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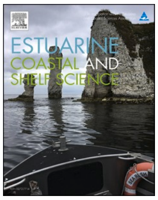

Seasonal variations of a coastal fish community in relation to environmental parameters - A case study of the Sylt-Rømø Bight, southeastern North Sea

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ABSTRACT

The Wadden Sea is a transition area between land, rivers, and the North Sea. It is of great ecological importance for a wide range of fish species that use it in the course of their life cycle for various purposes. It is a highly dynamic environment and is subject to strong seasonal patterns and annual variations in abiotic conditions. The Sylt-Rømø Bight (SRB) is a semi-enclosed tidal basin in the northern Wadden Sea between the islands of Sylt (Germany) and Rømø (Denmark). Monthly monitoring data of juvenile fish taken in the SRB from 2007 to 2019 were analyzed to determine the changes in species composition in comparison to previous monitoring programs (1989–1995). The long-term trends, common patterns, and potential effects of environmental parameters (sea surface temperature (SST), salinity, chlorophyll *a*, and the North Atlantic Oscillation (NAO) winter indices) were determined. In total, 55 species were recorded and only 22 of these together accounted for more than 95% of the total abundance for the entire monitoring. Results showed a changed species composition as we did not find two boreal, one Lusitanian, and one circum-temperate species recorded in the previous programs. Instead, one boreal, six Lusitanian, and one Atlantic species were observed for the first time. The fish community was dominated by high seasonal fluctuations of abundance with either dome-shaped, increasing, or decreasing trends. Dynamic Factor Analysis (DFA) partitioned the fish community into three seasonal assemblages based on SST preferences. Redundancy Analysis (RDA) revealed that environmental parameters explained 29 % of the variations in the fish community. These variances were partly a result of the spring immigration of Lusitanian species and the emigration of boreal species and vice versa in autumn. The absence of four previously reported species and the addition of eight new species support the hypothesis that warm-adapted species are increasing in the Wadden Sea. The inclusion of these seasonal variations into conservation and management practices is critical to the sustainable management of marine and coastal ecosystems covering spawning, nursery, and feeding grounds.

1. Introduction

The Wadden Sea is a transition area between land, rivers, and the North Sea and extends from the Netherlands to Denmark (Kabat et al., 2012). It is of large ecological importance for many fish species (Tulp et al., 2017), which require this area for at least one stage in their life cycle for various purposes (Tulp et al., 2008; van der Veer et al., 2015). The area acts as nursery grounds for post-larvae and juvenile fishes as the shallow water provides food and protection from predators. Furthermore, it offers an acclimatization area for seasonal migrants and permanent residents en route to marine or freshwater spawning areas (Elliott et al., 2007). The nursery function is of high significance as it ensures the survival and growth of juvenile fish, as well as protection, and connectivity to other habitats for recruitment into adults (van der Veer et al., 2022). The resident species spend all of their life in the Wadden Sea. In contrast, most non-resident species immigrate in spring

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and emigrate to the deeper North Sea in autumn (van der Veer et al., 2015), following the more rapid warming/cooling in the shallow areas compared to the deeper North Sea (van Aken, 2008a). Indeed, the Wadden Sea is highly dynamic and shows strong seasonal patterns and annual variability in abiotic conditions (Rick et al., 2023), therefore, species living in the area need to adapt to this variable environment.

Like other temperate coastal ecosystems, the environmental conditions in the Wadden Sea vary strongly on seasonal scales and also have changed significantly in the past decades (de Amorim et al., 2023), exposing fish communities to short-term variations and long-term changes (van der Veer et al., 2015). Changes in sea surface temperature (SST) and salinity play significant roles in ecological mechanisms such as production, predation, competition, migration, and changes in metabolic activities that limit organisms' distribution (Tulp et al., 2017). For instance, the migration patterns of fish due to SST variations or in search for nursery and spawning grounds differ among species based on their physiology and habitats. Pelagic species can migrate long distances while benthic species migrate locally (Daan et al., 1990). Moreover, during warm summers, the fish species of Lusitanian and Atlantic origins migrate northwards in the North Sea and Wadden Sea while boreal species migrate into the deeper North Sea and southwards during cold winters (Daan et al., 1990). Further, the abundance and distribution of various fish species correlate with primary productivity, riverine nutrient input, and large-scale climate oscillations such as the North Atlantic Oscillation (NAO) (Alheit et al., 2012; Capuzzo et al., 2018; Dippner, 1997).

The Sylt-Rømø Bight (SRB) is part of the northern Wadden Sea with a unique morphology as it is enclosed to the north and the south by causeways (Baird, 2012). Long-term data on abiotic drivers are available for this area, on average, SST increased by 1.11 °C from 1984 to 2019. Spring temperatures increased by 1.14 °C, summer by 1.24 °C, autumn by 2.04 °C, and winter SST cooled by −0.16 °C (Rick et al., 2023). Other parameters such as salinity, chlorophyll *a*, and nutrient loads also changed on seasonal and long-term scales (Rick et al., 2023). A report by Tulp et al. (2022) on long-term fish monitoring programs in the Wadden Sea showed changing species compositions and various trend patterns because of the changes in environmental conditions. These programs were conducted either seasonally or were restricted to some months which only provided limited information in the long term excluding what happens in the non-sampled months/seasons. One unique feature of the Wadden Sea is the strong seasonal variations compared to variations caused by global change. As fishes spend different times of the year in the Wadden Sea, consistent long-term monitoring that can allow the identification of community dynamics, seasonal patterns, interactions, and concomitant environmental drivers is necessary.

In 2007, high-resolution monthly monitoring of juvenile fish was initiated to investigate the fish fauna of the SRB with special interests in changes in species composition, migration patterns, trends, and community structure (Asmus et al., 2020). These data were analyzed to investigate the changes in species composition assuming an increase in warm-water adapted species over a longer time scale in comparison to two previous series from 1989 to 1995 in Herrmann et al. (1998) and Vorberg & Breckling (1999). Further, the potential effects of the seasonal changes of SST, salinity, chlorophyll *a*, and the NAO winter indices

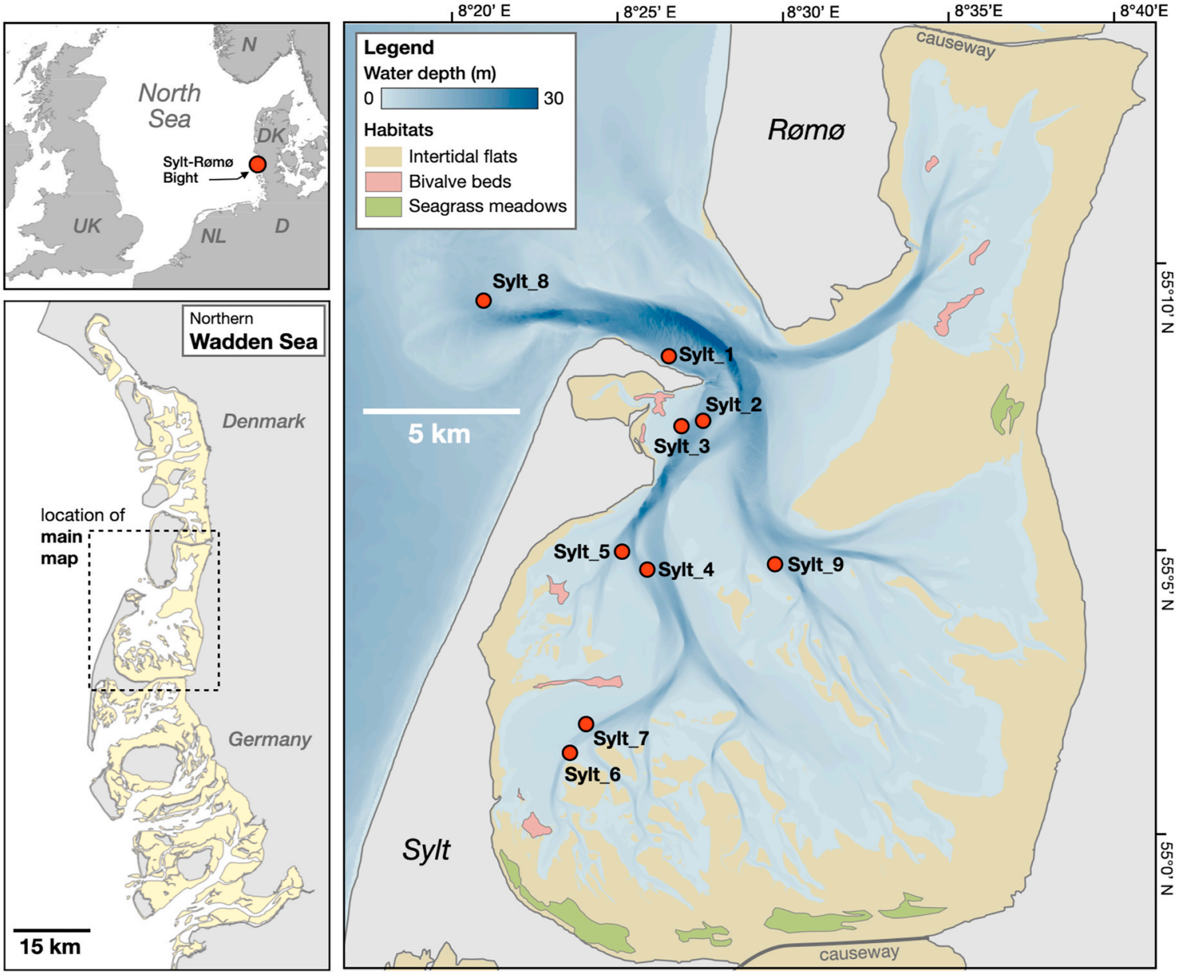

Fig. 1. Location of the Sylt-Rømø Bight on the eastern seaboard of the North Sea (top left) and the northern Wadden Sea (bottom left). Main map: Intertidal flats, bivalve beds, seagrass meadows, and tidal channels with varying water depths. Black dots with labels Sylt_1 to Sylt_9 represent the positions of sampling areas.

on species abundances, trends, and common patterns were investigated.

2. Materials and methods

2.1. Study site

The Sylt-Rømø Bight (SRB), (54°52′ to 55°10′N, 8°20′ to 8°40′E) is a semi-enclosed tidal basin between the islands of Sylt, Germany, and Rømø, Denmark. Two causeways to the north and the south connect the bight to the mainland and restrict water exchange with the adjacent tidal environments (Fig. 1). The bight covers a total area of 404 km^2 including 135 km^2 of tidal flats (Baird, 2012). It is connected to the open North Sea through a 2.8 km wide channel where 8–12 % of the bight's water is exchanged per tidal cycle. Little freshwater with minimal nutrient input from the surrounding land is discharged into the bight (Baird, 2012).

2.2. Fish monitoring

The sampling of fish has taken place monthly since 2007 and is continuing at seven locations inside the SRB and its tidal inlet (Sylt_1 to Sylt_7). Complementary two locations, Sylt_8 and Sylt_9 (Fig. 1) were sampled quarterly and the data from these are not included in this paper. Here we analyzed the data until 2019. Fish were sampled at each station using a 17 m long mini bottom trawl with a mouth measuring 7 m width, 3 m height, and mesh sizes of 32 mm in the wings, 16 mm in the mid part, and 6 mm in the cod end for 15 min at a speed of approximately 2 knots (Asmus et al., 2020). This sampling targets juvenile fish as adult individuals of many species can avoid the net and the mesh size is too large for the larval stages. For consistency, the same sampling equipment and net were used. Besides, sampling time of day, towing speed, and towing time were kept constant for the entire monitoring. An exception was in June 2013 when a new research vessel was put in place, in the early stages of its operation, technical issues limited fish sampling and caused data gaps until April 2014. Unfortunately, we did not compare the catch efficiency of our sampling method with another sampling gear. Nevertheless, the efficiency did not change over time since the same procedures were followed as well as the sampling equipment. Sampled fish were sorted based on morphology and morphometry and then identified to species level using the identification keys in Miller and Loates (1997) and Muus and Dahlstrøm (1978). The identified fish were counted and the total lengths were measured to the nearest 5 mm. If the sample size was large, the total wet weight of all individuals of an abundant species was established and subsamples were taken. These subsamples were weighed, counted, and measured and results were extrapolated to determine the total abundance in the haul.

2.3. Sampling and data of abiotic parameters

Water temperature and salinity were measured at each sampling station during fish sampling. However, salinity measurements began in July 2008 so the missing data were complemented using the data from the Ecological Time Series of the Alfred-Wegener-Institute. Chlorophyll *a* data were obtained from the same dataset and all are described in Rick et al. (2023) and the dataset links therein. The normalized winter Hurrell NAO Index (PC-based) was obtained from NOAA (2020), (https://www.ncdc.noaa.gov/teleconnections/nao/).

2.4. Data analysis

The analyzed datasets consisted of time series of fish species abundances, SST (°C), salinity, chlorophyll *a* (μg/L), and NAO winter indices. Fish abundances were standardized per sampled area and represented as individuals/10000 m^2. All datasets were explored by seasons defined as winter (December, January, February), spring (March, April, May), summer (June, July, August), and autumn (September, October, and November). However, for the determination of the common patterns in the fish community, the actual monthly data were used. Fish were grouped into genera and species and classified into biogeographic guilds (i.e. boreal, Lusitanian, and Atlantic), and preferred habitats (i.e. benthic, benthopelagic, and pelagic) which together yielded nine different biogeographic guild-habitats. Fish species were ranked in order of abundance and those that altogether contributed to 95% of the total abundance of the entire monitoring were considered dominant species. Their monthly time series were determined by aggregating their abundances over all the sampling stations (Sylt_1 to Sylt_7). The monthly mean abundances were square-root transformed to stabilize the variances and trends over time determined by LOESS smoothing (Zuur et al., 2009) and described based on the visual inspection of smoothed curves. The monthly means of environmental parameters were used to determine the trends, for NAO, only winter indices were used. The seasonal cycles of SST and chlorophyll *a* were determined by averaging the estimates of seasonal effects for each month and repeating the sequence over all the years of the entire time series.

Dynamic Factor Analysis (DFA) was applied to identify the underlying common patterns in the fish community. The DFA method is suitable for short, non-stationary multivariate time series and can estimate common patterns, trends, and the effects of environmental factors on response variables (Erzini, 2005). The time series of square-root transformed monthly abundances of dominant species were modeled in DFA as a function of a linear combination of common patterns, an intercept, an explanatory variable, and noise. This was to find out if various fish species followed particular patterns and if these patterns were influenced by explanatory variables. Several DFA models were tested and the one with the lowest Akaike Information Criterion (AIC), was selected. The canonical correlations are absolute values of >0.75, 0.75–0.5, 0.5–0.3, and <0.3 which refer to the terms 'strong', 'moderate', 'weak', and 'minor' that illustrate the relationships between the original time series and common patterns. Canonical correlations < -0.5 or >0.5 are significant at $p < 0.05$ (Zuur et al., 2007a).

Redundancy analysis (RDA) (Zuur et al., 2007b) was performed on Hellinger-transformed seasonal mean fish abundances to determine the potential effects of explanatory variables on the fish community dynamics. Hellinger transformation gives low weights to species with low counts and many zeros while the seasonal means of environmental data were scale transformed. RDA permutation tests (999 permutations) were performed to determine the significant environmental variables. Variance partitioning of explanatory variables was performed to determine the contributions of each parameter to the variations in the fish community. For all tests, statistical significance was assumed if the p-value was below 0.05. Statistical analyses were calculated using the Software R version 4.2.3 (R Development Core Team, 2024) and DFA analyses by the Brodgar package (https://www.brodgar.com).

3. Results

3.1. The fish community

Fifty-five fish species belonging to three biogeographic guilds and three biographic habitats (altogether nine biogeographic guild-habitats) were sampled. There were varying species numbers for each biographic habitat; Atlantic-benthic (1), Atlantic-benthopelagic (1), Atlantic-pelagic (1), boreal-benthic (13), boreal-benthopelagic (5), boreal-pelagic (5), Lusitanian-benthic (18), Lusitanian-benthopelagic (2), Lusitanian-pelagic (9) (Table 1). Of the 55 species, eight had not been observed in the two previous investigations of Herrmann et al. (1998) and Vorberg and Breckling (1999). In contrast, four species that had been recorded in these previous studies were not found anymore. Two species were present in this study and in either of the previous investigations, red mullet (*Mullus surmuletus*) in Herrmann et al. (1998) and Montagu's sea snail (*Liparis montagui*) in Vorberg and Breckling (1999). Six of the new species were of Lusitanian origin while both

Table 1
List of fish species that were sampled in the present investigation in comparison to two previous investigations, their classification into biogeographic guilds and habitats; presence (+) and absence ().

Common name	Scientific name	Biogeographic guild-habitat	Herrmann et al. (1998)	Vorberg and Breckling (1999)	This study
European eel	*Anguilla anguilla*	Atlantic_benthic	+	+	+
Flathead grey mullet	*Mugil cephalus*	Atlantic_benthopelagic			+
Atlantic mackerel	*Scomber scombrus*	Atlantic_pelagic	+	+	+
Hooknose	*Agonus cataphractus*	Boreal_benthic	+	+	+
Five-bearded rockling	*Ciliata mustela*	Boreal_benthic	+	+	+
Lumpfish	*Cyclopterus lumpus*	Boreal_benthic	+	+	+
Saithe/Pollock	*Pollachius virens*	Boreal_benthic	+	+	+
Striped seasnail	*Liparis liparis*	Boreal_benthic	+	+	+
Montagus sea-snail	*Liparis montagui*	Boreal_benthic		+	+
Bull-rout	*Myoxocephalus scorpius*	Boreal_benthic	+	+	+
Longspined bullhead	*Taurulus bubalis*	Boreal_benthic	+	+	
Lesser sand-eel	*Ammodytes marinus*	Boreal_benthic	+		
Great sand-eel	*Hyperoplus lanceolatus*	Boreal_benthic	+	+	+
Rock gunnel	*Pholis gunnellus*	Boreal_benthic	+	+	+
Eelpout	*Zoarces viviparus*	Boreal_benthic	+	+	+
Dab	*Limanda limanda*	Boreal_benthic	+	+	+
Lemon sole	*Microstomus kitt*	Boreal_benthic	+	+	+
Turbot	*Scophthalmus maximus*	Boreal_benthic	+	+	+
Atlantic cod	*Gadus morhua*	Boreal_benthopelagic	+	+	+
Ten-spined stickleback	*Pungitius pungitius*	Boreal_benthopelagic			+
Fifteen-spined stickleback	*Spinachia spinachia*	Boreal_benthopelagic	+	+	+
Small sand-eel	*Ammodytes tobianus*	Boreal_benthopelagic	+	+	+
River lamprey	*Lampetra fluviatilis*	Boreal_benthopelagic	+	+	+
Herring	*Clupea harengus*	Boreal_pelagic	+	+	+
Houting	*Coregonus oxyrinchus*	Boreal_pelagic	+	+	+
Sea trout	*Salmo trutta*	Boreal_pelagic	+	+	+
Smelt	*Osmerus eperlanus*	Boreal_pelagic	+	+	+
Three-spined stickleback	*Gasterosteus aculeatus*	Boreal_pelagic	+	+	+
Silvery lightfish	*Maurolicus muelleri*	Circum-temperate/-tropical_pelagic	+		
Snake pipefish	*Entelurus aequoreus*	Lusitanian_benthic	+	+	+
Greater pipefish	*Syngnathus acus*	Lusitanian_benthic	+	+	+
Nilsson's pipefish	*Syngnathus rostellatus*	Lusitanian_benthic	+	+	+
Tub gurnard	*Chelidonichthys lucerna*	Lusitanian_benthic	+	+	+
Dragonet	*Callionymus lyra*	Lusitanian_benthic	+	+	+
Thicklip grey mullet	*Chelon labrosus*	Lusitanian_benthic	+	+	+
Lesser weever	*Echiichthys vipera*	Lusitanian_benthic			+
Red mullet	*Mullus surmuletus*	Lusitanian_benthic	+		+
Lozano's goby	*Pomatoschistus lozanoi*	Lusitanian_benthic			+
Common goby	*Pomatoschistus microps*	Lusitanian_benthic	+	+	+
Sand goby	*Pomatoschistus minutus*	Lusitanian_benthic	+	+	+
Painted goby	*Pomatoschistus pictus*	Lusitanian_benthic			+
Scaldfish	*Arnoglossus laterna*	Lusitanian_benthic			+
Solenette	*Buglossidium luteum*	Lusitanian_benthic	+	+	+
Flounder	*Platichthys flesus*	Lusitanian_benthic	+	+	+
Plaice	*Pleuronectes platessa*	Lusitanian_benthic	+	+	+
Brill	*Scophthalmus rhombus*	Lusitanian_benthic	+	+	+
Sole	*Solea solea*	Lusitanian_benthic	+	+	+
Whiting	*Merlangius merlangus*	Lusitanian_benthopelagic	+	+	+
Bib	*Trisopterus luscus*	Lusitanian_benthopelagic	+	+	+
Grey gurnard	*Eutrigla gurnardus*	Lusitanian_benthopelagic	+	+	
Allis shad	*Alosa alosa*	Lusitanian_pelagic			+
Twaite shad	*Alosa fallax*	Lusitanian_pelagic	+	+	+
European anchovy	*Engraulis encrasicolus*	Lusitanian_pelagic	+	+	+
Pilchard	*Sardina pilchardus*	Lusitanian_pelagic			+
Sprat	*Sprattus sprattus*	Lusitanian_pelagic	+	+	+
Garfish	*Belone belone*	Lusitanian_pelagic	+	+	+
Sand smelt	*Atherina presbyter*	Lusitanian_pelagic	+	+	+
Transparent goby	*Aphia minuta*	Lusitanian_pelagic	+	+	+
Horse mackerel	*Trachurus trachurus*	Lusitanian_pelagic	+	+	+

Atlantic and Boreal origins each had one species (Table 1). Of the new species, scaldfish (*Arnoglossus laterna*) was the most abundant with occurrences in 2017 and 2018 while Lozano's goby (*Pomatoschistus lozanoi*) was observed in 2008, 2009, and 2019. Flathead grey mullet (*Mugil cephalus*) was present in 2011 and 2018. Some species only had single individuals sampled; these included Allis shad (*Alosa alosa*) in 2007, ten-spined stickleback (*Pungitius pungitius*) in 2015, lesser weever (*Echiichthys vipera*) in 2017, painted goby (*Pomatoschistus pictus*) in 2007, and pilchard (*Sardina pilchardus*) in 2012.

3.2. *Trends of dominant fish species*

Of the 55 fish species, only 22 altogether accounted for more than 95% of the total abundance for the entire monitoring and were considered dominant species. Herring (*Clupea harengus*) was the most abundant species with seasonal mean abundance ranging from 2 in the winter of 2013 to 6343 ± 5256 (SD) ind/10000 m^2 in the summer of 2010. The second most abundant species were small sand eel (*Ammodytes tobianus*) that had seasonal means ranging from 0 in several winters to 1119 ± 677 (SD) ind/10000 m^2 in the summer of 2015. The 22 dominant species exhibited three major trend patterns that were either dome-shaped, decreasing, or increasing, however, the original time series showed strong seasonal fluctuations (Fig. 2). The monthly abundance of all 55 species combined showed a dome-shaped trend pattern that was a result of high abundances in 2010, 2012, and 2016 and low abundances at the beginning and the latter years. This was a result of similar trends patterns by dominant species, *C. harengus, A. tobianus,* and great sand eel (*Hyperoplus lanceolatus* (Fig. 2).

Some species showed decreasing trends from the beginning towards 2010 and 2012. These were Atlantic cod (*Gadus morhua*), hooknose (*Agonus cataphractus*), dab (*Limanda limanda*), bull-rout (*Myoxocephalus scorpius*), three-spined stickleback (*Gasterosteus aculeatus*), smelt (*Osmerus eperlanus*), whiting (*Merlangius merlangus*) flounder (*Platichthys flesus*), common goby (*Pomatoschistus microps*), sand goby (*Pomatoschistus minutus*), plaice (*Pleuronectes platessa*), and sprat (*Sprattus sprattus*) (Fig. 2). Four species (*M. scorpius, P. flesus, P. platessa,* and *S. sprattus*) had low abundances after 2012. *G. morhua, A. cataphractus, L. limanda, P. microps,* and *P. minutus* showed slight increases after 2012. However, *G. morhua, G. aculeatus, O. eperlanus*, and *M. merlangus* showed declines from 2017 to 2019 (Fig. 2).

Rock gunnel (*Pholis gunnellus*) had a relatively low abundance but showed an increasing trend from 2010 until 2019. Nilsson's pipefish (*Syngnathus rostellatus*) increased in abundance from 2007 to 2011 then declined until 2016 followed by a gradual increase until 2019. Eelpout (*Zoarces viviparus*) was present most of the years but with very low abundance. Striped seasnail (*Liparis liparis*), European anchovy (*Engraulis encrasicolus*), and horse mackerel (*Trachurus trachurus*) were present in some years with very low abundances while *A. laterna* was only present in the latter years (Fig. 2). The other species in Table 1 had too low abundances to determine their trends.

3.3. Seasonal assemblages and common patterns

The Dynamic Factor Analysis (DFA) model of three common patterns with SST as an explanatory variable plus noise had the lowest AIC (AIC = 10204.831) representing the best fit. This model was based on a symmetric, non-diagonal error covariance matrix that required fewer common patterns for adequate model fit. These patterns (thick dark lines in Fig. 3) each represented the common behavior of the original time series (thin dark lines in Fig. 3) of the 22 dominant fish species and had strong seasonal oscillations. The observed seasonal patterns were mainly the effect of seasonal SST variations. The estimated regression parameters for the explanatory variable showed that *C. harengus, S. sprattus, A. tobianus, S. rostellatus, G. aculeatus, H. lanceolatus, O. eperlanus, A. cataphractus, P. platessa, P. minutus, Z. viviparus*, and *L. limanda* had relatively large t-values (Table 2), representing strong relationships with SST.

The first common pattern showed a sharp drop from the beginning of the survey followed by seasonal fluctuations. An increase in 2009 was followed by drops and rises until 2019. The canonical correlations showed strong positive significant relationships for five boreal-benthic species (*A. cataphractus, L. limanda, M. scorpius, P. gunnellus,* and *Z. viviparus),* and three Lusitanian-benthic species (*P. microps, P. minutus,* and *P. platessa)*. Two Lusitanian-benthic species (*P. flesus* and *S. rostellatus)* had weak positive correlations. These species were more abundant in winter and spring and represented the winter/spring

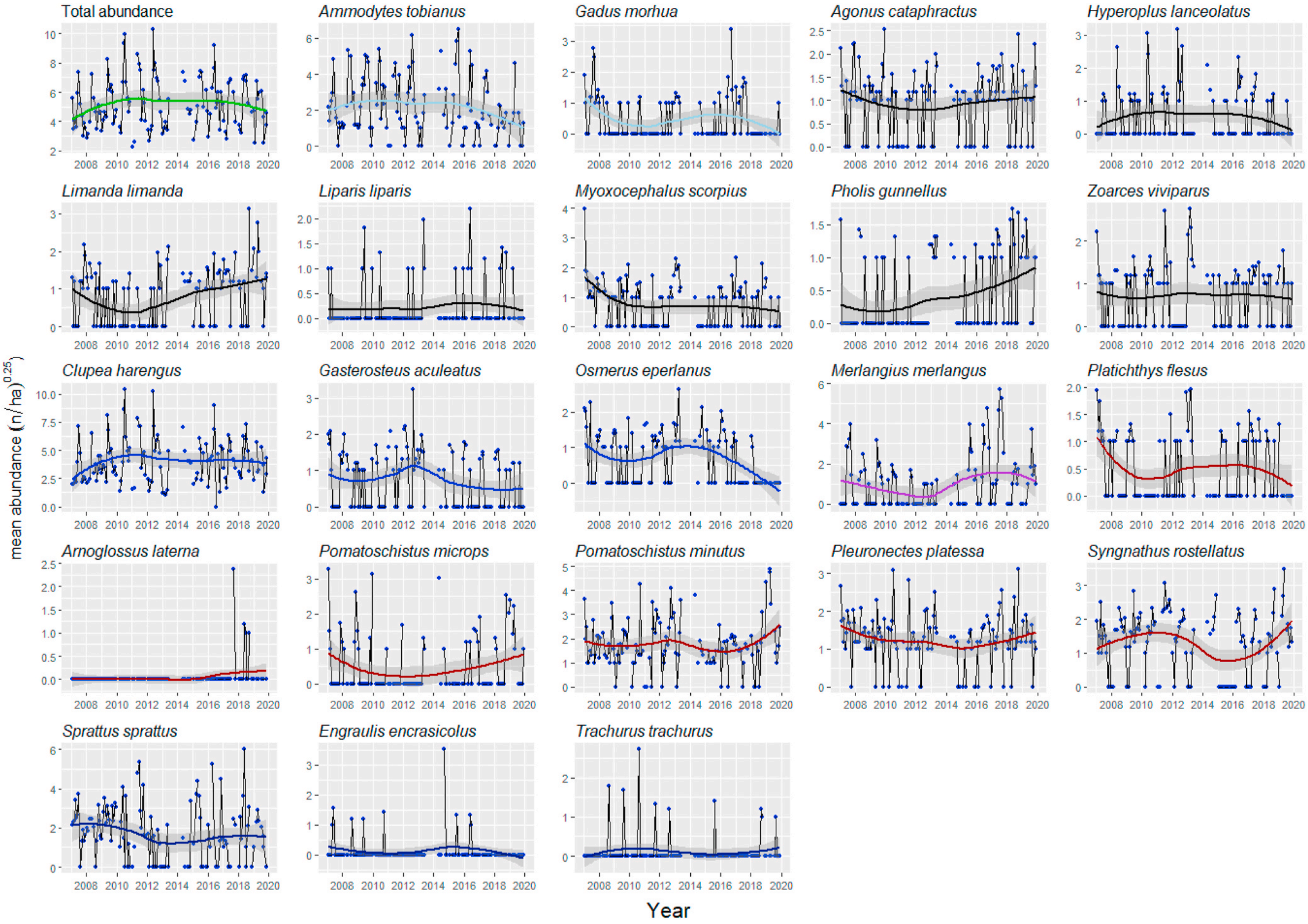

Fig. 2. The time series of the fourth root transformed the total abundance of all 55 species altogether and the abundance of the dominant species. Solid lines indicate the trends obtained by LOESS smoothing. The order of species arrangement is per the biogeographic guild–habitats (see Table 1). The grey shaded area is the 95% confidence interval.

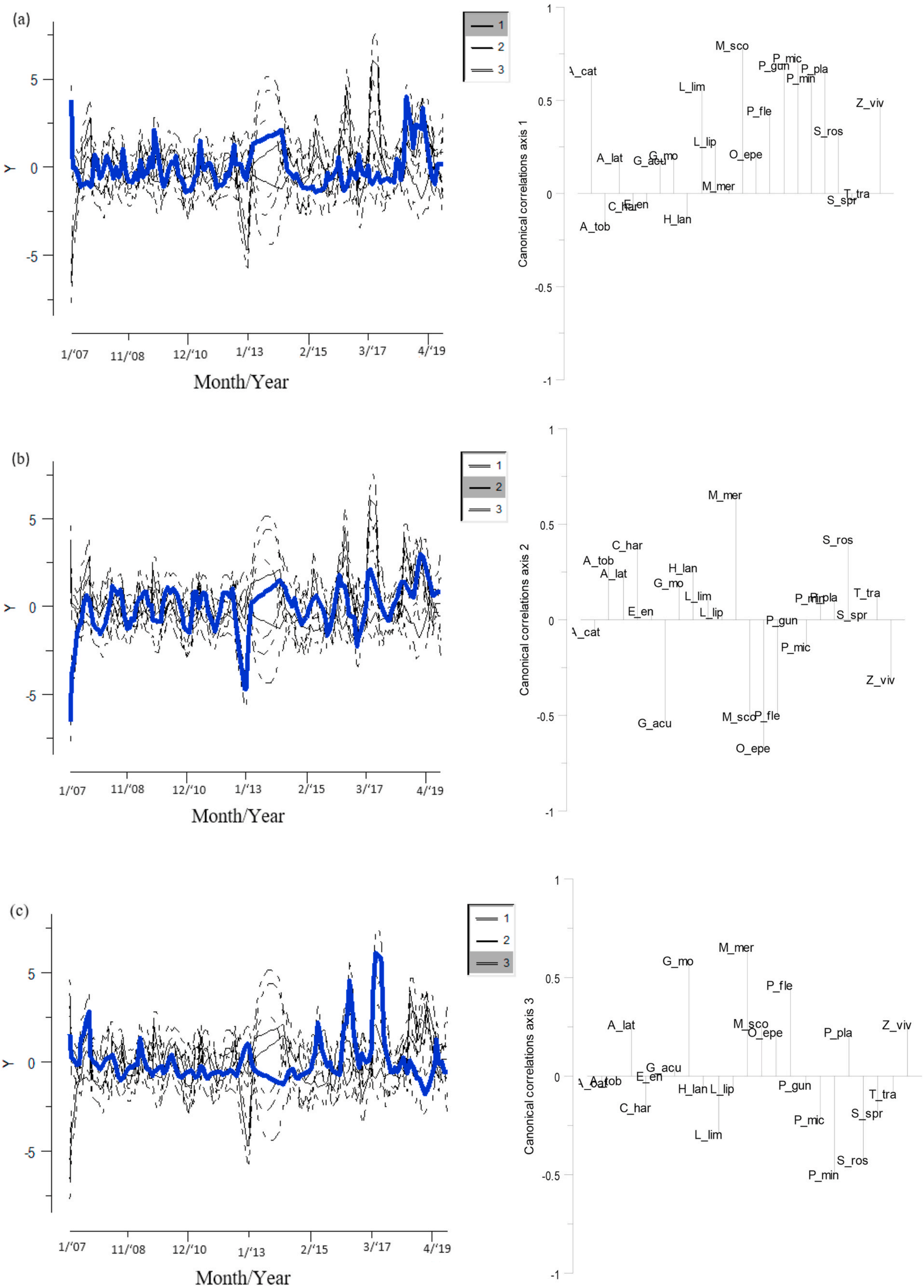

Fig. 3. Original time series (thin dark lines) and the DFA model containing three common patterns (thick dark lines) + explanatory variable (SST) + noise. The y-axis represents the patterns and the x-axis represents the months (January 2007 to December 2019). The first (a), second (b), and third (c) common patterns and canonical correlations, respectively. The common patterns are unitless (see Table 2 for the species' full names).

Table 2
The DFA estimated regression parameters, standard error (SE), and t-values for the explanatory variable (SST) and canonical correlations to the common patterns by fish species. (Spp_code represents the respective species names in DFA (Fig. 3).

Time series	Spp_code	Explanatory variable			Canonical correlations		
		Estimate value	SE	t-value	Pattern 1	Pattern 2	Pattern 3
Agonus cataphractus	A_cat	1.46	0.45	3.25	0.66	−0.06	−0.03
Ammodytes tobianus	A_tob	7.09	1.15	6.17	−0.18	0.32	−0.02
Arnoglossus laterna	A_lat	0.08	0.11	0.69	0.20	0.25	0.26
Clupea harengus	C_har	20.52	2.03	10.12	−0.07	0.39	−0.16
Engraulis encrasicolus	E_en	0.21	0.12	1.81	−0.06	0.05	−0.01
Gasterosteus aculeatus	G_acu	1.08	0.27	4.07	0.18	−0.54	0.04
Gadus morhua	G_mo	0.65	0.46	1.42	0.21	0.21	0.59
Hyperoplus lanceolatus	H_lan	0.78	0.22	3.64	−0.14	0.27	−0.06
Limanda limanda	L_lim	1.31	0.49	2.66	0.58	0.12	−0.29
Liparis liparis	L_lip	0.31	0.13	2.45	0.28	0.04	−0.06
Merlangius merlangus	M_mer	2.55	2.01	1.27	0.04	0.67	0.66
Myoxocephalus scorpius	M_sco	1.25	0.76	1.65	0.80	−0.50	0.26
Osmerus eperlanus	O_epe	0.93	0.28	3.27	0.21	−0.67	0.22
Platichthys flesus	P_fle	0.58	0.27	2.12	0.44	−0.49	0.45
Pholis gunnellus	P_gun	0.50	0.26	1.93	0.69	0.00	−0.05
Pomatoschistus microps	P_mic	1.01	0.71	1.42	0.73	−0.15	−0.22
Pomatoschistus minutus	P_min	4.66	1.65	2.83	0.62	0.10	−0.50
Pleuronectes platessa	P_pla	2.09	0.69	3.01	0.67	0.13	0.22
Syngnathus rostellatus	S_ros	2.69	0.63	4.27	0.33	0.41	−0.42
Sprattus sprattus	S_spr	4.82	0.72	6.66	−0.03	0.02	−0.19
Trachurus trachurus	T_tra	0.20	0.09	2.27	0.00	0.14	−0.09
Zoarces viviparus	Z_viv	1.01	0.37	2.74	0.49	−0.30	0.26

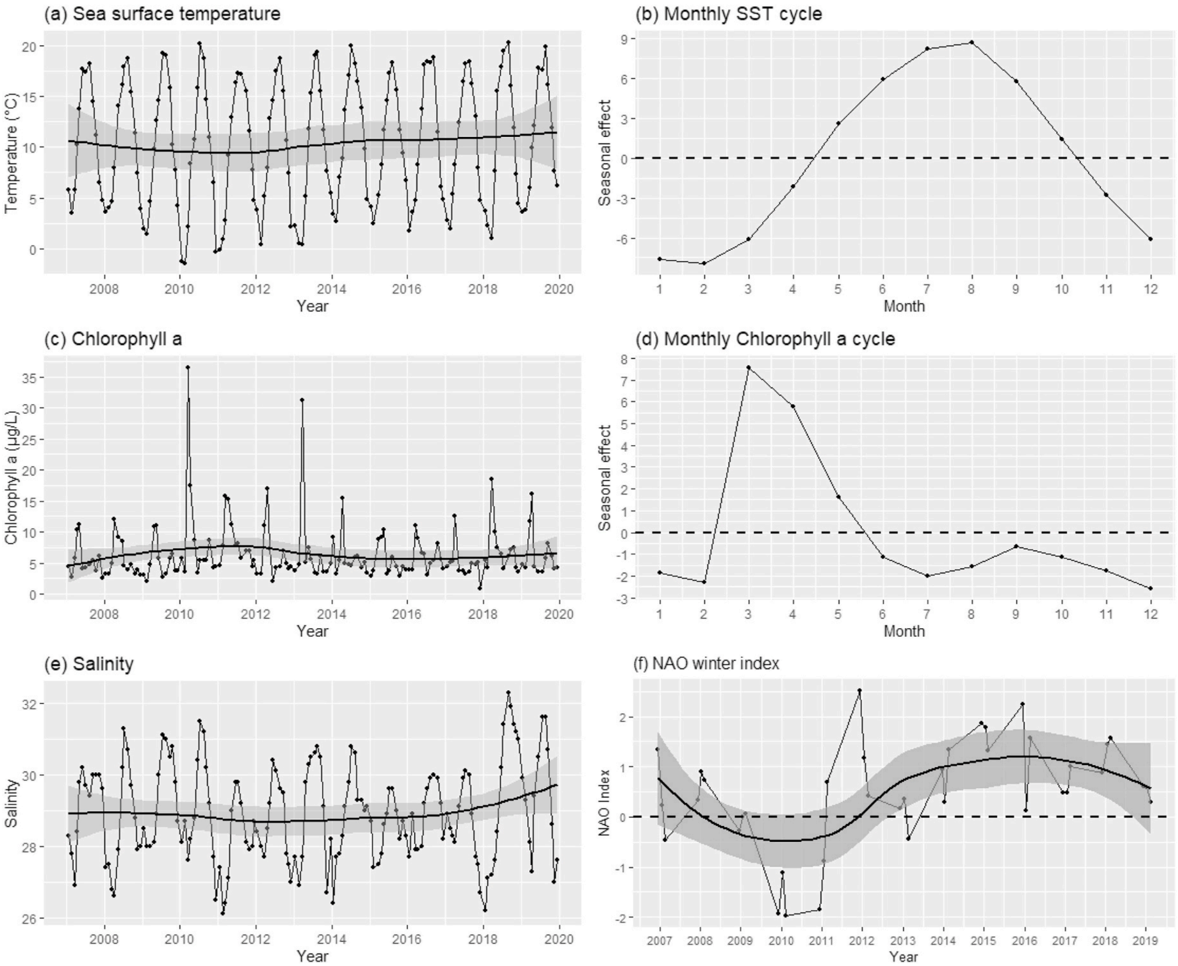

Fig. 4. Time series of environmental parameters; (a) SST, (b) monthly SST cycle, (c) time series of chlorophyll *a*, (d) monthly chlorophyll *a* cycle, (e) time series of salinity in the SRB, and (f) the monthly NAO winter indices.

assemblages. No species had significant negative correlations with this pattern (Fig. 3 (a)).

The second common pattern showed a sharp increase from the beginning of the survey followed by seasonal fluctuations until 2013 when a rapid fall occurred. This was followed by a sharp rise then seasonal fluctuations in an increasing order in the latter years. Canonical correlations showed that only *M. merlangus* had a strong significant positive relationship with this pattern while *C. harengus*, *S. rostellatus*, *A. tobianus*, and *H. lanceolatus* had weak positive correlations (Fig. 3 (b)). These species belonged to both Lusitanian and boreal origins and had high abundances in summer representing summer assemblages. *G. aculeatus, O. eperlanus, M. scorpius,* and *P. flesus* showed significantly strong negative correlations while *Z. viviparous* had a weak negative correlation (Fig. 3 (b)).

The third common pattern showed a decrease from the beginning of the survey followed by minimal seasonal fluctuations until 2016 when the highest seasonal rises were achieved for three consecutive years in an increasing order. In 2018, there was a sharp decline with no significant increase until 2019. *Gadus morhua* and *M. merlangus* had strong significant positive correlations while *P. flesus* had a weak one. These species had relatively high abundances in autumn and represent autumn assemblages. *Pomatoschistus minutus* and *S. rostellatus* had moderate negative correlations to this pattern (Fig. 3 (c)).

3.4. Inter- and intra-annual variations of abiotic parameters

There were strong seasonal variations in SST with February and August being the coldest and warmest months, respectively (Fig. 4). Warm winters occurred from the beginning of the survey to 2009/2010 and 2010/2011that had prolonged cold winters (Figs. 4 and 5). The mean winter SST was highest in 2007 and lowest in 2011. In 2012 and subsequent years, the mean winter SST was above 1.5 °C (Fig. 5). The mean summer SST was highest in 2018 and coldest in 2015 (Fig. 5). Overall, the SST patterns showed strong seasonal fluctuations to long-term trends (Fig. 4). Chlorophyll *a* showed peak concentration in the spring of 2010 after the prolonged cold winter (Fig. 4) and in 2013 that had a relatively low mean winter SST (Fig. 5). This was followed by relatively low concentrations until 2019. Chlorophyll *a* rapidly rises from February to March when the spring bloom occurs, then followed by a gradual decrease until July. A small bloom occurs in September but this is followed by a gradual decrease until February (Fig. 4). Salinity ranged from 26.1 to 32.3 with a mean of 28.9 ± 1.4 (SD). From 2014 to the latter years, salinity showed an increasing trend. Both negative and positive NAO winter indices occurred during the study period. Remarkable were the pronounced negative indices in the winters of 2009/2010 and 2010/2011 (Fig. 4).

3.5. Potential effects of environmental variables on the fish community

The RDA was performed with sea surface temperature (SST), salinity (Sal), chlorophyll *a* (Chl_a), NAO winter, and ordinal variables year and season as explanatory variables. The ordinal variables were included to investigate the combined effects of annual and seasonal variations of various parameters on the fish community. RDA with all the explanatory variables explained 56.41 % of variations (constrained) while 43.59 % were unexplained (unconstrained). The ordinal variables year and season were retained by RDA permutation tests and explained 29.4 % of the variations ($R^2 = 0.5641$, adjusted $R^2 = 0.2936$), ($p < 0.05$). Variance partitioning of explanatory variables showed that the factor year explained 10% while the seasonal variations of environmental parameters explained 18% of the variations in the fish community (Fig. 6 (a)). To find the significant environmental variables, ordinal variables were excluded from the second RDA model. The permutation tests retained SST, chlorophyll *a*, and salinity as important variables and significantly explained 17 % ($R^2 = 0.22$, adjusted $R^2 = 0.16.6$, $p < 0.05$) of the variations while NAO winter was excluded. Variance partitioning showed that SST was the most important variable that explained 10% of the variations while both salinity and chlorophyll *a*, each explained 2 % (Fig. 6 (b)). The combined effects of SST and salinity explained 14% while chlorophyll *a* and salinity explained 5% (Fig. 6). 71% of the variations were unexplained (Residuals = 0.71), (Fig. 6 (a)) suggesting other important variables that are currently unknown were missing from the model and could improve the results when included.

The RDA principal axis (RDA1) was correlated to winter and summer seasons, SST, salinity, and some years and together explained 20.66% of the variations. The second RDA axis (RDA2) explained 11.16% of the variations and was correlated to autumn and spring seasons, chlorophyll *a*, and several years. The longer arrows in Fig. 7 show important explanatory and response variables. *Gasterosteus aculeatus, O. eperlanus, Z. viviparous, P. minutus, P. microps, M. scorpius,* and *L. limanda* were positively correlated to winter seasons. *Clupea harengus* and *A. tobianus* were positively correlated to summer seasons while *S. sprattus* was positively correlated to spring seasons (Fig. 7). *Merlangius merlangus*, *S. rostellatus,* and G. *morhua* were positively correlated to the years 2016, and 2017, and negatively correlated with 2011 and 2012 as well as chlorophyll *a*. Species such as *A. laterna, E. encrasicolus, T. trachurus, L. liparis,* and *P. gunnelus* had very weak correlations with the environmental variables (Fig. 7).

4. Discussion

4.1. Fish species compositions

During the present monitoring, 55 fish species were documented in

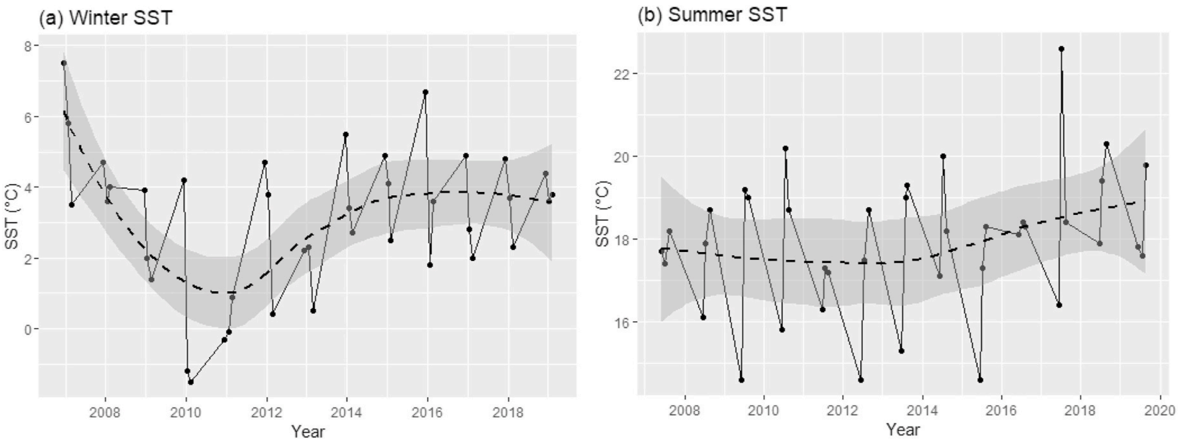

Fig. 5. Variations of winter and summer SSTs in the SRB between 2007 and 2019. SST measurements (dark lines) and a LOESS smoother of trends (dashed dark line).

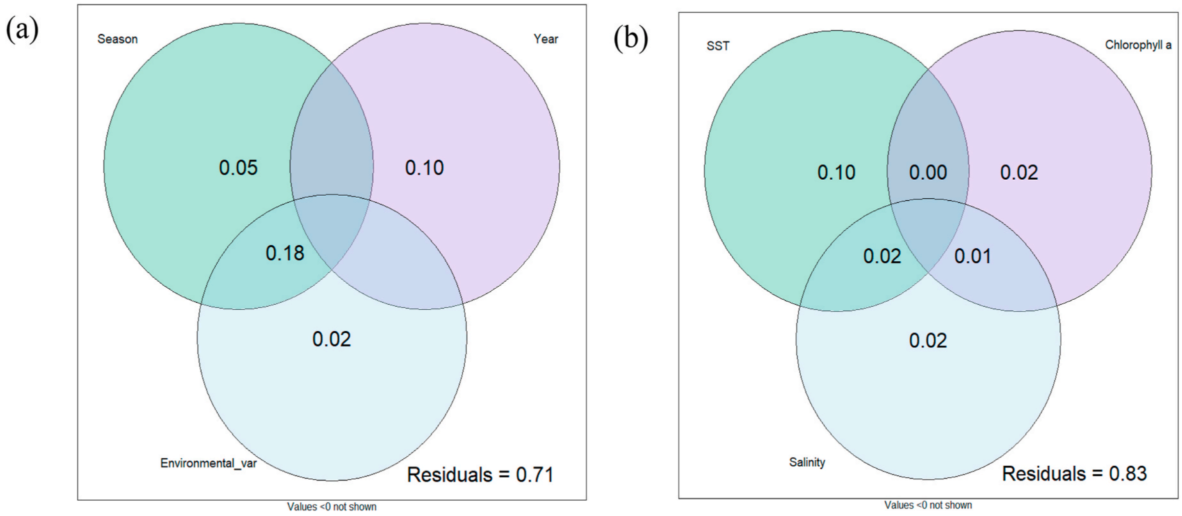

Fig. 6. Venn diagrams of variance partitioning of explanatory variables with respective percentage contributions to the variations in the fish community. (a) The ordinal variables year and season plus the combined effects of SST, salinity, and chlorophyll a as Environmental_var. (b) The percentage contributions of SST, chlorophyll *a*, and salinity. The residuals represent the unexplained variations.

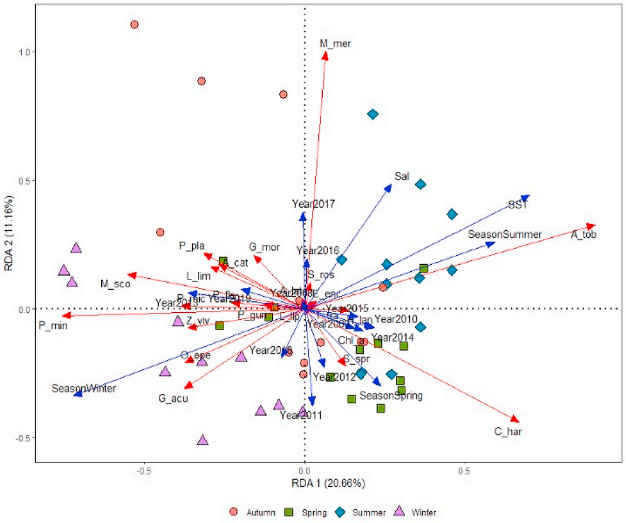

Fig. 7. RDA correlation triplot for the dominant fish species in the SRB, the explanatory variables sea surface temperature (SST), Sal (salinity), Chlorophyll *a* (Chl_a), and the ordinal variables year and season. Seasonal sample scores are shown in different shapes (See Table 2 for the species' full names).

the Sylt-Rømø Bight (SRB) and included eight new species that had not been recorded between 1989 and 1995 by Herrmann et al. (1998) and Vorberg and Breckling (1999). Two species that were absent in the present monitoring, Longspined bullhead (*Taurulus bubalis*) and lesser sand eel (*Ammodytes marinus*) were present in some monitoring programs in the Wadden Sea reported in Tulp et al. (2022). Similarly, silvery lightfish (*Maurolicus muelleri*) was found only in the German estuaries while grey gurnard (*Eutrigla gurnadus*) was present in all monitoring programs in Tulp et al. (2022). The higher number of Lusitanian species in the SRB was attributed to the relatively warm summers and autumns in the latter years compared to 1989 to 1994 (Rick et al., 2023) and supports the prediction of an increase in thermophile species and a decrease in the cold-water adapted species. However, these new species are still rare and have low abundances in the SRB. The SRB is an important transitional water system for catadromous species e.g. European eel (*Anguilla anguilla*) and anadromous species e.g. Twaite shad (*Alosa fallax), A. alosa, G. aculeatus,* houting (*Coregonus oxyrhynchus*), river lamprey *(Lampetra fluviatilis), O. eperlanus* and Sea trout (*Salmo trutta*). Fish of southern biogeographic origins such as European anchovy (*Engraulis encrasicolus*), red mullet (*Mullus surmuletus*), sardine (*Sardina pilchardus*), and snake pipefish (*Entelurus aequoreus*) was established in the North Sea (Dulvy et al., 2008), however, their occurrence in the SRB was rare, *E. aequoreus* was only present in 2007 and 2008.

Tulp et al. (2022) reviewed several fish monitoring programs between 2011 and 2020 along the Wadden Sea coastline, estuaries, large rivers, and around the North Sea Islands. Different sampling techniques were applied in these programs and a total of 124 fish species including 30 freshwater species were recorded. Of the 124 species, 42 were recorded in the coastal waters of Schleswig-Holstein, which was less than the SRB (55). Two new species in the SRB; *M. cephalus* and *A. alosa* were not recorded in the review of Tulp et al. (2022), though *A. alosa* was found earlier in the German Wadden Sea (Bolle et al., 2009). *Echiichthys vipera, A. laterna,* and *S. pilchardus* were recorded in other areas, but not in Schleswig-Holstein. *Pomatoschistus lozanoi* was recorded in the Dutch Wadden Sea while *P. pictus* and *P. pungitius* were only found in the German estuaries. The patchy occurrence of various species is a result of different sampling techniques and frequency, especially as most fish monitoring programs in the Wadden Sea occur in the spring/summer and summer/autumn periods (Tulp et al., 2022). Moreover, variations in abiotic factors such as SST, salinity, and nutrient input between the sampled areas (van Aken, 2008b; van Beusekom et al., 2019; van Walraven et al., 2017) play significant roles.

4.2. *Seasonal assemblages and common patterns*

Identifying shared trends and patterns in a fish community can demonstrate the key drivers of ecosystem dynamics and interactions (Zuur et al., 2007a). All the common patterns showed seasonal fluctuations with SST changes highlighting its significance in structuring the fish community in the Wadden Sea. High variability of abiotic conditions, especially SST, influences the fish phenology such as migration patterns. During winter, mature benthic fish species occur in deeper waters unlike the juveniles that occur in the coastal areas (Daan et al., 1990). Species that were positively correlated to the first common pattern were boreal-benthic and Lusitanian-benthic (Fig. 3) and were negatively correlated to SST (Fig. 7) explaining their high abundances in winter and spring. An exception to this migration behavior was *S. rostellatus*, which was also positively correlated to the second common pattern since it is warm-water adapted and a permanent resident in the SRB. Besides, the high winter/spring abundance of *P. minutus* and *P. microps* (Fig. 3) and their negative correlation to SST (Fig. 7) are attributed to their local migration to deeper areas with stable winter temperatures. Only at this time and in these depths our research vessel have access to these populations. However, they are more abundant in summer in intertidal habitats (Kellnreitner et al., 2012) that could not be sampled in the present monitoring because these areas are out of reach of our ship. The migration behavior was observed for *M. merlangus,* an exclusive late spring/early summer immigrant in the bight, while the opposite was true for *C. harengus* and *A. tobianus,* which emigrate in late summer. *Arnoglossus laterna, G. morhua, M. merlangus,* and *P. flesus* were positively correlated to the third common pattern and showed increasing trends from 2016 (Fig. 2), implying a shift in phenology as they are staying longer with warming autumn SSTs (Rick et al., 2023). In addition, *P minutus* stays longer in the shallow intertidal areas before the local migration to deep areas in winter (Fig. 3, c).

Osmerus eperlanus spawns in freshwater zones of estuaries (Camphuysen et al., 2017). They emigrate from the SRB into landward rivers in spring in search of spawning grounds hence the negative correlation to the second common pattern and SST (Figs. 3 and 7). In the western Dutch Wadden Sea, it peaked in the summer (van Walraven et al., 2017), attributed to differences in salinity between the two areas (Rick et al., 2023; van Aken, 2008b). *Ammodytes tobianus* hibernates in sandy substrates in winter (Camphuysen et al., 2017) explaining its positive correlation to SST and the second pattern (Figs. 7 and 3). Kellnreitner et al. (2012) and van Walraven et al. (2017) observed similar summer occurrences. Boreal species showed common patterns that were negatively correlated to SST while Lusitanian species were positively correlated in the Dutch Wadden Sea (Tulp et al., 2008). *Sardina pilchardus* and Seabream (*Diplodus sargus*) off the Portuguese coast also followed similar SST patterns (Leitão et al., 2014, 2016). *Platichthys flesus* and *M. scorpius* belonged to winter/spring assemblage (Fig. 3). In the western Dutch Wadden Sea, a similar occurrence was found for *P. flesus* but *M. scorpius* peaked in the summer (van Walraven et al., 2017). Erzini (2005) linked common patterns and trends to the life history characteristics of various fish species. Short-lived species were influenced by variations in environmental parameters as we observed in the SRB for the juveniles while the long-lived species were more susceptible to fishing.

4.3. *Fish population trends and the effects of environmental variables*

The fish populations were largely dominated by high seasonal fluctuations with either dome-shaped, increasing, or decreasing trends (Fig. 2) that were linked to variations in environmental parameters. Environmental variables significantly explained 29 % of the community variations, which was much lower when compared to other studies in the North Sea such as Pécuchet et al. (2015) who applied nine variables and explained more than 70% of variations. SST was significant and explained the highest portion of variations (Fig. 6) and its effects were visible in the species trend fluctuations. The correlations of temperature to the recruitment of fish are strong at the geographical limit of species ranges and less near the center (Myers, 1998). The SRB is located in the latitudinal center of distribution ranges for both the northern and southern species (Fig. 1). Thus, the 10 % variations in the fish community explained by SST show its significance. Species that were positively correlated to SST (i.e. *C. harengus, A. tobianus, H. lanceolatus,* and *S. rostellatus* (Fig. 7)) showed increasing trends with decreasing winter SST (Figs. 2 and 5). Historical records indicate trend fluctuations, especially for *C. harengus,* which had peak abundances after severe winters in the North Sea (Corten, 2013) and the Barents Sea (Aschan et al., 2013). After severe winters, the highest spring diatom bloom (Fig. 4), delayed copepod developments (Martens and Van Beusekom, 2008), and a decline of benthic organisms occur in the SRB (Armonies et al., 2001). This could lead to a mismatch between larval fish and copepods (Aschan et al., 2013) and prolong the high predation risk phase (Malzahn et al., 2007) potentially resulting in high mortalities during the critical period. On the contrary, the copepod, *Calanus finmarchicus,* which is the main food source for herring over-winters in the deeper waters along the Shelf Edge Current and is transported to the eastern North Sea by the Norwegian Trench Current (Gao et al., 2021). Therefore, calanoid copepod feeders (Kellnreitner et al., 2012) with spawning populations in the North Sea (Corten, 2013) had an alternative food source during and after prolonged cold winters (Fig. 2).

The recruitment of fish in an area depends on food availability, SST variations, predators, overfishing, etc (Corten, 2013). Species' SST preferences and food availability are the major parameters that explain differences in trends among fish species (Tulp et al., 2008). Species that were negatively correlated to SST (i.e. *G. aculeatus, O. eperlanus, P. minutus, P. microps, M. scorpius, L. limanda, P. flesus, P. platessa, A. cataphractus,* and *G. morhua*) showed decreasing trends with decreasing winter SST. *Sprattus sprattus* and *M. merlangus,* which were positively correlated to SST also showed decreasing trends with decreasing winter SST (Figs. 2 and 7). The similarity of decreasing trends and different responses to SST meant other additional parameters were driving the community variations. Food availability could be one of the parameters. For instance, *C. harengus* feeds in the pelagic zone and its high abundance results in less food available for demersal species with similar prey preferences (Pedersen and Fossheim, 2008). For example, *C. harengus'* consumption of *C. finmarchicus* reduced other species' consumption by more than 50 % in the Norwegian Sea (Utne et al., 2012). Similar inverse population patterns were reported for the Pacific sardine (*Sardinops caeruleus*) and the northern anchovy (*Engraulis mordax*) in the northern California Current System (Rodríguez-Sánchez et al., 2002).

A match between juvenile zooplanktivorous fish and copepods after normal winters from 2014 onwards could have increased their survival rates and competition for food. Thus, *C. harengus* and *A. tobianus* trends stabilized and even decreased in the latter years (Fig. 2) while some previously decreasing species showed increases. For *C. harengus*, warm winters correlated to positive NAO winter also mean less inflow of its larvae from the North Sea (Corten, 2013). Different trend patterns can be explained by differences in functional guilds, such as permanent residency or seasonal migrants, habitat preferences (Tulp et al., 2008), and spawning strategies. For permanent residents, any cause for trend fluctuations lies within the Wadden Sea (Tulp et al., 2017). There were some minor habitat changes in the SRB such as the increase of seaweed (*Sargassum muticum*) (Polte and Buschbaum, 2008) and seagrasses (*Zostera marina* and *Zostera notlei*) in summer (Horn et al., 2021) as well as the decline of mussel beds and the establishment of intertidal oyster beds in the last decades. These could have promoted the increase of *P. gunnellus* and *S. rostellatus* by providing suitable habitats. *Limanda limanda* spawns planktonic eggs in batches but the larvae settle in shallow waters (Camphuysen et al., 2017) thereby increasing their survival chances. This favors their recruitment hence the increasing trends in the SRB similar to the Dutch Wadden Sea (Tulp et al., 2022). However, it showed a decline in the German estuaries and North Frisia areas sampled in Tulp et al. (2022) which may be because of differences in sampling frequency and seasonality. Even sampling in the Dutch Wadden Sea starts in spring missing the winter peak abundances and might not provide the true trend patterns (Camphuysen et al., 2017). The low abundance of *P. platessa* (Fig. 2) is attributed to the SST increase that decreased the suitability for the nursery function for flatfishes in the Wadden Sea (van der Veer et al., 2022). Similarly, high frequencies of warm summers above the thermal tolerance of *Z. viviparus* caused its decline in the Wadden Sea (Pörtner and Knust, 2007). *Trachurus trachurus* is a pelagic schooling species that migrates inshore in the summer (Camphuysen et al., 2017). Its abundance remained low, however, the warm summers of 2010 (Fig. 4) might have favored its immigration (Jansen and Gislason, 2011).

Sprattus sprattus was negatively correlated to salinity (Fig. 7). In contrast, its recruitment was positively correlated to salinity in the western North Sea (Akimova et al., 2016) and Baltic Sea since low salinity hinders the reproduction of *G. morhua* its main predator (Ojaveer and Kalejs, 2010). This demonstrates an interplay of biotic and abiotic parameters in shaping the fish community. Chlorophyll *a* concentration is an indicator of productive feeding grounds for planktivorous fish and the variability of fisheries is highly associated with its seasonal changes (Lanz et al., 2009). High chlorophyll a enrichment with sufficient time lag for zooplankton increase and small pelagic fish with open-water spawning strategies to locate such areas is extremely important (Lanz et al., 2009; Pécuchet et al., 2015). The correlation of fish with chlorophyll *a* depended on species-specific phenology. For instance, *S. sprattus* was positively correlated to chlorophyll *a* (Fig. 7) since the juveniles move to estuaries in late spring (Camphuysen et al., 2017) resulting in a higher spring population in the SRB. Capuzzo et al. (2018) linked the recruitment of various fish species in the North Sea to bottom-up control, which was evident in the SRB, especially after prolonged cold winters. NAO was not significant in explaining the variations in the fish community similar to Tulp et al. (2008), unlike the positive correlations observed by Dippner (1997) between the recruitment success of *G. morhua*, saithe (*Pollachius virens*), *M. merlangus*, and *T. trachurus* in the North Sea. The warming North Sea associated with positive NAO in the 1990s was correlated with the re-introduction of *E. encrasicolus* and *S. pilchardus* (Alheit et al., 2012) but they are still rare in the SRB.

5. Conclusions

The seasonal variations of fish communities in temperate coastal waters and correlations with abiotic parameters were presented. Species composition changed compared to two previous investigations with four species being absent in the present study and eight new species which are still rare. The peak abundances of some species differed on a seasonal basis in comparison to other Wadden Sea areas, a feat that may be attributed to differences in environmental parameters and/or differences in sampling frequency and seasonality. SST was the main parameter driving the fish community. Interestingly, different species even those belonging to the same biogeographic guild-habitats showed different responses to SST variations. The environmental parameters applied in this study explained only 29 % of the variations in the fish community. The inclusion of more parameters could give a more detailed insight into the community dynamics and the interaction of factors. For instance, copepod data were not available during the study period but could improve our understanding in future research when included as we suspect food availability to be a very important driver. Future research could focus on biomass change over time as it was determined that eight commercially important fish species in the North Sea underwent reductions in asymptomatic body sizes in response to climate-induced temperature changes (Baudron et al., 2014). The high-resolution monitoring revealed high seasonal variations in the fish community in relation to environmental drivers. Incorporating these seasonal differences is critical for successful fish community management focusing on the local environments and should extend to wider spatial scales covering spawning, nursery, and feeding grounds. Further investigations on the connectivity between these areas and the driving forces to connectivity could answer more questions and shape decision-making for sustainable management of marine and coastal resources.

CRediT authorship contribution statement

Victor Odongo: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Harald Asmus:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Harald Ahnelt:** Writing – review & editing, Methodology, Conceptualization. **Maarten Boersma:** Writing – review & editing, Methodology, Conceptualization. **Johannes Rick:** Writing – review & editing, Validation, Methodology. **Karen Helen Wiltshire:** Writing – review & editing, Validation, Methodology. **Sabine Horn:** Writing – review & editing, Methodology, Conceptualization.

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.

Data availability

I have shared a supplementary material with the mean seasonal abundance data. Besides, I have provided the dataset links where the original data can be obtained upon request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2024.108723.

References

Akimova, A., Núñez-Riboni, I., Kempf, A., Taylor, M.H., 2016. Spatially-resolved influence of temperature and salinity on stock and recruitment variability of commercially important fishes in the North sea. PLoS One 11. https://doi.org/10.1371/journal.pone.0161917.

Alheit, J., Pohlmann, T., Casini, M., Greve, W., Hinrichs, R., Mathis, M., O'Driscoll, K., Vorberg, R., Wagner, C., 2012. Climate variability drives anchovies and sardines into the North and Baltic Seas. Prog. Oceanogr. 96, 128–139. https://doi.org/10.1016/j.pocean.2011.11.015.

Armonies, W., Herre, E., Sturm, M., 2001. Effects of the severe winter 1995/96 on the benthic macrofauna of the Wadden Sea and the coastal North Sea near the island of Sylt. Helgol. Mar. Res. 55, 170–175. https://doi.org/10.1007/s101520100077.

Aschan, M., Fossheim, M., Greenacre, M., Primicerio, R., 2013. Change in fish community structure in the Barents Sea. PLoS One 8. https://doi.org/10.1371/journal.pone.0062748.

Asmus, H., Hussel, B., Petra, K., Asmus, R., Rick, J.J., Wiltshire, K.H., 2020. Fish monitoring in the Sylt Rømø bight (2007 et seq). https://doi.org/10.1594/PANGAEA.911261 [WWW Document]. Alfred Wegener Institute - Wadden Sea Station Sylt, PANGEA. URL.

Baird, D., 2012. Assessment of observed and perceived changes in ecosystems over time, with special reference to the Sylt-Rømø Bight, German Wadden Sea. Estuar. Coast Shelf Sci. 108, 144–154. https://doi.org/10.1016/j.ecss.2011.06.006.

Baudron, A.R., Needle, C.L., Rijnsdorp, A.D., Tara Marshall, C., 2014. Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. Glob Chang Biol 20, 1023–1031. https://doi.org/10.1111/gcb.12514.

Bolle, L.J., Neudecker, T., Vorberg, R., Damm, U., Diederichs, B., Jager, Z., Scholle, J., Daenhardt, A., Lüerßen, G., Marencic, H., 2009. Trends in Wadden Sea Fish Fauna Part I: Trilateral Cooperation.

Camphuysen, C.J., Henderson, P.A., Velilla, E., Leopold, M.F., Kuhn, S., Somes, J.R., 2017. North Sea Fish and Their Remains. Royal Netherlands Institute for Sea Research & Pisces Conservation Ltd.

Capuzzo, E., Lynam, C.P., Barry, J., Stephens, D., Forster, R.M., Greenwood, N., McQuatters-Gollop, A., Silva, T., van Leeuwen, S.M., Engelhard, G.H., 2018. A decline in primary production in the North Sea over 25 years, associated with reductions in zooplankton abundance and fish stock recruitment. Glob Chang Biol 24, e352–e364. https://doi.org/10.1111/gcb.13916.

Corten, A., 2013. Food for thought: recruitment depressions in North Sea herring. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 70, 1–15. https://doi.org/10.1093/icesjms/fss187.

Daan, N., Bromley, P.J., Hislop, J.R.G., Nielsen, N.A., 1990. Ecology of North Sea fish. Netherlands Journal of Sea Research 26, 343–386.

de Amorim, F., Wiltshire, H.K., Lemke, P., Carstens, K., Peters, S., Rick, J., Gimenez, L., Scharfe, M., 2023. Investigation of marine temperature changes across Temporal and spatial Gradients: providing a Fundament for studies on the effects of warming on marine ecosystem function and Biodiversity. Prog. Oceanogr. 103080 https://doi.org/10.1016/j.pocean.2023.103080.

Dippner, J.W., 1997. Recruitment success of different fish stocks in the North Sea in relation to climate variability. German Journal of Hydrography 49.

Dulvy, N.K., Rogers, S.I., Jennings, S., Stelzenmüller, V., Dye, S.R., Skjoldal, H.R., 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. J. Appl. Ecol. 45, 1029–1039. https://doi.org/10.1111/j.1365-2664.2008.01488.x.

Elliott, M., Whitfield, A.K., Potter, I.C., Blaber, S.J.M., Cyrus, D.P., Nordlie, F.G., Harrison, T.D., 2007. The guild approach to categorizing estuarine fish assemblages: a global review. Fish Fish. 8, 241–268. https://doi.org/10.1111/j.1467-2679.2007.00253.x.

Erzini, K., 2005. Trends in NE Atlantic landings (southern Portugal): Identifying the relative importance of fisheries and environmental variables. Fish. Oceanogr. 14, 195–209. https://doi.org/10.1111/j.1365-2419.2005.00332.x.

Gao, S., Hjøllo, S.S., Falkenhaug, T., Strand, E., Edwards, M., Skogen, M.D., 2021. Overwintering distribution, inflow patterns and sustainability of Calanus finmarchicus in the North Sea. Prog. Oceanogr. 194 https://doi.org/10.1016/J.POCEAN.2021.102567.

Herrmann, J.P., Jansen, S., Temming, A., 1998. Consumption of fish and decapod crustaceans and their role in the trophic relations of the Sylt-Rømø Bight. In: Ökosystem Wattenmeer-Austausch-Transport- Und Stoffumwandlungsprozesse. Springer, Berlin Heidelberg, pp. 81–88.

Horn, S., Coll, M., Asmus, H., Dolch, T., 2021. Food web models reveal potential ecosystem effects of seagrass recovery in the northern Wadden Sea. Restor. Ecol. 29 https://doi.org/10.1111/rec.13328.

Jansen, T., Gislason, H., 2011. Temperature affects the timing of spawning and migration of North Sea mackerel. Cont Shelf Res 31, 64–72. https://doi.org/10.1016/j.csr.2010.11.003.

Kabat, P., Bazelmans, J., van Dijk, J., Herman, P.M.J., van Oijen, T., Pejrup, M., Reise, K., Speelman, H., Wolff, W.J., 2012. The Wadden Sea Region: towards a science for sustainable development. Ocean Coast Manag. 68, 4–17. https://doi.org/10.1016/j.ocecoaman.2012.05.022.

Kellnreitner, F., Pockberger, M., Asmus, H., 2012. Seasonal variation of assemblage and feeding guild structure of fish species in a boreal tidal basin. Estuar. Coast Shelf Sci. 108, 97–108. https://doi.org/10.1016/j.ecss.2011.02.020.

Lanz, E., Lopez Martinez, J., Nevarez Martinez, M.O., 2009. Small pelagic fish catches in the Gulf of California associated with sea surface temperature and chlorophyll. CalCOFI Reports 50, 134–146.

Leitão, F., Alms, V., Erzini, K., 2014. A multi-model approach to evaluate the role of environmental variability and fishing pressure in sardine fisheries. J. Mar. Syst. 139, 128–138. https://doi.org/10.1016/j.jmarsys.2014.05.013.

Leitão, F., Baptista, V., Teodósio, M.A., Hughes, S.J., Vieira, V., Chícharo, L., 2016. The role of environmental and fisheries multi-controls in white seabream (Diplodus sargus) artisanal fisheries in Portuguese coast. Reg. Environ. Change 16, 163–176. https://doi.org/10.1007/s10113-014-0726-5.

Malzahn, A.M., Clemmeses, C., Wiltshire, K.H., Laakmann, S., Boersma, M., 2007. Comparative nutritional condition of larval dab Limanda limanda and lesser sandeel Ammodytes marinus in a highly variable environment. Mar. Ecol. Prog. Ser. 334, 205–212.

Martens, P., Van Beusekom, J.E.E., 2008. Zooplankton response to a warmer northern Wadden Sea. Helgol. Mar. Res. 62, 67–75. https://doi.org/10.1007/s10152-007-0097-0.

Miller, P.J., Loates, M.J., 1997. Fish of Britain & Europe. HarperCollins, London.

Muus, B.J., Dahlstrøm, P., 1978. Meeresfische der Ostsee, der Nordsee, des Atlantik Biologie, Fang, wirtschaftliche Bedeutung, first ed. BLV.

Myers, R.A., 1998. When do environment-recruitment correlations work? Rev. Fish Biol. Fish. 8, 285–305.

NOAA, 2020. North Atlantic oscillation (NAO) [WWW document]. National Centers for Environmental Information (NCEI). URL. https://www.ncdc.noaa.gov/teleconnections/nao/.

Ojaveer, E., Kalejs, M., 2010. Ecology and long-term forecasting of sprat (Sprattus sprattus balticus) stock in the Baltic Sea: a review. Rev. Fish Biol. Fish. https://doi.org/10.1007/s11160-009-9130-5.

Pécuchet, L., Nielsen, J.R., Christensen, A., 2015. Impacts of the local environment on recruitment: a comparative study of North Sea and Baltic Sea fish stocks. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 72, 1323–1335. https://doi.org/10.1093/icesjms/fsu220.

Pedersen, T., Fossheim, M., 2008. Diet of 0-group stages of capelin (Mallotus villosus), herring (Clupea harengus) and cod (Gadus morhua) during spring and summer in the Barents Sea. Mar Biol 153, 1037–1046. https://doi.org/10.1007/s00227-007-0875-x.

Polte, P., Buschbaum, C., 2008. Native pipefish Entelurus aequoreus are promoted by the introduced seaweed Sargassum muticum in the northern Wadden Sea, North Sea. Aquat. Biol. 3, 11–18. https://doi.org/10.3354/ab00071.

Pörtner, H.O., Knust, R., 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science (1979) 315, 92–97. https://doi.org/10.1126/science.1135013.

R Development Core Team, 2024. R: A Language and Environment for Statistical Computing [WWW Document]. R Foundation for Statistical Computing, Vienna, Austria. URL. https://www.r-project.org/.

Rick, J.J., Scharfe, M., Romanova, T., van Beusekom, J.E.E., Asmus, R., Asmus, H., Mielck, F., Kamp, A., Sieger, R., Wiltshire, K.H., 2023. An evaluation of long-term physical and hydrochemical measurements at the Sylt Roads marine Observatory (1973–2019), Wadden Sea, North Sea. Earth Syst. Sci. Data 15, 1037–1057. https://doi.org/10.5194/essd-15-1037-2023.

Rodríguez-Sánchez, R., Lluch-Belda, D., Villalobos, H., Ortega-García, S., 2002. Dynamic geography of small pelagic fish populations in the California current system on the regime time scale (1931-1997). Can. J. Fish. Aquat. Sci. 1980–1988. https://doi.org/10.1139/f02-142.

Tulp, I., Bolle, J., Chen, C., Dänhardt, A., Haslob, H., Jepsen, N., van Leeuwen, A., Poiesz, S., Scholle, J., Vrooman, J., Vorberg, R., Walker, P., 2022. Fish. In: Kloepper, S., et al. (Eds.), Wadden Sea Quality Status Report. Wilhelmshaven, Germany.

Tulp, I., Bolle, L.J., Rijnsdorp, A.D., 2008. Signals from the shallows: in search of common patterns in long-term trends in Dutch estuarine and coastal fish. J. Sea Res. 60, 54–73. https://doi.org/10.1016/j.seares.2008.04.004.

Tulp, I., van der Veer, H.W., Walker, P., van Walraven, L., Bolle, L.J., 2017. Can guild- or site-specific contrasts in trends or phenology explain the changed role of the Dutch Wadden Sea for fish? J. Sea Res. 127, 150–163. https://doi.org/10.1016/j.seares.2016.10.001.

Utne, K.R., Hjøllo, S.S., Huse, G., Skogen, M., 2012. Estimating the consumption of Calanus finmarchicus by planktivorous fish in the Norwegian Sea using a fully coupled 3D model system. Mar. Biol. Res. 8, 527–547. https://doi.org/10.1080/17451000.2011.642804.

van Aken, H.M., 2008a. Variability of the water temperature in the western Wadden Sea on tidal to centennial time scales. J. Sea Res. 60, 227–234. https://doi.org/10.1016/j.seares.2008.09.001.

van Aken, H.M., 2008b. Variability of the salinity in the western Wadden Sea on tidal to centennial time scales. J. Sea Res. 59, 121–132. https://doi.org/10.1016/j.seares.2007.11.001.

van Beusekom, J.E.E., Carstensen, J., Dolch, T., Grage, A., Hofmeister, R., Lenhart, H., Kerimoglu, O., Kolbe, K., Pätsch, J., Rick, J., Rönn, L., Ruiter, H., 2019. Wadden sea eutrophication: long-term trends and regional differences. Front. Mar. Sci. 6 https://doi.org/10.3389/fmars.2019.00370.

van der Veer, H., Dapper, R., Henderson, P.A., Jung, A.J., Philippart, C.J., Witte, J.I., Zuur, A.F., 2015. Changes over 50 years in fish fauna of a temperate coastal sea: Degradation of trophic structure and nursery function. Estuar. Coast Shelf Sci. 155, 156–166. https://doi.org/10.1016/j.ecss.2014.12.041.

van der Veer, H., Tulp, I., Witte, J.I.J., Poiesz, S.S.H., Bolle, L.J., 2022. Changes in functioning of the largest coastal North Sea flatfish nursery, the Wadden Sea, over the past half century. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps14082.

van Walraven, L., Dapper, R., Nauw, J.J., Tulp, I., Witte, J.I., van der Veer, H.W., 2017. Long-term patterns in fish phenology in the western Dutch Wadden Sea in relation to climate change. J. Sea Res. 127, 173–181. https://doi.org/10.1016/j.seares.2017.04.001.

Vorberg, R., Breckling, P., 1999. Atlas der Fische im Schleswig-Holsteinischen Wattenmeer. Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning.

Zuur, A.F., Ieno, E.N., Smith, G.M., 2007a. Common trends and sudden changes. In: Analyzing Ecological Data. Statistics for Biology and Health. Springer, New York, pp. 289–320.

Zuur, A.F., Ieno, E.N., Smith, G.M., 2007b. Principal component analysis and redundancy analysis. In: Analyzing Ecological Data. Statistics for Biology and Health. Springer, New York, New York, NY, pp. 193–224. https://doi.org/10.1007/978-0-387-45972-1_12.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Things are not Always linear; additive Modelling. In: Mixed Effects Models and Extensions in Ecology with R. Statistics for Biology and Health. Springer, New York, NY, pp. 35–69. https://doi.org/10.1007/978-0-387-87458-6_3.