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Modelling of larval dispersal of Baltic flounder (*Platichthys solemdali*) revealed drifting depth as a major factor determining opportunities for local retention vs large-scale connectivity

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Abstract

For flatfishes, transportation of larvae to nursery areas is regarded a key mechanism for recruitment, with adaptations in larval behaviour to reach a suitable habitat. Here we model different possibilities of larval drifting of coastal spawning Baltic flounder *Platichthys solemdali* (recently identified as a species from European flounder *P. flesus*) to reveal opportunities for local retention vs large-scale dispersal to ensure settling in coastal nursery areas. Drifting depth, duration of drifting and effects of year and time during season were modelled using 1) a high-resolution local dispersal model, and 2) a large-scale connectivity database. The outcome revealed drifting depth as a major factor affecting larval dispersal. Drift at 10-22 m depth involved retention along the coast with the majority of larvae ($\geq 94\%$ or 69-93% according to 1 and 2, respectively) with end points ≤ 20 km from the coast enabling further successful migration to nursery habitats. Contrary, larval drift close to the surface resulted in advection with end points in the open sea (72-76%), i.e. loss of larvae, but with a small fraction (5-12%) displaying cross-basin connectivity. The results suggest, in agreement with depth distribution of spawning, a larval behaviour promoting drift in the lower part of the water mass, favouring retention close to coastal nursery areas. Obtained dispersal patterns may sustain both local recruitment but also connectivity with other areas, potentially explaining the low genetic diversity between areas for *P. solemdali*. Low inter-annual variability in dispersal patterns when drifting at 10-22 m depth suggests that larval drift is not a major bottleneck explaining recruitment variability in *P. solemdali* in the area. The study highlights the differences in life-history strategies of the species pair of flounder in the Baltic Sea; *P. flesus* spawning in the deep basins with extensive larval dispersal, and coastal spawning *P. solemdali* with, according to the model outcome, mainly local larval dispersal for sustaining a viable population, i.e. request for different management strategies.

Key words

Hydrodynamic modelling, vertical distribution, larval dispersal, larval retention, population specific behaviour

1. Introduction

Flatfishes display a complex life cycle including an ontogenetic metamorphosis as the larvae develop from bi-laterally symmetry to asymmetry, and shift from a pelagic to a demersal habitat. This shift normally occurs at the time when the larvae reaches coastal areas and settle in nursery areas with often specific habitat characteristics, e.g. depth, type of substrate and range in temperature and salinity, which favours growth and survival during the post-larval stage (see Able et al., 2005). Depending on habitat preferences of the species, nursery areas vary in size and distribution, and variability in the larval supply to nursery areas may govern the abundance of later stages and thus influence recruitment to the adult stock (Connell, 1985; Milicich et al., 1992). Thus, transportation of larvae to suitable nursery habitats is regarded a key mechanism for inter-annual variability in recruitment, in particular for flatfishes with specific nursery area preferences (van der Veer et al., 1998; Bailey et al., 2005). For example, modelling of egg and larval drift in North Sea plaice (*Pleuronectes platessa*) showed that the inter-annual variability in the distance of larval drift was correlated with the observed variation in the year class strength (Bolle et al., 2009), and similarly, Lacroix et al. (2013) showed that year-to-year variability in larval supply to nurseries varied with inter-annual variation in transportation pattern in sole (*Solea solea*) in the North Sea.

In general, flatfishes spawn with pelagic eggs at depths deeper than their nursery areas, and have, depending on connectivity between spawning- and nursery areas, adopted different strategies for larvae being transported to a suitable habitat for settlement. Offshore spawners may take advantage of currents for inshore transportation of eggs/larvae whereas species spawning more inshore may utilize retention features to maintain eggs/larvae in the area (see Bailey et al., 2005). Also, flatfish larvae may increase the probability to end up in a suitable nursery area by adjusting their vertical distribution. Modelling studies suggest that vertical migration may result in a significant departure from passive drifting (see Bailey et al., 2005; Leis, 2007; Sentchev and Korotenko, 2007) and several studies indicate both inter- and intra-specific adaptation in larval behaviour to local conditions to favour retention within, or drift into, an area to optimize settlement in a suitable nursery habitat (see Burke et al., 1998; Fox et al., 2006; Teodosio et al., 2016). However, some flatfish species produce demersal eggs and spawn in coastal areas at ≤ 20 m depth (see Bailey et al., 2005), a strategy that may

1 be an adaptation to maintain their propagules in proximity to suitable nursery areas (Pearcy,
2 1962).

3 In the brackish water Baltic Sea (Fig. 1), flounders (*Platichthys* spp) are the most abundant
4 flatfish and important target species in the fishery. Here, two genetically distinct ecotypes
5 (Hemmer-Hansen et al., 2007; Florin and Höglund 2008), recently identified as a species pair
6 (Momigliano et al., 2017; 2018a), with different spawning strategies exist; European
7 flounder (*P. flesus*; Linnaeus, 1758) spawning pelagic eggs in offshore deep basins below the
8 permanent halocline at 10-20 psu, and Baltic flounder (*P. solemdali*; Momigliano et al.,
9 2018a) spawning demersal eggs in coastal areas and on offshore banks at 6-9 psu (Nissling et
10 al., 2002; 2015; Ustups et al., 2013). These two flounder species are considered originating
11 from different colonization events to the Baltic Sea from the same ancestral population
12 (~8000 and 6500-5000 years BP, respectively; Momigliano et al., 2017). European flounder
13 occur mainly in ICES area 3.c. 22 to 3.d. 26 and 3.d. 28-2, but temporally also in the northern
14 Baltic Sea (3.d. 29 and 3.d. 32). Baltic flounder on the other hand is distributed in almost the
15 entire Baltic Sea except for in the northern Gulf of Bothnia (3.d. 31) and easternmost Gulf of
16 Finland (3.d. 32), with the highest abundancies in 3.d. 25-30 and 3.d. 32 (Fig. 1; Bagge, 1981;
17 Momigliano et al., 2018b; Florin et al., in prep). The species pair share feeding areas in
18 coastal waters during summer-autumn but utilize different spawning habitats in spring (Aro,
19 1989; Nissling et al., 2002), and further, share the same nursery areas, mainly shallow sandy
20 bays (e.g. Florin et al., 2009; Martinsson and Nissling, 2011). The respective spawning
21 strategy request for different strategies concerning settlement in suitable nursery habitats
22 along the coast; retention of larvae within the area of spawning or inshore transportation of
23 larvae originating from spawning in offshore deep basins, respectively.

24 Concerning factors influencing variability in recruitment of flounders (*Platichthys* spp) in the
25 Baltic Sea, several studies have focused on either factors affecting survival during the egg
26 stage (Nissling et al., 2002; 2017; Ustups et al., 2013; Petereit et al., 2014; Hinrichsen et al.,
27 2017) or during the juvenile stage post settlement in nursery areas (Aarnio et al., 1996;
28 Nissling et al., 2007; Jokinen et al., 2016; Ustups et al., 2016). Less attention has been
29 directed to the larval stage prior to settling, including transportation/drift from spawning
30 areas to suitable nursey areas. Recently however, survival and dispersal of flounder larvae of
31 the deep basin spawning species (European flounder) in the Central and Eastern Baltic Sea

(3.d. 24-26 and 28) was studied using biophysical modelling (Hinrichsen et al., 2018), and Petereit et al. (2014) studied drift of early European flounder larvae in the Western Baltic Sea (3.c. 22 and 3.b. 23), i.e. in the transition zone between the Kattegat (3.a. 21) and the Baltic Sea. To date larval drift patterns of the coastal spawning species, Baltic flounder (*P. solemdali*), have been considered in only one study, focusing mainly on larval export from a no-take zone area in the northern 3.d. 28-2 (Florin et al., 2013). Thus, lack of studies focusing on larval dispersal of Baltic flounder represents a gap in knowledge of flounder ecology in the Baltic Sea, a mechanism potentially influencing recruitment to the adult stock and explaining diversity in stock structure. Larval drift patterns of European flounder spawning in the offshore Baltic deep basins (in 3.d. 25-26 and SD 28) involved widespread dispersal, with settling from 3d. 29 in the northeast to 3.c. 22 in the southwest and including the Kattegat (3.a. 21; Hinrichsen et al., 2018; Fig. 1). In contrast, larval dispersal of Baltic flounder spawning in coastal areas can be expected to be limited due to the close proximity between spawning- and nursery areas, i.e. to display retention within the area (cf Pearcy, 1962). However, Baltic flounder, displays low genetic differentiation across different coastal areas (Florin and Höglund, 2008) suggesting connectivity between areas, potentially as a result of larval drift.

In the present study we use hydrodynamic modelling to explore the importance of different drifting possibilities of Baltic flounder larvae to ensure a high enough settling success in nursery areas, and thus sustain a viable population. As empirical data of larval drift characteristics of this newly identified species are lacking, we examine dispersal patterns in relation to different drifting depth, including a comparison of drift with free dispersal, under the assumption that larvae may adapt their behaviour to local conditions in optimizing probabilities for settlement in a suitable nursery area. The selected drifting depths (0 m/surface, 10 m and 22 m) are in agreement with what is known about the vertical distribution of European flounder larvae during the pelagic stage in both the Baltic Sea and the Kattegat-Skagerrak area (Moksnes et al., 2014; Hinrichsen et al., 2018); occurring at ca 0-30 m depth with the highest abundance at ca 0-20 m depth. This depth range is in accordance with what is known about the depth range of spawning of Baltic flounder; at ca 3-20 m depth (Bonsdorff and Norkko, 1994; Nissling et al., 2014), i.e. depths where hatching will occur and larval dispersal expect to start (see below). Additionally, potentially effects of

duration of drifting, i.e. the larval pelagic stage up to metamorphosis, as well as timing of spawning were considered. Two model exercises were carried out, using a high resolution local dispersal model and a large-scale connectivity database involving connectivity within the entire Baltic Sea, with the overall aim to evaluate the potential for local larval retention within the area to sustain the local spawning population vs extensive larval dispersal to other areas.

2. Material and methods

2.1 Study area

Both European flounder and Baltic flounder occur off Gotland (3.d. 28-2; Fig. 1), but the stock is at present dominated by Baltic flounder, ca 74% according to monitor fishing at site 2 (Florin et al., in prep). Spawning of Baltic flounder occur from April to June along most of the coast at ca 3-20 m depth (see Supplementary information; Nissling et al., 2014) at ca 7 psu. The eggs are demersal, with a specific gravity of in average $1.0160 \pm 0.0008 \text{ g cm}^{-3}$ (mean $\pm$ sd; Solemdal, 1971; 1973; Nissling et al., 2017) compared to ca 1.0056 g cm^{-3} of the water (at ca 7 psu and 4°C). Although eggs eventually may be stirred up during e.g. storm events, they will soon sink again; sinking rate $> 0.26 \text{ m minute}^{-1}$ according to measurements on cod (*Gadus morhua*) eggs (Nissling et al., 1994). Thus, the eggs can be expected to remain close to the site of spawning until hatching. Flounders (*Platichthys spp*) in the Baltic Sea have been shown to prefer sandy shallow areas ($< 1 \text{ m}$ depth) as nurseries (Aarnio et al., 1996; Florin et al., 2009; Martinsson and Nissling, 2011) but utilize, in the studied area (Gotland, 3.d. 28-2) frequently also other types of shallow habitats after settling; such as bedrock, gravel and soft sand (Martinsson, 2011). Studies in two nursery areas in proximity to site 1 showed that 80% and 85% respectively of newly settled individuals were Baltic flounder (Florin et al., in prep), and further, that the variability in larval supply is high. Recruitment indices assessed as the abundance of newly settled individuals during the period from early July to early September varied with a factor 5-10 during a nine-year period (Nissling and Wallin, in prep). Readings of daily increments in otoliths of newly settled individuals ($n=25$), suggested a drifting period from hatching to larval settling of in average 56 ± 13 days (mean $\pm$ sd; Martinsson and Nissling, unpublished). Although much is still

unknown about larval characteristics of Baltic flounder, the area represent a suitable area for studying larval dispersal patterns of this newly identified flounder species.

Sites of particle (representing virtual larvae) releases were chosen to cover the east coast of Gotland and to represent different topographic features of the coast as this potentially may influence the circulation pattern. At site 1 (Valleviken) the coast is heterogenic and the coastline convex, site 2 (Herrvik) is located off a headland and site 3 (Sudret) in a concave bay (Fig. 1).

2.2 Larval characteristic features

In accordance with the assumption that flatfish larvae may adapt their vertical positions to enhance probabilities for settlement in a suitable nursery habitat (see Bailey et al., 2005; Leis, 2007; Sentchev and Korotenko, 2007), effects of different larval drifting depths (surface, 10 m and 22 m) on the larval dispersal pattern was considered. Chosen drifting depths are in agreement with the vertical distribution of European flounder (*P. flesus*) larvae, derived from sampling in the Bornholm Basin (SD 25), Baltic Sea using a multi opening-closing net (Hydrobios, Germany) with sampling at 5 m layer intervals from the surface to the bottom, showing that larvae are distributed in the upper 30 m with the majority occurring at 0-20 m depth (Hinrichsen et al., 2018). These depths are in agreement with what is known about the depth range of spawning of Baltic flounder in the area; ca 3-20 m (Supplementary information), i.e. where hatching will take place and larval dispersal can be expect to start. In the Baltic Sea, larvae of European flounder migrate vertically from hatching in the deep layers below the permanent halocline (10-20 psu) to the surface layer (0-20 m depth) with a salinity of ca 7 psu (see Hinrichsen et al., 2016; 2018). Similarly, larvae of Baltic flounder, with the same size as European flounder at hatching (Wallin and Nissling, unpublished), and occurring at ca 7 psu, can be expected to be able to adjust their vertical position. Further, according to data presented in Hinrichsen et al. (2018) no clear differences in larval vertical distribution during night compared to during daytime exists and has not been considered in the model. Thus, the chosen drifting depths correspond to fixed depths, in agreement with depths in the large-scale connectivity database (see below). In addition, free dispersal, i.e. fully passive particle transportation with neutral buoyancy was considered in the experiment

using the local hydrodynamic model domain. For the particles at specified drifting depths the density was not relevant as there was no vertical movements.

Duration of particle drifting was based on data of the number of days from hatching to larval settling at metamorphosis (see Hinrichsen et al., 2018), derived from readings of daily increments in otoliths of newly settled flounder individuals ($n=25$;) from different cohorts sampled in nursery areas at Gotland (3.d. 28-2; site 1), i.e. Baltic flounder (see above); on average 56 ± 13 days (mean $\pm$ SD; Martinsson and Nissling, unpublished). Chosen days of drifting, 40, 50, 60 and 70 days, refer to the 10th and 90th percentile (44.2 and 70.4 days, respectively) and correspond to fixed times of drifting in the connectivity database.

The estimated maximum distance for a larvae to migrate from point of settlement to successfully being able to reach a nursery habitat was set to 20 km. This was based on data of larval length at settling (8 mm; Hutchinson and Hawkins, 2004) swimming speed in relation to body size (1 body length/s of a 10-20 mm larvae; see Bailey et al., 2005), size at arrival in nursery areas (15-20 mm; Martinsson and Nissling, 2011) and temperature dependent age-growth relationship as in Hutchinson and Hawkins (2004), with the addition of an assumed 50% reduction in distance due to non-directional movements as in Hinrichsen et al. (2018). To illustrate potential differences in end positions of particles/larvae depending on drifting depth, days of drifting or season, end positions in the local model are given for different zones according to distance from the coast, from ≤ 1 km to ≤ 20 km.

As opposed to in other areas where flounders (*Platichthys spp*) have been shown to prefer sandy shallow areas (<1 m depth) as nurseries, flounders in the studied area (Gotland, 3.d. 28-2) frequently also utilize other types of shallow habitats after settling (bedrock, gravel and soft sand; Martinsson, 2011). Thus, in the present study, habitat preferences were not considered in evaluating the probability to settle in a suitable nursery area, only the distance from the point of settling to the shore.

2.3 Start dates and positions of particle release

Spawning time of flounder in 3.d. 28-2 is known to occur from March to mid-June (based on spawning time of European flounder, *P. flesus*; Bagge, 1981), i.e. with hatching ca 1-3 weeks later depending on water temperature (see Hinrichsen et al., 2016). Baltic flounder (*P.*

solemdali) off Gotland, spawns in April-June, starting somewhat later and finishing spawning earlier compared to the European flounder (Nissling et al., 2014). Hence, in the experiments, 8 starting dates of particle releases were used, spanning from April 15th to June 13th. In the Result section starting dates of April 15-May 5 is referred to as early spawning and starting dates of May 24-June 13 to late spawning.

Spawning of Baltic flounder is known to occur off most of the east-coast of Gotland (3.d. 28-2; Fig. 1). In agreement with spawning areas of flatfish producing demersal eggs, occurring at <20 m depth (see Bailey et al., 2005), Baltic flounder have been found to spawn at ca ≤ 20 m depth with higher abundance of spawners at 10-20 m depth compared to at 3 m depth (monitoring fishing at site 2; Fig. 1; Table A1 Supplementary information). Thus, chosen positions of particle releases coincide with known spawning areas, including depth range, of Baltic flounder.

2.4 The local dispersal model

To describe the hydrodynamic conditions along the northeast coast of Gotland, site 1 Valleviken (Fig. 2), we used a high-resolution 3D-model reproducing the year 2014 (DHI, 2018). The domain spans from the northern end of island Fårö down to the easternmost peak of Gotland, about 70 x 40 km. The horizontal resolution was set to 200 m closest to the coast and the area of interest, thereafter the resolution becomes successively coarser out towards the open sea. Vertically the resolution was 0.5 m in the uppermost meter, 1 m-layers down to 25 m and then 2-m, 5-m and 10-m layers down to the maximum depth of about 100 m. The model was built with the hydrodynamical software MIKE 3 FM (DHI, 2017). It was forced at the surface with gridded meteorological data and at open borders with dynamic oceanographic data of temperature, salinity and current speed and direction from a larger, operative Baltic Sea model, the DHI Water Forecast. The model was validated with local observations of temperature and salinity for the modelled year (see DHI, 2018, for details).

Drifting Lagrangian particles representing virtual larvae were dispersed from five areas, about one square km each, along the coast with a depth between 10 and 20 m (Fig. 2). Based on the larval characteristics features described above we made four different model experiments; dispersal at 10 m, at 22 m, at surface and dispersal with free drifting in the

water column (see section 2.2 for approach). In this context, free drifting means that the modelled particles did not have any pre-destined drifting depth, but followed the flow field freely, while the particles with locked drifting depths resided at surface, 10 and 22 m or drifted 0.5 m above bottom when the over-all depth was less than the designated. No vertical swimming was modelled.

We released drifting particles representing larvae during the spawning season from mid-April to mid-June, with four start dates for surface- and free drifters and eight start dates for 10 m- and 22 m-drifters. We registered the positions of the particles after 40, 50, 60 and 70 days of dispersal and at each start we released 12 thousand particles from each of the five locations. We did not account for death, e.g. due to starvation or predation, but all particles were counted. In total, we simulated 1.74 million particles and we analysed 7 million positions in the experiment.

To compare the success of settling for the larvae between the different drifting possibilities we divided the area into zones based on the distance to the coastline; < 1 km to land, 1-3 km to land, 3-6 km to land, 6-12 km to land, 12-20 km to land and >20 km to land. We then sorted the end positions of the particles based on distance to land. The area closest to the hydrodynamic models borders out to open sea is excluded from the zones since the hydrodynamic conditions modelled there are not meant to be used for detailed analysis. We did no analysis of the difference between the five spawning sites, as they were pooled all through the calculations.

2.5 Large-scale connectivity database

To put the results from the local dispersal model into a larger context and investigate the fate of the larvae that left the local model domain, we used data from a connectivity database for the Baltic Sea region. The database consists of matrixes describing the connectivity due to passive dispersal of planktonic larvae during an eight-year period (1995-2002). The dispersal data was generated by using a Lagrangian biophysical particle-tracking model in flow fields generated with a 3D ocean circulation model.

BaltiX is a regional Baltic/North Sea configuration of the NEMO ocean model (Madec, 2010), with a horizontal resolution of 2 nautical miles (3.7 km), and a vertical resolution ranging

from 3 m at the surface and 22 m in the deepest parts. It is forced with tidal harmonics and SSH on the open boundary and with a dynamic downscaling of ERA 40 data set at the surface (see Hordoir et al., 2013, for details and validation). The particle-tracking model (TRACMASS; de Vries and Döös, 2001) calculated dispersal trajectories using interpolated velocity fields from the BaltiX model, updated every third hour, and the trajectories calculated with a 15-minute time step. The dispersal of drifting particles representing planktonic larvae, starting in every 3.7x3.7 km model grid cell where the depth is less than 100 m, was calculated, starting the 15:th of every month for eight consecutive years (1995-2002). The drifters in the different model experiments had fixed drifting depths at surface, 10 m, 22 m or 50 m, and drifted for 5, 10, 30 or 60 days. The choices of depths and larval duration were based on extensive field survey data for non-commercial, benthic species in the Baltic (Corell et al., 2012). The statistical probability of dispersal between the start points and the endpoints of the larval trajectories were stored in matrixes, and the data can be used for connectivity studies of any species in the Baltic Sea and Kattegat with some combination of the modelled behaviours. The database has been used in several connectivity studies, e.g. Moksnes et al. (2014), Rothäusler et al. (2015) and Larsson et al. (2017).

We used the database to investigate the dispersal from three spawning areas along the east coast of Gotland; the site 1 (Valleviken) area modelled in the local hydrodynamic model, and from two additional areas, site 2 (Herrvik) and site 3 (Sudret), along the east coast (Fig. 1). Each of the areas was represented by three 3.7 x 3.7 km model grid cell along the coast. We used matrixes describing the connectivity of larvae drifting at surface, 10 and 22 m for 60 days, with spawning in April, May and June. We extracted the dispersal pattern from the three areas and calculated the probability of the larvae to remain at the coast, disperse out to open sea or, for the surface drifters, travel cross-shelf. To remain at the coast was defined as staying within 20 km from the coast (within 5 model grid cells, 18.5 km), the estimated maximum distance for a larva to migrate to a nursery habitat after settling (Hinrichsen et al., 2018). The probability of staying within one grid cell (3.7 km) from the coast was given in addition. For 10 and 22 m drifters we also calculated the probability of the larvae to stay in the starting area or to drift southwards, eastwards or northwards along the coast of Gotland. All calculations were made both for all years and months separately and pooled together.

1 Since the horizontal resolution of the connectivity data base is about four times the size of
2 the start areas of the local connectivity model, 3.7 km compared to about 1 km, the results
3 are not fully comparable as some of the larvae will have started further out from the coast in
4 the large-scale model than in the local model.

6 **3. Results**

7 *3.1 Local larval dispersal*

8 The local hydrodynamic model revealed that particles drifting at the surface or freely in the
9 water mass drifted out of the model domain, whereas drifting at 10 and 22 m depth resulted
10 in end points within the domain, with the majority of drifters (91-92%) with end points less
11 than 1 km from the coastline. The time of the season or days of drifting had no major effect
12 on the dispersal pattern.

13 On average, 1.4% of the drifters had end points within the studied domain when allowed to
14 drift freely. Both the time during the season and the number of drifting days affected the
15 probability of retention in the area, but the share of drifters with end points within the
16 domain was low in all experiments, 0.2% for 70 days of drifting late in the season to 5.4% for
17 40 days early in the season (Table 1). For drifters locked to the surface, less than 0.1%
18 remained within the studied area irrespective of number of drifting days and time during the
19 season (Table 1). Contrary, drifting at 10 m depth resulted in on average 97.1% of drifters
20 with end points within the area with somewhat less particles remaining in the area early in
21 the season, 94.2%, compared to late in the season, 99.1%. Additionally, for drifting at 10 m
22 depth the experiment suggested a small effect of drifting-time, from 91.2% retention in the
23 domain when drifting 70 days to 97.1% at 40 days early in the season, but with no such
24 effect for drifting late in the season (Table 1). Drifting at 22 m depth yielded fully retention
25 within the studied domain irrespective of season or number of drifting days, >99% of
26 released particles (Table 1).

27 For particles drifting at 10 and 22 m depth, the clear majority ended up at a distance less
28 than 1 km from the shoreline (Fig. 3; Table 2). This was evident irrespective of days of
29 drifting or early or late in the season. Only a minor effect of the time spent drifting occurred;

drifting at 70 days at 10 m depth late in season resulted in 80.3% of particles with settling <1 km from the shore, and drifting at 70 days at 22 m depth in 84.6-87.3% of drifters with end points less than 1 km from the shoreline, compared to an overall average of 91.7%. Further, the experiment suggests that for drifters remaining in the studied area almost none settled >20 km from the shoreline when drifting at 10 or 22 m depth (Table 2).

The experiment suggests that most larvae display retention in the area with high probability to reach a nursery area along the coast, provided that they have the ability to stay drifting deep enough. Contrary, larval that drift in the upper part of the water mass, or are transported towards the surface, are dispersed away from the coast with low probability to remain in the spawning area or settle in proximity of a suitable habitat.

3.2 Large-scale larval dispersal

The outcome of the connectivity database revealed that most drifters had end points near the coast when drifting at 10 m and 22 m depth, with mainly a southward direction when not remaining in the release-area. Drift close to the surface on the other hand resulted to a large extent in advection from the area with end points in the open sea, but also along the Baltic coast in the eastern ICES 3.d. 28-2.

Drifting at 10 m depth resulted in end points mainly south of the release-areas (85-95% of the particles) with some remaining drifters in the start area (3-11%, Table A2 Supplementary information). Here, also drifting around the tip of Gotland and back up north again was considered “southward drifting”, and this happened at several occasions from all sites, but especially from site 2 and 3 (Fig. 4). Although southward drift was the dominating direction, occasions (years/time during the season) when most drifters remained in the release-area, or drifted towards the north, occurred (Table A2 Supplementary information).

When drifting deeper the dispersal directions are somewhat more evenly distributed. For the sites 1 and 2, drift at 22 m depth yielded end points in a southward direction (43-54% of the particles) or retention in the site (32-42%). Drifters released from site 3 at 22 m also mainly drifted southward (65% of the particles) but in addition also towards the east (32%), with only a minor fraction (3%) remaining in the start area (Table 3, supplementary

information). At this depth there is less transport around the south tip, and the over-all distances are shorter compared to drift at 10 m depth (Fig. 4). Further, the variability between occasions (years/time during the season) is still large, but the instances when all drifters go in just one direction are fewer than when drifting at 10 m depth (Table A3, supplementary information).

The majority of the drifters at 10 and 22 m remains within 20 km from the coast after 60 days of drifting, making it possible to reach a nursery habitat after settling; on average, the fraction varies between 69-83% when drifting at 10 m depth and between 88-93% when drifting at 22 m depth (Table 3). For both site 2 and 3 the chances of drifters having end points very close to the coast (within one grid cell, 3.7 km) are higher when drifting at 10 m than at 22 m depth, while for site 1 the chances are highest when drifting at 22 m depth. For site 1 and 2 the probability of remaining within 20 km from the coast, i.e. being able to successfully migrate to a nursery habitat, are about equal for drifting at 10 and 22 m depth (0.83-0.89%), while at site 3 the deeper drifting depth is, on average, more successful (0.93% vs 0.69%; Table 3).

The inter-annual variability of drifters with end-points ≤ 20 km from the coast (Table A4 Supplementary information) varied from 0.71 to 0.95% (mean $\pm$ sd 0.86 $\pm$ 0.08%) for site 1, from 0.77 to 0.90% (0.85 $\pm$ 0.05%) for site 2, and from 0.60 to 0.93% (0.81 $\pm$ 0.11%) for site 3, i.e. somewhat higher variability at site 3, when results of drifting at 10 and at 22 m were pooled. Almost all drifters had end points along the coast of Gotland. When drifting at 10 m depth a large share had connectivity with sites on the west coast of Gotland, and a few ones even reached within 20 km from the Swedish mainland and the island Öland, (western 3.d. 27; Fig. 4).

In contrast, surface drift involved extensive dispersal for most drifters (Fig. 5). Although a fraction, 17-18% for the respective site, of the drifters were retained along the coast, the majority were dispersed eastwards to south-eastwards to adjacent areas (3.d. 25, 26, eastern 3.d. 28-2 and 3.d. 29). On average 72-76% had end points in the open sea, whereas a small fraction, 5-12%, were transported cross-basin to the Baltic coast in the eastern 3.d. 28-2 (Table 4). On average, 24-28% of surface drifters had end-points ≤ 20 km from the coast, i.e. had the potential to reach a nursery habitat. However, the model yielded large

differences in dispersal pattern between years, e.g. retention along the coast was high in 1997, whereas almost no drifters remained along the coast in 1996, 2000 and 2001 (Table 5). Accordingly, cross-basin transportation to the eastern 3.d. 28-2 also varied among years, e.g. with a high fraction of drifters with end points along the coast in 1996, 1998 and 2000, but none in 1995 (Table 5).

The dispersal patterns obtained from the connectivity database coincide with the results of the local hydrodynamic model, i.e. larval drift at 10 m and 22 m depth result in mainly retention along the coast with high probability to reach a suitable nursery habitat. In contrast, drifting close to the surface involve to a large extent settlement far from the coast, i.e. loss of larvae, but also involve connectivity between spawning areas off Gotland and nursery areas along the Baltic coast. The model outcome suggests low variability in larval settling pattern between years when drifting at 10 m and 22 m depth, but highly variable and erratic larval dispersal if drift occur in the surface layer.

4. Discussion

The outcome of the experiments suggests that a majority of Baltic flounder (*P. solemdali*) larvae originating from spawning with demersal eggs off the coast of Gotland display retention in the area, with high probability to reach a suitable nursery habitat along the coast provided that they drift in deeper layers. In contrast, if larvae drift in the upper part of the water mass they are to a large extent dispersed away from the coast with considerably lower probability to settle in proximity of a suitable habitat, i.e. will be lost. However, results from the connectivity database indicate that larvae may drift to coastal areas along the Baltic coast in the eastern 3.d. 28-2, i.e. may be able to settle in a nursery area far away from the spawning site. According to the experiments, drifting depth is a major factor affecting the dispersal pattern of Baltic flounder, whereas duration of drifting and time of the season are of less importance for the dispersal pattern. The most pronounced decrease in dispersal occurred between particles locked to the surface and those drifting at 10 m depth with the highest retention for particles drifting at 22 m depth. The outcome indicated low inter-annual variability in larval settling along the coast, with a predominantly southward direction of dispersal, provided that drift occur at 10-22 m depth, but a highly significant effect of year

1 if larvae migrate/are transported to the surface layer. A small site-specific variability in drift
2 patterns was evident, e.g. at site 1 and 2 more larvae stayed within the spawning area
3 compared to site 3. This may be attributed to differences in bottom topography as well as
4 the shape/heterogeneity of the coastline influencing the pattern of currents. The results are
5 in agreement with those of Corell et al. (2012) where 80% of the total variation in dispersal
6 distance for invertebrate- and fish (*Gobiidae*) larvae in the Baltic Sea was explained by larval
7 depth distribution, together with duration of the pelagic larval stage. Moreover, the results
8 coincide with those in Florin et al. (2013) in which modelled Baltic flounder larval drift
9 patterns were averaged over two depth intervals, 0-2 m and 12-14 m, showing both larval
10 retention in the release area off the coast of Gotland (3.d. 28-2) and extensive dispersal to
11 offshore areas, i.e. in agreement with endpoints of drifters according to the respective
12 drifting-depth in our study.

13 Larval dispersal patterns are a complex feature including ocean circulation, duration of
14 planktonic stage and larval characteristics. E.g. for plaice, spawning areas may be located
15 close to nursery areas where currents are weak but located offshore in areas where
16 eggs/larvae may be transported onshore to nurseries by the current pattern (Gibson, 1999).
17 Further, several studies have shown that flatfish larvae are not dispersed fully passively, but
18 display species/population-specific vertical swimming behaviour in relation to local
19 circulation patterns affecting their dispersal/retention (e.g. Fox et al., 2006; Sentchev and
20 Korotenko, 2007; Leis, 2007). In agreement to this, an ability of the larvae to stay drifting in
21 the lower part of the water mass seem to be crucial for recruitment of the coastal spawning
22 Baltic flounder, i.e. for stock maintenance, as drifting in the upper part as well as free
23 dispersal to a large extent takes larvae far away from the coast and thus leads to loss of
24 recruits. As stated above, arrival to a suitable nursery area is probably not a random process;
25 flatfish larvae may optimize their probability to end up in a suitable habitat at settling in
26 coastal areas, i.e. adapt to local conditions to favour retention within, or transportation into,
27 an area depending on wind conditions and tidal currents (see Burke et al., 1998; Bailey et al.,
28 2005; Fox et al., 2006). In the North Sea with strong tidal currents, European flounder (*P.*
29 *flesus*) larvae have been found to occur in the water column during flood and in the bottom
30 layers during ebb to allow for shoreward drift and subsequent migration into favourable
31 nursery areas (Boss et al., 1995). In the Baltic Sea tidal currents are insignificant. Hence, in

the present study we focused on larval drift patterns when drifting at 0 m, 10 m or 22 m depth throughout development up to metamorphosis and settlement in accordance to what is known about vertical distribution of European flounder (*P. flesus*) in the area (Hinrichsen et al., 2018). Although empirical data of larval drift characteristics of Baltic flounder are lacking it can be expected that the larvae, similarly to larvae of European flounder (see above), is able to adjust their vertical position to favour settling in a suitable nursery habitat. Our results strongly indicate that a larval behaviour promoting drift in the lower part of the water mass favour retention along the coast with high probabilities for settlement in suitable nurseries. Further, larval drift at 10 m and 22 m depth (favouring retention of larvae in coastal areas), are in agreement with observations of depth distribution of Baltic flounder in spawning condition (stage 3; ICES, 2010). Monitor fishing off Gotland, at site 2, revealed higher abundancies of spawning Baltic flounder at 10 m and 20 m depth as compared to at 3 m depth (Nissling et al., 2014; Supplementary information), i.e. preferred depth range at spawning coincides with drifting depths that result in high probabilities for settlement in a suitable nursery area.

Thus, the two flounder species occurring in the Baltic Sea display different reproductive strategies. European flounder spawning in the deep basins below the halocline (occurring at 50-80 m depth) with larval migration to the upper part of the water mass involving extensive dispersal into coastal areas (see Hinrichsen et al., 2018), whereas Baltic flounder spawning in coastal areas allowing for mainly local dispersal along the coast (present study), respectively. Our results highlight the trade-off of the respective strategy in adapting to local environmental conditions, i.e. the production of demersal vs pelagic eggs to cope with brackish water conditions in the Baltic Sea. Compared to spawning with pelagic eggs in the Baltic deep basins at 10-20 psu (with adaptation of egg specific gravity to obtain neutral buoyancy; Nissling et al., 2017), spawning of Baltic flounder, *P. solemdali*, at low salinities (6-9 psu) in coastal areas involves demersal eggs and high egg mortality (Nissling et al., 2002). However, according to our results this strategy allows for high retention of larvae close to suitable nursery habitats (cf Pearcy, 1962), compared to extensive and erratic larval dispersal for European flounder (Hinrichsen et al., 2018). Further, according to the results from the model, larvae of Baltic flounder may potentially also drift to other coastal areas if transported/migrating into the upper part of the water mass. This may imply genetic

exchange between areas and thus contribute to the low genetic difference observed in Baltic flounder from different areas (Florin and Höglund, 2008).

According to the “supply side hypothesis”, stating that the number of flatfish-larvae that successfully settle in a nursery area is governing the abundance of later stages, recruitment is determined by variability in the larval supply (Connell, 1985; Milicich et al., 1992), potentially a result of inter-annual variability in larval drift pattern (Bolle et al., 2009).

Whether variability in drift patterns may influence the year-class strength of the flounder stock off Gotland (dominated by Baltic flounder; see above) is unknown, but recruitment indices (80-85% of sampled individuals determined to Baltic flounder; Florin et al., in prep) for two nursery areas in proximity to site 1 have varied with a factor 5-10 during a nine year monitoring period (Nissling and Wallin, in prep). Results from the large-scale connectivity database suggest low variability in larval settling along the coast between years for larval drift at 10-22 m depth; a factor 1.3 for site 1, and 1.2 and 1.5 for site 2 and 3, respectively. This indicates that variability in larval drift cannot explain the observed variability in larval supply to nurseries in the area, i.e. suggests that larval drift is not a major bottleneck in recruitment of *P. solemdali* off Gotland. Recruitment to the stock off Gotland may also be influenced by the reproductive success of the deep basin spawning European flounder (Ustups et al., 2013; Hinrichsen et al., 2016), including drift pattern variability (Hinrichsen et al., 2018), spawning in the Gotland deep basin, 3.d. 28-2 (Fig. 1). The variability in reproductive success of European flounder is high, depending on salinity and oxygen condition in connection to highly irregular saline water inflow events into the Baltic Sea (Nissling et al., 2002; 2017; Ustups et al., 2013) with poor survival up to the first feeding larval stage in the Gotland deep basin (3.d. 28-2) from the 1990s and onwards (Hinrichsen et al., 2016). Recent genetic analyses (Florin et al., in prep.) suggest currently mainly *P. solemdali* in the fishable stock off Gotland, ca 72% (fish ≥ 21 cm total length, i.e. minimum landing size, from site 2; Nissling, own data). Hence, at present the flounder stock off Gotland (western 3.d. 28-2) is built up mainly by *P. solemdali*. However, stock composition can be expected to vary depending on the reproductive success of European flounder, *P. flesus*, as shown for the flounder stock in the Gulf of Finland (3.d. 32). Here, European flounder dominated the stock in the early 1980s, were absent in 1993 and occurred in low proportions (10-11%) between 2003 and 2011 (Momigliano et al., 2018b).

The two flounder species share not only nursery areas but also feeding areas along the coast during summer-autumn as well as wintering areas in deeper waters, i.e. they are separated only during spawning in springtime (e.g. Nissling et al., 2015) representing a challenge in management of the flounder stock in the Baltic Sea. In the studied area, ICES 3.d. 28-2, both ecotypes are present (e.g. Nissling et al., 2002) although ICES currently treat the stock as being mainly European flounder, and thus pooled with the stock in 3.d. 26 to form a management unit (ICES, 2014). The findings in the present study, i.e. suggested strong connectivity between spawning areas along the coast and nursery areas, together with predominantly Baltic flounder in the stock off Gotland, suggests that recruitment to the fishable stock at present is mainly local. This, in turn, raises the question of a local management model, especially if the reproductive success of European flounder in the area will remain low as the findings in Hinrichsen et al. (2016) suggests.

4. Conclusions

The present study demonstrate the importance of vertical larval distribution for retention within, or dispersal from, an area. The results suggest, in agreement with depth distribution of spawning of Baltic flounder, larval drift in the lower part of the water mass for retention in the area with settling close to coastal nursery areas, whereas drift close to the surface involve dispersal away from the coast with loss of recruits but potentially settlement in other coastal areas. Obtained dispersal patterns may thus sustain both local recruitment but also connectivity with other areas, potentially explaining the low genetic diversity between areas for Baltic flounder. Hence, the results highlight the differences in life-history strategies of the species pair of flounder in the Baltic Sea; European flounder (*P. flesus*) spawning in the deep basins with larval migration to the upper part of the water mass and extensive larval dispersal (Hinrichsen et al., 2018), and Baltic flounder (*P. solemdali*), spawning in coastal areas allowing for mainly local larval dispersal along the coast (present study), i.e. request for different management strategies.

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Tables

Table 1 *The share of drifters with end positions within the model domain at various times of drifting, early (mid April-early May) or late (late May-mid June) in the season, when allowed to drift freely, drifting at the surface, and at 10 m and 22 m depth, respectively.*

Drifting days	Drifting with free dispersal		Drifting at surface		Drifting at 10 m		Drifting at 22 m	
	early	late	early	late	early	late	early	late
40	0.054	0.009	0.001	0.000	0.971	0.996	>0.999	~1
50	0.025	0.004	<0.001	0.000	0.950	0.996	>0.999	>0.999
60	0.010	0.002	<0.001	0.000	0.937	0.991	>0.999	>0.999
70	0.009	0.002	0.000	0.000	0.912	0.983	>0.999	0.997
Average	0.025	0.004	<0.001	0.000	0.942	0.991	>0.999	>0.999

Table 2 *The share of drifters with end positions in different zones according to distance (km) from the coastline, at various times of drifting, early (mid April-early May) or late (late May-mid June) in the season, when drifting at 10 and 22 m depth, respectively.*

Days/ km from land	Drifting depth 10 m											
	Early (mid April-early May)						Late (late May-mid June)					
	<1	1-3	3-6	6-12	12-20	>20	<1	1-3	3-6	6-12	12-20	>20
40	0.893	0.032	0.036	0.032	0.005	0.002	0.975	0.019	0.005	0.001	0.000	0.000
50	0.884	0.063	0.020	0.020	0.008	0.004	0.937	0.042	0.016	0.005	0.000	0.000
60	0.951	0.026	0.016	0.006	0.000	0.000	0.909	0.051	0.026	0.012	0.002	0.001
70	0.914	0.062	0.018	0.005	0.001	0.000	0.803	0.101	0.060	0.030	0.004	0.001
Tot	0.920	0.067	0.011	0.001	0.000	0.000	0.912	0.051	0.025	0.011	0.001	0.000

Days/ km from land	Drifting depth 22 m											
	Early (mid April-early May)						Late (late May-mid June)					
	<1	1-3	3-6	6-12	12-20	>20	<1	1-3	3-6	6-12	12-20	>20
40	0.948	0.046	0.005	0.001	0.000	0.000	0.951	0.040	0.007	0.001	0.000	0.000
50	0.921	0.074	0.005	0.001	0.000	0.000	0.939	0.044	0.015	0.002	0.000	0.000
60	0.917	0.072	0.010	0.001	0.000	0.000	0.923	0.063	0.012	0.002	0.000	0.000
70	0.873	0.107	0.018	0.001	0.000	0.000	0.846	0.130	0.020	0.001	0.002	0.001
Tot	0.917	0.073	0.009	0.001	0.000	0.000	0.918	0.066	0.013	0.001	0.001	0.000

Table 3 *The share of drifters ending up within 3.7 km or 20 km from the coast of Gotland (Fig. 1) or in the open sea after 60 days of dispersal, at 10 m and 22 m drifting depth.*

Site/ drifting depth	Stays along the coast of Gotland		Lost in open sea
	within 3.7 km	within 20 km	
1. Valleviken			
10 m	0.407	0.826	0.174
22 m	0.646	0.894	0.106
2. Herrvik			
10 m	0.516	0.829	0.171
22 m	0.301	0.879	0.121
3. Sudret			
10 m	0.398	0.687	0.313
22 m	0.321	0.929	0.071

Table 4 *The share of drifters with end positions along the coast of Gotland, reaching the east Baltic coast in eastern 3.d. 28-2 and ending up in open sea, after 60 days of drifting at the surface.*

Drift at surface Site	Stays along the coast of Gotland		Reaches cross-basin		Lost at open water
	within 3.7 km	within 20 km	within 3.7 km	within 20 km	
1. Valleviken	0.126	0.183	0.023	0.053	0.764
2. Herrvik	0.092	0.169	0.029	0.115	0.717
3. Sudret	0.098	0.181	0.024	0.062	0.757

Table 5 *The seasonal and inter-annual variability of ending up within 20 km from the coast of Gotland, travel cross-basin or end up in open sea after 60 days of*

dispersal at surface. (The averaged shares at the bottom line are those that are shown at column 2 and 4 in Table 4).

surface		Site 1. Valleviken			Site 2. Herrvik			Site 3. Sudret		
		Stays along coast	Drifts cross-basin	Lost at open water	Stays along coast	Drifts cross-basin	Lost at open water	Stays along coast	Drifts cross-basin	Lost at open water
1995	April	0.456	0	0.5442	0.4150	0	0.5850	0.3333	0	0.6667
	May	0.143	0	0.8571	0.5782	0	0.4218	0.5578	0	0.4422
	June	0	0	1	0	0	1	0.5034	0	0.4966
1996	April	0.075	0	0.9252	0	0	1	0.1293	0	0.8707
	May	0	0	1	0	0.8980	0.1020	0	0	0.9864
	June	0	0	1	0	0	1	0	0	1
1997	April	0.946	0	0.0544	0.8707	0	0.1293	0.0748	0	0.9252
	May	0.721	0	0.2789	0.3537	0	0.6463	0.6122	0	0.3878
	June	0.701	0	0.2993	0.6395	0	0.3605	0.6939	0	0.3061
1998	April	0.163	0	0.8367	0.2449	0	0.7551	0.4490	0	0.5510
	May	0	0.0748	0.9252	0	0.7007	0.2993	0	0	1
	June	0	0.8027	0.1973	0	0.5714	0.4286	0	0.8095	0.1905
1999	April	0.150	0	0.8503	0.0884	0	0.9116	0.0476	0	0.9524
	May	0.007	0.0068	0.9864	0	0.0272	0.9728	0.0204	0.0204	0.9592
	June	0	0	1	0.0136	0.0204	0.9660	0.0408	0	0.9592
2000	April	0.014	0	0.9864	0	0.1088	0.8912	0	0.0748	0.9252
	May	0	0.0884	0.9116	0	0	1	0	0.5510	0.4490
	June	0	0.0204	0.9796	0.0408	0.0272	0.9320	0.0068	0.0272	0.9660
2001	April	0	0	1	0	0	1	0	0	1
	May	0.048	0	0.9524	0	0	1	0	0	1
	June	0.048	0.1769	0.7755	0	0.2857	0.7143	0.0408	0	0.9592
2002	April	0.830	0	0.1701	0.7415	0	0.2585	0.7891	0	0.2109
	May	0.068	0.0952	0.8367	0.0680	0.1088	0.8231	0.0408	0	0.9592
	June	0.014	0.0068	0.9796	0	0	1	0	0	1
Average		0.183	0.053	0.764	0.169	0.115	0.717	0.181	0.062	0.757

Figure captions

Figure 1. The Baltic Sea with ICES subdivisions and Gotland (3.d. 28.2), the area studied.

Figure 2. The domain of the local dispersal model (left) and the five start areas in the domain (right) at site 1.

Figure 3a-b. End positions of drifters within the studied domain when drifting at a) 10 m depth, and b) 22 m depth, modelled with the local dispersal model at site 1. Dates of particle releases as well as number of days of drifting pooled.

Figure 4a-c. End positions of drifters released in a) site 1 (Valleviken), b) site 2 (Herrvik), and c) site 3 (Sudret), when drifting at 10 m and 22 m depth, respectively. The colour scale shows the number of drifters with end position in each 2-nautical mile grid cell after drifting for 60 days. Dates of particle releases pooled. Data from the large-scale connectivity database.

Figure 5a-c. End positions of drifters released in a) site 1 (Valleviken), b) site 2 (Herrvik), and c) site 3 (Sudret), when drifting close to the surface. The colour scale shows the number of drifters with end position in each 2-nautical mile grid cell after drifting for 60 days. Dates of particle releases pooled. Data from the large-scale connectivity database.

Figures

Figure 1.

Figure 2.

Figure 3.

Figure 4a-c.

Figure 5a-c.