with compliments
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Tidal, diel and longer term changes in the distribution of fishes on a Scottish sandy beach

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ABSTRACT: Fishes were sampled by seine and beam trawl over tidal and diel cycles on a sandy beach on the west coast of Scotland in June and August. Species composition of the catches of the 2 gear types differed. There was a significant positive relationship between depth (0 to 5 m) and species richness but a few species were restricted to depths of <5 m. Although significantly more species and individuals were caught at night and at low tide there was no evidence for the existence of distinct 'day' and 'night' communities. Differences between catches at high and low water were caused by the movement of a few species into the intertidal zone on the rising tide. Diel differences in abundance were principally due to an inshore migration of several species of gadoids at dusk and movement offshore at dawn. Longer term changes in abundance and distribution were attributed to predation and movement into deeper water.

KEY WORDS: Fishes · Sandy beach · Diel movements · Tidal movements · Habitat partitioning

INTRODUCTION

The distributions of animals are determined by a complex series of responses to both the physical and biological characteristics of their environment. These responses allow individuals to select those habitats that offer the best combination of a high potential for growth and reproductive output with the lowest risk of mortality. Individual requirements change, however, and a habitat that is suitable at one hunger state, time of day or stage in the life history may not be suitable at another. Consequently, many species move from one habitat to another at a variety of spatial and temporal scales. Furthermore, habitats themselves do not remain constant but vary regularly on a daily and seasonal basis. In coastal waters, aquatic species are subject to the additional changes caused by the tides whose effects are particularly dramatic in the intertidal and immediate subtidal regions. Species inhabiting such regions employ numerous strategies for dealing with tidally phased fluctuations in habitat suitability (Newell 1979, Brown & McLachlan 1991). Sessile species usually withdraw into protective structures whereas those capable of movement redistribute themselves to more favourable locations. These strategies, mainly associated with feeding and the avoidance of adverse physicochemical conditions and predators, lead to the complex tidal and diel movements that have been described for a wide variety of motile species (e.g. Edwards 1958, Tyler 1971, Janssen & Kuipers 1980, Burrows et al. 1994). Field studies of these movements require a variety of techniques and a complex sampling schedule if the influence of tidal and day/night effects are to be separated. Such investigations are essential if the ecology of shallow water organisms is to be fully understood.

This paper reports the results of a study designed to investigate the changes in distribution of fishes on a Scottish sandy beach over tidal and diel cycles. Specific objectives were to determine (1) whether the species composition and/or relative abundance of members of this fish assemblage differ between day and night, (2) how the species are distributed with depth and (3) how these depth distributions are affected by the state of the tide, the time of day and the time of year. Particular attention was paid to the differences and similarities in the distribution and movements of predators and their prey species.

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MATERIALS AND METHODS

Sampling 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. It is subjected to semidiurnal tides and low water of spring tides occurs at approximately midday and midnight. Mean tidal ranges are 3.3 m on springs and 1.1 m on neaps. 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. To provide as complete a description of the species present as possible, the fishes were sampled using 3 types of gear. A 2 m beam trawl, fitted with 3 tickler chains, had a stretched mesh of 15 mm in the body of the net and 3 mm in the cod end. At each sampling time a sequence of 5 trawl hauls lasting approximately 5 min were made parallel to the shore in decreasing depths of 4, 3, 2, 1, and 0.5 m. At 0.5 m the trawl was pulled by 2 people on foot. At greater depths it was towed by boat. A cyclometer attached to the trawl frame measured the distance towed. In addition, hauls were made with a 3 m beam trawl in depths of 5 m by a larger vessel, which also served as a floating laboratory for the sorting and preservation of specimens. In order to sample pelagic species adequately, following each trawling sequence single 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. When hauled, the net swept an area of approximately 1160 m^2. Further details of the methods are provided in Gibson et al. (1993). The catch from each haul was anaesthestised in a 50 mg l^{-1} solution of benzocaine and preserved in approximately 8% formalin.

Sampling regime and rationale. The investigation of the changes in fish distribution and abundance was coupled with a study of their diet (Gibson & Robb 1996) with particular reference to the role of fishes as predators on the juveniles of other fishes. Pilot studies had suggested that much of this predation took place at night. Consequently the sampling schedule represented an attempt 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 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). Sampling dates in June and August were separated by 1 wk so that both a high tide and low tide occurred as near to midnight as possible. This schedule allows the separation of 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. The actual dates and times of sampling are given in Table 1 together with the state of the tide.

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.

Data analysis. Abundance of the fishes caught by trawl was measured as the number of fishes caught per 100 m^2 trawled. This measure does not represent true abundance because the efficiency of the trawl is unknown, although it is likely to be of the order of 30 to 40% for *Pleuronectes platessa* (Kuipers 1975, Rogers & Lockwood 1989). Abundance of fishes in seine hauls was expressed as no. haul^{-1}. The data from trawls and seines were analysed separately because the catches are known to differ markedly in composition (Gibson et al. 1993).

Table 1. Details of sampling dates (1990) and times (British Summer Time) used during the investigation. Also shown are the predicted times of high water (HW), and low water (LW); high water height (Height, in meters above Chart Datum); and in parentheses, as decimal hours, the sampling times before (–) or after (+) high water

Date	Sample times (h)					Time of	Time of	Height
	SS–3	SS+1	MSSSR	SR	SR+3	HW	LW	of HW
14–15 Jun	19:03	23:03	01:17	04:31	07:31	22:37	16:28	3.4
	(–3.57)	(+0.43)	(+2.67)	(+5.9)	(–3.27)	10:47	05:11	3.0
20–21 Jun	19:06	23:06	01:18	04:31	07:31	16:30	22:48	3.4
	(+2.6)	(–6.08)	(–3.88)	(–0.67)	(+2.33)	05:11		3.6
6–7 Aug	18:15	22:15	01:23	05:31	08:31	18:58	01:09	3.9
	(–0.71)	(+3.26)	(–5.92)	(–1.78)	(+1.21)	07:18		3.7
14–15 Aug	17:57	21:57	01:27	05:47	08:47	00:50	18:25	3.0
	(–6.48)	(–2.88)	(+0.62)	(+4.95)	(–4.22)	13:00	07:03	2.9

The similarity between the species composition of the combined catches on each sample date was assessed by calculating percent similarity (Krebs 1989) after square root transformation to reduce the effect of the most abundant species. Percent similarity is given by:

$$P = \sum \text{minimum}(p_{1i}, p_{2i})$$

where p_{1i} = percentage of species i in sample 1 and p_{2i} = percentage of species i in sample 2. Spearman rank correlations between the percent species composition of the combined catches on each date were also calculated.

Analysis of variance was used to test the significance of changes in the total number of species, total number of individuals and the total weight of trawl and seine catches, together with the number and size of individuals of selected species contained therein. Trawl data were analysed with 2 alternative designs. In the first, variance due to the 3 crossed factors of depth, time of day and sample date and their 2-way interactions was tested over the residual variation (upper block in Table 7). Changes in catches during sampling periods may however be due in part to the influence of the tidal cycle. Low water occurred in the middle of the night on 2 dates (20 June and 6 August) and near dusk and dawn on the other dates (14 June and 14 August). A second design of ANOVA was used to detect these tidal influences in which differences in trends with the time of day among dates were assumed to reflect differences in tidal conditions. The state of the tide at the time of sampling was represented by the time relative to the closest high water, from low water 6 h before high water to low water 6 h after high water. Cosines, and sines, of the angular equivalent of the state of the cycle [$2\pi \times$ (time relative to predicted time of high water)/12.5 h] were included as covariates in the analysis. The cosines reflect changes from low water to high water while sines reflect differences between ebb and flood tide. Regression equations resulting from this analysis were used to predict values for each state of the tide. Seine hauls were analysed in a similar way to this second design but without the factor for depth.

The $\log_{10}$ of total numbers of species, numbers of individuals and weights of catches were used in the ANOVAs. Abundances of individual species were transformed using $\log_{10}(1+n)$ before analysis, while no transformation was applied to the total lengths of fishes. The irregular occurrence of most species in seines precluded the comparison of lengths among times and dates by ANOVA. Lengths of fish in trawls were analysed using mean lengths per haul in ANOVAs with weighting for the number of fish in each haul. Depth was considered as a covariate to reveal linear trends in length.

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 (Tables 2 & 3). Each trawl haul caught approximately twice as many species as each seine haul (Table 4). The trawl catches were dominated by 6 species (*Pleuronectes platessa, Limanda limanda, Pomatoschistus minutus, Eutrigla gurnardus, Gadus morhua* and *Trisopterus minutus*) whose abundance varied between dates. *L. limanda* was commonest in June whereas *T. minutus* was only common in August. These 6 species always made up >90% of the catch. The seine catches were more variable in composition, particularly in the numbers of the dominant species caught between dates. *G. morhua, Merlangius merlangus, Eutrigla gurnardus, Ammodytes tobianus, Clupea harengus* and *P. platessa* were most abundant and consistently made up >70% of the catches by number. Catch composition by weight presents a slightly different picture because the total weight was often affected by the presence of a few large individuals of *Pleuronectes flesus*. The main difference between the trawl and seine catches was the presence of greater numbers of the pelagic species *A. tobianus, M. merlangus* and *Pollachius virens* in the seine catches. An overwhelming proportion of all species caught were juveniles in their first year of life.

The species composition of the catches made at different times of day on each date varied considerably but, in general, similarity was greatest between adjacent times. There was a highly significant correlation between the rank orders of species abundance for all samples taken by trawl at different times of day on each date in June ($p = 0.006$ or less in all cases) but for only between 40 and 60% of the August trawl samples. The relatively few species caught in most seine hauls (Table 4) made an equivalent analysis for seine catches difficult but, where it was possible, samples taken at adjacent times of day were also the most similar. Very few species were caught exclusively during the day or at night and with one exception such species were represented by fewer than 6 specimens. The exception was *Melanogrammus aeglefinus*, which was caught only at night.

The species composition of the combined catches was very similar between dates within months for the trawl samples (Table 5) with the greatest similarity between adjacent samples. Similarity between the seine samples was lower overall but more consistent between sampling dates (Table 5). There was a significant correlation between the rank orders of species abundance for all samples taken by trawl ($p < 0.05$ in

Table 2. Species composition of the trawl catches as percentages of mean numbers (N) and weights (W, g) per 100 m^2. Species nomenclature follows Wheeler (1992)

Family	Species	14 Jun		20 Jun		6 Aug		14 Aug	
		N	W	N	W	N	W	N	W
Rajidae	*Raja clavata*	–	–	–	–	0.04	4.77	–	–
Clupeidae	*Clupea harengus*	–	–	–	–	–	–	0.03	0.01
Gadidae	*Gadus morhua*	6.62	7.99	5.89	9.33	2.68	5.07	6.51	6.82
	Melanogrammus aeglefinus	–	–	–	–	0.04	0.13	0.13	0.41
	Merlangius merlangus	0.05	0.15	0.07	0.16	0.43	0.71	1.74	2.83
	Pollachius pollachius	0.01	0.02	–	–	–	–	0.48	0.78
	Pollachius virens	0.02	0.02	0.01	0.02	–	–	0.33	0.94
	Trisopterus minutus	0.70	1.00	0.41	0.35	14.87	10.14	41.59	30.62
Lophiidae	*Lophius piscatorius*	–	–	0.02	4.90	–	–	–	–
Gasterosteidae	*Spinachia spinachia*	0.01	0.01	–	–	0.16	0.05	0.35	0.07
Syngnathidae	*Nerophis lumbriciformis*	0.11	0.03	0.02	0.01	0.11	0.01	0.17	0.02
	Syngnathus acus	0.01	0.01	–	–	–	–	–	–
	Syngnathus rostellatus	0.15	0.19	0.32	0.30	1.93	0.37	1.30	0.22
Triglidae	*Eutrigla gurnardus*	18.28	12.07	18.00	9.52	5.64	3.14	3.59	2.96
Cottidae	*Myoxocephalus scorpius*	1.11	2.20	0.62	1.18	0.29	1.83	0.17	2.04
Agonidae	*Agonus cataphractus*	1.85	2.59	2.31	2.95	0.43	0.29	0.55	0.48
Cyclopteridae	*Cyclopterus lumpus*	0.13	0.02	0.02	0.01	–	–	–	–
Pholidae	*Pholis gunnellus*	0.83	0.25	0.88	0.21	0.14	0.46	0.23	0.30
Trachinidae	*Echiichthys vipera*	0.09	1.58	0.19	2.47	0.62	1.76	0.81	2.56
Ammodytidae	*Ammodytes tobianus*	1.41	0.48	0.35	0.33	0.91	0.58	0.96	0.08
Callionymidae	*Callionymus lyra*	–	–	0.01	0.18	0.04	0.23	–	–
Gobiidae	*Gobiusculus flavescens*	0.01	0.02	–	–	–	–	–	–
	Pomatoschistus lozanoi	0.16	0.28	0.17	0.19	–	–	–	–
	Pomatoschistus minutus	2.75	4.89	1.82	5.02	3.68	2.73	4.33	2.68
	Pomatoschistus pictus	0.03	0.04	0.01	0.03	–	–	–	–
Scophthalmidae	*Scophthalmus maximus*	0.01	0.02	–	–	0.60	0.13	0.67	0.10
Bothidae	*Arnoglossus laterna*	–	–	–	–	–	–	0.03	0.06
Pleuronectidae	*Limanda limanda*	32.16	6.99	27.20	7.56	0.98	1.54	0.91	1.19
	Pleuronectes flesus	–	–	–	–	0.35	3.48	0.16	0.52
	Pleuronectes platessa	33.38	59.14	41.61	54.88	66.05	62.55	34.86	44.28
Soleidae	*Solea solea*	0.10	0.01	0.06	0.41	–	–	0.07	0.01
Total no. of species		24		21		20		23	
Mean no. 100 m^{-2}		78.3		54.6		15.6		17.1	
Mean weight 100 m^{-2}		41.5		36.7		48.1		56.7	
No. of samples		28		26		30		29	

all cases) but only between the 2 August samples for the seine catches ($p < 0.002$).

Depth, tidal, diel and seasonal influences on catch composition

Total number of species, individuals and weight of catch

The average number of species caught in trawls increased from approximately 5 in 0.5 m of water to around 10 in 5 m. Total number of individuals and total weights declined from 0.5 m to 4 m (Fig. 1A) but increased sharply to a maximum value at 5 m depth. The state of the tide did not affect trawl catches (Fig. 1C) but strongly influenced catches by seine. Most species, most individuals and heaviest catches were obtained 2 h after low water, while the least were caught 2 h after high water (Fig. 1F). Catches at night generally had more species, more individuals and were heavier than those taken in daytime in both trawls and seines (Fig. 1B, E; Tables 4 & 6; Table 7, significant Time of day effects).

The number of species and the number of individuals in trawls sharply declined between June and August, whereas the weight of the catch did not change significantly (Fig 1D). No such trends were seen in the seine catches (Fig. 1G).

The results summarised above and in Fig. 1 provide only a partial description of the complex changes that take place. A more detailed analysis of the interactions

Table 3. Species composition of the seine catches as percentages of total numbers (N) and weight (W, g). Species nomenclature follows Wheeler (1992)

Family	Species	14 Jun N	14 Jun W	20 Jun N	20 Jun W	6 Aug N	6 Aug W	14 Aug N	14 Aug W
Clupeidae	*Clupea harengus*	0.10	0.01	–	–	–	–	13.86	2.62
Gadidae	*Gadus morhua*	3.61	0.73	31.26	17.80	6.01	8.45	3.35	2.52
	Melanogrammus aeglefinus	–	–	–	–	0.28	0.97	0.23	0.35
	Merlangius merlangus	0.31	0.07	1.52	1.30	14.66	20.47	23.44	23.97
	Pollachius pollachius	–	–	–	–	0.09	0.07	0.35	0.23
	Pollachius virens	2.16	1.18	0.76	0.58	1.50	4.35	1.62	2.70
	Trisopterus minutus	0.31	0.04	0.44	0.09	6.77	3.94	4.39	2.25
Gasterosteidae	*Spinachia spinachia*	–	–	0.11	0.19	–	–	0.46	0.10
Syngnathidae	*Syngnathus rostellatus*	–	–	0.22	0.05	–	–	–	–
Triglidae	*Eutrigla gurnardus*	9.38	1.09	13.18	3.36	0.66	1.17	0.35	0.61
Cottidae	*Myoxocephalus scorpius*	0.10	0.01	0.55	0.07	–	–	–	–
Agonidae	*Agonus cataphractus*	–	–	0.33	0.02	–	–	–	–
Cyclopteridae	*Cyclopterus lumpus*	0.21	0.01	–	–	–	–	0.23	0.09
Trachinidae	*Echiichthys vipera*	–	–	1.31	5.51	0.85	1.73	0.69	1.11
Ammodytidae	*Ammodytes tobianus*	69.48	88.09	3.16	2.33	5.45	8.62	32.10	16.15
	Hyperoplus lanceolatus	0.52	1.13	–	–	–	–	0.11	0.12
Gobiidae	*Pomatoschistus lozanoi*	–	–	0.11	0.08	–	–	–	–
	Pomatoschistus minutus	–	–	0.11	0.14	0.09	0.02	0.92	0.11
Scombridae	*Scomber scombrus*	–	–	–	–	0.09	0.22	0.35	19.25
Scophthalmidae	*Scophthalmus maximus*	–	–	–	–	0.19	0.05	0.92	0.09
Pleuronectidae	*Limanda limanda*	0.31	0.01	18.41	1.79	0.28	0.26	–	–
	Pleuronectes flesus	0.31	1.20	2.29	30.63	0.47	11.95	0.81	15.40
	Pleuronectes platessa	13.20	6.44	26.03	34.13	62.41	37.01	15.82	12.31
Soleidae	*Solea solea*	–	–	0.22	1.91	0.09	0.70	–	–
Total no. of species		13		17		16		18	
Total numbers		970		918		1064		866	
Total weight		3621.4		2217.6		4466.3		5273.2	
No. of samples		5		5		5		5	

Table 4. Diel variations in species richness. Entries in the table are the number of species caught in each seine haul or the number caught at all depths by trawl for each sampling time. The sample dates are grouped according to whether low tide (LW) was at night or during the day

Gear	Date	SS−3	SS+1	MSSSR	SR	SR+3	Mean
Seine	LW in day						
	14 Jun	8	2	6	7	7	6
	14 Aug	7	14	9	8	5	8.6
	Mean	7.5	8	7.5	7.5	6	7.3
	LW at night						
	20 Jun	5	17	10	2	5	7.8
	6 Aug	2	11	13	3	1	6
	Mean	3.5	14	11.5	2.5	3	6.9
Trawl	LW in day						
	14 Jun	18	15	19	17	16	17
	14 Aug	13	17	19	14	15	15.6
	Mean	15.5	16	19	15.5	15.5	16.3
	LW at night						
	20 Jun	14	17	18	14	12	15
	6 Aug	12	12	15	13	12	12.8
	Mean	13	14.5	16.5	13.5	12	13.9

Table 5. Comparison of species composition of catches as percent similarity between dates. The similarities for the trawl samples are given above the diagonal and those for the seine samples below it. Percent similarity was calculated after square root transformation

	14 Jun	20 Jun	6 Aug	14 Aug
14 Jun	–	92	62	61
20 Jun	57	–	64	59
6 Aug	51	57	–	81
14 Aug	55	44	68	–

between the influences of depth, time of day and month is given below. Significant changes in the depth distributions of numbers of species, total number of individuals and total weight of catch were seen among the different times of day. More species were caught at shallower depths (1 to 3 m) in darkness (SS+1, MSSSR) and at SR than in daylight, while similar numbers were found at 5 m depth at all times (Fig. 2A). The number of individuals at 0.5 m was greatest at SS+1 and SR, while more fishes were caught at MSSSR at greater

Table 3. Species composition of the seine catches as percentages of total numbers (N) and weight (W, g). Species nomenclature follows Wheeler (1992)

Family	Species	14 Jun		20 Jun		6 Aug		14 Aug	
		N	W	N	W	N	W	N	W
Clupeidae	*Clupea harengus*	0.10	0.01	–	–	–	–	13.86	2.62
Gadidae	*Gadus morhua*	3.61	0.73	31.26	17.80	6.01	8.45	3.35	2.52
	Melanogrammus aeglefinus	–	–	–	–	0.28	0.97	0.23	0.35
	Merlangius merlangus	0.31	0.07	1.52	1.30	14.66	20.47	23.44	23.97
	Pollachius pollachius	–	–	–	–	0.09	0.07	0.35	0.23
	Pollachius virens	2.16	1.18	0.76	0.58	1.50	4.35	1.62	2.70
	Trisopterus minutus	0.31	0.04	0.44	0.09	6.77	3.94	4.39	2.25
Gasterosteidae	*Spinachia spinachia*	–	–	0.11	0.19	–	–	0.46	0.10
Syngnathidae	*Syngnathus rostellatus*	–	–	0.22	0.05	–	–	–	–
Triglidae	*Eutrigla gurnardus*	9.38	1.09	13.18	3.36	0.66	1.17	0.35	0.61
Cottidae	*Myoxocephalus scorpius*	0.10	0.01	0.55	0.07	–	–	–	–
Agonidae	*Agonus cataphractus*	–	–	0.33	0.02	–	–	–	–
Cyclopteridae	*Cyclopterus lumpus*	0.21	0.01	–	–	–	–	0.23	0.09
Trachinidae	*Echiichthys vipera*	–	–	1.31	5.51	0.85	1.73	0.69	1.11
Ammodytidae	*Ammodytes tobianus*	69.48	88.09	3.16	2.33	5.45	8.62	32.10	16.15
	Hyperoplus lanceolatus	0.52	1.13	–	–	–	–	0.11	0.12
Gobiidae	*Pomatoschistus lozanoi*	–	–	0.11	0.08	–	–	–	–
	Pomatoschistus minutus	–	–	0.11	0.14	0.09	0.02	0.92	0.11
Scombridae	*Scomber scombrus*	–	–	–	–	0.09	0.22	0.35	19.25
Scophthalmidae	*Scophthalmus maximus*	–	–	–	–	0.19	0.05	0.92	0.09
Pleuronectidae	*Limanda limanda*	0.31	0.01	18.41	1.79	0.28	0.26	–	–
	Pleuronectes flesus	0.31	1.20	2.29	30.63	0.47	11.95	0.81	15.40
	Pleuronectes platessa	13.20	6.44	26.03	34.13	62.41	37.01	15.82	12.31
Soleidae	*Solea solea*	–	–	0.22	1.91	0.09	0.70	–	–
Total no. of species		13		17		16		18	
Total numbers		970		918		1064		866	
Total weight		3621.4		2217.6		4466.3		5273.2	
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Table 4. Diel variations in species richness. Entries in the table are the number of species caught in each seine haul or the number caught at all depths by trawl for each sampling time. The sample dates are grouped according to whether low tide (LW) was at night or during the day

Gear	Date	Sampling time					
		SS–3	SS+1	MSSSR	SR	SR+3	Mean
Seine	LW in day						
	14 Jun	8	2	6	7	7	6
	14 Aug	7	14	9	8	5	8.6
	Mean	7.5	8	7.5	7.5	6	7.3
	LW at night						
	20 Jun	5	17	10	2	5	7.8
	6 Aug	2	11	13	3	1	6
	Mean	3.5	14	11.5	2.5	3	6.9
Trawl	LW in day						
	14 Jun	18	15	19	17	16	17
	14 Aug	13	17	19	14	15	15.6
	Mean	15.5	16	19	15.5	15.5	16.3
	LW at night						
	20 Jun	14	17	18	14	12	15
	6 Aug	12	12	15	13	12	12.8
	Mean	13	14.5	16.5	13.5	12	13.9

Table 5. Comparison of species composition of catches as percent similarity between dates. The similarities for the trawl samples are given above the diagonal and those for the seine samples below it. Percent similarity was calculated after square root transformation

	14 Jun	20 Jun	6 Aug	14 Aug
14 Jun	–	92	62	61
20 Jun	57	–	64	59
6 Aug	51	57	–	81
14 Aug	55	44	68	–

between the influences of depth, time of day and month is given below. Significant changes in the depth distributions of numbers of species, total number of individuals and total weight of catch were seen among the different times of day. More species were caught at shallower depths (1 to 3 m) in darkness (SS+1, MSSSR) and at SR than in daylight, while similar numbers were found at 5 m depth at all times (Fig. 2A). The number of individuals at 0.5 m was greatest at SS+1 and SR, while more fishes were caught at MSSSR at greater

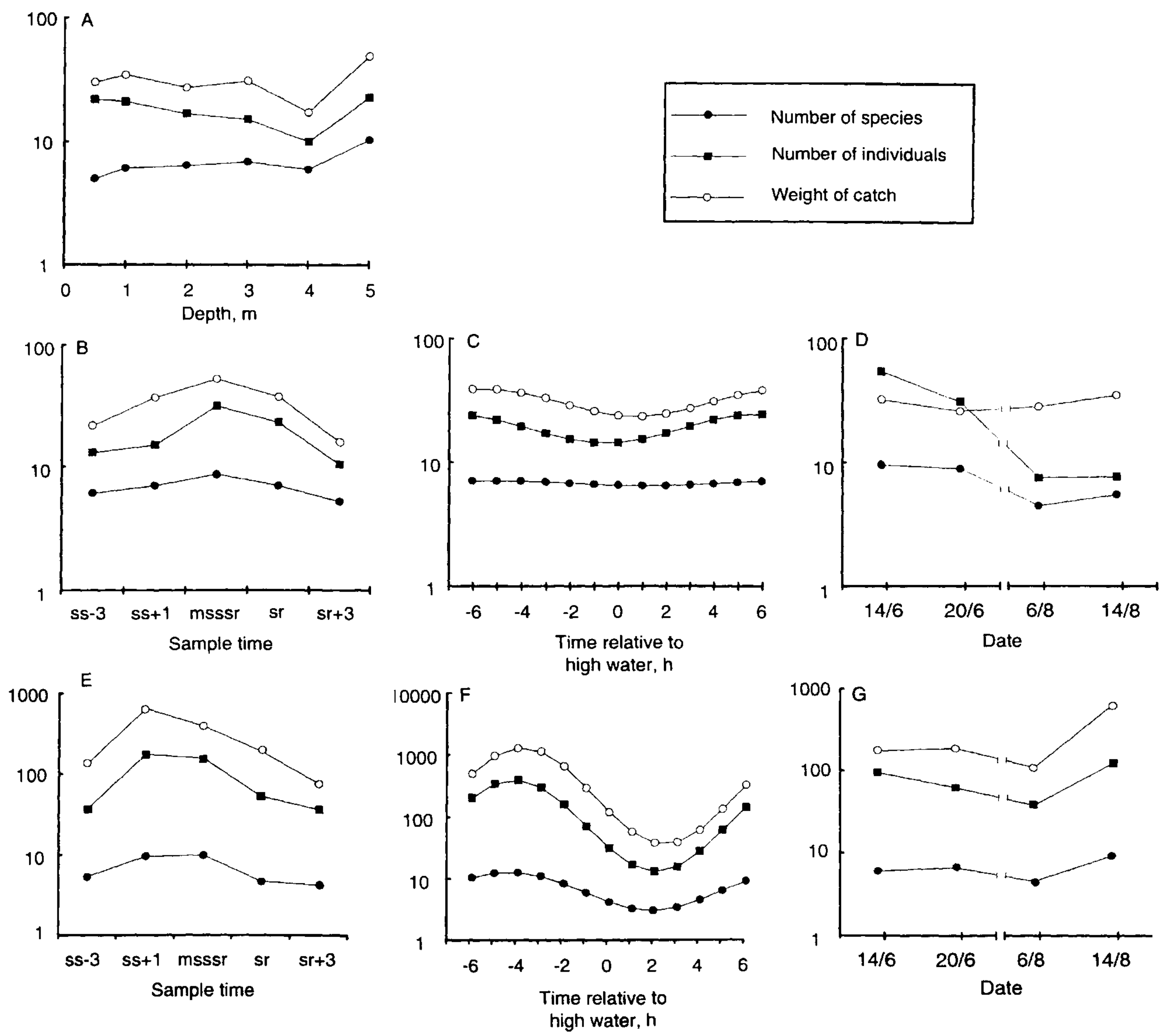

Fig. 1. Variation in geometric mean number of species, individuals and weight (g) for all catches combined. (A) Variation with depth. (B, E) Variation with sample time (B, trawls; E, seines). (C, F) Variation with time of tide (C, trawls; F, seines; values plotted are those predicted by the regressions — see text for further details). (D, G) Variation with date (D, trawls; G, seines); dates given as day/month

depths (Fig. 2B). Similar changes were seen in the weight of the catch (Fig. 2C).

Depth distributions also differed among the sample dates (Table 7: Depth by Date interactions). Fewer species were caught in the shallowest water in August than in June while similar numbers were caught at 5 m in the 2 months (Fig. 3A). Numbers of fishes in trawl catches remained relatively constant with depth on 14 June but declined steadily with depth on 20 June, whereas a decrease with depth from 0.5 to 4 m and an increase from 4 to 5 m were seen in both August samples (Fig. 3B).

The pattern of change in the numbers of fishes caught in trawls relative to the time of day varied with season. Day and night trawl catches had similar numbers of fishes in June, but catches in August were much larger at night (Fig. 3C).

Abundance of dominant species

The pattern of change in the overall catches is the resultant of the changing distribution of the dominant species and in this section the changing spatial and temporal distributions of these species are described. Dominant species were arbitrarily defined as those that exceeded 1.5% by number of the total catch on 2 or more sample dates.

Table 6. Diel variation in mean numbers (A) and weights (B) per seine haul and per trawl haul of 100 m^2 for the 4 sampling dates

Gear	Date	Sampling time SS−3	SS+1	MSSSR	SR	SR+3	Total
(A) Numbers							
Seine	LW in day						
	14 Jun	674	13	93	120	70	970
	14 Aug	24	254	66	180	342	866
	Total	698	267	159	300	412	1836
	LW at night						
	20 Jun	39	689	147	5	38	918
	6 Aug	2	370	628	63	1	1064
	Total	41	1059	775	68	39	1982
Trawl	LW in day						
	14 Jun	72.2	81.1	81.8	106.0	51.4	392.5
	14 Aug	5.8	12.6	25.9	28.4	11.2	83.8
	Total	78.0	93.7	107.6	134.4	65.6	476.3
	LW at night						
	20 Jun	63.8	81.8	53.0	19.0	43.4	261.0
	6 Aug	3.5	17.7	29.8	17.9	8.8	77.7
	Total	67.3	99.5	82.8	36.9	52.2	338.7
(B) Weights							
Seine	LW in day						
	14 Jun	3114.3	16.7	72.7	228.9	188.9	3621.4
	14 Aug	189.2	3311.2	461.2	398.5	913.0	5273.2
	Total	3303.5	3327.9	533.9	627.4	1101.9	8894.6
	LW at night						
	20 Jun	122.3	1635.4	331.5	35.8	96.3	2217.6
	6 Aug	4.4	1911.5	2152.4	396.0	2.1	4466.3
	Total	126.7	3546.9	2483.9	431.8	94.8	6683.9
Trawl	LW in day						
	14 Jun	36.5	47.5	58.8	52.0	21.7	210.5
	14 Aug	26.1	48.6	87.6	81.0	35.3	278.6
	Total	62.6	96.1	140.4	132.9	57.0	489.1
	LW at night						
	20 Jun	32.1	55.4	49.4	16.2	20.1	173.2
	6 Aug	16.0	60.2	88.1	52.7	23.4	240.4
	Total	48.1	115.1	137.4	69.0	43.5	413.6

The numbers of 4 dominant species (*Agonus cataphractus, Gadus morhua, Pomatoschistus minutus,* and *Trisopterus minutus*) significantly increased with depth. 0-group *Pleuronectes platessa* decreased in abundance with depth (Table 8; Fig. 4A) whereas all others showed no significant change in numbers with depth. The gadoids *G. morhua, T. minutus* and *Merlangius merlangus* were much more abundant at night (SS+1, MSSSR) than by day in both trawls and seines (Fig. 4B, D). 0-group *P. platessa*, while caught in trawls in similar numbers by day and night, were more abundant in seine catches at midnight (Fig. 4D; MSSSR vs other times, $F_{1,60}$ = 9.20, p = 0.0126). 1-group *P. platessa* were significantly more abundant at night in both trawls and seines. Only 2 species in trawls showed significant changes in abundance with the state of the tide: *M. merlangus* were slightly more abundant at the time of high water, while *P. minutus* were much less abundant in trawls taken at the time of high water. However, most species were significantly more abundant in seines taken 1 to 2 h after low water (Table 9, significant sine and cosine terms; Fig. 4E) and least abundant 1 to 2 h after high water.

Most species declined in abundance in trawls between June and August and only *Trisopterus minutus* and *Merlangius merlangus* increased from June to August. This consistent decrease in numbers was not evident in seine catches where only *Gadus morhua, Eutrigla gurnardus* and *Limanda limanda* were more abundant in June.

Not all of these trends were consistent among sampling occasions, as indicated by the significant interactions between the main variables for trawl catches (Table 8). *Gadus morhua* and *Merlangius merlangus* undertake a nocturnal inshore migration and increased in numbers in shallow water at night (Table 8: significant Depth by Time of day interaction; Fig. 5A, B). Although *Trisopterus minutus* also moved into shallow water at night the similarity of the *pattern* of distribution between day and night yielded a non-significant result in the ANOVA. 0-group *Pleuronectes platessa* also moved into shallower waters at night (Fig. 5C); most were caught in 0.5 m at SS+1 and SR whereas catches before sunset were greatest at 2 m depth.

Depth distributions varied significantly among the 4 sampling dates in 3 species (Table 8). *Gadus morhua* were absent from the shallowest depth on 2 dates (14 June and 6 August) but present on the other dates (Fig. 6A). *Pomatoschistus minutus* were much rarer in depths of less than 5 m in August than in June, while catches were similar at 5 m in the 2 months (Fig. 6B). A similar pattern of change was seen in the depth distribution of *Pleuronectes platessa*, which moved offshore from June to August (Fig. 6C).

The typical gadoid pattern of large catches at midnight generated significant Date by Time of day interactions for *Merlangius merlangus* and *Trisopterus minutus*. Differences in the size of catches among the 4 dates were much greater at MSSSR when the fishes were abundant (Fig. 7A, B). Changes in the abundance of *Pomatoschistus minutus* and 0-group *Pleuronectes platessa* with the time of day were not consistent on the 4 dates (Fig. 7C, D). The latter species was most abundant at SS-3 in June but at SR in August.

Table 7. Probabilities of *F*-ratios from analyses of variance on summary statistics of in seines and trawls (top half of table) and significance associated with these probabilities (bottom half of table). The number of individual fish and weight of the catch in g were transformed to $\log_{10}$ before analysis

Source	df	Trawls: No. of species	Trawls: No. in catch	Trawls: Weight of catch	Seines: No. of species	Seines: No. in catch	Seines: Weight of catch
Depth	5	<0.001	0.014	0.003			
Time of day (TOD)	4	<0.001	0.006	<0.001			
Date	3	<0.001	<0.001	0.461			
TOD by Depth	20	0.011	0.024	0.005			
Date by Depth	15	0.002	0.027	0.319			
Date by TOD	12	0.158	0.049	0.161			
Depth	5	<0.001	0.052	0.015			
TOD	4	<0.001	0.005	<0.001	0.039	0.303	0.481
Date	3	<0.001	<0.001	0.719	0.531	0.959	0.464
Cosine (Time relative to high water)	1	0.509	0.099	0.057	0.017	0.098	0.394
Sine (Time relative to high water)	1	0.643	0.653	0.421	0.002	0.007	0.014
Depth	5	***	*	**			
TOD	4	***	**	***			
Date	3	***	***	ns			
TOD by Depth	20	*	*	**			
Date by Depth	15	**	*	ns			
Date by TOD	12	ns	*	ns			
Depth	5	***	ns	*			
TOD	4	***	**	***	*	ns	ns
Date	3	***	***	ns	ns	ns	ns
Cosine (Time relative to high water)	1	ns	ns	ns	*	ns	ns
Sine (Time relative to high water)	1	ns	ns	ns	**	**	*

Significance: ***$p < 0.001$, **$0.001 < p < 0.01$, *$0.01 < p < 0.05$; ns: $0.05 < p$

Sizes of individual fishes

All species in trawls except *Agonus cataphractus* were significantly larger in August than in June (Table 10). *Pomatoschistus minutus* and 0-group *Pleuronectes platessa* and *Limanda limanda* increased significantly (Table 10) in length with depth. In June, *Pomatoschistus minutus* increased in length from 30 mm at 1 m depth to 60 mm at 5 m while 0-group *Pleuronectes platessa* increased from 30 mm to 45 mm over the same depth range. There was a smaller size increase for *L. limanda* in June, from 21 mm at 1 m depth to 24 mm at 5 m. Only 0-group *P. platessa* remained in sufficient numbers for comparison in August. Depth distribution of size was similar to that observed in June, average length increasing from 45 mm at 0.5 m to 60 mm at 5 m depth. *Gadus morhua* and *Eutrigla gurnardus* showed a more complex pattern of changes in size. By day, sizes of both species were similar at all depths. At night, however, larger fish were caught in shallower waters, indicating an onshore migration of large fish in darkness. This pattern for *G. morhua* resulted in significant effects of Time of day and interactions of Time of day with Depth (Table 10), while an increase in the gradient of size at night from shallow to deep water from June to August produced a significant Depth by Date interaction.

Average lengths of *Gadus morhua*, 0-group *Pleuronectes platessa* and *Pomatoschistus minutus* showed significant tidal influences (Table 10). *G. morhua* caught at high water were on average 8 mm larger than those caught at low water, while 0-group *P. platessa* caught at high water were 6 mm smaller than those caught at low water. *P. minutus* were 12 mm larger on flood tides than on ebb tides.

DISCUSSION

Species composition

As in previous studies on sandy beaches (e.g. Horn 1980, Ross et al. 1987, Romer 1990, Gibson et al. 1993) the fish assemblage on Tralee Beach is dominated by a few abundant species. Gross temporal patterns of change in the assemblage are therefore mainly a result of the changing distribution and abundance of these dominant species and the nature and extent of such change depends on the time scale at which they are measured.

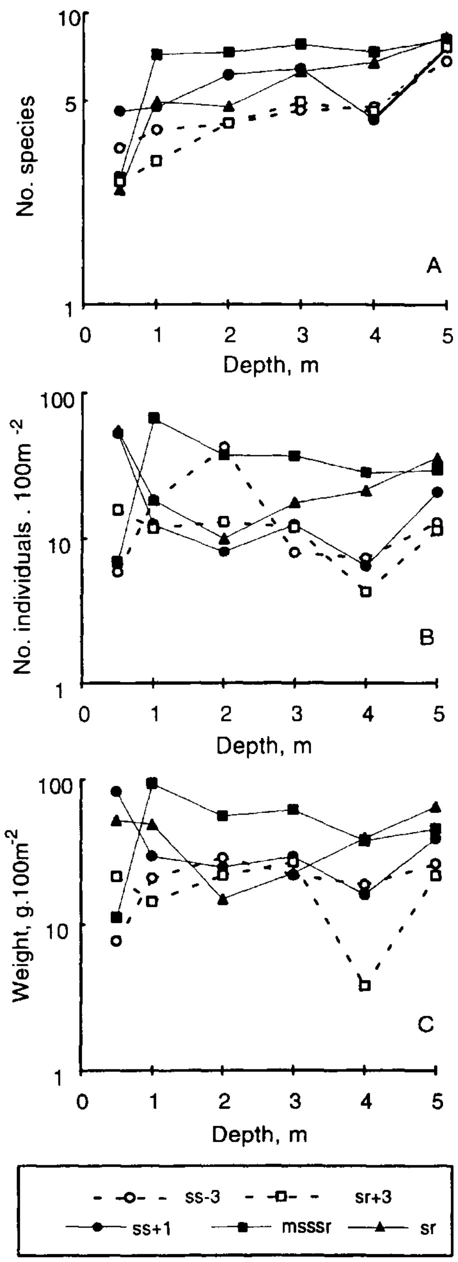

Fig. 2. Diel variation in depth of geometric mean number of species, individuals and weight for all trawl catches combined. (A) Species, (B) individuals, (C) weight

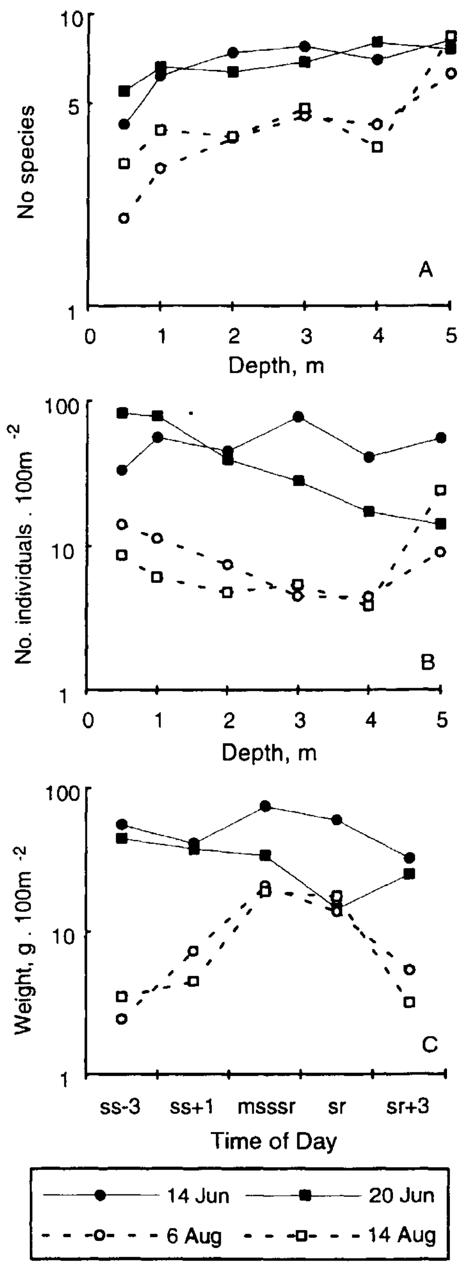

Fig. 3. Seasonal variation in depth of geometric mean number of species (A) and individuals (B), and seasonal variation in diel changes in numbers (C), for all trawl catches combined

The main temporal changes in assemblage structure (as measured by catch composition) were in seine catches over the tidal cycle. Many fewer species (about 50%) were caught by seine at high tide than at low tide (Fig. 1F, Table 11), a finding similar to that described by Lasiak (1984) for South African surf zone fishes. The difference can be attributed to the fact that hauls made at high water catch only those species that migrate upshore with the tide. High water samples therefore contained only flatfishes and gadoids (Table 11). Trawl samples covered a wider depth range than seines and so caught non-migrating species at all stages of the tide, with the result that there was no significant tidal variation in overall catch composition (Fig. 1C). Trawl samples taken intertidally at high tide contained fewer species than those taken at equivalent depths at low tide but the difference was much less marked at night, indicating a movement of many benthic species into the intertidal zone on nocturnal rising tides.

Table 8. Probabilities of *F*-ratios from analyses of variance on catches of common species in trawls (top half of table) and significance associated with these probabilities (bottom half of table). The numbers of individual fish of each species per 100 m^2 were transformed to $\log_{10}(1+n)$ before analysis. *A cat: Agonus cataphractus; E gur: Eutrigla gurnardus; G mor: Gadus morhua; L lim: Limanda limanda; M mer: Merlangius merlangus; P min: Pomatoschistus minutus; P pla* I: *Pleuronectes platessa* (I-group); *P pla* 0: *Pleuronectes platessa* (0-group); *T min: Trisopterus minutus*

Source	df	*A cat*	*E gur*	*G mor*	*L lim*	*M mer*	*P min*	*P pla* 0	*P pla* I	*T min*
Depth	5	0.030	0.459	<0.001	0.783	0.275	<0.001	<0.001	0.203	<0.001
Time of day (TOD)	4	0.633	0.518	<0.001	0.694	<0.001	0.501	0.739	0.008	<0.001
Date	3	0.006	<0.001	<0.001	<0.001	0.006	<0.001	0.015	<0.001	<0.001
TOD by Depth	20	0.098	0.602	0.032	0.304	0.005	0.852	0.024	0.483	0.072
Date by Depth	15	0.067	0.844	0.004	0.221	0.466	<0.001	<0.001	0.214	0.843
Date by TOD	12	0.141	0.843	0.331	0.876	0.008	0.020	0.006	0.362	<0.001
Depth	5	0.027	0.233	<0.001	0.761	0.217	<0.001	<0.001	0.214	0.005
TOD	4	0.304	0.446	<0.001	0.823	<0.001	0.705	0.826	0.041	<0.001
Date	3	<0.001	<0.001	<0.001	<0.001	0.007	<0.001	0.420	<0.001	<0.001
Cosine (Time relative to high water)	1	0.899	0.072	0.573	0.105	0.032	0.008	0.996	0.111	0.751
Sine (Time relative to high water)	1	0.339	0.309	0.840	0.688	0.872	0.649	0.147	0.507	0.076
Depth	5	*	ns	***	ns	ns	***	***	ns	***
TOD	4	ns	ns	***	ns	***	ns	ns	**	***
Date	3	**	***	***	***	**	***	*	***	***
TOD by Depth	20	ns	ns	*	ns	**	ns	*	ns	ns
Date by Depth	15	ns	ns	**	ns	ns	***	***	ns	ns
Date by TOD	12	ns	ns	ns	ns	**	*	**	ns	***
Depth	5	*	ns	***	ns	ns	***	***	ns	**
Time of day (TOD)	4	ns	ns	***	ns	***	ns	ns	*	***
Date	3	***	***	***	***	**	***	ns	***	***
Cosine (Time relative to high water)	1	ns	ns	ns	ns	*	**	ns	ns	ns
Sine (Time relative to high water)	1	ns	ns	ns	ns	ns	ns	ns	ns	ns

Significance: ***$p < 0.001$, **$0.001 < p < 0.01$, *$0.01 < p < 0.05$; ns: $0.05 < p$

In contrast to changes over the tidal cycle, changes in the species composition of the catches over the diel cycle were relatively small (Table 11) and there was no evidence for the existence of distinct, exclusive 'day' and 'night' communities (Helfman 1993). Although significantly more species were caught at night overall (Fig. 1B, E, Tables 4 & 7), the difference was slight and the major changes in assemblage structure observed were caused by the changing abundance of particular species rather than by their presence or absence. Romer (1990) came to a similar conclusion for a surf zone fish community in South Africa. There was no evidence of a difference between the 2 months in this respect in contrast to the finding by Nash (1986). Although some species were found only during the day or at night, with one exception (*Melanogrammus aeglefinus*) they were all rare and their absence at a particular time of day could be attributed to chance. Horn (1980) made a similar observation in a comparable study on the coast of California.

There was a marked difference between the trawl samples taken in June and August. Significantly fewer species were caught by trawl in August (Fig. 1D, Tables 4 & 7) and the difference between the catches in the 2 months is a reflection of the previously reported decline in both abundance and species richness that takes place in autumn and winter (Gibson et al. 1993). The absence of such a difference in the seine catches is probably a result of the recruitment of several pelagic species to the beach after the June samples were taken (see Table 3).

Depth distribution

There was a clear positive relationship between depth and species richness (Fig. 1, Table 7). This relationship partly explains why more species were caught by trawl than by seine. One other major reason for the difference is the greater number of trawl samples taken, thereby increasing the probability of capturing rarer species. The relationship between species richness and depth could be partly responsible for the significant change in numbers and weight with depth (Fig. 1A). In addition, however, many of the dominant species also increase in abundance with depth

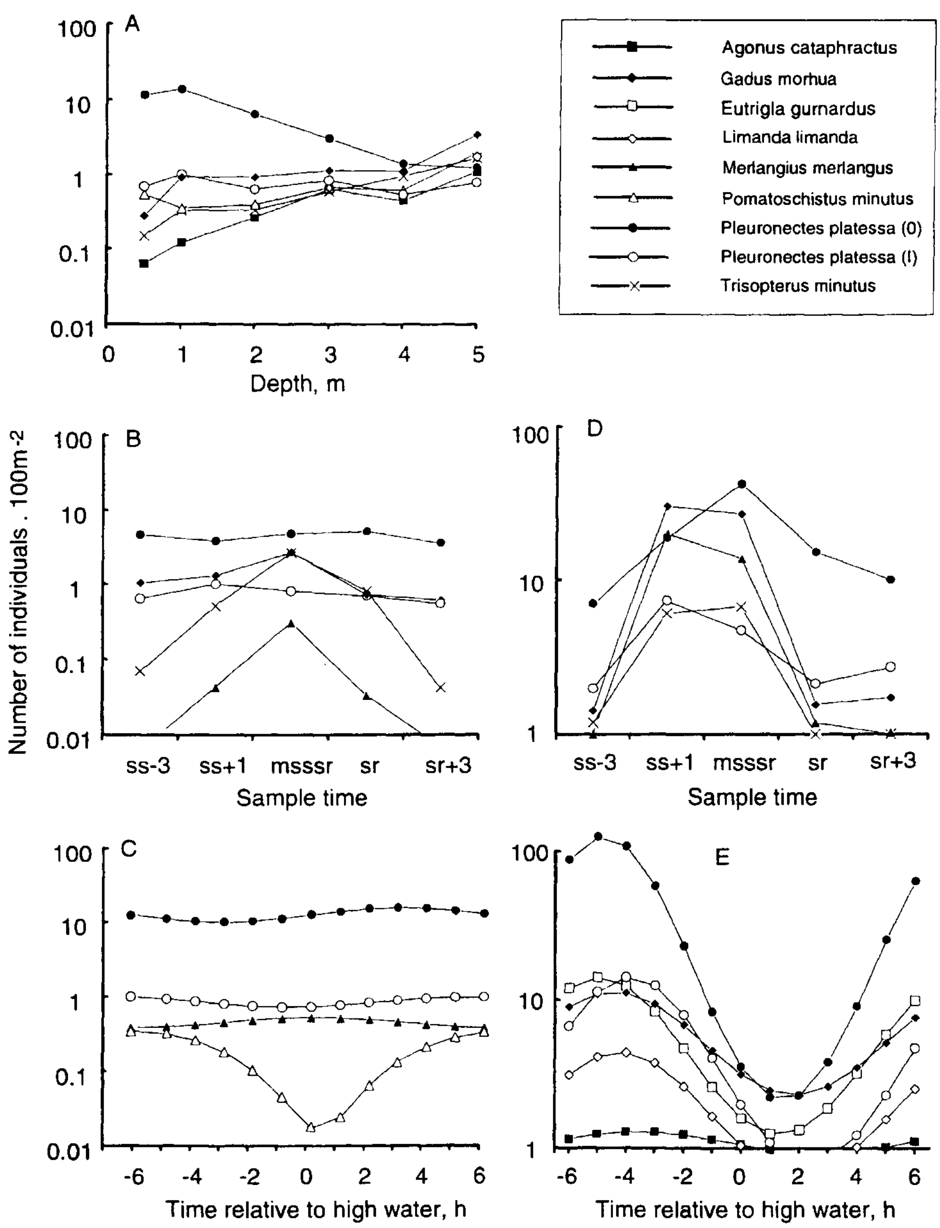

Fig. 4. Variation in geometric mean number of individuals for all catches combined. Only those species showing significant effects (Tables 8 & 9) are plotted. When not significant, data for *Pleuronectes platessa* are also plotted for comparison. (A) Variation with depth (trawls). (B, D) Variation with sample time (B, trawls; D, seines). (C, E) Variation with time of tide (C, trawls; E, seines; values plotted are those predicted by the regressions — see text for further details)

(Fig. 4A, Table 8). The change in total abundance is accompanied by a similar change in total weight (Fig. 1A) caused by a greater number of individuals at greater depths but also because 2 of the dominant species (*Pleuronectes platessa* and *Pomatoschistus minutus*) increase in size with depth (Table 10). The overwhelming dominance of 0-group *P. platessa* in the catches and their decreasing abundance with depth is responsible for the decreasing total numbers and weight observed down to 4 m. The increase at 5 m is mostly due to the predominance of gadoids at greater depths. Exclusion of *P. platessa* from the data set makes the relationship between numbers and depth more linear.

The narrow depth band sampled (0 to 5 m) represents the inner limits of the distribution of many species but others, particularly *Pleuronectes platessa* and *Scophthalmus maximus*, use very shallow waters as nursery grounds and the young of the year are most abundant in depths of <5 m (cf. Gibson 1973, Riley et al. 1981). Within the overall depth distribution of a species there is often a close positive relationship between size and depth. In *P. platessa* this relationship has even been accorded the status of a 'law' (Heincke's Law; Heincke 1913, Wimpenny 1953). Several of the gadoids caught in this investigation have a similar size-related depth distribution (Riley & Parnell 1984). Both cases represent examples of the wider phenome-

Table 9. Probabilities of *F*-ratios from analyses of variance on catches of common species in seines (top half of table) and significance associated with these probabilities (bottom half of table). The numbers of individual fish of each species per haul were transformed to $\log_{10}(1+n)$ before analysis. Species names abbreviations as Table 8

Source	df	*A cat*	*E gur*	*G mor*	*L lim*	*M mer*	*P min*	*P pla* 0	*P pla* I	*T min*
Time of day (TOD)	4	0.287	0.768	<0.001	0.324	0.007	0.745	0.077	0.003	0.031
Date	3	0.043	0.006	0.002	0.036	0.243	0.467	0.112	0.264	0.284
Cosine (Time relative to high water)	1	0.664	0.018	0.007	0.134	0.670	0.129	<0.001	0.006	0.373
Sine (Time relative to high water)	1	0.045	0.040	<0.001	0.016	0.329	0.222	<0.001	<0.001	0.321
TOD	4	ns	ns	***	ns	**	ns	ns	**	*
Date	3	*	**	**	*	ns	ns	ns	ns	ns
Cosine (Time relative to high water)	1	ns	*	**	ns	ns	ns	***	**	ns
Sine (Time relative to high water)	1	*	*	***	*	ns	ns	***	***	ns

Significance: ***$p < 0.001$, **$0.001 < p < 0.01$, *$0.01 < p < 0.05$; ns: $0.05 < p$

non whereby a species' overall niche is often subdivided into 'age-structured components' (Polis 1984). Various functions have been attributed to intra- and interspecific habitat partitioning by depth, principally the avoidance of competition, reduction of predation risk and the occupation of physiologically suitable abiotic conditions. In the present case, examples of both intra- and interspecific differences in depth distribution were observed. Both *P. platessa* and *Pomatoschistus minutus* were distributed in depth according to their size and, during the day, there was a clear separation between 0-group *P. platessa* and 2 of its major predators, *Gadus morhua* (Ellis & Gibson 1995) and the shore crab *Carcinus maenas* (van der Veer & Bergman 1987, Burrows et al. 1994).

Temporal changes in depth distribution

The overall patterns of distribution described in the previous section are not fixed but are continually changing. The changing distributions are caused by the movement of individual species into and out of shallow water at a variety of time scales. Not all species respond in the same way but 4 basic patterns can be distinguished.

Tidal movements. Several species migrate on- and offshore with each tidal cycle. The flatfishes *Pleuronectes platessa, P. flesus* and *Scophthalmus maximus* are the principal examples of this category. Absence of such a movement pattern is indicated by the lack of particular species in the seine and trawl catches made over the intertidal zone at high tide (see Table 11). Although pelagic species, particularly *Clupea harengus* and *Ammodytes tobianus*, were often caught at high tide, their presence in the intertidal zone is more likely to be the result of random movement than a directed shoreward migration. These tidal migrations may or may not be modified by a superimposed diel movement pattern (see below). Movement of fishes into the intertidal zone has been recorded in a wide variety of habitats (e.g. Tyler 1971, Kneib 1987, Sogard et al. 1989, Abou-Seedo et al. 1990, Gibson 1992) and is usually related to feeding on intertidal organisms that are only available at high tide. Avoidance of predators that may also move onshore with the rising tide has also been suggested as another function of these tidally related movement patterns (Girsa & Zhuravel 1983, Gibson 1988, Ansell & Gibson 1990).

Diel movements. Some species were found to be more abundant in shallow water at night, indicating an onshore migration at dusk followed by an offshore migration at dawn. A movement pattern of this type was most strikingly shown by the gadoid species *Gadus morhua, Merlangius merlangus, Trisopterus minutus* and *Melanogrammus aeglefinus*. Nocturnal inshore migration may therefore be a characteristic behaviour pattern of the juveniles of shallow water members of the Gadidae. It has certainly been recorded in several different locations for *G. morhua* (Pihl 1982, Clark & Green 1990, Keats 1990, Keats & Steele 1992) although the patterns of movement, and the functions attributed to them, differ between areas. The only other species clearly showing this pattern, particularly in the seine catches, was *Pleuronectes platessa*. Subsequent investigations using underwater television confirmed these movements and it has been suggested that the high seine catches at night can be partially explained by nocturnal movement of this normally benthic species into the water column, possibly in response to the nocturnal influx of bottom feeding predators (Burrows et al. 1994). Nash et al. (1994)

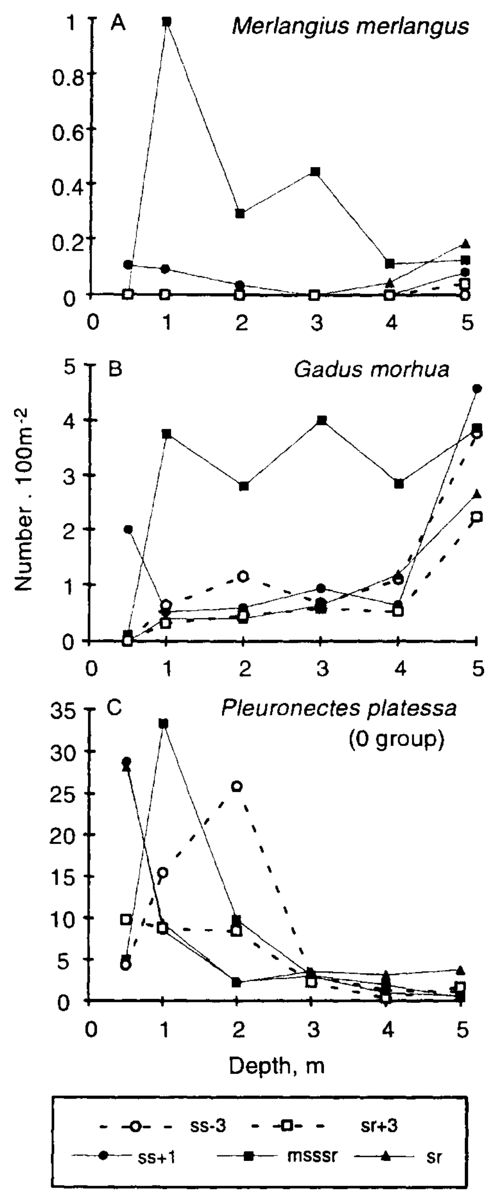

Fig. 5. Diel variation in numbers with depth for (A) *Merlangius merlangus*, (B) *Gadus morhua*, (C) 0-group *Pleuronectes platessa*. Trawl catches

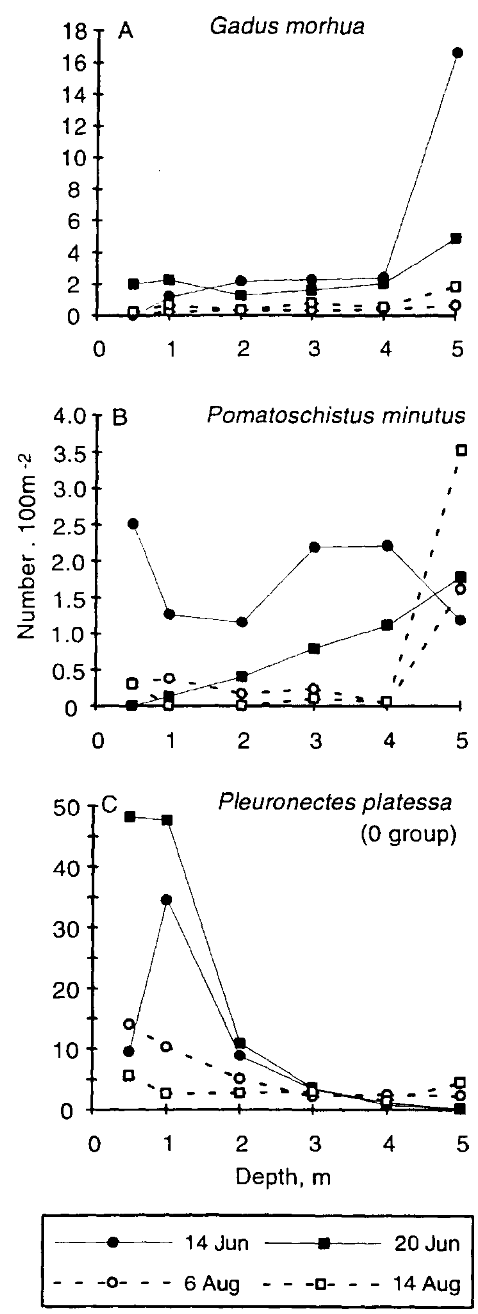

Fig. 6. Seasonal variation in pattern of depth distribution for (A) *Gadus morhua*, (B) *Pomatoschistus minutus*, (C) 0-group *Pleuronectes platessa*. Trawl catches

demonstrated that juvenile *P. platessa* are caught in higher numbers at night in September but showed no diel periodicity in catches in May/June. Increased numbers and size of fishes moving into shallower water at night have also been recorded in several other locations (Horn 1980, Ross et al. 1987, Wright 1989). Both feeding and predator avoidance have been cited as the function of such movements but the reverse argument has also been made, i.e. fishes avoid shallow water during the day because of increased predation risk from diurnal predators, particularly birds (Wright 1989). In the present case, the nocturnal movement into shallow water by *P. platessa* could be interpreted as a response to the equivalent movements by predators such as *G. morhua* and *Eutrigla gurnardus*, which are known to feed on small flatfishes (Edwards & Steele 1968, Ellis & Gibson 1995). It is likely, however, that no generally applicable conclusion can be drawn because species vary in their activity patterns and individuals in any one area will respond to local circumstances of prey availabil-

Table 10. Probabilities of *F*-ratios from analyses of variance on lengths of common species of fishes caught in trawls (top half of table) and significance associated with these probabilities (bottom half of table). Species names abbreviations as in Table 8. Data for *Limanda limanda* are for June only

Source	df	*A cat*	*E gur*	*G mor*	*L lim*	*M mer*	*P min*	*P pla* 0	*P pla* I	*T min*	*L lim*
Depth	1	0.264	0.047	0.646	0.543	0.276	<0.001	<0.001	0.032	0.748	0.027
Time of day (TOD)	4	0.196	0.269	0.002	0.351	0.361	0.891	0.667	0.845	0.896	0.563
Date	3	0.171	<0.001	<0.001	<0.001	0.009	0.003	<0.001	<0.001	<0.001	0.020
TOD by Depth	4	0.406	0.398	0.007	0.423	0.235	0.829	0.591	0.641	0.885	0.404
Date by Depth	3	0.101	0.020	0.006	0.963	0.277	0.197	0.201	0.313	0.001	0.766
Date by TOD	12	0.272	0.994	0.031	0.212	0.438	0.366	<0.001	0.531	0.311	0.048
Depth	1	0.262	0.150	0.085	0.007	0.545	<0.001	<0.001	0.097	0.307	<0.001
TOD	4	0.042	0.462	0.610	0.979	0.575	0.114	0.739	0.855	0.124	0.630
Date	3	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Cosine (Time relative to high water)	1	0.770	0.376	0.004	0.552	0.587	0.133	0.008	0.635	0.060	0.499
Sine (Time relative to high water)	1	0.323	0.433	0.201	0.746	0.267	0.010	0.018	0.506	0.109	0.078
Depth	1	ns	*	ns	ns	ns	***	***	*	ns	*
TOD	4	ns	ns	**	ns	ns	ns	ns	ns	ns	ns
Date	3	ns	***	***	***	**	**	***	***	***	*
TOD by Depth	4	ns	ns	**	ns	ns	ns	ns	ns	ns	ns
Date by Depth	3	ns	*	**	ns	ns	ns	ns	ns	**	ns
Date by TOD	12	ns	ns	*	ns	ns	ns	***	ns	ns	*
Depth	1	ns	ns	ns	**	ns	***	***	ns	ns	***
TOD	4	*	ns	ns	ns	ns	ns	ns	ns	ns	ns
Date	3	***	***	***	***	***	***	***	***	***	***
Cosine (Time relative to high water)	1	ns	ns	**	ns	ns	ns	**	ns	ns	ns
Sine (Time relative to high water)	1	ns	ns	ns	ns	ns	**	*	ns	ns	ns

Significance: ***p < 0.001; **0.001 < p < 0.01; *0.01 < p < 0.05; ns: 0.05 < p

ity, predation risk and abiotic conditions. Furthermore, any general conclusions as to the relative day/night abundance of fish populations depend mainly on the activity patterns of the dominant species; if the dominant species are diurnal (e.g. McCleave & Fried 1975) then more fishes overall will be caught during the day and vice versa.

Longer term movements. Virtually all species changed their abundance between June and August confirming the results of earlier studies (Gibson et al. 1993). Those that recruited to the beach early, i.e. prior to or during June, had decreased in abundance by August (e.g. *Pleuronectes platessa, Limanda limanda*). Species that increased in abundance between June and August were ones that recruited later (e.g. all gadoids except *Gadus morhua*). A large part of the decrease in abundance can be attributed to mortality but there was also evidence of an offshore movement of several species between June and August, shown particularly clearly by *P. platessa* and *Pomatoschistus minutus* (Fig. 6). Comparable seasonal movements have been commonly reported elsewhere (e.g. Creutzberg & Fonds 1971, Horn 1980, Ross et al. 1987). In the present investigation, fishes began to move offshore while physical conditions, particularly temperature and salinity, were comparable to earlier months and their movement may represent a change in their physiological requirements rather than the physical conditions themselves. Fonds et al. (1992), for example, have shown that there is a decrease in the optimum temperature for feeding as *P. platessa* grows and have suggested that movement into deeper, cooler water would maintain an optimum growth rate. In a wider sense, such patterns of 'behavioural enviroregulation' (Neill & Bryan 1991), whether on long or short time scales, serve to maximise metabolic scope and the capacity for growth. Growth in length itself also renders individuals less liable to predation by increasing their escape abilities and reducing the number and range of predators to which they are susceptible (Ellis & Gibson 1995). Movement into deeper water, where potential predators are larger and more numerous, may therefore only be advantageous once individuals have achieved a minimum size. For *P. platessa*, this minimum size appears to be approximately 70 mm (Gibson 1973).

No movement. No clear patterns of change in distribution could be detected in several species. This may

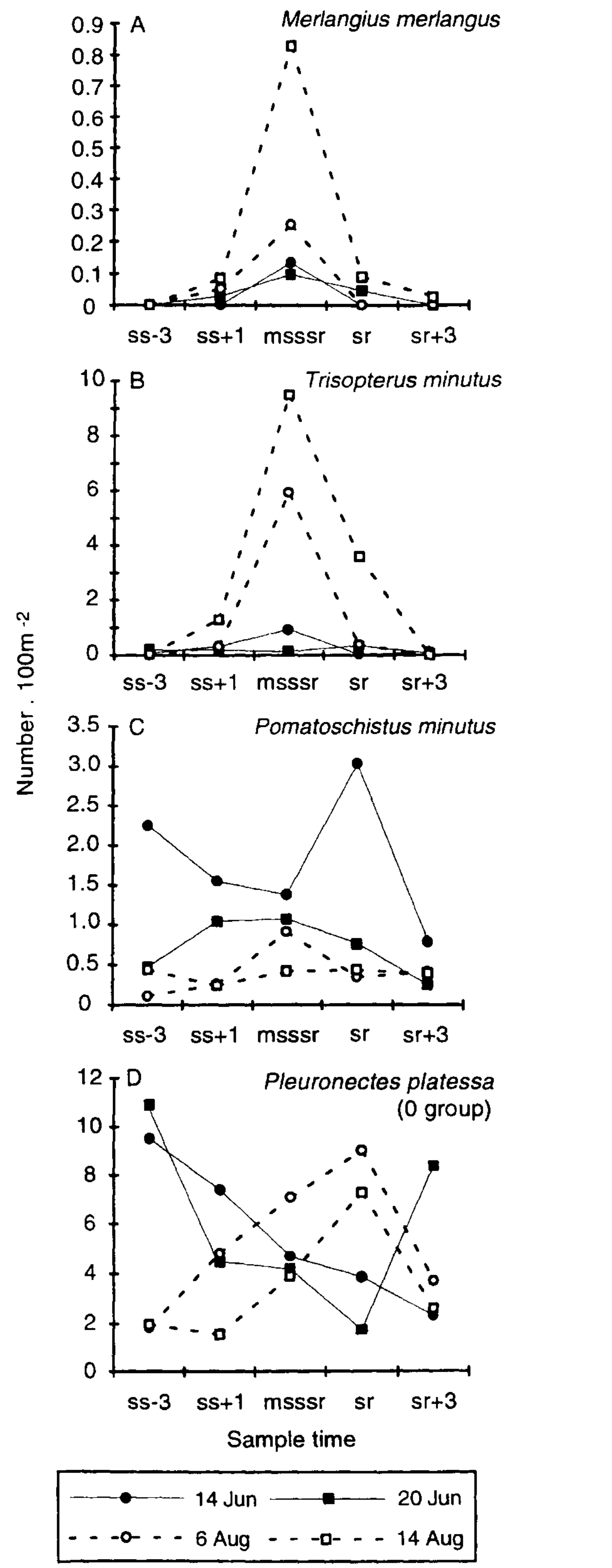

Fig. 7. Seasonal variation in the pattern of diel changes in abundance for (A) *Merlangius merlangus*, (B) *Trisopterus minutus*, (C) *Pomatoschistus minutus*, (D) 0-group *Pleuronectes platessa*. Trawl catches

Table 11. Comparison of species composition of catches made at high and low water during the day and night by seine, and by trawl at 0.5 and 1 m depth. Presence of a species indicated by X

	High water		Low water	
	Day	Night	Day	Night
Species caught by seine				
Clupea harengus			X	
Gadus morhua		X	X	X
Melanogrammus aeglefinus		X		
Merlangius merlangus		X	X	X
Pollachius pollachius		X		
Pollachius virens		X	X	X
Trisopterus minutus		X		X
Spinachia spinachia			X	X
Sygnathus rostellatus				X
Eutrigla gurnardus			X	X
Myoxocephalus scorpius			X	X
Cyclopterus lumpus			X	
Agonus cataphractus				X
Echiichthys vipera			X	X
Ammodytes tobianus			X	X
Pomatoschistus lozanoi				X
Pomatoschistus minutus			X	X
Scophthalmus maximus		X	X	X
Limanda limanda			X	X
Pleuronectes flesus	X	X	X	X
Pleuronectes platessa	X	X	X	X
Solea solea				X
Species caught by trawl				
Gadus morhua		X	X	X
Merlangius merlangus		X		X
Pollachius pollachius		X	X	
Pollachius virens		X		
Trisopterus minutus		X	X	X
Spinachia spinachia	X		X	
Sygnathus rostellatus	X	X	X	X
Eutrigla gurnardus		X	X	X
Myoxocephalus scorpius			X	X
Pholis gunnellus			X	X
Agonus cataphractus		X	X	X
Echiichthys vipera		X	X	X
Ammodytes tobianus		X	X	X
Pomatoschistus lozanoi				X
Pomatoschistus minutus	X	X	X	X
Scophthalmus maximus	X	X	X	
Limanda limanda		X	X	X
Pleuronectes flesus		X	X	
Pleuronectes platessa	X	X	X	X
Solea solea			X	

be a valid conclusion but is equally likely to be the result of small sample sizes or too great a variance between samples that prevented the detection of possible patterns. *Pleuronectes flesus*, for example, migrates intertidally in many areas, particularly at night (Wirjoatmodo & Pitcher 1984, Raffaelli et al. 1990), several other species of flatfishes are also caught in larger numbers at night (Nash et al. 1994) and sandeels (Ammodytidae) are strongly diurnal in their behaviour patterns (e.g. Winslade 1974) but none of these effects was detectable in the present investigation.

Sources of error and their effects on conclusions

The variety of species and sizes present in most fish communities means that no one method of capture is sufficient to sample them adequately. Consequently, any description of community structure and its temporal and spatial variations, especially if based on a single sampling method, is deficient in some respect. In the present investigation there were clear differences in the species composition of the catches made by trawl and seine but taken together they probably represent the best available estimate of assemblage structure at this site because both benthic and pelagic species were sampled. Nevertheless, each gear type is size- and species-selective and neither is 100% efficient. The major implications of this selectivity relate to differences between day and night. Numerous authors (e.g. Horn 1980, Nash 1986, Wright 1989) have discussed the contentious issue of whether observed increases in size and abundance of fishes caught at night are real or whether catches in the dark are larger and contain bigger fishes because net avoidance is lower at night. In the present case, the major nocturnal onshore movements of gadoids has also been observed using static underwater television (Burrows et al. 1994) and so is most unlikely to be solely an artefact of decreased gear avoidance at night. Such movements have also been detected elsewhere by acoustic tagging (Clark & Green 1990) and by direct observation (Keats 1990). Similarly, the movements of *Pleuronectes platessa* as described here are comparable to those observed using underwater television (Burrows et al. 1994).

A further problem encountered in investigations of the responses of fishes to rapidly changing tidal conditions, given the variable nature of successive samples (e.g. Lasiak 1984), is the difficulty of obtaining sufficient replicates for each tidal state. The logistics of repeat hauls within short time periods can be formidable, aside from any confounding effects of repetitive sampling in small bays. These difficulties can be overcome to some extent by a well designed sampling scheme, taking into account the changing phase of tidal and diurnal cycles, and followed by appropriate statistical analyses.

Accepting these reservations, this investigation has nevertheless provided good evidence for the existence of changes in fish distribution and abundance on tidal, diel and seasonal time scales with suggestions as to their function. The next stage of the study must be to determine the factors controlling such changes and their full biological significance.

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