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Research Article

Residents and Transients—Fish Community Dynamics in a Highly Anthropised Tidal North Sea Estuary Across the Annual Cycle

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Tidal estuaries provide important spawning, nursery and feeding habitats for a wide diversity of species and serve as transit areas for diadromous fishes. However, they are globally among the most impacted aquatic ecosystems, pressured by anthropogenic alterations and global change. Assessing local fish communities and their temporal dynamics is crucial to determine the ecological baseline of these ecosystems and to serve as an indicator of their ecological status. Here, we studied the fish community in a typical estuary of the Wadden Sea in central Europe, the strongly tidal and highly anthropised River Ems. Weekly bycatch samples from a commercial stow net fishery were analysed regarding fish community composition, individual length and biomass covering fourteen consecutive months. Thirty-nine diadromous, estuarine, marine and freshwater species were recorded, amending previously reported numbers upward. Total fish abundance peaked in November 2020 and was lowest in the first half of the year 2021, corroborating previous observations of a cyclical intra-annual community pattern in estuaries. The community structure changed significantly throughout the year, coinciding with variation in water temperature, dissolved oxygen concentrations, salinity and atmospheric pressure. During most months, European smelt (*Osmerus eperlanus*) and flounder (*Platichthys flesus*) dominated in abundance, and sand gobies (*Pomatoschistus* spp.), European eel (*Anguilla anguilla*), river lamprey (*Lampetra fluviatilis*), three-spined stickleback (*Gasterosteus aculeatus*) and European perch (*Perca fluviatilis*) occurred in substantial shares during single months. Some historically common species such as twaite shad (*Alosa fallax*), houting (*Coregonus* cf. *oxyrinchus*) and Atlantic salmon (*Salmo salar*) showed very low abundances. The non-native Western tubenose goby (*Proterorhinus semilunaris*) was first recorded in this area. Intra-annual changes in abundance and length composition of species of commercial or conservational interest, e.g., smelt and river lamprey, are discussed in detail. We show that high sampling resolution and complete annual coverage are crucial for a full picture of the fish community and conclude that the ecological status of the River Ems remains poor.

Keywords: annual cycle; biodiversity; community ecology; data-limited species; diadromous fish species; DNA barcoding; estuarine fish community; river Ems

1. Introduction

Tidal estuaries are characterised by the interplay of inflowing saline marine water and freshwater efflux through river discharge, which shape the physical characteristics such as horizontal and vertical gradients in salinity, density, pressure or turbidity [1, 2]. Through these complex hydrodynamics, estuaries provide a diversity of habitats and, for instance, serve as feeding and overwintering, spawning and nursery grounds for a variety of species [3, 4]. They also often feature high productivity and represent important migratory pathways for diadromous fish species [3–5]. Nowadays, most estuaries are increasingly under pressure through direct anthropogenic impacts and changing environmental conditions, such as weather anomalies caused by climate change [6–8].

A prime example of this global development is the here studied Ems estuary, located on the border between Germany and the Netherlands. The area was subject to severe anthropogenic alterations, such as repeated deepening to allow the passage of large vessels and coastline straightening for embankment [5, 9]. These morphological changes to the river flow caused the loss of important habitats (e.g., mudflats and shallow water zones) and strongly altered the natural current dynamics, leading to decreases in water quality, especially very high concentrations of suspended particulate matter and seasonal phases of pronounced oxygen deficiency [2, 10, 11]. As a consequence, and exacerbated by other anthropogenic impacts (e.g., reduced river continuity, eutrophication), the ecosystem has experienced a severe ecological deterioration, which was first noted through the drastic declines of single commercial fish stocks in the early 20th century and is now well documented for most components of the estuarine fauna (e.g., [5, 9, 12–15]).

To mitigate future deterioration, inform targeted restoration measures and monitor their effectiveness, baseline ecological knowledge and continuous monitoring of the estuarine ecosystem structure and function are essential [5, 16]. The structure and temporal dynamics of the estuarine fish community are particularly useful indicators of ecological status [17]. Fish are mobile organisms, and their distribution and demographics are influenced by multiple abiotic and biotic factors, such as tide, estuarine morphology, habitat connectivity, salinity, temperature and prey availability [9, 18, 19]. Anthropogenic disturbances and long-term changes within ecosystems are thus often reflected in the composition and population dynamics of fish communities [17].

To serve this purpose in the Ems estuary, a biannual fish community monitoring scheme was established in 2006 under the European Water Framework Directive (WFD), complementing previous studies which focused largely on commercially relevant species (e.g., [5, 15, 20–22]). Yet, the existing knowledge is based on snapshot analyses which, in a highly seasonal ecosystem like the Ems estuary, cannot fully resolve the dynamics and variability of the fish community [17, 21, 23, 24]. This study provides the first continuous picture of the fish community in the upper Ems estuary, covering a full annual cycle across fourteen consecutive months via weekly stow net catches. We describe the intra-annual changes in the fish community composition and provide a comparison to previous season-specific studies. Species-specific abundance dynamics and size distribution are discussed with particular emphasis on the most common species and such of high ecological interest, i.e., diadromous, endangered and non-native species.

2. Methods

2.1. Study Site. The Ems River is approximately 370 km long and drains into the North Sea through the Ems-Dollard estuary, located on the border between Germany and the Netherlands (Figure 1). The region is characterised by a temperate climate with strong seasonality, marked by cold winters with high precipitation and warmer summers [10]. The estuarine (tidal) section of the Ems measures around 100 km in length from the island of Borkum up to the Herbrum tidal weir, which separates it from the upstream river course ([5, 10, 21]; Figure 1). Since 2003, the estuary is subdivided by the Ems barrage at Gandersum, although this barrage is only closed occasionally and thus does not severely disrupt the river continuity (Figure 1; [14]). The estuary is classified as meso- to macrotidal [25], with tidal amplitudes increasing from approx. 2.5 m in the outer estuary up to 5 m near the tidal weir [2].

2.2. Sampling Strategy. The data analysed in this study were produced alongside a project monitoring the downstream migration of European eel *Anguilla anguilla* L. 1758 [26, 27]. Fish specimens were collected from five stationary stow nets placed in the lower, tidally influenced Ems River near Leer, Germany (53°14′49.7″N 7°23′47.5″E, Figure 1). Stow nets (Figures 2(a), 2(b)) are a fishing gear traditionally used in northern German estuaries [28] and frequently used in similar community-monitoring studies [21, 29]. To catch and retain fish during the full tidal cycle, an elongated catch chamber was knitted into the inside of the cod end. Captured fish that try to escape the cod end are presumed to swim close to the mesh and therefore end up in this interior catch chamber.

The nets were operated by a local fisher and were emptied daily as part of the *A. anguilla* monitoring. For this study, quantitative assessments focused on the total catch of one main net (referred to as 'MN'; maximum aperture: 3.5 × 7 m, mesh size in the cod end: 12 mm), usually collected during effluent water and shortly before low tide. MN samples were collected once per week, representing the catch of approximately 24 h, with exposure times ranging between 11 and 28.5 h. Samples were stored on ice during transport and frozen at −20°C within a few hours after catch.

Sampling was carried out consistently from November 2020 to December 2021, except for two subsequent weeks in February 2021, when sampling was not possible due to ice drift on the river, resulting in a total of 57 hauls. To improve the documentation of rare species, presence/absence data from four additional adjacent nets (hereafter: 'AN', maximum aperture: 3.5 × 7 m, mesh size in the cod end: 10–12 mm) were recorded from April 2021 onwards.

2.3. Species Identification and Biometrics. Species identification based on morphological features was conducted on thawed samples. To confirm morphological species identification, a total of 50 specimens were additionally DNA

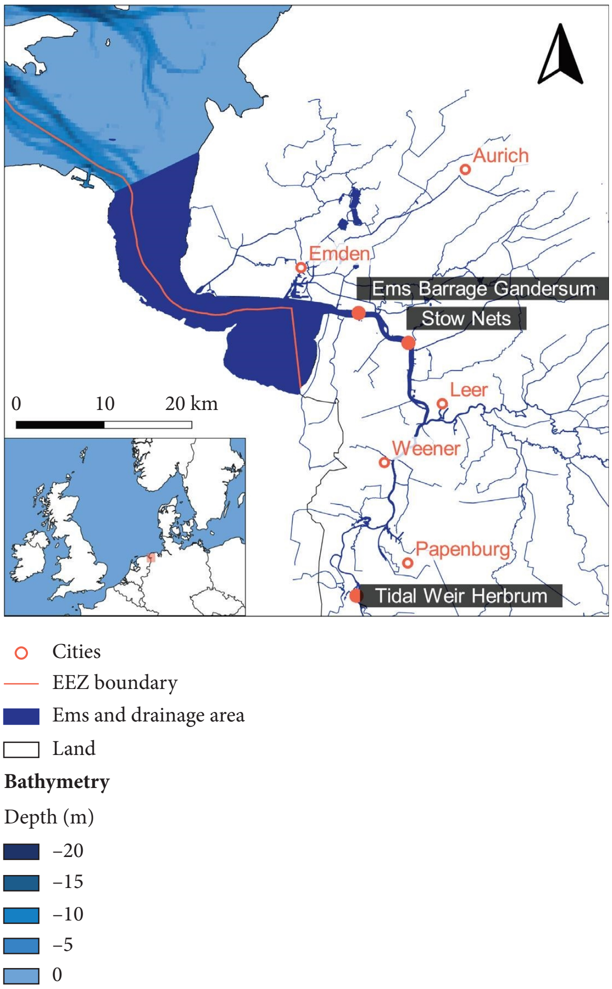


Figure 1: Map of the study area indicating the Ems estuary and location of sampling between Leer and Terborg. The barrage at Gandersum is closed occasionally to allow the passage of large cruise ships produced in a shipyard upstream or in case of storm surges [14].

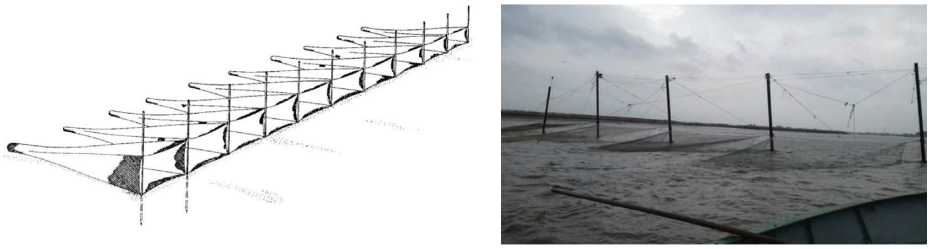

(a) (b)

Figure 2: (a) Schematic drawing of a stow net (source: [30], p. 286) and (b) image of the stow nets used in this study (photo: S. Blum).

barcoded for mitochondrial Cytochrome Oxidase I and/or 16S rRNA and compared via BLAST with NCBI Nucleotide Sequence Database [31]. If species identification was still ambiguous, genus names were used in further analyses. Owing to the high number of individuals in the catch, a representative subsample was examined morphologically and genetically for Pleuronectidae and sand gobies *Pomatoschistus* spp. In the former, only European flounder *Platichthys flesus* L. 1758 was identified, the latter contained two species: the common goby *Pomatoschistus microps* (Krøyer 1838) and the sand goby *Pomatoschistus minutus* (Pallas 1770). Since a quantitative distinction between the two species was not possible due to the physical state of several specimens, they were pooled under *Pomatoschistus* spp. in all subsequent analyses.

Total length and mass of every fish specimen were recorded during morphological examination after thawing. To enable live release of the endangered and protected European river lamprey *Lampetra fluviatilis* (L. 1758), a random subsample of 10 individuals per haul (if available) was weighed and photographed on-site for image-based length measurements in ImageJ [32], following the method described and validated for *A. anguilla* by Höhne et al. [33]. Lengths and mass of all *A. anguilla* specimens were recorded from all nets (MN + AN) for an in-depth eel monitoring described in Höhne et al. [27]. Damaged specimens (e.g., partially devoured by seals) were excluded from length and mass measurements and all subsequent biometric analyses but included in quantitative analyses, such as biodiversity indices, if their head was present.

2.4. Ethical Statement. The collection of fish specimens complied with German animal welfare laws, guidelines and policies as approved by the State Fisheries Department Bremerhaven, Germany, under the permit reference number 65432-2. Protected specimens were released at the capture site after biometric measurements had been taken.

2.5. Data Analysis. All statistical analyses were conducted in R (version 4.3.1, [34–37]). Quantitative analyses of diversity and community structure were only conducted on abundance data (MN), as body mass data could not be obtained for ~11% of all specimens (eels and lampreys ($n = 396$), as well as damaged individuals). To describe the taxonomic diversity in the total catch, species richness and Shannon–Wiener index [38, 39] were estimated through the 'vegan' package in R [40]. Sampling coverage was estimated through coverage indicators using the 'entropart' package [41–43].

Abundances were normalised for any comparison among hauls, since duration and net aperture varied among them. The effective (i.e., submerged) net opening was dependent on the tide, therefore, we first computed the effective net opening in 5-min intervals (equation (1)) and then took the average per haul. The overall average haul duration and submerged net opening surface (24.24 h and 21.16 m^2) was defined as one standard unit effort, and consequently, all abundance data were normalised to catch per unit effort (CPUE, equation (2)). Six hauls were excluded from this computation, because data on exposure time or water level (and thus effective net opening) were not available. Consequently, 51 hauls and 3789 individuals were considered in all CPUE-based analyses.

$$\begin{aligned} &(\mathrm{a})\ \text{if } l_t < h_{\max}\colon a_t = w * \left(h_{\max} - \mathrm{dif}_t\right),\\ &\text{else: } a_t = a_{\max} = w * h_{\max},\\ &(\mathrm{b})\ a_i = \frac{\sum_{Ni}^{t} a_t}{N_i}. \end{aligned} \tag{1}$$

Equation (1)—Effective net area a [m^2] per haul i and time step t, with net width $w = 7$ m, maximum net height $h_{\max} = 3.5$ m, water level l_t, tide-dependent difference between water level and top net edge dif_t [m] and total number of time steps t per haul N_i.

$$\mathrm{CPUE}_i = \frac{\mathrm{a} * \left(\left(\mathrm{T} * n_i\right) / \left(T_i\right)\right)}{a_i}. \tag{2}$$

Equation (2)—Normalised abundance (CPUE) per haul i, with mean net area $a = 21.16\,\mathrm{m}^2$; mean haul duration $T = 24.24$ h; number of fish n_i, haul duration T_i [h] and effective net area a_i [m^2].

Temporal fluctuations in the total CPUE were compared through generalised linear models (glm) [44, 45]. Alternative model formulations were assessed through the Akaike information criterion (AIC) as well as diagnostic plots, and post hoc pairwise monthly comparisons of estimated marginal means were based on the final glm (CPUE ~ 'month'; gamma distribution; identity link) [46]. Sampling coverage was also investigated for seasonal and monthly subsamples, as well as hauls, through coverage indicators or rarefaction curves, using the R packages iNEXT and entropart ([42, 47, 48]). Based on this, we decided to refrain from any comparison of alpha diversity (univariate diversity measures) between temporal subsets ([48–50]; and Figure S1).

Temporal differences within the taxonomic composition of catches were investigated via a Bray–Curtis dissimilarity matrix and a principal component analysis (tb-PCA) computed on log-chord transformed monthly community samples [40, 51]. We also included available environmental data as explanatory factors in the ordination (transformation-based redundancy analysis, tb-RDA). Environmental parameters (water temperature, salinity, turbidity, current velocity, current direction, water level, atmospheric pressure and dissolved oxygen concentration [DOC]) were obtained by a measuring station (53°12′58.3″N 7°25′26.9″E) operated by the local water authority WSV Ems-Nordsee, scaled and averaged per month. The final reduced model formula was chosen through a permutation-based forward selection process ('adespatial' package [52]), and results were visualised in triplots [53].

For eight of the most abundant species, we graphically analysed individual length and biomass data. Hereby, species were categorised into ecological guilds (freshwater, diadromous, marine estuarine opportunist or estuarine resident), according to the definition by Elliott and Dewailly [3] and Thiel et al. [54]. For European smelt *Osmerus eperlanus* (L. 1758), twaite shad *Alosa fallax* (Lacepède, 1803) and *L. fluviatilis,* maturation stages were assumed according to the length-age groups specified in Scholle et al. [21] and Thiel and Salewski [55].

3. Results

3.1. Total Catch. A total of 57 hauls was analysed with regard to fish community composition over the fourteen months of the study, recording 39 fish and lamprey species from 20 families (Tables 1 and 2). The MN catches comprised a total of 4103 specimens of 30 species, while nine additional species were identified in the other four nets (AN). Most common were freshwater ($n = 18$) and diadromous species ($n = 11$), followed by estuarine resident ($n = 3$) and marine estuarine opportunist species ($n = 6$). Three non-native species were recorded: round goby

Neogobius melanostomus (Pallas 1814), Western tubenose goby *Proterorhinus semilunaris* (Heckel 1837) and Siberian sturgeon *Acipenser baerii* Brandt 1869 (Tables 1 and 2).

The total normalised main net sample (i.e., each haul standardised to 24.24 h and 21.16 m^2 net aperture) had a richness of 29 species (assuming two species of the genus *Pomatoschistus*), a Shannon–Wiener index of 1.89 and a sampling coverage of 99.9%. With a share of 62.5%, the total MN catch was dominated by *P. flesus* and *O. eperlanus* (Table 1). *Pomatoschistus* spp. also occurred in substantial relative abundances (10.6%), while *L. fluviatilis*, pike-perch *Sander lucioperca* (L. 1758) and three-spined sticklebacks *Gasterosteus aculeatus* L. 1758 were subdominant with relative abundances of 7.5%, 4.7% and 4.1%, respectively. All other species ($n = 23$) occurred in abundances below 3%. Species that were recorded in the other nets (AN, but not in the MN) were recorded within a maximum of four hauls (Table 2).

The catch per unit effort in the MN (Figure 3(a)) differed significantly throughout the year (F-test $p = 0.003$, $\chi^2_{(11)} = 28.21$), but post hoc contrasts did not show any significant differences between months. The highest monthly average CPUE was 167.5 ± 83.3 ind./24 h/21 m^2 in November, and the lowest mean CPUE was recorded in March with 16.9 ind./24 h/21 m^2.

3.2. Intra-Annual Trends. According to the rarefaction curves, sufficient sampling coverage was reached in April, June, July, August, September and November (both years) (Figure S1). February and March were represented in CPUE-based analyses only by one haul, respectively, due to sampling limitations during ice drift. Monthly differences in the community composition were mostly driven by *S. lucioperca*, *O. eperlanus*, *Pomatoschistus* spp. and *Chelon* cf. *ramada* (Figure S2). The most distinct community structure was found in June and July (Figure S2) due to the presence of several rare species (Table S1). The monthly community structure was significantly influenced by water temperature, atmospheric pressure, DOC and salinity ($F_{(4,9)} = 4.27$, $p = 0.001$), which together explained 50.2% of the total variance. Water temperature and DOC were highly negatively correlated ($r_{(49)} = -0.95$, $p < 0.001$) and clearly followed an annual cycle with highest temperatures and lowest DOC in July (Figure 4). Salinity showed a less prominent trend but shared a medium negative correlation ($r_{(49)} = -0.60$, $p < 0.001$) with DOC. Pressure was not significantly correlated with the other environmental factors (Figure 4).

In several species, occurrence and abundance showed distinct patterns throughout the study (Figures 5(a), 5(b), 5(c)). Similarly, individual length and biomass varied substantially over the year within most of the species analysed (except for *Clupea harengus* L. 1758 and *Chelon* cf. *ramada* (Risso 1827), Figures 6(a), 6(b)). For instance, cyprinids (*Carassius gibelio* (Bloch 1782), *Cyprinus carpio* L. 1758) were almost solely detected during summer and autumn months, while grey mullets prevailed in autumn and winter. Juvenile *P. flesus* (> 10 cm) were present year-round but substantially increased in May and peaked in abundance in August (Figures 5(b), 6(a), and 6(b)). *Gasterosteus aculeatus* showed abundance peaks in February and December 2021, and a notable drop in mean total length in June. *Sander lucioperca* occurred only very scarcely except for two hauls in June and July 2021, which contained high numbers of juvenile individuals (mean TL ≈ 49 mm).

In the MN, 12 out of the 28 taxa present after normalisation were found in more than half of the sampled months (Figure 3). *Platichthys flesus* and *O. eperlanus* were present almost year-round and dominated the catches (relative abundances > 10%) with abundance peaks in August and November, respectively (Figures 3(b), 5(a), and 5(b)), except for May to July 2021, when *O. eperlanus* abundances approached zero (Figure 5(a)). Compared to only these two species, which occurred rather regularly (min. 75% of all hauls) in the MN, six species were regularly present in all nets combined: *A. anguilla*, *G. aculeatus*, *O. eperlanus*, *P. flesus*, *Perca fluviatilis* L. 1758 and *Abramis brama* (L. 1758). All abundance, length and mass data gathered from the MN (Table S1) as well as additional abundance (presence/absence) data from all nets (Table S2) are available in the supporting information.

4. Discussion

4.1. Patterns in the Fish Community. The recorded species widely represent the typical upper estuarine fauna in temperate European low-land rivers, mostly characterised by limnic and diadromous, and to a lesser extent by marine and estuarine species (e.g., Ems [13, 56, 57]; Elbe [29]; Zeeschelde [58]; Thames [59]; Severn [60]). In addition, with *Carassius gibelio, Coregonus* cf. *oxyrinchus* (L. 1758)*, Leucaspius delineatus* (Heckel 1843) and *A. baerii*, we identified four freshwater and diadromous species that have not been recorded in the biannual WFD monitoring within the previous 10 years [13, 56, 57, 61–71]. Another six species (*Leuciscus aspius* (L. 1758), *Misgurnus fossilis* (L. 1758), *Silurus glanis* L. 1758, *Tinca tinca* (L. 1758), *Esox lucius* L. 1758 and *Petromyzon marinus* L. 1758) were only reported once or twice within the past 10 years. *Alburnus alburnus* (L. 1758) and *P. semilunaris* were observed for the first time within this study and recaptured in 2023 during the WFD monitoring [62]. The very high sampling coverage and comparisons to previous studies indicate that we sampled essentially the entire species community. However, we found nine more species with quadruple sampling effort and using a smaller mesh size (AN).

The observed species richness (39 fish species in total) was considerably higher than the numbers previously reported in single studies of the lower Ems—usually varying between 14 and 20 species [13, 56, 57]. Species richness is positively correlated with sampling effort [49, 50], which will likely account at least partly for the differences between studies. However, the sample size was usually much higher in the comparative WFD monitoring scheme (e.g., [13, 56, 57]), which underlines that in the present study, the higher species richness is mostly caused by higher intra-annual resolution compared to bi- or annual sampling schemes.

Table 1: Total catch composition in the analysed stow net (MN) from Nov 2020 to Dec 2021 (57 hauls), sorted by abundance.

Species	**Common name**	**Guild**	**CPUE**		**TL (mm)**				**BM (g)**			
			(nr/24 h/21 m^2)	**(%)**	**Mean**	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**
Platichthys flesus (L. 1758)	European flounder	e.r.	1182.2	32.0	89.8	56.1	20	400	20.9	54.6	0.1	574.2
Osmerus eperlanus (L. 1758)	European smelt	d.	1128.7	30.5	83.8	35.4	36	230	6.1	14.2	0.1	121.1
Pomatoschistus spp.	Sand gobies	e.r.	392.1	10.6	40.9	19.0	14	89	1.1	2.4	< 0.1	43.0
Lampetra fluviatilis (L. 1758)	European river lamprey	d.	276.2	7.5	371.9	74.0	280	730	84.3	20.2	29.0	134.0
Sander lucioperca (L. 1758)	Pike-perch	f.	172.4	4.7	56.6	22.4	33	190	2.2	6.2	0.2	60.6
Gasterosteus aculeatus L. 1758	Three-spined stickleback	d.	150.2	4.1	55.8	11.8	22	79	1.8	0.9	0.1	6.4
Anguilla anguilla[†] (L. 1758)	European eel	d.	90.6	2.5	552.1	165.8	190	1100	397.5	360.8	10.0	2970.0
Clupea harengus L. 1758	Atlantic herring	m.e.o.	66.7	1.8	91.7	18.0	65	200	4.6	6.4	1.1	59.6
Chelon cf. *ramada* (Risso 1827)	Thinlip grey mullet	d.	61.0	1.7	146.8	20.8	105	230	32.3	13.2	9.9	109.5
Perca fluviatilis L. 1758	European perch	f.	47.7	1.3	64.9	23.7	32	140	4.4	5.9	0.3	36.6
Cyprinus carpio L. 1758	Common carp	f.	46.7	1.3	57.3	17.9	29	103	167.9	1142.2	0.2	8000.0
Abramis brama (L. 1758)	Freshwater bream	f.	20.2	0.6	111.8	66.3	36	280	27.5	59.9	0.3	260.0
Alosa fallax (Lacepède 1803)	Twaite shad	d.	8.5	0.2	397.8	61.6	320	510	609.9	242.0	285.6	996.0
Carassius gibelio (Bloch 1782)	Prussian carp	f.	5.6	0.2	66.4	22.3	48	94	5.6	4.6	1.4	12.3
Tinca tinca (L. 1758)	Tench	f.	4.1	0.1	89.5	27.7	59	124	12.0	11.1	2.1	27.0
Rutilus rutilus (L. 1758)	Roach	f.	3.9	0.1	120.8	95.7	37	270	65.6	119.8	0.4	278.7
Sprattus sprattus (L. 1758)	European sprat	m.e.o.	3.7	0.1	79.0	17.2	63	101	2.9	2.4	1.3	6.4
Gymnocephalus cernua (L. 1758)	Ruffe	f.	3.5	0.1	114.7	16.6	97	130	17.9	9.5	8.8	27.8
Silurus glanis L. 1758	Wels catfish	f.	2.9	0.1	99.3	7.0	92	106	6.5	1.7	4.8	8.3
Pungitius pungitius (L. 1758)	Ninespine stickleback	d.	2.9	0.1	37.3	2.9	34	39	0.3	0.1	0.3	0.4
Proterorhinus semilunaris (Heckel 1837)	Western tubenose goby	f., n.n.	1.9	0.1	72.0	7.0	67	80	4.8	1.3	3.5	6.1
Salmo salar L. 1758	Atlantic salmon	d.	1.9	0.1	165.0	49.5	130	200	55.2	40.9	26.3	84.1
Alburnus alburnus (L. 1758)	Bleak	f.	1.7	0.1	117.0	NA	NA	NA	9.3	NA	NA	NA
Solea solea (L. 1758)	Common sole	m.e.o.	1.7	< 0.1	210.0	28.3	190	230	95.8	31.7	73.4	118.2
Leuciscus aspius (L. 1758)	Asp	f.	1.0	< 0.1	690.0	NA	NA	NA	2690.0	NA	NA	NA
Coregonus cf. *oxyrinchus* (L. 1758)	Houting	d.	1.0	< 0.1	250.0	NA	NA	NA	121.3	NA	NA	NA
Leucaspius delineatus (Heckel 1843)	Belica	f.	1.0	< 0.1	45.0	NA	NA	NA	0.6	NA	NA	NA
Misgurnus fossilis (L. 1758)	Weatherfish	f.	0.9	< 0.1	55.0	NA	NA	NA	220.0	NA	NA	NA
Salmo trutta[‡] L. 1758	Sea trout	d.	< 0.1	< 0.1	160.0	NA	NA	NA	46.9	NA	NA	NA
Not classified			14.6	0.4	42.4	NA	NA	NA	NA	NA	NA	NA

Note: Guild refers to the ecological guild after Elliott and Dewailly [3] and Thiel et al. [54] (f. = freshwater, d. = diadromous, e.r. = estuarine resident, m.e.o. = marine estuarine opportunist, and n.n. = non-native). CPUE: abundance as number of individuals per 24.24 h haul duration and 21.16 m_2 net opening (normalised haul). CPUE values are based on 51 hauls, for which the necessary environmental data existed.

Abbreviations: BM = biomass (wet mass), SD = standard deviation, and TL = total length.

[†] TL and BM data for *Anguilla anguilla* were included from a larger sample size, calculated as a weekly average over all five stow nets.

[‡] *Salmo trutta* was only caught in one haul, which had to be filtered during normalisation due to a lack of data.

Estuarine fish communities vary spatially, following longitudinal gradients in abiotic factors, most notably salinity [72]. Towards the coast, marine species become more frequent and freshwater species disappear; accordingly, the estuarine species richness is usually considerably higher than that in the oligohaline area studied here [13, 29, 56, 57]. Since we identified 39 species in the oligohaline zone alone, fish species richness also in the entire Ems estuary might be higher than previously assumed (20–44 species; [13, 20, 56, 57, 61–71]). For estuaries in this latitude, fish species richness generally ranges between 40 and 120 species [19]. For instance, in the nearby Elbe River, it amounts to about 60 species [23, 29, 72]. Given the afore mentioned differences in sampling effort and the consistently poor ecological status of the tidal Ems (e.g., [10, 13, 56, 57]), our findings likely do not indicate an ecological improvement.

With a Shannon–Wiener index of 1.89 and a few highly dominant species, evenness in our catches was comparably low [38]. Among southern North Sea estuaries, patterns of low evenness were described for the Zeeschelde, Elbe and Ems (e.g., [13, 23, 29, 56–58]). Which species dominate the estuarine communities varies greatly among studies; most prominent in the Elbe and Ems estuaries are *O. eperlanus* (up to 98.5%), *P. flesus*, *Pomatoschistus* spp., *C. harengus* and other clupeids (e.g., [13, 23, 29, 56, 57]).

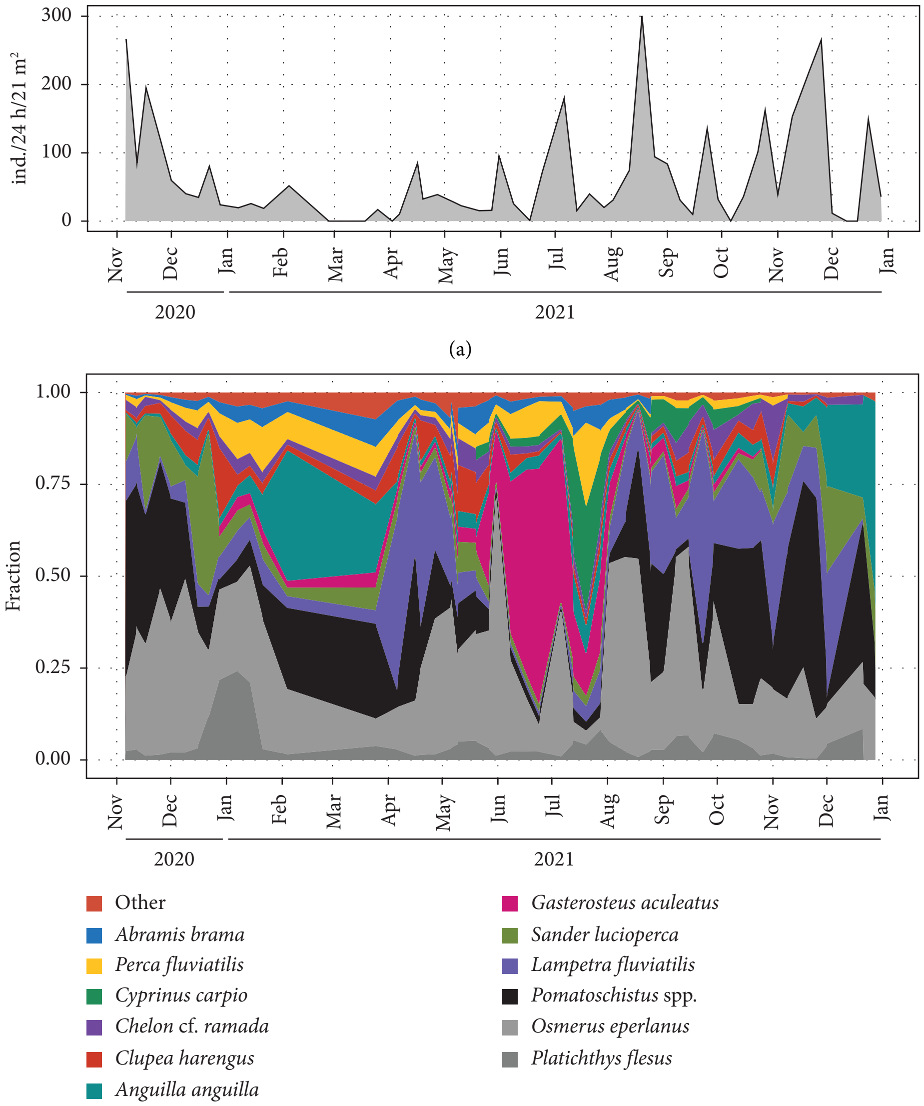
Significant differences in the monthly catch per unit effort indicate a cyclical intra-annual variation with catch rates considerably lower in the first half of the year, an annual maximum abundance in November, followed by a winterly decrease in catches during both years. This has been observed in several previous studies; typically, estuarine fish abundance is higher in autumn versus spring (e.g., [13, 58])—even though Thiel et al. [72] reported different trends for the Elbe estuary (with abundance maxima during summer).

Over the fourteen months studied, we observed significant changes in the monthly community structure, mainly caused by fluctuations in the abundances of *S. lucioperca, O. eperlanus, Pomatoschistus* spp. and *C.* cf. *ramada*. Half of the intra-annual community variance was statistically explained by variation in water temperature, DOC, salinity and atmospheric pressure. Estuaries are inhabited by many species that undergo diadromous or potamodromous migrations, which are largely driven by environmental variation, such as seasonal changes in temperate regions ([18, 23, 29, 73, 74]). Abiotic changes caused by anthropogenic drivers may additionally affect community structure [73, 74]. Although causal coherencies could not be resolved within this study, the environmental conditions in the Ems River in 2021 were far from favourable for all species. This

TABLE 2: List of species that were detected additionally in the other four stow nets (AN) between April and December 2021 (39 hauls), including the number of hauls with the presence in at least one of the four nets.

Family	**Species**	**Common name**	**Guild**	**Present in the no. of hauls**
Acipenseridae	*Acipenser baerii* Brandt 1869	Siberian sturgeon	f., n.n.	1
Leuciscidae	*Blicca bjoerkna* (L. 1758)	White bream	f.	4
Moronidae	*Dicentrarchus labrax* (L. 1758)	European seabass	m.e.o.	1
Esocidae	*Esox lucius* L. 1758	Northern pike	f.	1
Liparidae	*Liparis liparis* (L. 1766)	Striped seasnail	m.e.o.	2
Gobiidae	*Neogobius melanostomus* (Pallas 1814)	Round goby	f., n.n.	1
Petromyzontidae	*Petromyzon marinus* L. 1758	Sea lamprey	d.	4
Pleuronectidae	*Pleuronectes platessa* L. 1758	European plaice	m.e.o.	1
Sygnathidae	*Sygnathus* sp.	Pipefish	e.r.	1

Note: Guild refers to the ecological guild after Elliott and Dewailly [3] and Thiel et al. [54] (f. = freshwater, d. = diadromous, m.e.o. = marine estuarine opportunis, e.r. = estuarine resident, and n.n. = non-native).



(a)

(b)

FIGURE 3: (a) Total catch (normalised to CPUE [ind./24 h/21 m^2]) per month and (b) percent share to total CPUE per species or taxon.

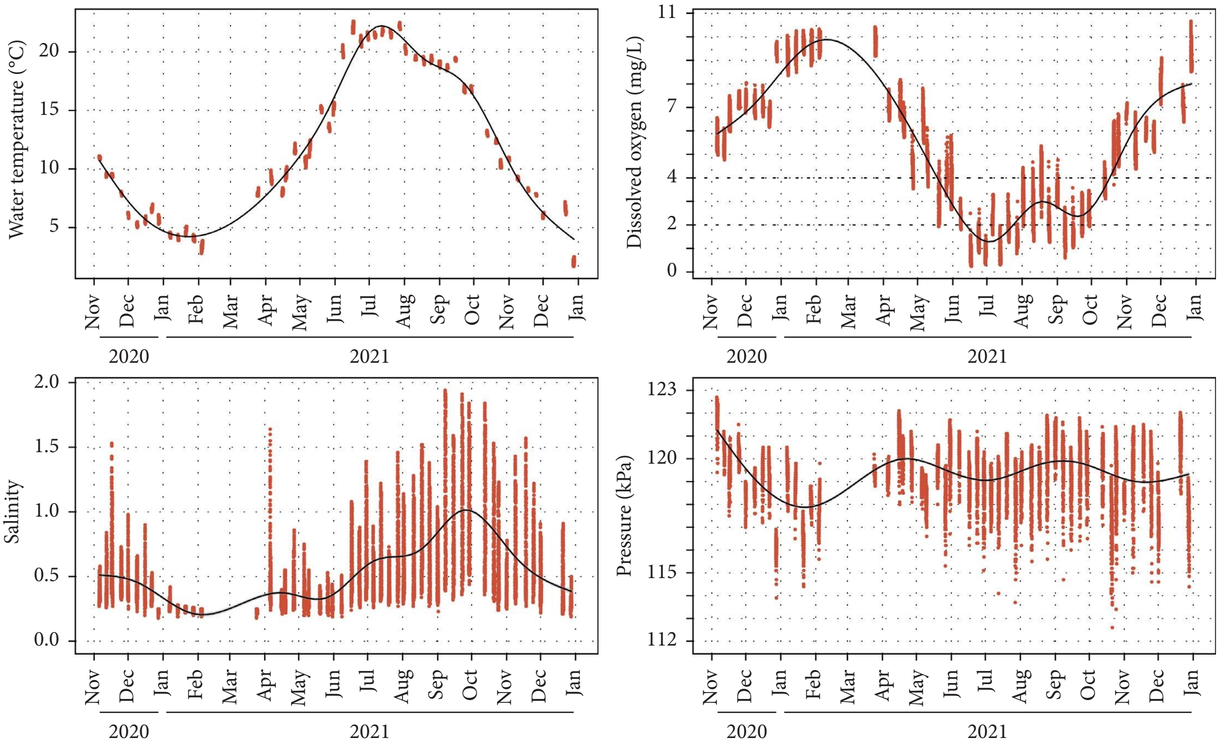
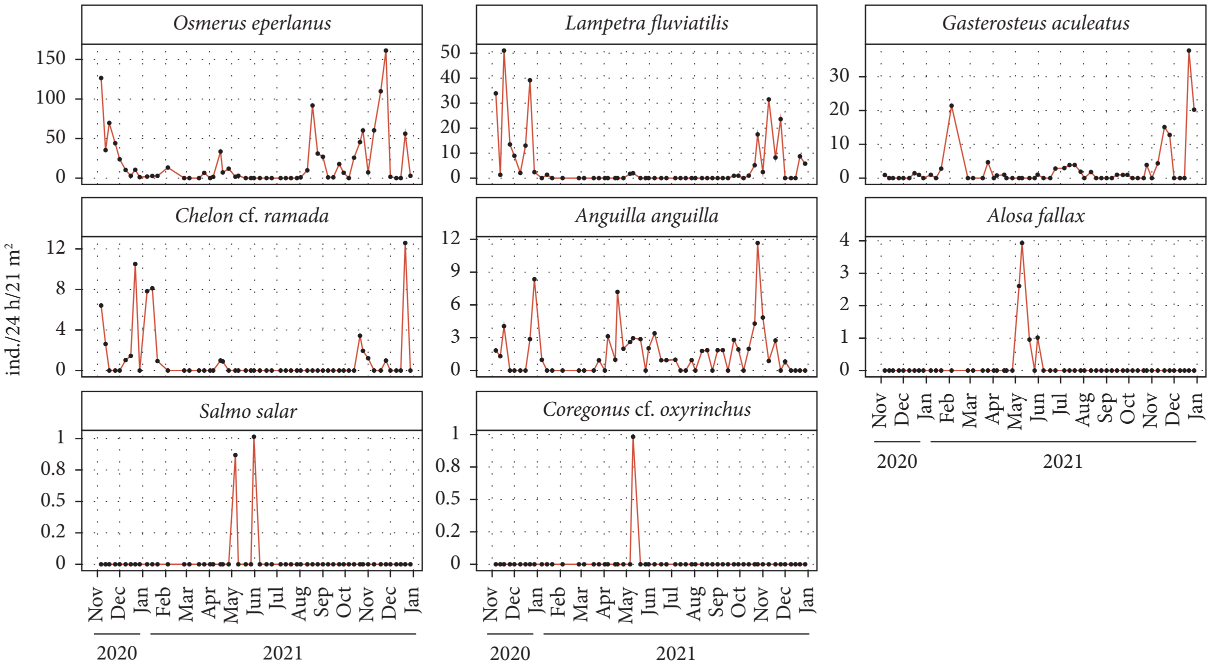
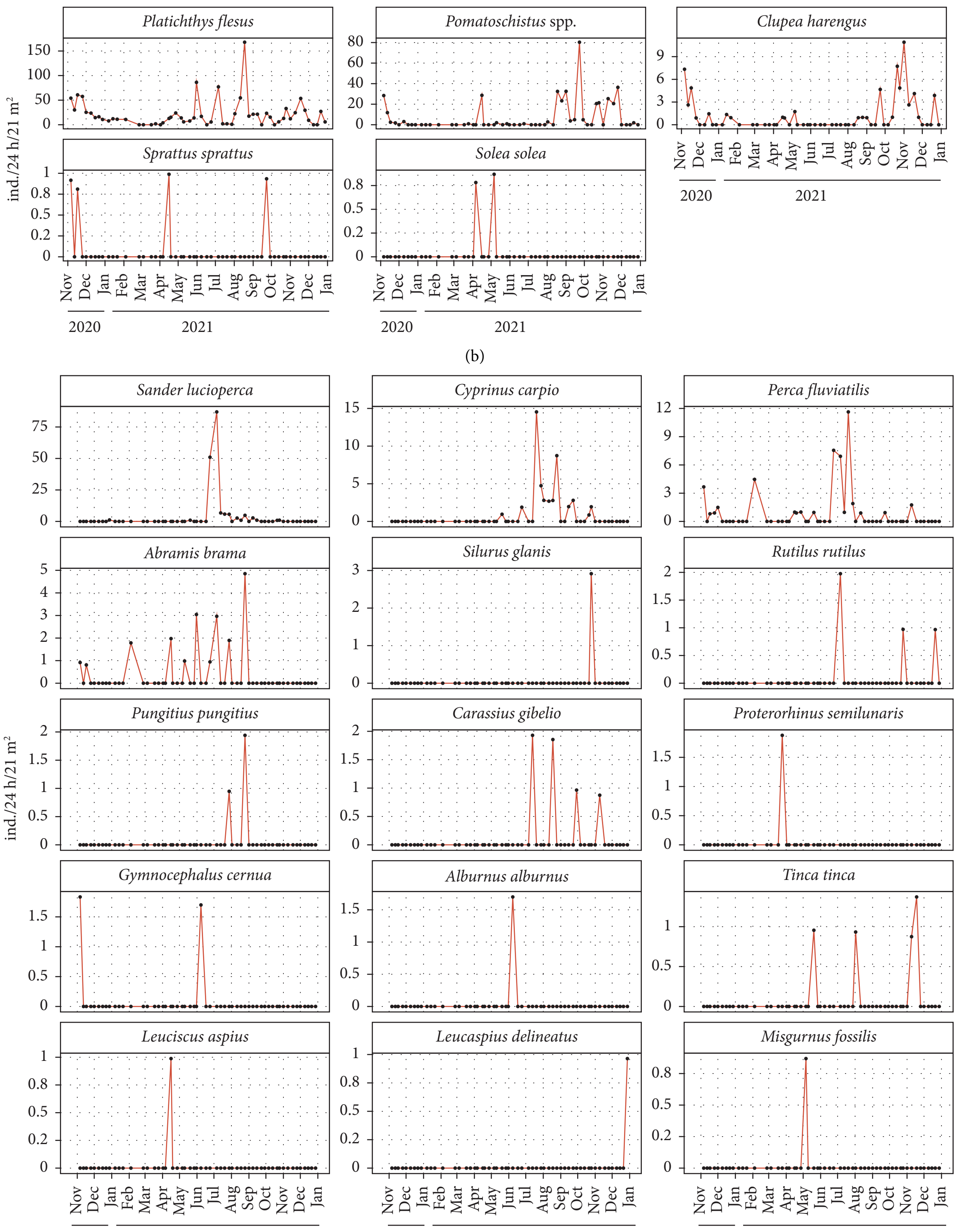


FIGURE 4: Annual trajectory of the four significant environmental parameters such as water temperature, atmospheric pressure, dissolved oxygen concentration and salinity. Regression lines were fitted by generalised additive models (geom_smooth, method = 'gam').



(a)

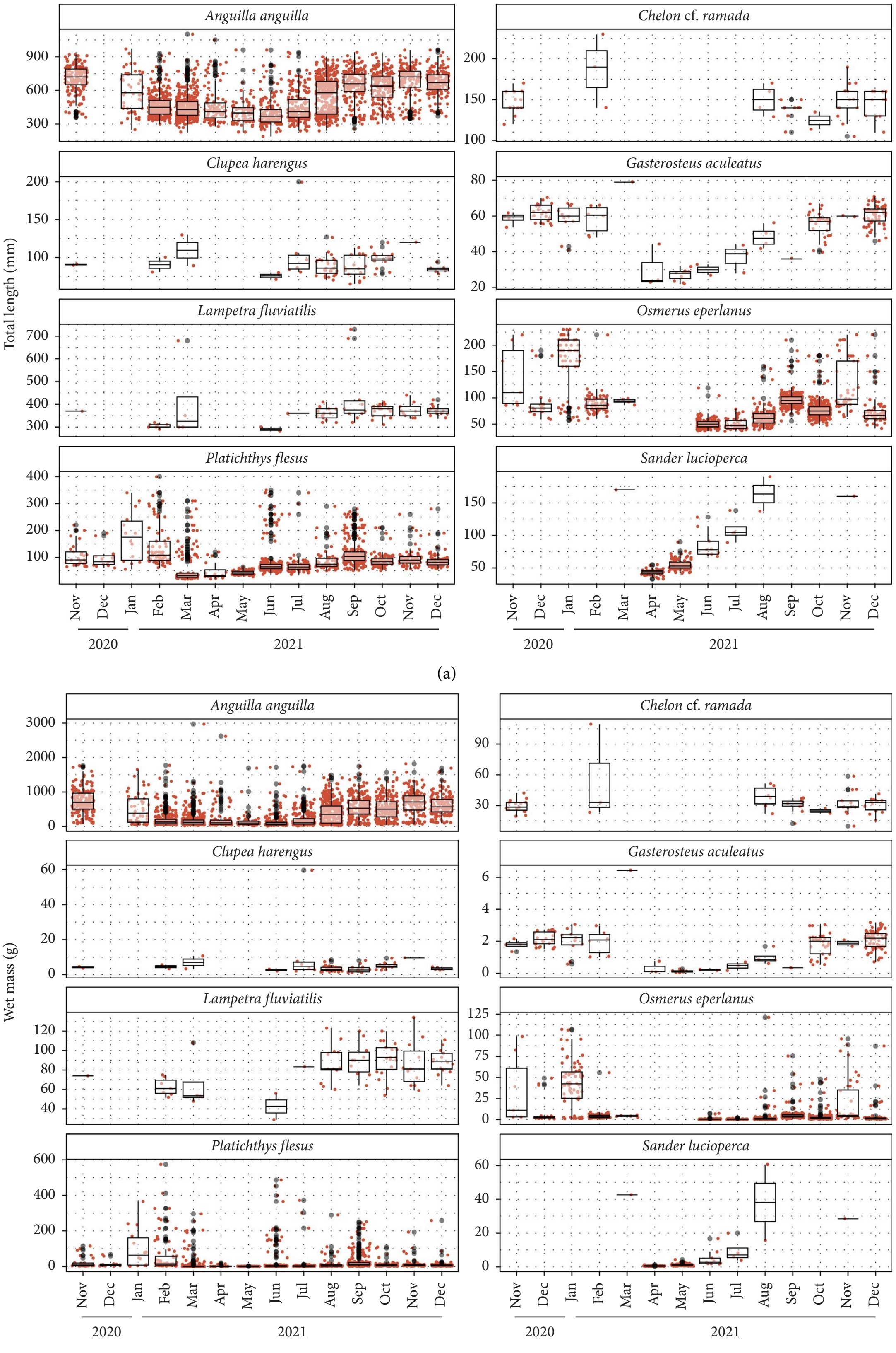
FIGURE 5: Continued.



(b)

(c)

Figure 5: Normalised abundance (CPUE [ind./24 h/21 m^2]) per haul for single species or taxa, grouped as (a) diadromous, (b) estuarine (including estuarine residents and marine estuarine opportunists) and (c) freshwater species according to the ecological guilds defined by Elliott and Dewailly [3] and Thiel et al. [54].



(a)

(b)

FIGURE 6: Individual length (mm) (a) and body mass (g) (b) per month for eight of the most abundant species in the main net (MN).

was demonstrated, for instance, by the complete absence of *O. eperlanus* in eleven subsequent hauls from May to July 2021 coinciding with the lowest DOC in the sampling period, up to hypoxic conditions ($\text{mean}_{\text{DOC}} = 1.98$ mg/L; $\text{min}_{\text{DOC}} = 0.24$ mg/L). *O. eperlanus* is known to exhibit a comparatively low tolerance to oxygen depletion [72, 75]. Despite—or because of—these hypoxic conditions, we found the most distinct community compositions in June and July 2021 with the highest proportions of rare species and peak abundances of juvenile *S. lucioperca*. It should be noted that the shifts in single-species abundance led to shifts in both evenness and dominance patterns (e.g., *Pomatoschistus* spp. in September 2021, *L. fluviatilis* during single weeks in November and December 2020), which may partially explain the differences in dominance among previous studies, which were usually conducted as single spot-checks (e.g., twice per year). Dedicated studies of environment- and season-modulated community change in estuaries, as well as research into the tolerance of single species to environmental changes are needed to better understand causal relationships and forecast estuarine community composition under climate change. This is important regarding single-species conservation, but also from a broader perspective, as community structure and diversity critically related to ecosystem function and services (e.g., [76]).

4.2. Species of Particular Ecological or Scientific Interest. Several species that were historically frequent and characteristic to northern German estuaries are now rare or completely absent; particularly mentionable in this regard are the twaite shad *A. fallax*, as well as European sturgeon *Acipenser sturio* L. 1758, Atlantic salmon *Salmo salar* L. 1758 and *Coregonus oxyrinchus* [12, 15, 77–80]. On an ecosystem scale, our results do not change this picture; we made, however, some notable catches with regard to the conservation or reintroduction of these formerly important and partly data-limited species [15, 81, 82].

An example is *A. fallax*, present in the MN with only nine adult individuals (TL 32–52 cm; seven hauls in May and June 2021), but 338 additional specimens were recorded anecdotally between 23 April and 11 June 2021 in AN (anonymous fisher, pers. comm.). We further recorded at least three specimens of *Coregonus* cf. *oxyrinchus* (one in MN (TL = 25 cm, 121.3 g); two subsequent 'present' records in AN, May 2021). *Coregonus* sp. are stocked in the River Ems to artificially support its return to the area [9], but they were not present in any of the recent WFD monitoring efforts [13, 56, 57, 61–71]. Moreover, we caught at least five *S. salar* specimens (two in MN (TL: 13 and 20 cm); three 'present' records in AN, May and July 2021). One of the latter was an ascending adult *S. salar* measuring a total length of 107 cm. *Salmo salar* was fully extinct in this area in the 1950s and is now again rarely present in the Ems, potentially owing to occasional returnees from reintroduction measures or straying individuals [80].

Lampetra fluviatilis is another data-limited diadromous species, protected by European law and endangered or in decline in most of its habitat [82]. In our catches, *L. fluviatilis* was quite frequent with a relative abundance of 7% (296 individuals in MN). The vast majority was caught from October to December and consisted of presumable adults (TL of 30–40 cm) on their autumnal upstream spawning migration [55]. Interestingly, four additional individuals were caught during two weeks in May 2021 in MN (one of them exceptionally large with a TL of 70 cm) and the species was present in AN during all recorded hauls in April and May 2021. Several other studies (e.g., in Finland, Sweden and Great Britain) recorded another (smaller) abundance peak in spring, in the otherwise highly seasonal occurrence. Different authors attribute this spring peak either to local overwinterers, or a potential second spawning migration which could occur in some river lamprey populations but has not been detected in the latest studies in the nearby Elbe River (reviewed in [55]).

Northern European anadromous *O. eperlanus* populations use estuaries such as the Ems-Dollard as spawning and nursery areas [21, 83], which was well reflected in this study. Half of the *O. eperlanus* catches consisted of presumable subadults (6–10 cm), which were present almost year-round. Presumable adults (> 10 cm) were caught primarily from November 2020 to March 2021 prior to the spawning season (mid-February to late March [22]). Very small individuals (< 6 cm) were present, partly in substantial shares, from August 2021 until the end of the year. Since large parts of the historical local spawning grounds are today considered unsuitable for the successful reproduction of *O. eperlanus* [13, 22], these presumable young-of-the-years (YOY) are noteworthy, but further information such as data on larval survival would be needed to interpret the ecological meaning of this finding.

Of particular interest is also the non-native *P. semilunaris*, of which at least six individuals were caught in the study period (two in the MN, March 2021). Prior to our findings, *P. semilunaris* has never been recorded in the Ems in any (publicly available) scientific publications, nor in the regular WFD monitoring reports [13, 56, 57, 61, 63–71]. Single findings have been made, however, in the nearby channel 'Mittellandkanal' [88], and in 2023, additional specimens were recorded for the first time during the regular WFD monitoring [62]. This suggests that *P. semilunaris* might be slowly establishing in the area. Research on the ecological consequences of non-native *P. semilunaris* occurrence is scarce to date. In other western European river systems, the species has apparently established only small populations, which has so far limited its ecological impact [84–86].

4.3. Limitations. As this study was run alongside a monitoring study of *A. anguilla* migration patterns [26, 27], the data are not suited to answer all ecologically relevant questions on the fish community structure. Owing to weather conditions and generally lower species abundance in winter and spring, these months are undersampled. Catch sizes also varied strongly among hauls (between 1 and 301 ind./24 h/21 m^2), as well as months (17–675 ind./24 h/21 m^2), which is why we chose to refrain from any comparison of univariate alpha diversity measures (e.g., species richness, evenness) between temporal subsets, as these are particularly dependent on sample size and coverage [48–50]. While less pronounced, this does also affect the multivariate comparison of community structure to some extent and should be kept in mind when working with these data [87].

Notably, our catches are several magnitudes lower than those of comparable studies in the area (e.g., [13, 62, 64, 65]) which, however, differ in the methodology (e.g., stow net placement, mesh size in the cod end). Particularly, the mesh size of 12 mm applied in this study has most likely led to an underrepresentation of small species (e.g., Gobiidae) and juvenile individuals in the MN [29]. Based on the comparison to previous community studies in the area (see above) and considering the high temporal resolution and coverage of this study, we expect that this has not substantially affected species richness, but it most certainly reduced the abundance estimates of small specimens.

Moreover, species abundance and population structure vary greatly between years because of interannual differences in recruitment, adult survival, or changes in migratory behaviour [29]. For example, numbers of *P. flesus* and adult *O. eperlanus* (> 100 mm) drastically decreased, whereas *Pomatoschistus* spp. were far more abundant in November 2020 vs. November 2021. Such fluctuations greatly affect spot-check monitoring results, as also evident in the biannual Ems monitoring scheme [13, 56, 57, 61–71]. To critically investigate seasonal dynamics in the fish community, such interannual fluctuations must be clearly distinguished, which would require more data covering multiple years.

Nevertheless, this depiction of a full annual cycle provided critical insights on rare and data-limited fish species, such as salmonids, *A. fallax*, *L. fluviatilis* and *O. eperlanus*. It may also serve as a base to design or adjust sampling schemes in the Ems and similar estuaries, depending on the target species and research question. As adopted in the WFD monitoring for transitional waters, two samples in spring (end of April or May) and autumn (September or October) are crucial to capture most variance [21]. Our results indicate that a third summer sampling in June or July might be desirable in studies that aim to analyse the full community. We also note that community shifts, for instance caused by migrations, may happen on very short time scales; see, for instance, the single abundance peak of *O. eperlanus* in April, during a presumable spawning migration event. This calls for extended periods of high-resolution sampling, i.e., multiple hauls during at least 3 weeks in spring, summer and autumn sampling periods. To detect invasive species at an early stage, sampling times need to be adapted, which was demonstrated by the highly seasonal occurrence of *P. semilunaris* in March and April.

Data Availability Statement

The original datasets generated and analysed within this study will be made publicly accessible via 10.6084/m9.figshare.28659578 upon publication. All relevant data are available from the corresponding author upon reasonable request.

Disclosure

All authors interpreted the results, edited, and approved the final manuscript version.

Conflicts of Interest

The authors declare no conflicts of interest.

Author Contributions

L.H., R.H., W.H., L.M., M.F. and S.R.B. conceived the study. S.R.B, B.M., L.H., M.F. and J-D.P. contributed to data collection. S.R.B. and J-D.P. performed data analysis. M.F., J-D.P., L.M. and R.H. obtained funding. S.R.B. and L.M. wrote the first manuscript draft.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.
Supporting Information 1. Table S1: Abundance, length and mass in the main net (MN) per species and month.

Supporting Information 2. Table S2: Presence or absence in all nets (AN) per species and haul.

Supporting Information 3. Figure S1: Interpolation and extrapolation of Hill number with order $q = 0$ (species richness) of monthly samples based on normalised abundance of individuals (CPUE [ind./24 h/21 m^2]). Curves that reach an asymptotic value indicate sufficient sampling coverage for that month. Created with R iNEXT [47, 48].

Supporting Information 4. Figure S2 a, b: Triplots of transformation-based redundancy analyses of environmental factors on log-chord transformed monthly community structure. Dots represent monthly community samples. Orange arrows represent species; only species that contributed most to community variance are displayed, hereby defining the 'circle of equilibrium contribution' in

Scaling 1 as a threshold ($r = \text{sqrt}(d/p)$, where d = number of displayed dimensions and p = number of non-zero eigenvalues). Yellow arrows represent environmental variables; only significant (following permutation-based forward selection) variables are displayed. Length of arrows indicates the relative importance of that variable or species to overall monthly community variance. Scaling 1 (a) Euclidean distance between samples (months) represents dissimilarity in community composition (i.e., dots closer to each other share a more similar species community). Scaling 2: (b) The angle between arrows relates to correlation (i.e., arrows pointing in the same direction are positively correlated). WT = water temperature. PR = atmospheric pressure. DOC = dissolved oxygen concentration. SAL = salinity. Species are abbreviated with the first two letters of each genus and species name.

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