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Feeding ecology and growth of O-group flatfish (sole, dab and plaice) on a nursery ground (Southern Bight of the North Sea)

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The food composition of O-group sole *Solea solea*, dab *Limanda limanda* and plaice *Pleuronectes platessa* on a nursery ground at Gravelines, France, included 17–25 taxa. Sole (new settlers) fed mainly on harpacticoid copepods and when ⩾50 mm in size, on polychaetes (Terebellidae). Dab (<40 mm) consumed mainly polychaetes (Magelonidae and Spionidae), and later amphipods, polychaetes (Spionidae) and Hydrozoa. O-group plaice diet was dominated by polychaetes (Terebellidae), crustaceans and molluscs at all sizes. O-group sole, dab and plaice did not compete for food resources, each species being specialized in different prey items. Growth rates during May–July 1998 varied between 0·5 and 0·67 mm day^{-1} for sole, 0·12 and 0·24 mm day^{-1} for dab and 0·55 and 0·81 mm day^{-1} for plaice. For sole and plaice, these estimates were similar to those recorded in other nurseries and also close to the maximal growth predicted by experimental models. This suggests that their growth was not limited by food during the first summer of life.

Key words: flatfish; feeding ecology; competition; resource utilization.

INTRODUCTION

Recruitment variation in fish is considered to be a major cause of fluctuations in adult population size. Although much research has been done on predation and starvation in early larval stages, there is increasing evidence that mortality of late-larval and early-juvenile stages may affect year-class strength (Sissenwine, 1984; van der Veer *et al.*, 1990; Myers & Cadigan, 1993; Witting & Able, 1993). Nevertheless, which factors determine the abundance, growth and survival of juveniles remain questionable. Rijnsdorp *et al.* (1992) hypothesized that the relative abundance of flatfish was related to the available surface area of nursery grounds, thereby implying competitive interactions when nursery grounds have an intrinsic carrying capacity. Studies on juvenile flatfish concluded that growth rates in the nursery were generally maximal and that food was present in excess and therefore never limited growth (Kuipers, 1977; Zijlistra *et al.*, 1982; van der Veer, 1986; van der Veer *et al.*, 1991; Rogers, 1994). However, in some areas in the western Wadden Sea, growth rate of O-group plaice appeared to be influenced by food abundance and quality (van der Veer & Witte, 1993; Berghahn *et al.*, 1995).

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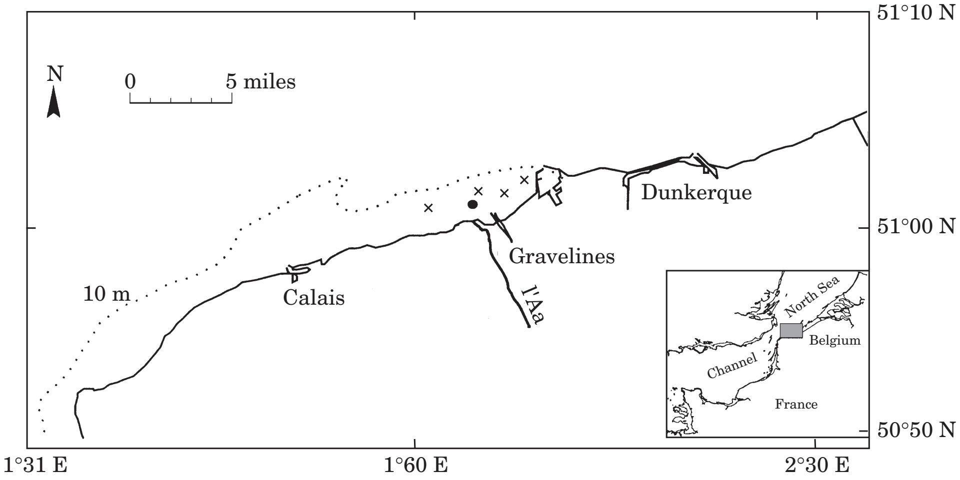

FIG. 1. Study area with location of the benthos (●) and demersal fish sampling stations.

These studies have brought up two types of questions. First, whether growth and mortality of young fish of the same species can be affected by the availability of food items and its partitioning between different size classes. In the second place, whether interspecific interactions may reinforce this regulation of growth and survival, due to similarities in diets when several species use the same nursery grounds. This is particularly true in the Southern Bight of the North Sea where sole *Solea solea* (L.), dab *Limanda limanda* (L.) and plaice *Pleuronectes platessa* (L.) form important components of the demersal fauna. These species spawn offshore and their larvae are transported to shallow coastal nursery grounds where they settle (van der Veer *et al*., 1990; van der Land, 1991; Rijsndorp *et al*., 1992; Bolle *et al*., 1994). The partitioning of food resources between these three commercially important flatfish was investigated because of their similarity in body morphology, size and preference for benthic prey. The goal was to assess the feeding ecology of early juvenile sole, dab and plaice during the first months after settlement in the shallow sandy bottom areas of the Southern Bight of the North Sea. The competition for food between species was evaluated by comparing the availability of benthic prey at the nursery and the diet composition of each species by size classes. Estimates of growth were used to assess whether growth was food limited.

MATERIALS AND METHODS

STUDY AREA AND SAMPLING

The study area was in the southern part of the North Sea near Gravelines (France) (Fig. 1). This site has been the focus of a long-term study on benthos (Dewarumez *et al*., 1992). The bottom of the subtidal zone studied (0–10 m depth) consisted of fine sand (70–90%) and mud (1–12%). At this depth, the benthic fauna was dominated by an *Abra alba* community all along the coast (Carpentier *et al*., 1997).

Demersal fish were sampled with a 3 m beam trawl (6 × 6 mm mesh codend) equipped with one tickler chain. The trawl was hauled from the 12·5 m RV Sepia II. Each haul was taken parallel to the coast and against the tidal current, at a speed of 2·5 knots and covered 1000 m on average. Samplings were carried out during daylight, on 8 May, 16 June and 7 July 1998, at four stations at around 5 m depth (Fig. 1). Corresponding to the settlement period of juveniles of the three targeted species, the spring and early summer periods were chosen because individuals were most numerous, allowing interspecific competition to be studied under the most appropriate conditions.

Fish were preserved in a 7% formaldehyde-sea water solution or in 95% ethanol (for later otolith analyses). In the laboratory, all fish were identified and counted to determine the density and to analyse the fish community composition (not presented in this study). The densities were standardized as numbers of individuals per 1000 m^2. Water temperatures and salinity were measured on every sampling occasion at each station.

GROWTH ANALYSES

O-group flatfish were measured for total length (L_T) to the nearest mm. For each species, length-frequency distributions were established and growth was calculated as length increase measured from May to July sampling dates. Growth of the O-group plaice and sole was analysed by comparing observed growth in the field with simulated growth using experimentally established growth equations obtained under optimal feeding conditions. For plaice, Glazenburg's equation (unpubl. data) was used:

$$\Delta L = 1{\cdot}3T + 1{\cdot}7 \text{ (mm month}^{-1}\text{)}$$

in which ΔL is the predicted monthly increase in length (mm month^{-1}) and T is the mean water temperature (°C) over the period of observation.

For sole, the following relationship between the mean water temperature (T, °C) and mean length (L, cm) derived by Fonds (1979), (in Rogers, 1994) was used to provide an indication of the maximum daily growth rate (ΔL) (mm day^{-1})

$$\Delta L = 0{\cdot}325\ (0{\cdot}14T + 0{\cdot}036L - 1{\cdot}2)$$

DIET COMPOSITION

To process the gut (stomach+intestine) content, all juvenile samples were divided into seven size classes (15–30; 31–40; 41–50; 51–60; 61–70; 71–80; 81–90 mm). Individuals analysed were selected at random in each size class. Prey items were identified under a stereomicroscope, to the nearest taxon or species, and counted. Food composition was expressed as a percentage of frequency of occurrence (% O, the percentage of gut in which a certain prey item occurred) and percentage composition by number (% N, the number of a particular prey item as a proportion of the total number of all prey items in the entire gut contents).

BENTHOS SAMPLING AND ANALYSIS

The benthos was sampled on 15 June 1998 at one station in the subtidal area (Fig. 1). Benthos samples were taken with a Van Veen grab digging 0·1 m^2 to a depth of 8–13 cm. Ten samples were taken and sieved (1 mm mesh) on board, then preserved in a 4% formalin-sea water solution. One extra sample was collected for sediment analyses. After sorting, the benthic organisms were identified, as often as possible at the specific level and counted. Biomass (ash free dry weight) was determined separately for the main species, the rare species being weighed together. An annual mean of the structure of the benthic community is also given using trends observed during the long-term survey (Carpentier *et al*., 1997).

RESULTS

From May to July, water temperature increased from 12 to 18° C. The salinity was stable at *c*. $S = 34{\cdot}5‰$.

LENGTH FREQUENCY DISTRIBUTION AND GROWTH

In early May, O-group plaice (14–80 mm) were the most abundant at 36·3 ind. 1000 m^2 (Fig. 2). O-group sole and dab were less abundant (mean density 7·2

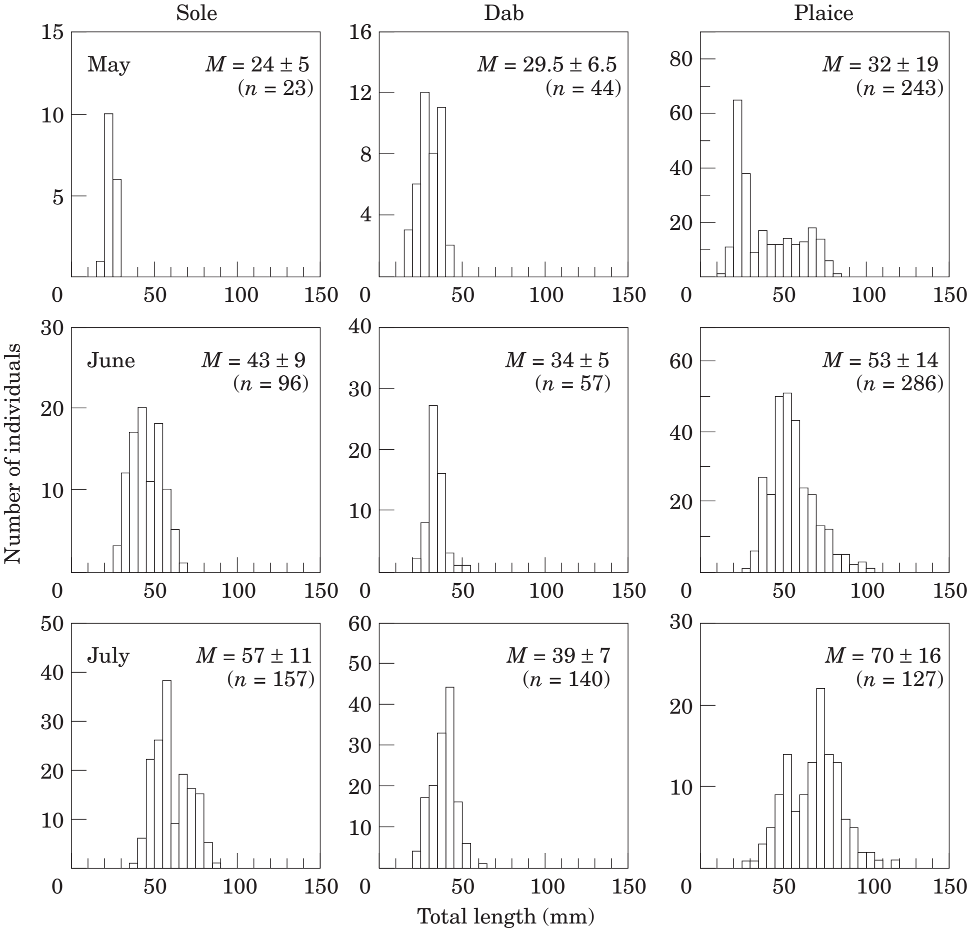

FIG. 2. Length-frequency distribution of O-group sole, dab and plaice in May, June and July. n, Number of individuals; M, median size (L_T mm ± S.D.).

and 8 ind. 1000 m^2, respectively) and smaller than plaice. The bimodal length-frequency distributions in May for plaice and in June for sole indicate that immigration to the nursery was a continuous process in which new immigrants mixed with older ones. As a result of the settlement of newly arrived fish, the population density of sole and dab increased to a maximum in July. At this time, the three species were equally abundant (mean density, ind. 1000 m^{-2}: 17·7 (sole), 15·1 (dab) and 14·7 (plaice)). The length frequency distributions were not normal and therefore, for each sampling date, the median length was estimated rather than the mean length. Median lengths increased almost linearly from May to July from 24 to 57 mm in sole, 29·5 to 39 mm in dab and 32 to 70 mm in plaice. Mean growth between May and June and between June and July was respectively 0·5 and 0·67 mm day^{-1} for sole; 0·12 and 0·24 mm day^{-1} for dab and 0·55 and 0·81 mm day^{-1} for plaice. When the bimodal length distributions are taken into account, the growth estimates for each separate modal group become slightly higher and more comparable with those of laboratory estimates. For example, for sole growth between June and July was 0·64 and

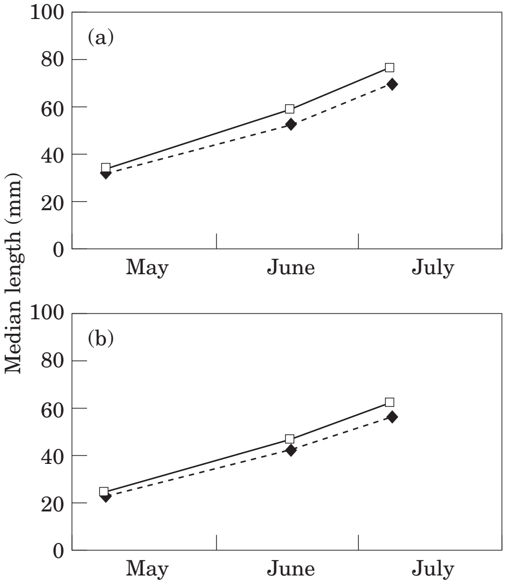

FIG. 3. Mean length (◆) of O-group plaice (a) and O-group sole (b) compared with simulated maximal growth (□) according to growth models obtained under optimal food conditions in the laboratory.

$0{\cdot}77\ \mathrm{mm\ day}^{-1}$. There was a high similarity between observed and simulated lengths of O-group sole and plaice (Fig. 3), suggesting that growth was not food-limiting during the summer.

DIET COMPOSITION

A total of 153 guts was examined, taken from newly settled juveniles as follows: 55 sole, 38 dab and 60 plaice. Empty stomachs occurred in 40% of sole, 15% of dab and 8% of plaice, and empty intestines only in 2% of sole. There were 9–12 taxa among the food organisms and dab and plaice fed on a wider range of prey species than did sole (Table I). Differences in diet composition were observed between species and between size classes.

SOLE

The dominant prey items in sole were polychaetes (79·2%O; 3·6%N) mainly *Lanice conchilega* and crustaceans (73·9%O; 93·4%N) mainly harpacticoïd copepods; Cumacea and Amphipoda were also important prey items (Table I). Harpacticoid copepods are the main components of the new settlers' diet (15–40 mm) (100%O; 96%N); planktonic copepods (and among them, *Temora longicornis*) and Cumacea constitute secondary prey. At a size >50 mm, sole replace copepods in the diet progressively by polychaetes (*Lanice conchilega*; 40–86%O) and secondarily, by Amphipoda (29–50%O) (Fig. 4).

DAB

Prey items were dominated by polychaetes (92·2%O; 66%N), crustaceans (86·8%O; 10·1%N) and molluscs (42·1%O; 15%N) (Table I). The new settlers ($\leq$40 mm) consumed mainly harpacticoid copepods, polychaetes (palps of *Magelona mirabilis* and Spionidae species) and bivalvia (*Mysella bidentata*)

Table I. Frequency of occurrence (%O) and percentage composition by number of taxa (%N) in the diet of the three flatfish species (others: prey unidentified due to their state of digestion or rare prey items (e.g. echinodermas)

	Sole		Dab		Plaice	
	%O	%N	%O	%N	%O	%N
Hydrozoa	—	—	10·53	0·93	—	—
Nematoda	9·43	0·31	2·63	0·19	15·00	1·26
Polychaeta	79·25	3·58	92·11	66·08	96·67	71·61
Bivalvia	15·09	0·83	42·11	15·01	35·00	6·29
Ostracoda	—	—	7·89	0·56	—	—
Calanoida	3·77	0·18	0·00	0·00	1·67	0·14
Harpacticoida	60·38	89·97	28·95	3·15	16·67	5·17
Cirripedia	—	—	—	—	1·67	0·14
Caridea	1·89	0·04	5·26	1·30	16·67	2·10
Mysidacea	—	—	2·63	0·19	8·33	2·10
Cumacea	33·96	2·33	10·53	2·22	21·67	3·08
Amphipoda	20·75	1·18	34·21	4·63	13·33	2·52
Pisces	—	—	—	—	10·00	1·54
Others	35·85	1·18	52·63	5·00	25·00	2·52
No. taxa	9		11		12	

(Fig. 4). At a size >40 mm, dab consumed amphipods (65%O), polychaetes (Spionidae; 80%O) and Hydrozoa (*Obelia* sp; 30%O). There was a net increase of amphipods in the diet with fish size, replacing progressively the palps of Magelonidae and harpacticoïd copepods. In all size classes, the diet was completed with bivalve molluscs and Spionidae species.

PLAICE

O-group plaice (15–90 mm) did not show a shift in prey consumption as a function of fish size. The main prey were polychaetes (96·7%O; 72%N), crustaceans (55%O; 14·5%N) and molluscs (35%O; 6·3%N) (Table I). The predominant polychaetes in the diet and for all size classes was *Lanice conchilega* (70%O; 52·4%N). Magelonidae (principally palps of *Magelona mirabilis*) and Aphroditidae were also important prey, particularly for the new settlers. Nephthydidae (*Nephtys* sp.) were consumed only by plaice >70 mm. Among crustaceans, Caridae (particularly juvenile *Crangon crangon*), copepods (mainly harpacticoids), cumaceans and amphipods were the most frequent (Fig. 4). The molluscan prey consisted almost entirely of bivalve siphons. Metamorphosing sole larvae (9 mm L_S) and fish eggs were recorded exceptionally.

TEMPORAL VARIATION IN THE DIET

In May, most of the flatfish were recently settled individuals. During this period, the major preys consumed ($\%O \geq 50$) for sole and dab were harpacticoid copepods, palps of *Magelona mirabilis* for dab and plaice, Spionidae species for dab and *Lanice conchilega* for plaice (Table II). In June, harpacticoid copepods remained the major prey in the diet of sole with Cumacea also, whereas dab and plaice fed mostly on polychaetes. In July, as in June, *Lanice conchilega* was

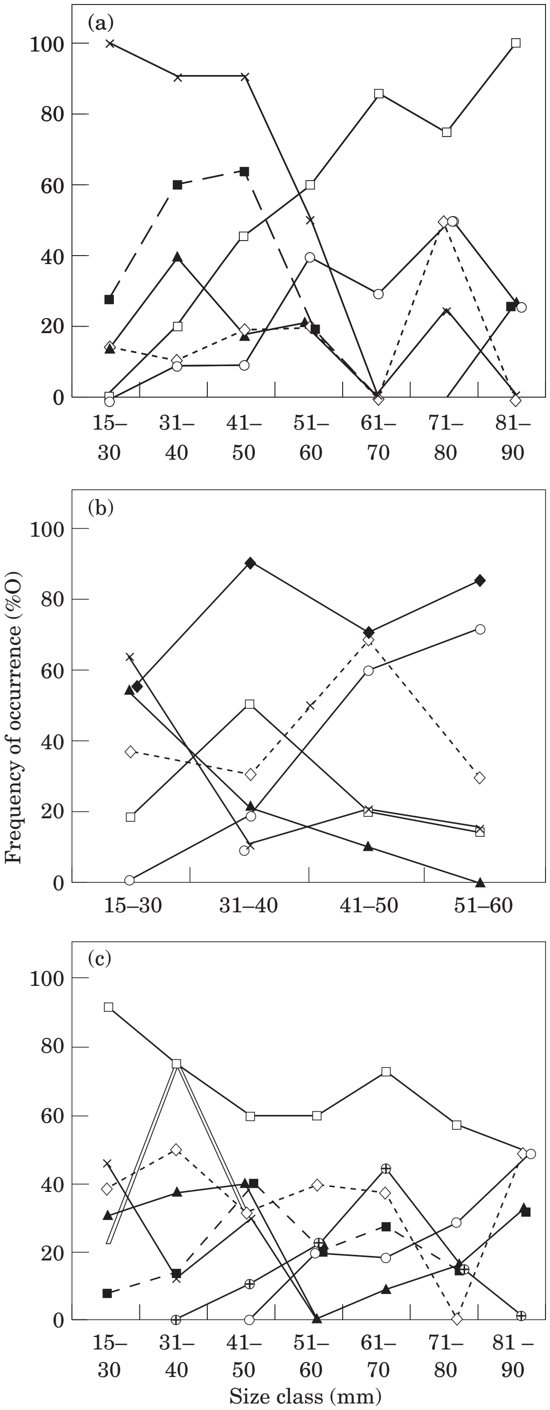

FIG. 4. Frequency of occurrence of the most important prey items (%O ≥ 20) in the diet of different size classes for (a) sole; (b) dab and (c) plaice. —□—, *Lanice conchilgea*; —▲—, Magelonidae palps; —■—, Spinidae; ═□═, Aphroditidae; —×—, Harpacticoidea; —⊕—, Crangonidae; – –■– –, Cumacea; —○—, Amphipoda; – –◇– –, Bilvalvia.

TABLE II. The most important prey items (%O ≥ 20) of the dominant size class in the three flatfish species in May, June and July

	May			June			July		
	Sole	Dab	Plaice	Sole	Dab	Plaice	Sole	Dab	Plaice
Polychaeta									
Spionidae species		+¶			+¶			+¶	
Magelona mirabilis		+¶	+¶		+¶		+	+	
Lanice conchilega			+¶	+	+¶	+¶	+¶	+	+¶
Nephtys sp.									+
Aphroditidae			+						
Phyllodocidae			+						
Bivalvia									
Bivalvia siphon			+		+	+		+	
Mysella bidentata		+						+	
Crustacea									
Temora longicornis	+								
Harpacticoida species	+¶	+¶	+	+¶			+¶		
Cumacea	+			+¶		+		+	+
Crangon crangon						+			+
Amphipoda					+	+	+	+¶	+

¶, Major prey items (%0 ≥ 50).

consumed in high proportion by the three flatfish. Nevertheless, other major prey for sole were harpacticoid copepods, and Spionidae species and amphipods for dab.

BENTHOS ANALYSES

The sediment of the sampling station was dominated by fine and medium sand (92%). In June, the benthic community was dominated by *Lanice conchilega* (3592 m^{-2}), *Abra alba* (376 m^{-2}) and *Notomastus latericeus* (331 m^{-2}) (Table III). The other important species were *Tellina fabula* (66 m^{-2}), *Nassarius reticulatus* (46 m^{-2}), *Nephtys hombergii* (42 m^{-2}), *Pectinaria koreni* (37 m^{-2}) and *Mysella bidentata* (35 m^{-2}). Since the sampling occurred before the main recruitment period of benthic species, the results were compared with mean values calculated over one year. The annual mean densities of species were different because they included all the recruitment of benthic species (Table III). In fact, a lot of species, absent in the June sampling, were recruited in late June–early July especially *Magelona mirabilis* (214 m^{-2}), *Spiophanes bombyx* (130 m^{-2}), *Eumida sanguinea* (83 m^{-2}), and *Phyllodoce mucosa* (67 m^{-2}).

The biomass (AFDW) was very high in June 1998: 107·9 g m^{-2} (Table IV). The main species regarding the biomass were *Abra alba* (41·9 g m^{-2}), *Notomastus latericeus* (27·8 g m^{-2}), *Lanice conchilega* (11·2 g m^{-2}), *Spisula subtruncata* (8·5 g m^{-2}), *Nassarius reticulatus* (5·3 g m^{-2}) and *Ensis directus* (5·1 g m^{-2}). The same species dominated the biomass throughout the year. However, the annual mean biomass was lower than the late spring biomass: 53·6 g m^{-2}.

TABLE III. Density (individuals m^{-2}) of the main benthic species in June 1998 and the mean annual density calculated from long-term survey data

Species	Density (ind. m^{-2}) in June 1998	Annual mean density (ind. m^{-2})
Spiophanes bombyx	0	130
Magelona mirabilis	0	214
Notomastus latericeus	331	251
Phyllodoce mucosa	1	67
Eumida sanguinea	8	83
Lanice conchilega	3592	1947
Nassarius reticulatus	46	42
Mysella bidentata	35	30
Spisula subtruncata	28	42
Tellina fabula	66	23
Abra alba	376	311
Ensis directus	18	49
Species richness	28	65
Total density	4685	3577

TABLE IV. Biomass (AFDW) of the main benthic species (mg m^{-2}) and the mean annual biomass calculated from long-term survey data

Species	Biomass (mg m^{-2}) in June 1998	Annual mean biomass (mg m^{-2})
Spiophanes bombyx	0·0	27·2
Magelona mirabilis	0·0	162·2
Notomastus latericeus	27778·6	5564·3
Phyllodoce mucosa	14·2	52·4
Eumida sanguinea	0·0	28·4
Lanice conchilega	11249·6	6328·4
Nassarius reticulatus	5307·6	6933·8
Mysella bidentata	13·9	11·2
Spisula subtruncata	8549·3	6463·5
Tellina fabula	535·7	230·3
Abra alba	41941·9	10012·5
Ensis directus	5141·1	6730·4
Other	7351·3	11052·3
Total biomass	107883·2	53596·9

DISCUSSION

In the North Sea, flatfish comprise 29% of the total biomass of demersal fish (Daan *et al.*, 1990). Like most marine fish, flatfish exhibit significant year-to-year variations in recruitment. Recruitment may depend upon the availability of suitable nursery habitat that provides vital functions enhancing growth and survival. Apart from predation, the availability of suitable food is usually considered to be a key factor affecting growth and mortality of young fish (Poxton *et al*., 1983; van der Veer & Witte, 1993; Gibson, 1994; Berghahn *et al*., 1995).

During the planktonic larval stage, sole, dab and plaice have distinct diets and competition for food between them is largely avoided (Last, 1978). After metamorphosis, sole, dab and plaice settle in late spring and early summer, generally at sizes from 11 to 20 mm, in shallow coastal nursery grounds (Russell, 1976; Poxton *et al*., 1983; Amara *et al*., 2000). For sole, the transition from the pelagic to the benthic lifestyle, which occurs at the end of metamorphosis, does so without nutritional crisis or growth arrest (Lagardère *et al*., 1999; Amara *et al*., 2000).

FEEDING ACTIVITY

Despite their similarity in benthic lifestyles, competitive interactions between juvenile flatfish settling on the nursery grounds of the Southern Bight were not observed at the time of maximal abundance of juveniles. The very low number of empty guts suggests that the three flatfish species were able to sustain a high feeding activity altogether. Compared with other flatfish species, sole, dab and plaice have a rather small stomach and a long alimentary tract, which explains why food passed rapidly through their stomachs (de Groot, 1971; Kuipers, 1977). According to Beyst *et al*. (1999), it was thus advisable to analyse the whole gut to compare the diet of the three species. Nevertheless, sole had a relatively high number of empty stomachs, which may have been due to the very small size of this organ, but also to a nocturnal feeding activity while samples were taken during daytime. In addition, juvenile soles, feeding mainly on small prey and at a high frequency (Marchand & Masson, 1989; Amara & Bodin 1995), do not need a storage capacity for large prey, as compared with other Pleuronectidae (de Groot, 1971).

SHIFTS IN PREY

Many benthic juvenile fish pass through an important meiobenthic feeding stage (Hogue & Carey, 1982; de Morais & Bodiou, 1984), and at a certain size (30–45 mm) an ontogenetic shift to larger macrofaunal prey usually occurs (Gee, 1987; Shaw & Jenkins, 1992; Aarinio *et al*., 1996). Such a shift in prey composition as a function of fish size, may reduce intraspecific competition and probably interspecific competition if the species shows distinct differences in time of settlement or depth distribution. In the North Sea, plaice settle from March to June (van der Veer *et al*., 1990), whereas sole and dab settle later from May to July (Rijsndorp *et al*., 1992; Bolle *et al*., 1994; this study). The distribution of O-group flatfish varies with depth, for example in the U.K. coastal areas, O-group sole were at maximum densities in depths of 0–5 m. Plaice are concentrated more in shallow waters, whereas juvenile dabs have peak densities at 5–10 m in depth (Riley *et al*., 1981).

Some shifts in prey preference as a function of fish size were observed in this study, but only for the sole and dab juveniles. Sole juveniles replaced harpacticoid copepods progressively by polychaetes (*Lanice conchilega*) and secondarily by Amphipoda when they reached a size >50 mm. A similar shift in prey was observed on the French Atlantic coast by Castel & Lasserre (1982) and Marchand & Masson (1989). Since the settlement period was a continuous process in which new immigrants mixed with older ones (Amara *et al.*, 1994, 2000), intraspecific competition in sole was then reduced since small juveniles took smaller prey (copepods) rather than larger juveniles (e.g. amphipods). Similar observations led to the same conclusions for dab.

DIET COMPOSITION AND RESOURCE PARTITIONING

Newly settled juveniles (15–30 mm) of sole, dab and plaice fed on small prey (e.g. palps of polychaetes and harpacticoid copepods). However, the relative importance of these prey in their diets differed between species. New settled sole fed almost exclusively on harpacticoid copepods (97%N), whereas in dab and plaice, the polychaetes formed the most important part of their diet (61 and 82%N, respectively), even if the new settlers also fed on harpacticoid copepods. Furthermore, both dab and plaice did not ingest the same polychaete species, with the Spionidae and Magelonidae in the new settler dab diet, whereas *Lanice conchilega* characterized the plaice's diet. Since the benthic community in June is dominated by *Lanice conchilega* (3592 m^{-2}) these results suggest that plaice consumes preferably the most abundant species, whereas dab utilizes any available food source. According to Wyche & Shackley (1986) this is probably due to differences in feeding posture between the two species.

The analysis of food composition showed that direct competition for food of recently settled flatfish was largely avoided by a partitioning of different types of food. With size increasing, individuals fed on larger prey (e.g. amphipods, cumaceans and Crangonidae). When some overlapping in the diet of flatfish species was observed, this concerned prey species which were highly abundant in the area such as *Lanice conchilega*, *Magelona mirabilis*, and bivalve siphons (*Tellina fibula*), which were also an important source of food. Consumption of parts of polychaetes (e.g. palps) and molluscs (e.g. siphon) by juvenile sole, plaice and dab has been observed by several authors (Edwards & Steele, 1968; Kuipers, 1977; de Vlas, 1979; Lagardère, 1987; Beyst *et al.*, 1999). In the Balgzan intertidal area (Wadden Sea), de Vlas (1979) showed that the total share of regenerating parts of benthic animals in the food intake of juvenile plaice was about 36% of the total predation. The high capacity for regeneration of all these organs (palps, gills and siphons) provided a continuously renewed source of food without concomitant mortality of prey.

Recent studies on the feeding ecology of juvenile flatfish suggested that interspecific competition for food was unlikely (Aarinio *et al.*, 1996; Beyst *et al.*, 1999). This was attributed both to a spatial segregation of feeding habitats and to feeding behaviour which differed between species. The Pleuronectidae, such as dab and plaice, were visual day-feeders able to use visual clues in their search for food, but also chemical clues. In contrast, sole being mostly non visual night-feeders, used mostly olfaction to feed on sedentary or slow-moving prey found in or near the bottom (Holmes & Gibson, 1983). Lagardère (1987) thought the nocturnal habit of the juvenile sole to be mainly responsible for avoiding competition. The present study supports these suggestions, indicating that the food composition of the three flatfish species varied greatly. Thus, interspecific competition for food was minimized owing to the specialization of each species on a different type of food and also by the differences in settlement period and depth distribution (feeding habitat).

GROWTH

Growth was estimated from length frequency distributions, a current method of calculation that is correct if the length frequency distributions are not influenced by effects of migration, mortality or gear efficiency. The effect of migration is probably negligible during the period of study since sole and plaice have very restricted distributions during their early juvenile phase (Riley *et al.*, 1981; Rogers, 1992; Gibson, 1994). Although the beam trawl has been used extensively for research into the ecology and population dynamics of juvenile flatfish, few studies have presented efficiency data, largely because of the practical difficulties involved in their estimation (but see Kuipers, 1975; Rogers & Lockwood, 1989; Kuipers *et al.*, 1992). The efficiency of the 3 m beam trawl used in this study has not been assessed, but Riou (1999) compared the relative efficiencies of a 2 m and a 3 m beam trawl. He found no significant difference for the O-group plaice and flounder. The efficiency of the 2 m beam trawl decreased considerably with the length of the plaice: from *c*. 100% at *c*. 50 mm to 15% at 200 mm length (Kuipers, 1975). Since the length of the sampled flatfish varies between 20 and 80 mm during this study, the bias in the efficiency measurements could, be low and probably not influence the length frequency distribution obtained. This assumption is reinforced by the fact that the length frequency distributions were similar to those observed during the same period in other areas sampled with a 2 m beam trawl (Kuipers, 1977; de Vlas, 1979). Besides, growth estimated here was in the range of those recorded in other nurseries and also for some flatfish reared experimentally. Growth of 0-group sole varied between 0·5 and 0·67 mm day^{-1}, which were similar to those estimated on the North Wales nursery ground (0·54 and 0·58 mm day^{-1}) (Rogers, 1994), but higher than those from the Vilaine estuary (0·49 mm day^{-1}), the Eastern Channel nursery (0·42 mm day^{-1}) (R. Amara *et al.*, unpubl. data), or a Swedish nursery ground (0·44 mm day^{-1}) (Phil, 1989). When fed *ad libitum* in hatchery on-growing systems, growth of reared juvenile sole may vary from 0·8 to 1·3 mm day^{-1} (M. Fonds, pers. comm.), 0·66 mm day^{-1} (Ramos & Rouros, 1985) and 0·64 mm day^{-1} (Howell, 1977), to 0·40 mm day^{-1} (Mo, 1991). For plaice, present growth (0·55 and 0·81 mm day^{-1}) was also in the range of those recorded in other nursery areas: 0·19–0·62 mm day^{-1} on the port Erin Bay nursery (Nash *et al.*, 1994), 0·56 mm day^{-1} in the Dollard (Ems estuary) (Jager *et al.*, 1995) and 0·56–0·66 mm day^{-1} in the Wadden Sea areas (Berghahn *et al.*, 1995). Maximum growth of juvenile plaice reared in the laboratory at temperatures of 10–18° C with unlimited food varies from 0·4 to 0·8 mm day^{-1} (Fonds *et al.*, 1992). Present results with dab showed the lowest growth rate, compared with the sole and plaice. Few studies referred to the summer growth of 0-group dab, estimated at 0·5 mm day^{-1} in the Clyde Sea area (Poxton *et al.*, 1983) and 0·49 mm day^{-1} in the Eastern Channel nursery (R. Amara *et al.*, unpubl. data). Lower and rather similar values were obtained from the Wadden Sea (0·25 mm day^{-1}, Bolle *et al.*, 1994) and from this study (0·11 and 0·24 mm day^{-1}). In the present case, the low growth cannot been explained by food limitation: all dab examined had food in their gut. Bolle *et al.* (1994) showed that 0-group dab were not restricted to shallow coastal nurseries and therefore a size-selective sampling bias cannot be excluded. On the other hand, dab are serial spawners with a prolonged spawning period (Daan *et al.*, 1990). As settlement is a continuous process, the arrival of newly settled dab until July reduced the mean size of the O-group juveniles and then the estimated growth.

By comparing the observed growth with the expected growth, obtained from experimentally established models, it was feasible to predict a maximal growth in relation to water temperature. This has shown that growth of 0-group plaice and sole was maximal, which suggested that feeding conditions were optimal in the Southern Bight and that growth was determined only by prevailing water temperatures. Based on such a comparison, previous studies in the Wadden Sea (Zijlstra *et al.*, 1982; van der Veer, 1986; van der Veer *et al.*, 1991; D. Mengedoht, unpubl. data) and in the port Erin Bay nursery (Nash *et al.*, 1994) also concluded that 0-group plaice achieved maximum possible growth in summer. The same was concluded for growth of 0-group sole from the North Wales nursery grounds (Rogers, 1994).

CONCLUSION

This study illustrates differences between diets of juveniles of three closely related flatfish species sharing the same nursery ground. Newly settled sole, dab and plaice apparently do not compete for food resources in the Southern Bight nursery grounds. Differences in settlement periods and depth distributions of these juveniles probably contribute to reduce interspecific competition for food. Growth of sole and plaice during their first summer was close to the maximal growth predicted by experimental models, suggesting that growth was not limited by food. However, use of shallow coastal nursery areas is an important phase of the life history of many marine organisms. In the nursery studied, juvenile flatfish do not occupy the nursery area in isolation and the role of potential competitors must also be taken into account. During the summer, 9–15 demersal fish species were caught in the nursery ground (C. Maryniak & R. Amara, unpubl. data). The highest catches were of *Pomatoschistus* sp. gobies with a maximum density in July (140 fish 1000 m^{-2}), dragonet *Callionymus lyra* (40 fish 1000 m^{-2}), and weever fish *Echiichthys vipera* (80 fish 1000 m^{-2}). The brown shrimp *Crangon crangon* was also abundant in July. Both goby and the brown shrimp competed with flatfish juveniles by feeding on crustaceans (copepods, cumaceans, amphipods, isopods and mysids), bivalve molluscs and polychaetes (Hamerlynck & Cattrijsse, 1994; Rogers, 1994). Since most of these prey are also consumed by 0-group flatfish (Edward & Steele, 1968; Ansell & Gibson, 1990; Beyst *et al*, 1999; this study), this probably entailed interspecific competition in late summer, when the density of gobies and *Crangon crangon* increased. This was the case in a flatfish nursery ground in the Bay of Biscay (France), where competition during July and August was identified between sole and sand gobies for annelids (Le Mao, 1986). However, the shallow coastal waters in the southern Bay of the North Sea is highly productive (Dewarumez *et al.*, 1986, 1992) and may provide the food required by the O-group flatfish. Kuipers (1977) came to the same conclusion by studying the total food-intake of juvenile plaice in the Wadden Sea.

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