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Nursery area utilization by turbot (*Psetta maxima*) and flounder (*Platichthys flesus*) at Gotland, central Baltic Sea

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To reveal the temporal and spatial utilization of a preferred nursery ground habitat by 0-group turbot and flounder in the Baltic Sea, sampling was conducted in six sandy bays in early–mid-July to early–mid-September 2003–2005 off the coast of Gotland (ICES SD 27 & 28-2). Settlement and peak abundance of turbot occurred from late July–early August to early September and from mid-August to early September, respectively. Settlement of flounder occurred from early–mid-July with decreasing numbers over time, except in 2005. Peak abundance of 0-group flounder occurred in late July–early August to mid-September, suggesting a considerable temporal overlap with 0-group turbot. 0-group turbot and flounder also overlapped in respect to depth with preference for 0.2 and 0.6 m over 1 m. The spatial and temporal overlap of the species was verified by a logistic regression analysis; the probability of sampling 0-group flounder when 0-group turbot was caught in a haul was 0.84 (0.80–0.87, 95% CI).

Introduction

Conclusions concerning the factors that affect the variability in recruitment of flatfishes, as summarized by Van der Veer *et al*. (2000), have in general been derived from studies of commercially important species such as plaice (*Pleuronectes platessa*) and sole (*Solea solea*) in the North Atlantic, mainly the North Sea area. The findings stress that variability in recruitment is generated during the egg- and larval stages under the control of large scale abiotic factors, and that density-dependent mortality after settlement dampens recruitment variability as the early juveniles concentrate in the nursery grounds (Beverton 1995). However, according to the "species range hypothesis", proposed by Miller *et al*. (1991), factors controlling flatfish recruitment vary due to differences in life history traits between species and over species range of distribution.

The life history traits of flounder (*Platichthys flesus*) and turbot (*Psetta maxima*) in the Baltic Sea differ from those in e.g. the North Sea in accordance with abiotic conditions. Due to brackish water, with salinity as a strong evolutionary force, populations with specific reproductive strategies have evolved (Bagge 1987, Nissling *et al*. 2002). Two genetically distinct (Florin *et al*. 2005, Hemmer-Hansen *et al*. 2007) flounder populations inhabit the Baltic Sea, one spawning offshore in the Baltic deep basins (ICES SD 24–26 and 28-2) with highly buoyant pelagic eggs (enabling neutral buoyancy in the brackish water), and one in coastal areas and on off-shore banks (ICES SD 25–30) with demersal eggs (Bagge 1981, Nissling *et al*. 2002). In contrast, turbot in the Baltic Sea only spawn in coastal areas and on off-shore banks (ICES SD 24–29) and produces demersal eggs (Nissling *et al*. 2006).

In the North Sea, variation in hydrodynamic and wind conditions have been shown to control the transportation of plaice larvae to the nursery grounds and therefore works as factors generating variability in recruitment (Pihl 1990, Van der Veer *et al*. 1998). This might be of less importance in controlling the recruitment of turbot and flounder in the Baltic Sea since they spawn along the coast, i.e. close to the 0-group nursery grounds. Further, predation by the brown shrimp (*Crangon crangon*) and shore crab (*Carcinus maenas*) have been shown to dampen recruitment variability after settling and thereby regulate the year-class strength of plaice in the North Sea (Van der Veer and Bergman 1987, Pihl 1990, Van der Veer *et al*. 2000). However, the shore crab does not inhabit the central Baltic Sea and the abundance of brown shrimp within the nursery areas is low during the period when 0-group turbot and flounder are present (A. Nissling unpubl. data). Hence, other controlling and regulating factors will come into play in affecting the recruitment of flounder and turbot in the central Baltic Sea. Flatfishes in general normally display low variability in recruitment (Beverton 1995, Iles and Beverton 2000). In contrast, recruitment of flounder and in particular turbot in the Baltic Sea is known to vary (Florin 2005). Furthermore, Molander (1964) observed, when focusing on turbot recruitment, that peaks in the year class strength of turbot coincided with weak year classes of flounder in the Baltic Sea. This suggests an interaction between the species that may occur during the juvenile stage, which affects 0-group turbot negatively, as both species utilize shallow sandy bays as nursery grounds (Kostrzewska-Szlakowska 1990, Aarnio 1996, Florin *et al*. 2009).

To assess potential controlling and regulating mechanisms affecting recruitment of turbot and flounder in the Baltic Sea, information about nursery ground utilization of the two species is needed. Thus, the aim of the present study was to assess the temporal and spatial distribution of the two species within typical nursery grounds in terms of (i) settlement patterns and peak abundances, (ii) depth distribution, and additionally (iii) to examine the overlap between 0-group turbot and flounder at a small-scale to reveal the potential for species interaction eventually affecting survival of turbot. The study is a part of a research programme at Ar Research Station, Gotland University, aiming to reveal mechanisms affecting recruitment of turbot and flounder in the Baltic Sea.

Material and methods

Sampling

Juvenile flounder and turbot were sampled in shallow sandy bays around Gotland, central Baltic Sea (ICES SD 27 and 28-2) (Fig. 1) in 2003–2005. Sampling was conducted in early–mid-July to mid-September with two (2003–2004) to four (2005) sampling occasions per month. A total of six bays were examined, but only bay B and C were sampled every year (Table 1). The fish sampled were also used in another study (Nissling *et al*. 2007).

A total of 1094 samples were taken, using a beach seine (mesh-size 4 mm and 2 mm in the wings and cod end respectively), at 0.2, 0.6 and 1 m depths. On each sampling occasion, generally five samples were taken from each depth. In each sample the number of flounder and turbot juveniles were counted and the length of each individual (L_t, 0.5 mm accuracy) was measured. 0-group juveniles were separated from 1-group juveniles by comparing length distributions, which were bimodal from the time at settlement onwards (Fig. 2). The mean lengths (± SD) of 0-group individuals sampled following the first recorded settlement were 28 ± 4 and 19 ± 5 mm for turbot and flounder, respectively. Thus, flounder ≤ 20 mm and turbot ≤ 30 mm were regarded as newly settled fish. In total, 4760 flounders and 1028 turbots were sampled. The length of each haul together with the width (4.5 m) of the beach seine was used to calculate the area covered (on average 120 m^2). The densities of 0-group flounder and turbot were calculated from the area cov-

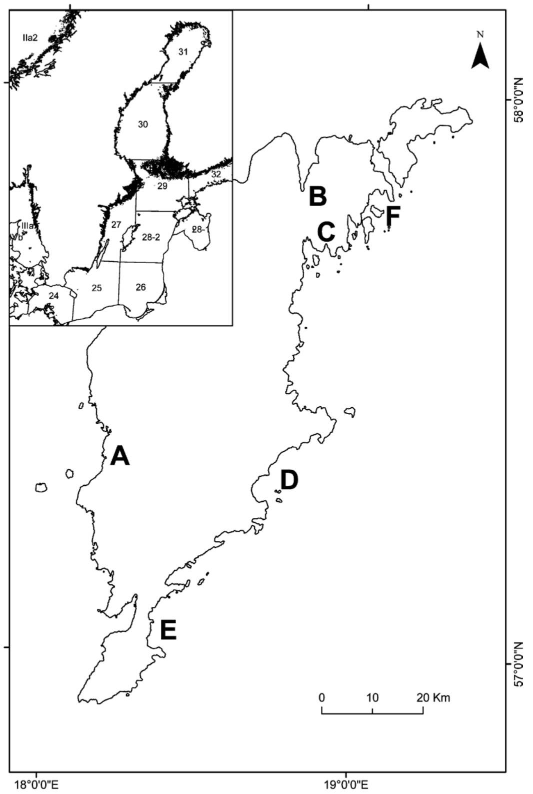

Fig. 1. The Baltic Sea with ICES subdivisions (SD) and location of sampling areas (bays A–F) at the coast of Gotland, central Baltic Sea (ICES SD 27 & 28-2) (based on GIS layers from the Baltic GIS Portal and ICES).

ered in each haul and expressed as the number of individuals 100 m^{-2}.

Statistical analyses

The general depth distribution of 0-group turbot and flounder was analysed using the PERMANOVA software (Anderson 2001, McArdle and Anderson 2001), which uses permutational analysis of variance. The Euclidian distance was used and Monte-Carlo *p* values presented (Anderson and Robinson 2003). Using densities *per se* in the analysis misleading results might be attained as the abundance could vary greatly between sample occasions. Hence, to maintain the relative differences (or similarities) in density between depths, the relative abundances of 0-group turbot and flounder in each haul on each occasion was calculated by dividing the density of each haul by the total density of all hauls on the occasion. Further, although several hundred of hauls were sampled at each depth, only six independent observations per depth could be used in the analysis, i.e. the mean relative abundance at each bay. The depth distribution was analysed using the model:

$$y = \alpha + \mathrm{Sp} + \mathrm{De} + \mathrm{Sp} \times \mathrm{De} + \varepsilon \tag{1}$$

Table 1. Arrival to (week), peak abundance (week), and the mean density (ind. 100 m^{-2}) at peak abundance for 0-group turbot and flounder for bays A–F.

		Time at settlement (week)		Peak abundance (week) (week)		Peak abundance density (ind. 100 m^{-2}) (mean ± SE)	
Year	Bay	Flounder	Turbot	Flounder	Turbot	Flounder	Turbot
2003	A	28	31	31	38	6.75 ± 1.69	3.69 ± 1.44
	B	28	30	30	31	7.07 ± 1.42	10.41 ± 2.57
	C	28	33	35	35	4.29 ± 1.29	3.06 ± 0.88
	E	28	33	33	33	1.72 ± 0.43	1.67 ± 0.34
2004	A	29	31	35	35	3.04 ± 0.95	1.33 ± 0.3
	B	29	33	33	37	4.22 ± 1.11	0.94 ± 0.32
	C	31	33	35	37	0.32 ± 0.13	0.95 ± 0.37
	D	29	33	35	33	1.72 ± 0.50	0.75 ± 0.22
	E	29	32	31	37	3.30 ± 2.01	0.26 ± 0.12
2005	B	28	30	36	33	8.37 ± 1.86	2.49 ± 0.95
	C	28	30	33	33	7.06 ± 1.51	3.19 ± 1.45
	F	28	30	35	33	30.56 ± 5.32	2.11 ± 0.63

where y is the mean relative abundance in a bay, α is the intercept, Sp is the factor Species with two levels (0-group turbot and flounder), De is the factor Depth with three levels (0.2, 0.6 and 1 m) and ε is the error term.

The sample occasions from first settlement of the species were used until last week in August. Samples taken in September were excluded since these might have biased the results as the species starts to migrate towards deeper waters in autumn.

Significant results using PERMANOVA may be due to differences in either the mean or the variance between groups (Anderson 2001). Therefore, tests of homogeneity of variance were performed using PERMDISP. The results revealed no significant difference in variance between the groups. Consequently, the dataset was not transformed in the analysis.

PERMANOVA was also used to analyse the general size distribution of 0-group turbot and flounder stratified according to depth. As for the previous analysis, the observations consist of six independent observations per depth, i.e. the mean length at each bay. The size distribution was analysed using the model:

$$y = \alpha + \text{Sp} + \text{De} + \text{Sp} \times \text{De} + \varepsilon \qquad (2)$$

where y is the mean length in a bay, α is the intercept, Sp is the factor Species, De is the factor Depth and ε is the error term.

No 0-group turbot was caught at 1 m depth in bay D. As PERMANOVA requires balanced datasets, a dummy calculated by using the mean of the observations at 1 m in the other bays was added to the dataset. The mean square for the residuals was therefore recalculated using the appropriate number of degrees of freedom. No significant difference in variance among groups were found using PERMDISP, thus no transformation was applied to the dataset in the analysis.

Moreover, a logistic regression with a binary response variable (present/absent) was conducted in SPSS 17.0 using a generalized linear model with the binomial distribution and the logit link function to assess the spatial overlap of 0-group flounder and turbot on a small scale, i.e. within each sample. Samples containing both species were assigned the value 1 and samples containing only turbot were assigned the value 0. In this way, the analysis estimated the probability of finding flounder when turbot was present in a sample. This procedure was undertaken as 0-group turbot was less abundant as compared with 0-group flounder.

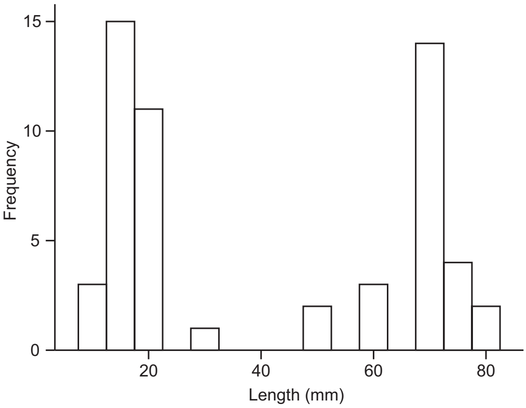

Fig. 2. Length distribution of flounder at first encounter of 0-group individuals (week 28) in bay B in 2003 at the coast of Gotland, central Baltic Sea (ICES SD 27 and 28-2).

Results

Temporal distribution

The settling pattern varied somewhat between years (Table 1 and Fig. 3). 0-group flounder arrived earlier to the nursery grounds than 0-group turbot. For flounder, a peak of newly settled individuals was recorded in early–mid-July (week 28–30) in 2003 and 2005 and in mid–late-July (week 29–31) in 2004, levelling off and resulting in few arriving individuals onwards. In 2005, however, settlement continued with new cohorts arriving throughout the sampling period, e.g. shown as a second peak in September in bay C (Fig. 3). For turbot the main settling period lasted from late July-early August to early September (week 31/32–36) in 2003 and 2005, but was somewhat later in 2004.

For 0-group fish in general (all sizes pooled) the highest abundances of flounder were recorded from late July-early August to mid-September (week 31/32–37). For turbot peak abundance occurred in mid-August–early Sep-

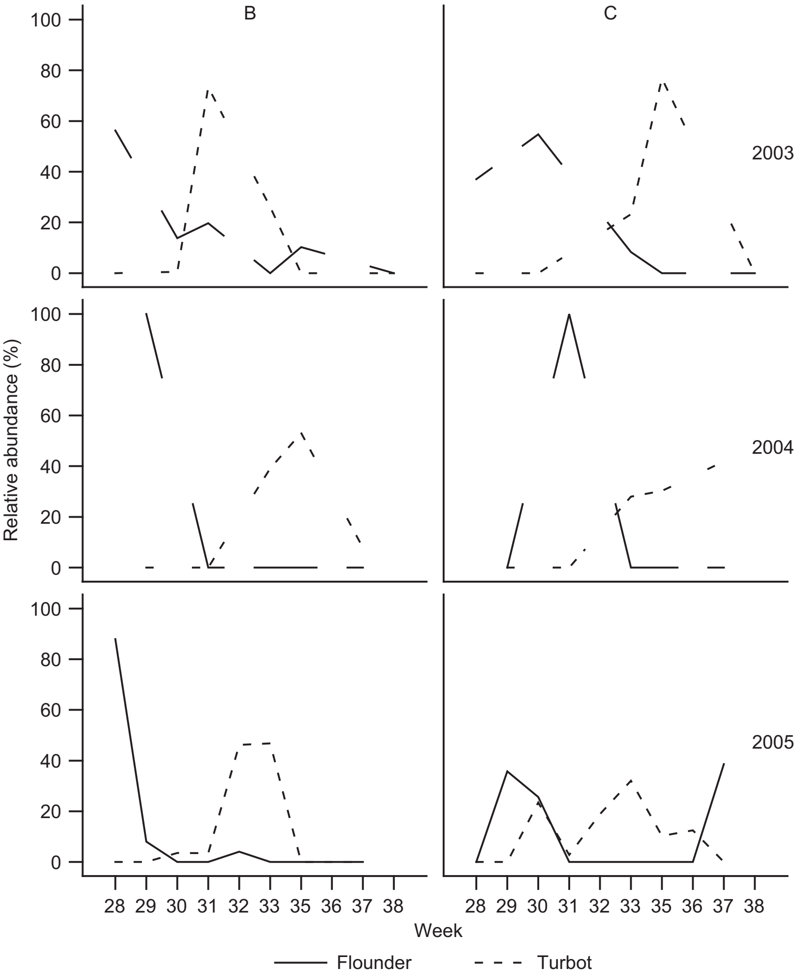

Fig. 3. Relative abundance (percentage of total density), in bays B and C for all years (2003–2005), of newly settled individuals of flounder (≤ 20 mm) and turbot (≤ 30 mm) at the coast of Gotland, central Baltic Sea (ICES SD 27 and 28-2).

tember, week 33–36 (Figs. 4 and 5). Due to later settlement, peak abundance of 0-group turbot occurred somewhat later in 2004 as compared with the other years, as shown for bay B and C (Figs. 3 and 4). Comparisons of peak abundance reveal a considerable temporal overlap in habitat utilization between the two species.

One-year old individuals were found on the nursery grounds during the entire period. The numbers decreased over the season for flounder, whereas the largest amounts of 1-group turbot were recorded in early August–early September (week 32–37). However, the share of 1-group fish differed significantly between turbot and flounder, 3% (33 ind.) and 25% (953 ind.), respectively, showing that flounder uses the nursery ground to a higher extent the second year.

For both species, mean density at peak abundance varied considerably between years (Table 1). e.g. between 7.06 ± 1.51 (SE) and 0.32 ± 0.13 (SE) ind. 100 m^{-2} in 2005 and 2004, respectively, for 0-group flounder in bay C and between 3.06 ± 0.88 and 0.95 ± 0.37 ind. 100 m^{-2} in 2003 and 2004, respectively, for 0-group turbot in bay C.

Spatial distribution

0-group flounder and turbot expressed the same depth distribution and showed preference for 0.2 and 0.6 m over 1 m depth. No significant interaction between the factors Species and Depth was found ($F_{2,30} = 1.63$, $p = 0.21$), whereas there was a significant effect of the factor Depth ($F_{2,30} = 26.95$, $p < 0.001$). The following pairwise com-

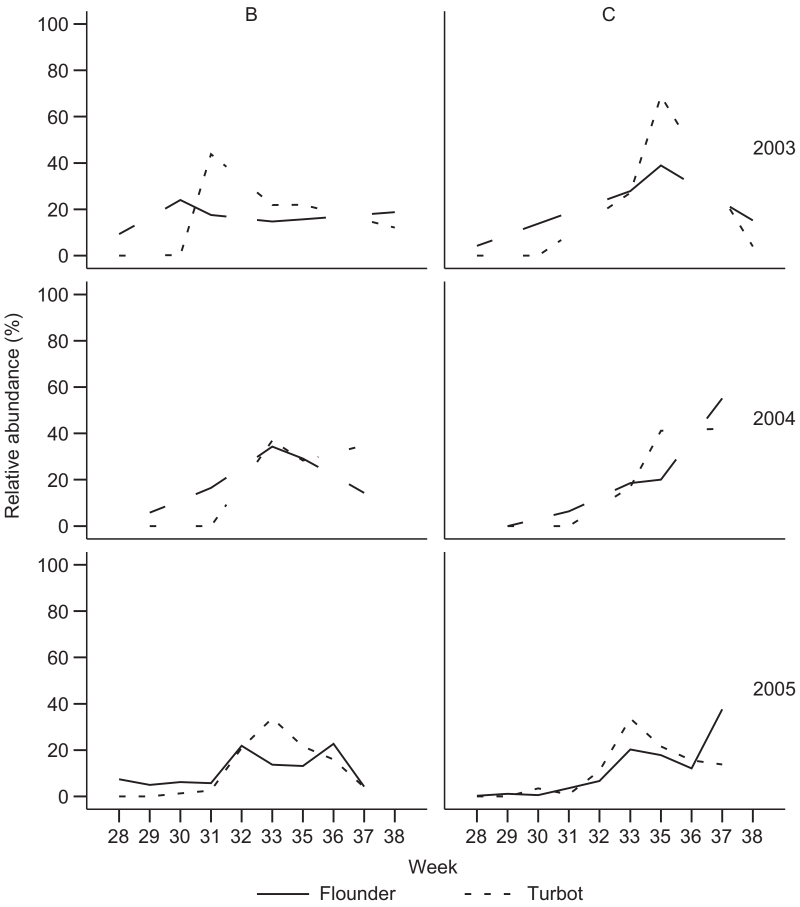

Fig. 4. Relative abundance (percentage of total density), in bays B and C for all years (2003–2005), of 0-group flounder and turbot (all sizes pooled) at the coast of Gotland, central Baltic Sea (ICES SD 27 and 28-2).

parisons showed that the mean relative abundance did not differ between 0.2 and 0.6 m depth (p = 0.1), but was significantly lower at 1 m (p < 0.001) as compared with that at other depths (Fig. 6).

When analysing the size distribution over the depths both species shared a tendency of larger size at greater depths. No significant interaction between the factors Species and Depth was found ($F_{2,29} = 0.37, p > 0.05$), whereas there was a significant effect of the factor Depth ($F_{2,29}$ = 26.95, p < 0.01). The following pairwise comparisons showed a significant difference between 0.2 and 1 m (p < 0.01), and almost a significant difference between 0.6 and 1 (p = 0.05), and between 0.2 and 0.6 m (p = 0.06) (Fig. 7).

The logistic regression showed a strong spatial overlap of 0-group turbot and flounder (Wald χ^2 = 126.94, df = 1, p < 0.001) within a sample. The probability of 0-group flounder being present in each haul when 0-group turbot was caught was 0.84 (0.80–0.87, 95% CI). Moreover, when co-occurring in samples 0-group flounder was on average 3.2 ± 0.41 (SE) times more abundant than 0-group turbot.

Both species were found in all bays examined and in all years, but densities varied considerably among locations (Table 1), e.g. in 2004 estimated densities of 0-group flounder varied between 0.32 ± 0.13 (SE) and 4.22 ± 1.11 (SE) ind. 100 m^{-2} in bay C and B, respectively. Similarly, for 0-group turbot estimated densities in 2004 varied between 0.26 ± 0.12 (SE) and 1.33 ± 0.3 (SE) ind. 100 m^{-2} in bays E and A, respectively.

Discussion

Flounder utilize the nursery grounds for a longer time, both as 0- and 1-group, as settling started

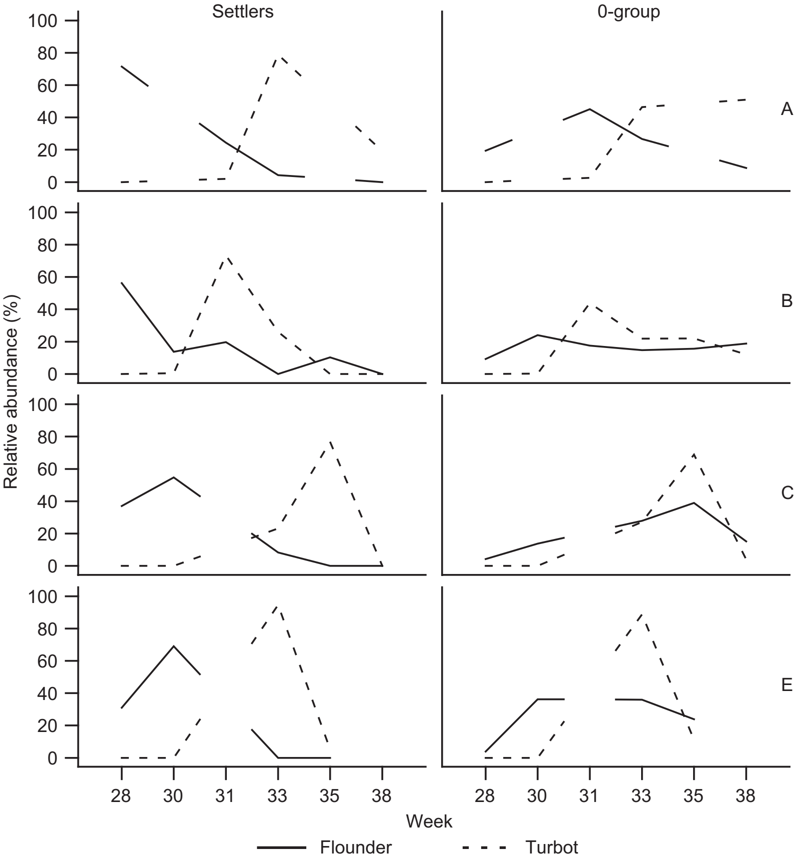

Fig. 5. Relative abundance (percentage of total density), in bays A, B, C and E in 2003, of newly settled- and 0-group individuals of flounder and turbot (all sizes pooled) at the coast of Gotland, central Baltic Sea (ICES SD 27 and 28-2).

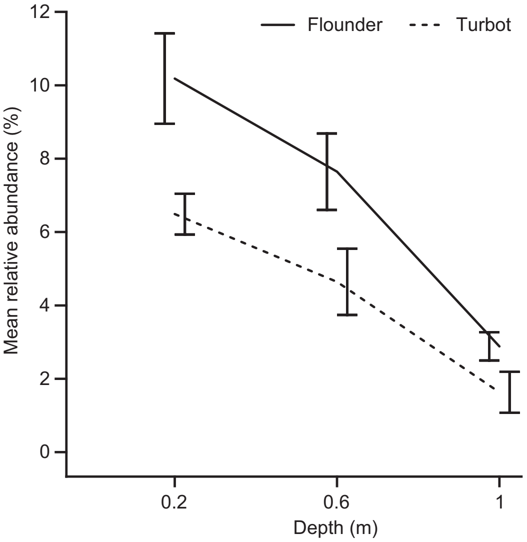

Fig. 6. Depth distribution (mean relative abundance in a haul ± SE), all bays (A–F) and years (2003–2005) included, of 0-group flounder and turbot in nursery grounds at the coast of Gotland, central Baltic Sea (ICES SD 27 and 28-2).

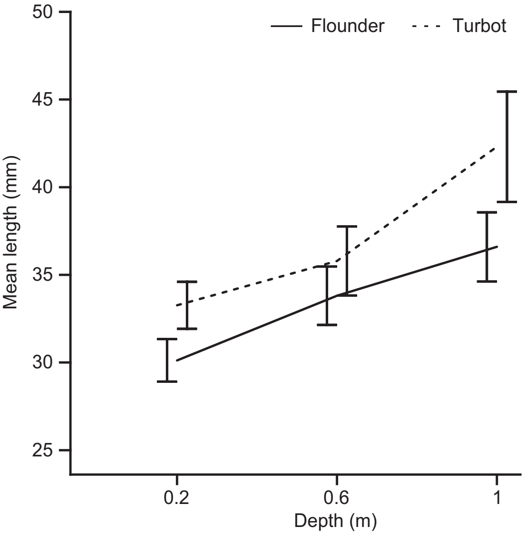

Fig. 7. Size-specific depth distribution (mean length ± SE), all bays (A–F) and years (2003–2005) included, of 0-group flounder and turbot in nursery grounds at the coast of Gotland, central Baltic Sea (ICES SD 27 and 28-2).

earlier in the season and a larger proportion of 1-group individuals were found within the nursery grounds as compared with turbot. Earlier settlement of flounder can be expected as flounder spawns earlier in the year, March–May, whereas spawning of turbot peaks in June–early July in the central Baltic Sea (Bagge 1981, authors' pers. obs.). The longer settling period of flounder in 2005 may reflect that cohorts from both coastal- and offshore-spawning populations were settling in the bays. The latter population spawns in the Gotland basin at > 70–80 m depth (ICES SD 28-2), i.e. the larvae have to be transported to the coast and may consequently appear at the nursery grounds later in the season. The occurrence of larvae originating from the offshore spawning population will, however, vary due to varying salinity and oxygen conditions, influencing the reproductive success (Drews 1999, Nissling *et al*. 2002), and varying wind and hydrodynamic conditions affecting the transportation to nursery grounds along the coast. Hence, the appearance can be expected to vary significantly between years, potentially reflecting the differences in settling patterns (Table 1 and Fig. 3).

The observed pattern of nursery ground utilization may also be related to differences in food preferences. After an ontogenetic shift at ≈ 40 mm length, endobenthic fauna as chironomids, amphipods and additionally oligochaetes are important food items of flounder up to ≈ 85 mm (Aarnio *et al*. 1996, Nissling *et al*. 2007). Contrary, turbot successively feed on larger food. At lengths < 30 mm, turbot uses a mix of copepods, chironomids and amphipods. At 30–55 mm lengths they feed mainly on mysids and additionally on amphipods, and at lengths above 55 mm increasingly on fish (mainly juvenile *Pomatoschistus* spp. and *Gasterosteus* spp.) (Aarnio *et al*. 1996, Nissling *et al*. 2007). The availability of endobenthic fauna is rather stable, both in terms of abundance and size, throughout the season (Aarnio *et al*. 1996). In contrast, epibenthic organisms (such as juvenile fish) preferred by turbot, not only vary spatially and temporally, but also vary in size over the season due to growth. Hence, flounder utilizes a food source with low variability in abundance and in size, i.e. allow settling during a long period and form a suitable food source for also 1-group fish. For turbot, on the other hand, preferred food organisms (juvenile fish in a certain size-range) when reached > 55 mm (Nissling *et al*. 2007) are available only during a short period during the season. Lower food availability for 0-group turbot is indicated by a considerable proportion of individuals with empty stomachs (without gut content), i.e. a lower feeding incidence as compared to 0-group flounder (Nissling *et al*. 2007).

Analysis of depth distribution of 0-group fish revealed a significant preference of both species for 0.2- and 0.6-m depths over 1-m depth. Further, a size-specific depth distribution was found, which indicated that smaller individuals are found in shallower water. In contrast to the present study, Florin *et al*. (2009) found no significant contribution of depth in explaining the abundance of 0-group flounder and turbot at a regional scale in the northern Baltic Sea. However, the design of this study was different and carried out in several types of substrates that may be more important as compared with depth in explaining the abundances. Moreover, the results of the present study is in agreement with findings reported by Gibson (1973) in a sandy bay off Scotland, where the centre of distribution was at < 0.5 m depth and < 1 m for 0-group turbot and flounder, respectively. Gibson (1973) also noted a significant relationship between fish size and depth (shown for juvenile plaice) with small fish occurring in shallow water. The observed distribution may reflect either feeding conditions or predation mortality, but also involve reduction of intra-specific competition, as argued by Gibson (1973). The brown shrimp is known to predate heavily on in particular early-juvenile flatfish (Van der Veer and Bergman 1987, Wennhage 2002). Although it usually occurs in low abundances at nursery grounds in the central Baltic Sea, it has been observed to be less abundant at 0.2- as compared with 0.6- and 1-m depths. Contrary to that of brown shrimp, abundance of mysids was significantly higher at 0.2- than at 0.6–1-m depths (A. Nissling unpubl. data). Hence, survival probabilities of specifically small turbot may be enhanced in shallow waters. Further, as derived from experiments on plaice and flounder, the optimum temperature for feeding and growth is negatively correlated with fish size (Fonds *et al*. 1985). Hence, newly settled juveniles may benefit from normally higher temperatures at smaller depths (Widbom, unpublished data) in nursery areas at Gotland during the season. Maximum growth of 0-group flounder has been reported to occur at 18–22 °C (Fonds *et al*. 1992). The corresponding values for 0-group turbot is 20–23 °C (Imsland *et al*. 2000).

As opposed to Riley *et al*. (1981), who found that 0-group turbot dwell at exposed beaches at salinities > 32 psu as compared with estuaries at < 28 psu for 0-group flounder around the coast of England and Wales, the present study demonstrated considerable co-occurrence of the species. The co-occurrence suggests a potential for inter-specific interactions. This may explain the observed negative correlation between feeding incidence of turbot < 30 mm and density of 0-group flounder (Nissling *et al*. 2007), and that peaks in the year class strength of turbot were observed to coincide with weak year classes of flounder in the Baltic Sea (Molander 1964).

In an earlier study, Nissling *et al*. (2007) found that the diets of 0-group turbot and flounder differed in general but overlapped to some extent for turbot < 30 mm and flounder > 40 mm. Flounder may have reached sizes > 40 mm at first arrival of turbot since flounder settlement occurs earlier. Therefore, turbot might have to compete for food at settling. However, the prey items shared (amphipods and chironomids) display stable abundances within the season and occur in high densities (Bonsdorff and Blomqvist 1993, Nissling *et al*. 2007), i.e. competition for the shared prey items is less likely to occur. This concurs with the general view that macrohabitat overlap is inversely related to competition (Schoener 1983). The association between habitat overlap and diet partitioning, i.e. differences in diet, have also been observed by Piet *et al*. (1998) when studying flatfish assemblages in the southern North Sea.

There is a potential for 0-group turbot and flounder to interact by interference. Turbot preys on fast moving epibenthic prey by vision at the bottom and in the water column. The feeding behaviour is characterized by burying into the sediment waiting for prey and when detected a short stalking behaviour is employed followed by a rapid lunge (Holmes and Gibson 1983, D. Nygren pers. comm.). Contrary, flounder uses both vision and chemical cues (De Groot 1971, Holmes and Gibson 1983) and search for food by slowly swimming along the bottom (Holmes and Gibson 1983). Potentially, the prey of turbot or turbot itself may be disturbed by flounder searching along the bottom, thereby reducing the feeding success of turbot.

Aiming at evaluating the timing of nursery ground utilization as a basis for future studies (e.g. growth and mortality rates) of juvenile turbot and flounder in the Baltic Sea, the sampling period, i.e. from early–mid-July to mid-September, covered the main settling period as well as peak abundance of turbot. Concerning flounder, however, settlement of 0-group fish was not fully covered as the abundance of fish < 20 mm peaked already in early mid-July (week 28) and probably started earlier. Further, at least in some years (2005), settlement of flounder may continue in September, i.e. 0-group abundance may peak later. Thus, for studies involving 0-group flounder the sampling period should be extended by beginning somewhat earlier and finished later to cover "late settlers". Considering depth distribution, depth strata sampled seem to, in accordance with Gibson (1973), cover the main occurrence of 0-group fish; the vast majority occurred at < 1 m depth, 87.4% and 81.6% for turbot and flounder, respectively. Regarding the potential for studying ecology of 1-group flounder appearing at the nursery grounds throughout the season, the sampling scheme conducted is inappropriate; 1-group flounder occur in high abundances already early in the season and probably have a different depth distribution as larger individuals occur more offshore as observed by e.g. Gibson (1973). Moreover, the 1-group fish appearing at the nursery grounds probably represent only a part of the population.

In summary, turbot and flounder in the Baltic Sea showed high temporal and spatial overlap within the shallow, sandy nursery grounds investigated. However, flounder utilized the nursery grounds for longer period of time both as 0- and 1-group, which may be explained by the differing feeding preferences of the species. The differing diets probably also reduces competition between the species, thus enabling the observed coexistence. The results of this study can be used to design studies aiming at assessing which controlling and/or regulating mechanisms within typical nursery grounds, i.e. shallow sandy bays, that affect variability in recruitment of the species.

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