

**A TRANSPORT OF FLOUNDER LARVAE (*Platichthys flesus* L.)
INTO MARIAGER FJORD**

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ABSTRACT Flounder larvae (*Platichthys flesus* L.) were studied from April to June 2000 in Mariager Fjord, Denmark. Low density (1.0 individual per 100 m³) of larvae was found in the fjord during the sampling period and most larvae were found in April. Flounder larvae were observed to utilise the tidal currents for their upstream transport. Higher densities of flounder larvae were found in the surface layer during flood than ebb tide, whereas the opposite pattern was found near the bottom of the water column. The hypothesis that flounder larvae are hatched in the fjord was rejected because no flounder larvae at the early stage II and I was found in the samples. The transport time needed by larvae for upstream migration over a distance of 9 km was about 3.5 – 4 days. Hatch date analysis showed that flounder larvae in Mariager Fjord were hatched in two different periods and they might represent two different cohorts of larvae.

**SỞI VAN CHUYEN CAI BOI LOAI CAI BON (*Platichthys flesus* L.)
O VONH MARIAGER**

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TÓM TẮT Cá bột loài cá Bón (*Platichthys flesus* L.) được thu mẫu ở vùng biển ngoài khơi bờ biển Đan Mạch từ tháng 4 đến tháng 6 năm 2000 tại vịnh hẹp Mariager, Đan Mạch. Kết quả nghiên cứu cho thấy, mật độ cá bột rất thấp, trung bình 1 con/100 m³ và phần lớn tập trung vào tháng 4. Cá bột loài cá Bón vận chuyển từ vùng nước bên ngoài vào bên trong vịnh nhờ sức chênh lệch của dòng triều. Mật độ cá bột trên tầng mặt cao hơn tầng đáy vào những lúc triều cao và có xu hướng ngược lại khi triều thấp. Giả thuyết cho rằng cá bột của loài cá Bón *Platichthys flesus* được sinh ra trong vịnh Mariager là không hợp lý mà cá bột của loài cá này phải được vận chuyển từ bên ngoài vào bên trong vịnh. Thời gian vận chuyển trung bình mà cá bột đi được trong khoảng cách 9 km từ bên ngoài vào bên trong vịnh là 3,5 – 4 ngày. Phương pháp phân tích đồng vị cacbon tại của cá cho thấy rằng, cá bột loài cá Bón *Platichthys flesus* nổi vào hai thời kỳ khác nhau trong năm.

I. INTRODUCTION

The flounder, *Platichthys flesus* L., is widely distributed in the northeastern Atlantic, ranging from the Mediterranean and Black Sea to the Baltic, Barent and White Sea (Jager 1998; Bos 1999). In western European waters, adult flounders spawn offshore in the North Sea from January to April (Russell 1976; Van der Land 1991). Highest concentrations of flounder eggs have been observed in February along the Dutch West Coast, the eastern English Channel and the area north-west of Helgoland (Van der Land 1991). After hatching, the larvae drift with the water currents towards the coastal nursery grounds in the tidal flats (Berghahn 1987; Van der Veer et al. 1991) or in estuaries (Kerstan 1991; Hutchinson & Hawkins 1993; Bos 1999) where they complete metamorphosis, settle in intertidal areas and develop into juveniles. The nursery areas of flounder extend from the brackish water regions of estuaries into freshwater habitats of rivers (Kerstan 1991). So flounder is able to survive in habitats with large range of salinity, and that explains its success in this wide geographic area (Van der Veer & Groenewold 1987; Robin 1990).

Larval fish migration is important for recruitment and stock unity (Cushing 1975), especially for species spawning offshore whose larvae utilise coastal nursery grounds. This process is governed by two main phases: firstly, larvae move shoreward, more or less passively, and secondly they react to some stimuli and

aggregate near nursery grounds (Boehlert & Mundy 1988). Each process is regulated by diverse environmental factors, initiating different behavioural responses. Larvae take an advantage of advective tidal transport, they sink to the bottom in periods of low current velocity and are redispersed in the water column by turbulent mixing when current velocity increases again. In addition to the processes described above, larvae may actively influence their transport by swimming. A combination of passive transport mechanisms and active dispersal may be expected to result in more effective inshore transport of fish larvae into nursery areas (Norcross & Shaw 1984).

Coastal waters fjords and estuaries are considered as nursery areas for several flatfish species (Zijlstra 1972). Like many other flatfish species (Rijnsdorp et al. 1985; Champalbert & Marchand 1994), selective tidal stream transport of flounder larvae to the nursery grounds have been studied by many authors (Jager 1998, 1999; Jager & Mulder 1999; Bos 1999). Jager (1998) and Bos (1999) described such behaviour in the Ems Estuary of the Wadden Sea and the Elbe River. Hutchinson & Hawkins (1993) observed metamorphosing larvae moving upstream with the advancing tide in the river Itchen. Bos et al. (1995), Jager (1998, 1999) and Bos (1999) found tidal variation in larval concentrations of flounder larvae in different water layers during the tidal cycle, and the highest concentrations of flounder larvae were observed near the surface during flood tides. This means

that flounder larvae take an advantage of tidal currents to move upstream to the nursery areas during flood tides.

Mariager Fjord is located on the East Coast of Jutland, Denmark, and is connected to Kattegat. The fjord is about 40 km long, but almost everywhere less than 2 km wide. The fjord is microtidal with a tidal range of only 20-30 cm (Christiansen & Kristensen 1988). The water exchange with the sea is relatively small because the inner part of the fjord is deeper than the outer part (Fallesen et al., 2000), so the water exchange in and out of the fjord is limited to a winding and deep channel held open by the tide. During prevailing westerly winds the surface outflow increases and this is compensated by an inflow along the bottom of water from the Kattegat (Fenchel et al. 1995).

Adult flounders, *Platichthys flesus* L, with ripe oocytes in the gonad have been found in the fjord (Sprensen and Carl, pers. comm.) and the juveniles of flounder have been collected on the tidal flats inside of the fjord during May and June 1999 (Carl, pers. comm.). On the other, there is a large and deep basin inside of the fjord with the conditions similar to deep waters. From the above information together with low water exchange in and out of the fjord lead me to the hypothesis that flounder larvae are annually produced in the fjord. The objectives of this study are to test the two null hypotheses that flounder larvae are hatched in the fjord and they are homogeneously distributed in the water column during the tidal cycle.

Furthermore I wish to estimate the transport time of flounder larvae from the entrance to the middle part of the fjord.

II. MATERIALS AND METHODS

1. Tidal data

Tidal measurements at Als Odde and Grenå were recorded at every 15 minutes in the period January 1999 to March of 2000. The result of tidal measurements showed a very high correlation between peaks of high and low water at these two stations. Because of missing tidal measurements at Als Odde from April to June of 2000, tide at Als Odde during this sampling period was back-calculated from the tidal measurements at Grenå.

2. Sampling sites and field work

Two stations (Als Odde: 56°42' 460" E & 10°12'120" N, and Havnø: 56°42'344" E & 10°09'956" N) in Mariager Fjord (Fig. 1) were sampled ten times during daytime from April to June 2000. Ichthyoplankton samples were taken with a plankton net (diameter 60 cm) with 300 µm mesh size deployed from a speed boat. A flowmeter (General Oceanic) was suspended in the middle of the net to estimate the volume of water filtered. The net was towed at a speed of 1.7 to 2.8 knots through the water, from the surface to near bottom (deep) in the opposite direction to the tidal current. Towing time used to collect was 5 minutes samples from 5 to 17 of April, corresponding to from 23 to 101 m³ of water filtered, and from 27 of April to 21 of June it was 10 minutes, corresponding to 97 to 174 m³ of water

filtered. Samples were immediately fixed in 96 % ethanol after filtering out seawater.

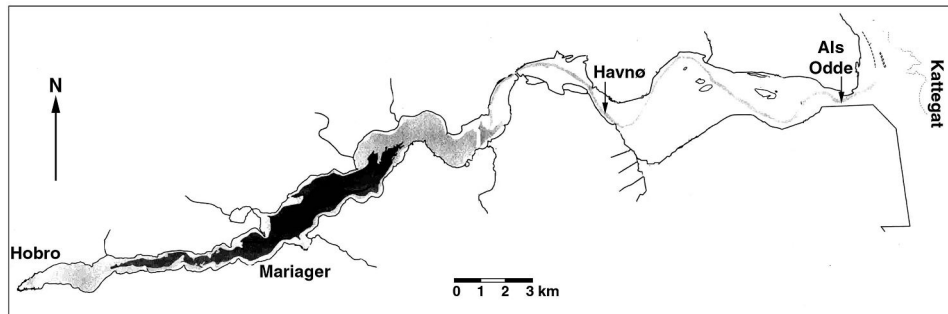


Fig. 1: Two sampling stations (Als Odde and Havnø) in Mariager Fjord. Arrow shows sampling position

3. Vertical sampling

The two sampling stations are shallow, with the maximum depth of about 6.0 to 8.5 m. Vertical sampling was conducted at three different depths: surface (0 – 0.5 m), midwater (3 – 3.5 m) and near bottom (deep: 5 – 5.5 m), depending on tide. The net was weighted down with a depressor of about 15 kg to ensure its vertical position when taking samples at mid and deep water. The net was lowered as fast as possible to the certain depth. Towing speed was kept constant as much as possible and the depth of the net were determined by measuring the angle and the length of the wire. The angle between wire of the net and sea surface was checked every one or two minutes and necessary adjustments were made by reeling in or releasing wire. Samples taken approximately 1 – 4 hours before high water slack were considered as flood samples and the rest of samples were considered as ebb samples.

Density of flounder larvae in the whole water column and in each depth strata were calculated by dividing the number of larvae with the filtered volume in the sample and then standardized to 100 m³. To compare the abundance of flounder larvae at Als Odde and Havnø I used a randomization test of the mean difference of depth integrated abundance (individuals per 100 m³) (Manly 1997).

4. Ontogenetic stage of larvae

After one or two days of fixation, fish larvae were sorted out under a dissecting microscope and preserved in 96 % ethanol. A total of 30 flounder larvae were identified and staged according to criteria developed for plaice by Ryland (1966) using a dissecting microscope. Two larvae caught on 5 April was too degraded to be staged and measured. The total length of 30 larvae was measured to the nearest 0.1 mm with a vernier calliper before removal of the lapillar and sagittal otoliths. No correction for

shrinkage was performed.

5. Otolith removal and polishing

Lapillar and sagittal otoliths of larval and juvenile flounders were extracted under a dissecting microscope using a polarized light source and fine insect needles mounted on handles. After removal, both the lapillar and sagittal otoliths of the larvae and the upper lapillar otolith of the juveniles were mounted on a single glass slide in thermoplastic resin (crystal bond). The surface of the lapillar otoliths of flounder juveniles was polished with a wet sandpaper (particle size 0.1 – 3 μm) under a light microscope.

6. Otolith analysis

Unpolished otoliths of flounder larvae were viewed under a Leitz Wetzlar microscope with oil immersion at 1000 times magnification, whereas lapillar otoliths of juveniles were viewed at 200 times magnification. The light microscope was equipped with a CCD video viewing system connected to a computer. The image of otolith was viewed on the screen of the computer. Otolith increments were counted from the initial ring of the hatching to the otolith edge at approximate screen magnification of 5600x for larval otoliths and 1250x for juvenile otoliths. Because it was difficult to count the increments in the otolith core area, I measured the distance from the hatch mark to a visible ring where the counting was started. This distance was normally less than 20 μm and that could be considered as the period of the larval stages. The number of increments along this distance was calculated by dividing it with the average increment width of known age larvae (see below).

Counting was repeated three times on each otolith, with an interval of at least two days in order to make sure that the last counting was completely forgotten. The repeated counts did not vary more than ± 2 increments for the larvae and ± 3 increments for the juveniles. The mean of the increment counts was used as age.

7. Transport time of larvae

The transport time of larvae was estimated by comparing the average increment counts of otoliths of flounder larvae caught at the two stations, Als Odde at the entrance and upstream at Havnø, at the same sampling date. The distance between these two sampling stations is about 9 km. All flounder larvae caught at each sampling date were used for analysis.

To test the hypothesis that flounder are not transported into the fjord I compared the ontogenetic stages of larval development and the average increment counts of otoliths of flounder larvae collected at the entrance Als Odde and upstream at Havnø in different time periods. The significant difference between the increment counts at the two different stations was tested by Kruskal-Wallis test (non parametric data).

8. Hatch date analysis

A total of 105 juveniles of flounder collected on the tidal flat out of the entrance of the fjord on 19 and 27 of June 2000 at low tide using a push net and 30 larvae from plankton samples were used for hatch-date analysis. Age of wild flounder larvae and juveniles was corrected using the equation from figure 2 (Increment = $0.973 * \text{Age of fish} - 1.637$). Larval and

juvenile flounders were grouped in 5 day intervals when analysing hatch date.

III. RESULTS

1. Abundance and vertical distribution of larvae

A total of 32 larvae were caught from April to June 2000. Most flounder larvae were caught in April, and only two larvae were found on 16 and 22 of May at Als Odde (Fig. 2). Mean densities of larvae at the two stations increased from the beginning up until

middle of April, and then gradually decreased from the end of April until June 2000. Average densities of flounder larvae per 100 m³ at Als Odde and Havnø were 1.1 individual (s.e. = 0.3, n = 31) and 0.7 individual (s.e. = 0.3, n = 14), whereas mean densities for the whole water column of the fjord was 1.0 individual (s.e. = 0.3) per 100 m³. There was not a significant higher average densities of flounder larvae at Als Odde than Havnø (randomized test of mean difference, P = 0.21).

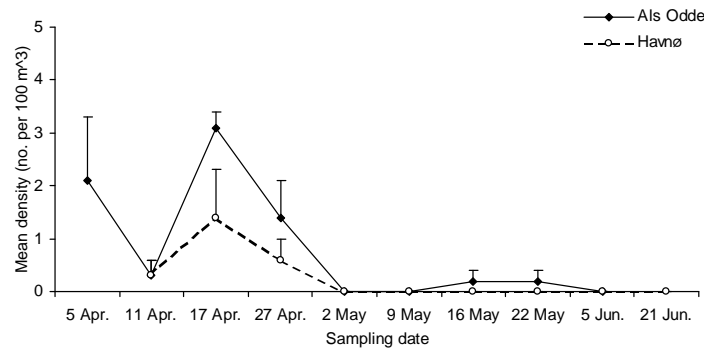


Fig. 2: Larval densities of flounder (mean ± s.e.) at the two sampling stations. The pattern of vertical distribution of larvae varied within tidal cycles

Larvae were found in all samples of the surface layer during flood tides, and densities tended to be higher than

in mid-water and near bottom layers. The opposite pattern was found during ebb tides (Fig. 3).

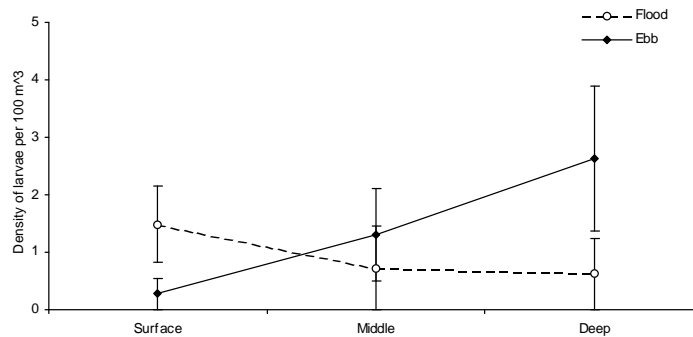


Fig. 3: Vertical distribution of flounder larvae at Als Odde between flood and ebb tides. Error bar shows standard error

2. Ontogenetic stages of larvae

No flounder larvae at ontogenetic stage I and II were caught during the sampling (Table 1). The least developed ontogenetic stage found in the samples at two stations of the fjord was III. Most of larvae caught at both stations were stage III, and only 13.3 % (n = 4) of the larvae staged (n = 30) were found in stage IV and V during the sampling period. About 13.6 % (n = 3) of the larvae caught at Als Odde (n = 22) were stage IV and V, whereas about 62 % (n = 5) of the larvae caught at Havnø (n = 8) were stage IV or close to stage V. So most of flounder larvae

caught in the fjord were in the process of metamorphosis, and high percentage of the metamorphosis stages IVa, IVb and V were found in the samples.

The total length of the larvae caught in the samples at two stations ranged from 5.6 to 9.3 mm. About 40.9 % (n = 9) of the larvae caught at Als Odde were in the group of 8.0 – 9.9 mm long, and 37.5 % (n = 3) at Havnø (Fig. 4). About 40 % (n = 12) of the total larvae caught in all samples were at 8.0 – 9.9 mm in length. There was no significant differences in the average total length of the larvae between the two stations (t-test, $t=0.605$, $P > 0.05$).

Table 1: Percentage of flounder larvae caught at Als Odde and Havnø for each ontogenetic stage and sampling date (only sampling dates when flounder larvae were found in the samples)

		Als Odde					Havnø			
		5 Apr.	11 Apr.	17 Apr.	27 Apr.	16 May	22 May	11 Apr.	17 Apr.	27 Apr.
Larval stage	I	*	-	-	-	-	-	-	-	-
	II	*	-	-	-	-	-	-	-	
	IIIa+b	*	100	71.4	33.3	100	100	100	66.7	-
	IIIc	*	-	28.6	41.7	-	-	-	-	-
	IVa	*	-	-	8.3	-	-	-	33.3	50
	IVb	*	-	-	8.3	-	-	-	-	50
	V	*	-	-	8.3	-	-	-	-	-

* Larvae were degraded

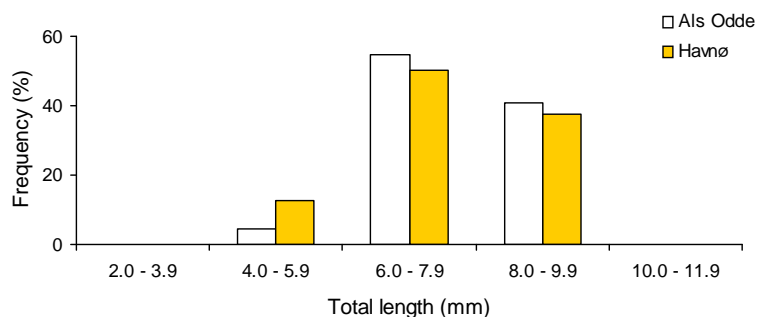


Fig. 4: Frequency distribution of total length of flounder larvae at Als Odde (n = 22) and Havnø (n = 8)

3. Ageing of larvae

Increments on otoliths with a diameter less than 40 μm were difficult to count, and it was easier to read increments of otoliths with a larger diameter. Increment on otoliths was most clearly seen under light microscope at 1000 times magnification (Fig. 5).

All flounder larvae caught were older than 15 days (Fig. 6). Increment counts at Havnø on 17 and 27 of April were significant higher than at Als Odde (Kruskal-Wallis test, $P = 0.014$ and $P = 0.003$ respectively). This

indicates that larvae at the upstream station were older than at the entrance of the fjord.

4. Estimation of transport time

Mean increment counts in the samples of 17 and 27 April at the entrance station were less than that at upstream station about 4 to 3.5 days (Table 2). So, the transport time needed by larvae for upstream migration over a distance of 9 km from Als Odde to Havnø was estimated to about 3.5 - 4 days, and approximately covering the time for 8 flood tides.

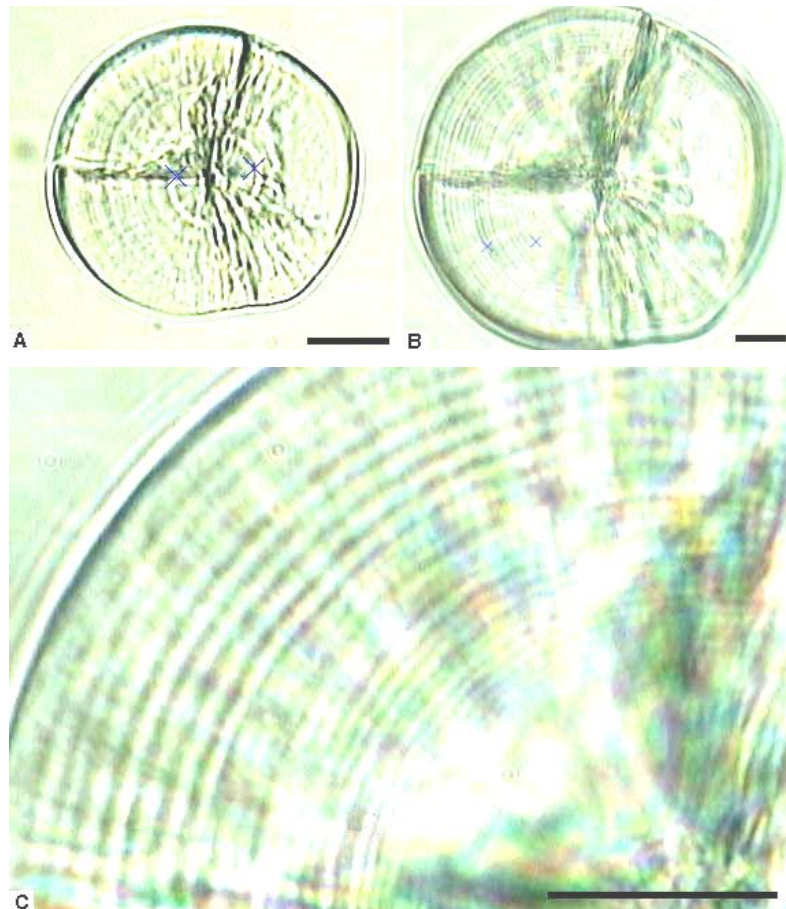


Fig. 5: Sagitta ($\varnothing 72.6 \mu\text{m}$) of a flounder larva with 34 increments and a total length of 9.2 mm at three different magnifications (A: 200x; B: 400x and C: 1000x). Scale bars = 10 μm

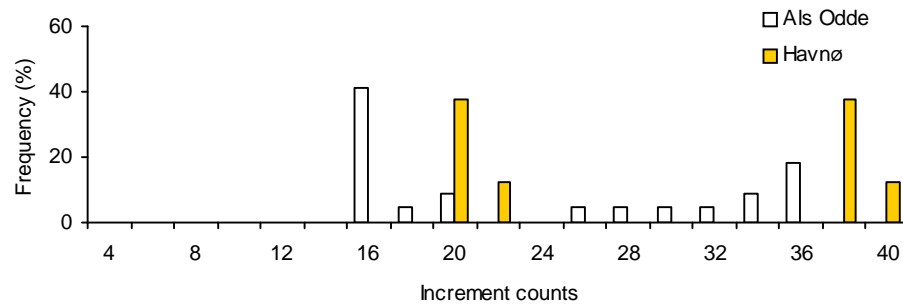


Fig. 6: Frequency distribution of increment counts of flounder larvae at Als Odde (n = 22) and Havnø (n = 8)

Table 2: Number of flounder larvae studied, median sagittal diameter (μm) and median counts of daily growth increments at two sampling stations

	Als Odde						Havnø		
	5 Apr.	11 Apr.	17 Apr.	27 Apr.	16 May	22 May	11 Apr.	17 Apr.	27 Apr.
	1	1	6	12	1	1	1	3	4
Sagittal diameter(μm)	35.7	31.4	35.8	61.4	60.2	48.5	33.7	42.4	74.8
Increment counts	17.0	16.0	16.0	34.5	26.0	27.0	16.0	20.0	38.0

5. Hatch check analysis

Flounder larvae that migrated into and settled on the tidal flat in front of the entrance to the fjord were primarily hatched from middle of March until late of April, with a maximum peak of hatching from 20 of March to 5 of April and small peak from 10 to 25 of April (Fig. 7A & 7B). The patterns of frequency distribution of increment counts between flounder larvae and juveniles were more or less similar and there might be two different cohorts of flounder larvae arriving at the fjord. This means that larvae caught in the April and May samples may have survived and contributed to the population of early

juvenile flounders.

Distribution of increment counts of flounder larvae on 17 and 27 of April showed that there were two different cohorts of flounder larvae represented in the samples (Fig. 8). The first cohort was about 16 increment counts on 17 of April and they were still present in the samples of 27 April with about 34 increment counts. The second cohort was present in the samples of 27 April with about 18 increment counts. Length distribution of wild juveniles flounder caught at the entrance of the fjord also showed the same pattern, average total length of the first cohort was about 41 mm and the second cohort was about 25 mm (Fig. 9).

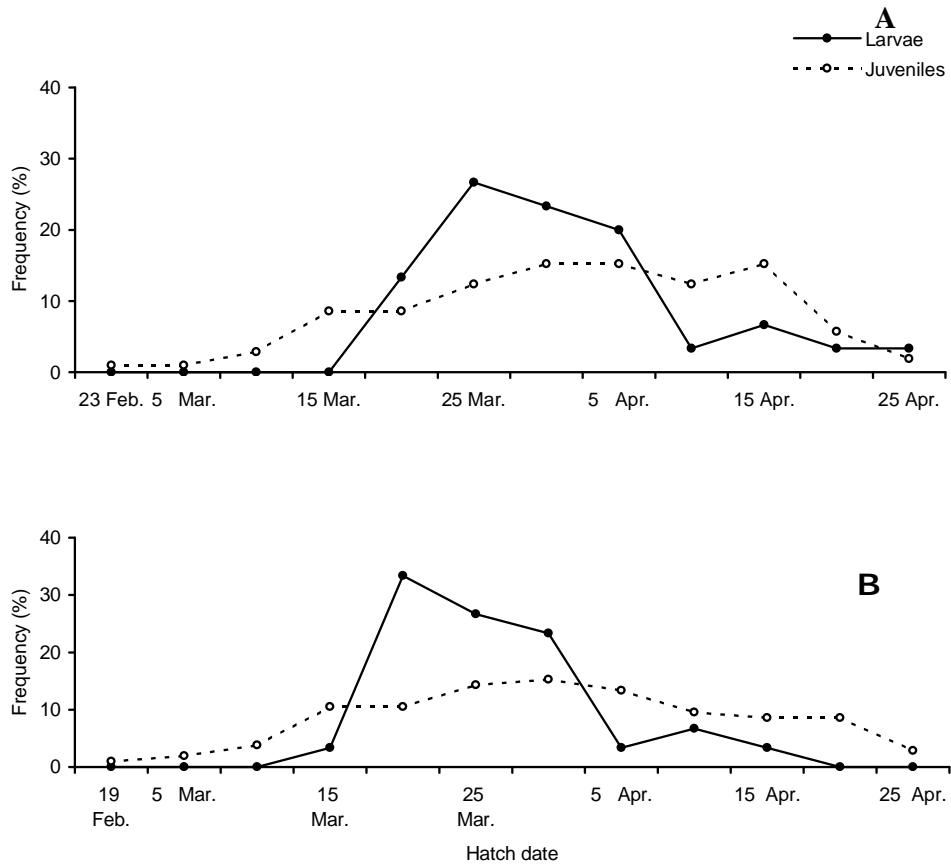


Fig. 7: Temporal distribution of hatching for flounder larvae (n=30) and juvenile (n=105).
 A: uncorrected; B: corrected by the equation:
 $\text{Age of fish} = 1.027 \cdot \text{Increment} + 1.628$

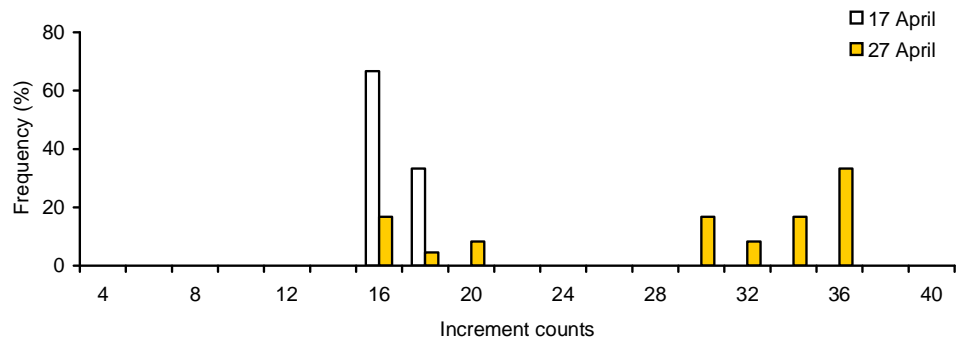


Fig. 8: Increment count distribution of flounder larvae at Als Odde on 17 April (n = 6) and 27 April (n = 12)

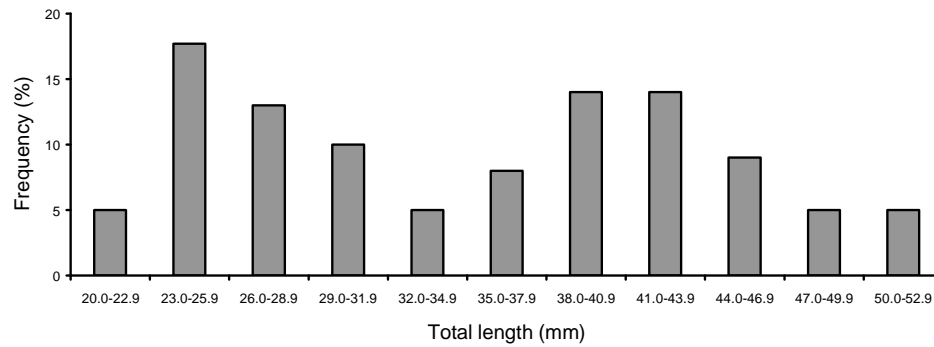


Fig. 9: Length distribution of wild juvenile flounders on 19 and 27 of June 2000 (n = 105)

IV. DISCUSSIONS

1. Abundance of larvae

The mean larval densities observed in this study (1.0 individuals per 100 m³) indicated that a low amount of flounder larvae was present in the water column of Mariager Fjord and this value was considerably lower than those observed in the western Wadden Sea (3.7 individuals per 100 m³; Van der Veer et al., 1991), or in the Elbe River (55 individuals per 100 m³; Möller & Dieckwisch 1991). This may be considered as an indication that Mariager Fjord is not a suitable area for the settlement of flounder larvae. All samples were taken during the daytime, and so flounder larvae with a larger size could possibly avoid the net, and this could contribute to reduce the mean densities of larvae in the water column. However, towing speed was quite fast compared to swimming speed of larvae, and some sticklebacks and pipefish with a size longer than 2 cm were caught in the samples. So avoidance of flounder larvae from the net was not likely.

Mean density of larvae at the entrance (Als Odde) of the fjord was

higher than at upstream (Havnþ) indicating that only a few of the flounder larvae were transported into the fjord and that the larvae were mostly retained at the entrance of the fjord where they settled. A high percentage of flounder larvae at stages IV, V (close to metamorphosis; Ryland 1966) and at a total length of 8.0 – 9.9 mm (size to settlement; Muus 1967) was found in the samples at the entrance, and the higher mean density of post-metamorphosed flounder larvae collected by a drop-trap (1 m²) on the tidal flat at the entrance compared to inside of the fjord during May and June 2000 (Carl, pers. comm.) supported the idea mentioned above.

The periodic appearance of flounder larvae in the fjord may be influenced by wind or predation. Flounder larvae were only found in April and on 16 and 22 of May. This suggests that the appearance of flounder larvae in the water column of the fjord may be related to wind speed during that time. Strong wind pushes up the water from the Kattegat into the fjord and flounder larvae may be transported together with these water masses because the immigration of

larval flatfish in the areas with small mean tidal amplitude depends on passive transport by wind stress and residual currents (Pihl 1990). It seemed to me that wind speed in April was much stronger than that in May and June, and that coincided with high density of flounder larvae in the April samples. Unfortunately, I did not have wind data during this sampling period in order to see how well these two parameters were related. On the other hand, the disappearance of flounder larvae in the water column of the fjord may be related to the outburst of predation. Van der Veer (1985) found that the immigration of both plaice and flounder larvae was abruptly terminated by the outburst of predatory coelenterates such as the ctenophore *Pleurobrachia pileus* and the scyphomedusa *Aurelia aurita*. During the beginning until middle late of May 2000, I found plenty of big medusa with a diameter of about 3 to 20 cm in the samples. This could be an explanation for the termination of flounder larvae in the May and June samples of the fjord.

Densities of early juvenile flounders from a drop trap sampling in front of the entrance of the fjord in May and July 2000 were much higher than that at Als Odde and Havnø (Carl, pers. comm.). This, together with a few larvae occurring in the water column of the fjord, leads me to another hypothesis that flounder larvae are transported from the Kattegat into a large tidal flat in front of the entrance of the fjord where they complete metamorphosis and settlement. The tidal flats outside the fjord may be a suitable settling habitat for the metamorphosed larvae, and flounder larvae mostly settle here on the tidal

flats and only a small amount of these are transported into the fjord by wind and tidal currents. After their settlement on the tidal flats, a part of post-metamorphosed flounder larvae migrate into the fjord. The difference between the areas of initial settling of plaice and their appearance in the demersal samples in the Wadden Sea (Van der Veer et al. 1991) supports this hypothesis.

2. Vertical distribution of larvae

Flounder larvae utilised tidal currents for their upstream transport in Mariager Fjord. Flounder larvae were found at higher densities in the surface layer during flood than ebb tide, and higher densities of larvae were found at deeper layer during ebb than flood tide. This indicated that flounder larvae were able to detect differences between ebb and flood tide by ascending from the bottom to the surface layer during flood and descending close to the bottom during ebb tides. However, significant differences of larval densities at three different depths between flood and ebb tides were not clearly confirmed because very few flounder larvae were found in the samples at a certain depth during flood or ebb tide. Therefore, it was difficult to test the difference in density of flounder larvae in different water layers between flood and ebb tides. So flounder larvae might take an advantage of the strong currents in the surface layer during the flood tides in order to travel from this place to others and in order to avoid the currents on the surface pushing them back during ebb tides they descended to the bottom (Campos et al. 1994; Bos et al. 1995; Grioche et al. 1997; Jager 1999). The small sample size and the limited

sampling time could influence on the result. Flounder larvae were very rare in the water column, so sampling time should be longer in order to catch more larvae. The migration of flounder larvae between tidal cycles and between places may be caused by the changes of the abiotic environmental factors such as temperature and salinity.

Tidal changes in these abiotic characteristics may control larval migration by influencing the behaviour of larvae (Gibson 1997, Jager 1998). Higher salinity on the surface during flood than ebb tide may have caused a high density of larvae on the surface layer. However, the difference in salinity between surface and deep layers in the fjord is about 1 – 2 ppt (Fenchel et al. 1995), so it is not the main factor influencing the migration of larvae. Flounder larvae are negatively buoyant in both fresh and salt water (Jager & Mulder 1999), and without swimming the highest concentrations would be expected near the bottom during tidal phases. On the other hand, the migration of flounder larvae between tidal cycle could be governed by the difference of food concentrations in different water layers. High food concentrations in the surface layer during flood and in the deep layer during ebb tides could attract flounder larvae swimming up and down.

In this study flounder larvae were found to be transported from the entrance (Als Odde) to upstream station (Havnø) of the fjord and that might be caused by the change of salinity. Measurements from April to August 2000 showed that salinity at the entrance was much higher (about 10 ppt) than further upstream of the

fjord (Carl, pers. comm.). On the other hand, the migration of flounder larvae in the fjord may be related to other factors such as food availability and settlement habitats. Burke (1995) found that prey gradients influenced the segregation of southern flounder (*Paralichthys lethostigma*) and summer flounder (*Paralichthys dentatus*), which share habitats during larval stages. He suggested that the abundance of mysids upstream of nursery areas may attract the southern flounder, whereas the abundance of polychaetes in saltmarsh habitats in the lower estuary may attract the summer flounder. Köpcke and Kausch (1996) found higher densities of copepod *Eurytemora affinis*, which is the main prey of flounder larvae, in the tidal Elbe than outside. In conclusion, despite the lack of proper statistical testing the differences in larval concentrations between flood and ebb tides reject the hypothesis that flounder larvae are homogeneously distributed in the water column during tidal cycles.

3. Origin of flounder larvae

No larvae at the early stage I and II, and no larvae younger than 16 days old were caught during the three months sampling. It was not due to the fact that mesh size of the net was too large to catch the larvae at stage I and II as early stages of flounder larvae were caught with a 300 µm mesh net in the North Sea (Campos et al. 1994). The explanation could be that sampling was started too late compared to the hatching period. Hatch date analysis showed that flounder larvae hatched in a long period from 15 of March to 25 of April. Sampling was started on 5 April and if it was late compared to the first hatching period, then I could be able to

catch the larvae of early stage I and II from the second hatching peak. However, the flounder larvae at stage I and II, and less than 16 days old were not found in the samples on all sampling dates. On the other hand, flounder larvae were not found in the inner part of the fjord from March to June 2000 (Sprensen, pers. comm.). The result from increment counts of flounder larvae showed that larvae at the entrance were younger than further upstream. Both results, early ontogenetic stages and increment counts of larvae, supported the idea that flounder larvae in Mariager Fjord must come from the Kattegat and did not hatch in the fjord.

There were two different cohorts of flounder larvae represented in the samples, indicating that the arrival of flounder larvae in Mariager Fjord might originate from spawnings at different time or from different spawning areas. Muus (1967) found that there are two different spawning areas (Kattegat and Belt Sea) of flounder in the Kattegat. However, the distribution of increment counts in Fig. 9 did not fit the two different cohorts of larvae on 17 and 27 of April. Mean increment counts of larvae caught on 17 of April was 16 and if these larvae still remained in the water column until 27 of April, then they should only reach about 27 increment counts. However the result showed 34 increments for the first cohort on 27 of April. Again, a small number of flounder larvae caught in each date could influence the result. If sampling size was big enough, then some older larvae should be observed in the samples from 17 April or younger larvae in the samples of 27 April.

In conclusion, the hypothesis that flounder larvae originate from spawning in Mariager Fjord was rejected, in other words, flounder larvae in the fjord must be transported in from the Kattegat.

4. Transport time of larvae

The transport time needed by flounder larvae transported over a distance of about 9 km from the entrance (Als Odde) to upstream (Havnø) of the fjord was about 3.5 – 4 days, and this was approximately the duration of 8 flood tides. Theoretically, larvae could be able to travel a distance of about 7 – 10 km per flood tide at the water current speed of 0.5 m/s. However, slow transport of larvae in Mariager Fjord could be explained by the unstabilization of tidal level between tidal cycles during sampling period. Low tidal range between high and low tide, low current speed (about 0.2 cm/s) and maximum currents taken place shortly during flood tides (only 2.5 – 1 hours before high water slack) contributed to reduce the transport speed of flounder larvae in the fjord. Furthermore, ebb tides may push larvae back even though they sink down to the bottom during this tidal phase.

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