity in diet between nursery grounds increased as cumaceans, amphipods, and mysids became more dominant components in the diet. This change from a basically grazing diet, to one where larger, more mobile prey are hunted, may be an enforced change resulting from the fish grazing the smaller organisms below an acceptable minimum density. While it is difficult to be certain, benthic studies by McIntyre and Eleftheriou (1968), and Edwards, Finlayson, and Steele (1969) suggest that this is not the case, although it could be the cause of changes in initial diet between years (Steele et al., 1970). There are, however, reasons to believe that the change in diet is simply a function of the fishes' increase in mean size.

Allen (1935) described how the prey organisms in the diet of perch increased in size as the fish increased in size thereby enabling the fish to take their daily ration in fewer, larger portions. This is apparently what the 0-group plaice do too. There appears to be an optimal relative size for prey organisms between 0.5 and 10 % of the fishes' body weight. Presumably if the prey is larger than 10 % of the size of the fish, the fish will experience difficulties in handling the prey, and thus a

high attack failure rate. If the relative size falls below 0.5 to 1 % the fish will need to spend so much time searching and grazing that the energy demand may become too high. Thus diet changes to keep the cost of feeding (time and energy) within acceptable limits. This strategy is not peculiar to the 0-group plaice. Last (1978 a, b) has shown the same form of succession in the diets of gadoid and pleuronectid larvae, including plaice larvae.

As well as describing a similar increase in prey size as the predator grows, Allen (1935) pointed out that as food is taken in fewer, larger portions the occurrence of empty stomachs will increase. As noted already, the occurrence of empty stomachs in 0-group plaice increased toward the end of the year, and they were observed most frequently in the largest fish (Fig. 4). However, the change in diet cannot offer a satisfactory explanation as to why there was such a high occurrence of fish with both stomach and gut empty during the period May–July, in addition to those with only stomach or gut empty. It may be an observation which is peculiar to flatfish, and associated with metamorphosis. Examination of the results in Figure 4 shows that there is a peak in this occurrence in July, which is at about, or shortly after, the time of peak recruitment to the nursery (Lockwood, 1974 b, 1980 a). The peak occurrence also coincides with fish which are less than 20 mm long. At this length they are not true 0-groups but stage IV larvae (nomenclature of Ryland, 1966). At stage III the larvae have normal teleost eye configuration, i.e. bilateral symmetry, but during stage IV the left eye migrates to the right side of the head, and the skull undergoes torsion in a comparatively short period (less than one week). At metamorphosis Riley (1966) recorded a fall in feeding rate from about 250 *Artemia* nauplii per day for stage III larvae to 50 nauplii per day for stage IV larvae. The higher rate was restored very quickly once metamorphosis was completed (stage V). These laboratory observations parallel the field observations shown in Figure 4. Either the fish cease to feed, i.e. the attack rate falls to zero, because the major morphological reorganization inhibits their appetite, or the fish continue to feed, i.e. the attack rate is constant or increases, but due to the rapidly changing eye–mouth configuration the fish fail to capture the prey they attack. Unfortunately neither Riley (1966), nor Wyatt (1972) give information on attack rates. The occurrence of completely empty alimentary systems in these fish indicates that the phase lasts for at least 1 to 2 days (Riley, 1966). A comparatively prolonged period as this for such a small animal may increase the probability of capture due to falling energy reserves, but it is not in real danger of starvation as Wyatt (1972) found that plaice larvae can survive 25 days without food, and will resume feeding after at least 7 days without food.

As is often the case when analysing the results from field work it is difficult to come to very firm conclusions. There are many variables which are beyond the control

of the observer, or which cannot be monitored for logistical reasons. From the results described here it appears that the diet of 0-group plaice may change in response to the fishes' increase in size, and will probably continue to do so until maturity. It is also apparent that in any particular sampling period the daily food intake of the larger fish in the population was greater than that of the small fish, but in relative terms (percentage body weight) the feeding rate was constant. As the mean size of the population increased the relative feeding rate decreased, much as is expected, but the absolute feeding level fell also. The inclusion of data from another area, and the knowledge that 0-group plaice cease to feed in winter, suggest that this decrease was a seasonal effect. It may be a response to decreasing day length, e.g. insufficient time to catch more food. The possibility that the reduced feeding level is the consequence of reduced prey abundance is discounted, as there is also a large 0-group dab (*Limanda limanda* L.) population in Filey Bay, which is known to feed on similar organisms throughout the winter (Arntz, 1971).

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