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Piscine predation on juvenile fishes on a Scottish sandy beach

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Predation by larger fishes is a major cause of mortality for the populations of juvenile fishes on a sandy beach on the west coast of Scotland. Predation was concentrated on the most numerous species (0-group *Pleuronectes platessa*) in June but with the decline in numbers and growth in size of this species, the fish predators had changed their diet in August to feed principally on small sandeels (Ammodytidae). Six major predatory species had taken 95 per cent of all fish found in predators' stomachs and could be roughly divided into three categories according to their piscivorous tendencies and their abundance. (1) Common species in which fishes formed the main item of their diet (*Gadus morhua*). (2) Species in which fishes formed only a relatively minor constituent of the diet but which, by virtue of their abundance, potentially had a significant predatory impact (I-group *P. platessa*). (3) less abundant species whose diet consisted principally of fishes. The intensity of predation was generally greatest at night for *G. morhua* but during the day for I-group *P. platessa*. The distributions and movements of the dominant prey species can be interpreted in the light of their predator–prey relationships. The most common benthic species, 0-group *P. platessa*, move off- and onshore with the ebb and flow of the tides and concentrate in shallow water at night. Such movements would have the effect of maintaining the majority of the population in depths where predation pressure from nocturnally onshore-migrating gadoids and other predators is likely to be minimized.

Key words: predation; sandy beach; feeding; *Pleuronectes platessa*; *Gadus morhua*.

INTRODUCTION

Sandy beach fish populations have been studied in many parts of the world (see Brown & McLachlan, 1990 for review) and a common finding is that such populations consist predominantly of juveniles (Modde, 1980; Lasiak, 1981, 1986; Senta & Kinoshita, 1985; Peters & Nelson, 1987; Bennett, 1989; Gibson *et al.*, 1993 among others). In temperate regions the influx of larvae and juveniles at the end of the adults' breeding season is generally followed by a decline in numbers, imposing a strong seasonal variation on population size. The decline in numbers is usually attributed to a combination of emigration and mortality. Mortality is often heavy and, although its causes are not well known, predation is usually considered to be a major contributory factor (Beverton & Iles, 1992). Because detailed studies of sandy beach food webs are scarce, the identity of the predators has been established only rarely and is inferred mostly from the presence of likely piscivorous species in the same area (Tyler, 1971; Toole, 1980; Kramer, 1991). Where predators have been identified, they are usually other fishes (Macer, 1967; Edwards & Steele, 1968; Lockwood, 1972;

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Brown & McLachlan, 1990) or decapod crustaceans (van der Veer & Bergman, 1987; Sekai *et al.*, 1993).

This paper reports the results of a field study designed to investigate the nature and extent of predation upon juvenile fishes on a Scottish sandy beach with particular reference to predation by other fishes. The study had three principal objectives. (1) To determine the piscine predators of juvenile fishes and the relative importance of the various prey species in their diets. (2) To determine temporal variations in predation intensity on fishes over tidal, diel and longer time scales. (3) To determine whether the distribution and movements of the prey species are related to those of their predators. The investigation forms part of a wider study of the ecology of sandy beach fish populations (Gibson *et al.*, 1993, 1995; Burrows *et al.*, 1994).

MATERIALS AND METHODS

STUDY AREA

The study area was situated at Tralee Beach in Ardmucknish Bay on the west coast of Scotland (56°29′ N, 5°25′ W). This beach is approximately 1 km long, faces southwest and is bordered by rocky headlands. Mean tidal ranges are 3·3 m on springs and 1·1 m on neaps. Low water of spring tides occurs at approximately midday and midnight. Below the low water mark the substratum consists mainly of fine sand, whereas intertidally it is coarser and less well sorted. The infauna is dominated by polychaetes, particularly *Lanice conchilega* and *Pygospio elegans*. The macrocrustacean epifauna and fishes are described in detail elsewhere (Gibson *et al.*, 1993).

SAMPLING METHODS

All fishes, both predators and prey, were sampled using three types of gear. A 2-m beam trawl (15-mm stretched mesh with 3-mm liner in the codend) was towed for approximately 5 min parallel to the shore in depths of 0·5, 1, 2, 3 and 4 m. At 0·5 m the trawl was pulled by two people on foot. At greater depths it was towed by boat. Hauls were also made with a 3-m beam trawl in depths of 5 m by a larger vessel. To sample pelagic species adequately, hauls were made with a 36 × 1·8 m beach seine with an 8-mm mesh in the central portion. The net was set by boat parallel to, and approximately 50 m from, the shore at a depth of 1 to 1·5 m. Further details of the sampling methods are given in Gibson *et al.* (1993, 1995). The catch from each haul was anaesthetized in a 50 mg l^{-1} solution of benzocaine and preserved in approximately 8% formalin.

SAMPLING REGIME AND RATIONALE

Pilot studies had suggested that many of the predators likely to feed on young fishes were either absent during the day or were more active at night. Subsequent more detailed studies (Gibson *et al.*, 1995) confirmed this initial impression. Consequently, the sampling schedule was designed to sample fishes at times when predation was considered to be most likely and compare these samples with others taken during the day. Specifically, samples were taken on 2 days in each of June and August 1990 at 3 h before sunset (SS − 3), 1 h after sunset (SS + 1), midway between sunset and sunrise (MSSSR), at sunrise (SR) and 3 h after sunrise (SR + 3). In June SS and SR were at approximately 22.00 and 04.30 hours BST whereas in August they were at approximately 21.00 and 05.45 hours BST respectively. Sampling dates in the 2 months were separated by 1 week so that both a high tide and low tide occurred as near to midnight as possible. This schedule allows the separation of possible tidal and diel effects. Sampling of all depths with each gear took approximately 1 h but time constraints in the face of changing light and tide did not allow replicate hauls to be taken. Predicted (neap) high water heights were identical on the two June sampling dates but differed by 0·9 m in August. The weather conditions were comparable on all sampling dates.

LABORATORY METHODS

All fishes were sorted from each haul, identified, counted, measured (total length to the nearest mm), damp dried and weighed to the nearest 0·01 g.

Based on previous qualitative studies of their diets only those individuals of cod *Gadus morhua* L. and other benthic and demersal species >50 mm total length were selected for further examination. Where numbers allowed, up to 10 individuals from each haul were examined.

The stomachs were removed, opened and an estimate of fullness made by eye on a scale of 0–5 (0 = empty; 1 = empty–<25% full; 2 = 25–<50% full; 3 = 50–<75% full; 4 = 75%–full; 5 = distended). Each stomach was then weighed, emptied and weighed again to give a wet weight of the contents by difference.

Prey items were identified to the lowest taxonomic category and to species if possible, counted, and an estimate made of the volume of each prey type. Volume was measured by gently compressing all items of one prey type to a uniform thickness (1·1 mm) between glass microscope slides resting on millimetre graph paper. The number of squares on the graph paper covered by the food were then counted and multiplied by 1·1 to give the volume in mm^3. The volumes of large prey items were measured by displacement of water in a small measuring cylinder.

DATA ANALYSIS

Temporal and spatial differences in dietary composition on a presence or absence basis were tested using the χ^2-test or, where this was invalid due to small expected values, the Fisher exact test. Two questions were asked concerning possible variations in feeding intensity. First, does the proportion of feeding individuals in the population change over the tidal and diel cycle? Secondly, does the intensity of feeding change with time? The second question was examined using visual estimates of stomach fullness and the actual weight of stomach contents. These two methods of estimating feeding intensity, which are frequently used but rarely compared, differ in their accuracy although the former has the advantage of being rapid once a scoring scheme has been developed. Consequently, analysis of changes in feeding intensity was carried out in three ways for each date: (1) a comparison of the proportions of fish with empty stomachs in each sample period; (2) an analysis of the distribution of fullness scores for each sample period (Kruskal–Wallis test) and (3) an examination of the changes in the food weight : body weight ratio for each sample period (Kruskal–Wallis test). In addition, the relationship between fullness score and the ratio of food weight to body weight was examined. All statistical tests were done using the SAS statistical package (SAS Institute, Inc., 1990).

RESULTS

SPECIES COMPOSITION OF THE CATCHES

Thirty-three species were caught, 31 by trawl and 24 by seine, with 22 species common to both gears. The trawl catches were dominated numerically by six species [plaice, *Pleuronectes platessa* L. (39% of total catch); dab *Limanda limanda* (L.) (24%); grey gurnard, *Eutrigla gurnardus* (L.) (15%); cod (6%); poor cod, *Trisopterus minutus* (L.) (6%) and sand goby, *Pomatoschistus minutus* (Pallas) (3%)], whose abundance varied between dates. *L. limanda* was commonest in June whereas *T. minutus* was only common in August. The seine catches were more variable in composition, particularly in the numbers of the dominant species caught between dates. *P. platessa* (31%), sandeel *Ammodytes tobianus* L. (27%), *G. morhua* (11%), whiting *Merlangius merlangus* (L.) (10%), *E. gurnardus*

TABLE I. Diets of predator species examined

Predators	*E. vip.*	*E. gur.*	*M. sco.*	*G. mor.*	*M. mer.*	*P. vir.*	*M. aeg.*	*P. fle.*	*P. pla.*	*T. min.*	*P. min.*	*P. pol.*	*A. cat.*	*L. lim.*	*P. loz.*
No. examined	67	25	17	400	105	56	11	44	554	74	207	11	56	40	3
No. with food	40	23	15	370	91	55	11	20	449	72	88	10	49	22	2
Min. length	70	52	85	50	51	51	84	72	62	51	51	67	55	73	57
Max. length	129	143	143	139	143	129	124	375	171	104	87	103	134	122	60
Prey species															
Teleostei Total	92·3	91·6	89·9	71·7	74·3	29·5	31·5	13·9	12·8	9·0	8·8	6·5	1·4	—	—
Polychaeta Total	3·4	1·8	0·7	10·9	8·1	3·2	36·6	24·5	81·3	37·9	59·8	1·8	17·1	93·6	71·4
Harmothoe sp	—	—	0·1	0·1	—	—	—	—	0·2	—	1·5	—	16·2	0·3	—
Nephtys sp	—	—	—	0·7	5·0	—	—	—	8·7	—	0·1	—	0·1	—	—
Nereidae	3·4	—	—	0·8	0·9	2·6	—	21·2	5·8	0·2	3·7	—	0·1	—	—
Eulalia sp	—	—	—	0·7	0·1	0·1	—	—	1·9	26·8	11·4	—	—	6·6	34·7
Spionidae	—	—	—	0·4	—	—	—	—	2·3	—	—	—	—	0·2	—
Lanice body	—	1·8	0·5	6·9	1·2	—	6·0	—	23·9	5·9	37·5	—	—	79·0	6·1
Lanice tentacles	—	—	—	—	—	—	—	0·9	0·1	—	0·4	—	—	6·9	20·4
Arenicola marina	—	—	0·1	—	0·5	—	—	2·3	35·7	—	—	—	0·8	0·6	—
Other Polychaeta	—	0·0	—	1·4	0·5	0·5	30·5	0·1	2·9	5·0	5·3	1·8	—	—	10·2
Crustacea Total	4·2	5·2	8·9	16·3	16·0	62·0	20·5	61·5	3·3	43·9	18·5	91·6	79·8	3·0	20·4
Copepoda	0·0	0·0	—	1·1	0·1	1·1	7·7	—	—	6·5	3·0	6·8	1·5	0·2	4·1
Cirripedia	—	—	—	0·1	0·0	0·5	—	—	—	9·3	0·3	0·4	0·1	—	2·0
Mysidacea	0·6	0·1	0·0	0·4	0·2	1·9	0·7	0·2	0·0	2·1	—	2·5	1·5	—	2·0
Isopods Total	1·0	—	0·3	2·5	1·8	19·3	—	1·9	0·0	1·4	—	30·7	6·2	0·0	—
Idotea sp	1·0	—	0·3	2·2	1·0	17·3	—	1·5	—	0·3	—	25·5	5·9	—	—
Amphipoda Total	0·4	0·3	0·5	4·2	4·8	14·2	11·1	10·4	0·4	18·8	7·1	36·9	38·6	1·6	10·2
Talitridae	—	—	—	0·3	0·2	1·3	—	5·7	0·0	—	—	0·4	0·2	—	—
Gammarus sp	0·2	0·2	—	1·9	2·1	10·9	—	4·4	—	0·9	1·3	35·5	31·4	—	—
Bathyporeia sp	0·1	0·0	0·5	0·9	1·4	1·6	1·0	0·1	0·2	5·7	1·3	—	0·4	1·6	4·1
Other Amphipoda	—	0·0	0·0	0·0	1·1	1·1	0·4	10·1	0·2	0·2	12·2	4·5	1·1	6·7	—
Decapoda Total	2·3	4·8	8·0	7·0	8·7	22·9	1·0	48·9	2·8	2·0	7·2	6·3	23·1	1·1	—
Crangon crangon	2·0	4·8	6·9	3·9	7·8	15·9	1·0	48·9	1·1	0·8	—	4·1	1·2	—	—
Other Decapoda	0·3	—	1·1	3·1	0·9	7·0	—	—	1·7	1·2	7·2	2·2	21·9	1·1	—
Other Crustacea	—	—	—	1·1	0·5	2·2	—	—	0·1	4·0	0·9	8·1	8·9	0·0	2·0
Unidentified tissue	—	—	—	0·7	0·3	1·5	6·0	—	0·1	8·2	1·8	—	1·1	0·1	—
Weed	0·0	1·2	0·5	0·2	0·6	—	—	0·1	0·0	—	1·9	—	0·3	0·3	8·2
Miscellaneous	—	0·2	0·0	0·4	0·7	4·2	5·4	0·0	2·4	1·1	9·1	0·2	0·2	3·1	—

Values in table are volume of each prey item as percentage of total food volume. All sampling dates combined.

Key to species names: *E. vip.*, *Echiichthys vipera*; *E. gur.*, *Eutrigla gurnardus*; *M. sco.*, *Myoxocephalus scorpius*; *G. mor.*, *Gadus morhua*; *M. mer.*, *Merlangius merlangus*; *P. vir.*, *Pollachius virens*; *M. aeg.*, *Melanogrammus aeglefinus*; *P. fle.*, *Pleuronectes flesus*; *P. pla.*, *Pleuronectes platessa*; *T. min.*, *Trisopterus minutus*; *P. min.*, *Pomatoschistus minutus*; *P. pol.*, *Pollachius pollachius*; *A. cat.*, *Agonus cataphractus*; *L. lim.*, *Limanda limanda*; *P. loz.*, *Pomatoschistus lozanoi*.

TABLE II. Percent frequency of occurrence of fishes in predator stomachs

Predator species	June			August		
	NT	NF	%*F*	NT	NF	%*F*
Echiichthys vipera	30	14	47	37	11	30
Eutrigla gurnardus	17	16	94	8	6	75
Myoxocephalus scorpius	6	4	67	11	9	82
Gadus morhua	195	94	48	205	32	16
Merlangius merlangus	22	3	14	83	12	14
Pollachius virens	26	1	4	30	3	10
Pollachius pollachius	—	—	—	11	1	9
Melanogrammus aeglefinus	—	—	—	11	2	18
Trisopterus minutus	11	1	9	63	0	0
Pleuronectes flesus (I group)	24	3	13	20	1	5
Pleuronectes platessa (I group)	328	29	9	226	29	13
Pomatoschistus minutus	162	9	6	45	0	0
Agonus cataphractus	48	1	2	8	0	0

NT, Total number examined; NF, number with fishes in the stomach; %*F*, percentage with fishes in the stomach. Data for the months of June and August are shown separately.

(6%) and herring *Clupea harengus* L. (3%), were most abundant. Full details of the species composition of the catches are given elsewhere (Gibson *et al.*, 1995) but in general, the catches consisted of juveniles of large species and juveniles and adults of small species, reflecting the nursery ground characteristics of the study area.

OCCURRENCE AND RELATIVE IMPORTANCE OF FISHES AS PREY

Twenty-one species considered as possible predators of fishes were examined. Six were rare (<five individuals) and have been excluded from further analysis. Of the remaining 15 species, 13 had recognizable remains of fishes in their stomachs (Table I). In seven of these 13 species, fishes were a dominant prey item (>25% total volume) and in five of these, fishes made up >70% of the diet by volume. The most common piscivorous species were cod, whiting, grey gurnard, lesser weever *Echiichthys vipera* (Cuvier) and short-spined sea scorpion *Myoxocephalus scorpius* (L.). Those species in which fishes formed only a minor dietary item or which were absent from the diet, fed principally either on polychaetes or crustaceans (Table I). There was a general correspondence between the percent occurrence of fishes in the diet and their importance by volume (compare Tables I and II).

IDENTITY OF FISHES EATEN

Although the presence of fish remains in the stomachs could be recognized easily, identification of the species eaten was more difficult and dependent on the degree of digestion. Nevertheless, in most cases a species or group could be assigned to each set of remains. Predation was most common on small flatfishes and sandeels (Table III). Gobies, gurnards and gadoids were eaten also, particularly by *M. scorpius*. There was little evidence of cannibalism by any species.

TEMPORAL CHANGES IN THE PROPORTION OF FISHES IN DIETS

Where the data were sufficient to make an objective assessment, the proportion of predators with fishes in their diet decreased from June to August in cod (χ^2 test, $P<0{\cdot}001$) but no significant changes were detectable in plaice or lesser weever ($P>0{\cdot}05$) (Table II). In grey gurnards and cod there was a change in the principal prey item from flatfishes in June to sandeels in August (Table III). The larger size of the sandeels meant that although fewer individual predators were feeding on fish, the relative total volumes of fish in their diets did not change between the 2 months.

In both June and August a significantly higher proportion of cod contained fish in their stomachs at night (Fig. 1, $P=0{\cdot}004$ and 0·03 respectively). For plaice in both June and August, the pattern seen in cod seemed to be reversed with an apparently higher proportion of predators with fish in their stomachs during the day (Fig. 1). When treated separately the effect was not significant for either month ($P=0{\cdot}218$ and 0·073 respectively) but when the data for the 2 months were combined the effect was significant at $P=0{\cdot}029$ (Fig. 1). The proportion of weevers eating fish was more or less constant throughout the five sampling periods (Fig. 1). There were no clear indications that fishes made up a significantly different proportion of the diet at night in cod, plaice or weevers in either month.

SPATIAL DIFFERENCES IN DIET COMPOSITION

There was no difference in the proportion of cod that fed on fish at different depths in June (Fig. 2, $P=0{\cdot}193$). In August however, a higher proportion of cod caught in depths of 1 m or less had fish in their stomachs than those caught in 2–5 m (Fig. 2, $P<0{\cdot}0001$). The latter effect was highly significant for plaice in both months (Fig. 2, $P<0{\cdot}0001$) but not for weevers in either month (Fig. 2, $P=0{\cdot}974$). There was no evidence that fish caught at different depths had been feeding on different prey types.

TEMPORAL CHANGES IN FEEDING INTENSITY

Only cod and I-group plaice were sufficiently numerous to allow temporal changes in feeding intensity to be investigated in detail.

Proportion of empty stomachs

In cod, the lowest proportion of fish with empty stomachs occurred at night (Fig. 3) but this effect was only just significant ($P=0{\cdot}049$) when the data from both months were combined. The opposite trend was seen in plaice in August where the highest proportion of empty stomachs was found in the middle of the night and early morning (Fig. 3, $P<0{\cdot}001$). There was no significant difference between sample times in this respect in June (Fig. 3, $P=0{\cdot}125$).

Stomach fullness

Cod generally had fuller stomachs during the hours of darkness and a representative pattern is shown in Fig. 4. However, the distribution of fullness scores between sample times differed significantly only on 14 June ($P=0{\cdot}021$) and 14 August ($P=0{\cdot}0007$). Plaice showed a similar pattern to cod in June ($P=0{\cdot}006$, Fig. 4) but the distribution of fullness scores was not significantly different on 20

TABLE III. Relative importance of fish prey species as percentage of total volume of fish eaten

Prey species	Predator species												
	A. cat.	*E. gur.*	*G. mor.*	*M. aeg.*	*M. mer.*	*M. sco.*	*P. min.*	*P. pol.*	*P. vir.*	*P. fle.*	*P. pla.*	*T. min.*	*E. vip.*
(A) June													
Agonus cataphractus	—	—	—	—	—	11·6	—	—	—	—	—	—	—
n	—	—	—	—	—	1	—	—	—	—	—	—	—
Limanda limanda	—	—	11·2	—	—	4·0	62·8	—	—	24·7	3·6	80·7	—
n	—	—	14	—	—	2	2	—	—	1	1	1	—
Pleuronectes platessa	—	—	—	—	—	3·8	—	—	—	—	—	—	10·7
n	—	—	—	—	—	2	—	—	—	—	—	—	2
Unid. flatfish	—	89·3	73·6	—	—	—	13·4	—	—	—	1·3	—	—
n	—	35	118	—	—	—	2	—	—	—	1	—	—
Gadoids	—	10·4	—	—	—	17·9	—	—	—	—	—	—	—
n	—	3	—	—	—	1	—	—	—	—	—	—	—
Gobies	100·0	—	0·5	—	24·7	38·4	—	—	—	—	0·8	—	—
n	1	—	1	—	1	1	—	—	—	—	2	—	—
Gurnards	—	—	1·1	—	—	23·2	—	—	—	—	—	—	17·8
n	—	—	2	—	—	2	—	—	—	—	—	—	2
Sandeels	—	—	9·8	—	61·7	—	—	—	100·0	55·6	92·5	—	38·2
n	—	—	5	—	1	—	—	—	1	1	27	—	9
Unid. roundfish	—	—	3·0	—	13·6	—	—	—	—	19·8	0·6	18·1	33·1
n	—	—	6	—	1	—	—	—	—	1	1	1	7
Unid. fish	—	0·3	0·9	—	—	1·1	23·8	—	—	—	1·3	1·2	0·2
n	—	1	9	—	—	1	5	—	—	—	5	2	1

(B) August													
Myoxocephalus scorpius	—	—	0·3	—	—	—	—	—	—	—	—	—	—
n	—	—	1	—	—	—	—	—	—	—	—	—	—
Echiichthys vipera	—	0·9	—	—	—	—	—	—	—	—	—	—	—
n	—	1	—	—	—	—	—	—	—	—	—	—	—
Limanda limanda	—	—	1·6	—	—	—	—	—	—	100·0	—	—	—
n	—	—	1	—	—	—	—	—	—	1	—	—	—
Scophthalmus sp	—	—	2·0	—	—	—	—	—	—	—	—	—	—
n	—	—	1	—	—	—	—	—	—	—	—	—	—
Unid. flatfish	—	10·0	—	—	—	—	—	—	—	—	—	—	5·1
n	—	1	—	—	—	—	—	—	—	—	—	—	1
Gadoids	—	—	—	—	—	27·5	—	—	—	—	—	—	—
n	—	—	—	—	—	3	—	—	—	—	—	—	—
Gobies	—	—	0·1	—	16·9	9·6	—	—	—	—	—	—	—
n	—	—	1	—	1	1	—	—	—	—	—	—	—
Gurnards	—	—	—	—	—	46·7	—	—	—	—	—	—	—
n	—	—	—	—	—	5	—	—	—	—	—	—	—
Sandeels	—	89·1	95·8	—	79·6	5·1	—	100·0	92·4	—	99·5	—	39·5
n	—	16	47	—	17	1	—	1	2	—	36	—	3
Unid. roundfish	—	—	0·2	—	3·5	11·2	—	—	7·6	—	0·5	—	55·4
n	—	—	1	—	1	2	—	—	1	—	2	—	7
Unid. fish	—	0·1	—	100·0	—	—	—	—	—	—	—	—	—
n	—	1	—	2	—	—	—	—	—	—	—	—	—
No. prey eaten	1	58	207	2	22	20	9	1	3	4	76	4	32
No predators examined	56	25	400	11	105	17	207	11	56	44	554	74	67
Fish/predator	0·02	2·32	0·52	0·18	0·21	1·18	0·04	0·09	0·05	0·09	0·14	0·05	0·48
% total fish eaten	0·2	13·2	47·2	0·5	5·0	4·6	2·0	0·2	0·7	0·9	17·3	0·9	7·3

n, No. individuals eaten. Species codes as Table I.

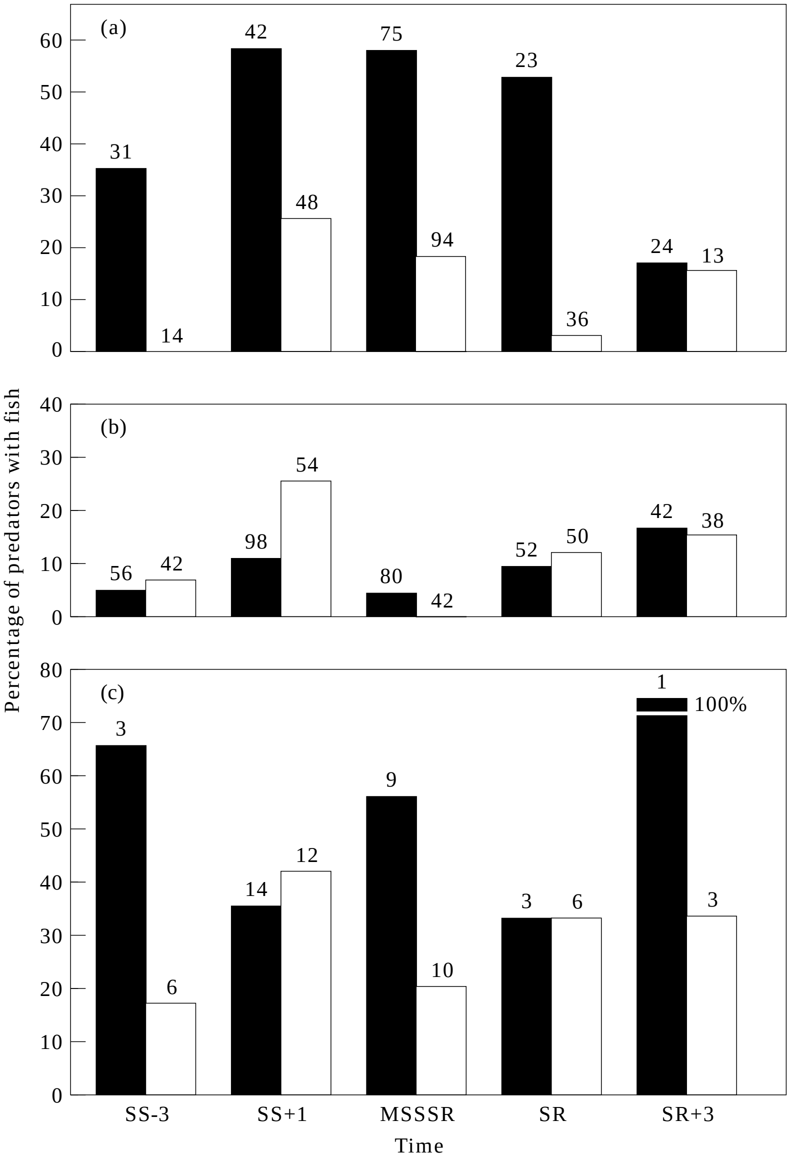

FIG. 1. Variation in the percentage of predators with fish in their stomachs over the five sampling periods for (a) cod, (b) plaice and (c) weevers. Sample sizes are given above each bar. ■, June; □, August. SS − 3, 3 h before sunset; SS + 1, 1 h after sunset; MSSSR, midway between sunset and sunrise; SR, sunrise; SR + 3, 3 h after sunrise.

June ($P=0{\cdot}052$) or 6 August ($P=0{\cdot}11$). On 14 August the pattern was reversed with a significantly greater proportion of higher fullness scores during the day ($P=0{\cdot}0006$, Fig. 4).

Weight of food in stomachs

Analyses of the changes in food weight : body weight ratios between sampling times showed a consistent pattern for cod for each date in that the greatest

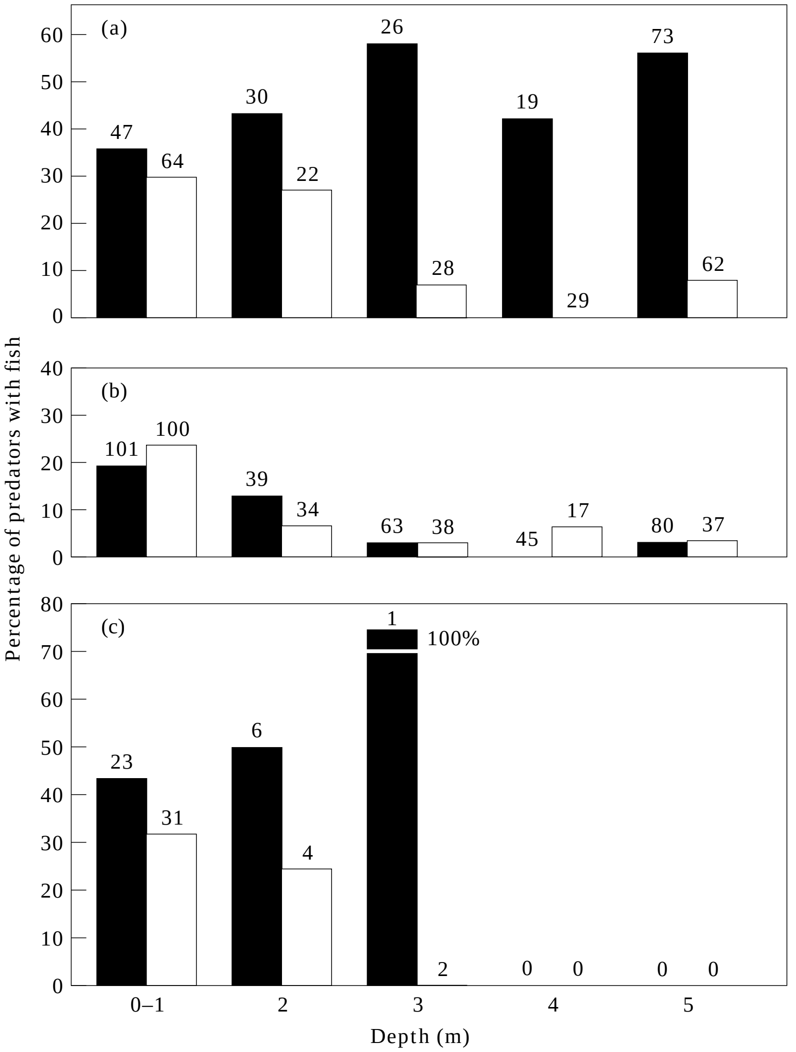

FIG. 2. Variation in the percentage of predators with fish in their stomachs with depth of capture for (a) cod, (b) plaice and (c) weevers. Sample sizes are given above each bar. ■, June; □, August.

weight of food was most frequently found in the stomachs during the night hours (Fig. 5), although the differences were significant only on 14 June ($P = 0{\cdot}0064$) and 14 August ($P = 0{\cdot}0001$). For plaice, the food weight : body weight ratios were significantly different between times for each date but the pattern of change in feeding intensity was less clear. There was a tendency, however, for the highest ratios to occur during the hours of daylight (Fig. 5).

In none of the analyses of feeding intensity could any unambiguous effects of tidal state be detected but there may be an indication of such an effect in the observation that there were significant differences in both measures of feeding intensity for cod only on 14 June and 14 August when high water occurred during darkness. A similar effect on fullness scores was detected on the same dates for plaice, and to a lesser extent in food weight : body weight ratios, where

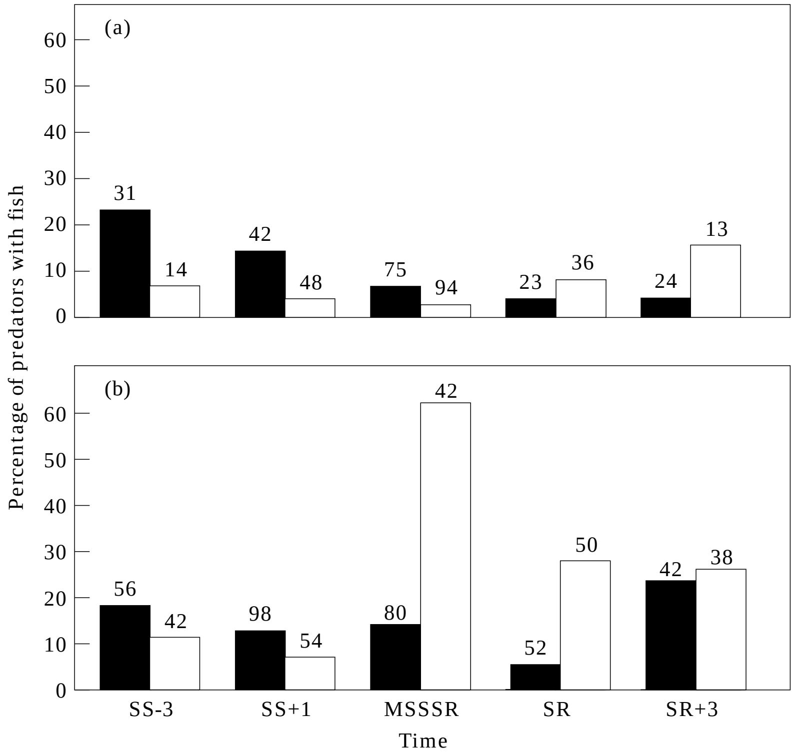

FIG. 3. Variation of the percentage of predators with empty stomachs over the five sampling periods for (a) cod and (b) plaice. Sample sizes are given above each bar. ■, June; □, August. Abbreviations as Fig. 1.

the significance of the differences was much greater ($P<0{\cdot}005$) on 14 June and 14 August than on 20 June and 6 August ($P<0{\cdot}05$).

Relationship between stomach fullness and food weight

The relationship between stomach fullness score and food weight as a percentage of body weight was non-linear in all cases examined (Fig. 6) and the variation in food weight as a percentage of body weight associated with a given fullness score increased markedly with increasing fullness score. The two methods give essentially the same results (see previous two sections) and for the detection of feeding patterns over time the fullness method may be preferable on the basis of its speed. The considerable overlap in the food weight : body weight ratios for a given fullness score (Fig. 6) can be attributed to at least three factors:

(1) Inconsistency in score allocation. Inconsistency is most likely at the beginning of an investigation and decreases with experience and increased sample size.

(2) Differences in density among prey types. An unavoidable source of variation caused by variations in weight per unit volume of different prey. Crustaceans and molluscs with shells, for example, are likely to be denser than polychaetes and it was noticeable in plaice that low food weight : body weight

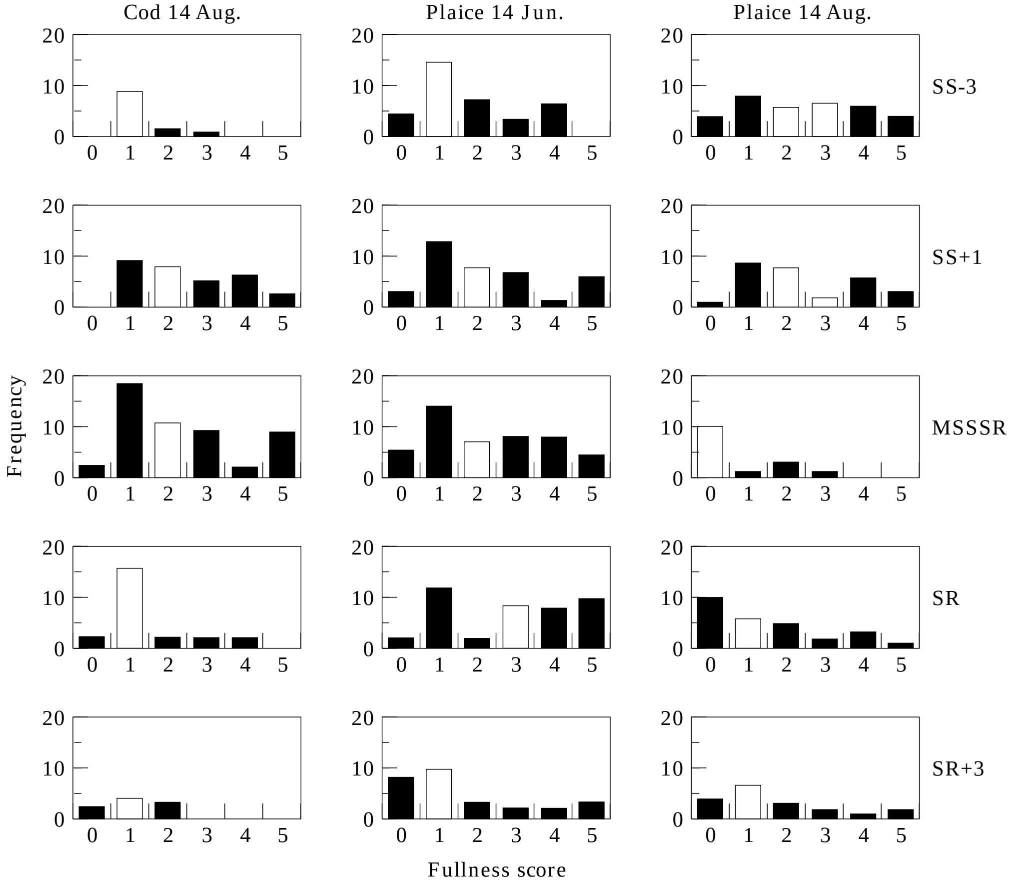

FIG. 4. Variation in the distribution of stomach fullness scores over the five sampling periods for cod on 14 August and plaice on 14 June and 14 August. The median point of the distribution is indicated by a white bar. Two white bars indicate that the median falls between the two fullness scores indicated. Abbreviations as Fig. 1.

ratios for a given fullness score were usually associated with the presence of the polychaete *Arenicola marina*.

(3) Differences in 'packing qualities' among prey types. There are two possible sources of variation here. First in the packing qualities of regular and irregular items of equivalent volume and secondly the difference between the volume occupied by one large prey item and numerous small ones of equivalent weight.

DISCUSSION

The study of predator–prey interactions provides two basic types of information. One is the importance of the prey in the diet of the predator and the other is the impact of the predator on the prey population. In the present case, juvenile fishes were major components (>50% by volume) of the diet of one-third (5/15) of the predators examined (Table I). Assessment of the dietary importance of a

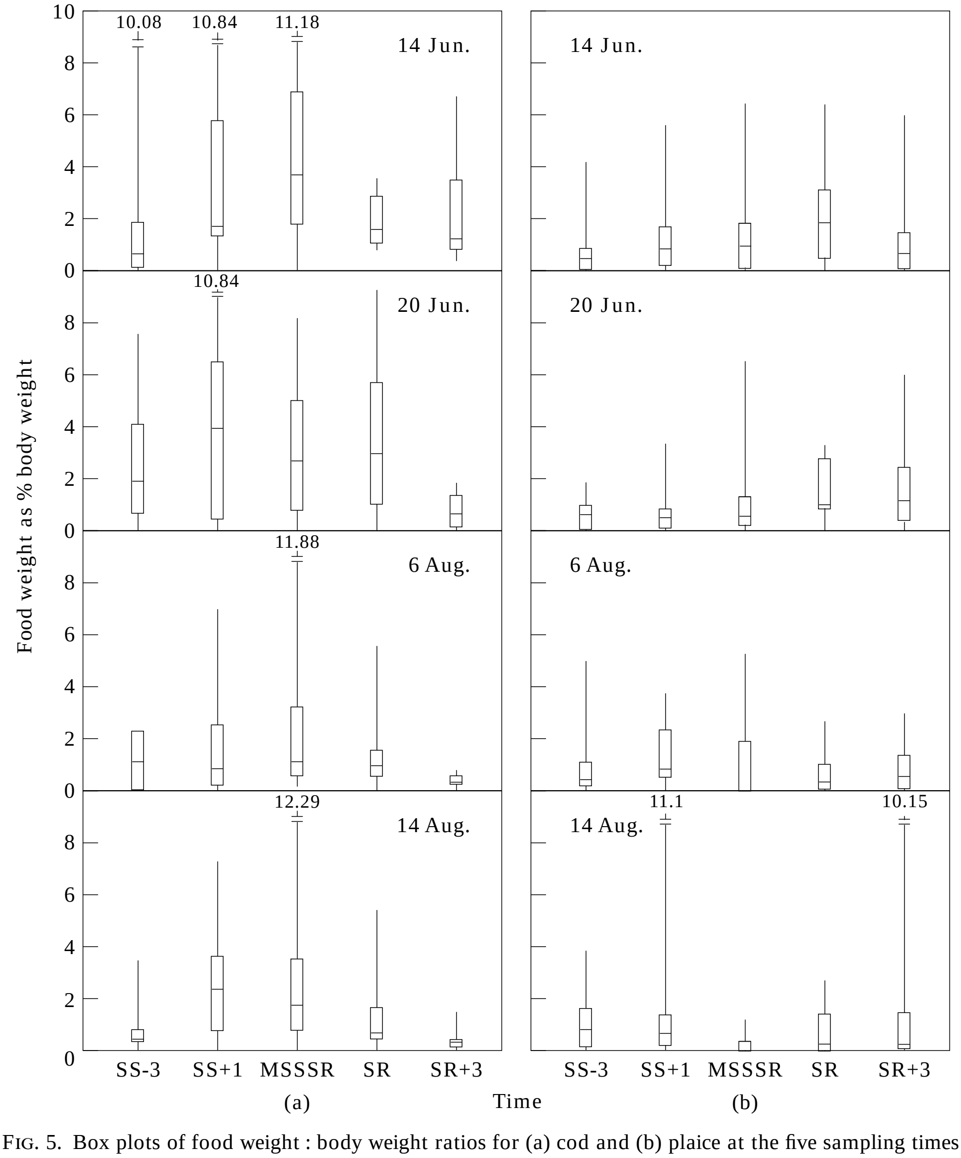

FIG. 5. Box plots of food weight : body weight ratios for (a) cod and (b) plaice at the five sampling times on each date. For each sample time the maximum, minimum and median values are shown together with the 25 and 75 percentiles. Abbreviations as Fig. 1.

particular prey item in terms of its contribution to the total volume of food consumed can be misleading, however, especially in the case of large, relatively rare items such as fish. One large prey item can contribute a disproportionate amount to the total volume and result in an overestimate of its importance to the predator population as a whole. Nevertheless, there was a general correspondence between the three measures used (% volume, Table I; % occurrence, Table II; number of prey individuals, Table III) for assessing the contribution of fish to the diet of the predators (see also Macdonald & Green, 1983). For the assessment of the impact of a predator species on the prey population, the most

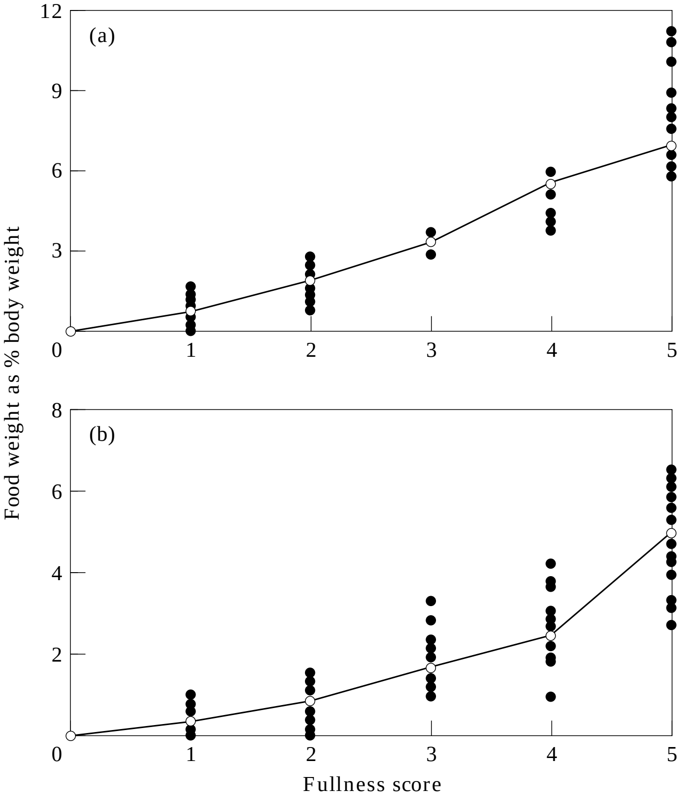

FIG. 6. Two examples of the relationship between food weight as a percentage of body weight and fullness score for (a) cod and (b) plaice on 14 June 1990. ○, Median point of each distribution.

relevant measure is the number of individual prey taken by each predator species. From this viewpoint (Table III), six species were important predators on fish: cod, whiting, gurnard, sea scorpion, plaice (I-group) and weever. These six major predators, which had taken 95% of all fish found in predators' stomachs (Table III), can be divided roughly into three categories according to their piscivorous tendencies and their abundance. In order of decreasing predatory impact they are: (1) common species in which fishes formed the main item of their diet (cod); (2) species in which fishes formed only a relatively minor constituent of the diet but which, by virtue of their abundance, had a significant predatory impact (I-group plaice); (3) less abundant species whose diet consisted principally of fishes (gurnard, short-spined sea scorpion, whiting, weever). The piscivorous tendencies of young cod are well documented (e.g. Edwards & Steele, 1968; Robb & Hislop, 1980; Pihl, 1982; Hawkins *et al.*, 1985) but have rarely been studied in detail (Ellis & Gibson, 1995). I-group plaice have also been recorded as consuming fishes in small but regular quantities (Riley & Corlett, 1966; Macer 1967; Wyche & Shackley, 1986). The rarer species encountered in the area also eat fish elsewhere (weever: Riley & Corlett, 1966; Macer, 1967; Edwards & Steele, 1968; gurnard: Wheeler, 1969; whiting: Nagabushanam, 1965; Gordon, 1977; Robb & Hislop, 1980; Hall *et al.*, 1990; short-spined sea scorpion: Wheeler, 1969).

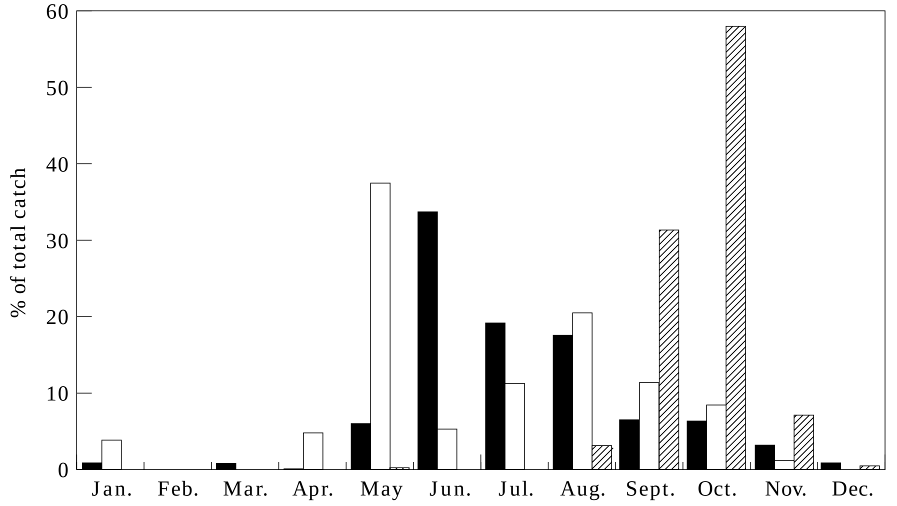

FIG. 7. Changes in abundance of 0-group plaice (■) and the sandeels *Ammodytes tobianus* (□) and *Hyperoplus lanceolatus* (▨) based on total catches over the period April 1986 to December 1989 (Gibson *et al.*, 1993 and unpublished data).

The main prey species eaten (Table III) reflect their relative abundance at the study site where the dominant small fishes are 0-group plaice and dabs, *Pomatoschistus* spp. and *Ammodytes tobianus* (Gibson *et al.*, 1993, 1995). The changing importance of the main prey species from flatfishes in June to sandeels in August (Table III) is a reflection of their changing size and relative abundance. In June, 181 flatfishes were found in the stomachs of 773 individuals of eight predator species whereas in August 270 individuals of four predator species had eaten only five flatfishes (Table III). This greater vulnerability of small flatfishes to a wider range of fish predators has been studied in detail by Ellis & Gibson (1995). Conversely, 604 individuals of six predator species ate 44 sandeels in June but in August 611 individuals of eight predator species were found to have fed on a total of 123 sandeels (Table III). 0-Group plaice decrease in abundance from June to August (presumably as a result of predation) but also outgrow their fish predators on this beach at a length of approximately 45 mm (Ellis & Gibson, 1995). The date at which plaice exceed this length depends upon their settlement time and growth rate but the population mean length usually exceeds 45 mm in mid to late July. In the present study the mean lengths of 0-group plaice in June and August were 33·6 (2·6% of population >45 mm) and 52·1 mm (70·5% of population >45 mm) respectively. After June, 0-group *Ammodytes tobianus*, together with small numbers of *Hyperoplus lanceolatus* (Le Sauvage) recruit to the beach (Fig. 7) and their small size and abundance renders them vulnerable to gurnards, cod, whiting and plaice (Table III). Subsequently, *H. lanceolatus* is the most abundant sandeel species (Fig. 7). The overall impact of fish as predators on any one prey species therefore depends on their relative abundances, the abundance of alternative prey and the predator–prey size relationship. Actual mortality of fishes due to predation is thus a complex interplay between year class strengths of predator and prey, relative times of recruitment and growth rates. From the prey's point of view, highest survival will be attained when the

0-group settles early, grows rapidly and is only subject to predation from a poor predator year class in the previous year and the late arrival (and hence small relative size) of predatory 0-group gadoids. The theme of ' match and mis-match ' of predators and prey in this context is developed more fully by Ellis & Gibson (1995).

Of the main piscivorous predators, only cod and I-group plaice were caught in sufficient numbers to allow any detailed analysis of temporal changes in feeding intensity. Taking all measures of feeding intensity into consideration, cod fed at all times of the day and night but both the proportion of fish feeding and feeding intensity tended to be greater at night (Figs 3–5). In addition, a larger proportion of individuals ate fish at night than during the day but this difference was not reflected in an increase in the relative volume of fish prey consumed during the hours of darkness. The prey population will therefore suffer a higher predation intensity after dark as a result of the marked increase in the number and size of cod in shallow water after sunset (Burrows *et al.*, 1994; Gibson *et al.*, 1995). Similar nocturnal inshore feeding migrations of cod have been described elsewhere (Pihl, 1982; Keats, 1992; Keats & Steele, 1992; Methven & Bajdik, 1994). In June this predation was focused on small flatfishes whereas in August the fish prey consisted predominantly of sandeels taken mostly in water <1 m deep (Fig. 2).

For plaice the situation was more complex because a greater proportion fed on fish during the day and in water of <1 m depth but the pattern of change in feeding intensity was different between the 2 months. In June, there was no difference in the proportion of empty stomachs over the sampling period and the greatest degree of stomach fullness was found at night. In contrast, in August more fish had empty stomachs at night and the greatest degree of fullness was found during the day. A possible explanation for the difference between the 2 months may be the difference in the length of, and the light intensity during, the dark period. In June the period between sunset and sunrise lasts approximately 6·5 h and, given clear skies, the light intensity at the latitude of the study site (56°N) may still be sufficient for visually-mediated feeding. In August, nights are darker and the sunset–sunrise interval is approximately 8·7 h. These constraints may not apply to the cod which can detect prey in the dark using non-visual sense organs and consequently is capable of feeding both day and night (Brawn, 1969; Chinarina & Troschicheva, 1975; Ansell & Gibson, 1993).

The distributions and movements of the dominant fish species can be interpreted in the light of their predator–prey relationships. The most common benthic species, 0-group plaice, undergo regular shifts in distribution that are phased with the tidal and diel cycles moving off- and onshore with the ebb and flow of the tides and concentrating in shallow water at night (Gibson, 1973; Kuipers, 1973; Burrows *et al.*, 1994; Gibson *et al.*, 1995). Such movements would have the effect of maintaining the majority of the population in depths where predation pressure from nocturnally onshore-migrating gadoids and other predators would be minimized. It has been suggested elsewhere (Burrows *et al.*, 1994) that 0-group plaice may further reduce their susceptibility to nocturnal benthic-feeding predators by swimming in the water column at night. In addition, there is a strong positive relationship between length and depth in 0-group plaice, dabs and sand gobies (Gibson, 1973; Gibson *et al.*, 1995). Such a differential distribution of the size classes would serve to counteract the vulnerability of the smallest fishes to the increased range of predators in deeper water (Ruiz *et al.*, 1993, Gibson *et al.*, 1995). Avoidance of predation by these means is not complete however, as indicated by the presence of many larger predators in shallow water at night and by their stomach contents. Avoidance of shallow water by the predators during the day provides some respite from predation for the small fishes in shallow water. It may also be an antipredator strategy of the predators themselves by reducing their vulnerability to diurnal surface-feeding birds. Unfortunately too little is known about the ecology of young sandeels, the other major prey item, to make similar inferences on the biological factors determining their shallow water distribution.

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References

Ansell, A. D. & Gibson, R. N. (1993). The effect of sand and light on predation of juvenile plaice (*Pleuronectes platessa*) by fishes and crustaceans. *Journal of Fish Biology* **43,** 837–845.

Bennett, B. A. (1989). Fish community of a moderately exposed beach on the southwestern Cape coast of South Africa and an assessment of this habitat as a nursery for juvenile fish. *Estuarine Coastal and Shelf Science* **28,** 293–305.

Beverton, R. J. H. & Iles, T. C. (1992). Mortality rates of 0-group plaice (*Pleuronectes platessa* L.), dab (*Limanda limanda* L.) and turbot (*Scophthalmus maximus*) in European waters. II. Comparison of mortality rates and construction of life table for 0-group plaice. *Netherlands Journal of Sea Research* **29,** 49–59.

Brawn, V. M. (1969). Feeding behaviour of cod (*Gadus morhua*). *Journal of the Fisheries Research Board of Canada* **26,** 583–596.

Brown, A. C. & McLachlan, A. (1990). *Ecology of Sandy Shores.* Amsterdam: Elsevier.

Burrows, M. T., Gibson, R. N., Robb, L., Comely, C. A. (1994). Temporal patterns of movement in juvenile flatfishes and their predators: underwater television observations. *Journal of Experimental Marine Biology and Ecology* **177,** 251–268.

Chinarina, A. D. & Troschicheva, N. V. (1975). Food-procuring reactions of the Atlantic cod, *Gadus morhua morhua*, and the short horn sculpin, *Myoxocephalus scorpius*, in the absence of visual reception. *Journal of Ichthyology* **15,** 990–997.

Edwards, R. R. C. & Steele, J. H. (1968). The ecology of 0-group plaice and common dabs at Lochewe. I. Population and food. *Journal of Experimental Marine Biology and Ecology* **2,** 215–238.

Ellis, T. & Gibson, R. N. (1995). Size-selective predation of 0-group flatfishes on a Scottish coastal nursery ground. *Marine Ecology Progress Series* **127,** 27–37.

Gibson, R. N. (1973). The intertidal movements and distribution of young fish on a sandy beach with special reference to the plaice (*Pleuronectes platessa* L.). *Journal of Experimental Marine Biology and Ecology* **12,** 79–102.

Gibson, R. N., Ansell, A. D. & Robb, L. (1993). Seasonal and annual variations in abundance and species composition of fish and macrocrustacean communities on a Scottish sandy beach. *Marine Ecology Progress Series* **98,** 89–105.

Gibson, R. N., Robb, L., Burrows, M. T. & Ansell, A. D. (1995). Tidal, diel and seasonal changes in the distribution of fishes on a Scottish sandy beach. *Marine Ecology Progress Series*, **130,** 1–17.

Gordon, J. D. M. (1977). The fish populations in inshore waters of the west coast of Scotland. The food and feeding of the whiting (*Merlangius merlangus*). *Journal of Fish Biology* **11,** 513–529.

Hall, S. J., Raffaelli, D., Basford, D. J., Robertson, M. R. & Fryer, R. (1990). The feeding relationships of the larger fish species in a Scottish sea loch. *Journal of Fish Biology* **37,** 775–791.

Hawkins, A. D., Soofiani, N. M. & Smith, G. W. (1985). Growth and feeding of juvenile cod (*Gadus morhua* L.). *Journal du conseil. Conseil International pour l'Exploration de la Mer* **42,** 11–32.

Keats, D. W. (1990). A nocturnal inshore movement of juvenile cod *Gadus morhua* L. in eastern Newfoundland. *Journal of Experimental Marine Biology and Ecology* **139,** 167–173.

Keats, D. W., Steele, D. H. (1992). Diurnal feeding of juvenile cod (*Gadus morhua*) which migrate into shallow water at night in eastern Newfoundland. *Journal of Northwest Atlantic Fisheries Science* **13,** 7–14.

Kramer, S. H. (1991). Growth, mortality, and movements of juvenile California halibut *Paralichthys californicus* in shallow coastal and bay habitats of San Diego County, California. *Fishery Bulletin* **89,** 195–207.

Kuipers, B. R. (1973). On the tidal migration of young plaice (*Pleuronectes platessa*) in the Wadden Sea. *Netherlands Journal of Sea Research* **6,** 376–388.

Lasiak, T. A. (1981). Nursery grounds of juvenile teleosts: evidence from the surf zone of King's Beach, Port Elizabeth. *South African Journal of Science* **77,** 388–390.

Lasiak, T. A. (1986). Juveniles food and the surf-zone habitat: implications for teleost nursery areas. *South African Journal of Zoology* **21,** 51–56.

Lockwood, S. J. (1972). An ecological survey of an 0-group plaice (*Pleuronectes platessa* L.) population, Filey Bay, Yorkshire. Ph.D. Thesis, University of East Anglia.

Macer, C. T. (1967). The food web in Red Wharf Bay (North Wales) with particular reference to young plaice (*Pleuronectes platessa*). *Helgoländer wissenschaftliche Meeresuntersuchungen* **15,** 560–573.

Macdonald, J. S. & Green, R. H. (1983). Redundancy of variables used to describe importance of prey species in fish diets. *Canadian Journal of Fisheries and Aquatic Sciences* **40,** 635–637.

Methven, D. A. & Bajdik, C. (1994). Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. *Canadian Journal of Fisheries and Aquatic Sciences* **51,** 78–90.

Modde, T. (1980). Growth and residency of juvenile fishes within a surf zone habitat in the Gulf of Mexico. *Gulf Research Reports* **6,** 377–385.

Nagabushanam, A. K. (1965). On the biology of the commoner gadoids in Manx waters. *Journal of the Marine Biological Association of the United Kingdom* **45,** 615–657.

Peters, D. J. & Nelson, W. G. (1987). The seasonality and spatial patterns of juvenile surf zone fishes of the Florida east coast. *Florida Science* **50,** 85–99.

Pihl, L. (1982). Food intake of young cod and flounder in a shallow bay on the Swedish west coast. *Netherlands Journal of Sea Research* **15,** 419–432.

Riley, J. D. & Corlett, J. (1966). The numbers of 0-group plaice in Port Erin Bay 1964–66. *Report of the Marine Biological Station Port Erin* **78,** 51–56.

Robb, A. P. & Hislop, J. R. G. (1980). The food of five gadoid species during the pelagic 0-group phase in the northern North Sea. *Journal of Fish Biology* **16,** 199–207.

Ruiz, G. M., Hines, A. H. & Posey, M. H. (1993). Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. *Marine Ecology Progress Series* **99,** 1–16.

SAS Institute Inc. (1990). *SAS Procedures Guide.* Version 6, 3rd edn. SAS: Cary, NC.

Sekai, T., Kinoshita, I. & Tanaka, M. (1993). Predation by crangonid shrimp on juvenile Japanese flounder under laboratory conditions. *Nippon Suisan Gakkaishi* **59,** 321–326.

Senta, T. & Kinoshita, I. (1985). Larval and juvenile fishes occurring in surf zones in western Japan. *Transactions of the American Fisheries Society* **114,** 609–618.

Toole, C. L. (1980). Intertidal recruitment and feeding in relation to optimal utilization of nursery areas by juvenile English sole (*Parophrys vetulus*: Pleuronectidae). *Environmental Biology of Fishes* **5,** 383–390.

Tyler, A. V. (1971). Surges of winter flounder, *Pseudopleuronectes americanus* into the intertidal zone. *Journal of the Fisheries Research Board of Canada* **28,** 1727–1732.

van der Veer, H. W. & Bergman, M. J. N. (1987). Predation by crustaceans on a newly-settled 0-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. *Marine Ecology Progress Series* **35,** 203–215.

Wheeler, A. 1969. *Fishes of the British Isles and northwestern Europe.* London: Macmillan.

Wyche, C. J. & Shackley, S. E. (1986). The feeding ecology of *Pleuronectes platessa* L., *Limanda limanda* (L.) and *Scophthalmus rhombus* (L.) in Carmarthen Bay, South Wales, U.K. *Journal of Fish Biology* **29,** 303–311.