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Predation of whiting and haddock on sandeel: aggregative response, competition and diel periodicity

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The predation of haddock *Melanogrammus aeglefinus* and whiting *Merlangius merlangus* on sandeel *Ammodytes marinus* was investigated based on intensive sampling [performed with a bottom trawl (GOV) equipped with a small meshed codend cover; sediment samples were taken with a van Veen grab] in a restricted area of *c.* 15×20 nautical miles in the northern North Sea during a 5 day period in July 1996. The analysis of the spatial distribution of predators revealed a pronounced aggregation of whiting in the south-west part of the area, where sandeel catches were also highest. This pattern was thought to be the result of an aggregative behaviour of whiting. The sandeel concentration most likely reflected a restricted patch of coarse sediment of the preferred grain size for sandeels to bury in. In haddock the aggregation was less obvious. Both predators fed almost exclusively on sandeel in the south-west part of the area with haddock stomachs containing more sandeel than whiting stomachs. The stomach contents in both predators increased rapidly during the night, indicating that the predators were targeting burying sandeels. This would explain the competitive advantage of the benthivorous haddock.

Key words: aggregative response; haddock; North Sea; predation; sandeel; whiting.

INTRODUCTION

The importance of aggregations of animals in predator and prey interactions is a dominant topic of general ecology and especially in aquatic environments much attention has been given to the schooling behaviour of fishes. Generally it is assumed that schooling reduces the risk of an individual being attacked (Pitcher & Parrish, 1993). More recently, this generally reduced per capita attack rate was questioned, since an aggregative response of the predators on the aggregations of prey may counterbalance the dilution effects of aggregations (Turchin & Kareiva, 1989; Connell, 2000). Investigations of the aggregative response of predators in marine fishes are rare, however, and the few existing ones were mostly made in coral reefs applying direct observations and habitat manipulations (Connell & Gillanders, 1997).

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The predation of whiting *Merlangius merlangus* (L.) and haddock *Melanogrammus aeglefinus* (L.) on sandeel *Ammodytes marinus* Raitt in the open North Sea was investigated, where such techniques as direct observations and habitat manipulations cannot be applied. All the three species form large populations which support intensive fisheries. Although the whiting predation on sandeel it at present the strongest feeding interaction among North Sea fish populations with an annual consumption of *c.* 700 000 t sandeel (ICES, unpubl. data), little is known about the predators behaviour and functional response to its main prey.

The investigation of feeding interactions of such populations is traditionally done from stomach samples taken either on station grids of routine surveys or in limited areas without any *a priori* knowledge of the feeding situation. Such samples reveal typically a broad mixture in the diets reflecting mainly spatial effects of food availability (Bogstad *et al.*, 1995; P. Degnbol unpubl. data). Insights into the feeding behaviour, other than coarse categorizations of predators as piscivorous or benthivorous are often not possible from such samples.

In order to raise the chances of revealing the underlying feeding processes a different sampling strategy was employed: the stomach contents of dominant predators in a routine ground fish survey were scanned continuously and an intensive sampling exercise carried out once a specific feeding situation was encountered. The preferred situation was characterized by intensive feeding of a restricted size class of a predator species on one or very few different prey items. Ideally these prey items should also be sampled by the trawl thus allowing a comparison of size compositions in stomachs and trawl catches as well as an analysis of spatial patterns of the interaction.

In two previous papers (Mergardt & Temming, 1997, Temming & Mergardt, 2002) the analysis of whiting samples taken according to this sampling strategy off the Scottish coast in May to June 1992 was presented. These whiting were feeding exclusively on 2 year-old sandeel. The analysis revealed a diel periodicity of food intake with a peak at night and a 4 day long mean interval between two successive meals of these large sandeel in an average predator. Sandeel were found in whiting stomachs all over the investigation area, spatial effects did not exist or could not be resolved with these data. Haddock, although abundant in the whole sampling area in 1992, did not feed on these relatively large sandeel at all, confirming the competitive advantage of whiting, which is known to be the more effective piscivore (Jones, 1954; Hislop *et al.*, 1997).

In 1996 the sampling programme was repeated in the same area but somewhat later in the season after the settlement of a new sandeel year class in July. A modified GOV-trawl with an attached codend cover to enhance the catchability of the net for small potential prey fishes was used. In 1996 a completely different situation of the same feeding interaction between sandeel as prey and whiting and haddock as predators was encountered: (1) the prey was only encountered in a small sub-area of the total sampling area, (2) both haddock and whiting were feeding intensively on sandeel in this sub-area and (3) the sandeel were much smaller compared to the previous investigation. The analysis of the 1996 data focused on the main hypothesis that predators display aggregative behaviour on the prey concentration and additionally on competition between haddock and whiting and the diel pattern of food intake.

MATERIALS AND METHODS

SAMPLING SITE AND GEAR

Whiting and haddock were trawled from a small area (*c.* 15×20 nm) at 54°53′ N; 0°54′ W during day and night from 18 July to 22 July 1996 (Fig. 1). Due to legal restrictions of the daily work time the start of the 10 h working periods was shifted by 3 h every day over the 5 sampling days to achieve day and night samples. A total of 35 hauls was carried out with the ICES standard GOV-trawl (towing time: 30 min). Initially trawling at randomly chosen positions was restricted to a 10×10 nautical mile box (box D), since the analysis of fish distributions and catch variability in several such boxes with fixed locations is part of a standardized fishing programme carried out since 1987 (Ehrich & Stransky, 2001).

Since the on-board inspection of stomachs revealed a pronounced spatial pattern of stomach fullness with high values in the south-west corner of the standard sampling area, the sampling area was expanded in this direction. For a total of 16 hauls the GOV was equipped with a cylindrical codend cover with a mesh-size of 6 mm to improve the estimates of the abundance of small prey fishes, which were not sufficiently retained by the 20 mm mesh-size of the GOV codend. Prey fishes <10 cm total length (L_T) are known to be the dominant prey of predatory fishes between 25 and 30 cm L_T as investigated here (Hislop *et al.*, 1997; Floeter & Temming, 2003).

Start positions and tow directions within the box were determined randomly. Tow duration was 30 min at 4 nautical miles h^{-1} at depths between 77 and 118 m. The mean ± S.D. bottom temperature in the sampling area was measured as 9·0 ± 0·7° C. Basic data on catches are given in Table I.

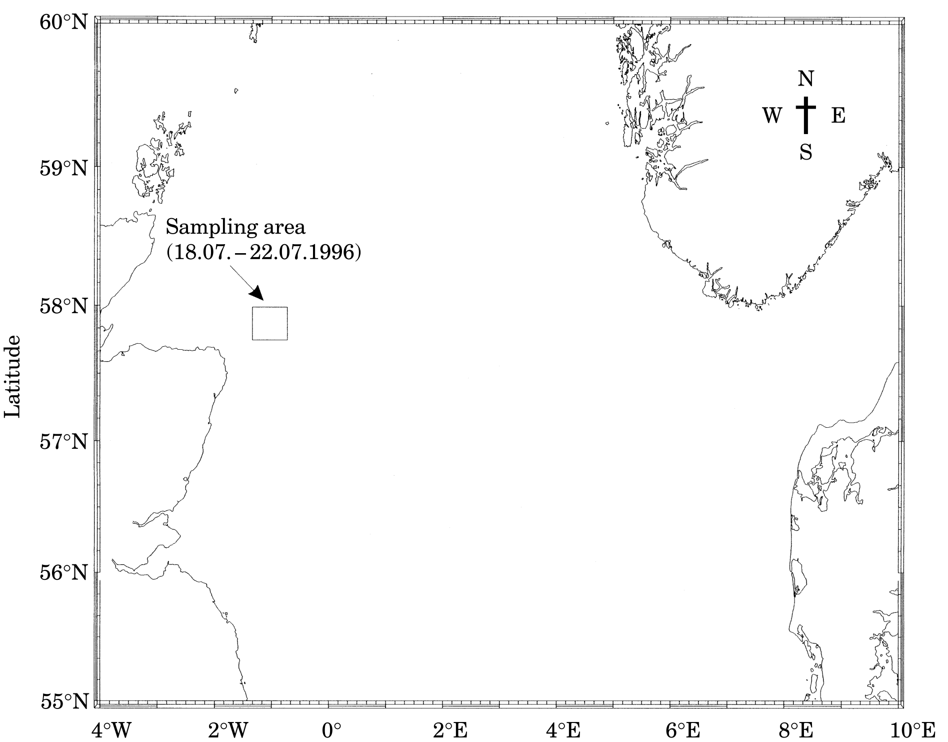

FIG. 1. Location of the sampling area.

TABLE I. Catch rates of whiting, haddock and sandeel from trawl hauls and number of whiting and haddock stomachs with and without food

Day in July 1996	Time (hours)	Station	Number of stomachs and per cent empty (in parentheses)		Predator catch rate (number per 30 min)		Prey (sandeel) catch rate (number per 30 min)
			Whiting	Haddock	Whiting	Haddock	
18	0655	597*	45 (60·0)	53 (1·9)	135	1055	0
	0851	598*	38 (71·1)	51 (15·7)	705	1731	0
	1051	600	37 (64·9)	41 (22·0)	508	2969	–
	1252	601	24 (79·2)	29 (34·5)	269	1629	–
	1443	603	24 (70·8)	29 (44·8)	340	2309	–
	1555	604	25 (72·0)	30 (30·0)	632	1717	–
	1743	606	23 (60·9)	30 (23·3)	391	2129	–
19	0438	608	47 (25·5)	49 (8·2)	195	819	–
	0625	609	16 (43·8)	29 (0)	446	935	–
	0737	610	47 (42·6)	53 (15·1)	148	993	–
	0919	611	31 (54·8)	29 (24·1)	173	1644	–
	1129	612	45 (71·1)	51 (11·8)	129	1107	–
	1310	613	55 (50·9)	55 (25·5)	316	1586	–
	1345	614	16 (62·5)	58 (24·1)	n.a.	n.a.	–
20	0210	615*	59 (23·7)	59 (15·3)	1751	777	11
	0328	616*	42 (73·8)	58 (15·5)	297	282	6
	0516	617*	26 (65·4)	29 (10·3)	434	1529	1
	0648	618*	44 (43·2)	27 (22·2)	106	1412	0
	0806	619*	49 (51·0)	28 (28·6)	433	1870	0
	0919	620*	53 (43·4)	29 (17·2)	827	831	0
	1041	621*	24 (54·2)	26 (15·4)	675	1152	0
	2249	623*	28 (75·0)	58 (22·4)	302	881	0
21	0007	624*	62 (46·8)	51 (2·0)	373	927	0
	0120	625	56 (60·7)	30 (10·0)	441	853	–
	0242	626	46 (56·5)	29 (0)	103	766	–
	0401	627	28 (39·3)	54 (16·7)	133	404	–
	0506	628	29 (69·0)	28 (10·7)	430	813	–
	0616	629	59 (42·4)	60 (6·7)	1706	1328	–
	0733	630	61 (1·6)	50 (0)	927	866	–
	1943	631*	No data	56 (16·1)	1880	881	45
	2128	632*	59 (18·6)	57 (10·5)	3426	2205	46
	2326	633*	53 (26·4)	59 (6·8)	2422	2095	362
22	0057	634*	53 (7·5)	53 (1·9)	3253	917	665
	0225	635*	47 (4·3)	53 (0)	1549	935	257
	0436	636	51 (3·9)	51 (0)	2685	1008	–

*, stations with codend cover.

Fish density for the two predator species is expressed as total numbers and biomass per species per 30 min tow. The relationship between the total catch of a species and the numbers in the size fraction that was chosen for stomach analysis (25–29·9 cm) was investigated by regression analysis.

BIOLOGICAL SAMPLES

From each haul a minimum of 30 whiting and haddock (size class 25–29·9 cm L_T) were sampled at random, if sufficient numbers were available. Stomachs of fishes with no signs of regurgitation (everted swimbladders or gill rakers with attached digested food material) were immediately deep frozen at $-30°$ C. For one station (614) the exact catch rates are not available due to a severe net damage, while stomach samples were taken from the available fishes. The whiting stomachs from station 631 were lost through a freezer break down. A total of 1402 whiting and 1532 haddock stomachs were analysed.

In the laboratory the contents of each stomach was analysed separately with regard to individual food particles, mass fractions per prey group and total stomach content wet mass. Individual prey fishes were identified to species and measured (L_T) to the nearest mm below and classified into three stages of digestion: 1, intact prey; 2, partly digested; 3, progressed digestion. Prey groups were categorized into species, in the case of fishes, and total invertebrates. For each prey group the total mass was determined.

STATISTICAL TREATMENT OF STOMACH DATA

The data originating from the box were grouped into four quadrants: NW, NE, SE and SW. The stations outside the box were grouped into one category SW_OB. Data were further grouped into four time of day categories: 2300–0459, 0500–1059, 1100–1659 and 1700–2259 hours. Grouped box-plots of the total stomach content of individual fish were constructed for the two predators to visualize the variability and the sampling design with regard to time of day and spatial coverage.

Statistical tests were only performed based on a even coarser grouping to minimize the total number of pair-wise comparisons: for this purpose the area outside of the box (SW_OB) was contrasted with the SW quadrant and with the other three quadrants treated as one unit (N + SE). Time of day was separated into 'night' and 'day'. 'Night' was defined arbitrarily as 1927–0721 hours, since samples from SW_OB were available for this time period only. This period includes the hours between sunset and sunrise (2315–0500 hours) as well as the dusk and dawn periods. All comparisons were made using the Mann–Whitney test (SPSS for Windows) for two independent samples (two tailed). The tests were done with total stomach content and with sandeel mass in the stomach as the explained variable.

Finally a generalized additive model (binomial with logit link function, McCullagh & Nelder, 1989) was fitted to the presence and absence data of sandeel in the predator stomachs. For this model time of day, area, predator species and predator size were used as explanatory variables. Computations were made using S-Plus for Windows.

A simple linear regression was applied to investigate the explanatory power of the mean amount of sandeel in the stomachs (mean over all stomachs from one station) on the densities of whiting and haddock.

SEDIMENT SAMPLES

The spatial pattern of sediments was analysed to reveal a rough indication of sandeel distributions independent of the trawl data. From a total of 23 stations located inside and outside of the box sediment samples were taken by means of a van Veen grab. These samples were analysed at the Federal Maritime and Hydrographic Agency of Germany. The grain size distribution was estimated from a sub-sample that was sieved through a standard Wentworth series of sieves ranging from 2000 to 63 µm mesh. The sediment was characterized by the modified median of the cumulative frequency curve for the grain size distribution based on linear interpolation. The median was modified by calculating the mean of the 16, the 50 and the 84% percentiles of the cumulative frequency distribution. In addition, the percentage of very fine sediments (<125 µm) was used to characterize the sediment in relation to sandeel habitat requirements (Jensen, 2001).

RESULTS

PREDATOR DISTRIBUTION

The length distribution of both predators was similar and unimodal ranging from 16 to 41 cm with most of the fishes in the size range 22–30 cm L_T. While the predator densities are displayed for all size classes, stomachs were only analysed from the size range 25–29·9 cm where piscivorous feeding behaviour is fully established. The relationship between the total catch (N_{total}) and the catch in the 25–29·9 cm size class ($N_{25–29·9}$), however, was very close and >90% of the variance was explained for each predator species: $N_{25–29·9} = 0·550$ $N_{total} + 2·664$ (haddock, $r^2 = 0·927$) $N_{25–29·9} = 0·446$ $N_{total} + 36·58$ (whiting, $r^2 = 0·914$). Given the statistical dependence of both variables, these regressions are not considered as a result but rather indicate that the density of the size class 25–29·9 cm is directly proportional to the total density. In the following fish density refers to total catches, unless explicit reference is made to the size class 25–29·9 cm.

Whiting biomass catch rates varied between 15·7 (station 618) and 451 kg per 30 min (station 634). Catches >100 kg per 30 min occurred only in the south-west corner of the box and in those stations outside of the box further to the south-west (stations 630–636) [Fig. 2(a)]. The highest catch rates were also obtained at stations outside of the box with up to 451 kg per 30 min. Overall the mean catch rate of the stations outside of the box (290·6 kg per 30 min) exceeded that of stations within the box (70·4 kg per 30 min) by a factor of four. The same relationship existed for the mean numbers of whiting per 30 min in the size class 25–29·9 cm, when catch rates in the box were compared with those from the area outside, the difference being highly significant (Mann–Whitney test, $P = 0·001$).

Haddock catch rates varied in a similar range between 51·4 and 485 kg per 30 min. The catches of haddock were more evenly distributed over the entire investigation area with high catch rates both within and outside of the box [Fig. 2(b)]. High catches within the box were also not associated with the south-east corner but rather with the north-west corner. The mean catch rate was higher on the stations located outside of the box (278·3 kg per 30 min) compared to the mean catch rate within the box (163·2 kg per 30 min) by a factor of 1·7. The catch rates of haddock of the size class 25–29·9 cm, however, were only 20% higher in the area outside of the box and this difference was not significant (Mann–Whitney test, $P = 0·442$).

PREY DISTRIBUTION IN THE TRAWL CATCHES

The distribution of sandeel can only be described from the 16 tows with the codend cover attached to the net. The mean number of sandeel caught on stations outside of the box was 275 per 30 min compared to 1·6 per 30 min in stations within the box (Table I). The highest catch obtained outside of the box amounted to 665 per 30 min compared to only 11 per 30 min inside of the box. The other two prey species that were found in high numbers in the codend cover, herring *Clupea harengus* L. and Norway pout *Trisopterus esmarki*

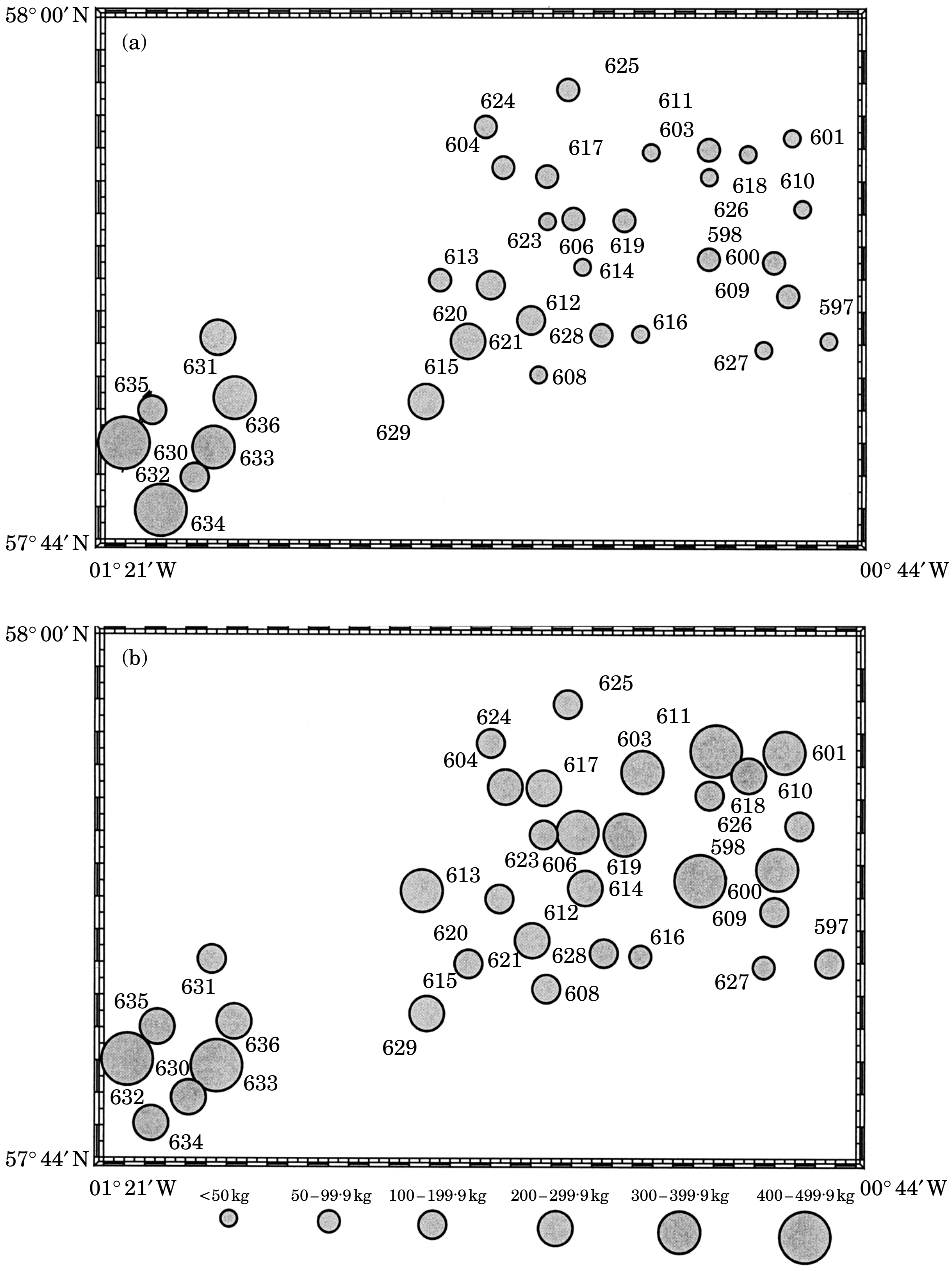

FIG. 2. Spatial distribution of (a) whiting and (b) haddock densities (total catch biomass of all length classes).

(Nilsson), were not found to any major extent in the predator stomachs. Norway pout catches reached peak values both in the box (18 394 per 30 min) and outside (10 563 per 30 min), while catches of herring were high only outside of the box (maximum 1958 per 30 min).

SEDIMENT DISTRIBUTION

The sediment samples revealed mostly fine sand from stations at the circumference of the box with median grain sizes varying from 130 to 231 µm (Fig. 3). In the southern part of the box a band of stations was characterized by medium sands with median grain sizes between 325 and 382 µm [stations 612, 614, 616 and 622 (the last was not fished)]. Outside of the box the majority of stations revealed medium sands with median grain sizes between 254 and 435 µm, the coarsest sediment was found in station 632 outside of the box. The fraction of very fine sediments varied between 40·9 and 0·3%. Stations with a high proportion of very fine sediments were found more in the northern part of the box, while lower proportions were found in the SW including the stations outside of the box, where the station with the least fraction of very fine sediments was located.

STOMACH CONTENTS: SPATIAL EFFECTS

In order for direct comparisons to be made between stomachs sampled inside and outside of the box, the mean value of the samples from within the box was based only on those stations which were trawled between 1927 and 0722 hours because this was the time interval sampled outside of the box. This period included night hours as well as dusk and dawn.

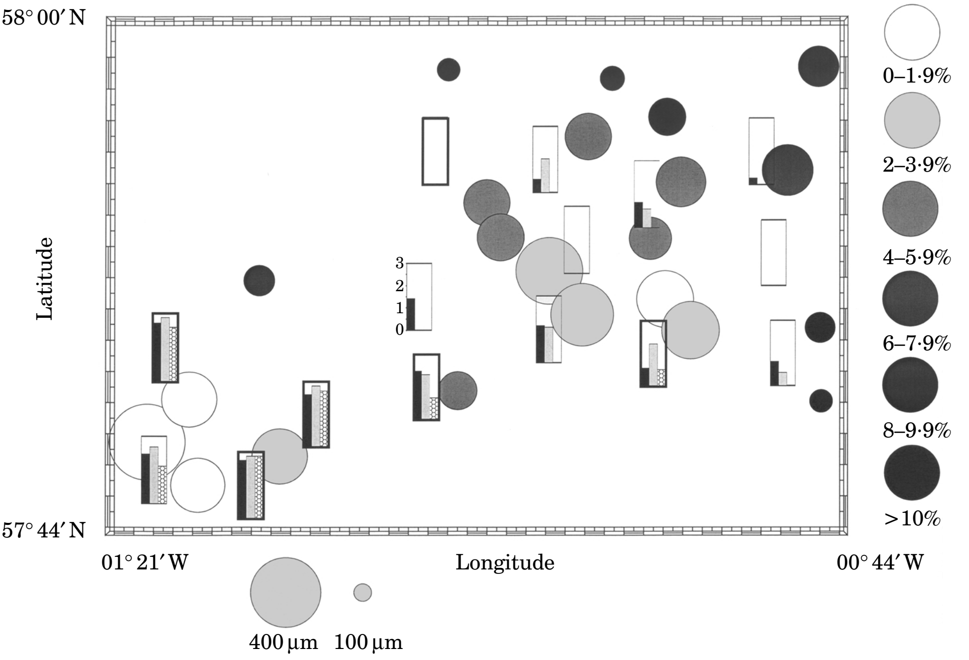

FIG. 3. Median grain size and fraction of very fine sediments of the sediment samples (circles) and ▒, the catch rates of sandeel in the GOV including the catches from the codend cover [$\log_{10}$(number per 30 min)]; ■, the number of sandeels in whiting stomachs [$\log_{10}$(mean number per 100 stomachs); □, the number of sandeels in haddock stomachs [$\log_{10}$(mean number per 100 stomachs)]. A bold frame around the bar chart indicates night samples.

Prey composition

The dominant prey species of whiting was sandeel, which occurred in the stomachs from 25 stations (406 stomachs, 284 in SW_OB, 111 in SW and 11 in SE, NE and NW) and accounted overall for 66% of the stomach contents. Sandeel dominance was most extreme in stations outside of the box and in the south-west corner of the box with 53–93% of the stomach content mass being composed of sandeel [Fig. 4(a)]. Generally high stomach contents (>1 g) corresponded with pure fish diets (99% fishes). The other relevant fish prey were herring and Norway pout accounting overall for 8·62 and 4·86% of the diets in whiting, respectively. Norway pout, however, occurred in only 46 whiting stomachs (seven in SW_OB, 39 in the box). Herring occurred in only 35 whiting stomachs (31 in SW_OB and four in the box). The total contribution of invertebrates to the whiting diet amounted to only 4·49%.

Haddock stomachs revealed a greater share (33·39%) of invertebrates in the diet while the fish diet was clearly dominated by sandeel (86·84% of all fish). The spatial distribution of the sandeel component in the haddock diet resembled closely that of whiting: high shares in the south-west corner of the box and in stations outside [Fig. 4(b)]. The stomach content mass of haddock was positively correlated with the share of sandeel in the diet, as observed in whiting.

Herring and Norway pout accounted for only 0·68 and 1·36% of the fish fraction. Norway pout occurred in only 12 haddock stomachs (one in SW_OB, 11 in box) and herring occurred in four haddock stomachs (one in SW_OB and three in box).

Empty stomachs

The percentage of empty stomachs in whiting varied between 1·6 and 79·2% (Table I) the largest value being 50 times higher than the smallest. The lowest values were observed in samples taken outside of the box, ranging between 1·6 and 26·4% at stations 630 and 636. The mean value outside of the box amounts to 10·5% compared to 49·4% form stations inside the box.

The percentage of empty stomachs in haddock varied between 0·0 and 44·8%. The mean value within the box (10·9%) is about twice as high as the mean from stations outside of the box (5·3%).

Stomach content mass by sub-area

Whiting median stomach contents were zero in all quadrants within the box and *c.* 2 g for the area SW_OB in the night period. The SW quadrant deviated from the other three within the box with a much higher 75% percentile value [Fig. 5(a)]. The overall mean ± S.D. mass of whiting stomach contents from stations within the box (0·503 ± 1·292 g) amounted to only one fifth of the overall mean from stations outside of the box [2·576 ± 2·861 g, Fig. 4(a)].

In haddock the median stomach content was below 1 g in all four quadrants of the box [Fig. 5(b)]. Only the area SW_OB revealed median values >1 g with a maximum >3 g by night. The quadrant SW deviated from the other three quadrants in the box with a higher median and especially a much higher 75% percentile [Fig. 5(b)]. The overall mean ± S.D. mass of haddock stomach contents from all stations outside of the box (3·186 ± 3·499 g) exceeded that of all stations inside of the box (0·955 ± 1·449 g) by a factor of three [Fig. 4(b)].

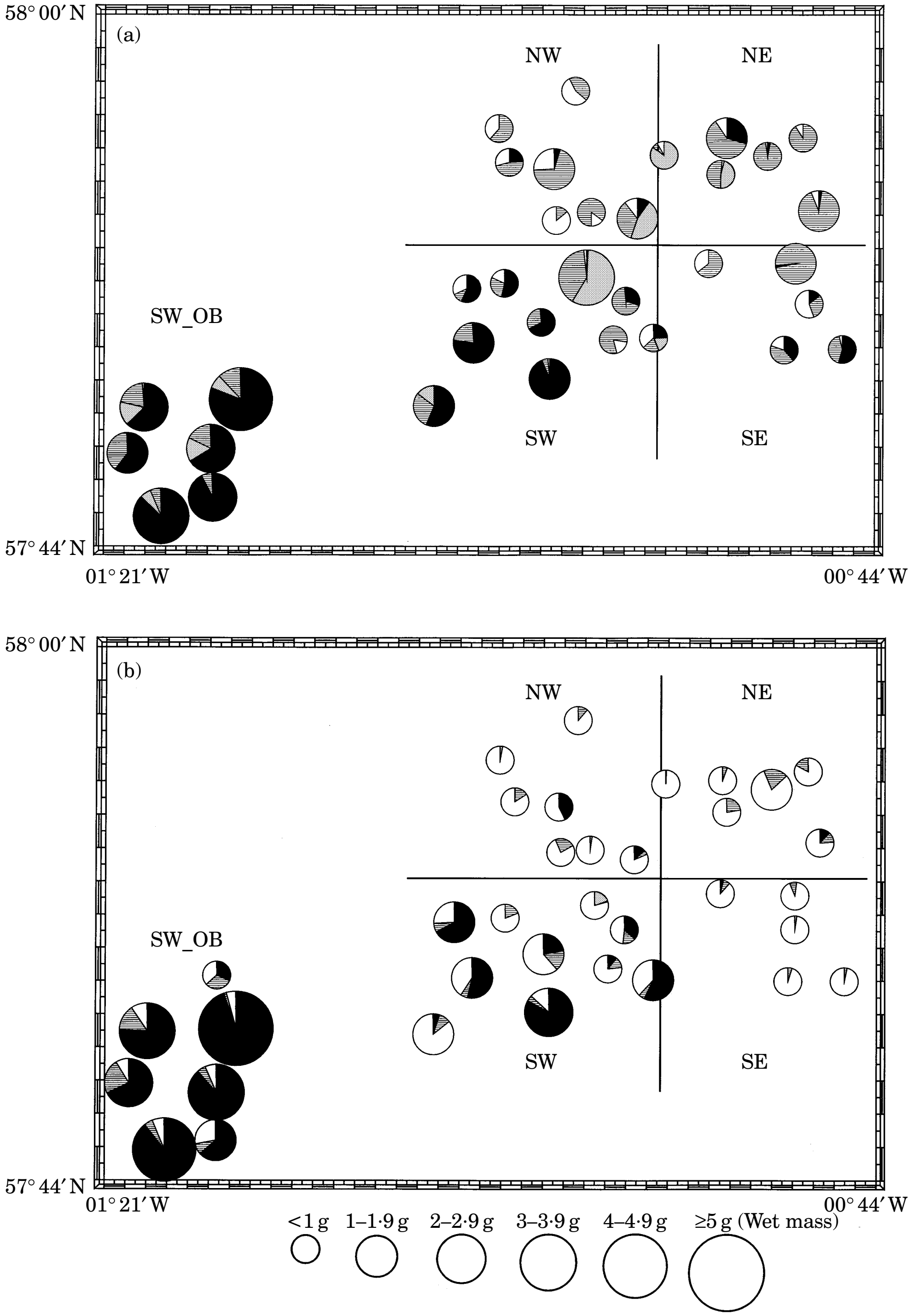

FIG. 4. Prey composition of (a) whiting and (b) haddock stomachs. (●, sandeel, ●, herring, ⊜, undefined fish prey and ○, invertebrates). Box: sub-areas NW, NE, SW and SE; outside of the box: SE_OB (see text).

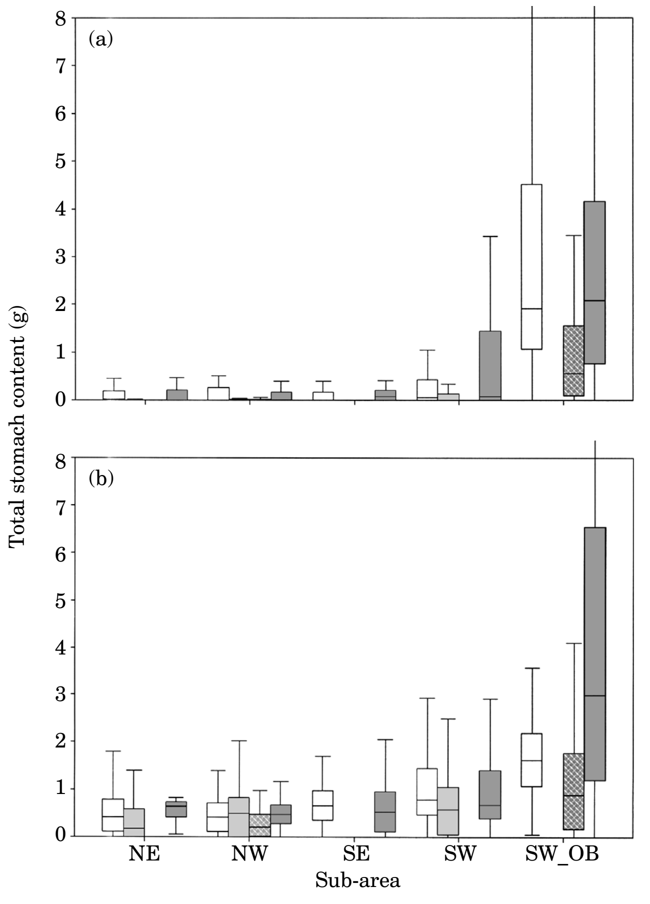

FIG. 5. Grouped box-plots of total stomach content of (a) whiting and (b) haddock by time of day and sub-area (see Fig. 4). Time of day is divided into four periods: 0500–1100 hours (□), 1100–1700 hours (▒), 1700–2300 hours (▩), 2300–0500 (■).

Statistical comparisons between the three larger sub-areas revealed highly significant differences between all combinations of the three sub-areas SW, SW_OB and N + SE for both day and night stations and for both variables (total stomach content and mass of the sandeel in a stomach) with only one exception: for whiting the total stomach contents did not differ significantly from each other in sub-areas N + SE and SW during night hours (Table II).

The GAM model revealed two significant variables: area (as a factor) and time of day (continuous). Predator species and predator L_T (with in the range 25–29·9 cm) were insignificant as explanatory variables. The total explained deviance amounted to 42·6% and sub-area as a factor explained 34·5% of deviance (Table III).

The regression of whiting abundance of the mean amount of sandeel in the stomachs explained 48% of the variance [Fig. 6(a)] and the regression was highly significant ($n = 32$, $r^2 = 0{\cdot}48$, $P = 0{\cdot}000$). If only the night stations were used the explained variance increased to 61% ($n = 24$, $r^2 = 0{\cdot}61$, $P = 0{\cdot}000$). The same regression for haddock (all times) explained only 0·7% of the variance [Fig. 6(b) and was not significant ($n = 33$, $r^2 = 0{\cdot}01$, $P = 0{\cdot}640$).

TABLE II. Significance levels from statistical comparisons of total stomach contents and sandeel mass in stomachs from different sub-areas of the investigation area. Area N + SE includes NW, NE and SE. All comparisons are based on the Mann–Whitney test (two tailed)

			N + SE/SW		SW/SW_OB		N + SE/SW_OB	
Target Variable	Time	Comparison:	Haddock	Whiting	Haddock	Whiting	Haddock	Whiting
Total stomach content	Day*	*n*	360/254	351/236	254/379	236/324	360/324	351/324
		P	0·000	0·000	0·000	0·000	0·000	0·000
	Night†	*n*	320/219	298/193	219/0	193/0	320/0	298/0
		P	0·001	0·157				
Sandeel mass in stomachs	Day	*n*	360/254	351/236	254/379	236/324	360/324	351/324
		P	0·000	0·000	0·000	0·000	0·000	0·000
	Night	*n*	320/219	298/193	219/0	193/0	320/0	298/0
		P	0·000	0·000				

†night: from 1927–0721 hours. The sampling period in area SW_OB covers dusk, night and dawn hours.
*day: from 0722–1926 hours. Times not sampled in the area SW_OB.

TABLE III. Summary of the GAM model fit. A binary model was used to describe the presence and absence of sandeel (sandeel_pa) in the stomachs of whiting and haddock using time of day as scatterplot smoother and sub-area as factor. Predator species and predator total length (in the range 25–29·9 cm) were not significant as explanatory variables and were excluded from the model. The S-Plus syntax was: 'model <- gam[sandeel_pa~sub-area + s(time of day), family = binomial, link = logit]'

	Deviance	Explained deviance (%)	d.f.	χ^2 *P*-value
Null deviance	3369·291		2933·0	
Residual deviance	1869·769		2927·2	
Explained deviance	1499·522	44·5	5·8	
Variables/factors				
Sub-area	1210·309	35·9	1·8	<0·001
Time of day	144·771	4·3	1·0	<0·001
Smoother of time of day	29·861	0·9	2·8	<0·001

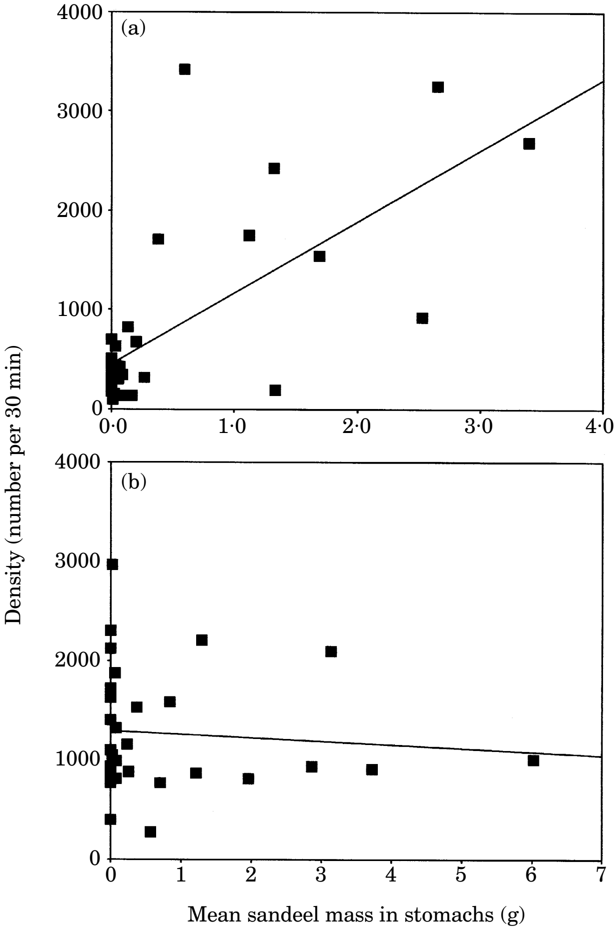

FIG. 6. Regressions of (a) whiting and (b) haddock densities on the mean mass of sandeel in their respective stomachs. (a) The curve was plotted by: $y = 455 + 718x$.

PREY SIZE DISTRIBUTIONS IN STOMACHS AND TRAWL CATCHES

A total of 3357 sandeel were obtained from stomach contents of whiting and haddock out of which 1413 could be used to measure L_T. The majority of sandeel were between 50 and 75 mm. The L_T distributions from stomachs of both predators were very similar and closely followed the length distribution from the codend cover (Fig. 7).

STOMACH CONTENTS: TIME OF DAY EFFECTS

The time of day effect was only investigated from samples of the relatively homogeneous feeding situation, that was encountered on stations 630–636 outside of the box, where both whiting and haddock were feeding intensely on sandeel. These samples cover the time period from 1943 hours (21 July 1996) to 0436 hours (22 July 1996) in a sequence, while the sample from station 630 was taken at 0733 hours on 21 July 1996.

The percentages of empty stomachs decreased from values >15% in the early evening hours to <3% in the early morning hours in both predators with whiting having higher values throughout [Fig. 8(a)]. The mass of the sandeel fractions in the stomachs as well as the mean number of sandeel per stomach increased during the evening and night hours for both predators, with haddock having both higher mass and higher numbers of sandeels in their stomachs compared to whiting [Fig. 8(b)].

The frequency of predators with sandeel in their stomachs increased from about 20% in the early evening hours to almost 100% by the end of the night in

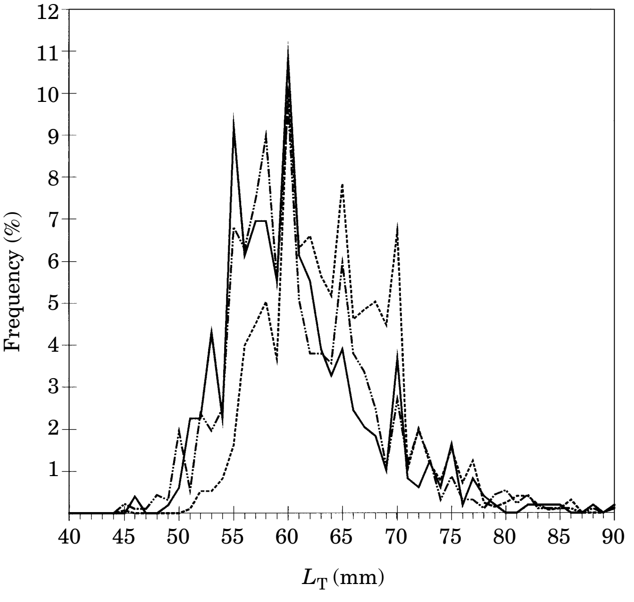

FIG. 7. Length frequency distribution of sandeel found in GOV catches with codend cover attached (┈┈┈, $n = 1404$) and from whiting (——, $n = 489$) and haddock (–·–·–, $n = 924$) stomachs.

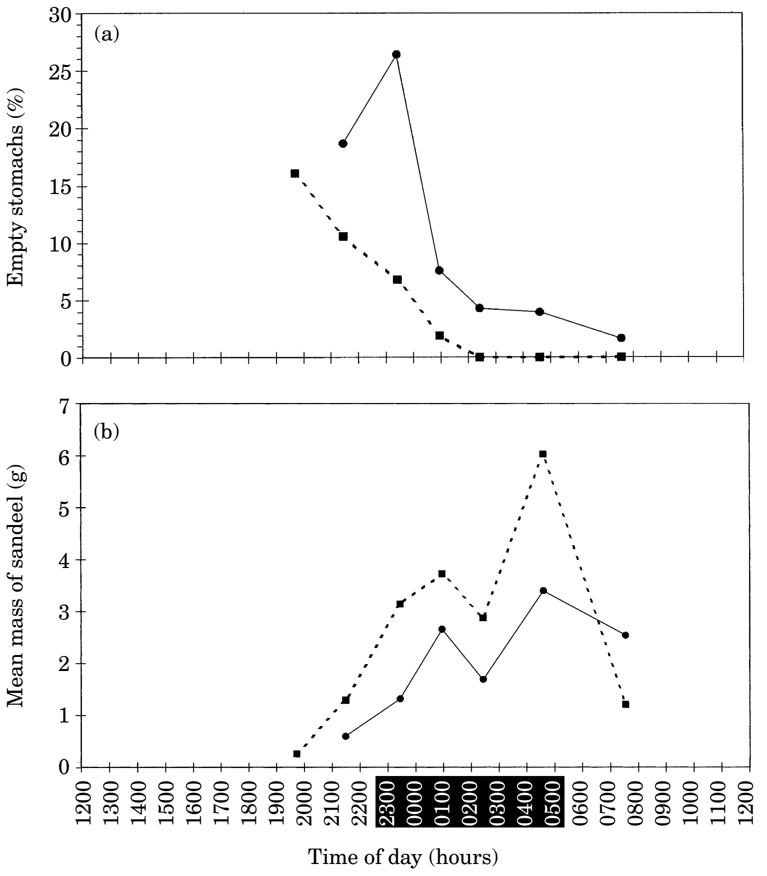

FIG. 8. (a) Percentage of empty stomachs and (b) mean wet mass of the sandeel in the stomachs of whiting (●) and haddock (■) sampled in the sub-area outside of the box (SW_OB) and time of day.

haddock. The pattern for whiting was very similar but on a lower level. If total stomachs contents from stations 630–636 are compared between the two predators, the difference in stomach content levels is statistically significant (Mann–Whitney two-tailed test, whiting $n = 324$, haddock $n = 379$, $P = 0{\cdot}035$).

The sandeels found in predator stomachs in the evening (1953 and 2128 hours) were mostly in a 'progressed' stage of digestion (stage 3). The share of fresh sandeels (stage 1) increased rapidly after 2128 hours in both predators (Fig. 9).

DISCUSSION

SPATIAL PATTERNS OF PREDATOR DENSITY

The trawl catches indicated a strong concentration of whiting in the southwest part of the investigation area mainly outside of the box area (SW_OB) while the SW part of the box showed intermediate densities of whiting. From the smaller sub-set of trawl catches that were performed with the codend cover

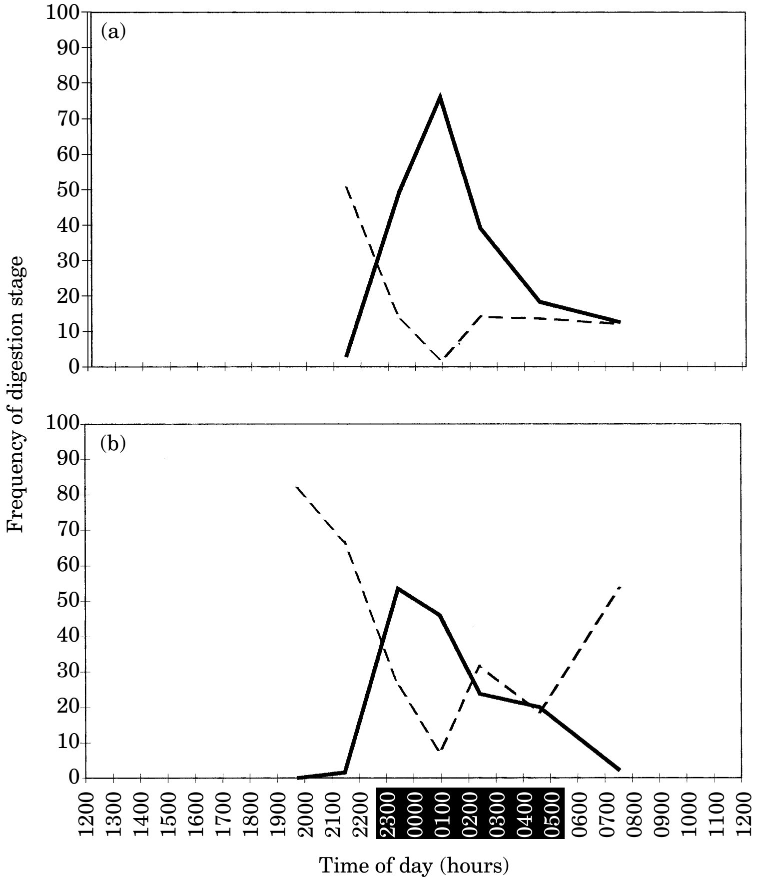

FIG. 9. Frequency distribution of stages [——, stage 1 (intact prey) and - - -, stage 3 (progressed digestion)] of digestion of sandeels found in stomachs of (a) whiting and (b) haddock samples in the small area outside of the box (SW_OB).

attached to the codend it appears, that the sandeel were also concentrating in the same sub-area as the whiting with highest catches in SW_OB and intermediate catches in the SW part. The sandeel data, however, were less reliable than those of the predators, since the catchability of the gear was both variable and low for sandeels, even with the codend cover attached. Sandeels are pelagic during the day and bury by night (Macer, 1966; Winslade, 1974). The GOV net is a ground trawl that may miss sandeel completely during the day hours when they are pelagic. By night, when the sandeel are completely buried the gear may also miss them, since it does not penetrate into the bottom. This assumption is supported by the exclusive restriction of the commercial trawl fishery on sandeel to daylight hours (Reay, 1970). High sandeel catches were obtained in the present investigation mainly in the evening and night hours in the small area outside of the box. This indicates that the sandeel were mainly accessible to the trawl when they stayed close to the bottom in the transition phase between their pelagic and their fully benthic lifestyle. The tows made in other stations at similar evening and night hours, however, did not reveal any substantial catches of sandeel. So overall the limited codend cover data suggest that high concentrations of sandeel were most likely restricted to the small area outside of the box, while intermediate concentrations occurred in the SW part of the box. The limited sediment data would support this interpretation: the station with the most suitable median grain size and the lowest fraction of very fine sediments was located in the area with highest sandeel catches. Stations with small median grain sizes and higher shares of very fine sediments were located more in the NE part of the box. This distribution pattern of sandeel is independently confirmed by the presence and absence pattern of sandeel in the stomachs of the two predators. If the two distribution patterns of predator and prey are viewed together, they basically indicate that whiting aggregate on their sandeel prey. This pattern is less obvious in haddock.

The stomach data of whiting and haddock strongly support the hypothesis of an active behaviour of the predators, because both predators were intensively and exclusively feeding on sandeel in the small area outside of the box. Stomach contents from other stations were much lower and sandeel were only found in the SW part of the box in smaller amounts. The SW part of the box area appeared as a transition area between the areas in the box with low stomach contents and a complete absence of sandeel in the stomachs and the small area outside of the box with high stomach contents and intensive sandeel predation.

Such an aggregative response of predators on a prey aggregation may be caused by two different mechanisms as suggested by Begon *et al.* (1998): 1) direct choice of a predator based on a visual comparison of different prey aggregations or patches and 2) changes in the swimming behaviour with decreasing speed and increasing frequency of turns following a random encounter of a prey aggregation. Investigations of the aggregative response of predators in aquatic environments are rare. The few existing studies concentrated mainly on diver observations in coral reefs (Hixon & Carr, 1997; Connell, 2000). In these environments the direct choice of predators is most likely the relevant mechanism. Predators encounter patches of different densities and dimensions in a short period of time and can base their decision of attack on relatively direct comparisons (Krause & Godin, 1995). Given the spatial dimensions of the present investigation area and the observed distribution patterns as well as the light limitations in water depths of >80 m it is unlikely that the observed aggregation of whiting reflects individual choice based on visual comparisons on these spatial scales. It is more likely that in the present case predators changed their swimming behaviour in an area with overall increased food supply. Since sandeel exhibit two principle modes of aggregation, it is not clear, if whiting deduce an increased density of the sandeel prey from the encounter with schooling sandeel or with benthic aggregations of buried individuals. These two forms of sandeel aggregation, however, are closely related with the time of day and therefore an investigation of the diel pattern of food intake could help to distinguish between the two types of encounter.

TIME OF DAY EFFECT AND VERTICAL MIGRATION

In a previous study (Mergardt & Temming, 1997) evidence for whiting feeding times around night time was found and it was concluded that whiting in principle encounter their sandeel prey during dusk and dawn, when their opposite vertical migration routes cross each other. Whiting are known to migrate into the pelagic by night and stay close to the bottom during the day (Blaxter & Parrish, 1958; Patterson, 1985). The encounter of ascending whiting and descending sandeel would imply that the whiting were feeding on schools of sandeel rather than on buried specimens. This interpretation, however, does not apply to the present data: the highest whiting catches were obtained by night and their stomach contents were continuously increasing during the night until dawn. These results imply that during the night whiting were staying close to the bottom and that sandeel were taken most likely from the sediment. The finding of this study that sandeel were taken around dusk and by night, however, generally confirms the data from the earlier study suggesting that whiting feed on sandeel in crepuscular and nocturnal modes rather than during daylight hours.

SEDIMENT PREFERENCE AND PREY AGGREGATION

It has been demonstrated that sandeel prefer very specific sediments with medium to coarse sands with median grain sizes between 0·25 and 2 mm and likewise avoid sediments with gravel or higher silt, clay and very fine sand fractions (Reay, 1970; Wright *et al*., 2000; Jensen, 2001). The ideal combination of the two sediment properties seems to exist only on very limited habitats such as exposed edges of sand banks (Hobson, 1986; Jensen, 2001). Hobson (1986) found that the burying habitat was a rather restricted patch of coarse sand of *c*. 0·1 ha that sloped sharply between depths of 5 and 10 m. The area around this patch was floored with either silt, fine sand or gravel with additional rocks. The small area outside of the box in the present investigation, where high sandeel densities were found, differed likewise from the remainder of the investigation area due to one station having the coarsest sand of the whole area (station 632 with median particle size 435 μm). According to Wright *et al*. (2000) and Jensen (2001) sandeel densities are inversely related to the fraction of very fine sediments. The same station (632) revealed also the smallest fraction of very fine sediments (0·3%) which makes this station most suitable as a sandeel habitat. Two of the neighbouring stations and one station in the box in the SW quadrant would be the next most attractive habitats with slightly lower median grain sizes and fractions of very fine sediments *c*. 2%. Sandeel densities in the codend cover roughly mirror this spatial pattern: highest densities outside of the box and intermediate densities in the SW part of the box. From the coarse station grid the dimensions of these suitable habitat patches could not be deduced, but it is most likely that the limitation of such optimal habitats may be the true cause for the aggregation of sandeel in the burying phase.

BEHAVIOURAL RESPONSE OF THE PREDATORS ON BURIED SANDEEL

The data revealed that haddock were consuming significantly higher amounts of sandeel during the evening and night hours than whiting. This result is somewhat surprising, since whiting is generally known to be the more effective piscivore, while haddock feed more on benthic organisms (Jones, 1954; Hislop *et al.*, 1997). The most likely explanation for the result is that the sandeel were taken out of the sediment, as was observed by Hobson (1986) for flatfish predators and sea sculpin. Hobson found that especially flatfishes seemed responsive to movements of the sediment above restless sandeel and attacked these by driving the jaws into the sediment. Girsa & Danilov (1976) observed that cod *Gadus morhua* L. feeding on *Ammodytes hexapterus* Pallas attacked sandeel that buried within their visual range immediately after they disappeared in the sediment. Likewise the sea sculpin in Hobson's (1986) observations reacted to sandeel becoming visible when reappearing after having been buried. It may be speculated that the benthic feeders like flatfishes or haddock are more effective in detecting buried sandeel, since they are not restricted to the visual observation of burying or emerging sandeels.

PERSISTENCE OF PREDATOR AGGREGATION

Hobson (1986) observed that predators started to concentrate in the vicinity of the sandeel refuge at the time when daylight was greatly diminished and sandeel started their burying. From the present data there is no direct evidence that the predators actually stay in the restricted area waiting for the sandeel to come back from their daytime feeding period in the pelagic. Remains of sandeel, however, were found in a progressed state of digestion in the stomachs of predators caught before dawn. This indicates that at least some predators fed successfully on sandeel also on the day before the main sampling. Maximum mean stomach contents in whiting in the early morning were *c.* 3 g. Applying the gastric evacuation model of Andersen (1999) it can be predicted that this amount of a 'lean' prey would be almost completely evacuated in 24 h at the given field temperature, so the low average stomach contents of whiting caught in the early evening would not contradict the hypothesis of a prolonged feeding stay of the predators on the sandeel ground. The finding that the whiting were not performing the night ascent as part of the typical vertical migration pattern (Blaxter & Parrish, 1958; Patterson, 1985) supports the view that whiting effectively maintained their position on this particular feeding ground. This interpretation might also apply to the observation of Turner *et al.* (2002) and D. Righton, K. Turner & J.D. Metcalfe (unpubl. data) who found that a group of cod tagged with data storage tags went through a period of strictly demersal behaviour with very limited vertical migration activity. This demersal period lasted from June to July. At this time of the year, 0 year-old sandeel start their nocturnal burying behaviour. After July, the tagged cod exhibited pronounced vertical migrations on a diel cycle, before June they stayed mostly in mid-water. While Turner *et al.* (2002) speculate that the cod were inactive and therefore probably not actively feeding in the demersal phase, an alternative explanation may be the active termination of the vertical migration resulting in an aggregation on a demersal prey concentration such as sandeel.

Aggregative response of predators has been suggested as a potential mechanism of density-dependent regulation of prey populations. The regulating effect, however, depends on the strength of the predators functional response (Connell, 2000). In the case of sandeel a potential regulation through aggregating predators is probably modulated through habitat limitation. If the ideal habitats, which allow fast and complete burying, are fully used at high population densities, increasing numbers of sandeel have to try burying in less suitable habitats with less success of the initial dive, thus raising their vulnerability to the predators. This process would have a stabilizing effect on the recruitment and hence the variability of the population.

SIZE PREFERENCE OF THE PREDATORS

The length frequency distributions of sandeel from the trawl catches (with codend cover attached) and both predator stomachs were very similar to each other: all sandeel prey probably belonged to the newly settled 0 year-group with L_T between 45 and 85 mm. Stomachs of both predators revealed higher proportions of sandeel <60 mm, when compared to the size distribution in the trawl catches. This difference probably reflects the selection properties of the codend cover and does not indicate selective behaviour of the predators in favour of the smallest prey. In essence the data do not suggest any size selection within the available size range of sandeel. While the GOV is capable of catching large sandeel (Mergardt & Temming, 1997), it is certainly not the ideal gear for quantitative sandeel catches. The complete absence of sandeel >11 cm and the very low numbers >8 cm in all hauls, however, suggest that larger sandeel were not present in the investigation area. The unselective feeding may therefore simply reflect this situation. In an earlier investigation (Mergardt & Temming, 1997) a similar situation was described: only large sandeel were found in the codend and in the stomachs of whiting while haddock stomachs contained only invertebrates and hardly any sandeel. They were obviously unable to catch the large sandeel with an average mass of 14 g. The results from both studies indicate that the process of size and species selection in the field is not necessarily a choice from a quasi-simultaneous offered spectrum of prey types, but rather a sequence of decisions on prey types, which are encountered in an extended area for a certain period of time. The decision is to either take the prey type encountered or to pass on. If such extended patches of homogeneous prey types occur frequently in the field, they should lead to relatively flat size preference functions where predators should always take the prey encountered within a broad range of appropriate sizes. The encounter of prey patches would then be the main determinant of the average predator stomach content composition at the meso – macro spatial scale as suggested by Floeter & Temming (2003).

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