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The feeding ecology of 0 year-group turbot *Scophthalmus maximus* and brill *Scophthalmus rhombus* on Irish west coast nursery grounds

P. S. Haynes*, D. Brophy, F. de Raedemaecker and D. McGrath

Commercial Fisheries Research Group, Department of Life Sciences, Galway-Mayo Institute of Technology, Galway, Ireland

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On sandy beach nursery grounds along the west coast of Ireland, 0 year-group turbot *Scophthalmus maximus* were found to consume six types of crustaceans, in addition to polychaetes. The 0 year-group brill *Scophthalmus rhombus* fed almost exclusively on mysids, even though nine taxonomic prey groups were identified in the sediment across the investigated beaches. Both species avoided non-motile organisms such as gastropods and bivalves, which were present in high abundances in the sediment and their growth and condition was not significantly related to the quantity or type of prey consumed, temperature or salinity. A high incidence of feeding was detected for both species over the duration of the study, suggesting that food was not limiting on west of Ireland nursery grounds. Temporal partitioning of settlement was detected between *S. maximus* and *S. rhombus*, indicating that inter-specific competition for food does not occur between these two flatfish species on west of Ireland nursery grounds.

Key words: diet; flatfish; growth; prey; temporal partitioning.

INTRODUCTION

Shallow inshore coastal areas serve as nursery grounds for many flatfish species during early life. These areas are described as highly productive habitats, with the availability of prey considered to be one of the key factors determining the quality of flatfish nursery grounds in terms of growth and survival (Gibson, 1994). While several authors investigating the feeding ecology of juvenile flatfish have concluded that food availability on nursery grounds is never limited (Karakiri *et al*., 1991; Amara *et al*., 2001), others have reported that variability in the type and quantity of prey available both within and between nursery areas can arise (Van der Veer & Witte, 1993; De Raedemaecker *et al*., 2011*a*). Seasonal fluctuations in benthic productivity within the nursery ground, can also affect the growth and survival of juveniles (De Raedemaecker *et al*., 2011*b*). Such differences may determine the abundance of juveniles eventually recruiting to the adult population, with larger individuals more likely to survive the nursery ground stage (Sogard *et al*., 2001).

Within a nursery ground, both intra and inter-specific competition, for available food resources can occur (Martinsson & Nissling, 2011). Certain strategies have

*Author to whom correspondence should be addressed. Tel.: +353857333058; email: paula.haynes@gmit.ie

evolved, however, to reduce competition both between and within flatfish species, thereby increasing the foraging efficiency and subsequent growth of individuals. Tactics exhibited by many flatfish species include temporal and spatial partitioning, whereby different species settle onto nursery grounds at different times throughout the year, and at different depths within the nursery. Resource partitioning, or different feeding habits have also evolved, with ontogenetic shifts in diet reducing intraspecific competition (Florin & Lavados, 2009). While competition is an important determinant of density-dependent mortality on nursery grounds, it may ultimately only arise if exceptionally high densities of juvenile flatfish occur (Nash *et al*., 2007).

In Ireland, turbot *Scophthalmus maximus* (L. 1758) and brill *Scophthalmus rhombus* (L. 1758) are valuable non-quota commercial flatfish species, with the juveniles known to inhabit nursery grounds along the west coast of Ireland (Haynes *et al*., 2010*a*). In general, temporal partitioning between the two species occurs along the Irish west coast, with 0 year-group *S. rhombus* settling onto beaches in March and April (P. S. Haynes, D. Brophy & D. McGrath, unpubl. data), whereas 0 year-group *S. maximus* do not arrive on the nursery grounds until later on in the year, in June and July (Haynes *et al*., 2011), and are present on beaches up until October to November (pers. obs.). On occasion, however, both 0 year-group *S. maximus* and *S. rhombus* of a similar size may co-occur, as a result of several cohorts spawned throughout the year. This suggests that competition between these two morphologically similar species might arise (Piet *et al*., 1998).

Both 0 year-group *S. maximus* and *S. rhombus* are described as visual daylight hunters, feeding primarily on moving organisms such as mysids and amphipods, as opposed to sedentary prey items (De Groot, 1971). While fishes are reported to be the main choice of prey for the juveniles of both species >10 cm total length (L_T) (Holmes & Gibson, 1983; Sparrevohn & Støttrup, 2008), studies have also found smaller *S. maximus* [3–5 cm L_T (Aarnio *et al*., 1996), 2·5–6 cm L_T (Beyst *et al*., 1999)], and *S. rhombus* [>6 cm L_T (Braber & De Groot, 1973), >5 cm L_T (Beyst *et al*., 1999)], to include fishes in their diet. In contrast to other juvenile flatfishes such as European plaice *Pleuronectes platessa* L. 1758 or European flounder *Platichthys flesus* (L. 1758), *S. maximus* and *S. rhombus* are reported to feed on a narrow range of prey items (Beyst *et al*., 1999), with 0 year-group *S. rhombus* known to be highly selective in the type of prey that they consume (Cabral *et al*., 2002). This restrictive diet may negatively affect the number of *S. rhombus* surviving to the end of the nursery ground stage, particularly if the preferred prey item within the inhabited nursery ground is scarce.

On the west coast of Ireland, recent studies have provided valuable baseline knowledge on the early life history of *S. maximus* (Haynes *et al*., 2010*a*, *b*, 2011). Basic data on the biology and ecology of juvenile *S. rhombus* from this geographical location are, however, lacking. The sparse distribution of *S. rhombus*, in addition to their inconsistent recruitment to nursery grounds in any part of the north-east Atlantic Ocean, has resulted in very little published information being available in the literature. In an attempt to expand on, or improve the data previously established for juvenile flatfishes on the west coast of Ireland, the feeding ecology and behaviour of 0 year-group *S. maximus* and *S. rhombus* was investigated.

The objectives of the present study were to: (1) describe the type of prey consumed by juvenile *S. maximus* and *S. rhombus* inhabiting nursery grounds, and investigate any differences in the availability of prey across months; (2) examine any temporal, spatial, or resource partitioning between 0 year-group *S. maximus* and *S. rhombus*; (3) identify the type of prey available in the sediment on nursery grounds, to determine if *S. maximus* or *S. rhombus* were actively selecting specific prey items; (4) determine whether either the growth or condition of *S. maximus* and *S. rhombus* was related to the abundance or type of prey consumed, or temperature and salinity values within nursery locations.

MATERIALS AND METHODS

NURSERY GROUNDS ASSESSED

Four shallow sloping sandy beaches were assessed for 0 year-group *S. maximus* and *S. rhombus* along the west coast of Ireland (Fig. 1). Inch and Brandon are located in the south-west of the country in County Kerry and Lahinch is on the west coast in County Clare; all three are exposed shores composed of coarse sediment. Silverstrand is composed of finer and soft sediment and is situated on the west coast, to the north side of Galway Bay.

SAMPLING PROCEDURE

The collection of fishes was weather dependent and the number of sampling replicates taken from each beach was inconsistent. Sampling on the Silverstrand nursery was undertaken between March and November and the remaining nursery grounds were assessed intermittently, between May and September (Table I). Fishes were captured using a small beach seine, 5·5 m long and 2 m deep, with a 5 × 5 mm mesh size. Sampling was carried out at depths of between 0 and 1 m. The 0 year-groups *S. maximus* and *S. rhombus* are known to reside predominantly in shallow depths on nursery grounds (Aarnio *et al*., 1996; Draganik *et al*., 2005; Sparrevohn & Støttrup, 2008) and the 0 year-group *S. maximus* in the Baltic Sea is reported to favour depths of between 0·2 and 0·6 m (Martinsson & Nissling, 2011). Sampling on a beach was carried out in a single day on a spring tide during daylight hours for the purpose of consistency. The number of hauls ranged between four and 13 depending on the beach. Preliminary identification of all 0 year-group flatfishes captured in the beach seine was carried out on the shore using morphological characters. Juvenile flatfishes were then placed immediately into liquid nitrogen, prior to being transferred to a −80° C freezer in the laboratory. Sampling was carried out *c*. 1 h before the time of low tide. Sampling on Silverstrand was also undertaken in June, but no 0 year-group flatfishes were captured given the high level of weed present on this beach during two sampling trips.

Bottom sea temperatures of the intertidal zone were recorded from randomly chosen locations (<1 m depth) within each nursery ground on each sampling occasion, in addition to salinity. To investigate the availability of prey within nursery grounds, four Van Veen grab samples (0·025 m^2) were taken from randomly chosen areas where 0 year-group *S. maximus* and *S. rhombus* were captured (0–1 m), within each beach on each sample date. Mean temperature and salinity values for each month are provided in Table II.

LABORATORY ANALYSIS

Frozen fishes were removed from the freezer and allowed to thaw overnight. As newly settled 0 year-group *S. maximus* and *S. rhombus* are almost identical, fin ray counts, which are species specific (Wheeler, 1969) were made for all fishes captured in order to verify that individuals had been correctly separated on the shore (Haynes *et al*., 2010*b*).

Sediment samples were sieved through a 0·5 mm mesh, to remove larger particles and retain any benthic organisms for identification at a later stage (ostracods were the smallest

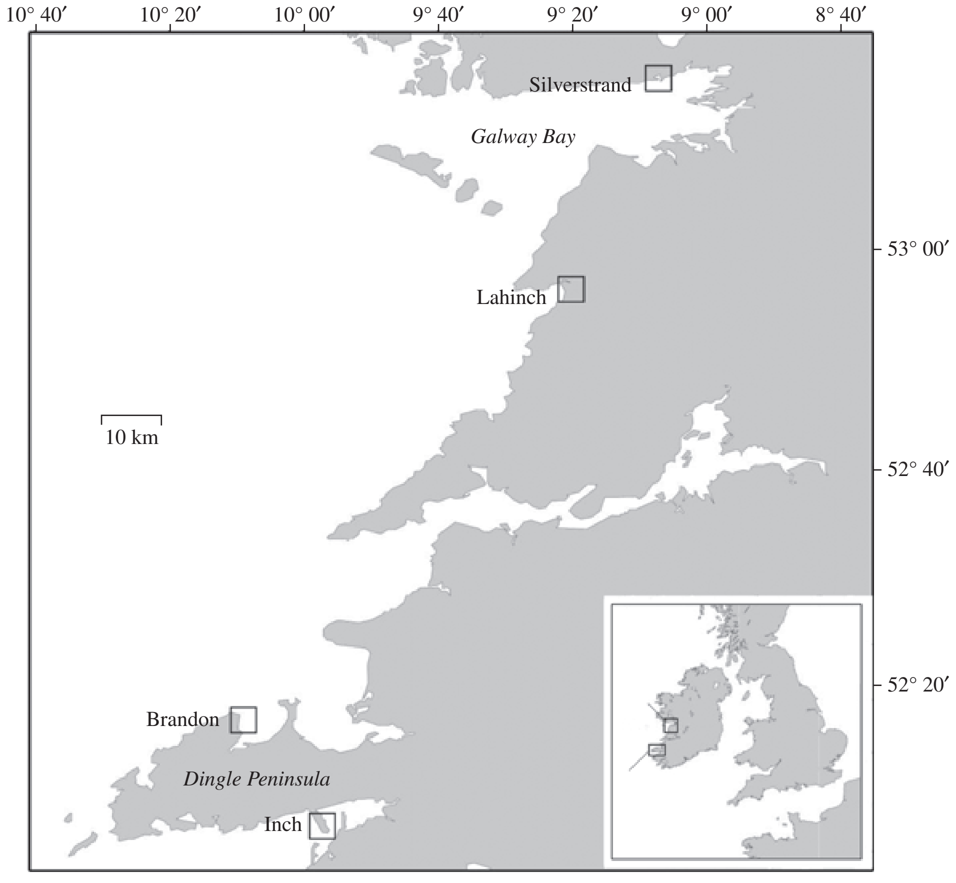

FIG. 1. The 0 year-group *Scophthalmus maximus* and *Scophthalmus rhombus* nursery grounds assessed along the west coast of Ireland.

benthic organism detected at <1·5 mm). All remaining prey and sediment particles were preserved in 10% formalin. Sediment samples were completely sorted under a stereoscopic microscope, with prey counted and identified to their main taxonomic group using the key by Hayward & Ryland (2003).

MORPHOLOGICAL ANALYSIS

The L_T, from the tip of the mouth to where the caudal fin ends was measured to the nearest 0·1 cm, and mass (m) was measured to the nearest 0·1 g for all captured flatfishes. The total abundance of prey present in the gut, stomach fullness and the total length and mass of the gut were recorded in order to assess whether any of these characters influenced the growth or condition of the fish. Fishes whose gut contents were emerging or absent were excluded from subsequent analyses. Stomach fullness was calculated by dividing the length of gut containing prey (mm) by the total length of the gut (mm) to obtain a percentage. The preferential selection of prey from the sediment by juvenile flatfishes was assessed using the Manly–Chesson selectivity index (α) according to the following formula:

$$\alpha_i = (d_i N_i^{-1})[\Sigma_{\mathrm{j}=1}^{\mathrm{k}}(d_i N_i^{-1})]^{-1},$$

TABLE I. Numbers of 0 year-group *Scophthalmus rhombus* (Tr) and *Scophthalmus rhombus* (Br) collected in each month from Irish west coast nursery grounds

Month	30 March		25 April		22, 23 and 26 May		7 and 22 June		7, 16, 20, 21, 24, and 29 July		16–19, 21 and 26 August		3 and 17 September		8 and 22 October		6 November	
Beach	Tr	Br	Tr	Br	Tr	Br	Tr	Br	Tr	Br	Tr	Br	Tr	Br	Tr	Br	Tr	Br
Inch	–	–	–	–	–	–	–	–	–	–	9	0	12	–	–	–	–	–
Brandon	–	–	–	–	–	–	–	–	0	10	3	0	–	–	–	–	–	–
Silverstrand	0	0	0	0	0	10	0	0	0	22	59	0	25	0	21	0	0	0
Lahinch	–	–	–	–	–	–	–	–	–	–	–	–	14	0	–	–	–	–

–, not sampled.

TABLE II. Mean ± S.D. temperature and salinity values recorded for each month on each nursery ground assessed

Month	May		June		July		August		September		October	
Beach	Temperature (° C)	Salinity	Temperature (° C)	Salinity	Temperature (° C)	Salinity	Temperature (° C)	Salinity	Temperature (° C)	Salinity	Temperature (° C)	Salinity
Inch	–	–	–	–	–	–	17·2 ± 0·2	31·3 ± 1·3	16·7 ± 0·2	30·0 ± 1·0	–	–
Brandon	–	–	–	–	17·2 ± 0·3	27·6 ± 1·6	17·2 ± 0·3	27·6 ± 1·6	–	–	–	–
Silverstrand	11·9 ± 0·1	26·4 ± 0·8	43·7 ± 0·4	29·2 ± 0·7	17·9 ± 0·2	31·7 ± 0·9	17·9 ± 0·2	31·4 ± 0·7	16·0 ± 0·8	30·0 ± 1·6	15·1 ± 0·1	29·0 ± 0·9
Lahinch	–	–	–	–	–	–	–	–	16·8 ± 0·2	31·7 ± 0·8	–	–

–, not recorded.

where $i = 1, 2, \ldots$, and k is the number of prey categories, d_i is the number or proportion of prey type in the diet and N_i is the density or proportion of prey in the environment (sediment samples). Prey types which are consumed relative to their abundance in the environment or are not selected, will have $\alpha_i = k_i^{-1}$; $\alpha_i > k_i^{-1}$, indicates a preference for a particular prey type and $\alpha_i < k_i^{-1}$ indicates selection against a specific item of prey (Mittelbach, 2002).

TEMPORAL AND SPATIAL PARTITIONING

Temporal, spatial and resource partitioning between 0 year-group *S. maximus* and *S. rhombus* was investigated between the months of May and October, on the nursery ground Silverstrand. Every month, the number of *S. maximus* and *S. rhombus* captured in each haul was recorded and the co-occurrence of the two species was examined. Gut content analysis was carried out for these fishes to determine if there was any overlap in the prey consumed. Temporal partitioning was also investigated for 0 year-group *S. maximus* and *S. rhombus* collected in August and September on Silverstrand, over a 6 year period, as part of an annual juvenile flatfish survey carried out on west of Ireland nursery grounds (Haynes *et al*., 2010*a*). The total number of fishes captured on a particular beach was divided by the number of hauls carried out, to compare the relative abundances of *S. maximus* and *S. rhombus* in each month.

GROWTH

Otolith increment widths were used to derive an index of daily growth after settlement. The first six and seven post-settlement increments [corresponding to 6 and 7 days after the deposition of the final accessory primordium (AP)], deposited by *S. maximus* and *S. rhombus* respectively, were measured to the nearest 0·1 μm along the longest axis. The selected number of increments for each species corresponded to the minimum number present on the otolith in the majority of individuals. Increments deposited upon completion of metamorphosis, or after the final AP, are more likely to represent the period when fishes are feeding on the nursery ground (Geffen, 1987). Sagittal otoliths were removed and cleaned and one of the pair was randomly selected for analysis. Cracked or unreadable otoliths were rejected. The selected otolith was mounted on a slide in Crystalbond (www.crystalbond.com), and polished until all increments in the region of interest could be clearly observed. Polished sections were examined using an Olympus BX51 (www.olympus.com) compound microscope under a ×1000 magnification, with analysis aided by Image Pro Plus Analyzer version 6.2 software (www.mediacy.com).

CONDITION

Residuals of the L_T and M relationship were used as a measure of condition in *S. maximus* and *S. rhombus*. This method of assessing condition is appropriate when dealing with a range of size classes (Blackwell *et al*., 2000). Residuals were calculated for each individual fish, using the regressions $\log_{10} L_T$ and $\log_{10} M$. Residuals of the relationship have previously been utilized to calculate the condition, and hence provide information on the habitat quality of 0 year-group flatfishes (Gilliers *et al*., 2006). A similar condition index based on L_T and M was used by Imsland *et al*. (1995) for reared *S. maximus* juveniles. A large negative mean residual value signifies that fishes are in poor condition; a large positive mean residual value is indicative of good condition, and a residual value close to zero indicates that fishes are in an average condition (Blackwell *et al*., 2000). As the prey type and quantity consumed is known to have an effect on the growth and condition of juvenile flatfishes, the biodiversity Shannon–Wiener index describing the diversity of prey in the gut was calculated for each individual, and plotted against the residual condition.

DATA ANALYSIS

Pearson's correlation was used to investigate if growth and condition were related to prey abundance and type, temperature and salinity using the statistical package MINITAB 15 (www.minitab.com). Prey composition and abundance in the gut of *S. maximus* and *S. rhombus* were analysed using a non-metric multidimensional scaling (MDS) ordination technique in PRIMER (Plymouth Routines in Multivariate Ecological Research) version 5 statistical package (Clarke & Ainsworth, 1993). Where large differences in scale occurred between variables the data were square-root transformed and a Bray–Curtis coefficient was calculated to produce a similarity matrix. To investigate differences in the taxonomic composition of prey in the gut between months, a one-way nested analysis of similarities (ANOSIM) was performed. Significant differences were explored using the *R*-statistic value, whereby a value close to one indicated a large difference between samples, with an *R*-value close to zero indicating a low difference between samples. Similarity percentages (SIMPER) were generated to determine the main taxonomic groups accounting for up to 90% of all prey consumed by *S. maximus* and *S. rhombus* on each beach. Given the low number of both *S. maximus* and *S. rhombus* collected on beaches differences in the prey consumed by fishes inhabiting separate locations were not statistically investigated, but were described. Mean ± s.d. values of the investigated variables were also calculated.

RESULTS

GUT CONTENTS

Scophthalmus maximus

A total of nine juvenile *S. maximus* collected over the duration of the study had empty guts; these tended to be smaller individuals (<3·5 cm L_T) and were not included in the analyses. Across beaches in the present study, juvenile *S. maximus* (4·5–7·5 cm L_T) consumed a total of seven taxonomic groups of prey, with four groups dominating the gut content of all captured individuals. The mean per cent numbers of prey items present in the gut of individual *S. maximus* are presented in Fig. 2.

The more detailed temporal analysis of the Silverstrand nursery ground revealed that juvenile *S. maximus* (2·5–7·5 cm L_T) consumed a total of eight taxonomic groups of prey between August and October, with four groups dominating the gut content of all captured individuals. The MDS plot showed that the taxonomic prey groups found in the guts of 74 *S. maximus* on Silverstrand were similar across months with a large amount of overlap observed (Fig. 3). ANOSIM detected no significant difference in the prey composition over the months of August, September and October on Silverstrand ($R = -0{\cdot}030$, $P > 0{\cdot}05$). The diet of *S. maximus* collected from Silverstrand between August, September and October was characterized by cumaceans (70%), mysids (15%), polychaetes (6%) and amphipods (1·3%). Additional prey items which featured in low abundances (<10%) in the diet of *S. maximus* on Silverstrand included isopods, decapods and amphipods. A mean ± s.d. fullness of the gut of all *S. maximus* was calculated as 70 ± 3%.

Scophthalmus rhombus

Juvenile *S. rhombus* consumed a total of three taxonomic prey groups; their gut contents were dominated by mysids and contained smaller proportions of amphipods and cumaceans. The MDS plot revealed a large amount of overlap in the type of prey consumed by 25 *S. rhombus* in May and in July on Silverstrand, with ANOSIM finding no significant difference in the prey items consumed ($R = 0{\cdot}028$, $P > 0{\cdot}05$). The mean ± s.d. gut fullness of *S. rhombus* collected on Silverstrand in May and July

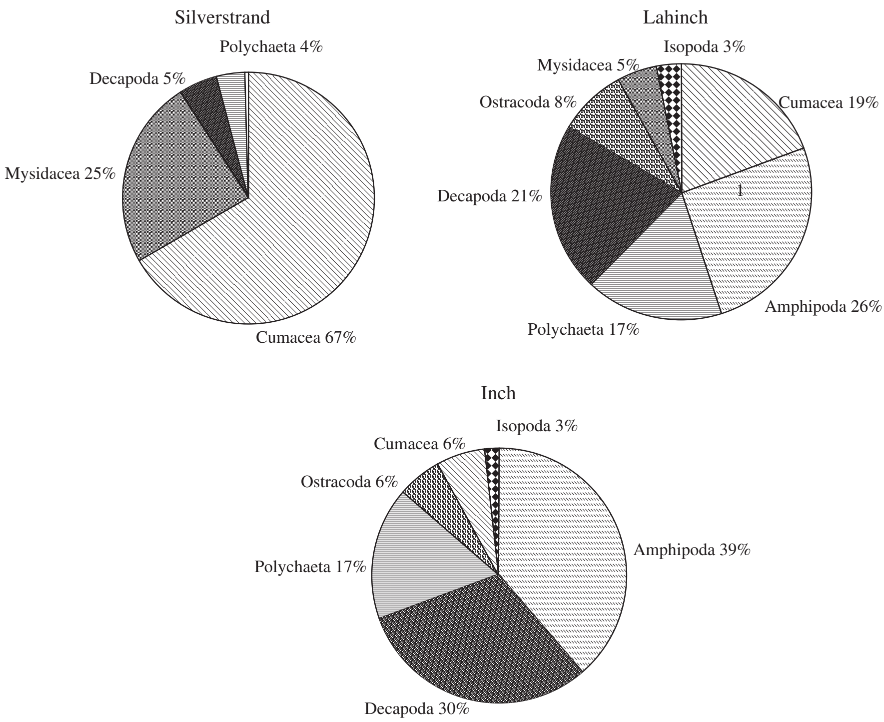

FIG. 2. Mean per cent number of prey groups present in the gut of individual 0 year-group *Scophthalmus maximus* on west of Ireland nursery grounds.

was 85 ± 12%. The prey consumed by *S. rhombus* were also similar across beaches, consisting predominantly of mysids, regardless of the habitat occupied (Fig. 4).

PREY AVAILABILITY

A total of nine groups of prey items were identified in the sediment across all four beaches, and consisted predominantly of crustaceans, polychaetes, bivalves and gastropods (Fig. 5). ANOSIM did not detect a significant difference in the composition of the sediment fauna between individual grab samples ($R = 0{\cdot}012$, $P > 0{\cdot}05$).

PREY SELECTIVITY

The Manly–Chesson index of prey selectivity showed that *S. maximus* exhibited a positive preference for six groups of crustaceans, in addition to polychaetes, with the main taxonomic group selected differing between nursery grounds. Juvenile *S. rhombus* showed a preference for mysids and amphipods. The highly abundant sessile organisms, gastropods and bivalves were avoided in all areas by both *S. maximus* and *S. rhombus* (Table III).

TEMPORAL PARTITIONING

The patterns of distribution of 0 year-group *S. maximus* (2·7–7·5 cm L_T) and *S. rhombus* (2·9–7·5 cm L_T) on the nursery ground at Silverstrand suggested that

FIG. 3. Plot depicting the similarity in the diets of 0 year-group *Scophthalmus maximus* collected on the nursery ground Silverstrand in August (▲), September (○) and October (■). Each symbol represents an individual fish.

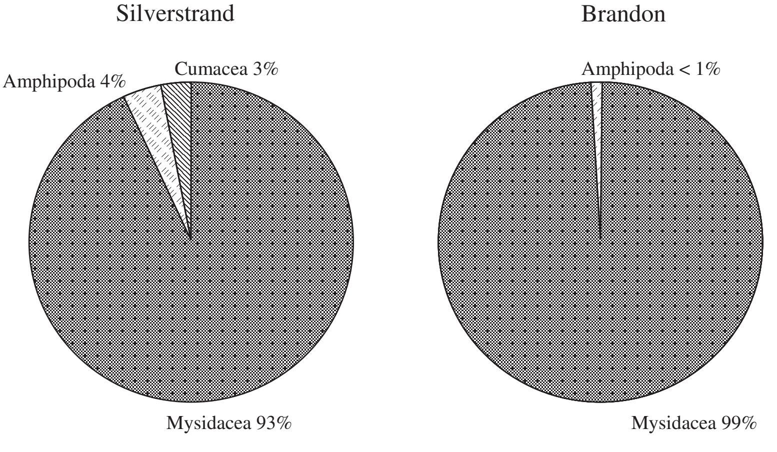

FIG. 4. Mean per cent number of prey groups present in the gut of individual 0 year-group *Scophthalmus rhombus* on west of Ireland nursery grounds.

temporal partitioning occurred between the two species; *S. rhombus* occurred in catches from May until August while *S. maximus* were found in the catches from August to October with peak densities occurring in early September (Fig. 6). There was an interval of 16 days when no sampling occured, between the last recording of *S. rhombus* and the first recording of *S. maximus*, but it is unlikely that either species occured at high densities during this period as peak settlement of *S. maximus* on the beach occurs in August and September (Haynes *et al*., 2011), whereas *S. rhombus* settle in March and April (P. S. Haynes, D. Brophy & D. McGrath, unpubl. data). Surveys conducted in August and September over a 6 year period also showed little temporal overlap in the distribution of *S. maximus* and *S. rhombus* (Fig. 7).

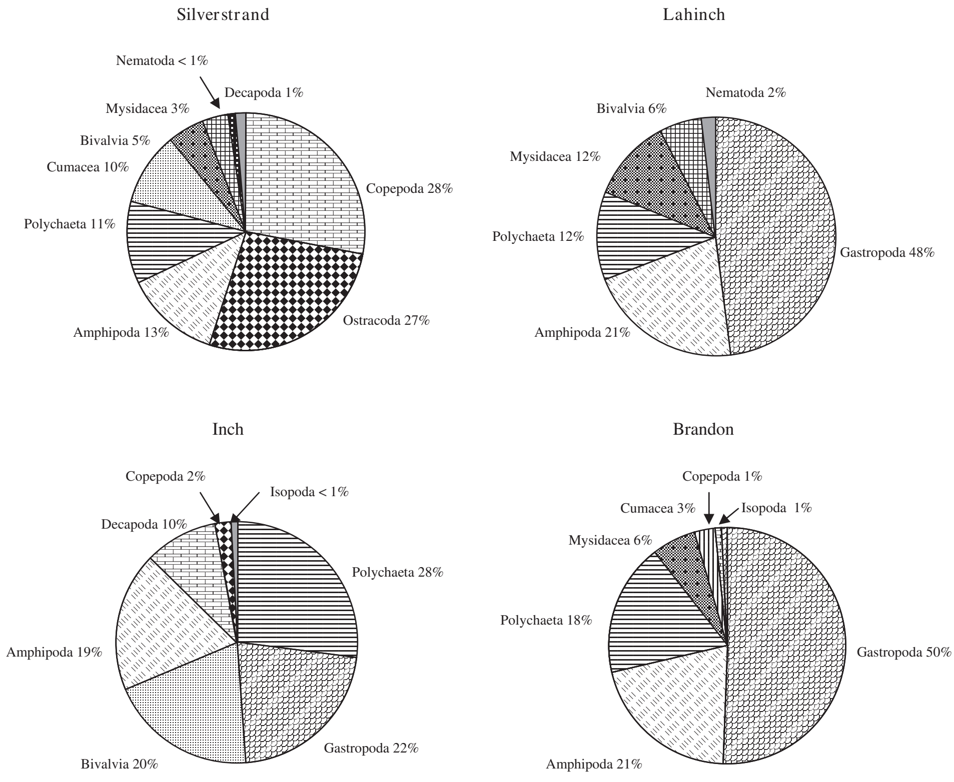

FIG. 5. Mean per cent number of all *Scophthalmus maximus* and *Scophthalmus rhombus* prey groups present per grab sample (0·025 m^2) on west Ireland nursery grounds.

TEMPERATURE AND SALINITY

Across nursery grounds bottom sea temperatures ranged between 11·8 and 18·2° C, with salinity values of between 25 and 34 also recorded between May and October.

GROWTH AND CONDITION CORRELATIONS

The growth and condition of each individual fish was not related to percentage gut fullness or the abundance of prey in the gut for *S. maximus* or *S. rhombus*. Mean growth and condition for each species on each sampling visit was not correlated with temperature or salinity values recorded on nursery grounds ($P > 0·05$). There was no significant correlation between the growth or condition of either *S. maximus* or *S. rhombus*, and the diversity of prey items in the gut, expressed using the Shannon–Wiener prey index ($P > 0·05$).

DISCUSSION

Juvenile *S. maximus* inhabiting nursery grounds along the west coast of Ireland consumed predominantly cumaceans, mysids, amphipods, decapods and polychaetes

TABLE III. Prey selectivity calculated using the Manly–Chesson index for juvenile *Scophthalmus maximus* and *Scophthalmus rhombus* on west of Ireland nursery grounds

Beach		Inch	Brandon	Silverstrand	Lahinch
Prey taxa	Fish species				
Polychaeta	*S. maximus*	−	n/a	−	+
	S. rhombus	n/a	−	−	n/a
Bivalvia	*S. maximus*	−	n/a	−	−
	S. rhombus	n/a	−	−	n/a
Gastropoda	*S. maximus*	−	n/a	−	−
	S. rhombus	n/a	−	−	n/a
Amphipoda	*S. maximus*	+	n/a	−	+
	S. rhombus	n/a	−	+	n/a
Mysidacea	*S. maximus*	−	n/a	+	+
	S. rhombus	n/a	+	+	n/a
Cumacea	*S. maximus*	−	n/a	+	−
	S. rhombus	n/a	−	−	n/a
Ostracoda	*S. maximus*	+	n/a	−	−
	S. rhombus	n/a	−	−	n/a
Decapoda	*S. maximus*	+	n/a	+	−
	S. rhombus	n/a	−	−	n/a
Copepoda	*S. maximus*	−	n/a	−	−
	S. rhombus	n/a	−	−	n/a
Isopoda	*S. maximus*	+	n/a	−	−
	S. rhombus	n/a	−	−	n/a

+, a preference for a particular prey item; −, selection against a prey item; n/a, fish was not present.

during the months when they were present in beach seine samples. The limited data available from three nursery grounds indicated a high degree of spatial overlap in the taxonomic prey items ingested by juvenile *S. maximus* although there was a lower incidence of cumaceans and a higher abundance of amphipods and decapods in the gut of fish collected from the two exposed shores (Lahinch and Inch), compared to the sheltered shore (Silverstrand). Although more replicate sites would be needed to confirm that these differences relate to the level of exposure of the beaches, the observations may reflect differences in the habitat structure between the locations (Nissling *et al.*, 2007; Florin *et al.*, 2009).

With the exception of cumaceans, the main benthic groups consumed by juvenile *S. maximus* along the Irish west coast were similar to those reported in studies of other nursery grounds in the north-east Atlantic Ocean. Juvenile *S. maximus* were observed to feed predominantly on mysids and *Crangon* sp. in the Kattegat (Sparrevohn & Støttrup, 2008) and on amphipods and mysids in the Baltic Sea (Florin & Lavados, 2009); polychaetes were also present in the guts of *S. maximus* in the Irish Sea (Jones, 1973). In contrast to other studies (Aarnio *et al.*, 1996; Ustups *et al.*, 2007; Sparrevohn & Støttrup, 2008; Florin & Lavados, 2009), fishes were notably absent from the diet of 0 year-group *S. maximus* in the present study; this may reflect the size range of the *S. maximus* examined. Although gobiids are reported to occur in the diet of juveniles <6 cm L_T (Aarnio *et al.*, 1996; Beyst *et al.*, 1999), in many areas fishes are not included as a food item until *S. maximus* reach larger sizes:

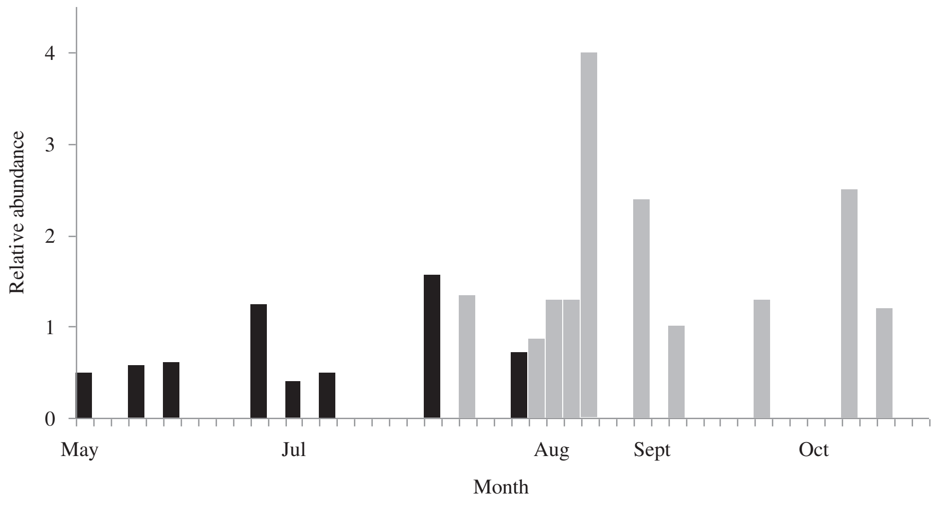

FIG. 6. Relative abundance of 0 year-group *Scophthalmus maximus* (■) and *Scophthalmus rhombus* (■) collected on the nursery ground Silverstrand (May to October, 2009).

7–8 cm L_T in the Baltic Sea (Stankus, 2003), 10 cm L_T along the Spanish coast (Iglesias *et al*., 2003), between 10 and 15 cm L_T in the southern North Sea and the Irish Sea (Braber & De Groot, 1973; Jones, 1973). Alternatively, the absence of fishes in the diet may be due to the low abundance of suitable fish prey on the nursery grounds (Beyst *et al*., 1999); no gobiids were caught in beach seines on the nursery grounds in the current study (pers. obs.).

Scophthalmus rhombus fed on a much smaller range of prey items than *S. maximus* in the current study, their diet consisting almost exclusively of mysids on both

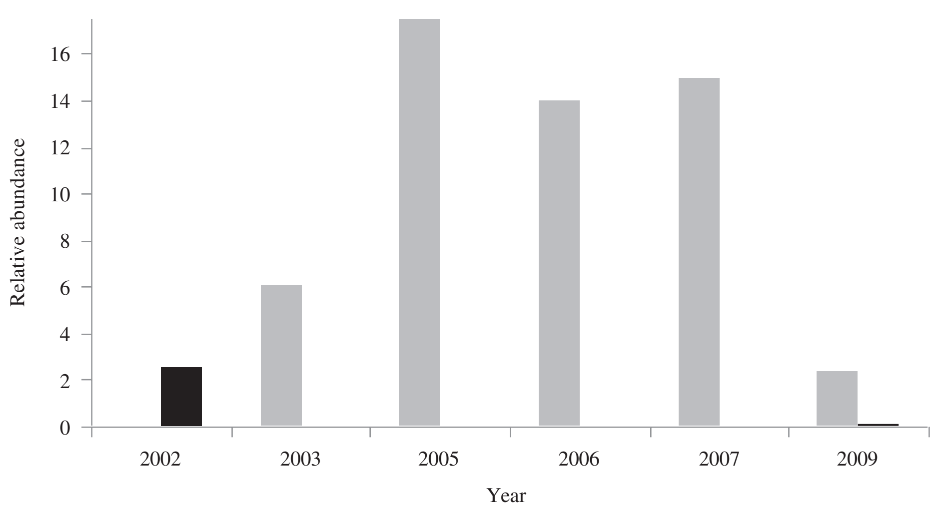

FIG. 7. Relative abundance of 0 year-group *Scophthalmus maximus* (■) and *Scophthalmus rhombus* (■) collected from Silverstrand on the west of Ireland on a single sampling occasion in August to September (2002–2009).

beaches examined. Selection of mysids by *S. rhombus* is common in other locations (Cabral *et al*., 2002). *Scophthalmus rhombus* reportedly start to consume fishes at relatively small sizes (5 cm L_T) (Braber & De Groot, 1973; Beyst *et al*., 1999). As with *S. maximus*, however, no fishes were identified in the guts of juvenile *S. rhombus* collected on the Irish west coast. Whether or not *S. maximus* and *S. rhombus* here are forced to consume less favourable prey items such as crustaceans in the absence of fishes is not known, though this has been previously suggested for juvenile *S. maximus* occupying other areas (Nissling *et al*., 2007). Consuming less favourable prey can negatively affect growth and hence survival in juvenile flatfishes (Sparrevohn & Støttrup, 2008).

In this study, both *S. rhombus* and *S. maximus* avoided non-motile prey items such as gastropods and bivalves, which were present in high numbers in the sediment, but were not identified in the diet of either flatfish species. This is consistent with the known feeding behaviour of both *S. maximus* and *S. rhombus* juveniles, which are more likely to consume mobile, fast moving prey in preference to sessile organisms (Holmes & Gibson, 1983). In general, juvenile flatfishes are opportunistic feeders and are reported to consume the most available prey item within the nursery (Darnaude *et al*., 2001; Cabral *et al*., 2002). In this study, however, evidence was found of selective feeding in 0 year-group *S. maximus* and *S. rhombus*. *Scophthalmus maximus* at Silverstrand preferentially fed on cumaceans, mysids, and decapods rather than the more abundant copepods and ostracods. A preference for mysids has previously been reported in the Kattegat where 0 year-group *S. maximus* actively consumed mysids and gobiids, even in the presence of similar abundances of chironomids and amphipods (Florin & Lavados, 2009). Juvenile *S. rhombus* exhibited a high level of prey selectivity for mysids, followed by amphipods, and did not consume the most abundant type of prey available as indicated by the sediment analysis.

In contrast to the more varied feeding behaviour noted for *S. maximus*, juvenile *S. rhombus* exhibited a high level of prey selectivity for mysids, followed by amphipods, and did not consume the most abundant type of prey available as indicated by the sediment analysis. The results suggest that *S. maximus* are more flexible than *S. rhombus* in terms of feeding behaviour and may more readily adapt their prey choice in response to food availability; this may partly explain the higher abundance and more widespread distribution of *S. maximus* on west of Ireland nursery grounds. The patchy distribution of prey in the sandy beach environment and movements of juvenile flatfishes within the nursery area make it difficult to describe the feeding conditions encountered by the fishes in the previous 24 h. Estimates of prey abundance in the environment relied on four grab samples from each beach on each sampling date. No significant difference was detected in the composition of the sediment fauna between individual grab samples on each beach. This suggests that although limited, the sediment data collected by the grab provided an accurate description of the feeding conditions within each beach. While the prey selectivity results must be interpreted with caution, they do signal some important differences in feeding strategies between *S. maximus* and *S. rhombus* and also indicate that feeding behaviour can vary between nursery areas. A more comprehensive sediment analysis would help to substantiate these observations.

Very little temporal overlap was observed in the distribution of juvenile *S. maximus* and *S. rhombus* on west of Ireland nursery grounds. In general, the two species did not co-occur on the nursery ground Silverstrand between May and October in

2009 or in August and September over a 6 year period. This may not reflect direct avoidance of competition by the two species; the timing of spawning and subsequent development rate of eggs and larvae are likely to have evolved to coincide with favourable conditions during the larval phase, such as prey availability, an absence of predators, or suitable transport processes (Bailey *et al*., 2005). In any case the observed temporal segregation of settlement in *S. maximus* and *S. rhombus* will either directly or indirectly reduce inter-specific competition on the nursery grounds. When two species of 0 year-group juvenile flatfishes co-occur, negative interaction or competition for available resources can occur; feeding in juvenile *S. maximus* in the Baltic Sea was found to be negatively correlated with juvenile *P. flesus* densities (Martinsson & Nissling, 2011). In this study, there was a high incidence of feeding for all captured individuals over the duration of the study and very few fishes had empty guts. This suggests that food was not limiting and these fishes did not experience competition when foraging for prey. Temporal partitioning is likely to maximize the feeding success of 0 year-group juvenile flatfishes that inhabit the same nursery grounds.

Growth and condition of *S. maximus* and *S. rhombus* were not related to the prey diversity, percentage fullness of the gut, prey numbers in the gut, or mean temperature and salinity values recorded on nursery grounds. A significant positive relationship was previously observed between the condition of *P. platessa* on western Irish nursery grounds, and the diversity of prey items present in the gut (De Raedemaecker *et al*., 2011*a*). That study, however, also observed considerable spatial and temporal variation in diet which was absent in the current study. Attempting to link otolith growth with biotic or abiotic variables can also be problematic, as otolith growth responds more gradually to changes in feeding conditions and metabolic rate, and represents a running average of fish growth rather than an instantaneous measure (Campana & Neilson, 1985). A longer time series or additional indices of growth and condition may be required, in order to identify any significant relationship between the variables investigated . Gilliers *et al*. (2006) recommend that several biological indicators should be used for assessing the habitat quality of 0 year-group flatfishes.

The present study has described the feeding ecology and behaviour of 0 year-group *S. maximus* and *S. rhombus* in a previously understudied location within their distribution range. Consistent with reports from other locations in the north-east Atlantic Ocean, *S. maximus* and *S. rhombus* on the Irish west coast consumed a narrow range of prey groups. *Scophthalmus maximus* and *S. rhombus* appear to target different prey groups, settle onto the nursery areas at different times and occur at low densities; competition between these two morphologically similar flatfish species is therefore unlikely. The high prey selectivity exhibited by *S. rhombus*, both here and also in other locations, may explain their exceptionally low occurrence in all areas of the north-east Atlantic Ocean (Gibson, 1994). Nonetheless, given the high incidence of feeding observed for both *S. maximus* and *S. rhombus* over the duration of the present work, food did not appear to be limited on west of Ireland nursery grounds.

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