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Using acoustic telemetry to locate flatfish spawning areas: Estuarine migrations of turbot *Scophthalmus maximus* and European flounder *Platichthys flesus*

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ABSTRACT

Estuaries are complex environments that provide important nursery areas for several fish species, but anthropogenic activities as well as low salinities may affect fish reproductive potential. This study investigated spawning migrations of turbot (*Scophthalmus maximus*) and European flounder (*Platichthys flesus*) in the estuary of Roskilde Fjord using acoustic telemetry. For turbot, migratory behaviour was coupled with salinity measurements to estimate likelihood of successful spawning. Turbot in Roskilde Fjord are stocked fish, whereas the European flounder represents a naturally occurring population. Telemetry data suggested that the two species exhibited different migration behaviours towards the spawning season. The migratory behaviour of turbot indicates that they remain in the southern parts of Roskilde Fjord where successful development of eggs and larvae may be limited by low salinity. In contrast, the majority of European flounder migrated towards more marine waters prior to the spawning season, and only a minority of the fish remained inside Roskilde Fjord during the spawning season. Consistent with previous studies, the present results indicate that European flounder perform partial spawning migration. Thus, European flounder may utilize a diversity of spawning areas, including the brackish waters in Roskilde Fjord estuary as well as more marine waters with elevated salinities. Our results are important for future management of spawning areas, recruitment dynamics and selection of suitable turbot populations for stocking.

1. Introduction

Coastal ecosystems are increasingly affected by a variety of human pressures (Lotze et al., 2006; Halpern et al., 2019). Exploitation of coastal resources, such as overfishing and land reclamation of shallow-water areas, often has direct effects on coastal ecosystems, but population growth, urbanization and industry also have several indirect, and often cumulative, effects (Vasconcelos et al., 2007; Halpern et al., 2008; Korpinen and Andersen, 2016; Brown et al., 2018; Lin and Yu, 2018;). Human alterations of coastal habitats can have unexpected effects on the ecosystems and may even obstruct various fish life stages, including spawning (Pihl et al., 2006; Brown et al., 2018; Martin and Adams, 2020). The diverse origins of human pressures in coastal ecosystems make them challenging to manage, especially since many of the major

activities responsible for these pressures occur on land (e.g. nutrient loading) and may be beyond the jurisdiction of the marine or national authorities (Tulloch et al., 2020).

Human activities in fish spawning areas may disturb or obstruct spawning (Dean et al., 2012; Armstrong et al., 2013; Martin and Adams, 2020). The protection of spawning areas may benefit fish populations and fisheries, concurrently, by increasing fish biomass, catch rates and recruitment (Armstrong et al., 2013; Erisman et al., 2017). For example, Heppell et al. (2012) observed an increased recruitment to the spawning population of Nassau grouper (*Epinephelus striatus*) in the Cayman Islands, after fishery closure in the spawning areas, while protection of a small area in New Zealand contributed recruits disproportionately to the surrounding recreational and commercial fisheries (Le Port et al., 2017). Resolving the timing and location of spawning areas could enable the

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establishment of protected spawning areas, which may increase future stock recruitment, unless fishing mortality remains unsustainable outside of the protected spawning areas and times (Grüss et al., 2014; Erisman et al., 2020). By knowing the timing and locations of spawning areas, efficient protection may be achieved by managing a relatively small spatial area (Armstrong et al., 2013; Erisman et al., 2017).

Estuaries are important for many marine fish species, partly because estuaries provide important juvenile habitats (Beck et al., 2001). Several flatfish species including European flounder (*Platichthys flesus*) benefit from estuaries as they often provide high food availability for both flatfish larvae, juvenile and adults (Vinagre et al., 2005; Dias et al., 2017). In addition, estuaries may provide a refuge from piscivorous fish predators (Whitfield, 2020), although this remains a contended and perhaps context dependent phenomenon (Wouters and Cabral, 2009; Baker and Sheaves, 2021). These findings indicate that habitat loss in estuarine nursery areas may have negative effects on nursery capacity, as witnessed in the Seine estuary (northern French coast) where habitat loss coincided with a 42% decrease in production of juvenile sole (*Solea solea*; Rochette et al., 2010).

Flatfish spawning may take place in marine waters, with larvae dispersing towards coastal areas and estuaries (Norcross and Shaw, 1984; Koutsikopoulos and Lacroix, 1992). For example, Ramos et al. (2017) showed increasing abundance of European flounder larvae from initial marine spawning grounds towards the inner estuary. Studies have revealed decreasing recruitment into juvenile habitats with increasing distance from the spawning area (Hare and Cowen, 1996; Paris et al., 2005), indicating that transport to nursery areas may be affected by the distance to local spawning areas. Recently, Baptista et al. (2020) showed that various factors (including local bathymetry and the probability of larvae detecting olfactory cues of nursery area) might influence the inflow of fish larvae to juvenile habitats and, thus, local recruitment. These findings suggest that the connectivity between spawning areas and juvenile habitats (which is often mediated by proximity) is essential for sustaining local populations, especially in species that utilize estuarine juvenile habitats, with a greater degree of hydrographic isolation from spawning areas. To manage estuarine and coastal fisheries sustainably, it is therefore important to know the location and quality of associated spawning areas and juvenile habitats, as well as the functional connectivity between them.

Turbot inhabit areas with great differences in physical conditions across its range and exhibit regional adaptation to temperature and salinity (Vandamme et al., 2014; Vilas et al., 2015). Within its European distribution, turbot exhibits genetically distinct populations. Genetically unique populations are found on the Irish Shelf, Northern Atlantic, North Sea and the Baltic Sea (Nielsen et al., 2004; Prado et al., 2018). In the Baltic region, turbot spawns in May and June (Støttrup et al., 2019). Few studies have investigated the spawning migration of turbot, particularly in relation to estuaries. Turbot in the Baltic Sea is considered mainly resident, with spawning migrations spanning less than 30 km (Aneer and Westin, 1990; Florin and Franzén, 2010). However, there are reports of individual fish performing considerably longer migrations (Florin and Franzén, 2010), and general patterns of connectivity between life-history stages of the species remain poorly understood in the transitional waters of the Baltic and the North Sea. Selection of spawning location and timing of spawning influence the environmental conditions experienced by the resulting eggs and larvae. This could be particularly important for turbot, because eggs and larvae are sensitive to salinity variation, with salinity levels for optimal egg buoyancy and larval development differing between populations (Kuhlmann and Quantz, 1980; Karås and Klingsheim, 1997; Nissling et al., 2006, 2013; Prado et al., 2018). Experiments on the embryonic development of turbot eggs suggest that turbot from populations in the North Sea exhibit the highest hatch viability (45–47%) at salinities ranging from 20 psu to 35 psu at an optimum temperature of 14 °C (Karås and Klingsheim, 1997). At lower salinity (15 psu), the hatch viability is only 6%, and at salinities \leq 10 psu, the hatch viability drops to 0% for the North Sea population (Karås

and Klingsheim, 1997).

In Denmark, turbot has been stocked into the estuarine area of Roskilde Fjord to support local fisheries. The stocked fish originated from a brood stock in Norwegian aquaculture (Stolt Sea Farm), acquired from the North Sea (Jørgensen et al., 2017), which is a population adapted to salinities reflecting fully marine seawater (Karås and Klingsheim, 1997; Vandamme et al., 2014; Vilas et al., 2015; Prado et al., 2018). In contrast, turbot from the Baltic Sea exhibit highest hatch viability (51%) at salinities approaching 15 psu (Kuhlmann and Quantz, 1980). While lower salinities have negative effects, Baltic Sea turbot hatch viability remains relatively high (26%) down to a salinity of 10 psu, and viable hatching has been recorded even at 6 psu (Nissling et al., 2006, 2013). Furthermore, Baltic Sea turbot hatch rates remain higher at elevated water temperatures compared to the North Sea conspecifics (Kuhlmann and Quantz, 1980; Karås and Klingsheim, 1997).

European flounder typically spawns in February–April (Cooper and Chapleau, 1998; Nissling et al., 2017; Støttrup et al., 2019) as reported for the Mondego estuary (Portugal), the Bay of Biscay (western French coast), and the Slack (northern French coast; Martinho et al., 2013). Populations of European flounder are often spawning in either offshore, coastal or estuarine areas but spawning areas may also vary between individuals within a population. In some estuarine areas, European flounder migrate offshore prior to spawning (Borsa et al., 1997). In the Baltic Sea, differences in reproductive strategy have led to sympatric speciation of the Baltic flounder (*P. solemdalii*) from the European flounder (Momigliano et al., 2017, 2018). Populations of the Baltic flounder spawn on the seafloor in shallow coastal areas, whereas the European flounder retains the offshore spawning migrations to the basins of the Baltic (Nissling et al., 2002; Nissling and Dahlman, 2010; Nissling et al., 2015). Other studies suggest that different individuals within the same European flounder population may spawn in either estuarine or coastal areas (Morais et al., 2011; Daverat et al., 2012). Such existence of migrant and resident individuals within a population is described as partial migration and occurs across a broad range of fishes (Chapman et al., 2012; Kasai et al., 2018; Ziegler et al., 2019).

A range of tools is available to locate spawning areas of marine fish. For example, visible tags combined with catch and recapture (Aneer and Westin, 1990; Florin and Franzén, 2010), analyses of strontium distribution in otoliths (Morais et al., 2011) as well as ichthyoplankton surveys combined with oceanographic data may be used to locate spawning areas of marine fish (Fox et al., 2008; Hinrichsen et al., 2018). Acoustic fish telemetry provides another approach to locate marine spawning areas (Hussey et al., 2015). Acoustic fish telemetry may be used to investigate the migration of individual fish and often provides numerous data points in space and time, which may be useful for accessing the location of individual fish both before, during and after the spawning season (Hussey et al., 2015). For example, Fairchild et al. (2013) used acoustic telemetry to locate spawning areas of winter flounder (*Pseudopleuronectes americanus*) in coastal and estuarine areas.

Our study investigated temporal and spatial migration patterns of turbot and European flounder in the estuary of Roskilde Fjord using acoustic fish telemetry. Specifically, the study had two main objectives: (1) describe dispersal of tagged turbot and European flounder from points of release, and (2) assess whether individuals of both species remain sedentary in an estuarine area or migrate towards more marine areas prior to the spawning season. The extent of the migrations performed by the two species was compared and used as indicator of the corresponding spawning areas (Fairchild et al., 2013). As the stocked turbot in Roskilde Fjord are not native to the area and were likely adapted to the North Sea's salinity, salinity data from relevant areas were collected and related to the turbot requirements for successful reproduction.

2. Materials and methods

2.1. Study area

The study was carried out in Roskilde Fjord (55° 48' 36" N, 12° 03' 36" E; Fig. 1), which is an estuarine area with an outlet into Kattegat. The Roskilde Fjord estuary is 40 km long with several narrow areas (Pedersen et al., 2014), a catchment area of 1200 km² and a surface area covering 123 km² (Flindt et al., 1997; Pedersen and Rasmussen, 2016). The water is shallow (mean depth is 3 m, whereas maximum depth is 32 m (Flindt et al., 1997; Pedersen and Rasmussen, 2016)). Temperatures range from 0 °C in winter to 22 °C in summer (Flindt et al., 1997). The seabed is dominated by sandy and muddy habitats, with eelgrass (*Zostera marina*) meadows occurring intermittently (Flindt et al., 1997). Commercial vessels dredge for blue mussels (*Mytilus edulis*) in the northern part of Roskilde Fjord in areas with a minimum depth of 4 m (Miljøstyrelsen, 2015). The study area is a Natura 2000 area with several species and habitats protected by the European Union. However, no fish species are explicitly protected under this framework. In Roskilde Fjord, recreational fisheries target a range of fish species, including turbot and

European flounder, using gill and fyke nets as well as rod and line angling.

2.2. Study species

Both turbot and European flounder are commonly found in marine and estuarine waters in the Atlantic Ocean, Black Sea, Mediterranean Sea and Baltic Sea (Muus & Nielsen, 2017). Inside Roskilde Fjord, both species are caught in recreational gillnet fisheries, while outside the fjord they are mainly caught as bycatch or by mixed fisheries in trawl and gillnets (ICES, 2016; Støttrup et al., 2019). In 2019, commercial landings in Kattegat and Skagerrak amounted to 153 t and 193 t for turbot and European flounder, respectively (ICES, 2019).

Aiming to create a reproducing local population of turbot, 45,000 juvenile turbot (5–10 cm) were released in the southern parts of Roskilde Fjord between 2011 and 2014 (Jørgensen et al., 2017). No releases of European flounder have been carried out in Roskilde Fjord. Prior to the releases of turbot, there was no turbot population in Roskilde Fjord, whereas naturally occurring European flounder are abundant in the northern parts of the study area. The northern distribution of the European flounder combined with the southern stocking locations of the turbot means that species distributions rarely overlap.

2.3. Deployment of acoustic receivers

Migrations of turbot and European flounder in Roskilde Fjord were tracked with an array of acoustic receivers (Fig. 1), similar to previous flatfish studies (Fairchild et al., 2013; Wada et al., 2017; Ziegler et al., 2019). Specifically, Vemco VR2W acoustic receivers (308 mm × 73 mm, Innovasea, Bedford, NS, Canada) were deployed throughout the study area to detect fish movements. Receivers were positioned 1 m below the water surface and attached to buoys anchored to the seabed using 12 kg anchors. Receivers were downloaded and cleaned bimonthly.

In February 2017, 16 receivers were deployed in the southern part of Roskilde Fjord (Fig. 1) prior to the release of tagged turbot in March 2017. The purpose of the receiver deployments was to ensure the detection of tagged turbot migrating north towards the more marine conditions outside of Roskilde Fjord (Fig. 1). Specifically, receivers were deployed west and east of Eskilsø island to detect turbot migrating north towards the outlet of the fjord. In addition, one receiver was deployed at the turbot point of release in the southern part of Roskilde Fjord (Fig. 1) to examine turbot dispersal, by measuring elapsed time from fish release until moving away from the release location, similar to previous studies (Christoffersen et al., 2019; Filous et al. 2020).

In December 2017, another nine receivers were deployed in the northern part of Roskilde Fjord (Fig. 1) prior to the release of tagged European flounder in November 2018. Four receivers were deployed both at Frederikssund and Dyrnæs (Fig. 1). Identical to the turbot releases, a single receiver was deployed at the release location to examine dispersal of tagged European flounder, by measuring elapsed time from fish release until moving away from the receiver at the release location (Fig. 4; Filous et al., 2020). All receivers used for the flatfish studies were terminated in 2020.

2.4. Fish capture, tagging and release

A total of 33 turbot and 27 European flounder were captured in Roskilde Fjord using gill nets. Mean total body length and body mass (\pm SE) of the captured turbot were 44.3 \pm 3.1 cm and 1888.6 \pm 70.9 g and European flounder 33.2 \pm 0.7 cm and 460.0 \pm 30.2 g. Turbot were captured in the southern parts of Roskilde Fjord (near turbot point of release), whereas European flounder were captured further north (near Frederikssund). Distributions of turbot and European flounder are generally not overlapping in Roskilde Fjord, precluding a common capture location. After capture, fish were gently transferred to a holding pen (3 m × 3 m × 4 m) and fasted for 2–3 days. Fasting was induced to

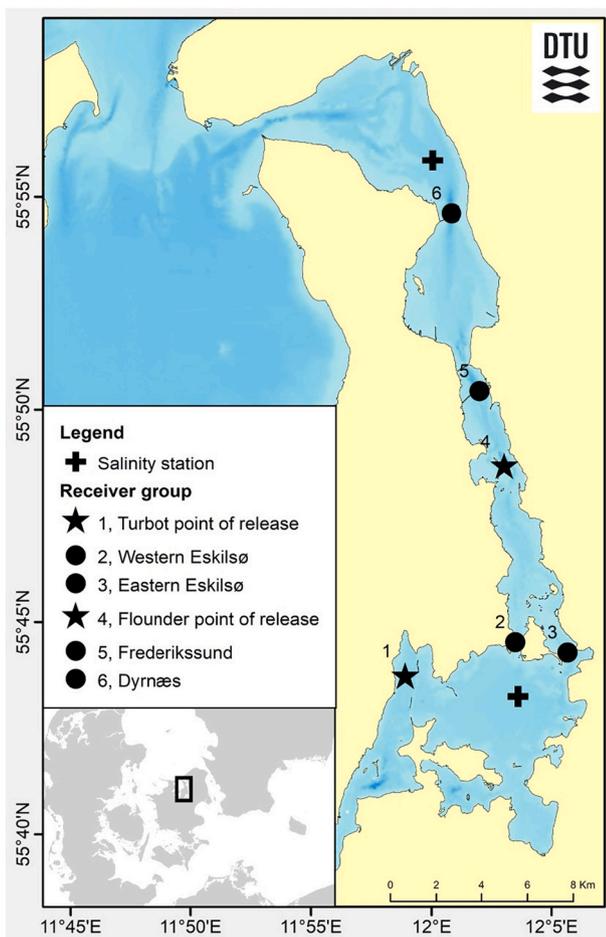


Fig. 1. Roskilde Fjord with the location of the six receiver groups (numbers 1 to 6) and two salinity stations in the southern and northern parts of Roskilde Fjord. Land is coloured beige and water in light blue. Tagged adult turbot were released at the turbot point of release. Adult European flounder were released at flounder point of release. Receiver groups 1–3 are referred to as the southern parts of Roskilde Fjord in the text, whereas receiver groups 4–6 are referred to as the northern parts of Roskilde Fjord. The island positioned between receiver groups 2–3 is referred to as Eskilsø island. Release locations differed between the two species because species distributions have insufficient overlap for a common release location. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

reduce any impact of digestive processes (Norin and Clark, 2017; Tirsgaard et al., 2014) on fish recovery after surgical implantation of telemetry transmitters. Fish were tagged with Vemco V8 coded transmitters (model V8-4L, 69 kHz, Power Output 144 dB re 1 μ Pa at 1 m, 8 mm diameter, 20.5 mm long, 2.2 g in air, 0.9 g in water; Innovasea, Bedford, NS, Canada) programmed to transmit an individual identification number at pseudorandom intervals ranging between 70 and 120 s for up to one year. Before tagging, fish were placed in an anaesthetic bath (benzocaine 0.004%) for 3–4 min, and transmitters were subsequently implanted into the fish coelomic cavity using standard surgical procedures (Svendsen et al., 2011; Piper et al., 2017; Jensen et al., 2019). The body sizes of the fish ensured a low ratio of transmitter mass to fish mass (< 1%). After handling and surgical procedures, fish were monitored in holdings tanks to confirm recovery. Upon recovery, fish were brought back to the net pen and kept there until release during the same day (i.e. within five hours). Turbot were released in mid-March 2017 (Fig. 1), prior to their spawning season in May and June (Støttrup et al., 2019). European flounder were released in mid-November 2018 (Fig. 1), prior to their spawning season in February–April (Cooper and Chapleau, 1998; Nissling et al., 2017; Støttrup et al., 2019).

2.5. Salinity in Roskilde Fjord

Salinity data (psu) were recorded by the Danish Metrological Institute and Aarhus University at two stations in the southern (55° 42' 78" N, 12° 04' 00" E) and northern (55° 55' 48" N, 12° 01' 40" E) parts of Roskilde Fjord throughout the turbot study period (2017–2018). Data collection involved conductivity, temperature and depth sensors (CTD) with an accuracy of ± 0.05 psu. Prior to measurements, the CTD was submerged into the water at a depth of 1–3 m for at least 1 min to avoid air bubbles in the CTD and equalize temperature differences between probe and water. Subsequently, the CTD was raised to 0.4 m depth and lowered slowly until reaching 0.2–0.5 m above the seabed. The salinity measurements provided data at 20 cm intervals from 0.4 m below the water surface to 0.2–0.5 m above the seabed. At both stations, salinity data were collected at least monthly. Salinity was not measured for the parallel European flounder study because the species is native to Roskilde Fjord and presumably adapted to local environmental conditions (Andersen et al., 2005; Nissling and Larsson, 2018).

2.6. Estimating successful turbot spawning by interviewing recreational fishers

Interviews with recreational fishers were used to assess reproduction of the stocked turbot in Roskilde Fjord. The fishers use fyke nets and gill nets and frequently report captures of juvenile European flounder. To assess successful spawning of the stocked turbot, fishers were interviewed during public meetings and during data collection on Roskilde Fjord. Specifically, this study gathered information concerning captures of juvenile turbot in Roskilde Fjord during the period 2016–2020. To distinguish juvenile turbot from juvenile European flounder, flyers and posters outlining morphological differences between the two species were shared with fishers in Roskilde Fjord. Subsequently, fishers examined their catches and reported captures of juvenile turbot to DTU Aqua. Because there is no native population of turbot in Roskilde Fjord, occurrences of juvenile turbot during 2016–2020 were interpreted as evidence of successful spawning by the turbot stocked in Roskilde Fjord. In contrast, absence of juvenile turbot in the catches of the fishers was interpreted as lacking evidence of successful spawning by the stocked turbot. Information from more than 50 recreational fishers fishing throughout the study area was gathered.

2.7. Data analyses

Data filtering and statistical analyses were performed with the

software R v. 4.0.2 (R Core Team, 2020). Acoustic signals are subject to code collisions (e.g. when coded transmissions coincide in time and produce false detections) so the data were initially checked and filtered to remove any non-target codes and incomplete transmitter-to-receiver transmissions (Heupel et al., 2006). To evaluate the dispersal of the tagged fish from the point of release, we defined date of dispersal as the last detection before a fish was not detected for at least 24 h by the receiver situated at the point of release. A Welch two-sample *t*-test was used to analyze differences in dispersal time between turbot and European flounder.

To identify patterns of turbot and European flounder migrations in Roskilde Fjord, we generated abacus plots of individual detections at each receiver group (e.g. at Frederikssund; Fig. 1) that indicate date of detection at a given receiver group for each tagged fish (Filous et al., 2020).

Two definitions of behaviour were used: migratory behaviour, defined as detections at receiver groups north of point of release, and non-migratory behaviour, defined as no detections at receiver groups north of point of release. Fischer's exact test was applied to analyze differences in proportions of migratory behaviour between turbot and European flounder.

European flounder migrations past Dyrnæs were defined as the last date of detection at the receiver group 6 at Dyrnæs (Fig. 1), similar to previous studies (Svendsen et al., 2011; Christoffersen et al., 2019). Influence of fish weight on timing of migration past Dyrnæs was tested by correlating fish body weight (g) with the number of elapsed days between fish release and migration past Dyrnæs using Pearson correlation analysis. A generalized linear mixed-effects model (GLMM) was fitted to examine the relationship of likelihood of migration past Dyrnæs with fish weight and identification number (ID) (Bates et al., 2015).

The water column of Roskilde Fjord is generally well mixed because of the shallow water (average depth is 3 m; Flindt et al., 1997). Therefore, this study used the mean salinity through the water column and calculated the mean monthly salinity for the southern and northern parts of Roskilde Fjord across the study period of turbot (March 2017 to February 2018).

3. Results

3.1. Comparing dispersal and migratory behaviour of turbot and European flounder

On the day of release, 32 of 33 tagged turbot and 24 of 26 tagged European flounder were detected at the point of release. The number of days spent at the point of release before dispersing ranged from 0 to 15 days (mean \pm SE; 2.2 ± 0.7) for turbot and from 0 to 3 days (0.4 ± 0.2) for European flounder (Fig. 4). A Welch two-sample *t*-test revealed a significant difference between the two dispersal times (mean difference = 1.8, $t = 2.6$, $p < 0.05$). The result indicated that turbot dispersed slower than European flounder (Fig. 4.). Moreover, Fisher's exact test showed a significant difference in the proportion of fish exhibiting non-migratory and migratory behaviour between turbot and European flounder ($p < 0.001$), with European flounder showing a higher tendency to migrate. Specifically, only 18% percent of the turbot exhibited migratory behaviour whereas 81% percent of the European flounder exhibited migratory behaviour. Both test results indicate that European flounder is more migratory than turbot.

3.2. Turbot migration in Roskilde Fjord

A total of 96455 detections were obtained from the 33 tagged turbot (Table 1). The fish were detected at three receiver groups: point of release (1), western Eskilsø (2), and eastern Eskilsø (3) (numbers in parentheses refer to positions in Figs. 1 and 2). The majority of turbot (94%; $n = 31$) were south of Eskilsø prior the spawning season (May and June; Fig. 2). In total, six of 33 turbot (18%) were detected at Eskilsø.

Table 1

Description of tagged and released turbot in Roskilde Fjord: identification number (ID), weight (g), total length (cm), date of first detection, date of last detection, time range in days (i.e. time between first and last detection), the total number of detections, and the total number of receivers that detected each ID. Point of release is described in Fig. 1.

ID	Weight(g)	Length(cm)	First detection	Last detection	Time range (d)	n detections	n receivers
2170	1780	42	2017-03-16	2018-02-02	323	2978	5
2171	2050	44	2017-03-16	2017-03-22	6	521	4
2172	1390	39	2017-03-16	2017-04-08	23	1530	5
2173	2140	45	2017-03-16	2017-03-16	0	3	2
2174	2070	44	2017-03-16	2017-04-09	24	3609	5
2175	2005	43.5	2017-03-16	2017-03-19	3	257	4
2176	1535	41	2017-03-17	2017-04-06	20	1229	9
2177	2018	45.5	2017-03-17	2017-04-01	15	6258	5
2178	1672	44	2017-03-17	2017-04-16	30	2233	5
2179	2590	49	2017-03-17	2017-04-19	33	2265	5
2180	1415	41	2017-03-17	2017-04-06	20	1388	5
2181	1970	45.5	2017-03-17	2017-03-31	14	229	5
2182	2200	47	2017-03-17	2017-03-30	13	1462	5
2183	1930	45.5	2017-03-17	2017-05-11	55	3745	4
2184	1750	42	2017-03-17	2017-03-31	14	434	6
2185	1836	45	2017-03-17	2017-03-21	4	448	4
2186	1472	41	2017-03-17	2017-03-31	14	7050	5
2187	1507	40	2017-03-17	2017-03-17	0	22	2
2188	1015	37.5	2017-03-17	2017-03-30	13	140	5
2189	2540	47.5	2017-03-17	2017-04-07	21	1361	5
2190	1830	45	2017-03-18	2017-04-22	35	12,784	5
2191	1420	42	2017-03-18	2017-04-08	21	99	4
2192	1925	46	2017-03-18	2017-05-14	57	3430	14
2193	1600	43	2017-03-18	2018-01-18	306	7006	8
2194	1644	45	2017-03-18	2017-04-06	19	1230	5
2195	1501	43	2017-03-18	2017-03-19	1	221	4
2196	2280	47.5	2017-03-18	2017-10-02	198	2170	5
2197	2213	48	2017-03-18	2017-03-28	10	635	5
2198	2538	49	2017-03-18	2017-06-11	85	270	5
2199	1284	39.5	2017-03-18	2017-06-05	79	762	8
2200	2326	48	2017-03-18	2017-04-26	39	6577	5
2201	2373	48.5	2017-03-18	2018-03-04	351	19,843	10
2202	2503	48	2017-03-18	2017-04-03	16	4266	5

Two turbot migrated past the receivers at western Eskilsø on the 28th and 29th March 2017, where they both were detected again on the 5th April 2017 and returned to the area south of Eskilsø on the 6th April 2017, prior to the spawning season (ID = 2176 and 2184). One turbot migrated past the receivers at eastern Eskilsø on the 5th June 2017 during the spawning season (ID = 2199 in Fig. 2). Another turbot was also detected at Eskilsø during the spawning season and migrated past the receivers at eastern Eskilsø on the 10th May 2017 and back again past the receivers at western Eskilsø on the 14th May 2017 (ID = 2192). Thus, the fish spent four days of the spawning season located north of Eskilsø, but returned to the area south of Eskilsø afterwards. One turbot was detected at the eastern Eskilsø on the 17th January 2018 where it stayed for two days but did not migrate past the receivers (ID = 2193). Another turbot was also detected on 17th January 2018 at eastern Eskilsø, where it stayed until the 4th March 2018 before returning south of Eskilsø (ID = 2201; Table 2.)

3.3. European flounder migration in Roskilde Fjord

A total of 27 European flounder were released, but only 26 were included in this study, as one European flounder was continuously observed at the point of release and assumed to be dead (Villegas-Ríos et al., 2020). In total, 14,369 detections were obtained from the 26 tagged European flounder (Table 2). The fish were detected at four receiver groups: point of release (4), eastern Eskilsø (3), Frederikssund (5) and Dyrnæs (6) (numbers in parentheses refer to positions in Figs. 1 and 3). Of the 26 European flounder released, 20 migrated past the receivers at Dyrnæs between 2 and 185 days after release (34.5 ± 10.6 days; mean \pm SE) (Fig. 5). Most tagged European flounder (69%; $n = 17$) migrated past the receivers at Dyrnæs prior to the spawning season (February to April); Fig. 5). Two migrated past the receivers at Dyrnæs

during the spawning season and one migrated past them after the spawning season (Fig. 5). Timing of migration past Dyrnæs (i.e. days after release) was not correlated with fish body weight ($p = 0.82$). Similarly, the likelihood of migration past Dyrnæs was not correlated with fish body weight ($p = 0.225$).

Among the 20 European flounder that migrated past Dyrnæs, four returned. Three returned to Dyrnæs on the 6th March 2019, 10th April 2019 and 28th May 2019 (ID = 3377, 4790 and 3381 in Fig. 3). One European flounder returned to Dyrnæs on the 9th May 2019 and was detected further south at Frederikssund on 20 May 2019 (ID = 4794). Returning European flounder spent 96–191 days past Dyrnæs (145.5 ± 35.0 days; mean \pm SE).

3.4. Salinity in relation to turbot migrations

Between the 1st March 2017 to 1st February 2018, salinity in the southern Roskilde Fjord ranged between 10.9 and 14.9 psu (12.7 ± 0.4 ; mean \pm SE) (Fig. 1). During the turbot spawning season in May–June (Støttrup et al., 2019), the salinity in the southern part of Roskilde Fjord ranged between 13.4 and 14.9 psu (mean $14.2 \pm$ SE), meaning that turbot eggs and larvae could have been exposed to relatively low salinities in the southern part of Roskilde Fjord.

In the northern part of Roskilde Fjord, salinity between the 1st March 2017 to 1st February 2018 ranged from 16.4 to 18.1 psu (17.3 ± 0.2) and ranged between 17.5 and 18.0 psu (mean = 17.8) during the turbot spawning season in May–June (Støttrup et al., 2019).

3.4.1. Captures of juvenile turbot in Roskilde Fjord during 2016–2020

Interviews with recreational fishers indicated no captures of juvenile turbot in Roskilde Fjord. In contrast, captures of juvenile European flounder were reported repeatedly, although mainly in the northern part

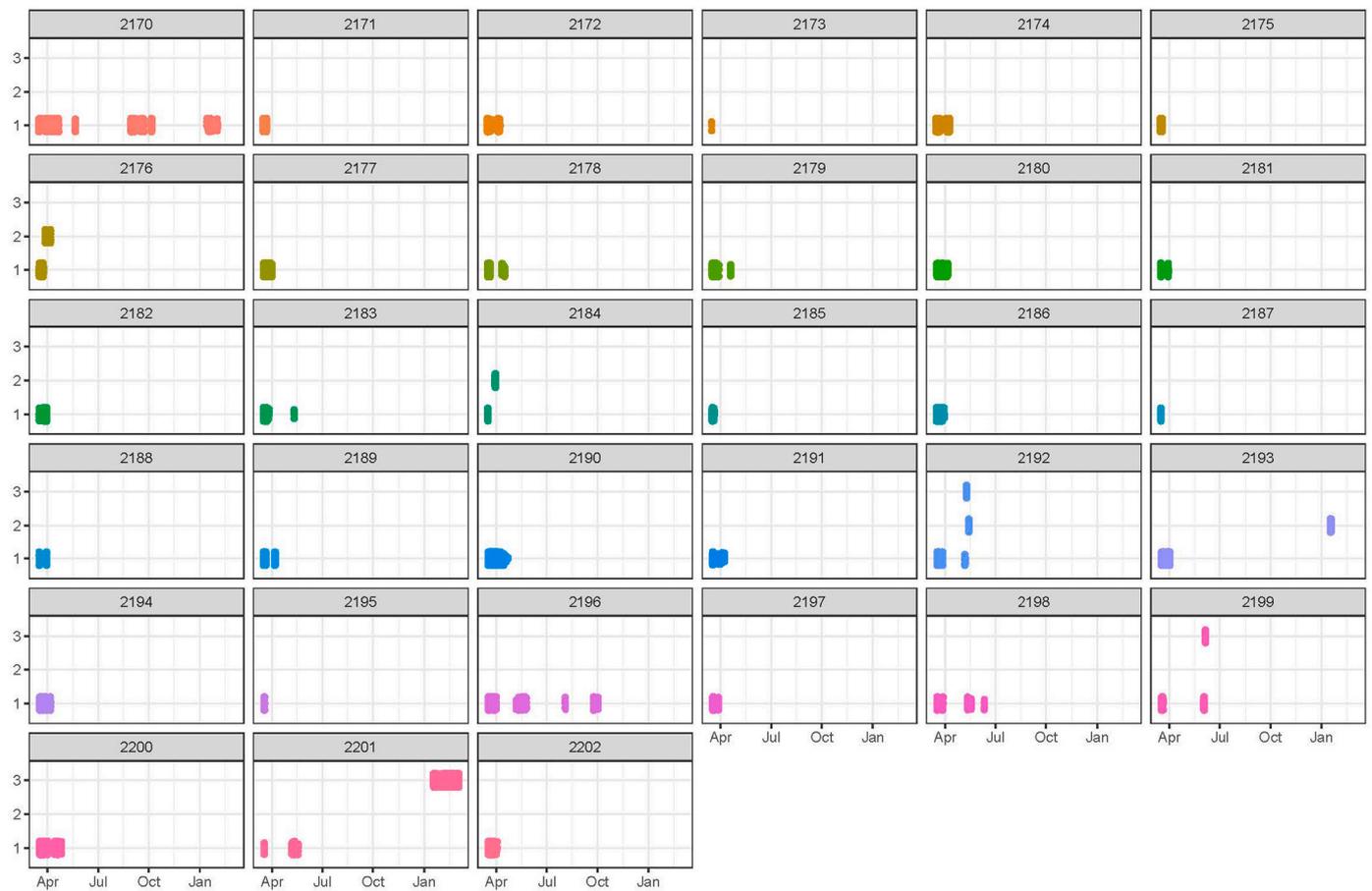


Fig. 2. Abacus plots of turbot detections in Roskilde Fjord from 16 March 2017 to 4 March 2018. Coloured dots indicate detections of each fish (ID) at the receiver groups 1–3 depicted in Fig. 1 as turbot were not detected at receiver groups 4–6. Dots have been jittered with height = 0.2 for visualisation of overlapping dots.

Table 2

Description of tagged and released European flounder in Roskilde Fjord: identification number (ID), weight (g), total length (cm), date of first detection, date of last detection, time range in days (i.e. time between first and last detection), the total number of detections, the total number of receivers that detected each ID, and whether a migration past Dyrnæs was recorded. Point of release, the Dyrnæs location etc. are described in Fig. 1.

ID	Weight(g)	Length(cm)	First detection	Last detection	Time range (d)	n detections	n receivers	Migrated
3377	782	39	2018-11-16	2019-04-07	142	2333	5	Yes
3378	395	33.5	2018-11-16	2018-12-05	19	51	8	Yes
3379	484	32.5	2018-11-16	2018-11-21	5	167	12	Yes
3380	706	36	2018-11-16	2018-12-03	17	453	9	Yes
3381	506	35.5	2018-11-16	2019-05-28	193	147	9	Yes
3382	523	38.5	2018-11-16	2018-11-19	3	139	9	Yes
3383	584	32.5	2018-11-16	2018-12-29	43	3732	5	No
3384	484	34.5	2018-11-21	2018-11-30	9	861	9	Yes
3385	466	38.5	2018-11-16	2018-11-16	0	10	1	No
3386	525	35.5	2018-11-16	2018-11-27	11	428	1	No
4780	484	32.5	2018-11-16	2018-12-12	26	630	9	Yes
4781	454	33.5	2018-12-06	2018-12-23	17	189	9	Yes
4782	761	36.5	2018-11-16	2019-02-10	86	1462	9	Yes
4783	411	33	2018-11-16	2018-11-23	7	607	9	Yes
4784	807	39	2018-11-16	2019-03-23	127	69	8	Yes
4785	407	34	2018-11-16	2018-12-05	19	157	12	Yes
4786	300	31	2018-11-16	2019-05-20	185	65	8	Yes
4787	270	28	2018-11-16	2018-12-30	44	919	9	Yes
4788	450	35.5	2018-11-16	2018-11-16	0	5	1	No
4789	334	29.5	2018-11-16	2018-11-25	9	1214	9	Yes
4790	405	30.5	2018-11-16	2019-04-15	150	284	9	Yes
4791	264	28	2018-11-16	2018-11-16	0	34	1	No
4792	290	29.5	2018-11-16	2018-11-28	12	97	8	Yes
4793	408	34	2018-11-16	2018-11-16	0	14	1	No
4794	268.5	27.5	2018-11-16	2019-05-24	189	191	9	Yes
4795	384	31	2018-11-16	2018-12-26	40	111	9	Yes

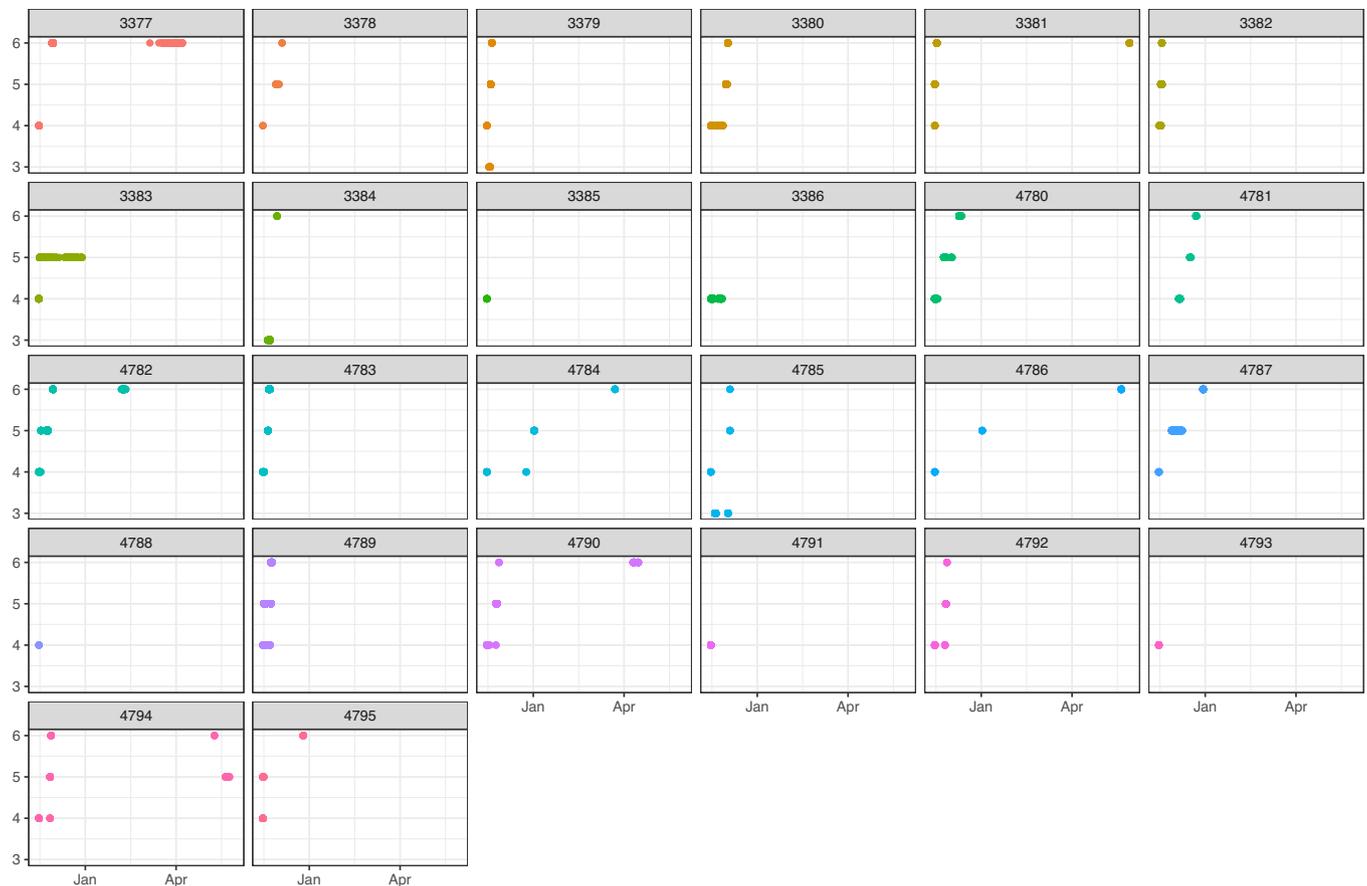


Fig. 3. Abacus plots of European flounder detections in Roskilde Fjord from 16 November 2018 to 28 May 2019. Coloured dots indicate detections of each fish (ID) at the receiver groups 3–6 depicted in Fig. 1 as European flounder were not detected at receiver groups 1–2.

of Roskilde Fjord (Fig. 1). More than 50 fishers using fyke nets and gill nets provided input for the assessment. The fact that fishers situated throughout the study area reported no captures of juvenile turbot indicated limited or absent turbot recruitment in Roskilde Fjord. The observations provided by the fishers suggested that the stocked turbot were largely unable to produce a sustainable population of turbot in Roskilde Fjord.

4. Discussion

This study used acoustic telemetry to investigate the spawning migration of individually tagged turbot and European flounder in an estuarine area (i.e. Roskilde Fjord). Following release, turbot exhibited slower dispersal than European flounder, despite the turbot being larger. Moreover, data suggest that only a minority of the turbot (6%) migrated north towards the outlet of Roskilde Fjord before and during the spawning season, whereas most European flounder (65%) migrated towards more marine areas prior to the spawning season. Consistent with previous studies, our results highlight limited migration and adult dispersal in turbot (Aneur and Westin, 1990; Florin and Franzén, 2010), in contrast to European flounder, which exhibits various migratory behaviours (Morais et al., 2011; Daverat et al., 2012). The majority of the tagged European flounder performed a spawning migration towards more marine waters. The minority that was more sedentary presumably either spawned within the estuary or did not migrate because they skipped a spawning season (Semushin et al., 2015). These findings indicate either a full or partial spawning migration in European flounder. The data suggest that European flounder recruitment to Roskilde Fjord is at least partially dependent on immigration of larvae and

juveniles from spawning areas in more marine waters. Finally, our findings suggest that the turbot of Roskilde Fjord are not making such spawning migrations and are therefore likely spawning in the southern parts of Roskilde Fjord. Whether or not such spawning activity is successful cannot be determined from our study. However, the absence of juvenile turbot captures by local fishers over five years (2016–2020) indicate limited or no new recruitment of turbot occurring in Roskilde Fjord as an outcome of the turbot stocked in Roskilde Fjord (2011–2014).

The turbot tagged in Roskilde Fjord are stocked fish, using a brood stock originating from the North Sea. The turbot brood stock is likely adapted to high salinities (> 30 psu) (Vandamme et al., 2014; Vilas et al., 2015; Prado et al., 2018), suggesting that survival of the resulting turbot eggs and larvae require salinities that exceed the salinities present in the southern Roskilde Fjord (Karås and Klingsheim, 1997). Furthermore, even if turbot was able to produce viable fertilised eggs, the narrow and shallow nature of the estuary makes it likely that physical interactions with the seafloor, vegetation and other structures would lead to high mortality. Although further research is required, these inferences may explain why no juvenile turbot were reported by local recreational fishers in Roskilde Fjord.

4.1. Assessment of turbot spawning success

Estuaries provide high food availability for flatfish larvae, juveniles, and adults (Sheaves et al., 2015). The high productivity provides important nursery areas for several flatfish species (Beck et al., 2001; Vinagre et al., 2005; Dias et al., 2017). Furthermore, estuaries are often characterized by a salinity gradient; a spatial pattern in the mixture of

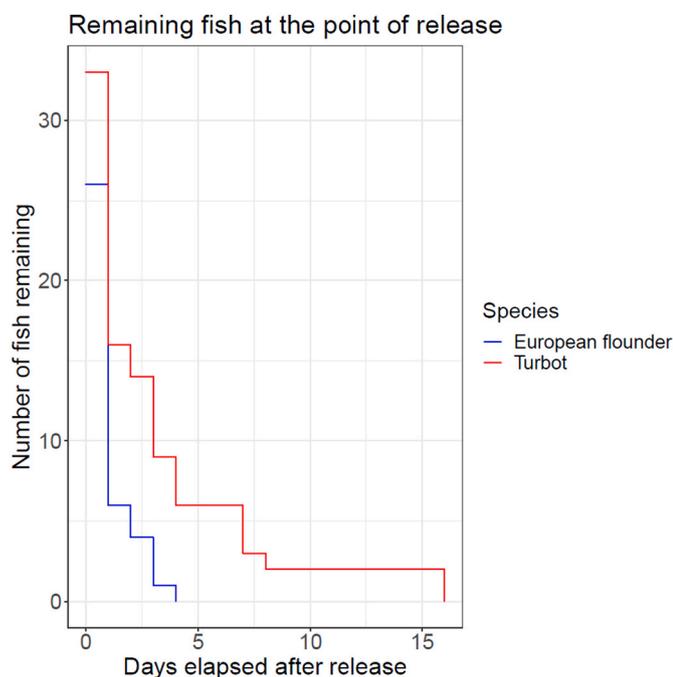


Fig. 4. Number of tagged fish remaining at the point of release (i.e. no dispersal from point of release) for turbot and European flounder. European flounder dispersed faster from the point of release than turbot, indicating a more stationary behaviour of turbot.

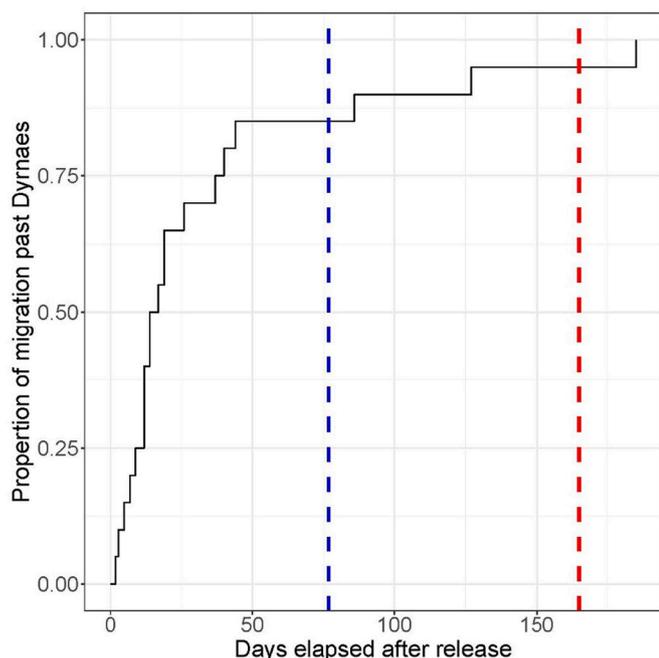


Fig. 5. Proportion of European flounder migrating past Dyrnaes from 18 November 2018 to 20 May 2019. Migration past Dyrnaes was defined as the last date of detection at the receiver group at Dyrnaes (see Fig. 1). The blue line indicates start of spawning season (1st February) and the red line indicates end of spawning season (30th April). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

water from seawater and freshwater (Cloern et al., 2017). Therefore, these shallow and transitional waters are also highly dynamic. Changes in temperature and salinity often have major impacts on the survival and growth rate of eggs, larvae and juvenile fish (Nissling et al., 2006; Neill

et al., 2011; Sales et al., 2016; Brown et al., 2019). Eggs from turbot in Roskilde Fjord likely have the highest hatch viability (45–47%) at salinities ranging from 20 to 35 psu and only 0–6% at salinities ranging from 10 to 15 psu (Karås and Klingsheim, 1997). Thus, spawning success of the turbot studied in Roskilde Fjord could have been constrained by low salinity, especially in the southern parts of Roskilde Fjord mean salinity was 12.7 psu during 2017–2018 and 14.2 psu specifically during the spawning season (Table 3), since the turbot originate from the North Sea population. However, the specific salinity preferences for the turbot broodstock used in Roskilde Fjord could be elucidated by laboratory studies investigating the survival of turbot eggs across a range of salinities. In contrast, turbot originating from the Baltic Sea may have favorable conditions for spawning in the southern part of Roskilde Fjord as they exhibit highest hatch viability (51%) at 15 psu and hatch viability remains relatively high (26%) down to a salinity of 10 psu.

In many locations, fish species are released to increase future harvest, but a growing number of species are released to reestablish reproducing local populations (Shute et al., 2005; Waples et al., 2007; Lyon et al., 2012). Many fish populations are adapted to local conditions (Fraser et al., 2011; Bourret et al., 2013; Prado et al., 2018), and fish from nonlocal brood stocks may have lower reproductive success in the wild when compared to locally originating brood stocks (Araki et al., 2008; Berejikian et al., 2009), which appears to be the case for turbot in Roskilde Fjord. Furthermore, divergence between hatchery and wild fish may occur due to genetic adaption to captivity. Stocks that have experienced severe genetic bottlenecks and/or selection in captivity may therefore have lower fitness in the wild (Araki et al., 2008; Berejikian et al., 2009). On this basis, we suggest that further stocking programs for estuarine areas like Roskilde Fjord should consider using turbot from wild or recently established brood stocks adapted to similar conditions to increase the probability of successful reproduction among the stocked fish.

4.2. European flounder migration and future perspectives

Previous studies suggest that European flounder performs spawning migrations towards marine waters (Summers, 1979; Borsa et al., 1997; Minier et al., 2000; Martinho et al., 2009). However, this might not be the case for all populations, as other studies indicate that European flounder may spawn in both estuarine and marine waters (Morais et al., 2011; Daverat et al., 2012). Most tagged European flounder (17 of 26) in our study migrated past Dyrnaes prior to the spawning season in early spring. The fish may have reproduced in the northernmost region of Roskilde Fjord, in the neighbouring estuary Isefjord, or in the more marine waters of the Kattegat further north. In support of our data indicating emigration from Roskilde Fjord, a recent study from this region and the neighbouring fjord reported the lowest European flounder catch per unit effort during the winter (Støttrup et al., 2018), perhaps reflecting that a large proportion of the adults leave the estuarine areas in the autumn and early winter.

Our findings may indicate that European flounder performs partial spawning migration, with the majority migrating towards marine waters, whereas some fish presumably spawn inside Roskilde Fjord, similar to previous studies (Morais et al., 2011; Daverat et al., 2012). However, it remains possible that not all individuals undertake a spawning migration every year, and that these individuals are resident in the estuary over the spawning season, without spawning (Semushin et al., 2015). Partial migration, where some individuals in the population migrate and others remain resident, is observed in numerous species (Jonsson and Jonsson, 1993; Chapman et al., 2012). Migration is often driven by predation and foraging, with trade-offs often changing temporally and spatially. Furthermore, these trade-offs may also vary between individuals, and studies have shown that decisions for migratory or resident behaviour are often related to the vulnerability of the individual fish to predation and its growth rate (Skov et al., 2011; Gillanders et al., 2015). Similar mechanisms may drive the various

Table 3

Mean monthly salinities (psu) in the southern and northern parts of Roskilde Fjord (Fig. 1) during the turbot study period (March 2017 to February 2018).

	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb
South 2017/2018	13.7	14.7	14.9	13.4	13.5	13.3	12.3	12.0	11.8	11.3	10.9	10.9
North 2017/2018	18.1	17.6	18.0	17.5	17.7	17.4	16.4	17.1	16.8	16.6	17.4	16.8

migration patterns observed here for the European flounder, although the present study did not observe any relationship between the likelihood of migration past Dyrnæs (towards more marine waters) and fish body weight within the tested range. Further investigations into the presence of mature fish with mature oocytes in Roskilde Fjord during the spawning season, and the presence of fertilised eggs and/or early-stage larvae, are needed to assess spawning and successful reproduction in the area.

The previous findings of European flounder performing spawning migration from estuarine waters towards more marine areas suggest that the European flounder examined in the present study emigrated from Roskilde Fjord to enter more marine waters (Summers, 1979; Borsa et al., 1997; Minier et al., 2000; Martinho et al., 2009). Hence, European flounder could utilize both Kattegat and Roskilde Fjord as spawning areas. Post-flexion larvae from Kattegat may use directional swimming to follow environmental nursery cues into estuaries (Baptista et al., 2020), suggesting that recruitment of European flounder post-flexion larvae from Kattegat could occur. Roskilde Fjord may therefore represent a juvenile habitat for European flounder spawned in Kattegat or inside the fjord, as indicated in Brown et al. (2019), largely because estuaries are beneficial habitats for flatfish larvae and juveniles due to high food availability (Vinagre et al., 2005; Dias et al., 2017).

Human alterations could affect European flounder spawning and nursery areas (Martin and Adams, 2020). For example, changes in substrate type could reduce the availability of prey species for flatfish (Nicolas et al., 2007) and reduce the possibilities for burying and hiding from predators (Gibson and Robb, 2000). A reduction of spawning and nursery areas may limit the population growth of commercially, recreationally and culturally important fish species such as European flounder (Rijnsdorp et al., 1992; Levin and Stunz, 2005; Fodrie and Levin, 2008; Sundblad et al., 2014). Management may therefore need to cover cross-realm conservation efforts, as European flounder utilize and migrate between estuarine and marine waters, which may be influenced by human activities on land and at sea, as well as climate change (Brown et al., 2018; Tulloch et al., 2020). For example, excessive commercial fishing of European flounder in Kattegat could affect recruitment into Roskilde Fjord, which is an important area for recreational fishing. Furthermore, the timing of human alterations in relation to spawning of the European flounder may affect the likelihood of successful spawning (Martin and Adams, 2020). For example, sand replenishment projects during the spawning season may inhibit successful settlement after spawning (Tulloch et al., 2020). Managers could use the information on the timing of European flounder spawning to plan seasonal restrictions and allow for certain human activities when the activities do not impact spatially explicit aggregations at specific life-history stages, for example, temporal restrictions on sand replenishment during settlement.

4.3. Study assumptions

The present study of the migratory behaviour of turbot and European flounder relies on several assumptions, including the following.

First, the tagged turbot and European flounder were caught in two different locations of Roskilde Fjord, because their geographical distributions are generally not overlapping in the area. Specifically, turbot mainly occurred in the southern part of Roskilde Fjord, whereas European flounder mainly occur in the northern part of Roskilde Fjord. Consequently, the tagged turbot and European flounder were released in the local areas where they were caught, which meant that tagged fishes were not transported between local areas, assumed to minimize

disturbances of the examined fish.

Second, there is no native population of turbot in Roskilde Fjord. This means that the tagged turbot originated from a non-local brood stock used for aquaculture in Norway, whereas the tagged flounder originated from a natural local population situated in Roskilde Fjord. Fish from non-local brood stock may have lower fitness in the wild compared to a locally adapted brood stock (Araki et al., 2008; Berejikian et al., 2009). Therefore, fish from a non-local brood stock may exhibit migratory behaviours that deviate from the migratory behaviours exhibited by fish from a locally adapted brood stock. It is difficult to disentangle how these observations may have affected our results, because there is no natural turbot population in Roskilde Fjord. However, our results revealing mainly resident behaviours in turbot in Roskilde Fjord are consistent with turbot findings elsewhere (Aneer and Westin, 1990; Florin and Franzén, 2010). Specifically, previous studies have shown turbot spawning migration spanning less than 30 km similar to our study (Florin and Franzén, 2010). On this basis, we consider our comparisons between turbot and European flounder valid.

Third, the tagged turbot (38–49 cm) and European flounder (28–39 cm) were assumed to be sexually mature. Maturation size may vary in time and space, but often, body size at maturation for males is smaller than for females. In the North Sea and surrounding regions, studies on female turbot indicate that about 50% of the fish are maturing at body sizes between 30 – 40 cm, and about 90% of the fish are maturing between 40–50 cm (Bromley et al., 2000; Heessen, 2010; ICES, 2012). For female European flounder in the Baltic Sea, 50% of the fish are mature at a body size around 21 cm (ICES, 2021). The body sizes for sexual maturation of turbot and European flounder in Roskilde Fjord are unknown, but the existing evidence indicate that most of the examined fish were mature, or maturing, during tagging and therefore likely ready for the following spawning.

Fourth, the year of tagging and release differed between turbot (2017) and European flounder (2019), and the fish may have been exposed to different environmental conditions. However, previous studies have shown that turbot and flounder facing different environmental conditions prior to their spawning seasons occurs naturally, because turbot and flounder are spawning during different seasons (Cooper and Chapleau, 1998; Nissling et al., 2017; Støttrup et al., 2019). Ideally, timing of tagging and release prior spawning should be the same for the two species, but the approach was not considered feasible because the spawning seasons differ widely (turbot and European flounder are spawning during the summer and winter/early spring, respectively). Moreover, tagging and release timing for the two species was also influenced by the availability of fish for tagging and boating support from local fishers engaged in the study. Therefore, the tagged turbot were released about 1.5 month prior their spawning season whereas the tagged European flounder were released about 2.5 months prior their spawning season.

Fifth, this study relied on detection of tagged fish by acoustic receivers deployed in several locations in Roskilde Fjord. Detections were ensured by deploying receiver groups (Fig. 1) in geographically narrow areas where a limited number of receivers were required to facilitate detection of tagged fish in the area. Receivers were examined regularly for biofouling removal and confirming that the individual receivers were functioning. Immediately before data download, test transmitters were deployed in the different receiver areas to confirm that the receivers were functioning as expected. Testing included range tests consistently revealing detection ranges exceeding 100 m. Receiver locations were decided accordingly and ensured overlapping detection ranges within

the receiver groups. This meant that undetected migration past a receiver group was considered unlikely, however, it is impossible to rule out the possibility completely. For example, tagged fish could have passed a receiver group while we were cleaning receivers and downloading detection data. This is the case because receivers are not capable of detecting tagged fish during data download or while receivers are out of the water for cleaning. In addition, severe weather conditions, or unusual underwater noise (e.g. heavy boat motors), may reduce detection ranges to an unknown extent. These considerations are likely to explain that two tagged European flounder apparently passed receiver group 5 at Frederikssund undetected, suggesting that passing a receiver group without detection may have happened in rare instances with unusual conditions. This is an important, although common, issue that needs to be addressed in future studies (Christoffersen et al., 2019).

5. Conclusion

The present study provides detailed information on migratory behaviour of stocked turbot and native European flounder in an estuary using acoustic fish telemetry. Data revealing turbot migration behaviour were coupled with salinity data to assess likelihood of successful spawning in the area. Our study indicates that most turbot remained in the southern part of Roskilde Fjord, where spawning may have been constrained by low salinity due to the Atlantic origin of the stocked turbot. Turbot originating from the Baltic Sea may be better suited for establishing a reproducing population in Roskilde Fjord due to their lower salinity requirements for embryonic and larval developments. In contrast to turbot, our results suggest that the majority of European flounder migrate towards more marine waters prior to the spawning season, while a limited number of fish presumably remained inside Roskilde Fjord during the spawning season. The various migration behaviours of European flounder prior to the spawning season may indicate partial spawning migration. Thus, European flounder may utilize both Roskilde Fjord and more marine waters as spawning areas. Although further research is needed, this information may help managers protecting spawning areas and selecting suitable populations matching local salinity conditions to ensure successful spawning after the hatchery fish are released.

Declaration of Competing Interest

None.

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