

Food and feeding ecology of five gadoid larvae in the northern North Sea

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The larval diets of five gadoids in the northern North Sea in May in both 1978 and 1979 are described and compared. Cod, Norway pout, saithe, and whiting larvae consumed similar types of prey and showed a general tendency to select increasingly larger prey with increasing body size. The haddock larvae exploited a wider range of prey types, and at comparable lengths they consumed smaller and slower moving organisms than did the other gadoid larvae. The diets of sandeels and long rough dab which were abundant in the area were also examined. The species-specific selectivity patterns with respect to size and mobility of prey fell into two categories: those dictated by the basic body morphology, and those determined by behavioural factors, which were intimately linked to adult behavioural patterns. Competition for food was potentially possible between late larvae, but it could not be identified as a factor causing shifts in dietary characteristics.

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Introduction

A density-dependent response to the utilization of food resources seems to be the primary stabilizing mechanism in fish populations, and this mechanism may operate at any stage of the life history (Jones, 1989; Rothschild *et al.*, 1989). Because larval mortality is an important component of recruitment variability, it is often assumed that density-dependent larval mortality plays an important role in the process of natural control, and that competition for food might be the main source of density-dependence (Shepherd and Cushing, 1980).

However, it has been difficult so far to test the larval competition hypothesis by direct measurements of food availability in relation to the density of larvae. This is partly due to the fact that a variety of endogenous or exogenous factors intervene in the process of prey selectivity, and partly because zooplankton cannot yet be sampled in a way that is properly representative of the amount of food which falls to the share of larvae of different species or sizes.

In a previous paper (Economou, 1987) I described the ecology of survival of the gadoid larvae in the northern North Sea and argued that the limits on survival were set primarily by prey density and prey size, and thus by the amount of food within the searching volume of the larvae. Bigger larvae appeared to experience greater foraging difficulties than smaller ones

because, due to the scarcity of large prey during the initial phase of the production cycle, their wider searching volumes alone did not sufficiently compensate for the higher food requirements. In this paper, data on the food and the feeding ecology of the gadoid larvae are presented, and ontogenetic changes in the species diets and the interspecific feeding similarities and differences are examined in order to determine the factors which affect prey selectivity and possibly to assess competitive interactions.

The species investigated are: Norway pout (*Trisopterus esmarkii*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), cod (*Gadus morhua*), and saithe (*Pollachius virens*). The food of two other larval species which were abundant in the area – sandeels (*Ammodytes marinus*) and long rough dab (*Hippoglossoides platessoides*) – has also been examined.

Material and methods

The sampling techniques and full details of the procedures followed in the field have been given elsewhere (Economou, 1987). Briefly, the surveys were carried out east of the Shetland Islands area in May 1978 and May 1979 on FRVs “Scotia” and “Clupea” of the Marine Laboratory (Aberdeen). Routine sampling took place

with the HSLE net, a modified version of the GULF III series of high-speed plankton samplers, fitted with nets of 0.25 mm (for sampling fish larvae) and 0.068 mm (for sampling zooplankton) mesh sizes. Supplementary sampling took place (non-quantitatively) with conical tow-nets, neuston nets, and a midwater trawl in order to capture sufficient late larvae for gut content analysis.

The fish larvae were extracted from the samples, identified to species, counted, and measured. The alimentary canal of the gadoid larvae was removed, the anterior part (from the oesophagus to the first point of inflection of the intestine) was opened, and the content was examined under a dissecting microscope. This part of the alimentary canal includes the stomach, which starts to differentiate in the smallest larvae from the lowest part of the oesophagus. With the growth of larvae the stomach becomes larger, but a real constriction separating it from the intestine does not appear until a size of about 15 mm is reached.

The number and kind of prey items in the guts were recorded. Because of the indigestibility of the crustacean shells, the size of most particles could easily be measured (cephalothorax length in copepods, carapace length in euphausiids, and maximum length in the other organisms), and using the zooplankton length to dry-weight relationships (Economou, 1987), the weight of the particles was reconstructed. The biomass estimates thus obtained represent the original weight of food at the time of ingestion and not the true weight at the time of sampling.

The similarity of the diet between species and between different size groups of larvae was examined using Morisita's (1959) index of interspecific association between planktonic communities, as modified by Obrebski and Sibert (1976). In applying this ecological approach to the study of the larval diets, fish larvae are treated as selective samplers and their stomach contents as samples. The index is $2\sum x_i y_i / \sum x_i^2 + \sum y_i^2$, where x_i and y_i are the proportions of the i th food item in larval species x and y respectively.

The index takes values between 0, when there are no food items in common, and 1, when all food items are common in the species under comparison and occur in the same proportions.

The feeding electivity of the gadoid larvae was studied by comparing the relative amounts of two species consumed with their relative abundance in the environment. An index suggested by Cock (1978) as the most suitable for studying electivity was used:

$$E = \frac{Ne/Ne'}{N/N'}$$

where: Ne = number of prey items I eaten; Ne' = number of prey items II eaten; N = number of prey items I in the environment; N' = number of prey items II in the environment.

This index provides better comparison of the electivity values obtained from different samples or localities than the most frequently used Ivlev's index of electivity, which is defined as the relative difference of the proportions of a prey item in the guts (r) and in the environment (p), $r - p/r + p$, and the main drawbacks of which have been stressed by Cock (1978), Jacobs (1974), and Strauss (1979).

In Cock's index, percentages rather than absolute values were used, and extra prey types were incorporated in the prey type II category. Preference is more strongly weighted than avoidance of a prey type, because the scale ranges from 0 (complete avoidance) to $+\infty$ (highest preference) and has its mid-value at +1 (fully random feeding). However, symmetrical scales for positive and negative preference can be obtained by taking the logarithm of the index and adding 0.01 to obtain a value when $E = 0$.

Results

The general composition of the diet

The numbers of larvae analysed for gut contents are shown in Table 1. The occurrence by number (N) and weight (W) of the main prey organisms is illustrated as cumulative percentages in relation to larval size in Figures 1 and 2. Frequency of occurrence (values F), calculated from the number of larvae which contained a particular organism out of the total number of larvae which contained food, are given in Table 2. (Tables presenting a detailed description of the larval gadoid species diets are available from ICES (Copenhagen) on request.)

Copepods and their developmental stages predominated in the diets of the gadoid larvae. The smallest larvae of all species fed principally on copepod nauplii and also took *Calanus finmarchicus* eggs. As the larvae grew, their feeding spectrum expanded and the importance of nauplii fell rapidly. Copepodites and the small copepod *Oithona similis* initially, and the bigger copepods *Pseudocalanus elongatus*, *Acartia clausii*, and *Temora longicornis* later, contributed significantly to the diet of medium-sized larvae. Cladocerans were of some importance only for cod and haddock larvae. *C. finmarchicus* gradually replaced all other prey organisms and it comprised the bulk of food of the largest larvae of all species, except haddock.

The fairly rapid change of the diet with larval size makes comparisons between species valid only among larvae of similar sizes. However, interspecific feeding differences are evident, although they are not as strong as the between sizes of larvae differences. Norway pout, cod, saithe, and whiting exploited the same components of the total food resource, but at comparable lengths they took different proportions of each prey type. Norway pout consumed more *P. elongatus*, while cod and

Table 1. Numbers of larvae analysed for gut contents.

Size groups (mm)	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	≥30	
1978 cruise																													
Norway pout		4	14	39	158	263	174	143	98	72	50	41	23	12	6	2	1	1											
Haddock		17	28	45	171	137	69	44	29	16	8	7	5	3	1		1				1								
Cod		2	11	17	35	25	19	16	5	2	1																		
Saithe				3	24	60	42	46	40	29	28	20	17	24	20	13	11	9	7	12	6	5	3	2	1	2	1	1	
Sandeels										9		42	46	49			48		50		42	21			15				25
1979 cruise																													
Norway pout	1	13	16	21	213	310	263	206	154	107	84	64	40	28	14	8	8	1		1									
Haddock	2	5	11	30	111	108	90	95	78	54	35	17	7	10	8	2	1		1	1									
Whiting	16	77	94	114	139	100	44	25	10	3	1																		
Cod			1	8	12	10	9	10	5	6	5	5	6	2															
Saithe				2	9	21	28	29	25	40	39	33	28	33	20	15	11	7	6	7	6	2	2		1	1			
Long rough dab						9		23	30			29		13		11		7		6		2	2						

Table 2. Percentage of larvae containing individual prey items (%F).

Fish species	Norway pout			Haddock			Whiting		Cod			Saithe			Sandeels		
	7-10	11-14	15-18	7-10	11-14	15-18	3-6	7-10	7-10	11-14	15-18	19-22	11-14	15-18	19-22	23-26	
1978 cruise																	
<i>Calanus</i> eggs	14.1	1.8		29.1	10.4				18.2				31.0	5.4	1.2		
Calanoid nauplii	60.3	20.8		72.1	73.1				75.5				56.8	10.5	3.3	1.9	0.0
<i>Oithona</i> sp.	35.7	20.6		24.3	79.4				38.6				48.7	37.5	7.4	6.9	0.0
<i>Pseudocalanus</i>																	
<i>elongatus</i>	53.7	55.8		39.6	65.5				36.1				17.1	18.2	3.3	0.0	2.4
<i>Acartia clausii</i>	2.7	5.0		0.5	0.0				47.5				41.8	40.8	28.9	23.0	0.0
<i>Calanus finmarchicus</i>	12.1	48.2		4.4	20.9				24.1				27.3	84.2	97.9	95.0	0.0
Fish larvae	0.0	0.0		4.9	34.8				0.0				0.0	5.3	6.3	0.0	0.0
<i>Evadne</i> sp.	0.0	0.7		7.9	27.1				3.6				1.8	2.3	4.8	1.9	7.4
1979 cruise																	
<i>Calanus</i> eggs	10.8	0.7		36.1	14.0				11.3				3.6	0.0	0.0	0.0	
Calanoid nauplii	80.3	62.1		51.6	94.6				100.0				85.3	52.6	34.4	6.8	
<i>Oithona</i> sp.	37.8	49.3		54.9	29.7				40.5				62.7	69.1	57.7	38.2	
<i>Pseudocalanus</i>																	
<i>elongatus</i>	32.9	37.5		42.3	12.3				8.4				14.2	9.0	10.3	8.3	6.5
<i>Acartia clausii</i>	0.5	1.3		0.7	1.3				5.6				37.5	2.3	21.2	13.7	21.0
<i>Calanus finmarchicus</i>	27.7	67.7		96.8	9.5				45.5				90.0	36.0	84.4	96.5	94.2
Fish larvae	0.0	0.3		0.0	3.0				0.0				9.2	1.0	1.4	1.3	0.0
<i>Evadne</i> sp.	0.0	0.0		0.0	13.8				3.1				26.7	1.3	1.1	1.7	0.0

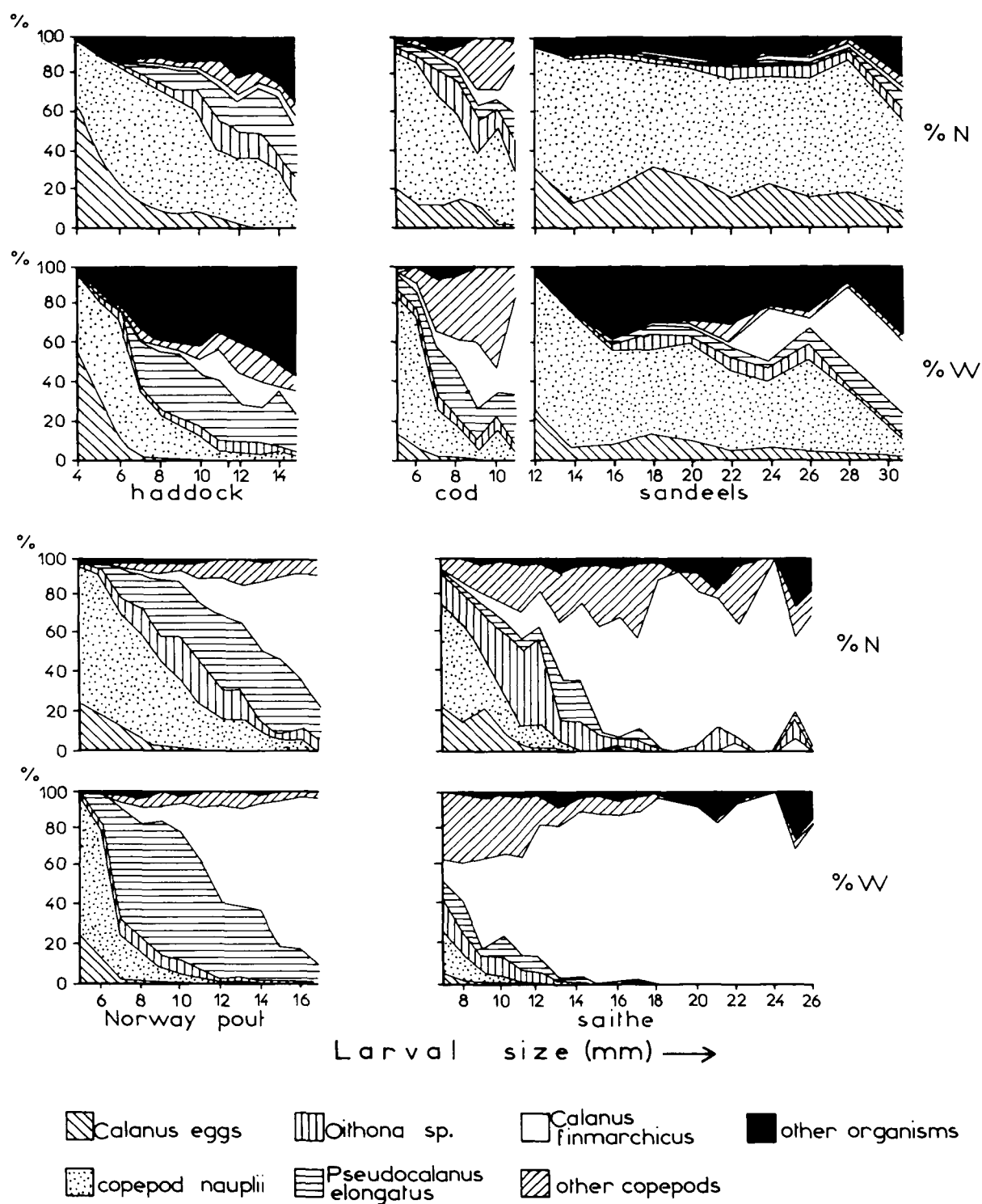


Figure 1. Cumulative percentage composition of the larval diets in numerical (%N) and biomass (%W) terms in 1978.

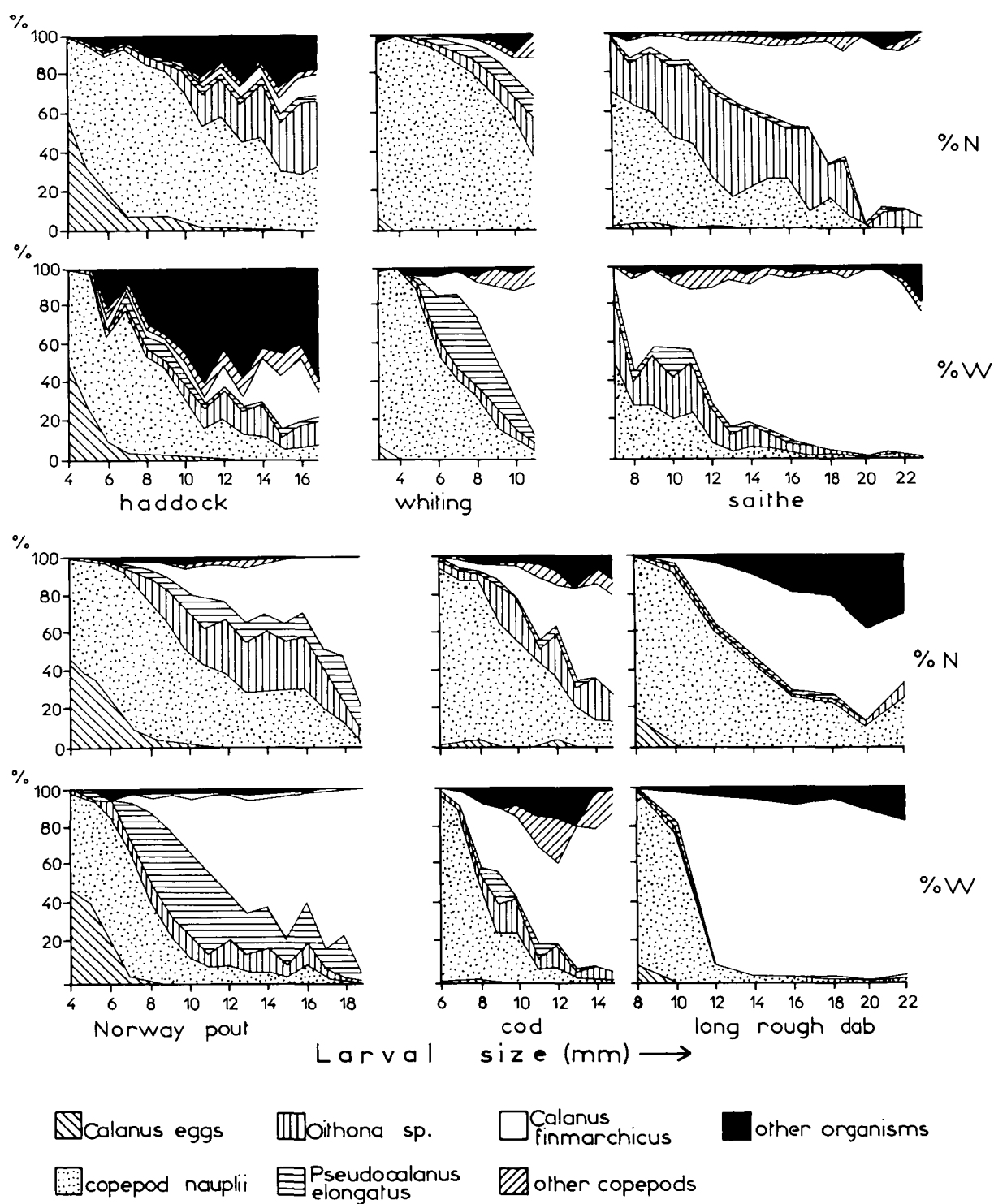


Figure 2. Cumulative percentage composition of the larval diets in 1979 in numerical (%N) and biomass (%W) terms.

saithe showed a higher preference for *A. clausii* than the other species.

Haddock larvae exploited a wider range of organisms, some of which were not utilized by the other gadoids. The haddock diet was characterized by the high contribution of copepod nauplii, larval euphausiids, fish larvae (mostly newly hatched whiting), cladocerans and non-crustacean prey items, such as appendicularians and larvae of bottom invertebrates. The majority of organisms selected by haddock larvae were slow-moving

forms. Copepods were of relatively low importance but egg-bearing females were highly selected. The fast-swimming *A. clausii* and *C. finmarchicus* were avoided, and usually only copepodites stage I of these species were taken. The slower copepods, *P. elongatus* and *T. longicornis*, were taken in higher proportions, and adults of these species were also found in the diet.

The food of sandeels consisted mainly of copepod nauplii and *C. finmarchicus* eggs, but appendicularians (*Oikopleura* sp.) comprised a substantial portion of the

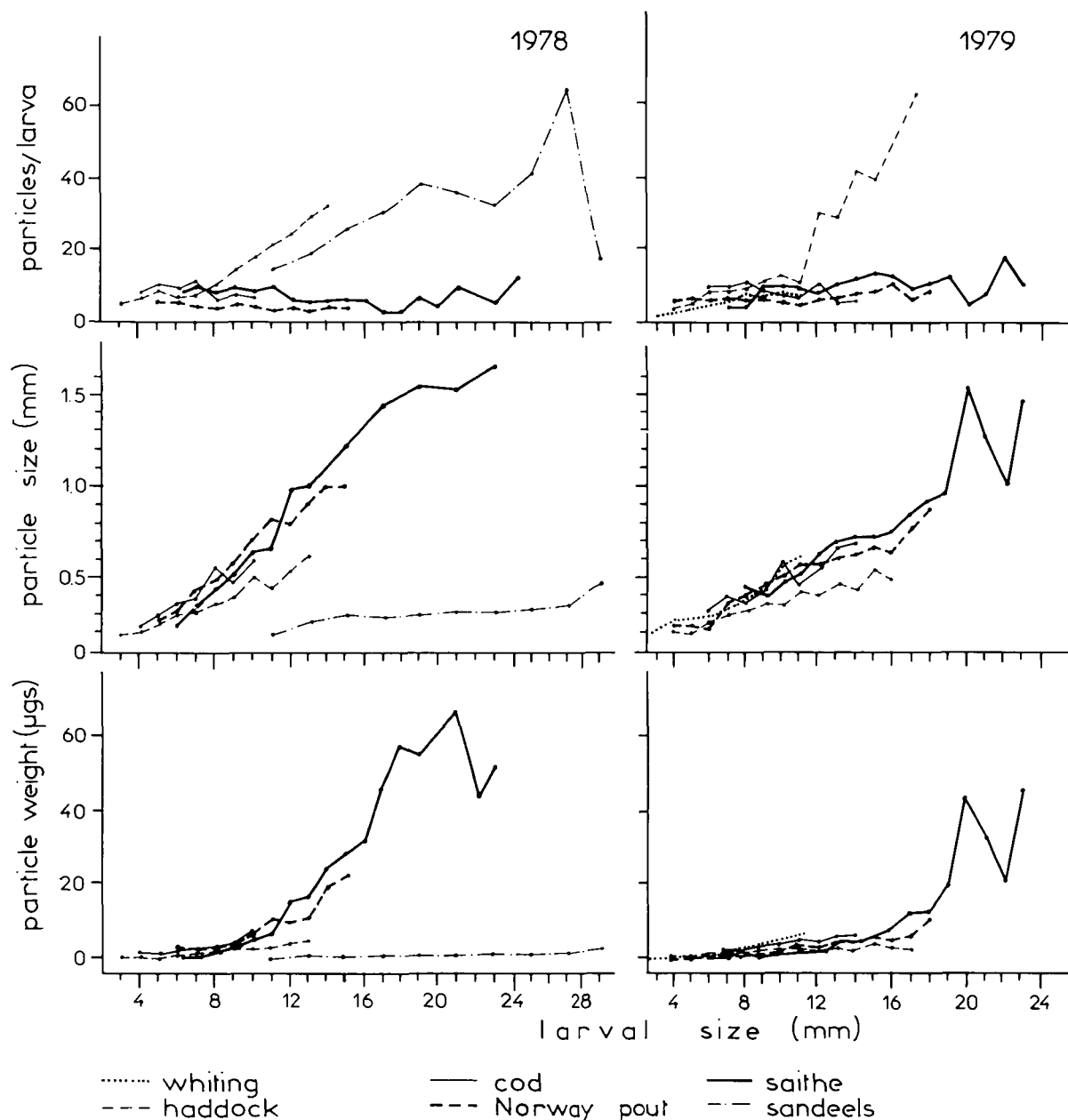


Figure 3 Average number, size, and weight of the ingested food particles.

diet. The long rough dab larvae fed predominantly on *C. finmarchicus* and to a lesser extent on appendicularians.

Some of the dietary differences between different species of gadoid larvae may be related to minor differences in their depth distribution compared with that of the zooplankton species. But the absence of a markedly defined vertical stratification of the gadoid larvae and the existence of a significant overlap in the horizontal distributions of the species examined (Economou, 1987), indicate that spatial separation was not responsible for most of the observed dietary differences.

Predator-prey size relationships

The average number of prey particles per larva, and the mean particle size and particle weight, are given in relation to larval size in Figure 3. Because the larvae of the species examined are visual feeders and stop feeding at night, only day-caught larvae were used in the estimation of the number of particles per larva.

The size of prey was clearly related to the length of larvae. With increasing larval size, progressively larger prey was taken, but at comparable lengths haddock took more and smaller particles than did the other gadoids. In sandeels, the change in prey size with the growth of larvae was even less and quite large larvae appeared to be feeding on very small prey.

There was a marked difference in the number and size distribution of organisms ingested in 1978 and 1979, reflecting differences in food availability. More and smaller particles were eaten in 1979 than in 1978. In fact, the abundance of large prey in the plankton was slightly lower in 1978, but the abundance of small prey was significantly higher in 1979 (Economou, 1987). Thus, a switch of preference in response to the size composition of prey is indicated.

Morphological and anatomical characters related to feeding

The change of diet with increasing larval size may reflect the development of the feeding apparatus and the improvement of the predacious feeding mechanism. The length and width at the broadest point of the upper jaw and the gape of the mouth to free opening, assumed to determine the prey capture success of larvae (Shirota, 1978a, b; Yasuda, 1960), and the diameter of oesophagus, which may influence the capability of ingestion, were measured for each size group of the five gadoid larvae. These are plotted in Figure 4 against the mean length, the range of lengths, and the maximum width of the prey consumed.

Although the haddock larvae had slightly larger mouth openings than the other gadoids, there were no

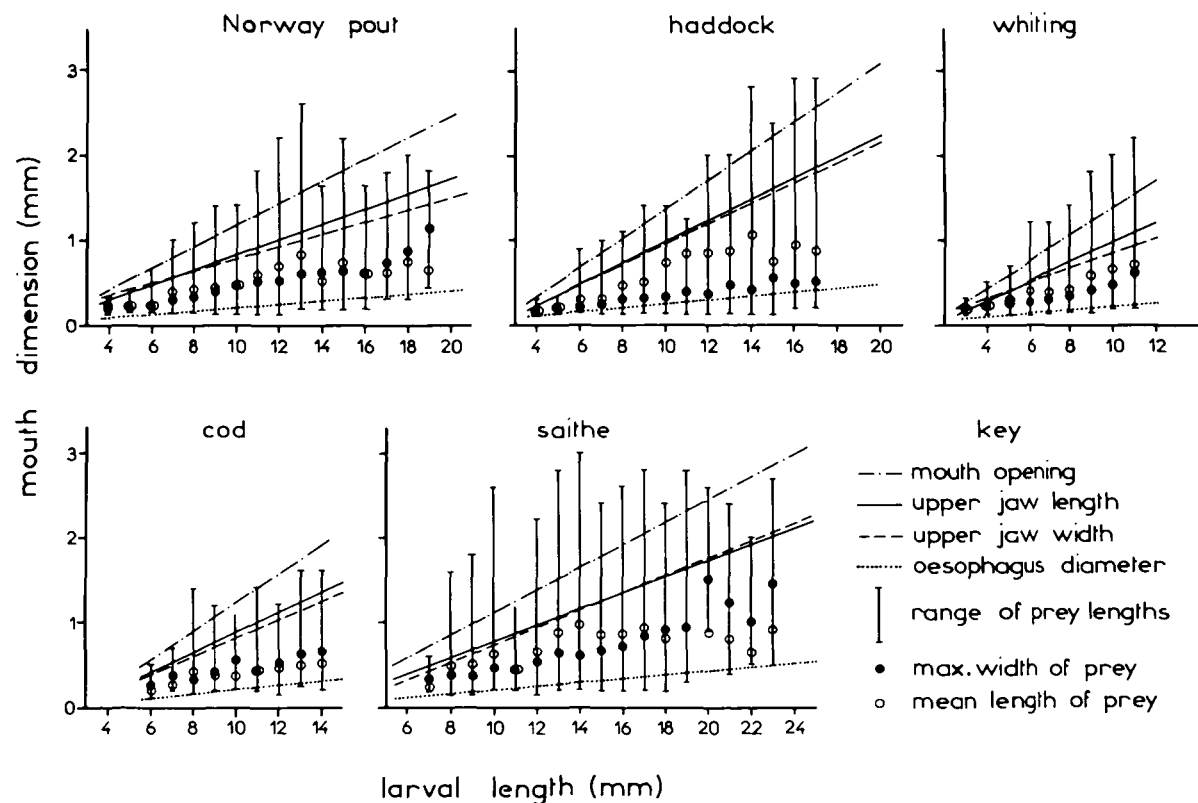


Figure 4. Relation between the mouth dimensions and the size of the ingested prey.

Table 3. Larval electivity in relation to average plankton composition. Values represent averages over 1 mm length groups.

Fish species	Norway pout		Haddock		Cod		Whiting		Saithe		Sandeels	Long rough dab
	1978	1979	1978	1979	1978	1979	1978	1979	1978	1979	1978	1979
Size range (mm)	7-15	7-15	7-15	7-15	7-11	7-15	7-11	7-15	7-15	7-15	14-28	10-20
<i>Calanus</i> eggs	-1.05	-1.21	-0.91	-0.66	-0.39	-1.49	-1.71	-0.71	-1.66	0.19	-1.84	-1.84
<i>Calanoid</i> nauplii	0.13	0.33	0.44	0.51	0.40	0.21	0.58	-0.46	-1.66	0.82	0.20	0.20
<i>Cyclopoid</i> nauplii	-1.40	-1.77	-1.16	-1.04	-1.08	-1.16	-0.76	-1.15	-1.25	-0.61	-1.69	-1.69
<i>Oithona</i> sp.	-0.26	-0.08	-0.32	-0.31	-0.15	-0.28	-0.39	0.09	0.29	-0.69	-1.21	-1.21
<i>O. spirinotris</i>	-1.32	-0.26	-1.73	-1.43	-0.32	-2.00	-1.15	-0.76	-0.50	-2.00	-2.00	-2.00
<i>Paracalanus parvus</i>	-0.49	-1.33	-0.62	-0.71	0.56	-2.00	-0.21	0.11	-0.16	-0.84	-2.00	-2.00
<i>Pseudocalanus elongatus</i>	0.80	0.60	0.41	-0.10	0.12	-0.68	0.56	-0.49	-0.36	-1.59	-0.77	-0.77
<i>Acartia clausii</i>	-0.24	-0.51	-1.88	-0.51	1.07	0.14	0.47	1.18	0.29	-1.59	-2.00	-2.00
<i>Calanus finmarchicus</i>	0.44	0.76	-0.42	-0.07	0.12	1.03	0.47	0.64	0.83	-0.94	0.54	0.54
<i>Microcalanus pusillus</i>	-1.24	-0.81	-0.70	-1.49	-2.00	-2.00	-2.00	-2.00	-1.88	-2.00	-2.00	-2.00
<i>Temora longicornis</i>	-0.04	-1.12	0.87	0.89	-1.53	-1.62	-1.32	-2.00	-2.00	-1.74	-2.00	-2.00
<i>Euphausiid</i> nauplii	-1.18	-0.89	0.72	0.80	-0.84	-0.83	-1.16	-1.11	0.38	-0.62	-2.00	-2.00
<i>Euphausiid</i> juveniles	-1.11	-1.50	0.47	0.55	-0.95	-1.62	-2.00	-1.63	-1.20	-1.51	0.10	0.10
<i>Eodone</i> sp.	-1.68	-2.00	1.43	1.60	-0.77	0.14	0.06	-0.03	-1.04	1.04	-2.00	-2.00
<i>Limacina retroversa</i>	-2.00	-2.00	-1.27	-0.76	-2.00	-2.00	-1.71	-2.00	-2.00	-1.82	-2.00	-2.00
Lamellibranch larvae	-2.00	-2.00	-1.44	-0.55	-2.00	-2.00	-1.49	-2.00	-2.00	-1.94	-2.00	-2.00
Appendicularians	-2.00	-1.94	-0.64	-1.08	-1.85	-1.56	-1.87	-1.84	-1.82	0.00	-0.01	-0.01

important differences in mouth morphology between species. As the dimensions of the mouth increased, increasingly larger prey was consumed, but the larvae continued feeding on small prey. Despite the fact that the haddock larvae consumed prey of the smallest average size, some of the particles ingested (relatively immobile forms, such as *Oikopleura* sp. and euphausiid calyptopis) were wider than the particles ingested by the other species.

No influence of body morphology on the kind and size of prey eaten by the gadoid larvae could be ascertained. The slightly more robust haddock larvae took the smallest and less evasive prey, while saithe larvae, the most slender among gadoids, took the largest and more active prey. The oesophagus, because of its distensibility, does not seem to be a limiting factor, and quite large prey can be ingested by the gadoid larvae if available. In contrast, the narrow elongated sande larvae fed almost exclusively on small prey.

Prey selection in relation to food availability

The electivity index (see Material and methods) for the most important prey types was calculated for 1 mm length intervals and averaged over a range of lengths (Table 3). The ontogenetic shifts of electivity with respect to prey type and prey size are shown in Figures 5 and 6 respectively.

The species-specific and size-related trends of electivity which are already known reappear, but it can now be seen whether they reflect preference for, or availability of, particular prey items. Haddock was the least selective species. The late haddock larvae tended towards a state of neutral electivity for most types and sizes of prey, indicating the gradual development of omnivorous feeding.

The species maintained a roughly similar ranking of electivity for most prey types in the two years (lack of consistency was observed only for *Calanus finmarchicus* eggs). The stability between years of the electivity trends for small and large prey confirms that the dietary switch towards smaller prey in 1979 reflected the high relative abundance of small prey in that year.

Feeding interactions between larvae

The interspecific and intraspecific associations of diets appear in Table 4. Dietary overlap was highest between species and size groups which fed predominantly on *C. finmarchicus*. The strongest intraspecific overlap was observed in saithe larvae.

There was a rapid increase of the zooplankton biomass during May (Economou, 1987), which implies a surplus of production over consumption by fish larvae and other pelagic predators. To test whether grazing by fish larvae altered the structure of the zooplankton

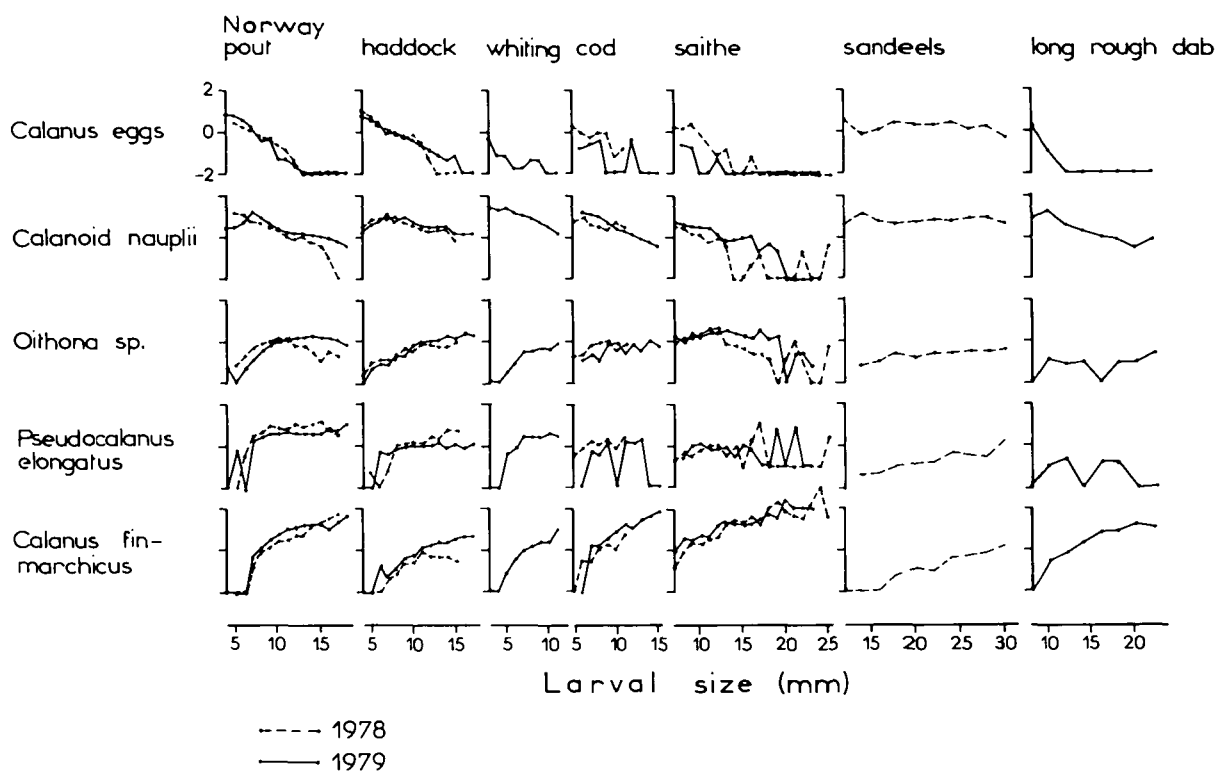


Figure 5. Electivity for the main prey groups in relation to larval size.

community, their density at each station in the three grid surveys of the 1979 cruise was correlated with zooplankton abundance and indices of relative abundance of the most important prey organisms (Table 5). The complexity of the system and the weakness of the correlations do not allow firm conclusions to be drawn

with regard to the possible impact of larvae on zooplankton. However, the consistent negative correlation between larvae and the relative abundance of *Calanus finmarchicus*, in conjunction with the high preference of larvae for this prey species, suggests that continuing grazing on juvenile stages reduces the net growth rate

Table 4. Intra- and interspecific overlap in the larval gadoid diets.

	Norway pout				Haddock				Whiting				Cod				Saithe			
	4	8	12	16	4	8	12	16	4	8	12	16	8	12	16	20	8	12	16	20
4	0.52	0.12	0.12	1.00	0.69	0.34	0.10	0.69	0.42	0.59	0.12	0.30	0.09	0.02	0.0					
8		0.52	0.49	0.49	0.78	0.52	0.28	0.64	0.97	0.70	0.30	0.50	0.30	0.17	0.13					
12			0.99	0.11	0.23	0.43	0.79	0.15	0.68	0.67	0.79	0.91	0.93	0.85	0.79					
16				0.11	0.22	0.41	0.78	0.15	0.65	0.68	0.79	0.92	0.94	0.89	0.83					
					4	0.64	0.31	0.08	0.66	0.39	0.55	0.10	0.28	0.08	0.02	0.0				
					8		0.64	0.23	0.80	0.68	0.78	0.19	0.43	0.15	0.05	0.01				
					12			0.62	0.38	0.52	0.61	0.51	0.56	0.40	0.25	0.21				
					16				0.10	0.41	0.57	0.75	0.82	0.80	0.67	0.61				
									4	0.52	0.74	0.13	0.37	0.11	0.03	0.0				
									8		0.70	0.46	0.61	0.45	0.34	0.29				
											8	0.60	0.85	0.66	0.56	0.51				
											12		0.85	0.88	0.72	0.65				
													8	0.94	0.82	0.76				
														12	0.92	0.87				
															16	0.99				
																20				

$$C_{ij} = \frac{2\sum x_{ij}y_{ij}}{\sum x_i^2 + \sum y_j^2}$$

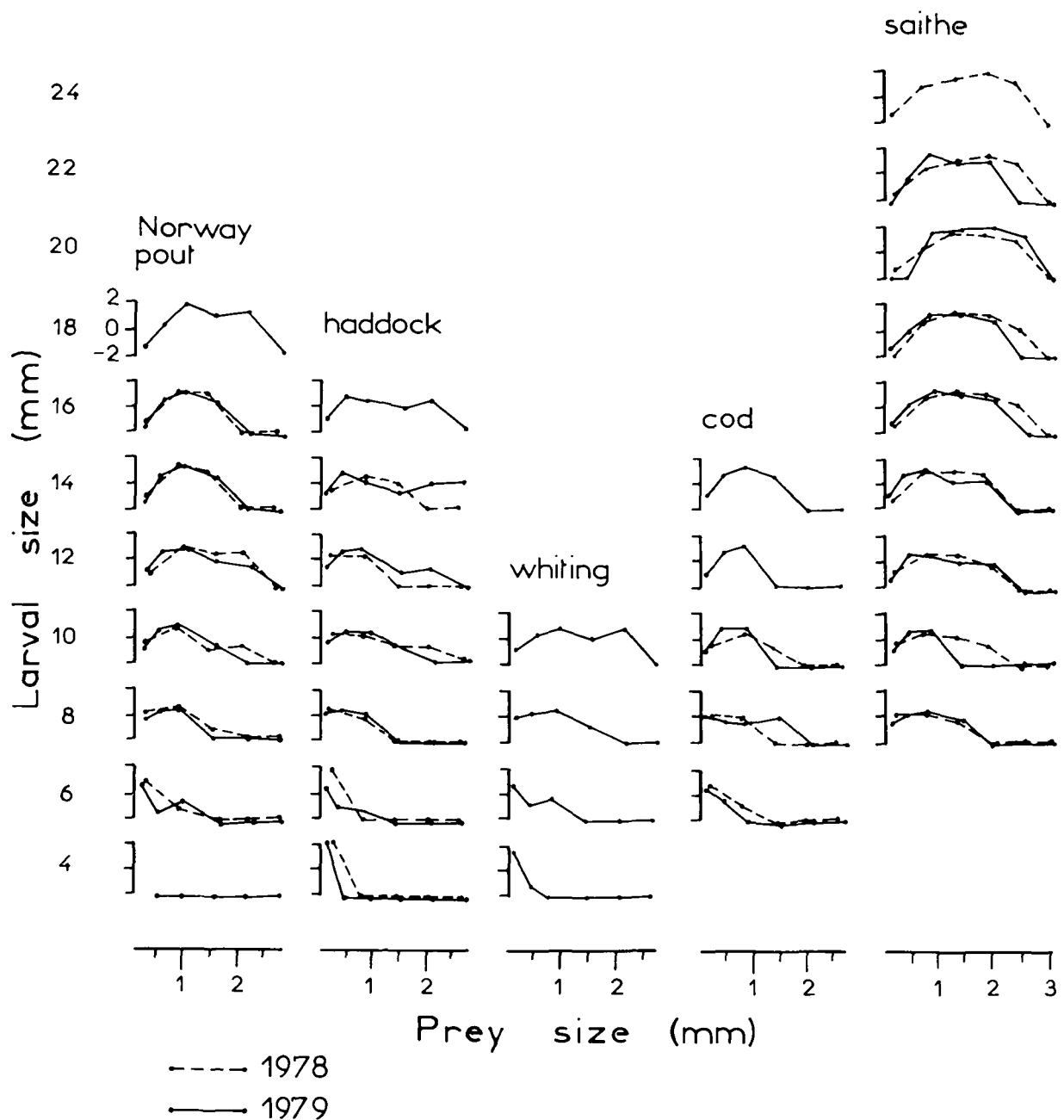


Figure 6. Electivity for prey size in relation to larval size.

of *C. finmarchicus* populations in areas of high larval density.

Discussion

The larval feeding behaviour

The mechanism by which adult planktivorous fish react to the prey has been seen as a function of prey size

(Confer and Blades, 1975) or apparent prey size, depending on the actual size of prey or on its proximity to the fish (O'Brien *et al.*, 1976). The "apparent size" model better explains the switch of selectivity in response to the higher relative abundance of small prey in 1979 and probably similar switches of selectivity described by Cohen and Lough (1983), Schmitt (1986a), and Grover and Olla (1987).

With the exception of haddock, the "robust" gadoid

Table 5. Correlation coefficients between larval density (nos m⁻³) and indices of zooplankton abundance (1979 cruise).

Survey period	9–10 May	13–18 May	29–30 May	All surveys
Number of stations	21	27	27	75
Measures of zooplankton abundance				
Total plankters (nos m ⁻³)	0.55	0.26	0.49	0.22
Total zooplankton biomass (mgs m ⁻³)	0.57	–0.18	–0.14	0.20
Biomass of most suitable prey (mgs m ⁻³)	0.39	–0.15	0.26	0.40
Relative abundance of selected zooplankters (Ne/Se) ^a				
<i>Pseudocalanus elongatus</i>	–0.00	–0.33	0.01	0.06
<i>Oithona</i> sp.	–0.01	–0.08	–0.57	–0.18
<i>Calanus finmarchicus</i> eggs	0.23	0.49	–0.05	–0.15
Calanoid nauplii	0.09	0.14	0.22	–0.06
<i>C. finmarchicus</i> copepodites 0.6–1.2 mm	–0.41	–0.60	–0.25	–0.07
<i>C. finmarchicus</i> adults	–0.04	–0.22	–0.25	–0.13
Total <i>C. finmarchicus</i>	–0.38	–0.55	–0.37	–0.10

^a Ne: The percentage contribution of the particular species to the total number of zooplankters at each station; Se: 100 – Ne.

larvae in this study and, so far as I am aware, all larvae of other gadoid species, the diets of which have been reported in the literature (Last, 1978a, 1980; Conway, 1980; Kendall *et al.*, 1987), tend to select copepods and generally evasive prey, and show increasing preference for larger prey as they grow. On the other hand, the diets of the “slender” sandeel larvae are characterized by the predominance of smaller and less active prey and by a slower rate of change in prey size with the growth of larvae (Last, 1980; Ryland, 1964; this study). Almost certainly, the difference of diets between “robust” and “slender” larvae reflects differences in swimming mode, manoeuvrability, and biting technique (see Braum, 1967; Hunter, 1972; Hunter and Kimbrell, 1980).

Mouth and prey size relationships such as those described above or which have appeared in the literature (Minton, 1977; Last, 1978a; Laroche, 1982) show that the increase in mouth gape with the growth of larvae is influential in determining electivity. However, it does not necessarily follow that species with the bigger mouths select the largest prey. The “opportunistic” haddock larvae utilize smaller on average prey than other more predacious gadoid larvae and thus their big mouth may be an adaptation towards omnivorous feeding.

Therefore, the divergence in feeding preferences between the larvae of haddock and of the other gadoids could not be ascribed to any obvious morphological differences. Feeding studies of 0-group cod and haddock indicate that the species specific electivity patterns observed in the larvae of these two species persist in later life stages: copepods and other crustaceans form the bulk of food in juvenile cod while non-crustacean and generally less active prey is more important for young haddock (Wiborg, 1960; Robb, 1981). Possibly, these feeding differences reflect differences in the species-specific behavioural patterns. I have argued elsewhere that the larval feeding behaviour represents

a rudimentary adaptation of the adult feeding behaviour (Economou, 1983). Among gadoids, juvenile and adult cod, saithe, whiting, and Norway pout are active predators on fish and evasive crustaceans while haddock is an omnivorous bottom feeder consuming passive and small prey (Jones, 1954; Raitt and Adams, 1965; Rae, 1967; Bergstad *et al.*, 1987; Macer and Easey, 1988). Thus, it appears from the data and the references cited that adult and larval fish feed on equivalent prey types with respect to relative size, motion, and ability to escape.

Differences in larval diets despite similarities in mouth size and morphology have also been reported for other species (Last, 1978b; Bainbridge and McKay, 1968; Laroche, 1982; Sumida and Moser, 1984). There have been discussions as to whether such interspecific differences represent a mechanism of resource partitioning leading to feeding niche separation (Last, 1978b; Minton, 1977; Laroche, 1982; Kane, 1984; Koslow and Naumov, 1988). In the case of the gadoid larvae examined in this study, preference for a particular kind of food may not necessarily be the selective force for feeding character displacement. The feeding divergence between larval haddock and the larvae of the other species may incidentally act to reduce trophic interactions, but the behavioural characteristics which effectively separate the larval species diets appear to represent independent adaptations of the adult behavioural patterns to the feeding opportunities in the planktonic environment.

Competitive interactions between larvae

The larval diets of four of the species investigated varied remarkably little, and although competitive interactions cannot be inferred from the similarity of the diets alone, feeding on the same components of the available food

resource is a necessary, though not sufficient, condition for competition between species to occur.

To establish competition as a critical survival factor, it must be shown that the food available within the normal larval searching range is inadequate to support larval growth and survival, and that this "local" food has been reduced to this low level by the grazing of the larvae themselves. However, it is difficult in practice to detect competition by demonstrating an effect of grazing on food availability. Because of seasonal productivity patterns in the planktonic environment, the supply of food varies continuously in time and is likely to be patchily distributed in space. Therefore, a test of the competition hypothesis requires measurement of the relative rates of zooplankton consumption and production, which is difficult with any reliability.

In practice, the existence or not of competition is usually inferred from assessments of the consumption rates under "average" conditions of larval and plankton densities, derived from the integration of catches over the trajectory of the sampling gear. I have estimated that at the observed size distribution of larvae and at the relative densities of larvae and prey organisms encountered during my research in the northern North Sea, the prey biomass overwhelmingly exceeded the larval biomass (Economou, 1987). Consumption rates were not estimated, but assuming normal consumption from theoretically estimated required rations it appeared that a relatively small amount of the standing crop of the suitable prey would be grazed down daily. Based on this evidence, I assumed that direct competition between larvae was not appreciable.

Most of the other studies of the trophic ecology of larval fishes which provide data on larval and zooplankton densities in sufficient detail for similar calculations do not indicate competitive interactions (Harding and Talbot, 1973; Rosenthal and Hempel, 1971; Lipskaya, 1987; Laurence, 1983). However, some impact of competitive grazing on prey density and hence on survival may be expected in years, areas, or seasons of extremely high levels of larval abundance and/or low zooplankton biomass (Smith and Lasker, 1978; Minton, 1977; Schnack and Böttger, 1981; Kendal *et al.*, 1987).

Therefore, under the assumption that the larvae and their prey are uniformly distributed in space, the prey biomass consumed daily rarely represents a significant proportion of the total available food resource. However, this kind of information is not adequate to ascertain the effect of grazing on the local food resource or of the impact of cumulative consumption on the population dynamics of the prey. Such an impact is suggested in this study by the negative association between density of larvae and relative abundance of some important prey species, and implies indirect competition between larvae occupying the same region at earlier and later times. In this sense, continuing and selective grazing early in the season will slow down the

net rate of increase of the prey and thus reduce the amount of food available later. This competition is likely to be intraspecific if "past" grazing by the small and medium-sized larvae of one species on the young developmental stages of the prey reduces the abundance of the large prey available to the late larvae.

It follows that competition for food may become more significant among larger (or late) larvae than among smaller ones, especially towards the end of the period of larval development. This has been demonstrated in laboratory experiments (Schmitt, 1986b) and is also implied by two other considerations. First, late larvae feed principally on large prey which are not replaced as fast as the small prey upon which smaller larvae feed; and second, the late larval development often coincides with the descending phase of the production cycle, when food availability is more likely to become a critical survival factor.

Summing up, cumulative and selective grazing by early larvae can alter the structure of the planktonic community and reduce the food supply to late larvae. The extent of this reduction may be proportional to the past grazing history, and hence to the past larval densities, in the water mass occupied by the larvae. Since relative dispersal is an important factor affecting larval densities in the field, the various ways developed by fishes for dispersing their reproductive products in time and in space (pelagic eggs and/or larvae, prolonged spawning seasons, or spawning in relation to particular hydrographic processes) may tend to minimize competitive interactions.

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