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The function of the Wadden Sea in the life cycle of small pelagic fish

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A R T I C L E I N F O

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A B S T R A C T

Most fish species require different habitats to complete their life cycle, with coastal areas often playing a crucial role as nursery areas for juveniles. The Wadden Sea is an important nursery area for juvenile fish in the North Sea ecoregion. Despite extensive research on the nursery function of the Wadden Sea for demersal species, its role in the life cycle of small pelagic fish (SPF) remains largely unknown. This limits our understanding of the Wadden Sea ecosystem, as SPF are the dominant component of the overall fish biomass and serve as important food source for higher trophic levels. We studied the role of the Wadden Sea in the life cycle of Atlantic herring (*Clupea harengus*), European sprat (*Sprattus sprattus*), European smelt (*Osmerus eperlanus*) and European anchovy (*Engraulis encrasicolus*) through monthly stow net and seasonal trawl surveys. Our study showed that SPF use the Dutch Wadden Sea primarily as juvenile habitat, with herring being the dominant marine juvenile representative. Length frequency distributions and genetic analysis revealed that the juvenile herring originated predominantly from southwestern waters, such as the English Channel. Additionally, the Wadden Sea still provides spawning grounds for herring and anchovy, with no substantial spawning observed for sprat. While smelt can complete nearly its entire life cycle in the Wadden Sea, it depends on connectivity to nearby freshwater for spawning. In summary, the Wadden Sea functions as a nursery for juveniles, and to a lesser extent as spawning grounds for adults. A thorough understanding of these functions is crucial for identifying bottlenecks and implementing effective conservation and management strategies.

1. Introduction

Most fish migrate between habitats to complete their life cycle (Harden Jones, 1968), with coastal areas often playing crucial roles, serving as nurseries, feeding, and/or spawning areas (Beck et al., 2001; Nagelkerken et al., 2015). The Wadden Sea, the largest unbroken system of gullies and intertidal flats in the world, is an important nursery area for juvenile fish in the North Sea ecoregion (Zijlstra, 1978; van der Veer et al., 2011). Eggs and larvae of species spawning in the North Sea are transported with currents and tides towards the coast, where they spend their early life stages, before returning to the deeper waters of the North Sea at a later stage (Bolle et al., 2005, 2009; Dickey-Collas et al., 2009).

While the nursery function for bottom-dwelling species in the Wadden Sea has been extensively studied in the past (van der Veer et al., 2011, 2022; Tulp et al., 2017), the assemblage of small pelagic fish (SPF) has received little attention to date. This lack of attention hampers the understanding of the Wadden Sea ecosystem, given that SPF are considered to be the dominant component of the overall fish biomass in the Wadden Sea (Couperus et al., 2016). However, information on the habitat use of SPF throughout their life cycles is unavailable, leaving the role of the Wadden Sea for each life stage unclear.

The Wadden Sea has been significantly impacted by large-scale infrastructure projects (Redeke, 1939; de Jonge et al., 1993). For instance, the Wadden Sea had an open connection to the Zuiderzee until the Afsluitdijk dam was built in 1932, closing off a large water body. This caused substantial changes in water currents and habitat availability (de Jonge et al., 1993) and resulted in major shifts in the fish community (Redeke, 1939), including the disappearance of large spawning populations of European anchovy (*Engraulis encrasicolus*, hereafter anchovy) and Atlantic herring (*Clupea harengus*, hereafter herring) (Boddeke and Vingerhoed, 1996). Until now, it was unclear whether the Wadden Sea still serves as spawning habitat for SPF.

Nowadays, the most abundant SPF in the Wadden Sea are herring and European sprat (*Sprattus sprattus*, hereafter sprat) (Couperus et al., 2016; Maathuis et al., 2024a). Together with European smelt (*Osmerus eperlanus*, hereafter smelt), they form a crucial component of the food

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web, providing the trophic link between zooplankton and piscivorous fish, birds, and sea mammals (Dänhardt and Becker, 2011). Furthermore, herring and sprat populations in the North Sea support important fisheries. Yet, the geographical origin and timing of spawning of SPF occurring in the Wadden Sea remained uncertain, particularly for herring, with its complex life history, involving multiple spawning grounds and distinct spawning periods (McQuinn, 1997; Payne, 2010). Drift modeling of Dickey-Collas et al. (2009) indicated that larvae in the Wadden Sea originate from the Downs winter-spawning herring population, which spawns in the English Channel. However, variations in herring body lengths and densities observed throughout the year indicate a mix of spawning origins (Maathuis et al., 2024a). Therefore, despite herring's dominance in the Wadden Sea, it remains unclear from which spawning populations they originate.

The function of the Wadden Sea in the life cycle of SPF was examined using four key species currently or historically dominant or with a significant role in the food web: herring, sprat, smelt, and anchovy. For each species, two hypotheses were tested: 1) the Wadden Sea serves as a juvenile habitat, with variations in spatial distribution among species, corresponding to their origin or life history; and 2) the Wadden Sea functions as a spawning ground (excluding smelt). In addition, a third hypothesis was formulated specifically for herring: 3) herring in the Wadden Sea originate from the Downs winter-spawning population.

Therefore, abundance, body length, and maturity were measured, incorporating temporal and spatial variation over a two-year period, using two fishing methods with different temporal and spatial coverage. In 2021–2022, a monthly stow net survey was conducted focusing on seasonal variation in three geographically distinct Wadden Sea areas. In 2022, a trawl survey was carried out in May and October in all tidal inlets and connecting channels, with a higher spatial resolution. Furthermore, genetic analyses of herring were conducted to identify the populations present in the Wadden Sea, providing insights into their geographical origin and spawning period.

2. Methods

2.1. Study area

The Wadden Sea is a large interconnected system of gullies, intertidal sand flats, mud flats, and salt marshes. It borders the North Sea coasts of the Netherlands, Germany and Denmark and is characterised by strong tidal currents. Although most of the Wadden Sea is shallow, with depths typically below 15 m, the inlets between the barrier islands connecting the Wadden Sea to the North Sea are up to 40 m deep. This study was done in six inlets, from west to east: Marsdiep, Vliestroom, Borndiep, Westgat, Lauwers, and the Ems-Dollard (Fig. 1). The inlets were grouped to represent three main areas: West (Marsdiep and Vliestroom), East (Borndiep, Westgat and Lauwers) and Ems-Dollard, in accordance with Tulp et al. (2017), and supported by a basin cluster analysis based on ecotopes (Baptist et al., 2019). The western area is the deepest, the eastern area is the most saline, and the Ems-Dollard is an estuary characterized by high turbidity levels and lower salinity.

2.2. Field sampling

Fish community composition and fish size distribution were assessed using two survey methods: a monthly stow net survey, and a seasonal trawl survey.

2.2.1. Monthly stow net survey

Each month from 22-3–2021 until 3-3-2022 fishes were caught in four inlets (Marsdiep, Vliestroom, Westgat and Ems-Dollard, Table 1) via stow net fishing. This is a passive fishing method using water currents driving fish into the net, held open by two 8-m beams. The nets were positioned vertically in the water during high current speeds at both incoming and outgoing tide during daytime. Weather permitting, nets were deployed on both sides of the ship and treated as a single haul. The nets covered the entire water column (average depth 5.3 m), with a stretched mesh size of 20 mm in the codend. Polyethylene codends were used in all months except April when, due to miscommunication, a nylon net with the same mesh sizes, but including hoops, was used. This resulted in catchability differences, where in April, fish smaller than 9 cm were hardly caught (Supplementary Fig. S1). However, we chose to include the April data in the analysis, as no alternative data were available. During some hauls, jellyfish (mainly *Mnemiopsis leidyi*), Bryozoa (*Electra pilosa*), or sea lettuce (*Ulva lactuca*) partially clogged the net, mainly between May and November. Fixed fishing locations were used, with backup sites designated for stormy weather (Fig. 1). Typically, these sites were near each other, except in the Ems-Dollard, where fishing occurred for 6 months in the Dollard (southern site Fig. 1), and for 5 months in the Westereems (northern site Fig. 1), located about 30 km northwest of the Dollard location. The Ems-Dollard is an open estuary, therefore the conditions in the Dollard, closer to the Ems river, differ from the Westereems. Not all inlets could always be fished, owing to adverse weather conditions, particularly in autumn and winter (Table 1). Altogether, 75 hauls were conducted, with an average

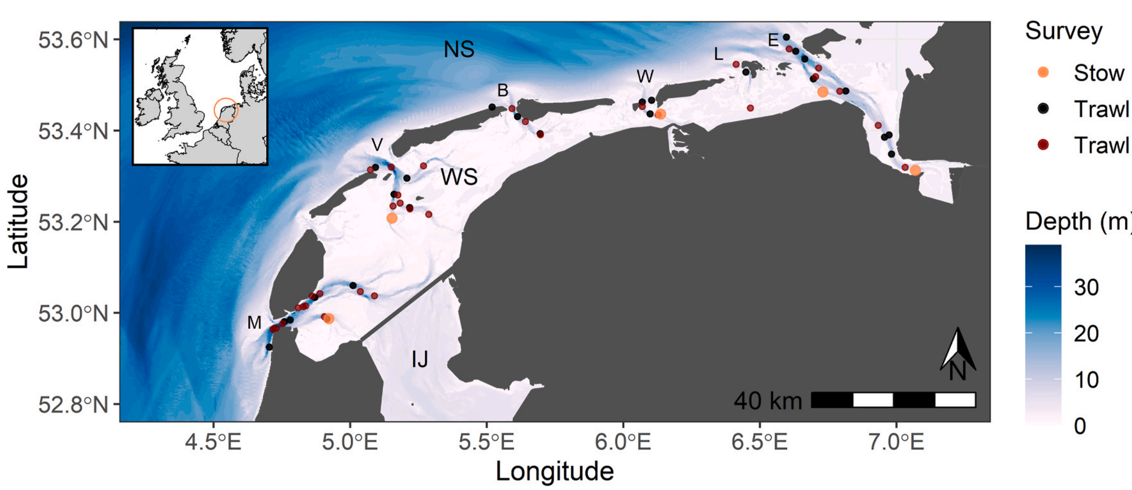

Fig. 1. Map of the study area showing Wadden Sea (WS), North Sea (NS) and Lake IJssel (IJ). Coloured circles represent sampling locations of the two surveys, with the six inlets denoted by their initial letters (M = Marsdiep, V = Vliestroom, B = Borndiep, W = Westgat, L = Lauwers, and E = Ems-Dollard). Stownet fishing occurred monthly in 2021–2022, and trawls were taken in May and Oct 2022. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Overview of sampling periods and sample sizes of hauls and individual fish used for final analysis. Abbreviations - Inlets: M = Marsdiep, V = Vliestroom, B = Borndiep, W = Westgat, L = Lauwers and E = Ems-Dollard; species: Her = herring, Spr = sprat, Osm = smelt and Ane = anchovy; * indicates fishing was conducted at the backup site Dollard instead of Westereems, and ** indicates a different net was used.

Survey	Sampling period	Number of hauls per inlet						Number of fish for maturity assessment				DNA samples
		M	V	B	W	L	E	Her	Spr	Osm	Ane	Her
Stow net	22–25 Mar '21	2	2	–	2	–	2	47	39	13	0	0
	26–30 Apr '21**	2	2	–	2	–	2*	34	17	45	2	0
	18–20 May '21	2	2	–	2	–	–	17	13	35	10	0
	21–24 Jun '21	2	1	–	2	–	2	24	36	42	0	0
	25–28 Jul '21	2	2	–	2	–	2*	27	23	77	8	0
	23–26 Aug '21	–	2	–	2	–	1	27	7	53	0	0
	19–22 Sep '21	1	1	–	2	–	1	24	25	38	10	0
	24 Oct-3 Nov '21	1	2	–	2	–	2*	48	40	65	0	0
	22–25 Nov '21	–	1	–	2	–	1*	37	22	49	0	0
	13–16 Dec '21	1	2	–	2	–	2*	76	48	73	0	0
	23–25 Jan '22	–	1	–	2	–	2*	61	39	50	0	0
	1–3 Mar '22	–	–	–	2	–	2	63	30	15	0	0
Trawl	9–18 May '22	6	4	3	3	1	8	120	36	19	174	17
	17–26 Oct '22	6	6	3	2	2	6	99	31	40	2	19
Sums	**Mar '21 – Oct '22**	**35**	**38**	**6**	**29**	**3**	**33**	**704**	**406**	**614**	**206**	**36**

haul duration of 48 min.

Flow velocity was measured throughout each haul, using two flow meters (General Oceanics, USA), positioned approximately 10 m behind the vessel to avoid interference with the net. Mean flow velocity and net opening area were used to calculate catch per unit effort (CPUE) as catch rate in numbers per 10000 m^3 water. Fish total length was measured to the nearest mm. Additionally, clupeid post-larvae were regularly caught but too small for accurate field identification, likely comprising a mixture of juvenile herring, sprat, and pilchard (*Sardina pilchardus*). Most were identifiable from 5 cm in length, with nearly all identifiable above 6 cm. Visibility, water temperature and salinity were measured during stow net sampling using a Secchi-disk and a Valeport mini CTD (Valeport Ltd, United Kingdom). Temperature ranged from 5 °C in February up to 21 °C in July, visibility ranged between 0.2 m and 2.2 m, and salinity fluctuated between 14 and 31, see Supplementary Fig. S2 for trends per area.

2.2.2. Seasonal trawl survey

Daytime trawl hauls were conducted over two fortnight periods in May and October 2022, across the six inlets (Fig. 1; Table 1). The trawl hauls were part of a hydro-acoustic survey covering all deeper inlets of the Dutch Wadden Sea, using a commercial fishing vessel. A semi-pelagic otter board trawl net, with a 17 m horizontal by 5 m vertical opening (based on sewing pattern dimensions) and a 10 mm mesh codend lining, was towed behind the vessel. Fishing speed averaged 3 knots through water, with hauls mainly executed in midwater, between 5- and 10 m depth. The average depth of the water column during fishing was 16.6 ± 7 m. In total, 50 hauls were conducted, with an average duration of 14 min. Haul duration was used to calculate CPUE, expressed as fish numbers per minute trawling. Fish total length was measured to the nearest mm.

2.3. Maturity assessment

Herring, sprat, smelt, and anchovy were collected during both surveys for assessment of fish maturity. For each area, up to 5 individuals per cm size class per month were collected. Under our permit for animal experiments, the minimum size for collecting herring, smelt, and anchovy was restricted to 8 cm, and to 6 cm for sprat. The maturity assessment followed the ICES M6 scale, where stages 1–4 represent immature, maturing, spawning, and spent, respectively (ICES, 2014). Stages 5 (omitted spawning) and 6 (abnormal gonad) were not observed. In total, 704 herring, 406 sprat, 614 smelt and 206 anchovy were assessed for maturity (Table 1).

2.4. Genetic assessment of herring

Fin tissue clips were collected from 36 herring during the trawl survey, 17 in May and 19 in October 2022, covering all observed sizes and all areas. Genotyping was performed using 59 single-nucleotide polymorphism (SNP) markers across 20 chromosomes to assign individuals to distinct herring populations, defined by spawning grounds and spawning seasons, following the procedure described by Seljestad et al. (2024). For nine individuals, >25% of the SNPs were missing due to low DNA quality genotypes. However, the most informative markers to discriminate herring populations relevant for this study were genotyped and thus these nine samples were not removed from further analysis. For assignment the R-package rubias (Moran and Anderson, 2019) was used, estimating individual posterior assignment probabilities by a fully Bayesian model conditional on the reference allele frequencies with a parametric bootstrapping correction (2000 MCMC iterations, 100 burn-in, 100 bootstraps). Bootstrap corrected posterior means of membership in each grouping were used to assign individuals to their most likely baseline population. We used the established baseline by Seljestad et al. (2024) for the assignment analysis.

2.5. Data analysis

Data analysis was conducted in R (version 4.3.1; R Core Team, 2023) and RStudio (version 2023.06.1; RStudio Team, 2023). CPUE data were aggregated per centimeter class (rounded down to the nearest integer) per haul. Two stow net surveys were delayed due to bad weather; however, to maintain consistency in data analysis, the period October 24 to November 3, 2021 was designated as October, and March 1 to 3, 2022 as February. To depict seasonal and spatial variation in SPF species and length composition while ensuring visibility of all species, CPUE data required fourth root transformation due to significant differences in catch rates, after which CPUE data were averaged per season and area. Furthermore, species-specific length frequency distributions were generated by averaging square root transformed CPUE data per bimonthly period and subsequently back transformed. Then proportions of maturity stages were calculated per cm class, per bimonthly period, and applied to the length frequency distributions. To provide an overview of the proportion of each maturity stage per length class, data from all months and locations were pooled. Both surveys were combined, and since we aimed for representative maturity sampling, no additional adjustments for catchability were made.

Length frequency distributions were used to identify the arrival of new year classes, with a notable reduction in sizes indicating the presence of young-of-the-year (YOY) individuals. To investigate spatial variation and potential origins of YOY herring using stow net catch data, average lengths and CPUEs were calculated per month per inlet for YOY herring (defined as herring smaller than 8 cm), and the two months of highest YOY influx were further examined. The 8 cm threshold was selected to capture the first peak of small herring observed in the monthly length frequency plots of herring (see Supplementary Fig. S3). This analysis was not conducted for the other species because of insufficient data (spatially or temporally).

Ethical statement

All sampling was performed in accordance with Dutch law concerning animal welfare. The protocol was approved by the Animal Ethical Commission of Wageningen UR (experiment code: 2020.D-0026.001; application: 40100202010984).

3. Results

3.1. Seasonal and spatial species composition

Herring was the most abundant SPF species in the Dutch Wadden Sea, followed by sprat (Fig. 2). Additionally, smelt, anchovy and clupeid post-larvae were observed regularly. Two other SPF species were only briefly observed: sandeel (*Ammodytes* sp.), typically buried in the sand for most of the year, was frequently caught in May, while pilchard was frequently caught in September. Clupeid larvae appeared in January and numbers peaked in May and June, before they were large enough to be identified. A spatiotemporal pattern in clupeid larvae abundance was present: increasing from west to east from spring to summer. Herring maintained high abundances year-round in all inlets. Sprat showed highest abundances in the West, except in spring 2021, where small sprat were most abundant in Ems-Dollard. Smelt was most prevalent in the Ems-Dollard and in the East. Smelt abundance in the Ems-Dollard varied with sampling location and was notably higher when sampled in the Dollard compared to the Westereems. Anchovy was present in all inlets, in low numbers throughout the year.

3.2. Herring

Herring abundance peaked in July and August. Herring sizes ranged from 4 to 27.7 cm, with the majority smaller than 12 cm. Individuals larger than 12 cm were observed from November to April (Fig. 3A, upper panel). Based on the stow net survey, the influx of YOY herring in 2021 began in June, reaching its peak in July and August. However, during the 2022 trawl survey, high abundances of herring around 5.5 cm were already observed in May. So the primary influx of YOY occurred early summer, but 5–6 cm herring were continuously caught until January.

Maturity estimates revealed that most herring were juvenile, from June until September even exclusively, while in other months individuals larger than 18 cm were also observed to be maturing, spawning, or spent (Fig. 3A, middle panel). Out of 704 individuals, 39 were found to be spawning, with 31 herring spawning in October, 1 in March, 6 in April, and 1 in May. The mean size of spawning individuals was 24.1 cm, with the smallest spawning individual measuring 19.5 cm. All spent individuals were larger than 21 cm, and primarily observed in April. Spawning herring were observed in several inlets (Fig. 3A, lower panel), with one notable observation in the Lauwers inlet, where 25 of the 31 herring spawning in October were caught.

The mean length of YOY herring was lowest in the western area in most months, especially during summer (Fig. 4A). CPUE per month shows that initially, the abundance of YOY increased in the West, followed by the East, and later in the Ems-Dollard area (Fig. 4B). This pattern suggests that YOY herring originate from southwestern waters. However, in the trawl data of May 2022, the west-east gradient is less apparent, as the Lauwers inlet (East area) shows the highest CPUE of YOY herring, with a mean total length of 5.2 ± 0.2 cm.

The suggestion that herring originate from southwestern waters is supported by genetic analysis, indicating that 28 out of 36 herring were winter-spawning Downs herring, and 6 were autumn-spawning herring (mainly North Sea autumn-spawning (NSAS) herring, Table 2). Additionally, in May, two spring-spawning herring were identified, which were assigned as western Baltic spring-spawning (WBSS) herring but with low posterior assignment probabilities (<80%). In May, herring measuring 8 cm were identified as NSAS, while the herring of 5–6 cm and 11–16 cm belonged to the Downs population. In October, all fish below 14 cm were classified as Downs, while those above 23 cm comprised a mixture of different populations.

3.3. Sprat

Sprat were present year-round. Their sizes ranged from 4 to 15.2 cm, with the majority being smaller than 8 cm (Fig. 3B, upper panel). Multiple peaks across the different lengths were observed, notably visible in the monthly length frequency distribution (Supplementary Fig. S3). In June, the peak of small sprat occurred at 8 cm, while in July, it occurred at 5 cm, suggesting the presence of a new year class. Sprat smaller than 5 cm were consistently observed from July until February. A second peak of YOY emerged in December, although with lower CPUEs than the July peak. The influx of sprat measuring 4–5.5 cm occurred locally, with the highest CPUEs observed in Marsdiep in July, and in Vliestroom in December. The sprat cohort entering the Wadden Sea in July showed a 2 cm increase in length frequency by September, while sprat entering in December reached only 6 cm by March.

Most sprat in the Dutch Wadden Sea were juveniles (Fig. 3B, middle panel). However, the first sprat began to mature at 6–7 cm, with 90% reaching maturation by 10 cm. Out of 406 assessed individuals, only 4 spawning sprat and 12 spent individuals were observed, all between March and July. Spawning sprat were exclusively observed in the western Wadden Sea (Fig. 3B, lower panel), while spent sprat were also observed in eastern areas. The average size of spawning and spent individuals was 11.5 cm, ranging from 8.8 to 12.7 cm.

3.4. Smelt

Smelt abundance varied by location and month, with the highest mean CPUE observed in October. Smelt sizes ranged from 4.2 to 24.7 cm. The length frequency plot shows two peaks from September to February: one representing YOY and another for older individuals, suggesting the presence of multiple year classes (Fig. 3C, upper panel). The influx of YOY started in late summer with a few individuals in July and August, yet the main peak occurred in September and October. YOY smelt were primarily observed in the Ems-Dollard and the eastern Wadden Sea, with only 5 YOY caught in the western Wadden Sea. Furthermore, the trawl survey also showed highest CPUEs for smelt in October, with dominance of the Ems-Dollard area. However, contrary to the stow net survey, smelt smaller than 8 cm were hardly caught during the trawl survey. Monthly length frequency distributions showed an increase in mean body length from around 5 cm upon influx to 7.5 cm by October, followed by stable lengths over the winter months, and from March onwards clear increase of body length again (Supplementary Fig. S3).

Most smelts were either juveniles or maturing individuals. From September to February, the first CPUE peak comprised solely of juveniles, while the second CPUE peak consisted of maturing individuals (Fig. 3C, upper panel). However, from March onward, maturity was less dependent on size, with juvenile, maturing, and spent individuals observed above 10 cm. At 14 cm, the percentage of maturing smelt surpassed the percentage of juvenile smelts (Fig. 3C, middle panel). No spawning individuals were observed in the Wadden Sea (Fig. 3C, lower panel), and larger fish were absent in February and March (Supplementary Fig. S3), indicating adults left to spawn in freshwater. Spent individuals were observed in April, with an average length of 15 cm, which were observed in all inlets except Vliestroom.

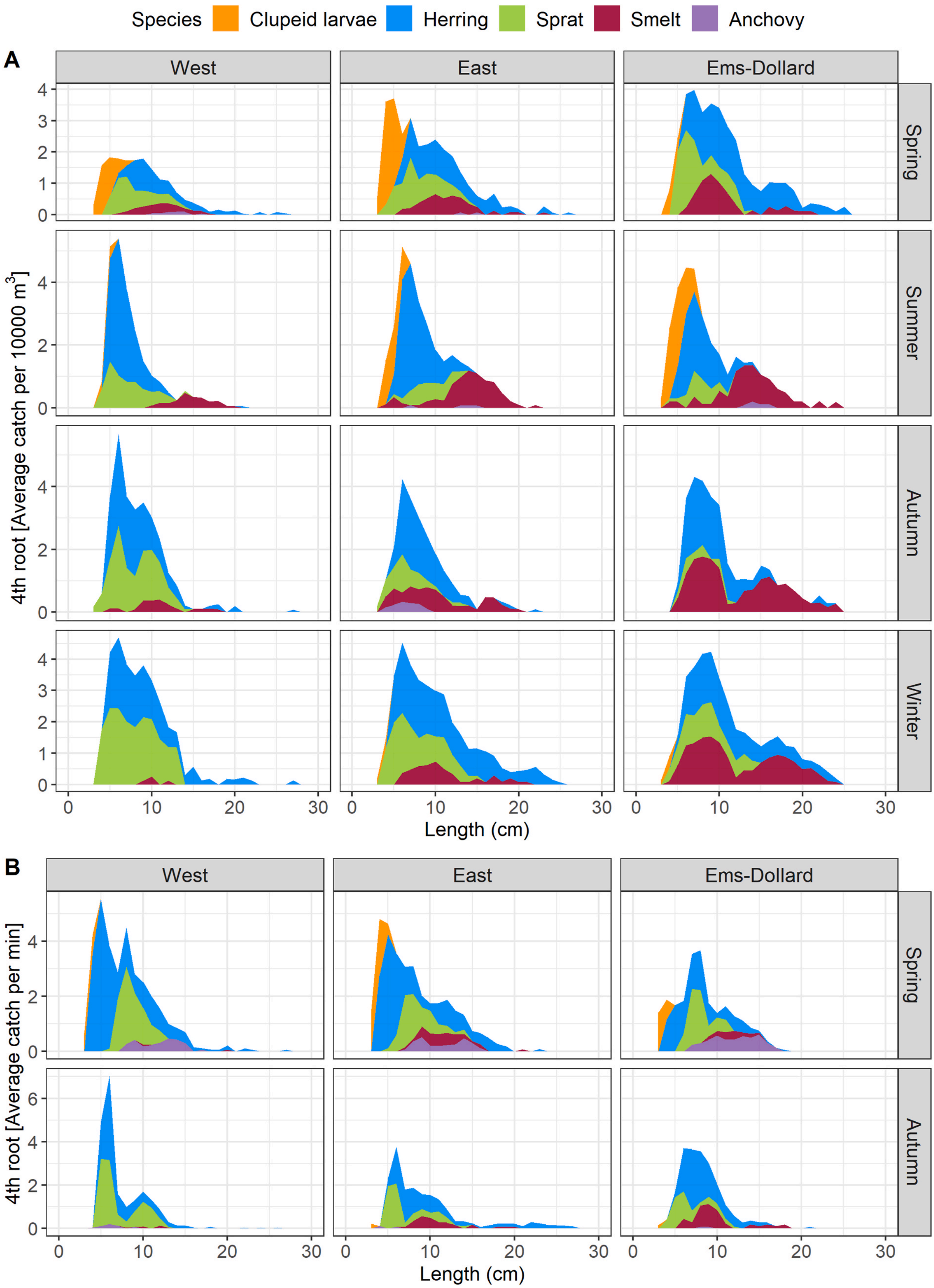

Fig. 2. Cumulative length frequency distributions of five species across different areas and seasons for A) stow net survey (2021–2022) and B) trawl survey (2022). The Y-axes denote fourth root transformed CPUEs, measured per 10000 m^3 (A) or per minute trawling (B). The colours denote different species, with clupeid larvae being unidentified post-larvae of the family Clupeidae. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

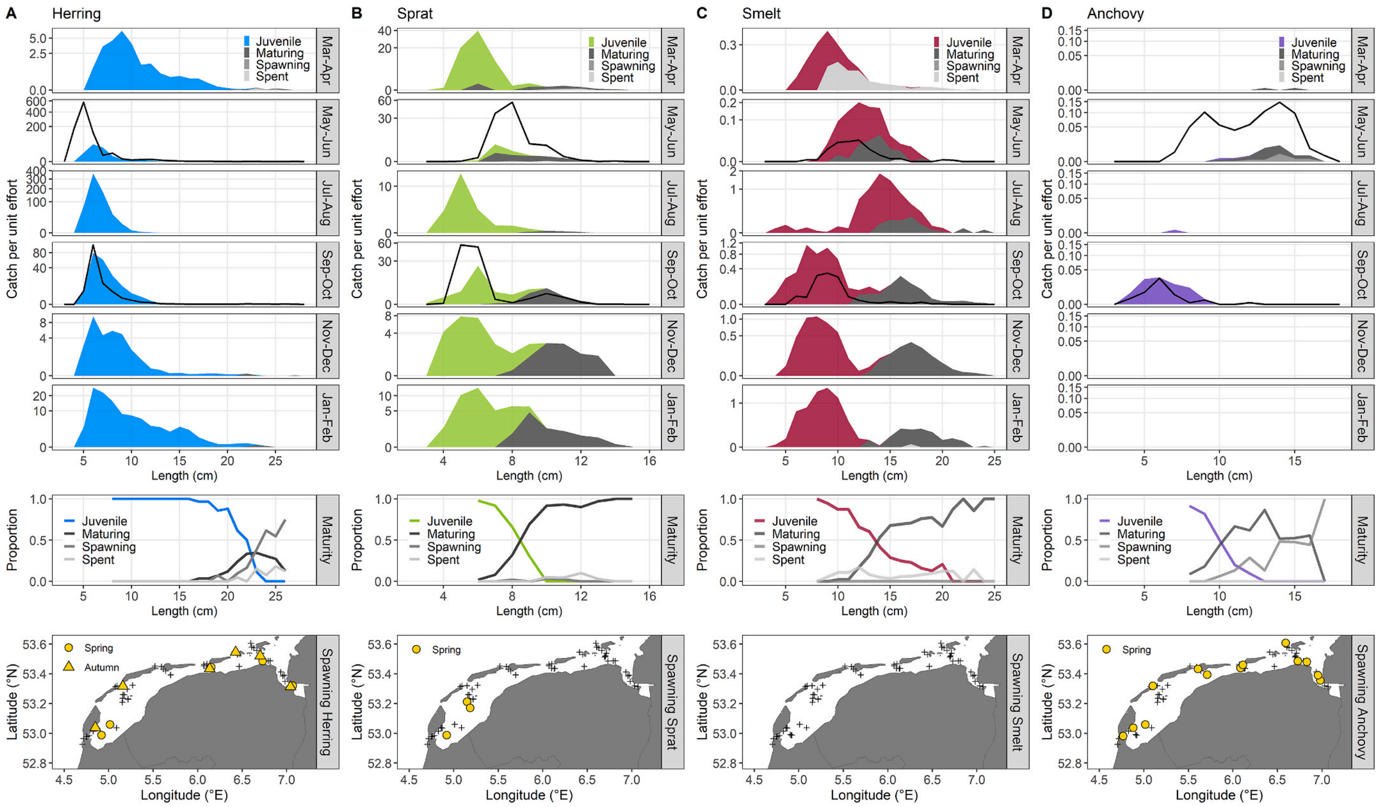

Fig. 3. Upper panels: length frequency distributions of small pelagic fish in the Dutch Wadden Sea captured by the stow net survey (coloured areas) per bimonthly period from March 2021 to February 2022, combined with data from the trawl survey in May and October 2022 (black line). The square root scaled Y-axes represent average CPUEs, with the stow net survey measured numbers per 10000 m^3 and the trawl survey per minute. Middle panels: proportions of small pelagic fish in specific maturity stages, averaged over both surveys, all months and locations. Lower panels: maps displaying locations where spawning individuals were observed during both surveys, with shapes denoting the period caught, and hauls without spawning individuals marked with '+'. Panels are arranged identically for each species: A) *Clupea harengus*, B) *Sprattus sprattus*, C) *Osmerus eperlanus*, and D) *Engraulis encrasicolus*. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

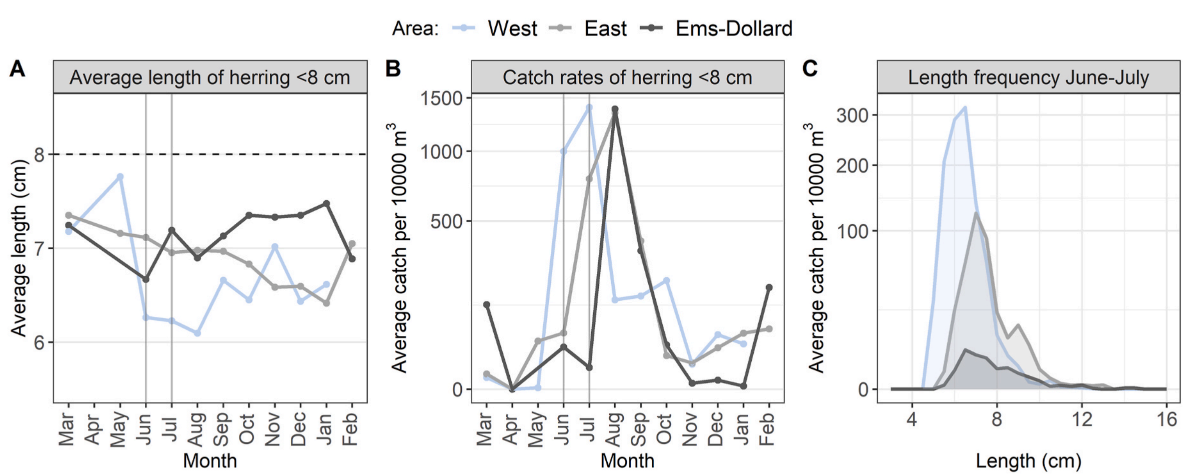

Fig. 4. A) Average length of herring smaller than 8 cm per month, with colours indicating area. B) Herring catch per unit effort (CPUE) per month and C) length frequency for herring in the main influx period (June and July) across three areas. CPUE is measured per 10000 m^3, and figure is based on monthly stow net data. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.5. Anchovy

Anchovy presence in the Dutch Wadden Sea was seasonal, with generally modest abundance (Fig. 3D, upper panel). The highest densities were recorded in May, observed across all inlets but highest in the Ems-Dollard area. The trawl survey revealed two peaks in length frequency in May: around 9 cm and 14 cm, with the largest individual measuring 17.5 cm. YOY were observed in autumn, albeit only locally: in September 2021 in Westgat and October 2022 in Marsdiep, with sizes starting at 4.3 cm.

In September–October, all anchovies were juvenile, while in May–June, the individuals were mainly maturing or spawning (Fig. 3D, upper and middle panel). Spawning was observed exclusively in May and June and occurred in all inlets (Fig. 3D, lower panel). The average

Table 2
Spawning ground population classification of 36 herring based on genetic analysis and stock assignment model. Area indicates catch location (ED = Ems-Dollard). Maturity stage is indicated as: juvenile (Juv), maturing (Mat) or spawning (Spa). Population shows the most likely population to which the individual belongs: Downs winter-spawners (Downs), North Sea Autumn Spawners (NSAS), Western Baltic Spring Spawners (WBSS), Baltic Autumn-Spawning herring (BASH). Assignment probability that an individual is assigned to the given baseline population and missing SNPs are provided.

Month	Length (cm)	Area	Maturity	Population	Probability	Missing SNPs
May	5.3	West	Juv	Downs	1.00	0
	5.3	East	Juv	Downs	0.97	1
	5.6	East	Juv	Downs	1.00	2
	5.7	West	Juv	Downs	0.99	0
	5.8	West	Juv	Downs	0.99	0
	8.1	ED	Juv	NSAS	0.98	0
	8.3	ED	Juv	NSAS	1.00	2
	8.8	ED	Juv	NSAS	1.00	0
	11.1	ED	Juv	Downs	1.00	8
	11.7	ED	Juv	Downs	0.91	5
	11.9	ED	Juv	Downs	1.00	22
	13.2	ED	Juv	Downs	1.00	2
	13.2	ED	Juv	Downs	1.00	23
	13.7	ED	Juv	Downs	1.00	0
	16.3	ED	Juv	Downs	1.00	36
	22.5	West	Spa	WBSS	0.63	13
	22.7	West	Spa	WBSS	0.80	19
Oct	5.8	West	Juv	Downs	1.00	16
	6.0	West	Juv	Downs	1.00	3
	6.2	West	Juv	Downs	1.00	4
	6.3	West	Juv	Downs	1.00	10
	8.5	East	Juv	Downs	0.93	3
	8.6	West	Juv	Downs	1.00	35
	8.9	East	Juv	Downs	1.00	5
	8.9	East	Juv	Downs	1.00	4
	13.2	West	Juv	Downs	0.98	19
	13.3	East	Juv	Downs	1.00	2
	13.3	East	Juv	Downs	1.00	16
	13.9	West	Juv	Downs	1.00	36
	23.0	West	Spa	BASH	1.00	1
	24.7	West	Mat	NSAS	1.00	2
	24.7	East	Spa	Downs	1.00	2
	26.7	East	Spa	Downs	0.99	7
	26.9	East	Spa	Downs	1.00	0
	26.9	West	Spa	NSAS	0.98	0
	27.3	East	Spa	Downs	1.00	2

size of spawning anchovy was 14.4 cm.

4. Discussion

4.1. Wadden Sea as nursery area for SPF

The presence of juvenile SPF, typically smaller than 10 cm, supports the hypothesis that the Wadden Sea serves as a juvenile habitat. Following Beck et al. (2001), there are four requirements for a juvenile habitat to qualify as nursery: if juvenile fish exhibit 1) higher densities, 2) accelerated growth, 3) improved survival, or 4) more successfully transition to adult habitats compared to other habitats. Below, we discuss the four factors outlined in Beck's paper, using our data and those available in literature.

The requirement of higher densities can be addressed using Tulp et al. (2017). They examined the biomass contribution of herring, sprat, and smelt across the Dutch Wadden Sea and along the Dutch coast. They found that smelt and herring predominantly inhabited the Wadden Sea, with smelt most prevalent in Ems-Dollard, while sprat was more abundant along the Dutch coast. Their study was based on a beam trawl survey, using gear that is not optimal for catching SPF. In the International Bottom Trawl Survey (IBTS), located further offshore, sprat is the dominant SPF species, followed by herring and eventually anchovy (Grift et al., 2004; ICES DATRAS Database, 2024). Moreover, in coastal acoustic surveys carried out in 2002–2003 in April and June along the Dutch coast, sprat dominated the catches while herring measuring 6–8 cm were almost absent (Grift et al., 2004). This finding was confirmed by a recent coastal survey in June 2023 (unpublished data Wageningen Marine Research), indicating that YOY herring are more bound to shallow waters like the Wadden Sea compared to sprat. Despite the challenges of comparing fish densities between different regions using fishing methods with different catchabilities, it appears that the Wadden Sea supports substantial numbers of herring, anchovy and smelt compared to neighboring waters. However, for sprat, this is less clear, as its distribution is more offshore. Within the Wadden Sea, comparing the pelagic habitat with salt marshes, herring and smelt occur in both habitats, while sprat and anchovy were mainly observed in deeper water (Friese et al., 2021). In these salt marshes, only small individuals were observed, frequently measuring below 4.5 cm.

Estuaries are typically highly productive because of nutrient inflow (Cloern et al., 2014) and are often warmer than offshore waters during spring and summer (van Aken, 2008), accelerating growth rates (Peck et al., 2012). For instance, optimal temperatures for the early life stages of sprat range between 18 and 22 °C (Peck et al., 2012), which is within the range of the water temperatures we observed in the Wadden Sea from June to September, the period of primary influx of YOY sprat. The seasonal shifts in our length frequency data indicate growth for sprat, smelt and herring. However, quantifying exact growth rates by tracking the size of specific cohorts over time was not feasible here due to immigration and emigration within the year.

Juvenile fish typically face high mortality due to predation. A modeling study investigating the survival of juvenile herring in the Scheldt estuary (southern North Sea), revealed that herring migrating to estuaries during their early life stages exhibited a 10-fold increase in survival compared to those remaining at sea, which was primarily attributed to decreased predation pressure in turbid estuarine waters (Maes et al., 2005). In the Wadden Sea, main predators of SPF include seabirds such as terns, and piscivorous fish such as whiting and sea bass (Baptist and Leopold, 2010; Cardoso et al., 2015; Maes et al., 2005). These predators primarily rely on sight for hunting, with terns often foraging at the boundary between turbid and clear water (Baptist and Leopold, 2010). Turbid waters may increase the survival rates of juvenile fish by reduced predation or increased plankton availability (e.g. Fiksen et al., 2002; Utne-Palm, 2002; Maes et al., 2005). The mean visibility measured during stow net fishing was 0.8 m, relatively low compared to the North Sea (Capuzzo et al., 2015), indicating that SPF can 'hide' in the Wadden Sea. However, the effect of turbidity on fish depends on species and intensity, as high turbidity can also negatively impact foraging success (Whitfield, 2021).

The presence of open connections through inlets suggests unhindered migration between the Wadden Sea and the North Sea (Couperus et al., 2016). However, for the anadromous smelt, obstacles like the Afsluitdijk hinder the connection with freshwater. Determining the contribution of juvenile habitats to adult populations, is essential for assessing the importance of the Wadden Sea on a population level, which requires large-scale sampling (e.g. van der Veer et al., 2024). Additionally, studying otolith microchemistry could potentially reconstruct fish movements and addressing natal origins through analysis of element profiles along otolith axes (Nachón et al., 2020).

In summary, the Wadden Sea exhibits relative high densities of juvenile SPF compared to neighboring areas, it has the potential for fast growth and increased survival rates, and offers good migration possibilities to contribute to the adult populations (apart from smelt). The Wadden Sea thus qualifies as a nursery area for SPF based on these criteria. Long-term trends show that the nursery function of the Wadden Sea is reduced for several flatfish species since the 1990's (van der Veer et al., 2011, 2022). Yet, there is no historical reference for SPF, making it difficult to assess long-term trends in their nursery function in the Wadden Sea. SPF have not been regularly sampled using pelagic gear, so historical records are limited. However, data from demersal surveys (which are suboptimal for pelagic fish) suggest a pattern of increasing pelagic species densities during the late 20th century, followed by a gradual decrease in recent decennia (Tulp et al., 2017).

4.2. Wadden Sea as spawning habitat for SPF

Spawning grounds vary between species and reproductive strategy. Anchovy and sprat are indeterminate multiple-batch spawners whose eggs are released in the water, while herring and smelt are determinate single-batch spawners that deposit eggs on suitable substrates (Belyanina, 1969; Frost and Diele, 2022; Petitgas, 2010). Historically, before the construction of the Afsluitdijk, anchovy, herring and smelt spawned in the Zuiderzee in large numbers, supporting an important fishery around the 1930s (ICES, 1903; de Jonge et al., 1993; Redeke, 1939). However, the closure of the Afsluitdijk drastically changed the ecosystem: a transition from an estuarine bay to a freshwater lake. This led to the disappearance of herring shortly after closure, and two decades later, anchovy also disappeared (Boddeke and Vingerhoed, 1996; de Jonge et al., 1993; Petitgas et al., 2012; Redeke, 1939). One of our objectives was to study if remnants of these historic spawning aggregations still occur. We observed spawning herring both in spring and in autumn. Spawning occurred in various inlets in the Wadden Sea, with a notable concentration in the northern part of the Lauwers inlet during autumn. In May, the highest CPUE for herring was recorded in the Lauwers inlet, with a clear size peak around 5 cm. Additionally, many spent herring were found north of Schiermonnikoog in January 2024 (unpublished results Wageningen Marine Research). These findings suggest a potential local spawning aggregation north of Lauwers, with subsequent juvenile development occurring in the Lauwers inlet. Additional surveys for eggs and larvae, complemented with genetic or microchemistry analysis, are necessary to confirm this.

Genetic analysis showed that spawning herring in October included both autumn-spawning and winter-spawning populations, with the latter group found in the Lauwers inlet. Two spring-spawning individuals revealed low assignment probabilities, suggesting they may belong to a population not represented in the baseline data. These two individuals, currently assigned to WBSS, may actually belong to a local coastal population. Historically, herring spawned in the Zuiderzee from mid-April until late May, providing a spawning ground with shallow brackish water, where eggs adhered to a substrate of firm sand and mud (ICES 1903). Generally, herring attach adhesive eggs to coarse seabed substrates or aquatic vegetation such as coarse sand, gravel, small rocks, shells, kelp, and other macroalgae, in habitats with strong currents to improve oxygenation and prevent sediment build-up on eggs (Frost and Diele, 2022). Presently, the largest spring-spawning populations are found in the Norwegian and Baltic Sea. Part of the herring along the UK and Irish coasts also spawn in spring, although these populations are generally smaller (Dickey-Collas et al., 2009; Petitgas, 2010). Sightings of spring-spawning herring have been recorded for the German Wadden Sea in the past decade: spawning herring have been observed in the Jade Bay in April, and herring eggs were found on harbour walls in Wilhelmshaven (personal communication A. Dänhardt). Additionally, in May 2013, substantial quantities of herring eggs were discovered on *Fucus* macroalgae in the Hörnumtief and the Holmer Siel (personal communication H. Büttger). To determine the origins of the spring-spawning herring in the Dutch Wadden Sea, and whether they are possible remnants from the old Zuiderzee stock, large-scale sampling of early life stages and genetic analyses is required.

Another species potentially remnant from a Zuiderzee stock is the anchovy. Currently, the main spawning areas for anchovy are located south of the North Sea, in the Bay of Biscay, and the Mediterranean (Bellier et al., 2007). In the Netherlands, spawning occurred historically in the northern part of the Zuiderzee, the upper section of the Dollard, and in the Oosterschelde estuary in June and July (ICES 1903). Following the closure of the Zuiderzee, smaller anchovy spawning areas persisted in the Oosterschelde estuary, and anchovy eggs were detected again in 1993–1994 in the western Dutch Waddenzee (Boddeke and Vingerhoed, 1996). Water temperature and salinity are key factors in determining suitable spawning conditions for anchovy, with a water temperature of 14 °C as the lower threshold for spawning (Ibaibarriaga et al., 2007). In our study, spawning anchovy were observed at temperatures close to this lower threshold. Although anchovy abundance in the North Sea fluctuates between years (Petitgas et al., 2012), there has been an increase in anchovy populations since the 1990s (Alheit et al., 2012). This increase was likely due to the expansion of suitable thermal windows, as warmer summers and fewer severe winters improved the productivity (Petitgas et al., 2012). Genetic analysis has shown that the North Sea and English Channel anchovy constitute a distinct population from the Bay of Biscay population (Petitgas et al., 2012). Therefore, it is plausible that anchovy spawning in the Wadden Sea represents part of local remnant populations that benefitted from improved thermal conditions in recent decades.

Historically, smelt also spawned in low saline areas of the Zuiderzee (Redeke, 1939). While smelt can complete nearly its entire life cycle in the Wadden Sea, it depends on connectivity to freshwater for spawning. Currently, only two sluice complexes provide connections between the estuarine Wadden Sea and freshwater Lake IJssel. However, excess freshwater is discharged during low water, resulting in a short migration window, a sudden transition between salt- and freshwater, and high water velocity. Microchemistry analysis showed no substantial contribution from the anadromous smelt to the spawning stock of the landlocked population (Tulp et al., 2013), suggesting no substantial contribution to the Lake IJssel population by anadromous smelt. Consequently, the primary spawning locations for anadromous smelt in the Wadden Sea nowadays are likely located upstream in the unobstructed rivers Ems and Elbe (Eick and Thiel, 2014; de Jager et al., 2019). This is supported by long-term stow net monitoring in the Ems-Dollard, showing large abundances of YOY smelt in late September upstream in the Ems river (Kopetsch, 2023).

In sprat, approximately 50% reach maturity at a size of 8 cm according to IBTS data in the North Sea (Heessen et al., 2015). In our sample of 137 individuals larger than 8 cm between March and August, only 3% were found to be spawning, and 8% were spent, suggesting that the Wadden Sea is not a primary spawning ground for sprat. Typically, sprat spawning areas are situated in the German Bight, Southern Bight and English Channel (Baumann et al., 2009; Munk et al., 2024), indicating that sprat generally spawns further offshore.

Concluding, the presence of spawning individuals in the Wadden Sea suggest that the area still provides spawning grounds for herring and anchovy. Meanwhile, limited spawning was observed for sprat and no spawning for smelt.

4.3. The life cycles of SPF using the Wadden Sea

Having identified the role of the Wadden Sea as nursery and spawning areas for the four species, we now examine their entire life cycles. Herring, the dominant juvenile representative, arrives in the Wadden Sea as clupeid post-larvae or YOY and remains as a juvenile to grow and develop. However, the abundance of herring larger than 12 cm was relatively low, indicating that most larger herring leave the Wadden Sea. The primary influx period of YOY herring occurred from late May onwards. Surprisingly, small herring were observed throughout the year, suggesting that the Wadden Sea is used as juvenile habitat by multiple herring populations. Our findings support our third hypothesis that herring in the Wadden Sea originate from the Downs winter-spawning population: 78% of the sampled individuals were Downs herring. This indicates a clear connectivity for herring between habitats in the English Channel and the Wadden Sea. Additionally, a west-east gradient in YOY herring length was observed: size was generally lowest in the western area, and an increase in abundance of small sized herring started initially in the western inlets. Driven by the counter-clockwise residual circulation in the North Sea, herring offspring are transported northeastward (Dickey-Collas et al., 2009), resulting in the initial influx of juveniles into the westernmost inlets of the Wadden Sea. While the primary peak of herring influx can now be attributed to autumn and winter spawners from southwestern waters, the origin of the smaller herring entering around November until January remains unclear.

Like herring, sprat arrives in the Wadden Sea as post-larvae or YOY, remaining to grow and develop. While most individuals were under 10 cm, sizes of up to 15 cm were observed regularly. Given that sprat rarely exceeds 16 cm (Peck et al., 2012), they can complete a substantial portion of their life cycle in the Wadden Sea. However, the origin of sprat in the Dutch Wadden Sea remains unclear. A study in the German Bight showed that sprat present in August (~7 cm) originated mainly from an area north of the Wadden Sea and were hatched from mid-March to mid-May (Baumann et al., 2009). Multiple cohorts were present, including a new cohort in October (~4 cm), which were born in July (Baumann et al., 2009). This situation is similar to what we observed in the Wadden Sea, indicating that sprat in the Wadden Sea originate from a wide range of North Sea spawning grounds and periods.

In contrast to herring and sprat, smelt eggs are deposited in freshwater and juveniles enter the Wadden Sea from freshwater areas. The Wadden Sea provides juvenile habitat for smelt, which typically enter at sizes around 5 cm in autumn, and exhibit clear growth throughout the season. Smelt show a distinct spatial distribution, with higher concentrations in the eastern part, close to the freshwater outflow of the river Ems. In the Netherlands, smelt exhibit two distinct life history strategies: a migrating anadromous population and a landlocked freshwater population in Lake IJssel. The level of interchange between these two smelt populations is still unclear. Currently, there is no evidence for a substantial contribution from the anadromous population to the spawning stock of the landlocked population (Tulp et al., 2013). However, large numbers of YOY landlocked smelt flush out with discharge water through the Afsluitdijk sluices into the Wadden Sea, with a peak in October (Tulp et al., 2013). Despite frequent captures of smelt along the Afsluitdijk in fyke monitoring (van Rijssel et al., 2023), we did not observe an influx of YOY freshwater smelt into the Western Wadden Sea. This might be caused by the study locations away from freshwater inlets, further towards the North Sea.

Anchovy used the Wadden Sea only seasonally: they spawned in May and the YOY were briefly present in autumn. Being at the northern part of its distribution range, temperature plays a crucial role for anchovy (Raab et al., 2013). Temperatures between 17 and 19 °C during the growing season had a strong positive effect on the anchovy CPUE the following year, indicating such temperatures are advantageous for growth and increase the overwinter survival of YOY anchovy (Raab et al., 2013). In September, the water temperature in the Wadden Sea was still 17 °C, but dropped quickly thereafter, potentially explaining why YOY anchovy were absent after October. Similar seasonal behavior was observed in the German Wadden Sea, where adult anchovy were present in June but migrated away to deeper waters after spawning (Alheit et al., 2012).

Our study primarily focused on post larval stages. To fully comprehend the role of the Wadden Sea in the full life cycle of SPF, additional studies are necessary. These should address questions such as whether the YOY are locally produced, and when and where these early life stages occur. Conducting egg and larvae surveys, along with techniques like otolith daily increment analysis will be essential (Baumann et al., 2009). Knowledge on the role of the Wadden Sea within the entire life cycle of SPF is crucial for effective management, both for the sustainability of populations as well as their functioning within the Wadden Sea ecosystem as important prey of higher trophic levels and as predators of zooplankton (Maathuis et al., 2024b).

This study examined the role of a shallow tidal ecosystem in the life cycle of four SPF species. Globally, research on the nursery value of coastal pelagic habitats is limited, with most studies focusing on subtidal soft bottoms, seagrass beds, and mangroves (Ciotti et al., under review), or on SPF in deeper waters due to sampling challenges in shallow depths (Brehmer et al., 2006; David et al., 2022). Yet, shallow coastal waters are widely acknowledged as critical habitats for many migratory pelagic fish species during part of their life cycle (e.g. Chícharo et al., 2012; Polte et al., 2017; David et al., 2022). Notably, in the Bay of Biscay, David et al. (2022) observed significantly higher SPF biomass, as well as larger and denser shoals, in shallow areas (<20 m) compared to deeper offshore waters. Furthermore, they found higher SPF densities in summer compared to autumn. While we observed year-round use of the Wadden Sea by SPF, our study also revealed seasonal variations in abundance, species composition and size structure. These findings highlight the importance of shallow nearshore habitats for different life stages of different SPF species throughout the year.

5. Conclusions

Our study represents one of the first dedicated efforts to comprehensively investigate SPF within the Dutch Wadden Sea, both in terms of temporal and spatial coverage. Our findings highlight the Wadden Sea's importance as a juvenile habitat for SPF, and its role in providing spawning grounds, particularly for herring and anchovy. The relative high densities of juvenile SPF compared to neighboring areas, the potential for fast growth, possible increased survival rates due to favourable turbid conditions and open migration possibilities towards the North Sea, support the qualification of the Wadden Sea as a potential juvenile nursery area for SPF. However, further studies are needed to evaluate the contribution to adult populations compared to neighboring areas. Our research reveals that multiple cohorts of herring and sprat from various North Sea spawning grounds use the Wadden Sea for growth and development. Genetic analysis indicated that most herring originated from the Downs spawning population. Furthermore, adult herring were observed in spawning stage during both spring and autumn, suggesting potential local spawning aggregations. While smelt can complete nearly its entire life cycle in the Wadden Sea, it relies on freshwater connectivity for spawning. Anchovy, a seasonal visitor, arrived in May to spawn, with YOY briefly appearing in autumn. Additional research on early life stages of SPF is essential for a comprehensive understanding of the role of the Wadden Sea in their life cycles.

CRediT authorship contribution statement

Margot A.M. Maathuis: Writing – original draft, Visualization, Project administration, Investigation, Formal analysis, Data curation, Conceptualization. **Florian Berg:** Writing – review & editing, Investigation, Funding acquisition, Formal analysis. **Bram Couperus:** Writing – review & editing, Investigation, Conceptualization. **Jan Jaap Poos:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Ingrid Tulp:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Conceptualization.

Declaration of generative Ai in scientific writing

During the preparation of this work the authors used ChatGPT, a language generation tool developed by OpenAI, in order to assist in diversifying word choice and grammar. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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Data availability

Data will be made available on request.

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