

Tidal transport of flounder larvae (*Platichthys flesus*) in the Elbe River, Germany

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Abstract

Flounder larvae (*Platichthys flesus* Linnaeus 1758) were observed to utilise the tidal currents for their upstream transport in the Elbe estuary. Differences in current speed between mid-water during flood and near bottom during ebb facilitated larval migration upstream. In 1995 larvae were collected in the tidal reaches of the Elbe River at 3 different depths in the water column (bottom, mid-water and surface) during four tidal cycles. During flood most larvae were found in mid-water, whereas during ebb most larvae were caught near the bottom. The hypothesis proposed by several authors of flounder populations spawning in the tidal Elbe was rejected, since early ontogenetic stages of larvae were absent from the catches. Otoliths were analysed to estimate the time needed by flounder larvae to complete their upstream migration from the entrance of the estuary to the feeding grounds. The diurnal nature of growth increments in the otoliths was corroborated. The average transport time over a distance of 49 km was estimated to be 6 d in April and 9 d in May.

Kurzfassung

Gezeitentransport von Flunderlarven (*Platichthys flesus*) in der Elbe

Es wurde beobachtet, daß Flunderlarven (*Platichthys flesus* Linnaeus 1758) die Gezeitenströme für ihren Aufwärtstransport in der Elbmündung nutzen. Die Unterschiede der Strömungsgeschwindigkeit in mittlerer Wassertiefe während der Flut und nahe dem Grund während der Ebbe ermöglichte den Larventransport flußaufwärts. 1995 wurden Larven im Gezeitenbereich der Elbe in drei verschiedenen Wassertiefen (Boden-, Mittelbereich und Oberfläche) bei 4 Gezeitenzyklen gefangen. Während der Flut wurden die meisten Larven im mittleren Wasserbereich angetroffen, während der Ebbe dagegen nahe dem Grund. Die von mehreren Autoren vorgebrachte Hypothese, daß Flunderpopulationen im Gezeitenbereich der Elbe laichen, wurde verworfen, da frühe Larvenstadien nicht in den Fängen auftraten. Otolithen wurden analysiert, um die Zeit zu errechnen, die Larven für ihre Wanderung flußaufwärts von der Flußmündung bis zu den Nahrungsgründen benötigen. Die Erscheinung der täglichen Zuwächse in den Otolithen wurde bestätigt. Die durchschnittliche Transportzeit über eine Entfernung von 49 km wurde für April mit 6 Tagen und für Mai mit 9 Tagen errechnet.

Introduction

The European flounder (*Platichthys flesus* Linnaeus 1758) inhabits tidal flats and estuaries throughout its extensive distribution area. This area includes the Black Sea, the Mediterranean Sea, the European Atlantic coast (including the British Isles and Ireland), the North Sea, the Baltic Sea, the Barents Sea and the White Sea. The ability of flounder to survive in habitats with low salinity and even fresh water explains its success in this wide geographical area (*e.g.* Robin 1990; Van der Veer and Groenewold 1987).

In western Europe, adult flounder leave estuaries to spawn in the North Sea (Russell 1976). Spawning starts mid-January and continues until April in the Southern Bight of the North Sea (Van der Land 1991). The pelagic eggs drift with the water currents towards the Wadden Sea (Campos *et al.* 1994) and after hatching, flounder larvae are thought to develop the ability to influence their drift direction (Gibson 1997). In the nursery areas of the estuaries larvae metamorphose, adapt to a bottom life and develop into juveniles.

The flounder is one of the most abundant species in the tidal Elbe River (Thiel and Bos 1998; Möller 1988), which may explain why most studies carried out in the tidal Elbe have dealt with the adult segment of the population (*e.g.* Schnakenbeck 1940; Tesch 1965). The first study into the distribution of juvenile flounder in the tidal Elbe was carried out by Kerstan (1991). He found high concentrations of 0-group flounders in the oligohaline and limnetic sections. Möller (1988) studied the distribution of flounder larvae in the tidal Elbe and found high densities in the fresh water tributaries, especially in the Este (Fig. 1). The importance of these low salinity sections as nursery and feeding grounds for flounder has been demonstrated by several studies (Ladiges 1935; Fiedler 1991; Kafemann *et al.* 1996).

Selective tidal transport has been observed in several fish species (*e.g.* Weinstein *et al.* 1980; Fortier and Leggett 1983) including flatfish (Champalbert and Marchand 1994; Rijnsdorp *et al.* 1985). Rijnsdorp *et al.* (1985) observed similar behaviour in plaice, *Pleuronectes platessa*, in the North Sea which are evolutionarily closely related to the flounder (Chapleau 1993). Selective tidal transport can be described as the utilisation of tidal currents to move in a specific direction or to maintain geographical position. If flounder larvae utilise selective tidal transport they should utilise currents with high velocities during flood tide and currents with low velocities during ebb tide.

Berghahn (1983) observed tidally influenced behaviour in newly metamorphosed flounder in the drainage gullies of the tidal flats in the Wadden Sea. Jager (1998) found that concentrations of flounder larvae varied during the tidal cycle. Both studies indicated the existence of tidally dependent behaviour in flounder, though they only concentrated on the accumulation of flounder on shallow tidal flats during the settlement period. The relatively deep channels of the Elbe estuary provided a good setting for the present study into larval transport, because differences in larval densities between surface and bottom were thought to be clearer than they would be in shallower estuaries and tidal flats.

Sterner (1916) and Möller and Dieckwisch (1991) caught relatively small larvae in the tidal Elbe. The long distance between the spawning grounds in the North Sea and settlement areas in the tidal Elbe led these authors to suggest that the flounder also spawned in the

tidal Elbe. However, this hypothesis has never been studied. The small size of the larvae could be an indication of the speed of larval migration and the efficiency in utilisation of tidal currents. In view of this interest arose in estimating the time that larvae need for their migration.

The first objective of this study was to describe the upstream transport mechanism of flounder larvae in the tidal Elbe. The second objective was to test the hypothesis that flounder also spawn in the tidal Elbe. The third objective was to estimate the transport time needed by the larvae to migrate from the estuary entrance to the upstream nursery.

Materials and methods

Study area and sampling

The tidal Elbe River, located in northern Germany (53°50'N; 9°20'E, Fig. 1) with a tidal range of more than 3 m, ranges from the weir at stream kilometre (Skm) 586 to Skm 740 in the Wadden Sea. The tidal Elbe River has been much affected by canalization for shipping, which has reduced the number of shallow-water areas and increased the current velocity and tidal range. The average maximum current velocity per tide is 0.95 m/s

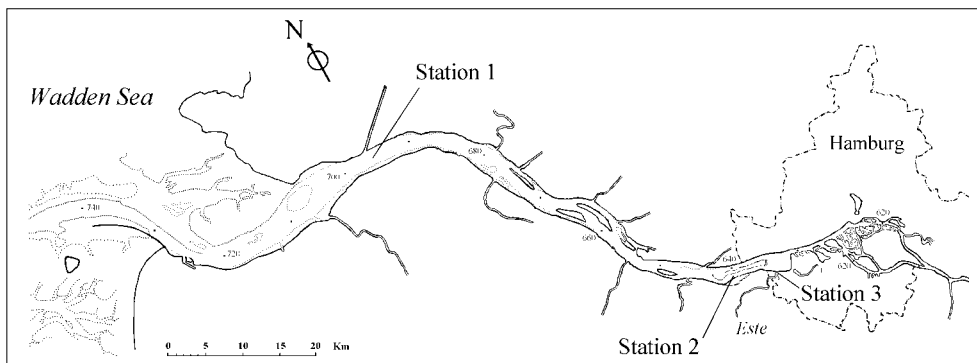


Figure 1: The tidal Elbe River with the sampling stations: 1) estuary entrance, 2) Hahnöfer Nebel and 3) mouth of the tributary Este. Black dots with numbers indicate stream kilometre of the main channel.

during ebb and 1.15 m/s during flood (Baumert and Zabanski 1994). The salinity ranges from 0.5 to 30 PSU and Kies *et al.* (1992) classified the tidal Elbe in 4 salinity sections: a limnetic section with a salinity less than 0.5 PSU (Skm 586-673), an oligohaline section with a salinity between 0.5 and 5 PSU (Skm 673-695), a mesohaline section with a salinity between 5 and 18 PSU (Skm 695-705) and a polyhaline section with a salinity between 18 and 30 PSU (Skm 705-740). Further details on the study area can be found in Thiel *et al.* (1996).

Plankton samples were taken with a bongo net (diameter 60 cm) with 500 and 1000 μ m mesh sizes. The net was weighted down with 20 kg ballast to ensure its vertical position

and was positioned in the water for 5 minutes. A flowmeter (General Oceanics®) was used to estimate the volume of water filtered by the net. Samples were immediately fixed in a 5 % formaldehyde solution buffered with sodium borate. In the laboratory, larval standard lengths were measured to the nearest 0.01 mm using an electronic drawing board, that was mirrored into one ocular of a stereomicroscope. The ontogenetic stage of larval development was determined after Ryland (1966) and Campos (1996). Surface water temperature and dissolved oxygen were recorded with an oxygen meter (OXI196, WTW®). Salinity was measured with a conductivity meter (LF196, WTW®).

Vertical sampling

The vertical distribution was investigated to detect differences in larval densities in relation to the tide. Samples were collected on 11th April and 8th May 1995, each covering two successive tidal cycles at Station 2 in the Hahnöfer Nebelbe (Fig. 1). The bongo net was lowered with a hydraulic crane from an anchored platform to three different depths: surface (0.5 m), mid-water (4 m) and near bottom (7 to 9 m). The maximum water depth was between 7.5 and 10.5 m depending on the tide.

The time needed to lower the bongo net to the deepest position of 9 m took 4 s. Since the bongo net was not a multiple closure net, it did fish at all depths, but for a relatively short period of time. However, in the case of 5 min hauls less than 3 % of the catching time was at a depth different to that aimed for. Therefore, samples were assumed to approximate discrete depth samples.

Transport time

The transport time was estimated by comparing the average increment counts of otoliths of flounder larvae collected at the entrance of the Elbe (Station 1; Skm 692) and upstream in the Hahnöfer Nebelbe (Station 2; Skm 643). At Station 1, larvae were collected at weekly intervals from 16th March to 23th May 1995 (Bos *et al.* 1995). As the vertical distribution survey at Station 2 was carried out in mid April and at the beginning of May, two estimations of transport time were made. The net was towed by the research vessel 'Tromper Wiek' at a speed of 1.5 m/s in the opposite direction to the tide, at an average depth of 1.5 m. At Station 2, larvae were collected on 11th April and 8th May when taking samples for studying on the vertical distribution.

Otolith analysis

Larvae were aged by counting the growth increments of the otoliths. Each pair of sagittae was dissected under a stereomicroscope with a magnification of 40 \times , fixed to a glass slide with mounting medium (DePeX, Serva®) and covered with a glass cover-slip. The stereomicroscope, equipped with a videocamera, was connected to an image analysis system (Optimas® 6.0) to study the sagittae on a video screen. Growth increments were counted and sagitta diameters were measured at a magnification of 400 \times .

Verification counts for all otoliths did not vary by more than ± 2 increments. Since underestimation is common in otolith studies (Campana 1992) the highest counts were

used for further calculations. Left and right otoliths were tested for morphological differences since flatfish have different left and right body sides after metamorphosis. No significant difference (Paired *t* test, $P = 0.34$, $n = 66$) was found between the diameter of the left and right otoliths and thus an average of both increment counts was used for further calculations.

Validation of daily growth in otoliths

The diurnal nature of the growth increment formation in the otoliths was investigated before the increment counts were used for exact time calculations. Larvae were collected at 4 h intervals during a 24 h period on 9th and 10th May 1997 at the mouth of the tributary Este (Station 3; Fig. 1). The marginal increment technique (Tanaka *et al.* 1981) was used to estimate the completion (C) of the increment on the edge of the otolith. It expresses completion (or width) of the increment being formed on the edge of the otolith as a percentage of the width of the immediately preceding increment:

$$C = \frac{W_n}{W_{n-1}} \cdot 100$$

where W_n represents the width of the increment in the process of formation and W_{n-1} the width of the previously formed increment. A magnification of 1000 \times was used.

Results

The mesh size of 500 μm was found to be too small to sample the larval fish population in the tidal Elbe, because this net already became full of excessive zooplankton and detritus after 1 min hauls. Therefore, the larval densities in the present study were based only on the catches of the 1000 μm net. Numbers of larvae caught with the 500 and 1000 μm nets did not differ significantly (Paired *t* test, $P > 0.05$, $n = 50$).

Vertical distribution

Larvae were found higher in the water column during flood tide than during ebb tide. Significantly higher larval densities (Mann-Whitney U-test, $P < 0.05$) were found in the April samples taken at 4 m depth during flood tide than during ebb tide, while at 8 m depth the opposite was true (Fig. 2A). No significant differences were found at 0.5 m depth (Mann Whitney U test, $P > 0.05$).

The May samples showed significantly higher larval densities (Mann-Whitney U-test, $P < 0.01$) at 4 and 8 m depth during flood tide than during ebb tide (Fig. 2B). Again, no significant differences were found at 0.5 m depth (Mann Whitney U test, $P > 0.05$). Average water temperature, dissolved oxygen and salinity were 10.9 $^{\circ}\text{C}$ (Standard deviation, $s = 3.1$), 9.5 mg/l ($s = 0.9$) and 0.38 PSU ($s = 0.05$), respectively. Water temperature varied slightly with time of day, whereas tidal changes in the above parameters were not observed.

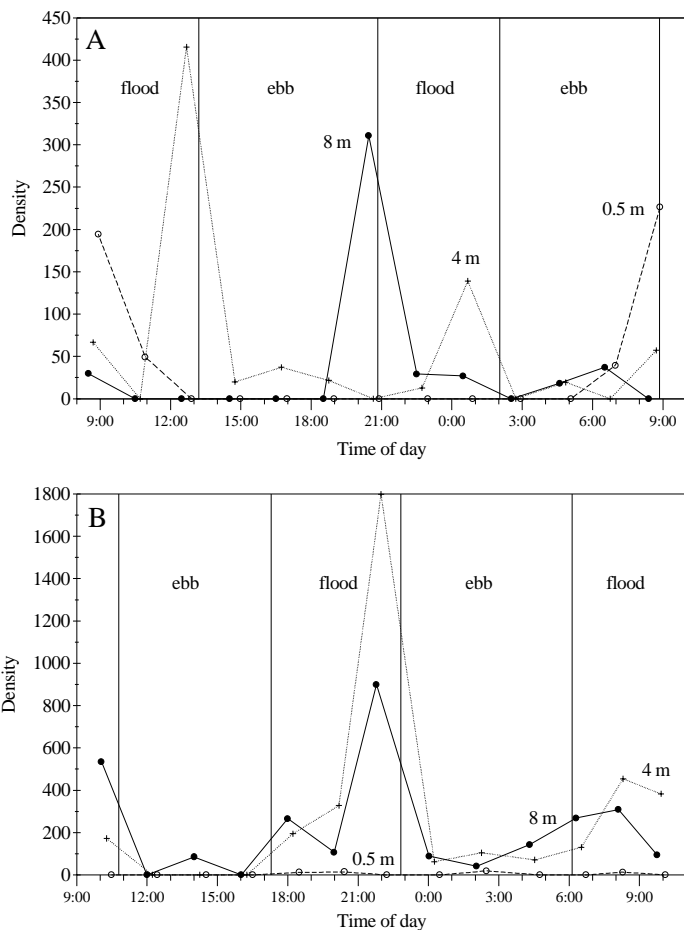


Figure 2: Larval densities [ind. $m^{-3} \cdot 10^{-3}$] at Station 2 found during two sampling periods at three different depths: 0.5 m (dashed line, \circ), 4 m (dotted line, $+$) and 8 m (solid line, \cdot). A: 11th and 12th April, 1995. B: 8th and 9th May, 1995. Vertical lines represent change of current direction.

Table 1: Percentage of flounder larvae caught at stations 1 and 2 for each ontogenetic stage and sampling date in 1995.

Larval stage	Station 1						Station 2	
	16 Mar.	19 Apr.	25 Apr.	3 May	10 May	17 May	11 Apr.	8 May
I	-	-	-	-	-	-	-	-
II	-	-	-	-	-	-	-	-
IIIa+b	-	-	-	-	-	-	-	-
IIIc	100	20	62	24	31	22	-	-
IVa	-	40	38	56	54	61	-	-
IVb	-	20	-	10	15	17	39	21
V	-	20	-	-	-	-	61	79

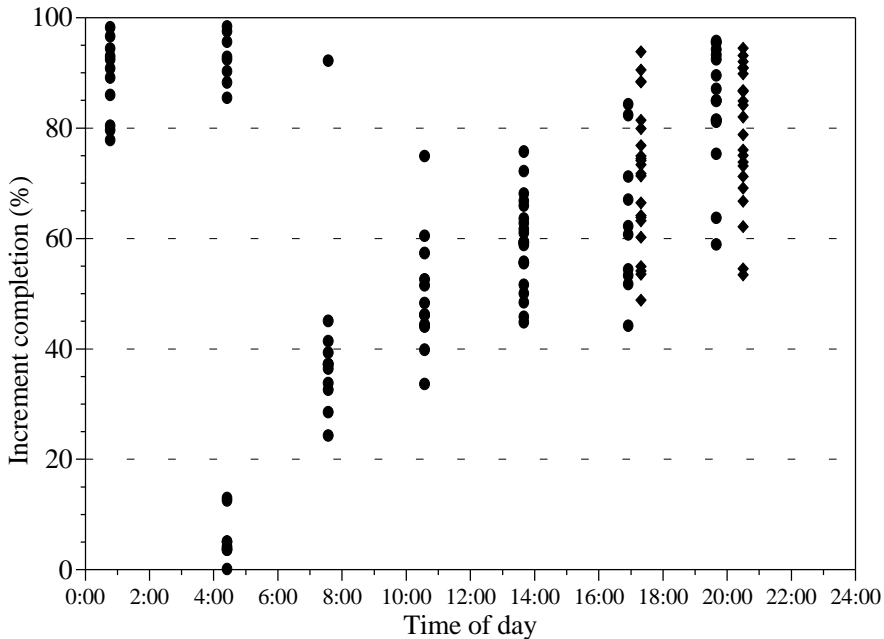


Figure 3: Diurnal variation in completion of the marginal increment in the sagittae ($n = 142$) of flounder larvae. Diamonds and dots represent samples from 9th and 10th May, respectively.

Ontogenetic stage of larvae

Flounder larvae at ontogenetic stages I and II were not caught during the sampling in 1995 (Table 1). The least developed ontogenetic stage found in the samples of the tidal Elbe was IIIc. Larvae caught at Station 1 had at least reached stage IIIc, and most of them were stage IVb. About 70 % of the larvae caught at Station 2 were stage V, whereas the rest of the larvae had at least reached stage IVb.

The average standard length of the larvae caught at Station 1 was 7.92 mm ($s = 0.66$). The average standard length of the larvae at Station 2 was 8.08 mm ($s = 0.64$) and 7.90 mm ($s = 1.30$), in April and May respectively.

Validation of daily growth in flounder otoliths

The analysis of the completion of the marginal increments corroborated the diurnal rhythm of increment deposition in the sagittae of flounder larvae (Fig. 3). A total of 142 sagittae were analysed, which had been extracted from larvae with a mean standard length of 8.65 mm ($s = 0.94$). Completion of the marginal increment of 95 % or more was only observed in larvae collected in the morning. New increments were being formed in the morning between 04:25 and 07:35 h. Deposition rates were higher during day time than during night time, which explained why deposition of more than 90 % had already been observed in specimens collected at 17:19 h.

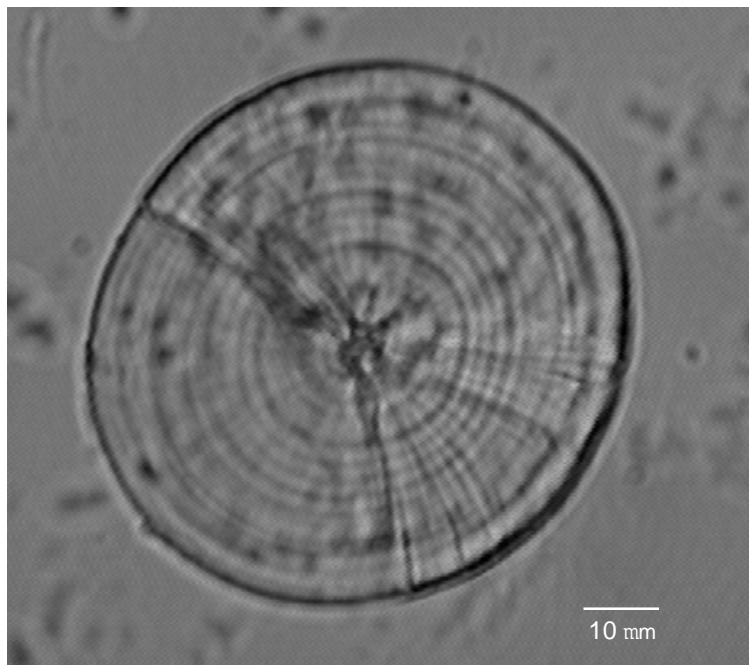


Figure 4: Sagitta (\bar{x} 76.9 μm) with 15 increments of a IIIc flounder larva with a standard length of 8.1 mm (Scale 1:1000).

Table 2: Number of flounder studied, median sagittal diameter (μm) and median counts of daily growth increments at Stations 1 and 2 in 1995.

	Station 1						Station2	
	16 Mar.	19 Apr.	25 Apr.	3 May	10 May	17 May	11 Apr.	8 May
Number of Flounder	1	9	13	21	13	23	31	28
Sagittal diameter (μm)	67.2	81.2	74.2	79.3	84.3	84.0	92.7	149.2
Increment counts	12.0	14.5	14.0	16.0	15.0	16.0	20.5	30.5

Ageing of larvae

Estimation of the number of growth increments in flounder otoliths, using the proven technique of light microscopy, was only found to be possible for otoliths with a diameter smaller than 250 μm . Otoliths with a diameter larger than 250 μm were too thick to let enough light through, which made exact counting difficult. 3.7 % of the otoliths studied had a diameter between 200 and 250 μm (Table 2). Whereas, 90 % had a diameter of less than 150 μm and daily rings were easily recognised (Fig. 4).

The increment counts were significantly higher (Kruskal-Wallis ANOVA, $P < 0.01$) upstream at Station 2 than at the entrance of the estuary at Station 1 on the all sampling dates (Table 2). Average increment counts of the larvae at the mouth of the estuary only

Tidal transport of flounder larvae (*Platichthys flesus*)

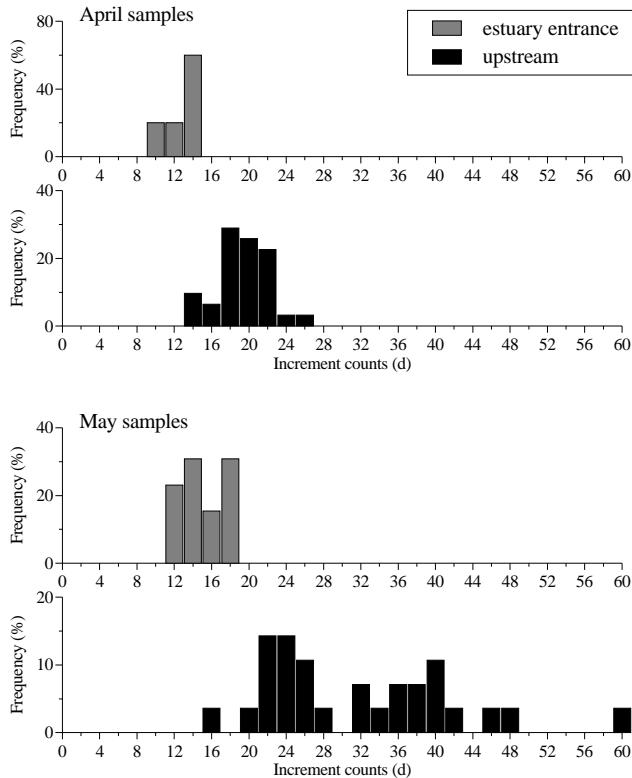


Figure 5: Increment count distributions in April and May at the entrance of the estuary (Station 1) and at the Hahnöfer Nebenelbe (Station 2).

varied on 12 to 16 days within a 3 month period, indicating that hatching took place during this extended period and that larvae only seemed to pass the entrance of the Elbe to migrate to upstream areas.

Increment counts were significantly higher for the May samples than for the April samples at Station 2 (Kruskal-Wallis ANOVA, $P < 0.01$). Furthermore, the range of increment counts in the May samples was higher than in the April samples.

Estimation of transport time

The frequency distribution of the increment counts of the April and May samples was more or less similar at the estuary entrance at Station 1 (Fig. 5). Upstream at Station 2, the frequency distribution of the increment counts in April was different to that in May (Fig. 5). In April the increment counts were normally distributed, whereas the May increment distribution was strongly skewed. This skewed distribution at Station 2 may have represented two cohorts of larvae, the first with more than 30 increment counts and the second with less than 30 increment counts (Fig. 5). The median increment count of both peaks would then have been 39.5 d and 24.0 d, respectively.

The transport time needed by the larvae for upstream migration over a distance of 49 km from Station 1 to Station 2, was 6 d in the middle of April (Table 2). At the beginning of May this transport time was 15 d (Table 2). However, the transport time would be 9 d if the distribution of the increment counts of the May samples from Station 2 consisted of two peaks of larvae and only the second peak was taken into account. This value was similar to the 6 d found in April and resulted in an average transport time of 7.5 d.

Theoretically, larvae would be able to travel a distance of about 10 km when only travelling during flood currents at an average water speed of 0.5 m/s. The transport time over a distance of 49 km would then approximately equal that of 5 flood tides (2.5 d). This means that the flounder larvae were able to utilise a tidal phase at an efficiency rate of about 42 and 33 % in April and May respectively.

Discussion

Tidal transport

The results of the present study indicate that flounder larvae utilised tidal currents for their upstream transport in the Elbe river. Flounder larvae were found to migrate in a specific direction, which means that they were able to detect differences between ebb and flood currents. Ebb and flood currents in estuaries usually differ in their abiotic characteristics, *e.g.* salinity. Tidal changes in these abiotic characteristics may control larval transport by influencing the behaviour of larvae (Gibson 1997).

Jager (1998) found salinity to be a governing factor in larval transport of flounder on tidal flats. An important difference between Jager's study and the present study was the salinity of the water at the sampling stations. Jager (1998) found mean salinities ranging between 5.7 and 11.8 PSU, whereas tidal migration of flounder larvae in the present study was observed in the limnetic part of the tidal Elbe, where there was a mean salinity of 0.4 PSU. So, the behaviour of flounder larvae in habitats, where salinity changes were of no importance, was additionally being influenced by at least one other factor.

Another factor which could have influenced the swimming behaviour of the larvae was food availability. Burke (1995) suggested that prey gradients guide the segregation of southern flounder (*Paralichthys lethostigma*) and summer flounder (*Paralichthys dentatus*), which share habitats during larval stages. The author proposed that the abundance of mysids in upstream oligohaline nursery areas may attract the southern flounder, whereas the abundance of polychaetes in saltmarsh habitats in the lower estuary may attract the summer flounder. Creutzberg *et al.* (1978) found in a laboratory experiment that feeding conditions have an effect on the swimming behaviour of plaice larvae (*Pleuronectes platessa*). Starvation induced pelagic swimming, whereas feeding induced the larvae to lay on the bottom.

Food availability may be an important factor guiding the migration of flounder larvae into estuaries and tidal rivers. In the tidal Elbe the main prey of flounder larvae is the copepod *Eurytemora affinis* (*e.g.* Fiedler 1991; Kafemann *et al.* 1996). Köpcke and Kausch (1996) found higher densities of *E. affinis* during ebb than during flood tides at the

entrance of the Elbe estuary in June 1993. A similar situation was observed upstream in the Hahnöfer Nebenelbe in July 1994. In the present study, flounder larvae may have moved to the bottom during ebb when enough food was available. During flood they actively foraged in the water column when prey density was relatively low.

Origin of flounder larvae

Estimation of the time needed by flounder larvae for their upstream transport from the entrance of the estuary to the nursery, only made sense if the hypothesis that the flounder also spawns in the tidal Elbe (Möller and Dieckwisch 1991) was rejected. Increment counts of the otoliths of larvae that hatched in the tidal Elbe, would have obscured the increment distributions (Fig. 5). During the present study, flounder larvae had less increments (were younger) at the entrance of the estuary than further upstream. Furthermore, the early ontogenetic stages of flounder larvae were absent from the catches. Both results support the idea that larvae came from the North Sea and did not hatch in the tidal Elbe.

In the North Sea, early stages of flounder larvae were caught with a 300 μm mesh net (Campos *et al.* 1994). The 500 and 1000 μm mesh sizes used in the present study may be considered to have been too large for catching larval stages I and II. However, the decision to only use the samples caught with the 1000 μm net was made because the 500 μm net was already full of excessive zooplankton and detritus after 1 min hauls. Therefore, the actual mesh size was probably smaller than 500 μm after the first minute of towing. If early stages of flounder larvae had been present in the tidal Elbe, it would be expected that the 500 μm net samples from the 5 min hauls would have contained at least some early stage larvae. But in 50 samples caught with the 500 μm net, the larval stages I and II were not found.

The hypothesis of flounder spawning in the tidal Elbe suggested that ripe adults would occur in the estuary. However, the literature concerning this flounder population has never mentioned such catches. Furthermore, flounder were found to leave the Elbe estuary when preparing to spawn and probably did not return to shallow areas after their first spawning (Ehrenbaum 1936). This phenomenon has also been observed in other estuaries (*e.g.* Nellen 1968). In conclusion, the hypothesis of a flounder population spawning in fresh water regions of the tidal Elbe can be rejected.

Transport time

The Hahnöfer Nebenelbe (Station 2) has been described as a nursery and settlement area for flounder (Möller 1988). This suggests that larvae prefer this area above other areas in the tidal Elbe and that they would try to reach it as fast as possible. In April, larvae were observed to reach this area in 6 d, whereas in May it took 15 d (Table 2). The distribution of the increment counts suggested that in April larvae reached Station 2 as fast as possible, since the distributions were more or less similar (Fig. 5). In contrast, larvae caught at Station 2 in May represented relatively old larvae that had already stayed in the estuary for a longer period of time (first cohort) and also relatively young larvae that migrated upstream as fast as possible (second cohort). To estimate a reasonable transport time for

these May samples it seemed fair only to use larvae with less than 30 increments, which resulted in a transport time of 9 d. Though, even if we except this, the transport took 3 d longer in May than in April. Again, food availability may have been an influence. Larvae may have migrated relatively fast due to low densities of prey species in April and may have migrated relatively slowly due to higher densities of prey species in May.

The suggestion of different cohorts of flounder observed in the tidal Elbe, was supported by observations in the North Sea. Campos (1994) observed two separate areas with high larval densities and suggested that these represent two different spawning areas. The observation of flounder upstream in the nursery which were smaller than downstream at the entrance of the Elbe estuary, made Möller and Dieckwisch (1991) think that spawning in the tidal Elbe was possible. These authors may also have observed different cohorts that possibly came from different spawning areas in the North Sea.

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