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Diel feeding patterns and the development of food webs in pelagic 0-group cod (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* L.), whiting (*Merlangius merlangus* L.), saithe (*Pollachius virens* L.), and Norway pout (*Trisopterus esmarkii* Nilsson) in the northern North Sea

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Stomach content analysis was used to investigate feeding interactions between pelagic 0-group gadoids in the northern North Sea. The species studied were cod (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* L.), whiting (*Merlangius merlangus* L.), saithe (*Pollachius virens* L.) and Norway pout (*Trisopterus esmarkii* Nilsson). The fish were caught at a site south-east of Shetland in late spring during 24 h depth-stratified fishing using a mid-water trawl. There was overlap in the range of prey consumed by the various species. Fish of 1–3 cm in length fed mainly on copepods and other invertebrates. Larger Norway pout continued to feed almost entirely on copepods, but the other species diversified as they grew to include fish in their diet, cod and whiting becoming almost entirely piscivorous. Haddock and saithe ate moderate amounts of fish combined with crustacea in roughly equal proportions. The depth at which the fish were caught did not appear to influence the range of prey consumed, but fish was slightly more prevalent in the diet of 0-groups caught near the surface. The results indicate that a food web of increasing complexity can develop during a relatively short time scale in late spring when the 0-group gadoids are pelagic. Generalised linear modelling revealed diel feeding patterns which were size-dependent and species-specific. In 2–3 cm cod, for example, peak feeding was during the period 1200–2000 h and high numbers of prey (mainly invertebrates) were consumed. The stomachs of the larger cod (3–5 cm) contained smaller numbers of mainly fish prey and peak feeding switched to 0000–0800 h. The piscivorous 0-groups were capable of eating relatively large prey items, providing the opportunity for larger individuals to eat younger or slower-growing individuals from the same year class. Whiting in particular were subject to substantial levels of cannibalism and inter-specific predation. Feeding interactions of this sort might be of sufficient magnitude to influence significantly the survival and recruitment of gadoids. High fecundity in whiting, coupled with multiple spawnings over a protracted period of time means that offspring from late spawnings could act as a food reserve for siblings from earlier spawnings. Such prey provide substantially more energy than the female invested in producing the original egg from which the prey was derived. This mechanism could prove to be an energy-efficient way of providing food reserves for the early offspring. It is also an efficient way of governing population size through density-dependent mortality.

Key words: 0-group, gadoid, fish, feeding, interactions, cannibalism, diel, depth, North Sea, cod, haddock, whiting, saithe, Norway pout.

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Table 1. The catch rates of pelagic 0-group gadoids and the number and size range used for stomach content analysis.

Species	Number of tows	Mean numbers caught per hour	Std Dev	Number of fish stomachs analysed	Mean length of fish (cm)	Std Dev (cm)	Minimum (cm)	Maximum (cm)
Cod	18	334	606	341	3.91	0.91	2.0	7.0
Haddock	18	699	1368	450	4.14	1.16	1.7	7.3
Whiting	18	1241	1308	388	3.21	0.81	1.5	5.1
Saithe	18	20	57	47	4.56	1.17	2.5	7.9
Norway pout	18	260	340	255	4.78	1.37	2.1	6.6

Introduction

Gadoids such as cod (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* L.), whiting (*Merlangius merlangus* L.), saithe (*Pollachius virens* L.) and Norway pout (*Trisopterus esmarkii* Nilsson) attain different sizes and tend to exploit different and predominantly demersal feeding niches as adults. However, as post-larval 0-groups in the northern North Sea during late spring they feed pelagically and their size range and geographical distribution patterns overlap. Often, high concentrations of more than one species are found in the same area and follow similar diel vertical migration patterns (Bailey, 1975; Bromley *et al.*, 1995). Potentially, competition between species and exposure to predation could be high during this phase of development (Rob and Hislop, 1980), and this might play an important role in governing survival and recruitment.

The present study was part of the ICES 1991 stomach sampling programme to investigate feeding interactions in North Sea fish. The diets of the pelagic 0-group gadoids in the northern North Sea were ascertained from stomach content analysis. The extent of feeding interactions, including cannibalism, was determined and the stomach content data were also used to investigate diel feeding patterns.

Material and methods

Research vessel cruises

In June 1991 the pelagic 0-group gadoids in the northern North Sea were surveyed by the research vessel ''Clupea''. Intensive 24 h sampling of three depth bands was undertaken at a site 60 miles south-east of Lerwick (60°00′N, 00°00′E) in the Shetland Islands between 17 and 20 June. The water depth was 147 m. A mixture of cod, haddock, whiting, saithe and Norway pout were present.

Fish were sampled with an International Young Gadoid Pelagic Trawl (IYGPT, Holden, 1981). Towing speed was 3 knots through the water, although this varied slightly since control over the depth of fishing was achieved through a combination of adjusting warp length and towing speed. The spread of the wing ends was approximately 10 m and the vertical gape of the net was approximately 8 m. The depth of the trawl headline below the surface and the configuration of the net during towing were monitored using a headline transducer.

The 24 h fishing cycle involved a series of 18 tows, each of 30 min duration. The standard sampling protocol was to undertake three tows within a 4 h period at depths of 10 m, 35 m, and near the bottom. This was repeated six times to give 24 h coverage. The sampling was undertaken in 8 h shifts and took 3 d to get full 24 h coverage. A temperature profile of the water column was also taken. Surface temperature was 10.3°C, declining to 8.3°C at a depth of 45 m.

The fish were preserved whole in 4% buffered formal saline for stomach content analysis in the laboratory and the results presented here are based on measurements made on preserved material. The length of each fish was measured to the nearest mm below and the prey items in the stomach were separated, identified, weighed (wet weight), and counted. Prey that were in an advanced stage of digestion and which could not be counted accurately were identified as far as possible and weighed (wet weight). The length of relatively intact fish prey was measured. The results were analysed using standard statistical techniques, including general linear modelling.

Results

The catch rates of the 0-groups are shown in Table 1. There was evidence that fish underwent a diel vertical migration, congregating at the surface in the evening and dispersing downwards in the day (Bromley *et al.*, 1995). Few fish were caught near the bottom. Analysis of variance of body length in relation to depth showed a slight tendency ($r^2<0.05$, $p=0.05$) for the haddock and whiting caught near the surface to be slightly larger than those in mid-water. However, the difference in length was small, of the order of 2–4 mm. The size of the other 0-groups was not significantly related to depth.

Table 2. Percentage by numbers of the various prey which could be recognised as distinct individuals in the stomachs of the pelagic 0-group gadoids.

Prey	Cod	Haddock	Norway pout	Saithe	Whiting
Copepods					
Calanus finmarchicus	16.74	5.99	77.79	15.98	26.93
Temora longicornis	0.6	0.1	—	—	—
Anomalocera pattersoni	—	—	—	7.1	—
Candacia spp	—	—	0.12	—	0.5
Caligus spp (parasitic copepod)	—	0.2	—	—	—
Copepods (not identified)	60.94	24.75	10.47	40.83	49.01
Amphipods					
Hyperia galba	—	0.29	—	—	—
Hyperoche spp	—	0.2	—	—	—
Gammaridae (not identified)	0.09	—	0.03	1.18	—
Hyperids (not identified)	0.43	16.99	0.18	1.18	2.87
Other crustaceans					
Pandalus montagui	—	0.1	—	—	—
Pandalus spp	—	2.06	—	—	—
Podon spp	—	—	—	—	0.1
Euphausiacea	7.47	2.16	10.17	1.78	0.2
Decapod larvae	1.8	21.12	0.65	15.98	0.69
Isopoda	—	—	—	2.37	—
Cirripedia	—	3.93	0.03	0.59	—
Crabs (not identified)	—	0.2	—	—	—
Crustaceans (not identified)	—	0.2	—	—	0.2
Other invertebrates					
Gastropoda	—	0.2	—	—	0.1
Mollusca	—	0.1	—	—	—
Nematoda (parasites)	0.09	0.39	—	—	0.1
Fish					
Cod (*Gadus morhua*)	0.09	—	—	—	—
Haddock (*Melanogrammus aeglefinus*)	—	0.2	—	—	—
Whiting (*Merlangius merlangus*)	0.69	0.88	—	—	2.87
Saithe (*Pollachius virens*)	—	0.1	—	—	0.1
Norway pout (*Trisopterus esmarkii*)	—	—	—	—	0.1
Gadidae (not identified)	1.46	4.32	0.06	1.78	2.57
Sandeels	1.37	0.39	—	—	0.2
Witch (*Glyptocephalus cynoglossus*)	—	0.29	—	—	—
Pleuronectidae	—	0.69	—	—	—
Dragonet (*Callionymus* spp)	—	0.2	—	—	0.1
Fish (not identified)	8.24	13.95	0.49	11.24	13.37

Diet of gadoids

The size ranges of the 0-groups used for stomach analysis are shown in Table 1. The mean percentage by numbers of the prey eaten by the various species of 0-group gadoids are shown in Table 2. There was overlap in the major categories of prey consumed by the various species of 0-groups. At the species level, *Calanus finmarchicus* were eaten by all the 0-group gadoids. Whiting were eaten by cod and haddock as well as by other whiting.

Most of the prey were partially digested and could not be identified to species level and it was not possible to make a complete assessment of the degree of overlap in the diets at the species level. When stomach contents are expressed in wet weight terms (Fig. 1) it can be seen that fish is important in the diet of all species except Norway pout. This was a size-dependent relationship (Fig. 2). With increasing size, cod and whiting became almost exclusively piscivorous. Haddock and saithe ate moderate amounts of fish combined with roughly equal proportions by weight of invertebrates, mainly crustacea. Norway pout, as they grew, continued to feed mainy on copepods. This divergence in feeding provides a mechanism for reducing interspecific feeding competition as the 0-groups get bigger.

Depth of capture had only a modest influence on diet composition. 0-groups caught in the upper regions of the water column contained 4–13% more fish in the diet compared with those caught in deeper water. However, in saithe the difference was 25%.

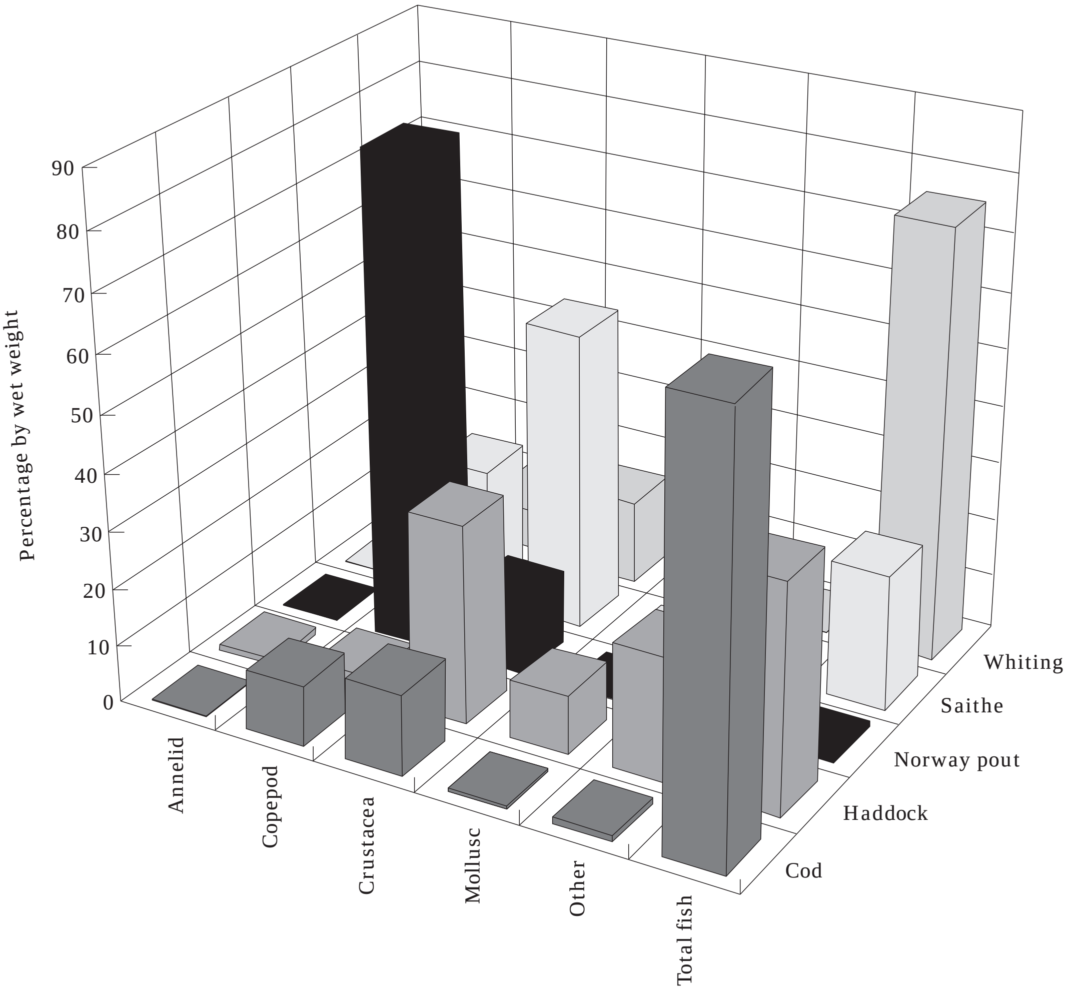

Figure 1. Percentage by wet weight of the main categories of prey eaten by the pelagic 0-group gadoids.

In general, the items of fish prey eaten by the 0-groups tended to weigh considerably more than the invertebrate prey. In 0-groups measuring 1–2 cm in length the stomachs contained numerous small invertebrate prey but larger piscivorous 0-groups contained fewer prey items (Fig. 3). This reflects an ontogenetic shift from feeding little and often to taking large meals at less frequent intervals. Norway pout, by contrast, continued to feed on increasing numbers of copepods (Fig. 3).

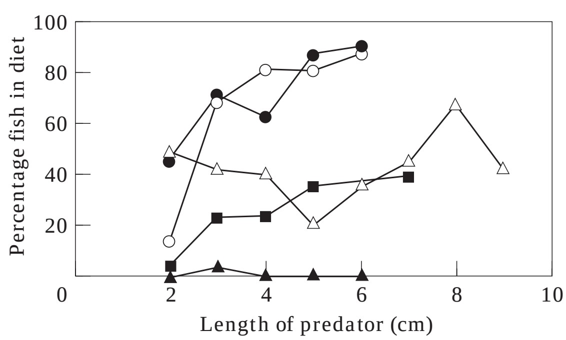

Figure 2. The proportion of fish in the diet in relation to the length of the pelagic 0-group gadoids. ▲ Norway pout, ■ saithe, △ haddock, ● whiting, ○ cod.

Relation between size of predator and prey

The relationship between predator size and the size of freshly ingested fish prey is shown in Figure 4. Cod, haddock, and whiting ate sandeels that were nearly as long as themselves and they consumed gadoids of up to half their own length, enabling the larger 0-groups within a cohort to predate the smaller ones. If it is assumed that the species composition of the fish that could not be identified matched that of the fish that could be identified (Table 2), then predation on whiting was considerable. In the larger whiting, cannibalism

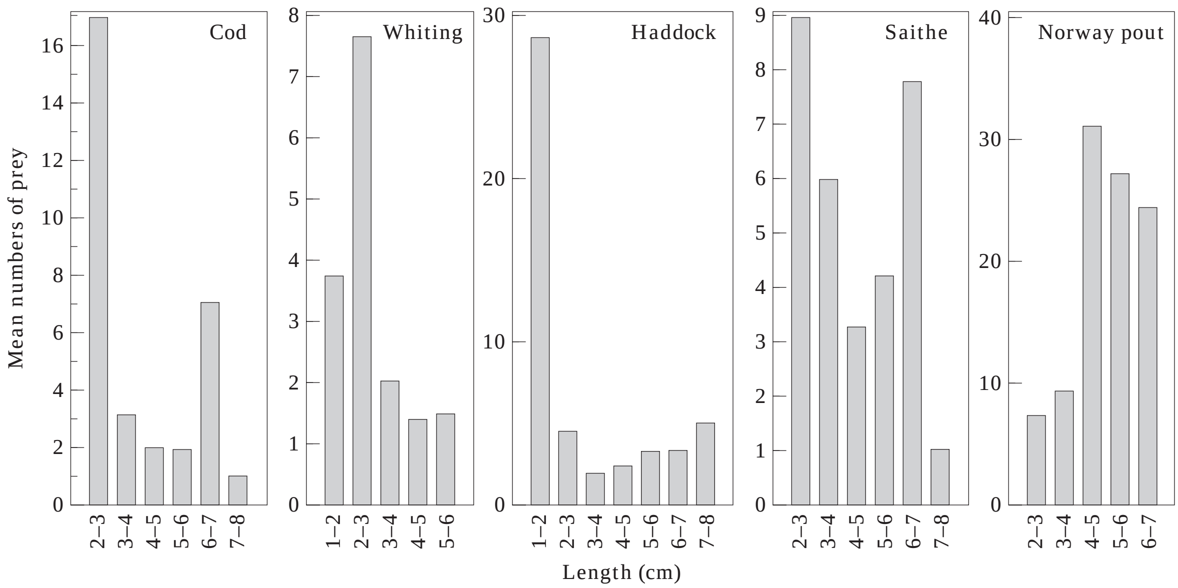

Figure 3. Relationship between the mean number of prey which could be recognised as distinct individuals in the stomach and the length of the pelagic 0-group gadoids.

accounted for up to 80% by weight of the diet. Cod and haddock also ate whiting, but sandeels were the most numerous fish in their diets.

Food web

The results show how an increasingly complex food web develops during the pelagic 0-group phase in spring and early summer. In the absence of larger 0-groups, progeny from early spawnings will pass through the pelagic phase without being subjected to significant levels of inter- or intra-specific predation from other 0-groups. Progeny from late spawnings will be subjected to increased predatory pressures from the older 0-groups and suffer the disadvantage that there will be no small 0-groups around on which they can feed. This pelagic

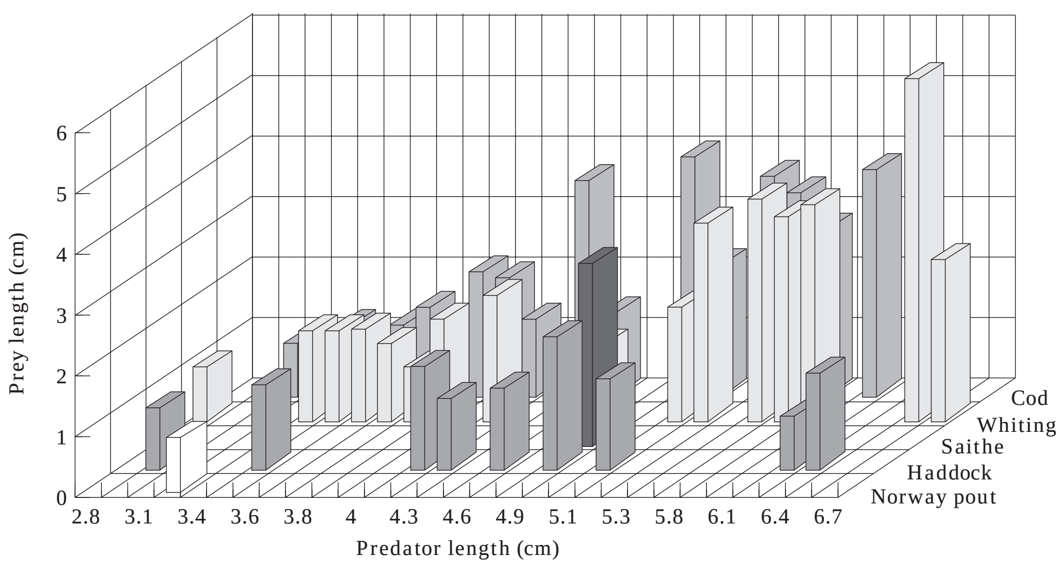

Figure 4. Length of fish prey in relation to length of the pelagic 0-group gadoids.

Table 3. Analysis of variance showing the significance of the relationship between the mean number of prey which could be recognised as distinct individuals in the stomach of feeding pelagic 0-group gadoids with time period during the day, length of 0-group in cm and period × length interactions (Type III Sums of Squares).

Predator, Model r^2 and mean number of prey per predator	Source of variation	d.f.	Mean square	F	P
Cod	Period	5	1188	21.6	0.0001
$r^2=0.69$	Length	5	1146	20.9	0.0001
$n=5.2$	Period × length	14	1023	18.6	0.0001
	Residual	197	55		
Haddock	Period	5	255	10.0	0.0001
$r^2=0.34$	Length	6	238	9.3	0.0001
$n=3.1$	Period × length	21	82	3.2	0.0001
	Residual	300	25		
Norway pout	Period	5	2670	5.0	0.0004
$r^2=0.36$	Length	4	769	1.4	0.2283
$n=21.2$	Period × length	18	417	0.8	0.7257
	Residual	125	538		
Whiting	Period	5	215	4.0	0.0016
$r^2=0.33$	Length	4	526	9.8	0.0001
$n=3.4$	Period × length	16	281	5.2	0.0001
	Residual	274	54		

food web is transitory and disappears when the 0-groups become demersal early in the summer.

Diel feeding patterns

A generalised linear model was used to investigate diel feeding patterns. The mean number of prey in the stomach was related to time period, body size and interaction terms in the following model:

$$N=\beta_0+\beta_1 \text{ period}+\beta_2 \text{ body length}+\beta_3 \text{ (period} \times \text{body length)}+\varepsilon\text{: } \varepsilon \sim N(0,\sigma)$$

Where N is the number of discrete prey items in the stomachs of fish that were actively feeding. The day was divided into six 4-h-periods, where period 1=0000–0400 h etc. Body length was a class variable with the 0-groups categorised into 1 cm length groups. β_0, β_1, β_2, and β_3 are constants.

In cod, haddock, and whiting (Table 3), ANOVA showed that the number of prey in the stomach was significantly ($p<0.05$) related to time period, predator length and the period × body length interactions. There were insufficient data to analyse saithe in this fashion.

Feeding intensity appeared to vary throughout the day in a size-specific fashion. These relationships can be seen in Figure 5. Cod of 2–3 cm in length, which fed mainly on invertebrates, exhibited peak feeding from 1200–2000 h. In cod of 3–5 cm, which were mainly piscivorous, there were fewer prey items in the stomach and peak feeding was from 0000–0800 h. In 5–6 cm cod feeding appeared to be concentrated in the middle of the day. Whiting of up to 4 cm in length followed similar trends to those exhibited by cod. In 2–3 cm haddock, peak feeding was also during 1200–2000 h, but larger haddock appeared to eat throughout the 24 h. In the case of Norway pout, ANOVA showed that prey numbers in the stomach were mainly related to the time period. This probably reflects the habit of all the sizes of Norway pout to concentrate their feeding on copepods. There was some indication of slight size-dependent variation in feeding pattern. Norway pout of 2–4 cm appeared to feed throughout the day but feeding was most intense from 0400–1600 h. Larger Norway pout tended to start feeding earlier in the day and appeared less prone to eat over the period 1600–2400 h.

The findings suggest there are complex feeding adaptations governing the timing of peak feeding, which could reduce feeding competition and might facilitate predator avoidance.

Discussion

High concentrations of pelagic 0-groups are often found in the same areas in the North Sea (Anon., 1984) and undergo similar diel vertical migrations (Bailey, 1975; Bromley *et al.*, 1995). The present study shows evidence of inter- and intra-specific feeding interactions, either through competition for food or through predation by the larger 0-groups on smaller ones. In whiting, this often took the form of cannibalism.

There was considerable overlap in the broad categories of prey eaten by different species of gadoids.

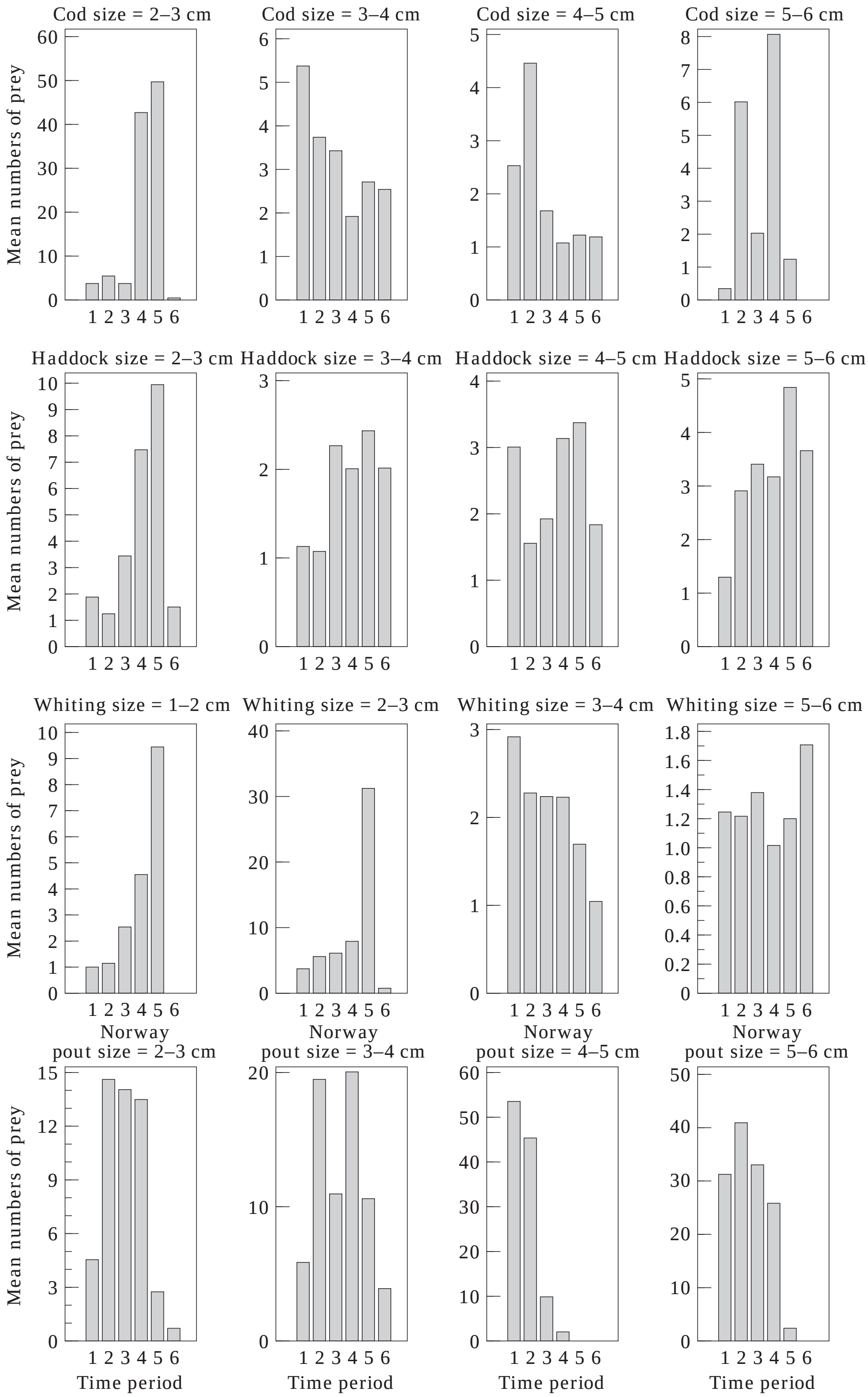

Figure 5. Relationship between the mean number of prey which could be recognised as distinct individuals in the stomach of the pelagic 0-group gadoids and the time period (Period 1 = 0000–0400 h etc.) when the fish were caught.

Often the prey was partially digested and could not be identified to species level. It was therefore not possible to get a complete picture of the overlap in the diets of the various 0-groups. Small 0-groups fed mainly on copepods and all ate *Calanus finmarchicus*, indicating that competition for food could be most intense at the early stages of 0-group development. Robb and Hislop (1980) and Robb (1981) found some evidence that larger 0-groups tended to specialize on different species of copepod. Extending the range of prey eaten to include fish would also tend to reduce feeding competition between species, as might varying the timing of peak feeding in a size-dependent fashion. However, the latter might reflect complex adaptations due to changes in the feeding behaviour associated with the transition to a piscivorous habit. Peak feeding in small 0-groups is probably related to the vertical migration patterns of their invertebrate prey near to the surface, but might also be modifed by predation pressures incuding those from piscivorous 0-groups.

The high fecundity and protracted spawning period exhibited by species such as cod and whiting (Kjesbu *et al.*, 1996; Hislop, 1984), coupled with the ability of the older pelagic 0-groups to eat relatively large prey items has led to the possibility of the 0-groups becoming cannibalistic (Nellen, 1986). In effect, the whiting from late spawnings acted as a food reserve for fish from earlier spawnings. This is not entirely disadvantageous since the fish from late spawnings, having fed and grown prior to being eaten, acted as an ever increasing food reserve for the progeny from early spawnings, at no subsequent energetic cost to the parent. If a form of density-dependent mortality is to be used as a strategy to regulate population size, it might as well be an energy-efficient strategy.

The results indicate that a food web of rapidly increasing complexity develops in the northern North Sea during June. Fish from early spawnings enter a simple food web and are not subjected to predation by larger 0-groups. Later progeny enter a more complex food web, where predation by larger individuals is an increasingly dominant force governing survival.

There are clear advantages therefore in being the first to pass through the pelagic phase since intra- and interspecific predation will be minimal. This could explain why the eggs spawned early in the season are often larger than those spawned later. With higher potential survival rates there will be pressure to invest a higher level of energy expenditure on reproduction during the early part of the spawning season. There are dangers, however, since if the fish spawn too early they might pre-empt the plankton production cycle. If progeny from early spawning fail to survive then offspring from later spawnings will not be subjected to high levels of predation and have an improved chance of survival.

The impact of predation on population size is dependent on a number of factors. The effect of inter-specific predation is related to the extent of the overlap in the distributions of the different species, and the timing of that overlap. This in turn depends on the timing of the development of the various species, their year-class strength, and the vagaries of weather, water currents and other such factors. Cannibalism likewise will vary depending on the level of survival of offspring from early and late spawnings. Predation on fish is therefore likely to be erratic and difficult to predict.

Studies undertaken during the mid-1970s (Robb and Hislop, 1980; Robb, 1981) indicate that fish were less prevalent in the diet of 0-group gadoids in the northern North Sea at that time. It is uncertain if this reflects normal inter-annual variability or is evidence of long-term changes in feeding patterns. Clearly, more research is needed to establish the full importance of the pelagic phase in governing the survival and recruitment of gadoids.

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