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Fish community dynamics in a cold temperate tidal lagoon in the Wadden Sea, in relation to changes in environmental conditions

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Fish community dynamics in a cold temperate tidal lagoon in the Wadden Sea, in relation to changes in environmental conditions

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Summary

Coastal marine ecosystems are characterized by high productivity and biodiversity supporting valuable coastal fisheries for centuries. The coastal ecosystems are of large ecological importance for many fish species, which require these areas for at least one stage in their life cycle for various purposes. The Wadden Sea is a transition area between land, rivers, and the North Sea and extends from Blåvands Huk in Denmark to Den Helder in The Netherlands. The Sylt-Rømø Bight (SRB) is one of the largest cold temperate lagoons in the northern Wadden Sea that is located between the islands of Sylt (Germany), Rømø (Denmark), and the mainland coasts. The coastal areas provide nursery functions where fish juveniles aggregate because of better feeding and refuge conditions promoting survival and growth and later emigrating. Permanent residents spend their entire lives in the coastal areas, which also act as acclimatization zones for diadromous species *en route* to marine or freshwater spawning habitats.

Like other coastal ecosystems, the Wadden Sea has undergone tremendous changes in abiotic and biotic conditions over the last decades due to climate change. Records of water temperature indicates an increase in annual average over the last decades and high inter-annual variabilities in seasonal patterns. These changes influence the reproduction, dispersal, recruitment, survival, growth, community composition, and migration patterns of coastal fish communities. Thus, this study aimed to investigate the potential effects of long- and short-term changes in environmental parameters including water temperature, salinity, chlorophyll *a,* and the North Atlantic Oscillation winter index on the fish community using a long-term monthly fish monitoring dataset, which was initiated in 2007 in the SRB. Additionally, the young-of-the-year (YOY) fish supply and potential effects of these parameters were investigated.

The general overview of the Wadden Sea and the potential effects of climate change on the fish communities are discussed in **Chapter 1**. In **Chapter 2**, the fish species composition based on the long-term monthly fish monitoring dataset from 2007 to 2019 was compared to two previous surveys from 1989 to 1995. In total, there were fifty-five fish species including six Lusitanian, one boreal, and one Atlantic species that were observed for the first time in the SRB. Unfortunately, four species present in the previous surveys were not found anymore. Three trend patterns (dome-shaped, increasing, or decreasing) were exhibited by various species that depicted the effects of winter temperature on recruitment and survival. The Dynamic Factor Analysis (DFA) revealed the partitioning of the fish community into seasonal assemblages based on species' temperature preferences that influence migration patterns. Changes in migration phenology were observed, as some species are staying longer related to warming autumn temperatures. Redundancy analysis (RDA) revealed that the seasonal variations of water temperature, salinity, and chlorophyll *a* significantly explained 18% while the inter-annual changes of environmental conditions explained 10% of the variations in the fish community.

In **Chapter 3**, the seasonal changes in fish community structure and diversity, in relation to changes in water temperature were assessed. Seasonal abundance fluctuations of six dominant species caused dissimilarities in community structures with higher percentage contributions when a particular species was in high abundance. Rank Abundance Curves (RACs) showed differences in seasonal species co-occurrence based on species-specific temperature preferences. The patterns were different between the benthic and pelagic habitats because of habitat preference and the transition of species such as small sandeel (*Ammodytes tobianus*) from juvenile pelagic to benthopelagic phases. General Additive Models (GAMs) revealed higher species richness at 5°C and 15°C, typical temperatures for winter/spring and summer/autumn seasonal transition phases, and indicate that emigration and immigration simultaneously occur in the bight. Species diversity was negatively correlated to water temperature because of the dominance of Atlantic herring (*Clupea harengus*) and *A. tobianus* in summer and whiting (*Merlangius merlangus*) in autumn (from GAMs and RACs). Spatial distribution and the utilization of intertidal habitats were assessed based on the correlations between diversity indices with water depth using generalized linear mixed-effects models (GLMMs). Species richness was negatively correlated to water depth since more species migrated to the intertidal habitats during high tide and retreated with ebbing waters. Evenness was positively correlated to water depth in the benthic habitats as populations were concentrated in smaller areas during low tide and widely distributed during high tide. In the pelagic habitats, evenness was positively correlated to water depth in areas close to seagrass meadows and bivalve beds. In contrast, evenness was negatively correlated to water depth in the deep tidal channels. There were no potential effects of water depth on the Shannon-Wiener Index, thus, further investigations on the spatial distributions of abundant and rare species in the bight are recommended.

In **Chapter 4,** the YOY fish survey was carried out in the deep tidal channels of the SRB between 2021 and 2023 to determine whether the bight acts as a spawning ground and/or a nursery ground and for which species. Fifteen fish species at different earliest developmental stages from the embryo, pre-flexion, flexion, post-flexion, and juveniles were sampled. Only a few species spawn in the bight while the majority are supplied from the North Sea and surrounding waters. Environmental variables including water temperature, salinity, and chlorophyll *a* explained 39% of the variations in YOY fish while 61% were unaccounted for indicating the potential effects of other parameters. The cohort structures of *C. harengus* revealed supply from two different cohorts of individuals hatched in autumn and spring. Nilsson's pipefish (*Syngnathus rostellatus*) had one cohort hatched within the bight, but sheltered in the brood pouch of the adult male, therefore showing higher survival.

In **Chapter 5**, the results are synthesized and compared to those of coastal areas in other regions of the world. Inferences are drawn from model projections and other studies of similar climate systems of what might occur if global warming continues. Critical reviews of the sampling methods and the knowledge gaps that future investigations and analyses could address are presented.

Zusammenfassung

Die marinen Küstenökosysteme zeichnen sich durch eine hohe Produktivität und Artenvielfalt aus, die seit Jahrhunderten eine einträgliche Küstenfischerei unterstützen. Küstenökosysteme sind von großer ökologischer Bedeutung für viele Fischarten, die diese Gebiete für mindestens eine Phase in ihrem Lebenszyklus für verschiedene Zwecke benötigen. Das Wattenmeer ist ein Übergangsgebiet zwischen Land, Flüssen und der Nordsee und erstreckt sich von Blåvands Huk in Dänemark bis Den Helder in den Niederlanden. Die Sylt-Rømø-Bucht (SRB) ist eine der größten kaltgemäßigten Lagunen im nördlichen Wattenmeer, die sich zwischen den Inseln Sylt (Deutschland) und Rømø (Dänemark) und den Festlandsküsten befindet. Küstengebiete dienen als Kinderstube, in der sich Jungfische in großer Zahl ansammeln, da sie dort bessere Nahrungsbedingungen sowie Zuflucht vor Räubern vorfinden, die das Überleben und das Heranwachsen und so das spätere Auswandern ermöglichen. Dauerhafte Bewohner verbringen ihr ganzes Leben in den Küstengebieten, die auch als Akklimatisierungszonen für diadrome Arten auf dem Weg zu Meeres- oder Süßwasser-Laichhabitaten dienen.

Wie andere Küstenökosysteme hat auch das Wattenmeer in den letzten Jahrzehnten aufgrund des Klimawandels enorme Veränderungen der abiotischen und biotischen Bedingungen erfahren. Die Aufzeichnungen der Wassertemperaturen zeigen einen Anstieg des Jahresdurchschnitts in den letzten Jahrzehnten und hohe jahreszeitliche Schwankungen zwischen den Jahren. Diese Veränderungen beeinflussen die Fortpflanzung, die Ausbreitung, die Rekrutierung, das Überleben, das Wachstum, die Zusammensetzung der Gemeinschaft und die Migrationsmuster der Fischgemeinschaften an der Küste. Ziel dieser Studie war es daher, die Auswirkungen lang- und kurzfristiger Veränderungen von Umweltparametern wie Wassertemperatur, Salzgehalt, Chlorophyll a und dem Winterindex der Nordatlantischen

Oszillation auf die Fischgemeinschaften anhand eines langfristigen monatlichen Fischmonitoring-Datensatzes zu bestimmen, der 2007 in der SRB eingeführt wurde. Außerdem wurden das Vorhandensein an Jungfischen (YOY) und mögliche Auswirkungen der genannten Umweltparameter auf diese untersucht.

Ein allgemeiner Überblick über das Wattenmeer und die möglichen Auswirkungen des Klimawandels auf die Fischgemeinschaften werden in **Kapitel 1** erörtert. In **Kapitel 2** wurde die Zusammensetzung der Fischarten auf der Grundlage des langfristigen monatlichen Fischmonitoring-Datensatzes von 2007 bis 2019 bewertet und mit zwei früheren Erhebungen von 1989 bis 1995 verglichen. Insgesamt gab es fünfundfünfzig Fischarten, darunter sechs lusitanische, eine boreale und eine atlantische Art, die zum ersten Mal in der SRB beobachtet wurden. Leider wurden vier Arten, die in den früheren Erhebungen vorkamen, nicht mehr gefunden. Drei Trendmuster (kuppelförmig, ansteigend oder abnehmend) zeigten sich bei verschiedenen Arten, die die Auswirkungen der Wintertemperatur auf die Rekrutierung und das Überleben darstellten. Die Dynamische Faktorenanalyse (DFA) zeigte die Aufteilung der Fischgemeinschaft in saisonale Artengruppierungen auf der Grundlage der Temperaturpräferenzen der Arten, die die Migrationsmuster beeinflussten. Es wurden Veränderungen in der Migration zwischen Wattenmeer und Nordsee beobachtet, da einige Arten aufgrund der wärmeren Herbsttemperaturen länger bleiben. Die Redundanzanalyse (RDA) ergab, dass die saisonalen Schwankungen der Wassertemperatur, des Salzgehalts und des Chlorophylls a 18% der Schwankungen in der Fischgemeinschaft erklärten, während die zwischenjährlichen Veränderungen der Umweltbedingungen 10% erklärten.

In **Kapitel 3** wurden die saisonalen Veränderungen in der Struktur und Vielfalt der Fischgemeinschaft als Reaktion auf Veränderungen der Wassertemperatur bewertet. Die saisonalen Schwankungen der Abundanz von sechs dominanten Arten führten zu unterschiedlichen Gemeinschaftsstrukturen mit höheren prozentualen Anteilen, wenn eine bestimmte Art in hoher Abundanz vorhanden war. Die Rangabundanzkurven (RACs) zeigten unterschiedliche saisonale Muster des gemeinsamen Vorkommens von Arten auf der Grundlage der artspezifischen Temperaturpräferenzen. Die Muster unterschieden sich zwischen dem benthischen und dem pelagischen Lebensraum aufgrund der Lebensraumpräferenz und des Übergangs von Arten wie dem kleiner Sandaal (*Ammodytes tobianus*) von der juvenilen pelagischen zur benthopelagischen Phase. Allgemeine additive Modelle (GAMs) ergaben einen höheren Artenreichtum bei 5°C und 15°C, den typischen Temperaturen für die saisonalen Übergangsphasen Winter/Frühjahr und Sommer/Herbst, und deuten darauf hin, dass Auswanderung und Einwanderung in der Bucht gleichzeitig stattfinden. Die Artenvielfalt war negativ mit der Wassertemperatur korreliert, da der Atlantische Hering (*Clupea harengus*) und *A. tobianus* im Sommer und der Wittling (*Merlangius merlangus*) im Herbst dominierten (aus GAMs und RACs). Die räumliche Verteilung und die Nutzung der intertidalen Lebensräume wurden anhand der Korrelationen zwischen den Diversitätsindizes und der Wassertiefe mit Hilfe von verallgemeinerten linearen Modellen mit gemischten Effekten (GLMMs) bewertet. Der Artenreichtum war negativ mit der Wassertiefe korreliert, da bei Flut mehr Arten in die Gezeitenzonen einwanderten und sich erst bei Ebbe wieder zurückzogen. Die Artengleichheit (Äquität, evenness) war in den benthischen Lebensräumen positiv mit der Wassertiefe korreliert, da die Populationen bei Ebbe in kleineren Gebieten konzentriert und bei Flut weit verteilt waren. In den pelagischen Lebensräumen war die Artengleichheit in Gebieten in der Nähe von Seegraswiesen und Muschelbänken positiv mit der Wassertiefe korreliert. Im Gegensatz dazu war die Artengleichheit in den tiefen Gezeitenkanälen negativ mit der Wassertiefe korreliert. Es gab keine Auswirkungen der Wassertiefe auf den Shannon-Wiener-Index. Daher werden weitere Untersuchungen zur räumlichen Verteilung von häufigen und seltenen Arten in der Bucht empfohlen.

In **Kapitel 4** wurde die Untersuchung der Jungfische in den tiefen Gezeitenkanälen der SRB zwischen 2021 und 2023 durchgeführt, um festzustellen, ob die Bucht als Laichgebiet und/oder Aufwuchsgebiet dient und für welche Arten. Es wurden fünfzehn Fischarten in verschiedenen frühesten Entwicklungsstadien vom Embryo bis zum Jungfisch beprobt. Nur einige wenige Arten laichen in der Bucht, während die meisten aus der Nordsee und den umliegenden Gewässern in die Bucht verdriftet werden. Umweltvariablen wie Wassertemperatur, Salzgehalt und Chlorophyll a erklärten 39% der Schwankungen der Abundanz der Jungfische, während 61% nicht berücksichtigt wurden, was auf die möglichen Auswirkungen anderer Parameter hinweist. Die Kohortenstrukturen von *C. harengus* zeigten, dass zwei verschiedene Kohorten von Individuen jeweils im Herbst und im Frühjahr geschlüpft sind. Bei der kleinen Seenadel (*Syngnathus rostellatus*) gab es nur eine Kohorte, die in der Bucht, geschützt im Brutbeutel des männlichen Elterntieres geschlüpft war, dadurch aber eine höhere Überlebensrate aufwies.

In **Kapitel 5** wird die Synthese der Ergebnisse diskutiert und mit Küstengebieten in anderen Klimasystemen verglichen. Aus Modellprojektionen und anderen Studien über ähnliche Klimasysteme werden Rückschlüsse darauf gezogen, was passieren könnte, wenn die globale Erwärmung anhält. Es werden kritische Vergleicheder Beprobungsmethoden vorgestellt und Wissenslücken dargestellt, die durch zukünftige Untersuchungen und Analysen geschlossen werden könnten.

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CHAPTER 1

GENERAL INTRODUCTION

1.0 General Introduction

1.1 Coastal fish communities and climate change

Fish are important components of ecosystems for material transfer and cycling. Fish contribute to high productivity and biodiversity, particularly for coastal marine ecosystems that have supported valuable coastal fisheries for centuries (Barbier et al. 2011). Coastal marine ecosystems are among the most socio-ecologically important habitats (MacKenzie and Schiedek 2007) and the world's most populated areas are near the coastal zones (Harley et al. 2006). As the human population grows, so does the dependence on the functioning of these valuable coastal and nearshore ecosystems and concomitant impacts (Bernhardt and Leslie 2013). Human drivers of ecosystem change include climate change, overfishing, mining, eutrophication, sedimentation, pollution, dredging, coastal development, biological invasion, etc. (Barbier et al. 2011). Among these, anthropogenically induced climate change threatens the most as it affects the coastal marine ecosystems extensively on spatial and temporal scales (Harley et al. 2006; Rutterford et al. 2023). Climate change poses severe threats to marine ecosystems and the economic and social systems that depend on them (Harley et al. 2006).

Some of the severe physiochemical changes in coastal ecosystems related to climate change include increasing air and water temperatures, sea level rise, and ocean acidification (He and Silliman 2019). Among these, increasing water temperature has great repercussions on marine ecosystems (IPCC 2023). Decadal-scale variations in ocean temperature and global warming have caused substantial damages and increasingly irreversible losses in coastal and open ocean ecosystems at all levels of biological organizations including organismal, population, and ecosystems (Rijnsdorp et al. 2009; Clark et al. 2020; IPCC 2023). Fish populations and associated phenologies are part of an intricate network of ecosystem relationships that can be influenced directly or indirectly by changes in water temperature. Fish species are characterized by species-specific temperature tolerances that influence their occurrences and migration patterns (van Walraven et al. 2017). Ocean warming influences individuals' performance, for instance, physiological and behavioral responses at various life stages. At the population level, ocean warming influences changes in transport and drifting processes that influence dispersal and recruitment (Harley et al. 2006). At the community level, ocean warming has led to physiologically driven species range shifts by shifting distributions to higher latitudes, and to deeper depths in subtidal systems (Dulvy et al. 2008; Poloczanska et al. 2013; Montero-Serra et al. 2015). Temperature effects on fish prey items can indirectly influence fish species, which may result in changes in the composition and dynamic coupling of food webs (Pörtner and Peck 2010).

The North Sea and the adjacent Wadden Sea have experienced tremendous temperature warming over the last decades. Continuous measurements from 1962 and ongoing at the marine stations in Helgoland (Helgoland Roads) and Sylt (Sylt Roads) (Dummermuth et al. 2023) reveal changes in water temperature. The mean water temperature has increased by 1.9°C in the North Sea and 1.8°C in the Wadden Sea (0.3°C per decade) from 1962 to 2019 (de Amorim et al. 2023). These changes influence fish communities in various ways. For instance, Perry et al. (2005) stipulated that two-thirds of North Sea fish species shifted with latitude and depth because of global warming. The cold-adapted fish species of northern distribution shifted their range northwards as well as the warm-adapted species of southern origin. For example, fish of southern biogeographic origin (warm-favoring Lusitanian species) such as anchovy (*Engraulis encrasicolus*), red mullet (*Mullus surmuletus*), European pilchard (*Sardina pilchardus*), and snake pipefish (*Entelurus aequoreus*) are now established in the North Sea and Celtic Sea (Dulvy et al. 2008; Hoístede et al. 2010). These have led to increased species richness in these areas. On the other hand, as cold-water favoring boreal species are shifting northwards, the number of taxa has decreased in areas such as the west of Scotland (Hoístede et al. 2010). Besides, the niches of cold water adapted species are contracting because of warming (Amelot et al. 2023).

The latitudinal and depth shifts have led to changes in species proportions in fish assemblages (Engelhard et al. 2011), changes in community structures (Clark et al. 2020; Rutterford et al. 2023), and ecosystem reorganizations (Beaugrand 2004). These have altered species interactions, as species do not interact with the same assemblage they had in the past (He and Silliman 2019) as well as changes in diet spectra and predator-prey relationships (Amelot et al. 2023). Water temperature influences the reproduction and spawning timing of fish. For instance, seasonal temperature variations in temperate areas such as the North Sea cause fluctuations in the timing of annual adult fish winter migrations from cool, shallow inshore waters to warmer, deeper offshore spawning grounds. This influences the start and rates of gonad development, the spawning timing, and larval duration (Genner et al. 2010). For instance, prolonged low water temperatures lengthen the egg incubation period and the vulnerable larval duration (Malzahn et al. 2003). On the other hand, warmer conditions promote faster larval growth and development (Berg et al. 2024). Thus, water temperature influence the timing, survival, and recruitment into nursery grounds. The coastal nursery grounds such as the Wadden Sea offer better feeding and refuge conditions that promote survival and growth before recruitment to adult populations (Tulp et al. 2008). However, these processes partly depend on favorable environmental conditions (Arevalo et al. 2023) and prey availability.

1.2 Large-scale climate oscillations and temperature variations in Western European

Large-scale climate oscillations such as the North Atlantic Oscillation (NAO) influence the climate and weather patterns of the North Atlantic and Western European regions (Rogers 1984;

Hurrell and Deser 2010). The NAO refers to the redistribution of atmospheric mass between the Arctic and subtropical Atlantic. This redistribution fluctuates between positive and negative phases producing large changes in surface air temperature, winds, storms, and precipitation over the Atlantic and adjacent continents (Hurrell and Deser 2010). The NAO affects the ocean through changes in gyre circulations, heat content, mixed layer depth, salinity, ice cover, and high latitude deep water formation (Hurrell and Deser 2010). Positive NAO winter indices indicate an intense Icelandic low and Azores high that causes strong westerlies across the North Atlantic, and above-normal temperatures in northwestern Europe (Wallace and Gutzler 1981). The negative NAO winter indices indicate smaller Sea Level Pressure differences, which cause weaker westerly winds and a decrease in winter and spring temperatures in northern Europe (Ottersen et al. 2001). Large changes in NAO, for instance, from one winter to the next, from one decade to the next, and within seasons, alter the structure and functioning of marine ecosystems (Hurrell and Deser 2010). Since the residual currents in the North Sea and adjacent waters depend very much on the wind conditions (Riepma 1980), the NAO indirectly influences the dispersal and recruitment of fish in various nursery grounds in northern European regions such as the Wadden Sea.

1.3 The Wadden Sea

About 8,000 years ago when the post-glacial sea level rise began to slow down below 10 mm/year, the Wadden Sea emerged with the formation of the seaward barrier of dune islands, sandy shoals, and landward areas of tidal flats and salt marshes (Reise et al. 2010; Kabat et al. 2012). The islands and marshlands adjacent to the intertidal area of the Wadden Sea belong to the oldest and most complex cultural landscapes in Europe and the present-day tidal flats were once farmlands that have been inhabited for more than 5,000 years (Kabat et al. 2012). Parts of this land had been flooded after large storm events until when land reclamation and protection by dykes began. Initially, these were defensive embankments for protecting the existing, already inhabited land against storm surges, and about 1200 years ago, the reclamation of salt marshes began (Wolff 1992).

The Wadden Sea is a 500 km long geographical unit that includes a mosaic of intertidal sand and mudflats, subtidal systems of inlets, channels, and creeks extending from Blåvands Huk in Denmark to Den Helder in The Netherlands (Fig. 1) (Kabat et al. 2012). The Wadden Sea is a transition area that forms a morphological boundary between land, rivers, and the North Sea (Asmus 2011). In the 1980s, the Wadden Sea was listed as a biosphere reserve subject to protection by several international conventions (Kabat et al. 2012). In 2009, the highest level of international recognition was attained when the Dutch and German Wadden Sea parts (approximately 87%) were recognized as World Heritage Sites (UNESCO 2009). The remaining 13% of the Danish side was recognized in June 2014 (UNESCO 2014).

The Wadden Sea has a total area of about 8000 km^2, including 25 inhabited islands and several smaller vegetated and barren high sands with a total area of about 2000 km^2 (Reise et al. 2010). It is subdivided into several systems by the catchment areas of the tidal inlets that exchange water with the North Sea separately (Fig. 1) and the mixing of water bodies of adjacent tidal systems is spatially and temporally limited (Asmus 2011). It has a complex matrix of habitats across environmental gradients of depth, salinity, exposure to hydrodynamics and wind, and substrates that accommodate a high diversity of aquatic and terrestrial species (Reise et al. 2010).

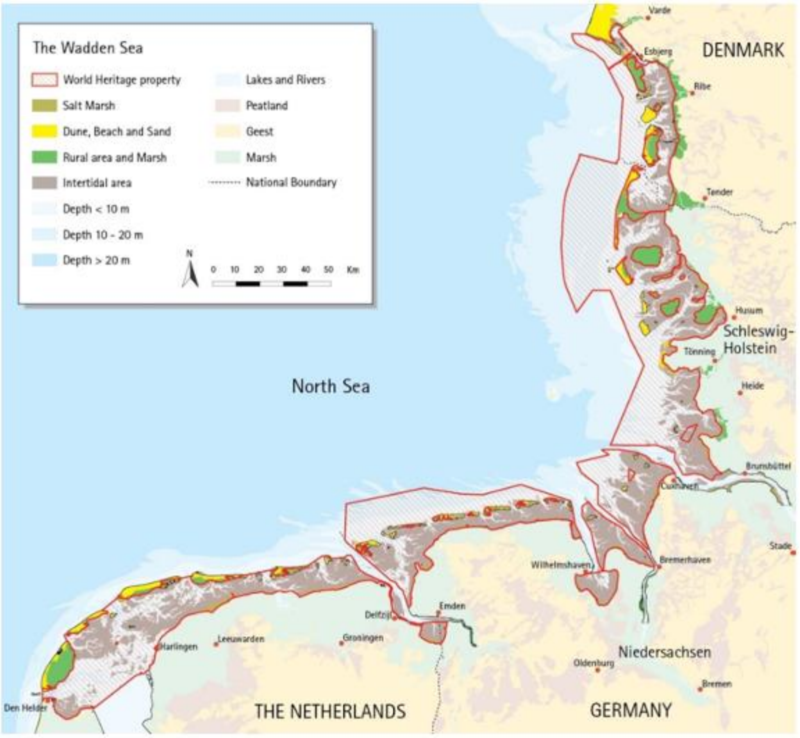

Figure 1 Map of the Wadden Sea World Heritage Site showing the areal coverage, natural habitats, intertidal areas, barrier islands, major estuaries, and the North Sea (© map adapted from Common Wadden Sea Secretariat 2024)

Ecologically, the Wadden Sea functions as a massive coastal ecosystem of unique composition that includes about 10, 000 species of plants, fungi, and animals (Reise et al. 2010). It is the world's largest coherent intertidal wetland with a total area of about 4700 km^2 that emerges twice daily at low tide (Fig. 1). In addition, the rich benthic fauna supports up to 6.1 million birds at the same time and on average 10 – 12 million birds per year (Blew and Südbeck 2005). Thus, it plays a key role in the functioning of the East Atlantic and the African-Eurasian flyway migrations by offering feeding, overwintering, and resting areas for energy replenishment after long-distance flights and breeding (Blew and Südbeck 2005). The high ecological productivity comprising of high bacterial remineralization rates, high imports of suspended microalgae and production by the bottom microscopic algae together constitute a food supply for zoobenthos such as molluscs suspension feeders, deposit-feeding worms, and small snails (Asmus 1987). These in turn provide food to shrimp, small crabs, and fish that use the intertidal flats as nurseries during high tide. During low tide, the intertidal habitats act as feeding grounds for wading birds (Reise et al. 2010).

1.4 Climate change and the Wadden Sea fish

The Wadden Sea is an important area for an array of fish species that use it for at least one stage in their life cycles. Many marine fish including flatfishes, groundfish, and pelagic species reach the Wadden Sea as larvae or post-larvae where they spend the juvenile stages benefitting from the high food availability and protection from predators (Tulp et al. 2022). The nursery areas are 10 – 20 times richer in food than the adjacent deeper waters (Reise et al. 2010). Like other temperate coastal ecosystems, the environmental conditions in the Wadden Sea have significantly changed in the past decades and vary strongly on seasonal scales (van Beusekom et al. 2019; Rick et al. 2023). Thus, fish communities have been exposed to long- and short-term changes (van der Veer et al. 2015). Varying trends and abundances across functional guilds of the Wadden Sea fish including marine juveniles, estuarine residents, diadromous species, marine seasonal, and marine adventitious have been reported by Tulp et al. (2008, 2017, 2022), and van der Veer et al. (2016). Shifts in species composition and abundance of typical fish species of the Wadden Sea due to increasing water temperature were observed as transient or warm water adapted species became more prevalent since 1980 simultaneous with a decline in cold water adapted species (Alheit et al. 2012; van der Veer et al. 2015).

An increase in spring and autumn temperatures has caused shifts in migration phenology such as early or late immigration and emigration of specific fish species in the Wadden Sea (van Walraven et al. 2017). Higher temperatures caused high mortality and significant population declines of eelpout (*Zoarces viviparous*) in the German Wadden Sea (Pörtner and Knust 2007). Furthermore, higher water temperatures caused a decline in the nursery function of the Wadden Sea to flatfish species such as plaice (*Pleuronectes platessa*), sole (*Solea solea),* and dab (*Limanda limanda*) (van der Veer et al. 2011, 2015, 2022). Increased water temperature has exceeded the optimum for the cold-water flatfish species, and has affected larval settling and habitat suitability for growth. As a result, *P. platessa, P. flesus,* and to a lesser extent *S. solea* larvae now settle earlier than before (Freitas et al. 2016; van der Veer et al. 2022). Besides, the 1-group *P. platessa* densities have declined while the 11-group has disappeared from the intertidal flats in spring and summer and is not found anymore in the subtidal and tidal channels in autumn (Freitas et al. 2016). The 11-group *P. flesus* almost disappeared while *L. limanda* densities declined at all age groups (van der Veer et al. 2022). On the other hand, the growth of young-of-the-year (0-group) *S. solea* increased as a result of longer periods with optimal growth conditions. On the contrary, the mortality rates for 0-group *P. platessa* have increased (van der Veer et al. 2015, 2022). Despite the population fluctuations in the Wadden Sea, the recruitment of *P. platessa* and *L. limanda* in the North Sea has not changed (van der Veer et al. 2022). Thus, other areas currently offer better nursery functions with favorable water temperatures. This may be attributed to the Wadden Sea being relatively fragile and warm at much faster rates than other coastal areas (MacKenzie and Schiedek 2007).

While the Wadden Sea waters generally become warmer, fish communities are also affected by temperature changes on seasonal scales. For instance, generally *P. platessa, L. limanda,* and Atlantic cod (*Gadus morhua*) abundances were declining from the 1980s but after the severe winter of 1995/1996, *G. morhua* abundance drastically decreased (Meyer et al. 2016). Warm winters on the other hand favor warm water-adapted species such as *S. solea* and

Pomatoschistus species (Meyer et al. 2016). Furthermore, severe winters cause a decline in benthic organisms that form part of prey items for fish (Armonies et al. 2001). Beukema and Dekker (2020) observed a decline in the survival of cockle (*Cerastoderma edule*) close to zero in all age classes after severe winters which further escalated the food limitation to benthic fish species. However, the recruitment of *C. edule* was enhanced after cold winters because cold temperatures caused a low abundance of its predators. This way, the long-term decline in its recruitment was compensated by increased survival after winter resulting in an absence of any long-term trend patterns (Beukema and Dekker 2020). The question is whether fish species can undergo similar population dynamics with the changing climatic patterns.

1.5 The Sylt-Rømø Bight: A case study site of investigation

The Sylt-Rømø Bight (SRB) is a semi-enclosed tidal lagoon located in the most northern part of the German Wadden Sea between the islands of Sylt (Germany) and Rømø (Denmark) (54°52’ to 55°10’ N, 8°20’ to 8°40’ E) (Baird et al. 2004). The area is protected as part of a larger national park extending from Blåvandshuk to the German-Dutch border under both German and Danish legislation and is part of the internationally recognized Wadden Sea World Heritage Site (UNESCO 2009, 2014). Commercially, only local (without crossing the international borders) mussels and shrimp fisheries are allowed in the area. Two causeways, a railway dam on the German side constructed in 1927 and a road on the Danish side constructed in 1943 connect the islands to the mainland and restrict water exchange with the adjacent tidal environments (Asmus 2011; Kabat et al. 2012). The lagoon is drained by three main tidal inlets Rømø Dyb, the Højer Dyb, and Lister Ley. All three meet within the 2.8 km wide Lister Tief tidal channel, which is located between the two islands and connects the bight to the North Sea (Fofonova et al. 2019). Through Lister Tief, 8 to 12 % of the bight’s water is exchanged per tidal cycle. The tidal range is

2 m and the water residence time ranges between 19 and 29 days (Reise et al. 1998). The bight covers a total aerial surface of 404 km^2, separated into an intertidal area of 135 km^2 and a subtidal area of 270 km^2 (Reise et al. 1998). The subtidal areas are separated into tidal gullies and shallow subtidal flats. The deepest parts are found in the tidal gullies with a maximum depth of 40.5 m below low water levels at Lister Tief. In comparison, the shallow subtidal flats with a total area of about 230 km^2 have a maximum depth of 5 m below low water levels (Fofonova et al. 2019).

The average water temperature in the bight varies from 5°C in winter (October to March) and 13°C in summer (April to September) and water temperature fluctuates between -1°C in winter and 22°C in summer. In addition, there are within-season variations in water temperature. For instance, the warm winters of 2006/2007 compared to the severe winters of 2009/2010 and 2010/2011 and warm summers of 1997 compared to 2011 (Rick et al. 2023). The area is characterized by lower salinities in winter and spring, and highs in summer and autumn with an overall range between 24 and 33 (Rick et al. 2023). Two rivers, Vidå and Bredeå, open out into the bight draining a catchment area of about 1554 km^2 (1081 km^2 and 473 km^2, respectively) (Asmus 2011). Thus, the salinity variability is mainly due to precipitation and evaporation (Rick et al. 2023). In all seasons, diatoms are the most prominent phytoplankton group in the bight. In addition, in late spring and early summer, the prymnesiophyte (*Phaeocystis globosa*) adds substantially to the photosynthetic biomass (Rick et al. 2023). Changes in nutrient concentrations have been observed in the area in the last decades (van Beusekom et al. 2019; Rick et al. 2023). However, despite the strong nutrient fluctuations, phytoplankton parameters such as chlorophyll *a* patterns did not change since planktonic algae are not only influenced by total concentrations of single nutrients but also by nutrient ratios (Rick et al. 2023).

The SRB is rich in plant and animal species whose productivity results in a complex system with a multitude of interactions between living and non-living components (Baird et al. 2004, 2007). The subtidal areas are mainly sandy substrates that are poor in benthic macrofauna (Armonies et al. 2018). The intertidal areas consist of eight contiguous habitat types named according to dominant species, community, or substrate type with characteristic biotic community compositions (Baird et al. 2007). These include mussel beds, where the mussel (*Mytilus edulis*) predominates, Arenicola flats where the lugworm (*Arenicola marina*) predominates, oyster beds dominated by oyster (*Magallana gigas*), seagrass meadows dominated by *Zostera noltii* and *Zostera marina*, and substrate types such as mud flats, sand flats, and sandy beaches (Baird et al. 2007; Asmus 2011). These habitats contain different proportions of flora and fauna, for instance, more than one million individuals have been examined and identified to species level on the sandy beach and sand flat extending 115 m between high and low tide in the SRB (Reise et al. 2010). Since 1993, the Japanese seaweed (*Sargassum muticum*) has been spreading in the shallow subtidal zones forming a habitat of dense canopies (Polte and Buschbaum 2008).

1.6 Past fish related research in the Sylt-Rømø Bight

Fish species perform various ecosystem functions. Fish act as prey items for harbor seals (*Phoca vitulina*) (De La Vega et al. 2016) and forms part of prey items for birds such as cormorants, gulls, terns, and herons (Elliott et al. 2002; Horn et al. 2019). Small-sized species such as common goby (*Pomatoschistus microps*) and sand goby (*Pomatoschistus minutus*) act as keystone species i.e. have a large impact on the community by transferring more energy from lower trophic levels up the food chain due to their high abundance and biomass (Pockberger et al. 2014). Fish may be eaten by cannibalistic individuals from the same or different species with different sizes depending on the prey density (Elliott et al. 2002). Fish play additional ecological roles within the SRB and the surrounding areas. For instance, their egesta become sediment particulate organic carbon (POC) that forms part of the energy source for benthic bacteria and invertebrates (Baird et al. 2007). Excess fish production is exported from the system through seasonal migrations and the relatively few predators (Baird et al. 2004, 2007). Besides, seasonal fish migrations export the secondary production of nitrogen and phosphorus from the bight to other areas (Baird et al. 2008).

Most of the fish research that has been conducted in the SRB has focused on one hand on the ecology of a single or a few species in terms of their presence/absence, feeding patterns, use of intertidal and subtidal zones, and resource partitioning (Herrmann et al. 1998; Polte and Asmus 2006; Polte and Buschbaum 2008; Kellnreitner et al. 2012). On the other hand, some fish species as part of the food web have been investigated (Baird et al. 2004, 2007, 2011, 2019; Baird 2012). The environmental conditions in the SRB have significantly changed in the past decades. For instance, the mean annual water temperature is higher than three decades ago (Rick et al. 2023), the number of severe and cold winters is decreasing (de Amorim et al. 2023) while summer and autumn are becoming warmer (Rick et al. 2023). Other parameters such as salinity and chlorophyll *a* also show inter- and intra-annual variations. There has not been a comprehensive analysis of the fish community dynamics in response to the long-term and seasonal changes in environmental regimes. Therefore, a comprehensive analysis of the fish community's responses to changing environmental conditions such as global warming is needed.

1.7 Objectives of the thesis

The main objective of this study was to conduct an in-depth analysis of the fish community dynamics in relation to the changing environmental conditions, mainly changes in water temperature using the long-term, high-resolution monthly fish monitoring data that has been conducted in the SRB since 2007 (Asmus et al. 2020). Different approaches were applied such as the guild approach, which is based on partitioning the components of fish biomass sharing similar functions and resources within a geographic region (Jiming 1982; Benoit et al. 2021). The guild approach was used to classify the species into small tractable units and correlate their occurrence to changes in temperature conditions. Species compositions were compared to previous investigations to assess whether fish species of the southern origins are increasing in the Wadden Sea with a concomitant decline in cold-water adapted species. Long-term trends, seasonal assemblages, and changes in community structure and diversity were correlated to changes in environmental conditions. Additionally, spatial distribution with changes in water depth and bedform morphology were investigated to assess the use of intertidal habitats for various purposes such as nursery and refuge during high tide. Despite years of research on the importance of the SRB and the Wadden Sea for fish reproduction e.g. Polte and Asmus (2006), there is still remarkably little knowledge on which species spawn in the bight and those supplied from the adjacent waters at different times of the year. Hence, I aimed to assess the species using the SRB as a spawning and/or nursery ground. In addition, the seasonal patterns of young-of-the-year (YOY) fish occurrences, abundance fluctuations, and cohort structures of the dominant species were correlated to the seasonal changes in environmental parameters. In summary, this thesis aims to address the following questions:

1. Did the fish species composition change in comparison to previous investigations?
2. Are there trends and common behaviours exhibited by various species in relation to changes in environmental conditions?
3. Does the fish community structure and diversity change with changes in temperature conditions?

4. Does fish utilize the intertidal habitats in the SRB during high tide?
5. Does the SRB act as a spawning and/or a nursery ground and for which fish species?
6. Do cohort structures of YOY fish differ between species at different times of the year?

1.8 Outline of the study

This thesis is based on the following publications:

1.8.1 Publication 1

Publication 1 addressed the first and second questions: Fish species composition was compared to two previous monitoring programs from 1989 to 1995 using the long-term monthly fish monitoring data from 2007 to 2019. The guild approach was used to classify the fish species into tractable units based on temperature preferences and to assess which guild dominates the SRB. Long-term trends and seasonal abundance fluctuations were determined and correlated to changes in water temperature. The common patterns based on temperature preferences of the 22 most abundant species were determined to assess the migration patterns, seasonal assemblages, and changes in migration phenology. Additionally, the potential effects of water temperature, salinity, chlorophyll *a,* and the North Atlantic Oscillation winter indices on the fish community were assessed.

1.8.2 Publication 2

Publication 2 addressed the third and fourth questions: The fish community structure and diversity were investigated using long-term fish monitoring data from 2007 to 2019 and corelated to long-term and seasonal changes in water temperature in the Wadden Sea. Seasonal variations in the community structure, seasonal species co-occurrence and the contributions of various taxa to the dissimilarities across seasons were assessed. Diversity patterns i.e. changes in species richness, evenness, dominance, and Shannon-Wiener Index were correlated to the seasonal changes in water temperature. Additionally, the spatial distributions and the utilization of intertidal and subtidal habitats were correlated to changes in water depth per tidal cycle and within the tidal channels.

1.8.3 Publication 3

Publication 3 addressed the fifth and sixth questions: Young-of-the-year (YOY) fish supply in the SRB was investigated to determine whether the area acts as a nursery ground and/or as a spawning ground and for which species. The YOY fish species were assessed based on the earliest developmental stages and species compositions were compared with the documented species from the long-term fish monitoring. Variations in YOY fish supply were correlated to environmental parameters with a specific focus on changes in water temperature. The cohort structures of the dominant YOY fish species were used to assess somatic growth, survival, and the number of cohorts present in the SRB.

1.8.4 General discussion

The synthesis of the results obtained from the three publications is discussed to give a general overview of the fish community ecology of the SRB. General aspects of the long-term trends and seasonal assemblages are discussed. The fish community dynamics are discussed and compared to coastal ecosystems in other regions of the world to asses the potential effects of climate change. Conclusions are drawn on the climate change effects on the Wadden Sea fish community, the significance of the high-resolution monitoring, and the knowledge gaps that could be addressed by future investigations.

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CHAPTER 2

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

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.

Keywords

Fish monitoring, species composition, seasonal assemblages, abiotic drivers, Dynamic Factor Analysis, Wadden Sea

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

2.0 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 to 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).

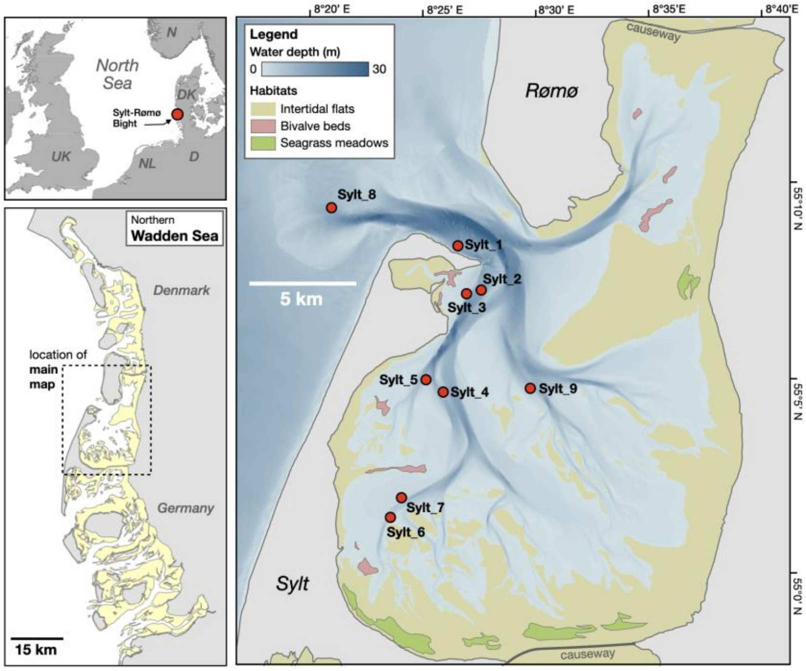

Fig. 1. Location of the Sylt-Rømø Bight on the eastern seaboard of the North Sea (top left) and the northern Wadden Sea (bottom left). Main map: Intertidal flats, bivalve beds, seagrass meadows, and tidal channels with varying water depths. Red dots with labels Sylt_1 to Sylt_9 represent the positions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

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 minutes 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 (ºC), 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 assess 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).

3.0 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 & 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 & Breckling (1999). Six of the new species were of Lusitanian origin while both 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.

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 & Breckling (1999)	This study
European eel	*Anguilla anguilla*	Atlantic_benthic	+	+	+
Flathead grey mullet	*Mugil cephalus*	Atlantic_benthopelagic			+
Atlantic mackerel	*Scomber scombrus*	Atlantic_pelagic	+	+	+
Plaice	*Pleuronectes platessa*	Lusitanian_benthic	+	+	+
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	+	+	+
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	+	+	+

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 trend 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.

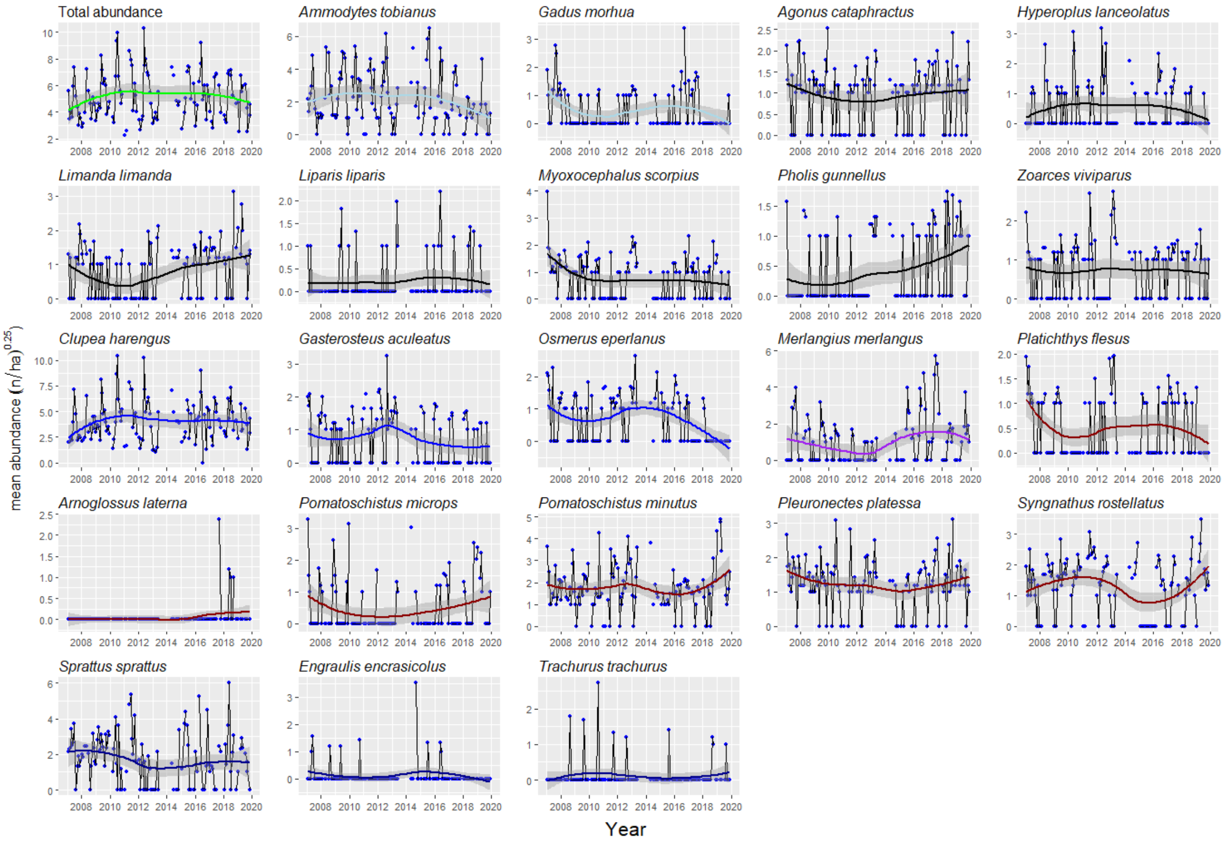

Fig. 2. The time series of the fourth root transformed the total abundance of all 55 species altogether and the abundance of the dominant species. Solid lines indicate the trends obtained by LOESS smoothing (different colors represent the biogeographic guild–habitats, (Boreal-benthopelagic (light-blue), boreal-benthic (black), boreal-pelagic (blue), Lusitanian-benthopelagic (purple), Lusitanian-benthic (dark-red), Lusitanian-pelagic (dark-blue). The grey shaded area is the 95% confidence interval.

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 blue 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 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)).

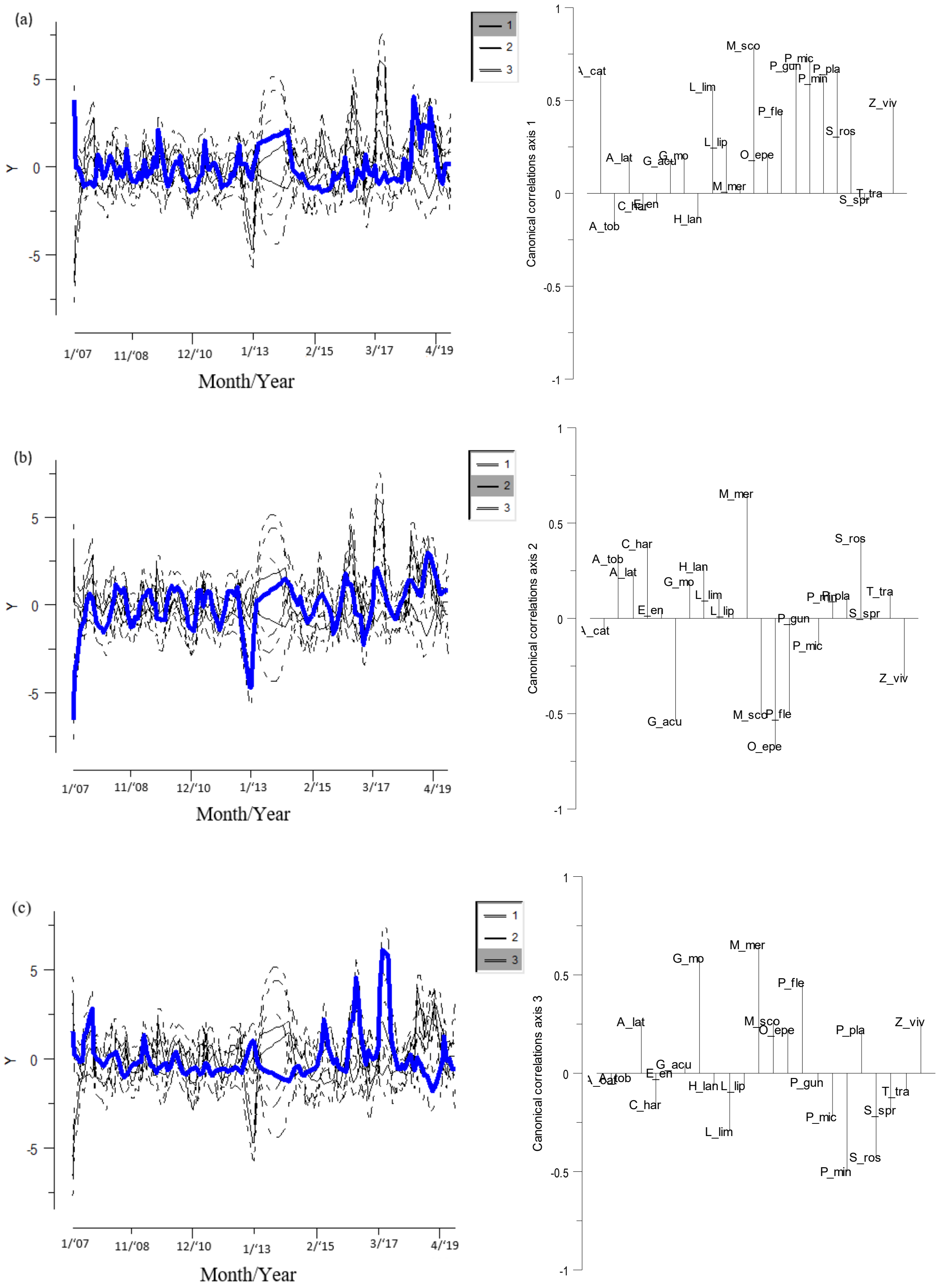

Fig. 3. Original time series (thin dark lines) and the DFA model containing three common patterns (thick blue lines) + explanatory variable (SST) + noise. The y-axis represents the patterns and the x-axis represents the months (January 2007 to December 2019). The first (a), second (b), and third

(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)

		Explanatory variable			Canonical correlations		
Time series	Spp_code	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

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 (Fig. 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 ºC (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).

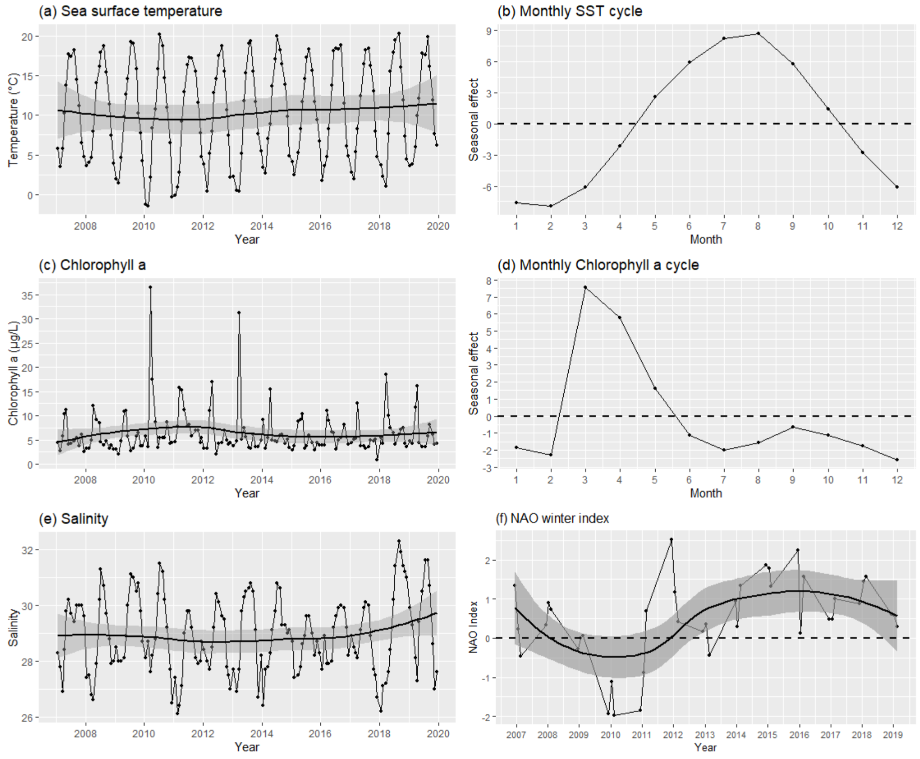

Fig. 4. Time series of environmental parameters; (a) SST, (b) monthly SST cycle, (c) time series of chlorophyll a, (d) monthly chlorophyll a cycle, (e) time series of salinity in the SRB, and (f) the monthly NAO winter indices

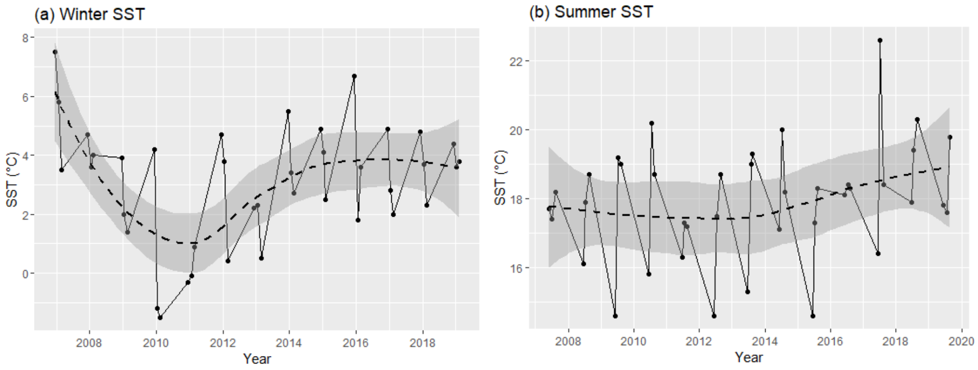

Fig. 5. Variations of winter and summer SSTs in the SRB between 2007 and 2019. SST measurements (dark lines) and a LOESS smoother of trends (dashed dark line)

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.

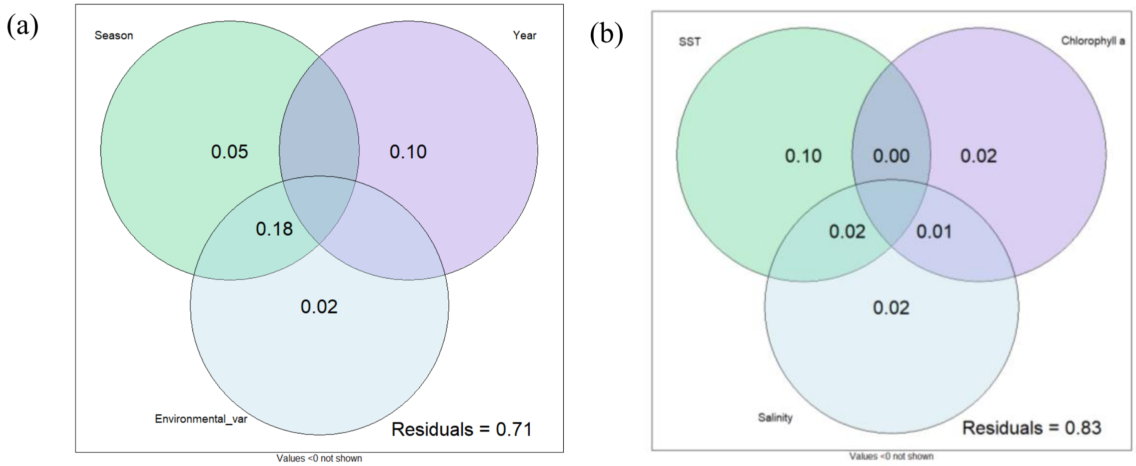

Fig. 6. Venn diagrams of variance partitioning of explanatory variables with respective percentage contributions to the variations in the fish community. (a) The ordinal variables year and season plus the combined effects of SST, salinity, and chlorophyll a as Environmental_var. (b) The percentage contributions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

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).

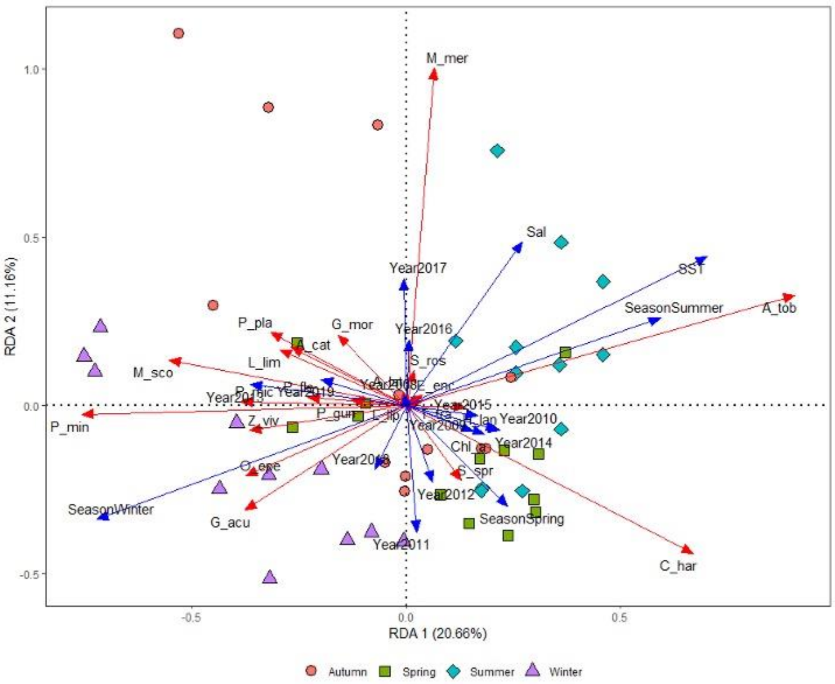

Fig. 7. RDA correlation triplot for the dominant fish species in the SRB, the explanatory variables sea surface temperature (SST), Sal (salinity), Chlorophyll a (Chl_a), and the ordinal variables year and season. Seasonal sample scores are shown in different shapes and colors, (See Table 2 for the species'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

4.0 Discussion

4.1 Fish species compositions

During the present monitoring, 55 fish species were documented in 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 (Fig. 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 (Fig. 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., 2016, 2014). *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 (Fig. 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 (Fig. 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 in the northern California Current System (*Engraulis mordax*) (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.

5.0 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.

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CHAPTER 3

Community structure and diversity changes for fish in a temperate tidal lagoon, in relation to changes in water temperature and depth

Community structure and diversity changes for fish in a temperate tidal lagoon, in relation to changes in water temperature and depth

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Abstract

Coastal marine ecosystems are characterized by high productivity and biodiversity supporting coastal fisheries for centuries. These ecosystems have undergone changes over the last few decades, experiencing shifts in seasonal patterns due to climate change. As a case study for responses of cold temperate coastal ecosystems to climate change, fish diversity changes in the Sylt-Rømø Bight (SRB), northern Wadden Sea; 54°58’40”N, 8°29’45”E, were analyzed using data from the monthly monitoring from 2007 to 2019. Results showed that the biodiversity changes correlated to seasonal water temperature changes. The spatial distribution of fish to intertidal areas for feeding and refuge was correlated to changes in water depth. Rank abundance curves (RACs) showed that a few species dominated the fish community and changed with seasons and habitat type. General Additive Models (GAMs) showed higher species richness (*S*) at 5°C and 15°C, which are seasonal transition phases for winter/spring and summer/autumn, respectively. Evenness (J) and Shannon-Wiener Index (H) decreased with increasing water temperature in the benthic and pelagic habitats while dominance increased. Generalized linear mixed-effects models (GLMMs) showed that *S* decreased while J increased with water depth in benthic habitats. Similar patterns were observed in the nearshore pelagic habitats contrary to the deep tidal channels. There were no significant effects of water depth on H. The diversity changes reveal the sensitivity of fish to changes in seasonal oceanographic processes and the use of intertidal habitats. Thus, the significance of shallow coastal habitats to the distribution of fish needs implementation in conservation and management measures.

Keywords

Cold temperate coastal ecosystems, Sylt-Rømø Bight, seasonal changes, ecotones, tidal influence, spatial distribution

Introduction

Coastal marine ecosystems are characterized by high productivity and biodiversity that have supported valuable coastal fisheries for centuries (Barbier et al. 2011). These ecosystems have undergone tremendous changes over the last decades due to climate change (Dulvy et al. 2008) and multiple anthropogenic stressors (Holm et al. 2024). Global warming for example has affected marine ecosystems and caused changes in phenology (van Walraven et al. 2017), and poleward movement of distributions in many species (Montero-Serra et al. 2015). Changes in community structure (Clark et al. 2020; Rutterford et al. 2023), predator-prey interactions (Durant et al. 2007), and shifts of bottom-dwelling species to deeper areas (Dulvy et al. 2008) are related to global warming. These changes have great implications for many species; here we focus on fish because of their high sensitivity to climate-driven environmental changes (Peck et al. 2013). For example, demersal fish species with limited movement capabilities must acclimatize or adapt to warming when they are no longer in their optimal ranges, otherwise, consequences such as population declines are inevitable (Rutterford et al. 2023). Such a scenario was reported for eelpout (*Zoarces viviparus*) whose growth and abundance decreased in the Wadden Sea because of rising water temperatures (Pörtner and Knust 2007).

The Wadden Sea is an important nursery ground providing rich feeding and refuge areas for many North Sea and resident fish species (Tulp et al. 2017; van der Veer et al. 2022). Global warming and the changes in seasonal environmental patterns can cause substantial changes in the nursery function by affecting species recruitment and diversity. For example, early timing of spawning, shorter egg and larval development times, and early immigration (van der Veer et al. 2022). Besides, temperature affects interspecific interactions such as predation rates between fish and key prey items (Edwards and Richardson 2004) which has implications on the total food web (Baird et al. 2019).

The Sylt-Rømø Bight (SRB) is one of the largest tidal catchments of the Wadden Sea and is located between the islands of Sylt (Germany), Rømø (Denmark), and the mainland coasts. Two causeways delimit the area to the north and south preventing water exchange with the adjacent tidal environments (Reise et al. 1998). The SRB comprises diverse subtidal and intertidal habitats such as mussel beds, seagrass meadows, and substrates of different grain sizes such as mudflats and sandflats (Baird et al. 2007). These offer feeding and refuge grounds for an array of different fish species (Kellnreitner et al. 2012). As a transient area between rivers Vidå and Bredeå and the North Sea, many individuals of anadromous species such as houting (*Coregonus oxyrinchus*) and catadromous species such as European eel (*Anguilla anguilla*) pass through during their migration (Odongo et al. 2024). Furthermore, during summers, individuals of the warm-adapted fish species of Lusitanian and Atlantic biogeographic origins migrate northwards in the North Sea and into the Wadden Sea, while boreal species migrate into the deeper North Sea and southwards in cold winters (Tulp et al. 2008).

Water temperature records in the SRB indicate an increase in annual means over the last decades and changes on seasonal scales with high inter-annual variabilities (Rick et al. 2023). There are more warmer days in summer and fewer cold days in winter compared to the 1962 to 1990 period (de Amorim et al. 2023) and autumns are also getting warmer (Rick et al. 2023). Temperature changes could influence the distributions and abundance of various fish species (Clark et al. 2020). Furthermore, the magnitude, duration, frequency, and temporal scales at which temperature changes are likely to occur, together influence fish community structure and diversity (Holbrook et al. 1994; Clark et al. 2020). Thus, diversity changes may either be a reflection of decadal fluctuations or directional changes in hydro-meteorological forcing (Beaugrand 2004) or short-term ones based on seasonal changes in water temperature (Corten and van de Kamp 1996). Additionally, the local habitat characteristics such as changes in water depth with tides influence the spatial distribution of fish through the movement of individuals between habitats in shallow coastal ecosystems (Couperus et al. 2016). In the SRB, water depth changes per tidal cycle and varies between different areas (Fofonova et al. 2019). Thus, the fish diversity in a specific location may vary based on differences in tidal velocity or change on short-term scales with tides.

The question arises whether there are potential effects of changes in water temperature on the community structure and diversity of fish in the SRB. As a tidal lagoon, there is a much shorter time effect on the diversity in different locations as fish may migrate to submerged intertidal areas for feeding and refuge during high tide and retreat with ebbing waters. Some fish species on the other hand may persist in different areas that differ in water depth within a tidal system. Therefore, we assessed the diversity of fish in the SRB using data from the monthly fish monitoring between the years 2007 and 2019 (Asmus et al. 2020). From the same dataset, changes in the fish community composition in comparison to previous investigations that took place from 1989 to 1995 (Herrmann, J.P., Jansen, S., Temming 1998; Vorberg and Breckling 1999) were determined. Additionally, trends and common patterns of the 22 most abundant species and the potential effects of water temperature, salinity, and chlorophyll *a* were assessed (Odongo et al. 2024). Here we focussed on the whole fish community and investigated the how the fish community structure and diversity changes as a response to the seasonal changes in water temperature. The spatial distribution and utilization of intertidal habitats during high tide were investigated to show the significance of shallow coastal ecosystems.

Materials and Methods

Study area

The Sylt-Rømø Bight (SRB) is a semi-enclosed tidal lagoon located between the islands of Sylt (Germany) and Rømø (Denmark) (Fig. 1) (central coordinates: 54°58’40N, 8°29’45E). The area is protected as a national park under both German and Danish legislation and is part of the internationally recognized Wadden Sea World Heritage Site (UNESCO 2009).

Commercially, only local (without crossing the international borders) mussels and shrimp fisheries are allowed in the area. The SRB is connected to the open North Sea through the Lister Deep, a 2.8 km wide tidal inlet, where 8 to 12 % of the bight's water is exchanged per tidal cycle and the water residence time ranges from 19 to 29 days. The bight covers a total aerial surface of 404 km^2, which includes 135 km^2 of intertidal area (Reise et al. 1998). The area is characterized by low salinities in winter and spring, and highs in summer and autumn with an overall range between 24 and 33 (Rick et al. 2023).

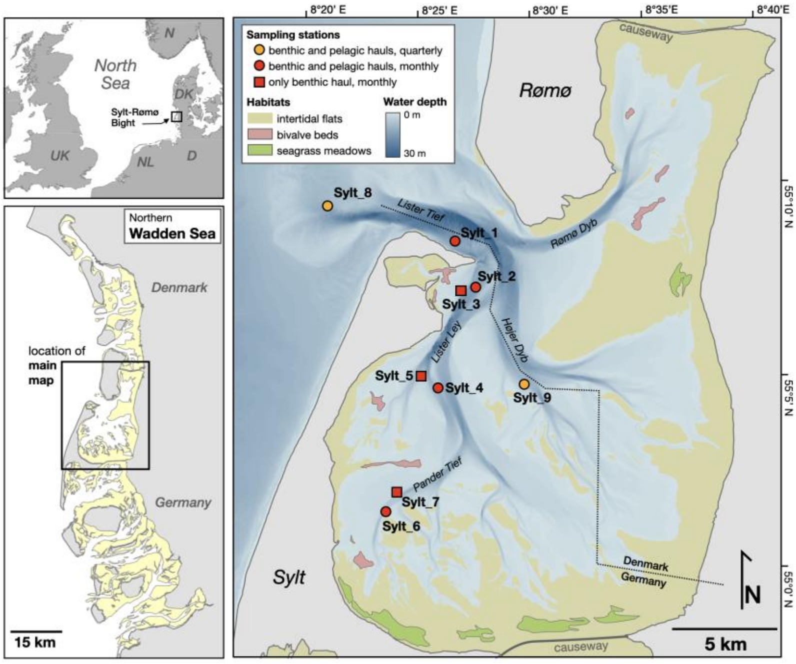


Fig. 1 Overview maps: Location of the Sylt-Rømø Bight on the eastern seaboard of the North Sea (top left) and the northern Wadden Sea (bottom left). Main map: Intertidal flats, bivalve beds, seagrass meadows, and tidal channels with varying water depths. Red dots, yellow dots, and red squares with labels Sylt_1 to Sylt_9 represent the positions of sampling areas and the sampling frequency (see legend). Map modified from Odongo et al. (2024), layout by authors based on own data and additional bathymetric data from BSH (2023)

Fish monitoring and data collection of environmental parameters

The details of sampling methods are described in Odongo et al. (2024) as we used the same dataset in Asmus et al. (2020). Fish monitoring took place monthly at seven stations inside the SRB and at two complementary stations, one outside the bight (Sylt_8) and one close to the Danish border (Sylt_9), which are sampled four times per year (Fig. 1). Water flow within the bight follows four major tidal channels and sampling mainly targeted the Lister Tief, Lister Ley, and Pander Tief that are all on the German side of the bight (Fig. 1). Due to international maritime boundaries and legislations, the Danish side of the bight was not sampled except the Sylt_9, which is located along the Højer Dyb (Fig. 1). All sampling stations were permanently submerged and the sampling gear is efficient with the capability of cruising at minimum water depths of 1.4 m. Sampling stations were chosen in such a way that they, together, are representative of the differences in the magnitude of tidally induced water currents, water depth, substrate type, and macrophyte systems. Sylt_1, Sylt_2, Sylt_4, and Sylt_8 are located in the deep tidal channels and differ in terms of water depth and tidal velocities from the other stations that are adjacent to the tidal channels (Fig. 1) (Fofonova et al. 2019).

Fish were sampled using research vessels MYA I (January 2007 to April 2013) and MYA II (from June 2013 onwards). In the early stages of MYA II operation, technical issues limited fish sampling and caused data gaps until April 2014. At each station, fish were sampled 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. Sampling per haul take 15 minutes at a speed of approximately 2 knots (Asmus et al. 2020). Both benthic and pelagic hauls were taken at the sampling stations that are located in the deep tidal channels while only benthic hauls were taken in the shallow stations where the vertical opening of the bottom trawl is quite similar to the total water depth (Fig. 1). Benthic hauls were always carried out directly above the sediments and targeted near-bottom communities. Pelagic hauls were always carried out in the middle of the water column, thus, the position of the sampling net changed relative to the total water depth and targeted the mid-water communities. In this paper, we refer to benthic hauls as benthic habitats while pelagic hauls are considered representatives of pelagic habitats. Sampled fish were sorted and identified to species level using the identification keys in Miller and Loates (1997) and Muus and Dahlstrøm (1978), then counted to determine species abundances. Respective sensors mounted on the onboard ferry box (Petersen 2014) measured various parameters such as water temperature and salinity while the ship's navigational echo sounder measured water depth at the start and the end of each haul. Due to strong tidal mixing in a shallow coastal system, sea surface temperature (SST) and water temperature are the same, thus, we use both terms in our analyses. The datasets are contained in the PANGEA repository (Felden et al. 2023) and the dataset links in this paper in Asmus et al. (2020) and Rick et al. (2023).

Data analysis

Non-parametric Kruskal-Wallis test was used to test depth differences between sampling stations. Similarly, same test was used to determine the differences in water temperature between seasons and between years. Then Dunn's test with Bonferroni corrections was performed for post hoc analysis to find significant differences between pairs.

Fish abundances in the benthic and pelagic hauls were standardized per sampled area (Individuals/10000 m^2). Rank Abundance Curves (RACs) were used to assess the seasonal species abundance distributions, the dynamics of co-occurring species, and the seasonal changes in community structures (Izsák and Pavoine 2012). This was done to elucidate the changes in species` use of the SRB at different times of the year. For this analysis, the monthly fish abundance data were aggregated into four seasons, winter (December, January, and February), spring (March, April, and May), summer (June, July, and August), and autumn (September, October, and November). The seasonal community dynamics in terms of changes in the relative abundances and the number of co-occurring species (Avolio et al. 2019) for benthic and pelagic habitats were assessed independently. Additionally, Jaccard's coefficient, analysis of similarity (ANOSIM), and similarity percentage (SIMPER) were used to further assess the differences in the seasonal community structures. Jaccard's coefficient assesses the similarity between seasons in terms of species presence/absence. ANOSIM compares ranked differences within- and between-groups that produce an R-value that approaches one when between-group differences are greater than within-group differences and vice-versa. R-values close to one signify higher dissimilarity between groups (James et al., 2023). SIMPER assesses the major taxa that are responsible for the observed differences between pair combinations (Clarke, 1993). SIMPER and ANOSIM analyses were based on the Bray-Curtis similarity coefficient at 999 permutations (Clarke 1993) on square-root transformed seasonal mean fish abundances.

Fish community diversity within the SRB for each month in each station was determined by computing diversity indices comprising species richness (*S*), evenness (J), dominance (D), and Shannon-Wiener Index (H). Species richness is a measure of the number of taxa present and was used to assess whether the numbers changed with time or changed per season. Evenness represents species abundance distribution in a community and ranges from 0 to 1. Low values indicate that one or few species dominate the community while high values indicate that relatively equal numbers of individuals belong to each taxon (Morris et al. 2014). The opposite is true for D, which also ranges from 0 to 1. Dominance was used to assess the abundance fluctuations of dominant species with changes in water temperature. Shannon-Wiener Index quantifies the uncertainty of randomly selecting a taxon based on the relative abundance of each species and was used to assess the distribution of both rare and abundant species. It ranges from 1.5 to 3.5 with high values indicating high diversity/ecological status (Morris et al. 2014).

General additive models (GAMs) in the *mgcv* package in R were used to assess the relationships between the diversity indices and the nominal variable (sampling station), ordinal variables (year and season), and continuous variable (water temperature). The GAMs were formulated as: $D_i \sim f(\text{water temperature})+\text{year}+\text{season}+\text{sampling station}+\varepsilon_i)$, where D_i = diversity index, $f()$ specifies the smoothing term, and ε_i is the error term that follows a normal distribution with zero mean ($\varepsilon_i \sim N(0,\sigma)$). The smoothing functions use a back-fitting algorithm to estimate the intercept and the smoothing curve and estimate one smoother at a time (Zuur et al. 2007, 2009b). The smoothing curves are estimated by cubic regression splines where the explanatory variables are divided into several intervals. In each interval, a cubic polynomial is fitted, and the fitted values per segment are connected using conditions that involve first- and second-order derivatives to form a smoothing curve (Zuur et al. 2009b). The smoothing curves were used to assess the non-linear relationships between water temperature and the diversity indices. The ordinal variables year and season were included in the GAMs to assess the inter- and intra-annual changes in fish diversity while sampling stations were to assess the spatial distribution patterns as sampling was concentrated in or adjacent to the main tidal channels (Fig. 1). Several combinations of explanatory variables were tested in GAMs and Akaike Information Criterion (AIC) was used to select the best model.

The Sylt-Rømø Bight is a tidal environment, water depth varies over each tidal cycle, and the bedform morphology differs within each sampling station. Generalized linear mixed-effects models (GLMMs) with identity link functions were used to model species diversity (*S,* J, and H) as linear functions of water depth where the intercept and slope changed per sampling station. This was to investigate the spatial distributions of fish with varying water depths at each sampling station. The mean water depth in meters (m), which was obtained by averaging depth at the start and the end of each haul, was used in GLMMs. The effect of the sampling station was included in the model as a random component where changes in water depth per sampling station had a different effect on the diversity. The variation around the intercept for each sampling station was assumed to be normally distributed with a certain variance. A small variance represented a small difference between sampling stations and vice versa. Further, a linear regression model with sampling station and water depth and the interaction between them, in other words, analysis of covariance (ANCOVA) was used to find their relationship with fish diversity. The GLMMs were formulated as $D_{ij} \sim depth_i + (depth_i|Station_j) + \varepsilon_i$), where D_{ij} is the diversity index at $depth_i$ in $station_j$, $depth_i$ is the fixed effect of water depth on a diversity index, $(depth_i|Station_j)$ is the interaction between water depth and sampling station, and ε_i is the error term ($\varepsilon_i \sim N(0,\sigma)$). For more details on model specifications and formulation for the GAMs and GLMMs, refer to Zuur et al. (2007, 2009a, b). Statistical significance was assumed for all tests if the p-value was below 0.05. The Software R version 4.3.1 (R Development Core Team, 2023) was used to perform all statistical analyses.

Results

Temporal changes in water temperature

Water temperature ranged from -1.5 to 22.6 °C during the survey period. Seasonal water temperature cycles that are typical in the Wadden Sea were observed as all seasons were significantly different from each other. No significant within-season mean temperature differences were observed except for the warm winter of 2006/2007 compared to the cold winters of 2009/2010, 2010/2011, and 2012/2013 (Fig. 2, d). For more information on changes in water temperature and significant differences, see Supplementary Information 1.

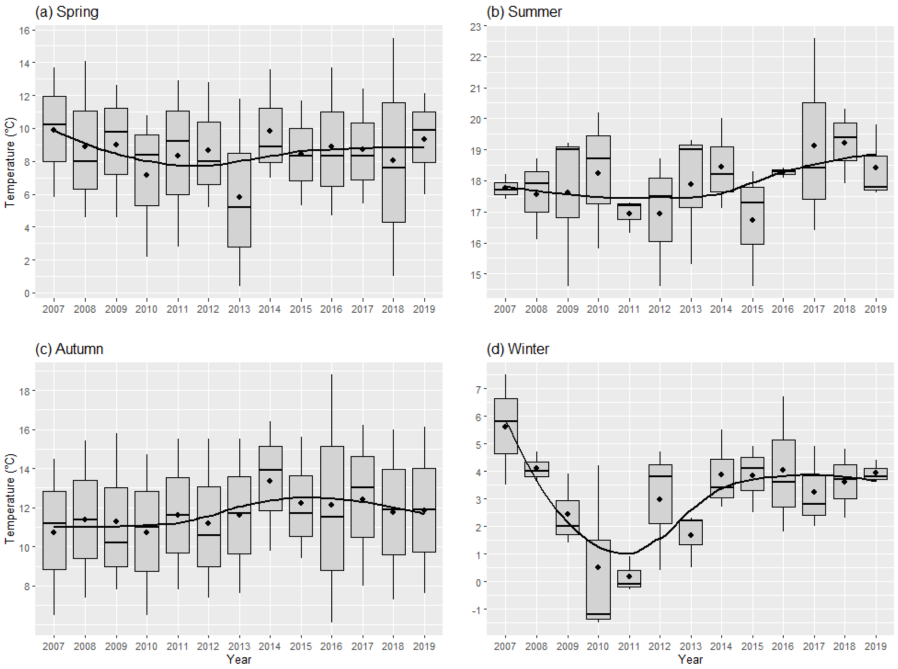


Fig. 2 Boxplots of the distribution of water temperature per season in the SRB. Each box represents the monthly measurements made in the seven stations (Sylt_1 to Sylt_7). The black dot indicates the seasonal mean, the horizontal line is the median, and the black line is the LOESS smoother of trends, see the different temperature ranges in the y-axis. Summer (b) and winter (d) temperature figures are also described in Odongo et al. (2024)

Spatial changes in water depth

Sampling of fish took place during daylight and more than four hours to sample half the number of stations. Thus, sampling at each of the stations generally occurred at different moments of the tidal cycle and under different meteorological conditions. Besides the influence of tides on water depth, transects differed within sampling stations as it was difficult to always maintain one transect due to strong tidal currents and the influence of wind velocity and direction. Therefore, towing directions and transects within the sampling areas differed and covered the edges, slopes, or centers of the tidal channels. Consequently, there were changes in water depth within each sampling station (Fig. 3). For more information on the significant differences in water depth between stations, see Supplementary Information 1.

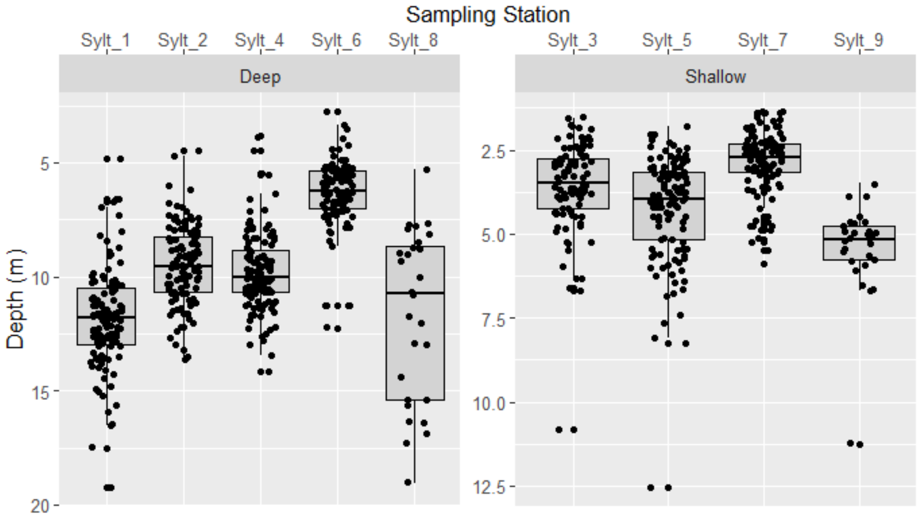


Fig. 3 Boxplots of depth variations per sampling station arranged as deep stations versus shallow stations. Each box and black dots represent all the measurements made per sampling station during the survey period. The horizontal line represents the median, and the Y-axis is reversed. Note the different scales in the Y-axis (see Fig. 1 for the location of sampling stations)

Species frequency of occurrence and relative abundances

In total, 55 fish species were found during the survey period and showed strong inter- and intra-annual abundance fluctuations. Some species were present all year round, others occurred only occasionally or were season-specific, while others were rare and present only in some years. Thus, only 22 species accounted for more than 95% of the total abundance for the entire survey. Table 1 and Table 2 show the details of the seasonal frequency of occurrence and the fluctuating abundances in both habitats. Herring (*Clupea harengus* Linnaeus 1758) was the dominant species while the second and subsequent rankings slightly differed between the habitats. Small sand eel (*Ammodytes tobianus* Linnaeus, 1758) was ranked second in the benthic habitats with 70% occurrence in summer while in the pelagic habitats, it was third-ranked with high occurrences in spring (Table 1 and 2). Sprat (*Sprattus sprattus* Linnaeus, 1758) was ranked third in the benthic habitats with high occurrence in spring followed by summer (Table 1). It was ranked second in the pelagic habitats with high occurrence in spring followed by winter (Table 2).

The sequence of species organization in terms of highly ranked to the least of the 22 abundant species differed per season. *Clupea harengus* was dominant in both habitats in all seasons. In the benthic habitats, *A. tobianus* was ranked second in spring and summer, sand goby (*Pomatoschistus minutus* Pallas 1770) in winter, and whiting (*Merlangius merlangus* Linnaeus, 1758) in autumn (Fig. 4). In the pelagic habitats, *S. sprattus* was ranked second in winter, summer and autumn, and *A. tobianus* in spring. Third and subsequent ranks differed per season (Fig. 4 and Fig. 5). The Relative Abundance Curves (RACs) show seasonal changes in species distributions and evenness. The steep gradients between first ranked to the second-ranked species in all habitats in spring and summer indicate uneven communities (Fig. 4 and 5). In the pelagic habitats, the relatively low steepness in winter and spring indicates a moderately even community as species abundances were almost in a similar range (Fig. 5).

Additional analyses of the seasonal changes in community structure showed that all winters compared to all summers had the highest percentage dissimilarity; ANOSIM, R = 0.63, $p = 0.0001$, SIMPER = 67.55%. The two seasons were 55% similar in terms of species presence and absence (Jaccard's coefficient = 0.55). The dissimilarities between other seasonal comparisons were lower, SIMPER ranged from 55 % to 58.49 %, ANOSIM, R < 0.3, $p < 0.001$, and Jaccard's coefficient was relatively higher and ranged from 0.62 – 0.79. In all seasonal community structure comparisons, six dominant species, *C. harengus, A. tobianus, M. merlangus, S. sprattus, P. minutus,* and Nilsson's pipefish (*Syngnathus rostellatus* Nilsson 1855) contributed the highest percentage dissimilarities. See Supplementary Table 1 for the details of the percentage contributions of different taxa to the dissimilarities between seasons.

Table 2 The total abundance, the percentage of each species to the total abundance, seasonal mean abundances, and the percentage seasonal frequency of occurrence of the 22 species in the benthic habitats for the entire survey. Spp_code show the species names in other analyses

Species			Total abundance	% of the total abundance	Seasonal mean abundance				% Seasonal frequency of occurrence			
Common names	Scientific names	Spp_code			Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
Herring	*Clupea harengus*	C_har	818841	67.6	1091.2	1989.7	368.1	137.6	30	56	10	4
Small sand eel	*Ammodytes tobianus*	A_tob	176934	14.6	180.8	540.8	47.6	2.7	23	70	6	0
Sprat	*Sprattus sprattus*	S_spr	69791	5.8	160.4	75.1	50.7	16.2	53	25	17	5
Whiting	*Merlangius merlangus*	M_mer	48971	4.0	10.6	137.0	71.0	0.7	5	63	32	0
Sand goby	*Pomatoschistus minutus*	P_min	35714	3.0	58.7	15.0	51.3	39.3	36	9	31	24
Nilsson's pipefish	*Syngnathus rostellatus*	S_ros	11717	1.0	15.4	17.5	16.6	2.4	30	34	32	5
Plaice	*Pleuronectes platessa*	P_pla	7346	0.6	5.4	13.4	7.3	8.0	16	39	21	23
Great sand eel	*Hyperoplus lanceolatus*	H_lan	5304	0.4	14.6	7.4	0.4	0.0	65	33	2	0
Bull-rout	*Myoxocephalus scorpius*	M_sco	4764	0.4	2.7	1.4	2.5	18.3	11	6	10	74
Common goby	*Pomatoschistus microps*	P_mic	4602	0.4	4.1	0.2	4.6	14.4	17	1	20	62
Three-spined stickleback	*Gasterosteus aculeatus*	G_acu	3934	0.3	4.6	4.5	1.0	8.9	24	24	5	47
Hooknose	*Agonus cataphractus*	A_cat	3715	0.3	3.5	2.0	5.9	6.4	20	11	33	36
Dab	*Limanda limanda*	L_lim	3331	0.3	4.5	0.8	6.4	3.8	29	5	41	25
Cod	*Gadus morhua*	G_mor	2923	0.2	0.4	7.0	4.5	1.6	3	52	33	12
Smelt	*Osmerus eperlanus*	O_epe	2667	0.2	3.0	1.2	1.7	7.3	23	9	13	56
Eelpout	*Zoarces viviparus*	Z_viv	2642	0.2	2.8	3.2	0.8	6.1	22	25	6	48
European anchovy	*Engraulis encrasicolus*	E_enc	1768	0.1	0.2	0.5	7.4	0.0	3	7	91	0
Fluonder	*Platichthys flesus*	P_fle	1278	0.1	2.1	0.4	0.6	3.0	35	7	11	45
Horse mackerel	*Trachurus trachurus*	T_tra	885	0.1	0.0	3.8	0.1	0.0	0	96	4	0
Gunnel	*Pholis gunnellus*	P_gun	814	0.1	1.6	0.7	0.5	1.0	43	19	12	26
Striped seasnail	*Liparis liparis*	L_lip	639	0.1	1.6	0.8	0.2	0.2	59	30	6	6
Scaldfish	*Arnoglossus laterna*	A_lat	261	0.0	0.1	0.0	1.1	0.0	7	3	89	1

Table 3 The total abundance, the percentage of each species to the total abundance, overall seasonal mean abundances, and the percentage seasonal frequency of occurrence of the 19 abundant species in the pelagic habitats for the entire survey period

Species		Total abundance	% of the total abundance	Seasonal mean abundances				% seasonal frequency of occurrence			
Common names	Scientific names			Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
Herring	*Clupea harengus*	300829	87.9	10087	12621	1423	401	29	22	25	23
Sprat	*Sprattus sprattus*	18472	5.4	331	518	685	111	36	14	22	28
Small sand eel	*Ammodytes tobianus*	10867	3.2	634	45	206	2	57	23	12	7
Great sand eel	*Hyperoplus lanceolatus*	3282	1.0	245	5	5	0	54	23	22	1
Nilsson's pipefish	*Syngnathus rostellatus*	2436	0.7	33	50	131	9	30	28	33	9
Three-spined stickleback	*Gasterosteus aculeatus*	1764	0.5	45	21	22	71	35	9	21	35
Horse mackerel	*Trachurus trachurus*	1752	0.5	0	143	3	0	0	82	18	0
Sand goby	*Pomatoschistus minutus*	716	0.2	32	8	6	14	25	7	26	43
Smelt	*Osmerus eperlanus*	496	0.1	17	2	6	19	20	11	16	53
Whiting	*Merlangius merlangus*	451	0.1	0	23	18	0	4	65	31	0
Plaice	*Pleuronectes platessa*	197	0.1	9	4	1	2	27	30	16	27
Common goby	*Pomatoschistus microps*	193	0.1	1	0	2	16	11	0	26	63
Fluonder	*Platichthys flesus*	159	0.0	9	1	0	3	49	8	8	36
Bull-rout	*Myoxocephalus scorpius*	92	0.0	3	0	1	3	30	11	19	41
Hooknose	*Agonus cataphractus*	82	0.0	3	1	2	2	22	22	19	38
Garfish	*Belone belone*	65	0.0	4	1	0	0	41	47	12	0
Lumpfish	Cyclopterus lumpus	63	0.0	1	0	4	2	16	3	63	19
Dab	*Limanda limanda*	62	0.0	1	0	5	0	40	13	40	7
Eelpout	*Zoarces viviparus*	49	0.0	2	0	1	1	46	8	15	31

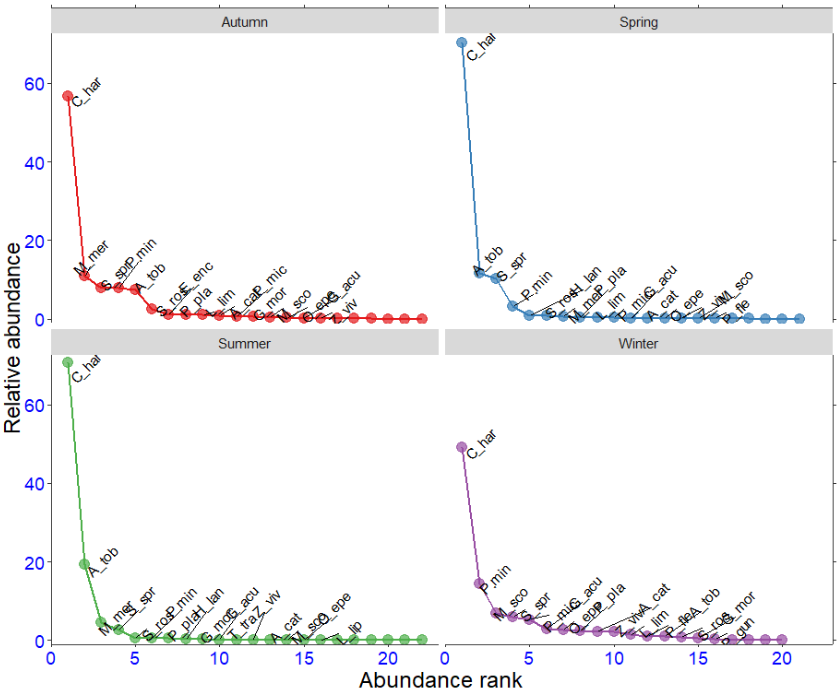


Fig. 4 Seasonal Rank abundance curves (RACs) of the 22 dominant fish species in the benthic habitat. The x-axis shows species ranked from the most abundant to the least, and the y-axis is the relative abundance (see the column Spp_code in Table 1 for species full names)

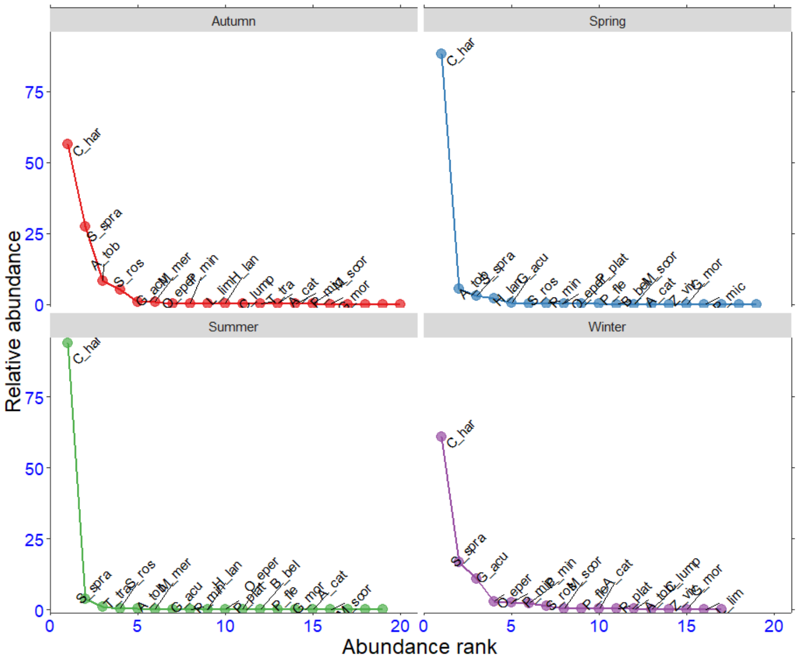


Fig. 5 Seasonal Rank abundance curves (RACs) of the dominant fish species in the pelagic habitat. The x-axis shows species ranked from the most abundant to the least, and the y-axis is the relative abundance (see the column Spp_code in Table 1 for species full names)

Temporal changes in fish diversity

The diversity indices, species richness (*S*), evenness (J), dominance (D), and Shannon-Wiener Index (H) varied both spatially and temporally over the study period. In general, there were higher taxa numbers in the benthic habitats compared to pelagic habitats (SI Fig. S1). Species richness *(S)* in benthic habitats was the highest in spring and summer. In contrast, *S* in pelagic habitats was low in summer (SI Fig. S1). Inter-annual differences in *S* were observed with high variabilities in both benthic and pelagic habitats (numerous outliers in SI Fig. S1). The General Additive Model (GAM) comprising smoothing terms of water temperature, sampling station and the factors year and season explained 15 % and 24 % of the variations in *S* in the benthic and pelagic habitats, respectively. Water temperature was significant and explained 4% and 11% variations in *S* in the benthic and pelagic habitats, respectively (Tables 3 and 4). Smoothing curves show higher *S* in temperatures between 4°C to 7°C and 13°C to 16°C in both habitats and remain stable when temperatures are above 19°C (Fig. 6). However, *S* ranged from 2 to 15 species (mean of 7.6±3.1 (SD), n = 100) between 19°C and 22.6°C in the benthic habitat and from 1 to 7 species (mean of 2.6±1.5 (SD), n = 42) in the pelagic habitats (SI Fig. S2). Thus, the wide 95% confidence bands indicate high uncertainty in *S* prediction when water temperature are >19°C. Numerical output of different GAMs for both habitats are summarized in Table 3 and Table 4, best models are shown in bold. The tables show various information on the performance of various models in explaining the variations in diversity indices. For instance, deviance explained which is equivalent to R^2 in linear regressions and the Akaike Information Criterion (AIC). The GAMs show that the factor year explained higher variability in *S* at 7 % (benthic) and 10 % (pelagic) habitats compared to the seasonal effect that explained only 2 % and 3%.

Table 4 Estimated parameters, standard errors, t-values, p-values, deviance explained, scale estimates, and Akaike Information Criterion (AIC) of the parametric components of the general additive models of the explanatory variables to the diversity indices in benthic habitats. Best models are shown in bold, s() represents the smoothing terms of water temperature

Diversity index	Explanatory variables	Estimate/ Intercept	SE	t-value	*p*-value	Deviance explained	Scale est.	AIC
Species richness (*S*)	**s(Temperature)+Year+Season+Station**	**7.47**	**0.51**	**14.57**	***	**15%**	**10.8**	**4385.1**
	s(Temperature)+Year+Season	8.11	0.43	18.95	***	13%	10.9	4390.8
	s(Temperature)+Year	9.16	0.36	25.46	***	10%	11.2	4405.6
	s(Temperature)+Season	6.88	0.26	26.70	***	6%	11.6	4429.3
	s(Temperature)	7.84	0.12	65.84	***	4%	11.8	4441.4
	Year+Season	5.99	0.41	21.01	***	8%	11.4	4419.1
	Year	9.40	0.36	26.12	***	7%	11.5	4426.8
	Season	7.13	0.24	29.69	***	2%	12.1	4458.2
	Station	7.28	0.32	22.60	***	2%	12.1	4465.6
Evenness (J)	**s(Temperature)+Year+Season+Station**	**0.56**	**0.03**	**16.69**	***	**17%**	**0.0**	**-167.2**
	s(Temperature)+Year+Season	0.53	0.03	18.87	***	15%	0.0	-169.2
	s(Temperature)+Year	0.47	0.02	19.98	***	13%	0.0	-156.3
	s(Temperature) + Season	0.49	0.02	29.97	***	12%	0.0	-169.2
	s(Temperature)	0.44	0.01	58.08	***	11%	0.0	-157.5
	Year+Season	0.49	0.03	18.03	***	11%	0.0	-139.5
	Year	0.46	0.02	19.18	***	3%	0.1	-79.7
	Season	0.46	0.02	30.22	***	8%	0.0	-134.2
	Station	0.47	0.02	22.20	***	1%	0.1	69.9
Dominance (D)	**s(Temperature)+Year+Season+Station**	**0.43**	**0.04**	**11.39**	***	**20%**	**0.1**	**25.2**
	s(Temperature)+Year+Season	0.42	0.03	13.47	***	18%	0.1	29.5
	s(Temperature)+Year	0.45	0.03	17.43	***	17%	0.1	27.3
	s(Temperature)+Season	0.51	0.02	26.83	***	11%	0.1	76.2
	s(Temperature)	0.54	0.01	62.30	***	10%	0.1	74.2
	Year+Season	0.43	0.03	14.22	***	15%	0.1	55.1

	Year	0.45	0.03	16.46	***	9%	0.1	103.0
	Season	0.53	0.02	29.93	***	7%	0.1	103.1
	Station	0.55	0.02	22.42	***	2%	0.1	156.4
Shannon (H)	**s(Temperature)+Year+Season+Station**	**1.22**	**0.08**	**14.54**	***	**22%**	**0.3**	**1361.3**
	s(Temperature) + Year + Season	1.25	0.07	17.75	***	19%	0.3	1374.3
	s(Temperature) + Year	1.22	0.06	20.90	***	19%	0.3	1369.8
	s(Temperature)+Season	1.01	0.04	23.54	***	12%	0.3	1425.5
	s(Temperature)	0.98	0.02	49.87	***	11%	0.3	1424.0
	Year+Season	1.23	0.07	18.06	***	15%	0.3	1406.4
	Year	1.24	0.06	20.45	***	9%	0.3	1454.5
	Season	0.97	0.04	24.27	***	7%	0.3	1457.7
	Station	0.96	0.05	17.43	***	2%	0.4	1508.9

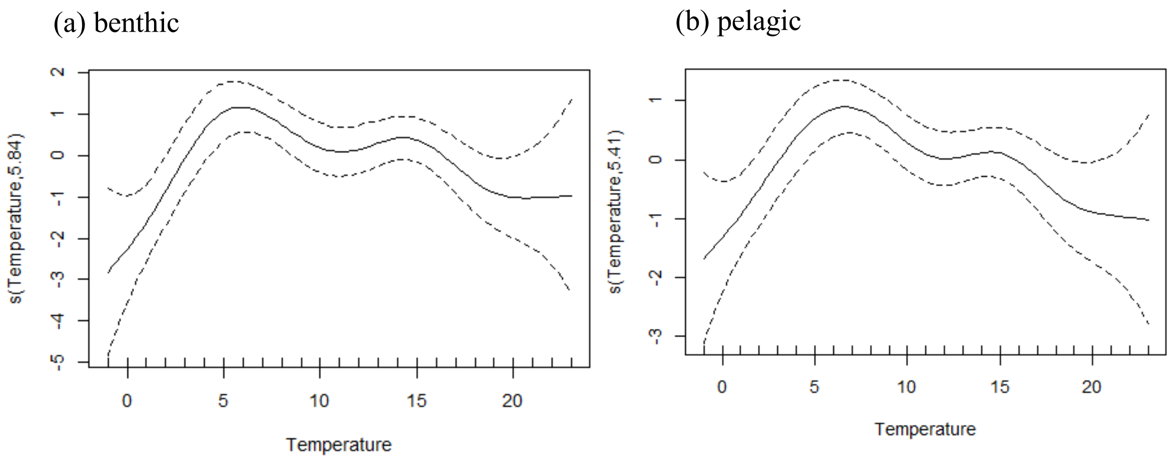
Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Table 5 Estimated parameters, standard errors, t-values, p-values, deviance explained, scale estimates, and Akaike Information Criterion (AIC) of the parametric components of the general additive models of the explanatory variables to the diversity indices in the pelagic habitats. Best models are shown in bold, s() represents the smoothing terms of water temperature

Diversity index	Explanatory variables	Estimate/ Intercept	SE	t-value	*p*-value	Deviance explained	Scale est.	AIC
Species richness (*S*)	**s(Temperature)+Year+Season+Station**	**4.65**	**0.34**	**13.65**	***	**24%**	**3.74**	**1831.91**
	s(Temperature)+Year+Season	5.08	0.29	17.32	***	19%	3.90	1845.48
	s(Temperature)+Year	5.08	0.29	17.38	***	19%	3.90	1842.11
	s(Temperature)+Season	3.86	0.10	38.91	***	11%	4.18	1863.83
	s(Temperature)	3.87	0.10	39.45	***	11%	4.18	1861.08
	Year+Season	5.31	0.35	15.11	***	14%	4.12	1863.96
	Year	5.30	0.30	17.58	***	10%	4.27	1876.53

	Season	3.89	0.21	18.17	***	3%	4.49	1889.15
	Station	3.55	0.22	15.96	***	4%	4.50	1892.58
Evenness	**s(Temperature)+Year+Season+Station**	**0.71**	**0.04**	**16.21**	***	**17%**	**0.06**	**48.27**
(J)	s(Temperature)+Year+Season	0.65	0.04	17.46	***	13%	0.06	58.18
	s(Temperature)+Year	0.65	0.04	17.11	***	9%	0.07	70.51
	s(Temperature) + Season	0.76	0.03	26.78	***	9%	0.06	51.46
	s(Temperature)	0.66	0.01	53.84	**	6%	0.07	60.62
	Year+Season	0.69	0.05	15.23	***	5%	0.07	81.18
	Year	0.64	0.04	16.65	***	3%	0.07	86.05
	Season	0.70	0.03	26.67	***	2%	0.07	73.54
	Station	0.70	0.03	25.82	***	3%	0.07	70.78
Dominance	**s(Temperature)+Year+Season+Station**	**0.54**	**0.05**	**11.15**	***	**15%**	**0.08**	**147.67**
(D)	s(Temperature)+Year+Season	0.51	0.05	10.08	***	12%	0.08	150.36
	s(Temperature)+Year	0.56	0.04	13.61	***	11%	0.08	150.84
	s(Temperature)+Season	0.61	0.01	44.49	***	8%	0.08	148.81
	s(Temperature)	0.61	0.01	44.84	***	6%	0.08	149.15
	Year+Season	0.52	0.05	10.47	***	8%	0.08	163.78
	Year	0.56	0.04	13.24	***	6%	0.08	166.45
	Season	0.59	0.03	19.91	***	2%	0.08	166.53
	Station	0.59	0.03	19.33	***	2%	0.09	170.97
Shannon	s(Temperature)+Year+Season+Station	0.86	0.08	10.21	***	20%	0.23	627.33
(H)	s(Temperature) + Year + Season	0.94	0.09	10.63	***	18%	0.24	627.85
	s(Temperature) + Year	**0.87**	**0.07**	**12.08**	***	**17%**	**0.24**	**626.28**
	s(Temperature)+Season	0.71	0.02	29.29	***	12%	0.25	633.68
	s(Temperature)	0.70	0.02	29.50	***	11%	0.25	633.15
	Year+Season	0.95	0.09	10.95	***	12%	0.25	649.46
	Year	0.89	0.07	11.96	***	8%	0.26	661.48
	Season	0.75	0.05	14.33	***	4%	0.27	662.26
	Station	0.72	0.06	13.02	***	1%	0.28	680.01

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1


(a) benthic

(b) pelagic

Fig. 6 Smoothing functions of water temperature (°C) for the additive models applied to species richness (*S*). The x-axis shows temperature values and the y-axis is the contribution of the smoother to the fitted *S* values for benthic and pelagic habitats. The solid line is the estimated smoother and the dotted line represents 95% confidence bands. The thin vertical lines along the x-axis indicate the temperature values of the observations

Evenness (J) varied both annually and seasonally in both habitats. Evenness was higher in winter and spring than in summer in most of the years. Evenness was higher in the pelagic habitats than in the benthic habitats (SI Fig. S3). Water temperature explained 11% and 6% variations in J in the benthic and pelagic habitats, respectively (Tables 3 and 4). In the benthic habitats, the smoothing terms of water temperature show that J decreases with increasing temperature up to 15°C followed by a minor increase. This is followed by a decline at temperatures above 18°C (Fig. 7, a). In the pelagic habitats, J decline with increasing temperatures up to 8°C then remain constant up to 11°C. This is followed by a further decrease to 15°C then an increase up to 19°C after which it remains constant (Fig. 7, b). The factor season explained a higher variability in J (8%) than the factor year (4%) in the benthic habitats (Table 3). In the pelagic habitat, both factors year and season explained low variability in J at 3 % and 2 %, respectively (Table 4).

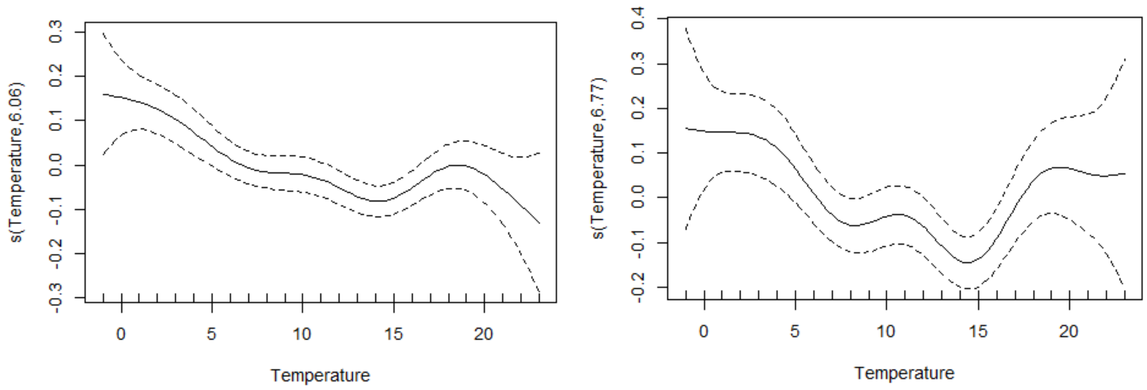

(a) benthic

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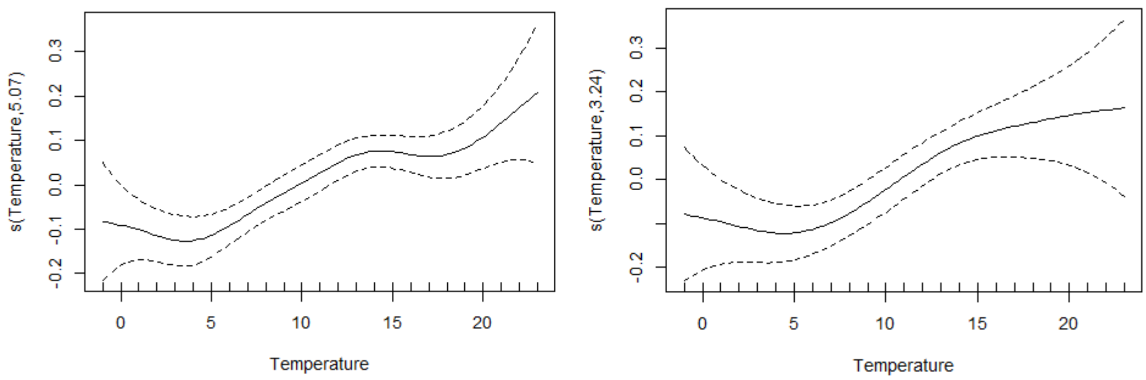
Fig. 7 Smoothing functions of water temperature (°C) for the additive models applied to evenness (J). The x-axis shows temperature values and the y-axis is the contribution of the smoother to the fitted J values for benthic and pelagic habitats. The solid line is the estimated smoother and the dotted line represents 95% confidence bands

Dominance (D) varied both annually and seasonally in both habitats. The highest values were found in most summers. However, in 2015 spring and autumn had higher values than summer in the benthic habitat while in the pelagic habitat, springs of 2009 and 2017 showed relatively higher values (SI Fig. S3). In the benthic habitats, smoothing terms showed that D is unstable at temperatures below 5°C then gradually increases up to 14°C after which it remains stable to 18°C. This is followed by an increase at temperatures above 19°C (Fig. 8, a). A similar pattern occurred in the pelagic habitat. However, the wide 95% confidence interval indicates the uncertainties in D at temperatures above 16°C (Fig. 8, b). Water temperature explained 10% and 6% variations in D in the benthic and pelagic habitats, respectively. The factor year explained 9% and 6% of the variability in D in benthic and pelagic habitats, respectively. The factor season on the other hand explained 7 % variability in benthic and only 2% in the pelagic habitats (Tables 3 and 4).


(a) benthic

(b) pelagic

Fig. 8 Smoothing functions of water temperature for the additive models applied on dominance (D). The x-axis shows the temperature values and the y-axis the value of the smoother to the fitted D values in benthic and pelagic habitats. The solid line is the estimated smoother and the dotted line represents 95% confidence bands

Shannon-Wiener Index (H) varied annually and across seasons in both habitats. Generally, H was high in winter and low in summer. However, in 2017 spring showed the highest H values in the benthic habitat, and springs of 2012, 2016, and 2017 had the highest values in the pelagic habitats (SI Fig. S4). Smoothing terms of water temperature showed a gradual increase in H from 1°C obtaining a maximum value at 5°C in both benthic and pelagic habitats (Fig. 9), which represents an equal proportion of all species at this temperature. As temperatures increase beyond 5°C, H gradually declines in all the habitats. However, in the benthic habitat, H was stable between 14°C and 18°C after which further decline occurs at higher temperatures. Water temperature explained 11% variability in H in both habitats. The factor year explained 9% and 8% variations in H while season explained 7 % and 4 % of the same in the benthic and pelagic habitats, respectively (Tables 3 and 4).

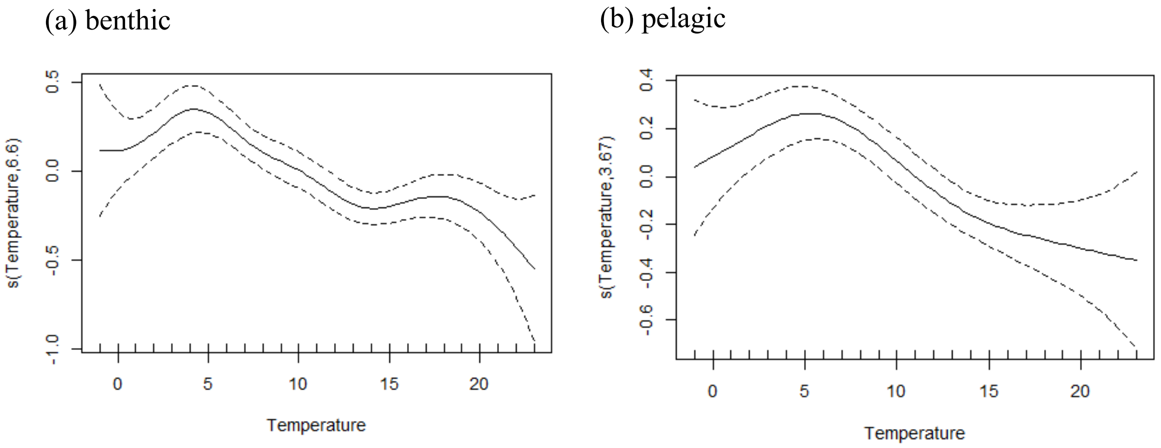
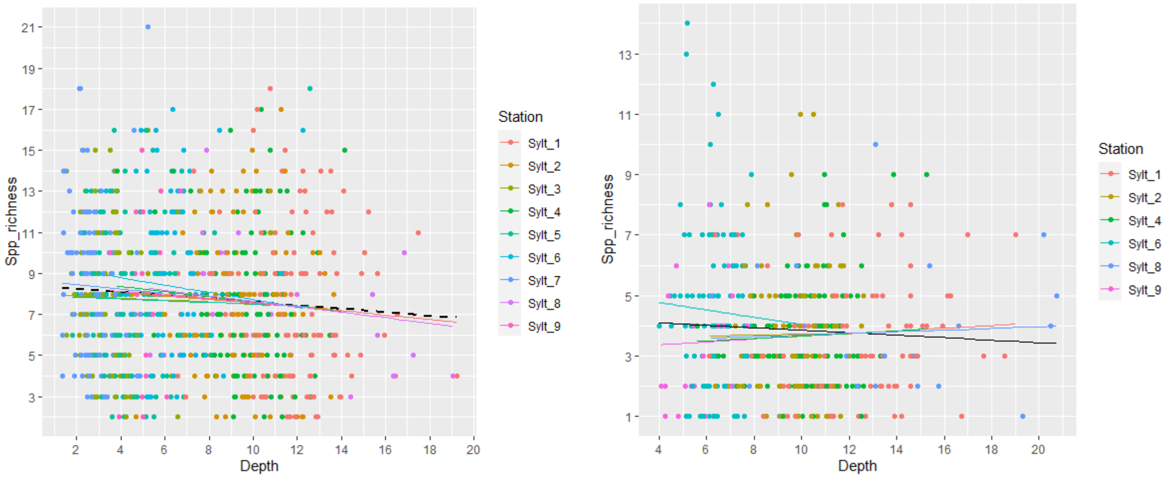


Fig. 9 Smoothing functions of water temperature for the additive models applied on the Shannon-Wiener Index (H). The x-axis shows the temperature values and the y-axis the value of the smoother to the fitted H values in the benthic and pelagic habitats. The solid line is the estimated smoother and the dotted line represents 95% confidence bands

Spatial distribution of fish with changes in water depth

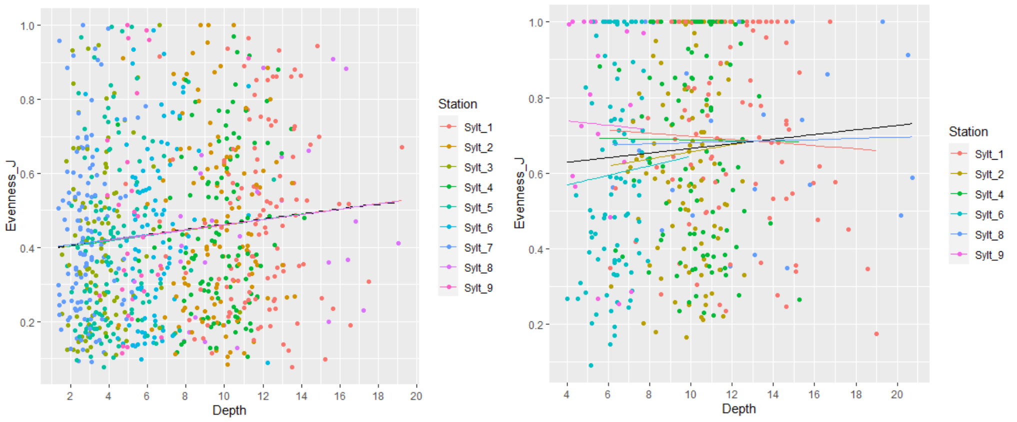
The tidal effects and changes in water depth within sampling stations on the distribution of fish were analyzed using generalized linear mixed-effects models (GLMMs). The different slopes and intercepts showed the distribution patterns in different sampling stations with changes in water depth. Generally, *S* decreased with increasing water depth in all sampling stations in the benthic habitats even though sampling was always slightly above the sediments irrespective of the water depth. The intercepts and slopes show minimal variations in *S* (variance (σ^2) = 0.59; sampling station, and σ^2 = 0.004; depth) between sampling stations in the benthic habitats regardless of whether the station was located in or adjacent to the deep tidal channels (Fig. 10, a). In the pelagic habitats, variations in *S* with water depth between sampling stations (σ^2= 1.14 (sampling station) and σ^2= 0.01 (depth) were observed. For instance, *S* decreased with water depth in Sylt_6 while Sylt_1 and Sylt_9 showed positive relationships between *S* and water depth (Fig. 10, b).


(a) benthic

(b) pelagic

Fig. 10 Random slope and intercept models (GLMMs) showing the variations of species richness (*S*) (y-axis) with water depth (m) (x-axis) at every sampling station in the benthic and pelagic habitats. Different intercepts show *S* variations per sampling station, the dark line represents the linear regression of combined depth effects on *S*

Evenness (J) increased with water depth in all sampling stations in the benthic habitats with no variations between stations (same intercept and slope, Fig. 11, a). In the pelagic habitats, J varied between sampling stations. For instance, Sylt_2 and Sylt_6 showed positive relationships between J and water depth while no depth effects were observed in Sylt_8. In the stations adjacent to deep tidal channels (i.e. Sylt_1, Sylt_4, and Sylt_9), J decreased with an increase in water depth (Fig. 11, b). Dominance on the other hand showed a slight decrease with an increase in water depth in all sampling stations in all habitats (SI Fig. S5). Individuals of various species utilized the submerged areas at high water depths resulting in equal abundance proportions in the sampled areas. There were minor variations in D with water depth between sampling stations. For instance, in the benthic habitats, Sylt_2 and Sylt_4 showed relatively steeper slopes than the other stations. Only Sylt_2 in the pelagic habitat showed such steepness (SI Fig. S5). There were no significant effects of water depth on H.


(a) benthic

(b) pelagic

Fig. 11 Random slope and intercept models (GLMMs) showing variations of evenness (J) (y-axis) with water depth (x-axis) at each sampling station in the benthic (a) and pelagic (b) habitats. Different intercepts show J variations per sampling station in the pelagic habitats. The dark line represents the linear regression of combined depth effects on J

Discussion

Species' relative abundances and seasonal distributions

This study investigated the potential effects of the seasonal changes in water temperature on the community structure and diversity of fish in the Sylt-Rømø Bight (SRB). In addition, the utilization of intertidal habitats during high tide and spatial distribution within and adjacent to the tidal channels were investigated. The species' frequency of occurrence showed the overall seasonal distribution patterns in the benthic and pelagic habitats and the transitions of some species between these habitats. For example, *A. tobianus* had the highest frequency of occurrence in spring in its pelagic phase (Table 2). Thus, its highest frequency of occurrence in summer in the benthic habitats (Table 1) shows its transition from pelagic to benthopelagic behavior that occurs in the middle of their juvenile stages (Laugier et al. 2015). For the pelagic species such as *C. harengus,* the highest occurrence in spring in the pelagic habitats (Table 2) in comparison to the highest occurrence in summer in the benthic habitats (Table 1) may also indicate differences in size distributions. *Sprattus sprattus* on the other hand was abundant in spring in both habitats (Table 1 and Table 2). Its high occurrence in winter in the pelagic habitats (28%) compared to benthic habitats (5%) (Table 1 and Table 2), may indicate differences in size distributions between the habitats. However, the area is relatively shallow (Fig. 3), therefore, the size distributions of different species between the habitats need further investigations

Community ecology aims to understand how communities are organized by identifying, describing, and explaining the patterns that underlie the structure and diversity across space and time (Verberk 2011), and the associated environmental drivers (Heaven and Scrosati 2008). In every community, a few species are always present in the highest numbers suggesting that there are general macro-ecological rules or processes such as migration patterns underlying the species distribution and abundances (Verberk 2011; Murphy and Smith 2021). These patterns portray how such communities function, the types of ecological interactions, the relationships of co-occurring species, and the manner they respond to environmental changes (Verberk 2011). However, such predictions must be able to take into account the multiple interacting processes operating across spatio-temporal scales that dictate where and when species occur (Murphy and Smith 2021). This brings the question as to whether the observed seasonal abundance rank patterns (Fig. 4 and 5) are related to temperature changes (Fig. 2), and/or ecological interactions such as competition and predation that can lead to the exclusion of other species or whether the other species simply prefer different habitats at different life stages. Furthermore, in a resource-limited environment, dietary competition occurs among individuals of the same species (Borcherding et al. 2019) posing the complexities of ecosystem functioning.

Temperature is a critical environmental parameter structuring the fish diversity patterns through physiological tolerances (Selleslagh and Amara 2008) that leads to seasonal changes through community reorganizations shown by the Rank abundance curves (Fig. 4 and Fig. 5). Accordingly, temperature influences reproduction, recruitment, migration patterns, and ecological relationships (Selleslagh and Amara 2008; Clark et al. 2020). *Clupea harengus* dominated all seasons because it is the most abundant species in the North Sea (Corten 1986), has bi-annual (spring and autumn) spawning (Bierman et al. 2010), continuous inflow of juveniles from the adjacent North Sea (Maathuis et al. 2023), and high consumption of prey items (Utne et al. 2012). Thus, it outcompetes species of similar prey items but can co-occur with species with diverse prey choices and similar temperature preferences such as *A. tobianus* (Kellnreitner et al. 2012), which also spawns twice per year (Laugier et al. 2015).

Merlangius merlangus has diverse prey choices (Kellnreitner et al. 2012; Ross et al. 2016) but overlapping temperature preferences to *C. harengus* and *A. tobianus* (Table 1). Therefore, *M. merlangus* co-occurs with both *C. harengus* and *A. tobianus* in late spring/early summer attaining high relative abundances in autumn (Fig. 4). This co-occurrence pattern changes depending on the temperature conditions, for instance, after the prolonged cold winters of 2009/2010 and 2010/2011, low recruitment of *M. merlangus* in the SRB were observed while there were strong recruitments of *C. harengus* and *A. tobianus* (Odongo et al. 2024). Such abundance fluctuations explain why *C. harengus* was highly ranked even in autumn since we used seasonal mean abundances in the analysis. *Pomatoschistus minutus* feeds on diverse prey items (Kellnreitner et al. 2012) but its high ranking in winter in the benthic habitats (Fig. 4) is related to its local migration to deeper areas to avoid the unstable winter temperature conditions in the shallow intertidal zones. The second-ranking of *S. sprattus* in the pelagic habitats in most of the seasons (Fig. 5) is related to its preferred habitat. Other species had low relative abundance distributions but their rankings fluctuated with seasons and habitats (Fig. 4 and 5). These observations support the temperature role in the species' co-occurrence and/or exclusions in habitat use.

Potential effects of temperature changes on the diversity patterns

The Wadden Sea is characterized by seasonal changes in water temperature (Fig. 2) (Rick et al. 2023). Rutterford et al., (2023) predicted that global warming could cause shifts in fish species composition across the Northeast Atlantic continental shelf with greater implications at higher latitudes. Our monthly monitoring of 13 years, which might be considered short in determining the effects of climate change on community structures revealed a strong influence of seasonal changes in water temperature on the phenology of various fish species. For instance, the effects of anomalous events such as the prolonged cold winters of 2009/2010 (Fig. 2), also described by Osborn (2011) and 2010/2011 resulted in low taxa numbers compared to the relatively warm winters of 2006/2007, 2007/2008, and 2008/2009 (SI Fig. S1). Such events also influenced the diversity in the seasons that followed. For example, the higher number of taxa in the summer of 2010 (SI Fig. S1) may have resulted from the delayed emigration of boreal species that coincided with the immigration of Lusitanian species. Similarly, the high dominance in the 2015 autumn (SI Fig. S3) which was contrary to other years is attributed to the delayed emigration of *C. harengus* and *A. tobianus* after the cold summer of 2015 (Fig. 2). In the Dutch Wadden Sea, van Walraven et al. (2017) reported delayed immigration and emigration of fish because of an increase in offshore temperature based on a 53-year survey. However, changes in the fish community assemblages depend on the capacity for and the rate of distributional changes between species under different climate change scenarios (Rutterford et al. 2023). This is why we observed varying diversity patterns resulting from either delayed or advanced migration related to inter-annual variations in water temperature. Other factors besides temperature though not investigated in this study, may additionally play significant roles. For example, there was high species richness in the spring of 2016 (SI Fig. S1) despite similar the spring temperature ranges from 2014 to 2017 (Fig. 2).

Diversity patterns reflect the underlying processes that shape ecological communities (Vasconcelos et al. 2015). Species richness has been used as the simplest metric to represent community diversity. Although limited in measuring ecological dynamics, it provides information on co-occurring species under different environmental conditions (Avolio et al.

2019). Furthermore, *S* is a better measure when the primary objective is to detect the effects of environmental parameters on community diversity (Magurran and Dornelas 2010). For example, the low number of taxa at lower and higher temperatures (Fig. 6). Higher species richness occurred at temperatures around 5°C and 15°C (Fig. 6), which are typical temperatures for seasonal transition phases for winter/spring and summer/autumn, respectively (Fig. 2). This is because immigration and emigration occur simultaneously in the SRB resulting in higher species numbers at the seasonal transition phases. This is further supported by Jaccard's coefficients, which showed high similarity in terms of species present between adjacent seasons (Supplementary Table 1) and explain why the factor season explained low variations in *S* in both habitats (Tables 2 and 3). Furthermore, the migration patterns explain why *S* was not subjected to the bi-modal nature of the number of temperature observations (highs around 5°C and 15°C) which are typical in the Wadden Sea (de Amorim et al. 2023) or the North Sea (Boersma et al. 2016) (see SI Fig. S2).

At 10°C and 18°C, which are the typical mean spring and summer temperatures, respectively (Fig. 2), similar species richness (Fig. 6) and evenness (Fig. 7, a) were observed. The species numbers were lower than those of the winter/spring and summer/autumn transition phases because only species that are adapted to specific temperatures use the habitats at specific times otherwise migrate to more favorable environments. The *S* patterns (Fig. 6), show that the emigration of *C. harengus* and *A. tobianus* and the immigration of *M. merlangus* and *T. trachurus* (Table 1) starts at 15°C achieving a relatively even community at 18°C. Beyond 18°C, *M. merlangus* becomes the dominant species as indicated by the decrease in evenness (Fig. 7, a) and an increase in dominance (Fig. 8, a).

Compound indices such as the Shannon-Wiener Index (H) and evenness (J) provide more information on community dynamics (Morris et al. 2014). Nearby communities or seasonal assemblages with similar taxa numbers can have different community structures

(Heaven and Scrosati 2008). For instance, 10°C (spring) and 18°C (summer) had similar species richness (Fig. 7) but different H (Fig. 9). The decrease in H with increasing temperatures indicates that the proportion of less abundant and/or rare species gradually declined with temperature increase and a few species dominated the community except between 15°C and 18°C because of the community transitions or ecotones (Fig. 9). Similarly, in the tidal habitats of the Irish Sea, seasonality played a bigger role in structuring the fish community (Jovanovic et al. 2007) as well as the English Channel where higher diversities were observed in winter and low in summer (Selleslagh and Amara 2008). The changes in H (SI Fig. S4) and the variations explained by year (Tables 2 and 3) indicate that the inter-annual variations of biotic and abiotic factors that cause abundance fluctuations influence diversity as well (Morris et al. 2014).

Spatial distribution of fish with changes in water depth

A greater range of local habitat types and environmental conditions support higher diversity (Morris et al. 2014). Species-area relationships assume that the availability of important features such as habitat size influences species numbers and abundances (Tittensor et al. 2010). Local habitats may contain various microhabitat types that comprise different growth forms such as seagrass meadows, seaweed (*Sargassum muticum*), or bivalve beds (Fig. 1) that contain a high diversity of benthic and epibenthic communities (Armonies et al. 2018). The intertidal habitats when submerged during high tide offer additional ecological functions such as more prey, camouflage, and refuge spaces that promote higher taxa numbers (Gratwicke and Speight 2005). The negative correlation between S and water depth (Fig. 10) shows that during high tide, fish migrate to the intertidal habitats and recede with ebbing currents. The migration decreases the total fish density per area as the total aerial coverage increases during high tide. Thus, a positive correlation exists between water depth and evenness (Fig. 11). On the other hand, a negative correlation exists with dominance (SI Fig. S5).

Tidally induced current velocities vary within the tidal cycle and differ in various sub-areas of the SRB. Maximum velocity, which is approximately 1.8 m s^{-1} occurs at the opening of Lister Tief (Fig. 1) and decreases towards the intertidal flats (Fofonova et al. 2019). Besides, the seabed morphology differs within sampling stations. Thus, the positive correlation between water depth and J indicates that fish concentrated in smaller areas during low tide and/or simply avoided the deeper parts within the tidal system irrespective of the tidal condition. The negative correlations in stations adjacent to subtidal channels (i.e. Sylt_1, Sylt_4, and Sylt_9) in the pelagic habitats (Fig. 11, b), show that a few species dominated these areas during high tide. These differences are attributed to species habitat preferences as Kellnreitner et al. (2012) observed that benthivorous fish species mainly dominated the shallower areas while planktivorous fish were mostly abundant in the deep areas. Similarly, in the Irish Sea, flatfishes were more abundant in shallow areas or near the receding water edges as they fed on macroinvertebrates (Jovanovic et al. 2007). In the Dutch Wadden Sea, higher densities of *S. sprattus, C. harengus, E. encrasicolus,* and pilchard (*Sardina pilchardus*) occurred during high tide and dominated the top 10 m of the water column (Couperus et al. 2016). These observations show the significance of tidal dynamics on habitat utilization and distribution of common and rare species.

Different aspects of the composition, structure, and functioning of natural communities vary independently so a suite of metrics is needed to cover all types of changes (Greenstreet et al. 2012). For example, current velocity and sediment characteristics are important structural factors that influence the spatial distribution and composition of macrofaunal species (Schückel et al. 2015) that offer diverse food sources to fish (Kellnreitner et al. 2012). Incorporating these different aspects of habitat structure and composition (Gratwicke and Speight 2005) could offer more information on habitat utilization. This could better explain the changes in diversity between sites than generalizing only on sampling stations, which was significant but explained low percentage variations of the diversity (Tables 2 and 3). Nevertheless, incorporating and disentangling singular or cumulative effects of parameters such as habitat dependencies and shared food resources for different fish species is complex as it varies across key life stages and space (Rutterford et al. 2023). Therefore, exploring the behavioral responses, distribution patterns, and abundances of singular species with abiotic responses and biotic interactions could determine further habitat preferences and provide more information on spatial distribution patterns.

Conclusion

The fish community structure and diversity patterns demonstrated high seasonal dynamics that were potentially driven by the changes in water temperature in a cold temperate coastal ecosystem. The seasonal transition phases of winter/spring and summer/autumn recorded higher species richness (*S*) because immigration and emigration occur simultaneously. The community was less diverse at very low temperatures because of the low *S* and abundances and constrained biological interactions whereas the low diversity at higher temperatures was related to the dominance of a few species and physical tolerance. The higher percentage variations of *S* explained by temperature in the pelagic habitats compared to the benthic habitats showed the high sensitivity of species' pelagic phases to temperature changes. Since temperature effects cut across food webs, incorporating its effects on all trophic levels could provide more information on the fish community dynamics as we targeted only one group or compartment of the food web. Additionally, an analysis of the size distributions of various species between benthic and pelagic habitats could provide more information on the use of these habitats at different times of the year. The GLMMs showed the spatial distribution with changes in water depth per tidal cycle and within and between sampling stations. Thus, the significant roles of the shallow and intertidal areas as important feeding and refuge grounds. The effect of water depth on the diversity patterns was less pronounced because of the low depth changes in the SRB in comparison to other North Sea areas. Nevertheless, the GLMMs showed the species distribution patterns in different habitats, which calls for further investigations on the role of habitat complexity on species richness, abundance, and the distribution of common and rare fish species. The spatial distribution patterns provide baseline information on the significance of shallow coastal systems for fish. This is useful not only in the Wadden Sea but can be used as a guideline for management and conservation measures for the maintenance of biodiversity and valuable coastal and offshore ecosystems.

Supplementary Information

The online version contains supplementary information including descriptions of temperature and depth changes as well as additional figures of diversity indices.

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Author contributions

VO conceptualized the research questions, and data analysis methods, wrote the first draft, and led the writing process. HA conceptualized the fish monitoring ideas and designed the sampling methodology and gear selection. MB, SB, and KH guided the manuscript structure and clarity, review, and editing. LS provided the map of the study area and editing. SR and VF review and editing. All the authors contributed to the drafts and gave final approval for publication.

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Data availability

Data will be made available upon request.

Declarations

Conflict of interest

The authors declare that there are no competing financial interests or personal relationships, which could influence the scientific work presented in this paper.

Ethical approval

All applicable national and international regulations on scientific monitoring in protected areas were followed during the sampling and handling of fish specimens. The National Park “Schleswig- Holsteinisches Wattenmeer” issued the permit and authorization to work in the Sylt-Rømø Bight.

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Supplementary Materials

Supplementary Information 1

Temporal variations in water temperature

There were no significant variations in the annual mean temperature between years, except for 2013 which had an annual mean of 9.23 ± 7.1 °C (SD), n = 13, and was significantly different from all other years that had means above 10°C (Kruskal-Wallis test, H12 = 44.6, p <0.0001, Dunn's test, p <0.05). Seasonal water temperature cycles that are typical in the Wadden Sea were observed as all seasons were significantly different from each other (Kruskal-Wallis test, H3 = 616.31, p <0.0001). No significant within-season mean temperature differences were observed except for the winter of 2006/2007, which was relatively warm and significantly differed from the cold winters of 2009/2010, 2010/2011, and 2012/2013, (Dunn's test, p <0.05) (Fig. 2, d). Even without the significant differences between the seasonal mean water temperatures in the other seasons, there were year-to-year differences in water temperature ranges. For instance, spring water temperature ranged from 0.4 to 15.5 °C, summer from 14.6 to 22.6 °C, autumn from 6.1 to 18.8°C, and winter from -1.5 to 7.5°C (Fig. 2). Therefore, we cannot solely rely on the seasonal means but additionally explore the effects of water temperature ranges as well.

Spatial variations in water depth

Sylt_1 located in the main tidal channel recorded the highest depth variability and the least occurred in Sylt_7 (Fig. 3). There were significant differences in water depth between sampling stations located in the deep tidal channels to those located adjacent to the channels (Fig. 3), (Kruskal-Wallis test, H8 = 672, p <0.0001). No significant differences in water depth occurred across stations located in similar depth ranges irrespective of the distances between them. For example, no significant differences between Sylt_6 and Sylt_9, Sylt_4 and Sylt_8, Sylt_3 and Sylt_7, Sylt_2 and Sylt_8 (Dunn's test, $p > 0.05$) (see Fig. 3).

Supplementary Information 2

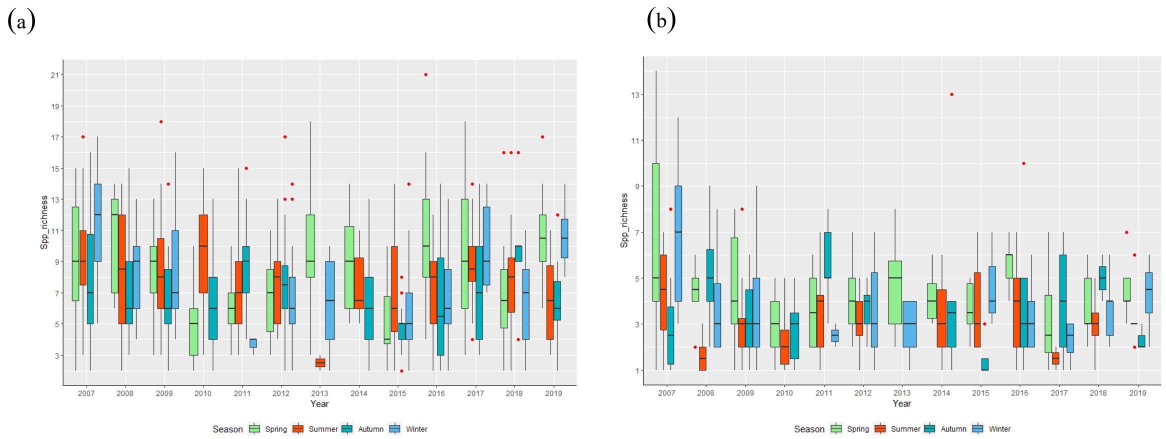


Fig. S1 Annual and seasonal variations of species richness in the benthic (a) and pelagic (b) habitats in the SRB. Note the different ranges in the y-axis

The number of temperature observations versus species richness

The number of observations for water temperature bins differed and *S* varied substantially even within the same temperature 1°C bin in both habitats. For example, 8 °C was the most observed temperature bin, but *S* in the benthic habitats ranged from 3 to 18 species (mean of 7.5± 3.6 (SD), n = 54). In contrast, 3°C only had half the number of observations, but *S* in benthic habitats also ranged from 3 to 16 species (mean of 9.6 ±3.6 (SD), n = 26) (Fig. 6, a). In the pelagic habitats, S was higher at 5 °C than at 8°C, although 8°C had the highest number of observations (Fig. 6, b). Therefore, the number of temperature observations did not influence *S* during the study period.

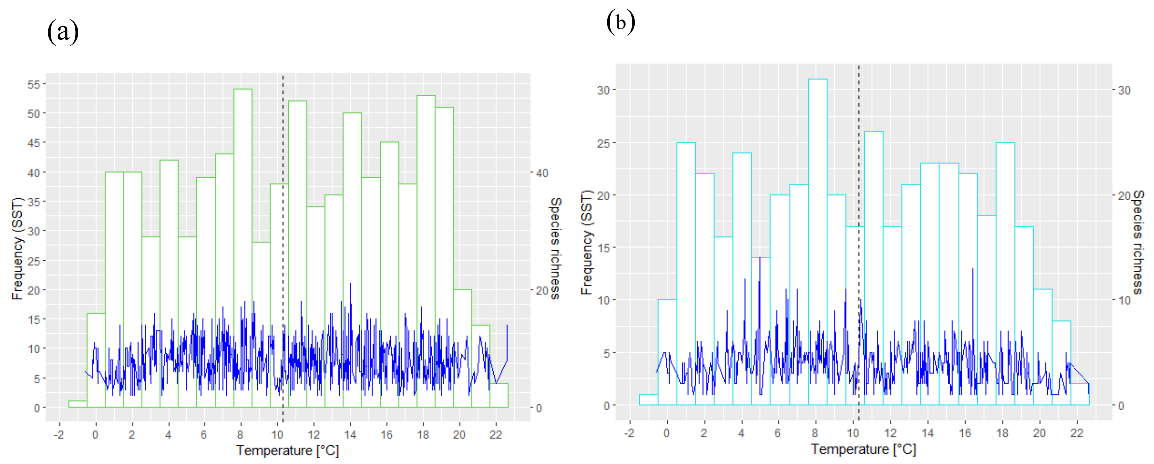
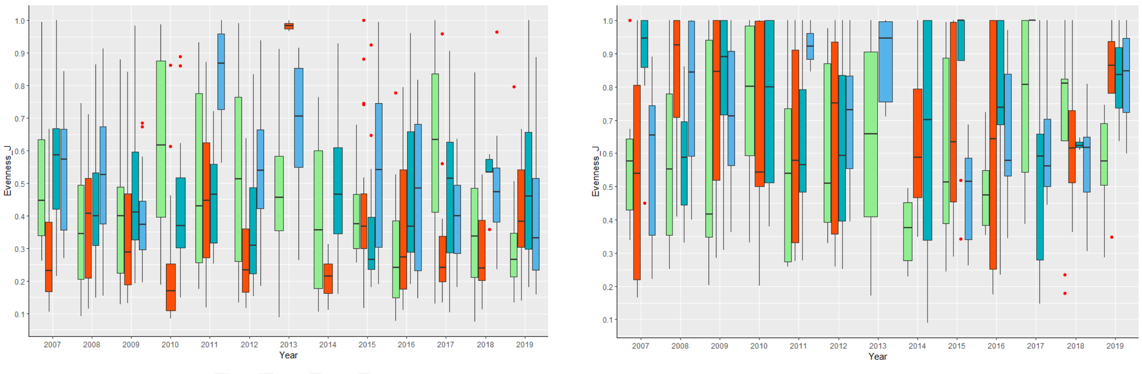


Fig. S2 Frequency distribution of the number of temperature observations (histogram, 1°C bins) in the benthic (a) and pelagic (b) habitats versus species richness (thin blue lines). The dotted vertical line is the long-term temperature mean. More measurements take place in the benthic habitats compared to pelagic habitats, thus, the differences in the number of temperature observations

(a) benthic

(b) pelagic



(c) benthic

(d) pelagic

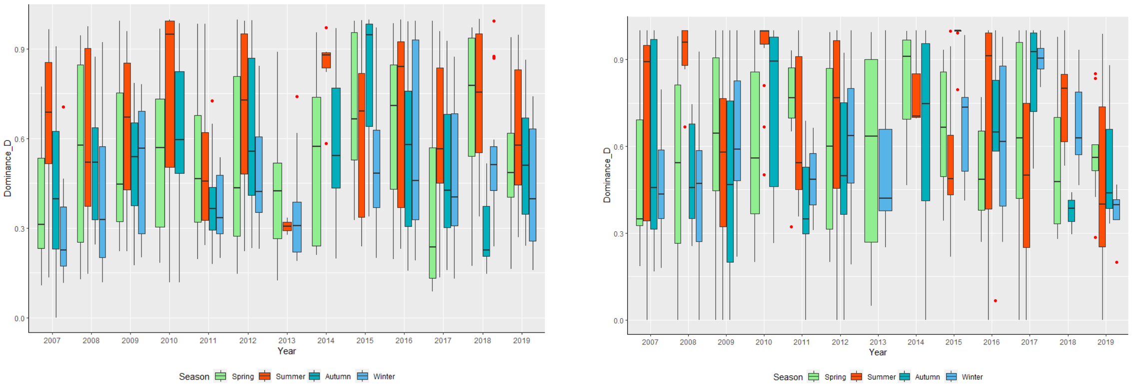
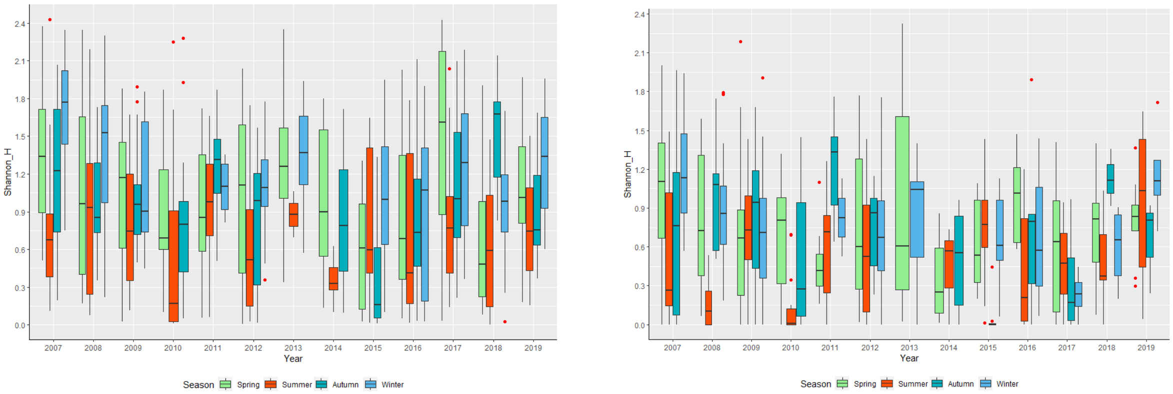
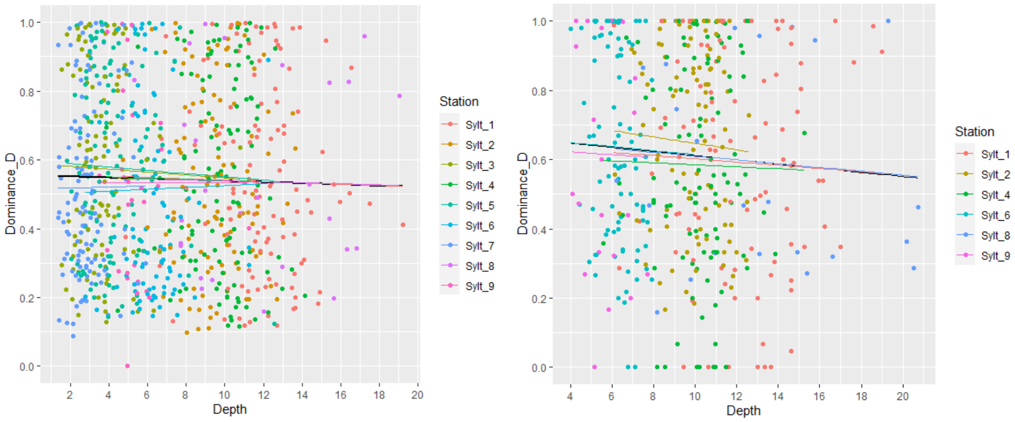


Fig. S3 Inter- and intra-annual variabilities of evenness (J) and dominance (D) in the benthic and pelagic habitats.



(a) benthic (b) Pelagic

Fig. S4 Intra- and inter-annual variabilities in Shannon Wiener Index in the SRB in the benthic (a) and pelagic (b) habitats



(a) benthic (b) pelagic

Fig. S5 Random slope and intercept models showing variations of dominance with water depth at each sampling station in the benthic (a) and pelagic (b) habitats

Supplementary Table 1

Table S1 Seasonal (the entire survey period) comparison of community structures by one-way ANOSIM (R values and significance levels), SIMPER (species' average and cumulative dissimilarity contributions), mean of transformed abundances (group 1 = left, group 2 = right on the Seasons column) and Jaccard's coefficients (see Table 1 for species full names)

Seasons	ANOSIM		SIMPER				Jaccard's coefficient
2007 - 2019	R	p	% average dissimilarity	% dissimilarity contribution		Cumulative % dissimilarity	
Winter vs Spring	0.21	0.0001	58.49	*C. harengus*	23.74	23.74	0.617
				A. tobianus	13.86	37.6	
				S. sprattus	9.772	47.37	
				P. minutus	7.927	55.3	
				S. rostellatus	4.033	59.33	
				M. scorpius	3.547	62.88	
				P. microps	3.416	66.3	
				O. eperlanus	3.028	69.33	
				G. aculeatus	2.97	72.3	
				L. limanda	2.604	74.9	
				M. merlangus	2.125	86.82	
Winter vs Summer	0.63	0.0001	67.54	*C. harengus*	29.42	29.42	0.549
				A. tobianus	17.03	46.44	
				M. merlangus	8.274	54.72	
				S. sprattus	8.237	62.95	
				P_minutus	4.043	67	
				S_rostellatus	3.525	70.52	
				G_aculeatus	3.092	73.61	
				P_microps	2.22	75.83	
				P_platessa	2.213	78.05	
Winter vs Autumn	0.12	0.0001	55.4	*S_sprattus*	9.258	30.96	0.659
				P. minutus	8.176	39.14	
				M. merlangus	7.732	46.87	
				A. tobianus	5.77	52.64	
				S. rostellatus	5.339	57.98	
				G. aculeatus	4.09	62.07	
				P. microps	3.873	65.94	
				M. scorpius	3.733	69.67	
				O. eperlanus	3.017	72.69	
				P. platessa	3.013	75.7	
Spring vs Summer	0.21	0.0001	58.03	*C. harengus*	31.21	31.21	0.788
				A. tobianus	16.59	47.8	
				S. sprattus	9.087	56.89	
				M. merlangus	8.252	65.14	
				P. minutus	4.597	69.74	
				S. rostellatus	3.168	72.9	
				G. aculeatus	2.269	75.17	
				H. lanceolatus	2.239	77.41	
				P. platessa	2.162	79.57	
				G. morhua	1.691	81.27	
Spring vs Autumn	0.13	0.0001	56.71	*C. harengus*	25.13	25.13	0.705
				A. tobianus	12.26	37.39	
				S. sprattus	8.844	46.24	

				P. minutus	7.877	54.11	
				M. merlangus	6.719	60.83	
				S. rostellatus	4.276	65.11	
				L. limanda	2.556	67.67	
				G. aculeatus	2.377	70.04	
				P. platessa	2.293	72.34	
				H. lanceolatus	2.189	74.52	
				P. microps	2.179	76.7	
				G. morhua	2.053	78.76	
				A. cataphractus	2.023	80.78	
Summer vs Autumn	0.28	0.0001	57.14	*C. harengus*	27.74	27.74	0.731
				A. tobianus	17.85	45.59	
				M. merlangus	9.765	55.35	
				S. sprattus	8.772	64.13	
				P. minutus	4.796	68.92	
				S. rostellatus	3.059	71.98	
				P. platessa	2.482	74.46	
				G. morhua	2.356	76.82	
				L. limanda	1.768	78.59	
				H. lanceolatus	1.613	80.2	

CHAPTER 4

Temporal variations of the young-of-the-year fish supply in the Sylt-Rømø Bight, southeastern North Sea

Temporal variations of the young-of-the-year fish supply in the Sylt-Rømø Bight, southeastern North Sea

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To be submitted to Fishes

Abstract

The maintenance of marine fish populations is critically dependent on fish larval supply and recruitment. Coastal zones provide spawning, nursery, and refuge grounds for various fish species that spawn offshore or inshore. In the Sylt-Rømø Bight (SRB), a tidal basin between the islands of Sylt (Germany) and Rømø (Denmark), the fish community has been subject to detailed investigations since 2007. However, the importance of the SRB as a spawning or a nursery ground supplied by the nearby waters has rarely been investigated. Weekly sampling of young-of-the-year (YOY) fish was conducted from 2021 to 2023 to show the area's role for most species. The potential effects of environmental variables sea surface temperature (SST), salinity, chlorophyll *a*, pH, and water depth on the species dynamics were investigated. Seventeen fish species at different earliest developmental stages from the embryo, pre-flexion, flexion, post-flexion, juveniles, and young adults were recorded. Herring (*Clupea harengus*) accounted for 46.9% while Nilsson's pipefish (*Syngnathus rostellatus*) accounted for 44.6 % of the total abundance and dominated the spring and summer seasons, respectively. Redundancy Analysis (RDA) showed a substantial correlation of 40% between the environmental variables and species abundances. However, 60% of the variations were unaccounted for indicating the potential influence of other parameters. The RDA permutation tests retained SST, chlorophyll *a*, salinity, and the factors year and season as significant variables. Water depth and sampling stations were not significant while pH had minor effects. The length frequency distributions of the *C. harengus* and *S. rostellatus* showed the population-level parameters such as somatic growth and cohort structures. These results support the significance of the SRB as an important spawning and nursery ground for commercial and non-commercial fish species, hence, its importance in the conservation and management of marine and coastal fishes.

Keywords:

Ichthyoplankton, fish larvae, nursery habitats, seasonal patterns, Wadden Sea, length frequency distributions

Key contribution:

The Sylt-Rømø Bight (SRB) acts as an important spawning ground for *Syngnathus rostellatus, Clupea harengus, Belone belone, Pomatoschistus minutus, Pomatoschistus microps* and a nursery ground for most species that are recruited at post-larval stages. The SRB provides an important acclimatization area for the critically endangered European eel (*Anguilla anguilla*) at the glass stage *en route* to freshwater habitats. The study showed high seasonal abundance variations and the sensitivity of YOY fish to changes in environmental conditions. The cohort structures of *S. rostellatus* and *C. harengus* showed the presence of individuals spawned within the SRB and those supplied from the surrounding waters as well as the differences in somatic growth and survival at the vulnerable early life stages.

1. Introduction

The maintenance of marine fish populations is critically dependent on the fish larval supply and recruitment [1]. Larval supply is the number of planktonic larvae available at nursery grounds while recruitment is the individuals that survive the larval stage and reach subsequent developmental stages [2]. Young-of-the-year (YOY) fish are the recruited individuals that have not reached one year of age [3]. The eggs and larvae of most marine fish species are planktonic [4] while most species spawning in the coastal zones lay demersal eggs [5] and other species' eggs are attached to hard substrates or macrophytes [6]. Some species show parental care in that fertilized eggs are carried by adult males in a brood pouch on their ventral surface until they leave as independent free-swimming juveniles [7,8]. The duration of planktonic stage is species-specific and lasts for weeks to months. This is particularly important as the planktonic stage plays a significant role in the distribution, dynamics, and recruitment into suitable nursery habitats [9]. The knowledge of spawning seasons and locations of various fish species is an important aspect of fisheries science and management. These locations can be identified by the presence of eggs and larvae in plankton surveys [10,11]. Spawning and recruitment are influenced by different aspects of oceanographic features such as upwelling and tidal mixing, frontal zones, and larval drift towards nursery grounds [2,12].

The planktonic eggs and larvae (ichthyoplankton) drift and disperse by ocean currents over short or long distances and are recruited into nursery habitats within the parent populations or away from the spawning grounds [13]. The physical processes such as changes in water temperature determine the timing of adult migration from cool inshore habitats to warmer offshore overwintering grounds that in turn trigger gonad maturation i.e. the timing of spawning [14,15]. The interaction between the physical and biological oceanic processes governs the larval responses to hydrodynamics and vertical migration by maximizing food intake based on the abundance of copepod nauplii at the same time avoiding predators [2,16]. In addition, the physical and biological processes influence horizontal swimming, growth rates, and planktonic duration [17].

Fish recruitment is the ultimate result of a complex chain of events including spawning, dispersal, drift by currents from spawning to nursery habitats, and surviving the vulnerable larval stage [18,19]. Early life survival is partially dependent on body size as was proposed by the "bigger-is-better" hypothesis, which states that larger species tend to have higher survival chances than small-bodied species that have longer periods in the planktonic stage [20]. The prolonged pelagic period extends their vulnerability to predation and the risk of starvation as they have limited energy in the yolk sac, and restricted swimming and prey-searching abilities [20]. Larger-bodied individuals at hatching are relatively resistant to starvation and have greater flexibility in the first feeding. The feeding success increases growth thereby decreasing mortality due to starvation and predation [21]. Variations in growth and survival rates occur even for larval fish of the same species that are spawned in different geographic locations and seasons [20,22].

The temporal distribution of body size can give vital information on species' survival and life history characteristics [23]. One of the reasons for size variations within populations is the exposure to different environmental conditions [24] as each individual in a cohort experiences a unique environment in its immediate proximity [25]. Temperature influences cohort distributions by altering the timing or onset of the adult reproductive seasons [15,23] and the competitive interactions between individuals through changes in energy demand and rates of size-dependent processes such as survival [26]. Temperature influences recruitment timing and patterns causing differences in cohort structures [27]. Thus, the length frequency distributions can be used to estimate somatic growth [28] and the presence of different cohorts in a population [29].

The Wadden Sea is a transition area between the open North Sea and land that stretches from the Netherlands to Denmark [30]. It offers a large nursery ground for various fish species that spawn offshore or inshore [31]. The YOY fish supply to the Wadden Sea from offshore spawning areas partly depends on the inflow of the North Sea water by currents and tides, which are regulated by several factors such as the morphology of the tidal basins and the prevailing wind conditions [32]. Early life survival of fish is dependent on the availability of suitable feeding grounds [33] with favorable abiotic conditions such as sea surface temperature (SST) and salinity, and biotic interactions such as prey availability and predation [34]. The fluctuating spawning times for most fish species are correlated with variations in water temperature [15] while salinity influences egg buoyancy [32], larval growth, and development [35]. The interactions between abiotic and biotic factors further influence the variations in YOY fish. For instance, low water temperatures lengthen the egg incubation period and cause slow growth rates, thus, longer larval duration [36]. In addition, low water temperatures can cause a mismatch with key prey items such as copepods [37], which is an important food source for YOY fish.

The Sylt- Rømø Bight (SRB) is a tidal basin in the Wadden Sea, southeastern North Sea [38]. The fish community and the seasonal assemblages in the SRB are well known through monthly monitoring that has taken place since 2007 [39,40]. Despite years of research on the significance of the SRB and Wadden Sea in general for fish reproduction e.g Polte et al. 2006 [6] and Ahnelt, et al. 2021[58], there is still little knowledge on which species use the SRB as a spawning ground and/or as a nursery ground. Therefore, weekly YOY fish sampling was initiated from February to October of the years 2021, 2022, and 2023. This was to investigate the YOY fish species in comparison to the documented species from the long-term fish monitoring [39,40] and to investigate the species that spawn in the bight and those that are supplied by the nearby waters.

The spatial and temporal patterns of YOY fish supply and the potential effects of abiotic parameters including water temperature, water depth, salinity, pH, and chlorophyll *a* on species dynamics were investigated. The cohort structures of the dominant YOY fish species were assessed to determine somatic growth and the presence of various cohorts at different times of the year.

2. Materials and Methods

2.1. Study area

The Sylt-Rømø Bight (SRB) (central coordinates; 54°58’40” N, 8°29’45” E) is a coastal tidal basin in the northern Wadden Sea located between the islands of Sylt (Germany) and Rømø, (Denmark) and the mainland coasts [38]. It is bound by two causeways that prevent water exchange with the adjacent tidal habitats in the northern and southern parts but connected to the North Sea by a 2.8 km wide channel between the two islands, the Lister Tief (Fig. 1). The bight covers a total area of 404 km^2, which includes an intertidal area of about 135 km^2. The mean tidal range is about 2 m and the mean depth is approximately 4.2 m at high tide [41]. In each tidal cycle, between 8 to 12% of the entire tidal water of the bight is exchanged with the North Sea through the Lister Tief (Fig. 1) and the residence time of the water within the bight is between 19 to 29 days [41]. The SRB is covered by different intertidal and subtidal habitats such as seagrass meadows, mussel beds, bivalve beds, and sand and soft bottom substrates of different grain sizes such as sandflats and mudflats [42].

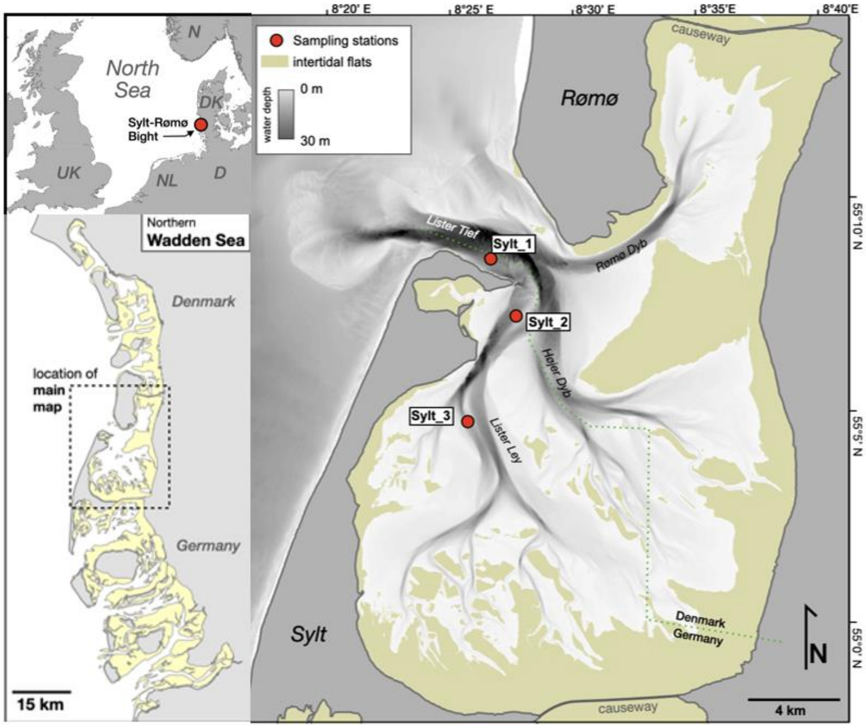


Figure 1. Map of the study area on the eastern seaboard of the North Sea (top left); N = Norway, DK = Denmark, D = Germany, and NL = The Netherlands) and the northern Wadden Sea (bottom left). The main map shows the subtidal and intertidal flats, variations in water depth, and sampling locations. Map layout by authors based on own data and additional bathymetric data from BSH [43]

2.2 YOY fish sampling

Sampling took place weekly from 10:00 am irrespective of the tide conditions from March 2021 to October 2023 at three stations along the main tidal channels of Lister Tief (Sylt_1), at the beginning of Lister Ley (Sylt_2), and towards the end of Lister Ley in the south (Sylt_3) (Fig. 1). Sampling was done using a Bongo frame equipped with nets of mesh sizes 300 µm and 500 µm, each with a mouth-opening diameter of 0.6 m and 2.5 m length. The mesh sizes ensure maximum sampling effort most of the newly hatched fish larvae are more than 2000 µm in length. Besides, the mesh sizes ensure maximum filtration efficiency by reducing clogging of nets by plankton and detritus [11]. The Bongo frame was centrally fitted with an 18 kg V-Fin depressor, which creates a negative lift and ensures sampling at one-third of the total water depth [33]. At the center of each Bongo net opening, a mechanical Flow Meter model HYDRO-BIOS 438 110 was mounted to measure the volume of filtered water [44]. Samples were collected by launching two horizontal hauls of the Bongo net at one-third of the water depth [33] per sampling station for 15 minutes from a research vessel Mya II belonging to Alfred-Wegener-Institut (AWI) [45]. The ship's mean average towing speed was 1.3 m/s and the direction during each haul was always opposite the direction of tide flow for efficiency. Respective sensors mounted on the ferry box on board the research vessel measured environmental parameters including pH, sea surface temperature (SST), and salinity for each haul. The ship’s navigational echo sounder measured water depth at the start and the end of each haul. The contents of each net per haul were gently flushed into marked sampling jars and seawater was added to avoid shrinkage until transfer to the laboratory.

The months of May were hardly sampled in all the years as the research vessel Mya II was in the yard for annual routine maintenance. In May 2021, we sampled using a tourist ship, Gret Palucca, and in May 2022 with the research vessel Uthörn belonging to the AWI. In all the trials, no fish samples were caught. Mya II was used to sample the first two weeks of May 2023.

2.3 Laboratory preservation and taxonomic identification

In the laboratory, organisms within samples were euthanized by adding clove oil into the jar containing samples. Ideally, 0.5 ml clove oil was added to 1 L sample volume then organisms were left in the solution for 10 minutes. Using a stereo microscope, fish samples were sorted based on the differences in morphological and meristic characteristics and then identified to the lowest possible taxonomic level following the description and identification keys in Camphuysen et al. 2017 [46], Munk et al. 2005 [7], and Rodríguez et al. 2017 [47]. The total lengths (TL) (tip of the snout to the edge of the fin fold in the pre-flexion larvae and the tip of the caudal fin in other developmental stages) of each specimen were measured. The developmental stages of the samples were determined based on the descriptions in the identification keys in Munk et al. 2005 [7]. In the first sampling year, after identification, samples were transferred into smaller jars containing seawater. Inside a fume hood, samples were fixed by adding an equal volume of 10 % formalin solution buffered by seawater so that the resultant sample volume in the jars had a concentration of 5 % formalin [11]. Samples were exposed to this concentration for 24 hours. Subsequently, samples were sieved and then a series of ethanol concentrations were added, firstly 30% for six hours, 50% for 24 hours, 70% for 24 hours, and lastly 70% for long-term preservation. In 2022 and 2023, after laboratory identification samples were frozen at -20 °C for long-term preservation.

Nilsson's pipefish (*Syngnathus rostellatus* Nilsson, 1855) has specialized parental care where females transfer the eggs to the brooding pouch in males for fertilization and brooding until they leave as free independent individuals [48]. Occasionally, we found male adults with developing embryos and larvae in their brood pouches. The larvae were extracted and counted but not included in the analysis since the adults were not targeted by the sampling method.

2.4 Statistical analyses

Fish density per Bongo net haul was obtained by the quotient of abundances and the volume of the filtered water then standardized to individuals per 100 m^3. The weekly time series of dominant species were determined by aggregating the mean abundances of sampling stations (Sylt_1 to Sylt_3). For trends and determination of environmental conditions during the survey period, data from the bi-weekly long-term monitoring of the hydro-chemical parameters in the Sylt Roads Long Term Ecological Research (Sylt Roads LTER) time series [45,49] were used.

Since the YOY fish abundance data were not normally distributed, non-parametric Kruskal-Wallis test was used to test the significance differences between sampling stations, seasons, and years after which the Dunn test was used for post hoc comparisons. For the seasonal comparisons, the weekly fish abundances and environmental parameters data were aggregated into four seasons, winter (December, January, and February), spring (March, April, and May), summer (June, July, and August), and autumn (September, October, and November).

Redundancy analysis (RDA), a form of constrained ordination [50] was performed on Hellinger-transformed fish abundances to determine the potential effects of water temperature, salinity, water depth, chlorophyll a, and pH on the fish community. Additionally, the nominal variables season and year were included in the RDA to determine the seasonal and annual patterns of species occurrences. The environmental data used in RDA analyses were measured in the field during sampling except for the mean weekly chlorophyll *a* data, which was obtained from Sylt Roads LTER. Mean depth in meters (m) was obtained by averaging depth at the start and the end of each haul. Hellinger transformation gives low weights to species with low counts and many zeros [51] while the environmental data were scale transformed. Type II scaling in the RDA was used to determine the correlative relationships between fish abundances and explanatory variables. The ordination results were visualized in a correlation triplot. Stepwise forward selection and permutation tests (999 permutations) were used to select the environmental variables that best explained the variations and their significance [50]. Variance partitioning of the significant explanatory variables was performed to determine how much variation in the community was attributable to each parameter.

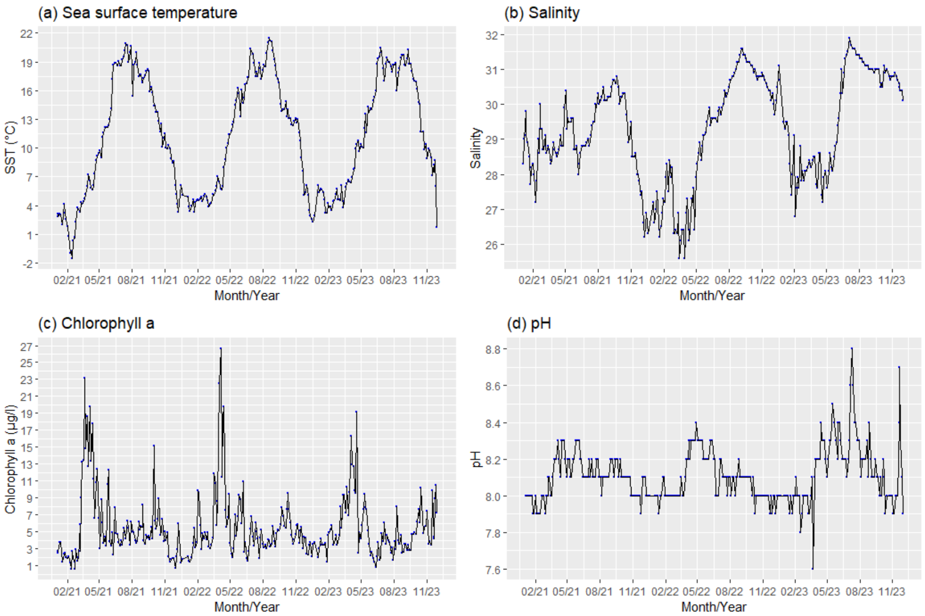
The monthly length frequency distribution of the dominant species per year was determined by the ggridges package in R [52] where the density estimates of length classes were plotted against time using ridgelines. This was to visualize the density distributions over time that can be used to infer growth and survival. Statistical significance was assumed for all tests if the p-value was below 0.05. Statistical analyses were calculated using the Software R version 4.2.3 [53].

3. Results

3.1 Seasonal patterns of environmental parameters

The annual and seasonal patterns of environmental parameters, sea surface temperature (SST), salinity, chlorophyll a, and pH are shown in Fig. 2. The lowest SST was recorded during the winter of 2021 at -1.5 °C while 2022 and 2023 recorded the lowest SSTs of 0.9 °C and 2.3 °C, respectively. Maximum summer SSTs ranged from 20.5 °C to 21.5 °C. There were significant differences in the mean seasonal SST across seasons (Kruskal-Wallis, H3 = 230, $p < 0.001$, Dunn`s test $p < 0.001$). Salinity ranged from 25 to 32, the low values were recorded in winter and highs in summer. There were significant differences in the mean annual salinity between 2021 and 2023 (Kruskal-Wallis, H2 = 12.9, p =0.001, Dunn's test, p <0.001) and across all seasons except between summer and autumn and between winter and spring.

Chlorophyll peaks around late March/early April when the spring bloom occurs followed by a gradual decrease to September/October when the autumn bloom occurs (Fig. 2). There were significant differences between all seasonal comparisons except between winter and summer (Dunn's test, $p > 0.05$). The pH ranged from 7.6 to 8.8 (Fig. 2). Significant differences in the mean annual pH occurred between 2022 and 2023 (Kruskal-Wallis, H2 = 6.68, p =0.035, Dunn`s test p= 0.032) and across seasons except between spring and summer.


(a) Sea surface temperature

(b) Salinity

(c) Chlorophyll a

(d) pH

Figure 2. Annual and seasonal patterns of environmental parameters; (a) sea surface temperature (SST), (b) salinity, (c) chlorophyll *a*, and (d) pH in the SRB during the study period

3.2 Spatial variations in water depth

Sampling took place at a fixed time of the day irrespective of the tide conditions and the tidal range in the SRB is 2 m. Besides, sampling transects varied within the sampling stations, as it was difficult to maintain the same transect due to strong water currents, wind direction, and wind velocity, thus, there were variations in water depth (Fig. 3). Higher variations in water depth occurred in Sylt_1 and Sylt_2, which were relatively deeper than Sylt_3 (Fig. 3).

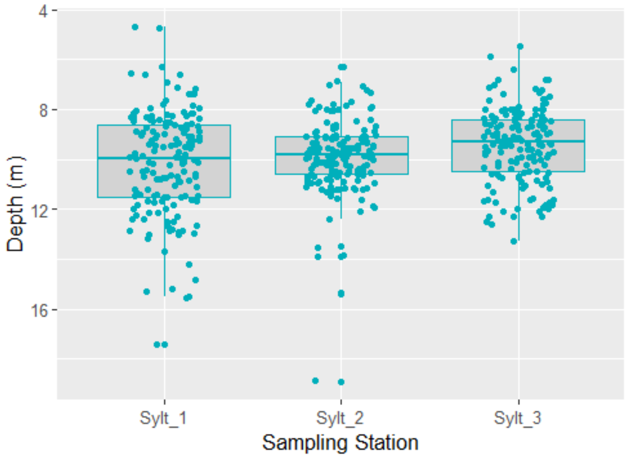


Figure 3. Variations in water depth per sampling station during the study period. Each box and point represents all the measurements in all three sampled years. Note the reversed Y-axis

3.3 The young-of-the-year fish

During the three years (2021 – 2023), 483 samples that contained 7203 YOY fish of 17 species belonging to 15 families (Table 1) were collected at the three sampling stations. The species were sampled at different developmental stages that included pre-flexion, flexion, post-flexion, juveniles, and two species as young adults (see Table 1). The abundances per stage varied per species. The larvae extracted from the brood pouches of *S. rostellatus* adult males (Fig. 4) were counted under a stereo microscope. The larvae from 12 male adults ranged from 59 to 78 individuals (Fig. 4), the higher numbers were found in bigger adults with longer lengths. All specimens sampled and described here were the released juveniles that were at the beginning of the free-swimming phases. Herring (*Clupea harengus* Linnaeus, 1758) was the only species sampled from the pre-flexion stage to juveniles with total lengths ranging from 10 mm to 60 mm. The pre-flexion stage was rare as post-flexion and juvenile stages were dominant. Three other species were sampled at the post-flexion and one post-leptocephalus stages. Eight species were exclusively at juvenile stages and two species as young adults were occasionally sampled (see Table 1). On any sampling day, some species were present in more than one developmental stage (Table 1) and collectively referred to as young-of-the-year (YOY) in the following sections.

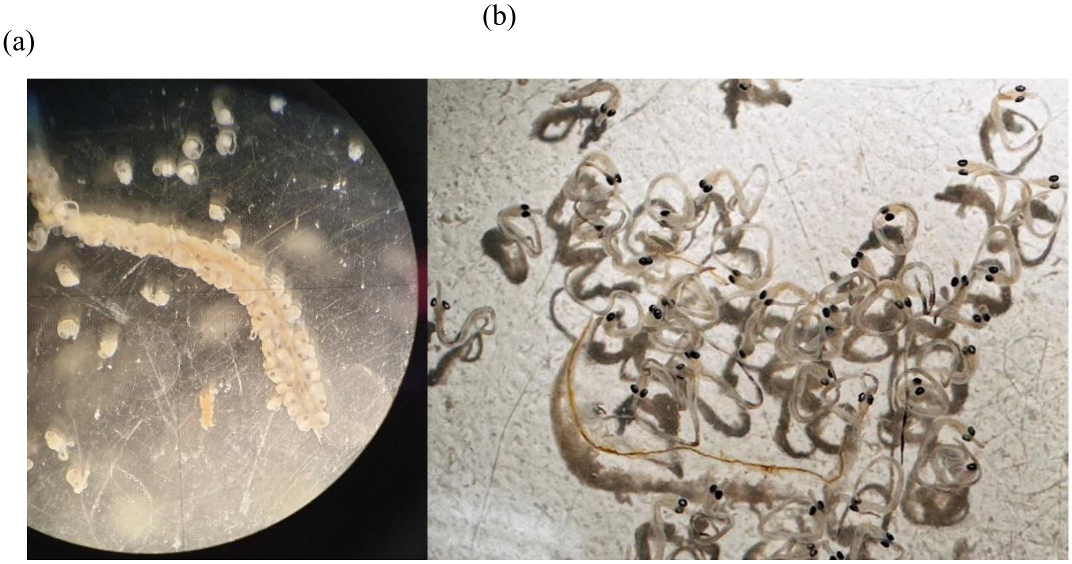


Figure 4. (a) Developing embryos and (b) larvae extracted from the brood pouch of *S. rostellatus* male adults. Photo by V. Odongo

Clupea harengus accounted for 46.9% of the total abundance and was present at the beginning of each sampling year (February/March) reaching peak abundances in spring that gradually declined to early summer. It had low abundances in late summer to early autumn but this trend was inconsistent (Fig. 5). There were significant differences in the annual mean abundances between 2021 and 2023 (Kruskal-Wallis, H2 = 5.8, p =0.055, Dunn's test, p =0.019). Similarly, there were significant differences in seasonal mean abundances between spring and summer and between spring and autumn (Dunn's test, $p < 0.001$). *Syngnathus rostellatus* juveniles with lengths ranging from 10 mm to 50 mm accounted for 44.6% of the total abundance. They were dominant in summer and autumn (Fig. 5). The abundances gradually declined towards the end of the year with no occurrence between February and June (Fig. 5). There were significant differences in the mean annual abundances between 2021 and the other years (Kruskal-Wallis, $H2 = 8.74$, $p =0.012$, Dunn's test, $p < 0.05$) and across mean seasonal abundances (Kruskal-Wallis, $H3 = 249$, $p < 0.001$, Dunn's test, $p < 0.0001$) except between winter and spring (Dunn's test, $p > 0.05$).

Plaice (*Pleuronectes platessa* Linnaeus*,* 1758) with lengths ranging from 8 mm to 55 mm was the only flatfish species that was present in the spring and summer of the sampled years (Fig. 5). Most of the *P. platessa* individuals were already metamorphosed and accounted for 3.5% of the total abundance. There were significant differences in the annual mean abundances between the years 2022 and 2023 (Kruskal-Wallis, $H2 = 7.07$, $p =0.0291$, Dunn's test, $p =0.023$). Seasonally, significant differences occurred between spring and autumn, and between summer and autumn (Dunn's test, $p < 0.05$). Smelt (*Osmerus eperlanus* Linnaeus, 1758) with lengths ranging from 10 mm to 45 mm was occasionally present in the sampling years with high occurrences in spring (Fig. 5) and accounted for 3% of the total abundance. The annual mean abundances significantly differed between 2021 and the other years (Dunn's test, $p < 0.05$). There were significant differences in the seasonal mean abundances between spring and autumn and between summer and autumn (Dunn's test, $p < 0.05$).

Sand goby (*Pomatoschistus minutus* Pallas, 1770) was occasionally present in the sampling years (Fig. 5) and accounted for 1.6% of the total abundance. Lesser sandeel (*Ammodytes tobianus* Linnaeus, 1758*)* with lengths ranging from 15 mm to 85 mm was present in the springs of all sampled years but with very low abundances to estimate annual patterns. The European eel (*Anguilla anguilla* Linnaeus*,* 1758) at the post-leptocephalus and juvenile (glass eel) with lengths ranging from 35 mm to 100 mm was present at low abundances in February 2022 and spring of

2022 and 2023. *Ammodytes tobianus* and *A. anguilla* abundances were summed up and plotted as low abundance (Fig. 5).

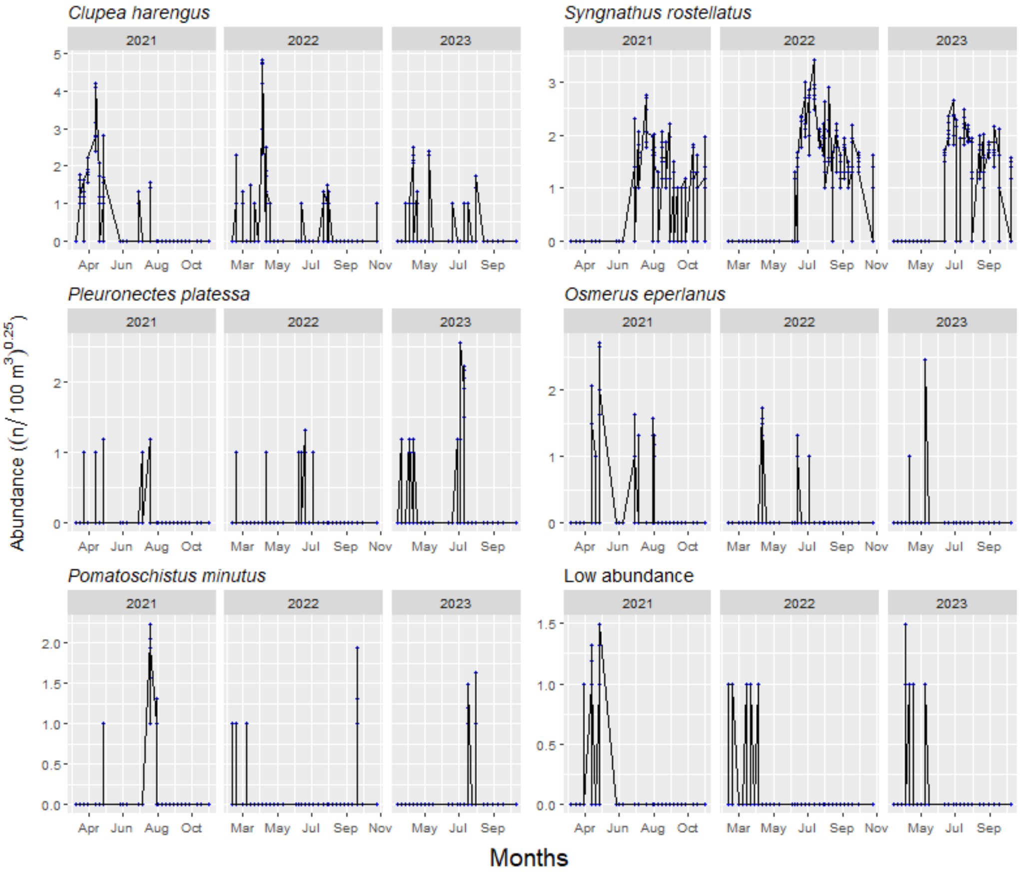


Figure 5. Time series of square-root transformed abundances of the dominant fish species and those that had low abundances (*A. tobianus* and *A. anguilla*) during the study period. These are the sum of the abundance of all developmental stages per sampling day

Table 6. The list of young-of-the-year (YOY) fish species belonging to 15 families and two young adult species that were sampled in the SRB during the study period. Common names and developmental stages in which the species were present are shown. For *Anguilla anguilla,* the earliest developmental stage was post-leptocephalus. ✓indicates presence and blank indicates absence. Species code is used as a reference for RDA triplot in section 3.4

Common name	**Family**	**Scientific name**	**Species code**	**Developmental stages**					
				Embryo	**Pre-flexion**	**Flexion**	**Post-flexion**	**Juvenile**	**Young adult**
Nilsson's pipefish	Syngnathidae	*Syngnathus rostellatus*	S_ros	✓				✓	
Herring	Clupeidae	*Clupea harengus*	C_har		✓	✓	✓	✓	
Sprat	Clupeidae	*Sprattus sprattus*	S_Spr				✓	✓	
Smelt	Osmeridae	*Osmerus eperlanus*	O_epe				✓	✓	
Plaice	Pleuronectidae	*Pleuronectes platessa*	P_pla				✓	✓	
Hooknose	Agonidae	*Agonus cataphractus*	A_cat					✓	
Lesser sandeel	Ammodytidae	*Ammodytes tobianus*	A_tob					✓	
Garfish	Belonidae	*Belone belone*	B_bel				✓		
Bull-rout	Cottidae	*Myoxocephalus scorpius*	M_sco					✓	
Lumpfish	Cyclopteridae	*Cyclopterus lumpus*	C_lum					✓	
Whiting	Gadidae	*Merlangius merlangus*	M_mer					✓	
Common goby	Gobiidae	*Pomatoschistus microps*	P_mic					✓	
Sand goby	Gobiidae	*Pomatoschistus minutus*	P_min					✓	
Horse mackerel	Carangidae	*Trachurus trachurus*	T_tra					✓	
European eel	Anguilidae	*Anguilla anguilla*	A_ang				✓	✓	
Three-spined stickleback	Gasterosteidae	*Gasterosteus aculeatus*	G_acu						✓
River lamprey	Petromyzontidae	*Lampetra fluviatilis*	L_flu						✓

Other species in Table 1 and not described above had very low frequency of occurrences with abundances ranging from four individuals to 10 for the entire monitoring period, thus, classified as rare species. These included lumpfish (*Cyclopterus lumpus* Linnaeus, 1758), whiting (*Merlangius merlangus* Linnaeus, 1758), and hooknose (*Agonus cataphractus* Linnaeus, 1758), all were present in spring 2021. Bull-rout (*Myoxocephalus scorpius* Linnaeus, 1758) was present in spring and summer 2021. Sprat (*Sprattus sprattus* Linnaeus, 1758) was present in spring 2021 and 2022 while garfish (*Belone belone* Linnaeus, 1761) was present in summer 2021 and 2023. The common goby (*Pomatoschistus microps* Krøyer, 1838) was present in winter 2022. Horse mackerel (*Trachurus trachurus* Linnaeus, 1758) was present during all summers. Young adults of three-spined stickleback (*Gasterosteus aculeatus* Linnaeus, 1758) were occasionally sampled in February and spring 2022, and 2023, and River lamprey (*Lampetra fluviatilis* Linnaeus, 1758) in February 2022.

3.4 Potential effects of environmental parameters

The RDA model with the explanatory variables SST, salinity, chlorophyll *a*, pH, water depth, sampling station, and the ordinal variables year and season was significant and were correlated to 43% (constrained) of the variations in the YOY fish community. The longer arrows for spring and summer seasons, SST, salinity, and chlorophyll showed that these variables were important for the community dynamics. Water depth and sampling station that are co-variates had no significant influence while pH had minor effects (shorter arrow). The rest of the variations at 57 % were non-redundant (unconstrained) with the environmental variables applied on the RDA. RDA1, the main axis significantly explained 36.3 % of the variations while RDA2 explained 5.2% of the additional orthogonal variations (Fig. 6). These percentages represent the species-environmental relationships summarized in the ordination triplot (Fig. 6). The environment variables SST and salinity were negatively correlated to chlorophyll *a* and pH. All these variables were positively correlated to RDA1 and explained the largest proportion of variations. The seasonal patterns were observed as chlorophyll *a* was positively correlated to spring season while high salinity and SST occurred in summer (Fig. 6). The winter season was not represented as only February of 2022 was sampled, similarly, the autumn season is not captured in the RDA triplot because only *S. rostellatus* was present in autumn but in low abundances compared to the summer.

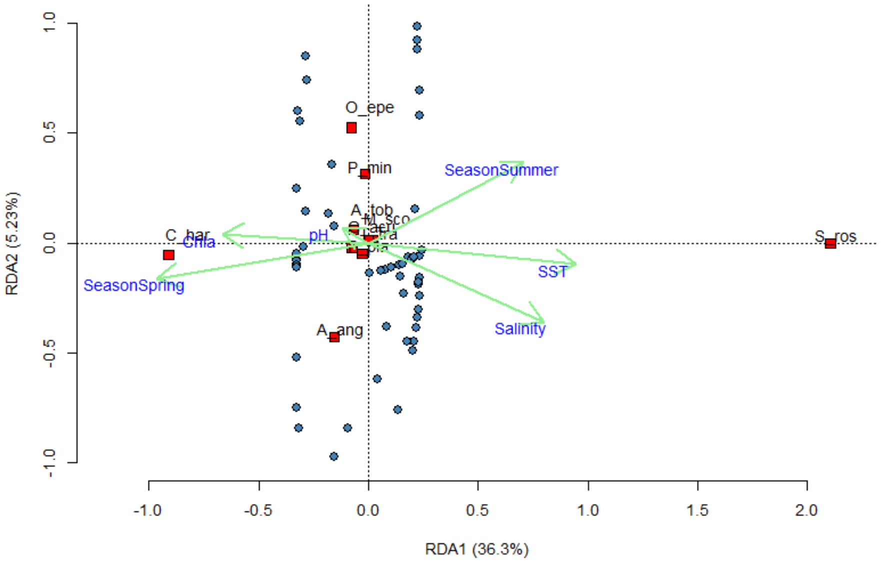


Figure 6. RDA correlation triplot for the fish species (sum of abundances of all developmental stages per sampling day) and environmental variables, and the variations explained by the RDA axes. See Table 1 for species names

Species are scaled proportional to the eigenvalues in the RDA triplot and depict the correlations of YOY fish to the environmental variables. For instance, *C. harengus* was positively correlated to spring season and high chlorophyll *a* concentration while *S. rostellatus* was positively correlated to summer season, salinity, and SST in RDA1. The ordinations of *O. eperlanus, P. minutus,* and *A. tobianus* show that they are more abundant in early summer while *A. anguilla* in winter and early spring in RDA2 (Fig. 6). In RDA scaling II that was applied, angles between variables reflect their linear correlations, which is equal to the cosine of the angle. Thus, *C. harengus* and *S. rostellatus* on RDA1 were not correlated with the other species in RDA2, which are at right angles since cos(90) = 0. *Pleuronectes platessa, T. trachurus,* and *M. scorpius* had low scores on both RDA1 and RDA2 axes (close ordinations at the center of the RDA triplot). Thus, weaker correlations to the environmental parameters. The rare species comprising *M. merlangus*, *P. microps, C. lumpus, B. belone, A. cataphractus, S. sprattus,* and *L. fluviatilis* were not included in the RDA.

Variance partitioning revealed that the factor year explained 2% ($p < 0.05$) while the seasonal changes of environmental parameters jointly explained 42% ($p < 0.05$) of the YOY fish variations (Fig. 7, a). The exclusion of nominal variables in second RDA showed that SST explained 7% ($p < 0.05$), salinity 2% ($p < 0.05$), and chlorophyll *a* 5% ($p < 0.05$) of the variations. The interactions of these parameters explained higher variations (Fig. 7, b). However, more than half of the variations (61%) were not explained by the environmental parameters that were included in the RDA model (Residuals = 0.61) (Fig. 7, b).

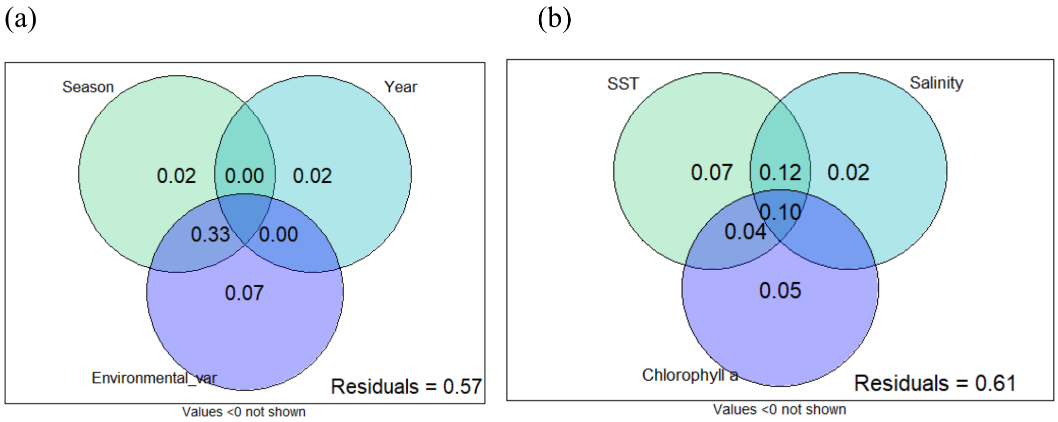


Figure 7. Venn diagrams of variance partitioning of explanatory variables with respective percentage contributions to the variations. (a) The ordinal variables year and season plus the combined effects of the seasonal variations of SST, salinity, and chlorophyll *a* as

Environmental_var. (b) The percentage contributions of SST, chlorophyll a, and salinity. The residuals represent the unexplained variations

3.5 Length frequency distribution of dominant species

The length frequency distribution of two dominant species *S. rostellatus* and *C. harengus* was determined to infer somatic growth and the presence of different cohorts. The newly released *S. rostellatus* juveniles were sampled from June in all the years. The minimal length was 10 mm although rare as 15 mm was the most observed minimal length. The maximum length in June was about 40 mm, although with low abundance proportions (Fig. 8) but showed that the release of juveniles starts earlier. The gradual increase in size with time was observed as the abundance proportion of smaller individuals decreased in the latter months while the proportion of larger individuals increased (Fig. 8). Besides, the right-shifting mid-points of lengths in Fig. 8 show somatic growth. The distribution pattern showed that only one cohort spread over several months within the season spawned in the SRB as the lower numbers of smaller larvae were sampled in the later months and varied across the years. For instance, in 2021, there were no larvae smaller than 20 mm that were sampled in October and November but they were present in the other years. This resulted in the bi-modal distribution pattern in October 2022 and 2023, which may be assumed as the presence of two cohorts (Fig. 8).

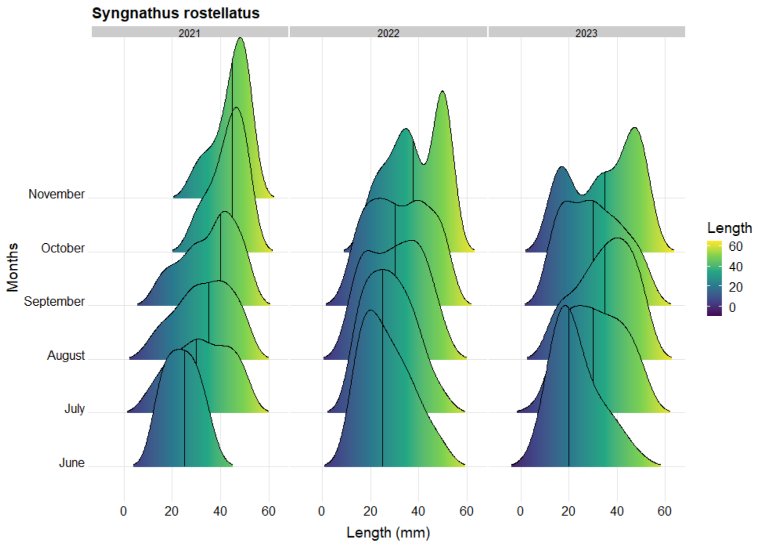


Figure 8. Length frequency distribution of the total monthly (sum of weekly abundances in all sampling stations) abundance of *S. rostellatus* in the sampled years. The x-axis is the length (mm) and the y-axis is the sampled months. The thin vertical dark line on the x-axis represents the mid-point of lengths

Clupea harengus showed a bimodal distribution pattern at the beginning of all the sampled years indicating the presence of larvae and juveniles from two cohorts. February 2021 was not sampled since the sea was frozen and February 2023 was due to technical reasons. In February 2022, *C. harengus* larvae and juveniles spawned in autumn 2021 with total lengths of more than 30 mm were the dominant cohort while the spring-spawned cohort with mean lengths of 10 mm had low abundance (Fig. 9). In March 2021 and 2022, the abundance of spring-spawned cohorts with median lengths of 10 mm was had high abundance than the autumn-spawned cohorts with median lengths of 30 mm. In March 2023, both cohorts had equal abundance proportions with a clear length difference of those less than 20 mm and those with lengths between 30 mm and 50 mm (Fig. 9). In April of all the sampled years, only one cohort was present in the community. The larval growth was observed in May 2023 and June 2021 shown by the right-shifting midpoints of lengths (Fig. 9). In July and August, only the spring-spawned cohort was sampled although with inconsistent occurrences over the years.

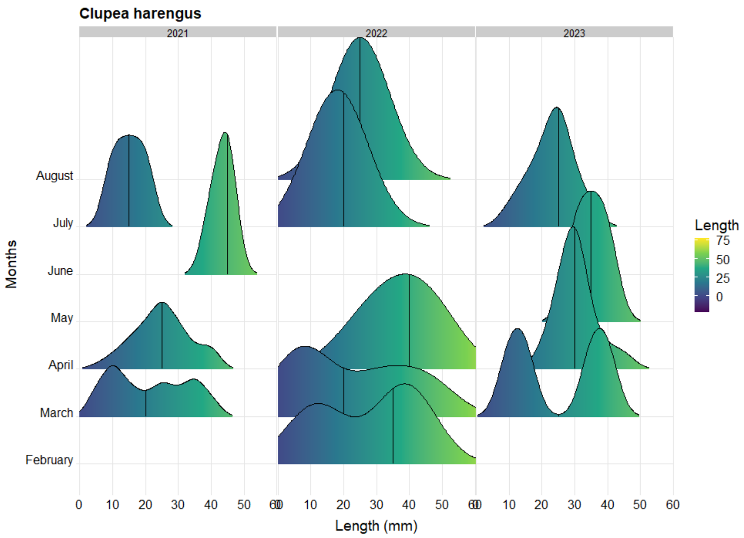


Figure 9. Length frequency distribution of the total monthly (sum of weekly abundance in all sampling stations) catch of *C. harengus* in the sampled years. The x-axis is the length (mm) and the y-axis is the sampled months. The thin vertical dark line on the x-axis represents the midpoint of lengths

4. Discussion

4.1 Young-of-the-year fish and the seasonal patterns

This study investigated annual and seasonal patterns of young-of-the-year (YOY) fish and the potential effects of environmental parameters on community dynamics in a temperate tidal lagoon. The study aimed to assess which fish species use the area as a spawning and/or a nursery ground. Seventeen species were found at different early developmental stages from embryos to young adults. *Clupea harengus* and *S. rostellatus* were the dominant species in spring and summer, respectively, and collectively accounted for 91.5% of the total abundance. Their abundances were followed by *O. eperlanus* (3.5%)*, P. platessa* (2%)*, P. minutus* (1.6%)*, A. anguilla,* and *A. tobianus* in decreasing order. In Odongo et al. 2024 [40], 55 fish species including juveniles and adults were recorded in the SRB. In the documented species from the monthly fish monitoring, *C. harengus* accounted for 67.6 % of the total abundance for the entire survey followed by *A. tobianus* (14.6 %), *S. sprattus* (5.8 %), *M. merlangus* (4 %), *P. minutus* (3 %)*, S. rostellatus* (1 %), and *P. platessa* (0.6 %) [Odongo et al. in review]. The seventeen species in this study were present in the 55 fish species previously recorded [40]. The differences in species abundance proportions between the two studies show that some species especially those spawning in the area are more abundant at early stages than those supplied from the adjacent waters. However, the abundance proportions change with the influx of juveniles of various species at different times of the year and use the area for nursery purposes.

The presence of a species at different developmental stages in an area can give information on spawning time and location. The individuals spawned in or around the studied location occur at the earliest stages at the beginning of the spawning seasons but this depends on whether the eggs are pelagic or demersal. *Clupea harengus* is a benthic spawner that attaches their eggs to substrates and macrophytes [7]. The presence at the pre-flexion stage indicates that these species spawn in the SRB. Polte et al., 2006 [6] found eggs of *C. harengus* attached to seagrass (*Zostera noltii*) and brown algae (*Fucus vesiculosus*) in the SRB. The low abundance at pre-flexion stages may indicate a low abundance of the spawning populations. Besides, the larvae are active swimmers [54] and may resist outgoing currents and remain in shallow nursery habitats that were not sampled in this study. The presence of adult males of *S. rostelattus* with larvae in brood pouches indicates its residency and spawning in the bight. *Syngnathus rostellatus* abundance has increased in the SRB

[40], which may be partially supported by the extra habitats provided by the brown algae (*Fucus vesiculosus*) and introduced Japanese seaweed (*Sargassum muticum*) [56].

The presence of *B. belone* at the post-flexion stage indicates that spawning may take place within the SRB or nearby waters. The species uses the intertidal seagrass meadows and *F. vesiculosus* habitats in the SRB as spawning grounds [6]. However, the species is rare in fish monitoring catches [40], probably because of very high swimming speeds and the capability to avoid sampling nets. Since *P. minutus* and *P. microps* spawn in the intertidal zones [57], we did not find the early life stages in our samples. High juvenile abundances of these species were caught mostly after strong winds that may have drifted them to the subtidal zones. Some species that were reported to spawn in the SRB but we did not find in this study include the marine ecomorph of *G. aculeatus* [6,58], *A. tobianus,* sand smelt (*Atherina presbyter*), European flounder (*Platichthys flesus*), European anchovy (*Engraulis encrasicolus*) [59]. This may be because of sampling only the deep tidal channels. Perhaps more species could be found at early developmental stages by sampling the intertidal and subtidal areas using different techniques at different depths.

Pleuronectes platessa is among the most abundant flatfishes in the SRB [40], however, we only found individuals at the post-flexion and juvenile stages. There was no evidence of spawning in the SRB but the presence of individuals at the post-flexion stage shows a faster drift of planktonic eggs from the nearby spawning grounds. The spawning locations of *P. platessa* are concentrated in the Southern Bight, English Channel, south of Dogger Bank [60,61], and the German Bight [7] which supplies the larvae to the Wadden Sea nursery grounds. *Pleuronectes platessa* larvae change from pelagic to demersal feeders upon arrival in tidal flats in the Wadden Sea thereby avoiding being swirled up by tidal currents and dispersed elsewhere [33]. This partly explains the low abundances (Fig. 4) as we sampled only the water column. Moreover, the low abundance could be correlated to the increasing water temperatures in the Wadden Sea, which has influenced the nursery functions for flatfishes [62].

The presence of *S. sprattus* individuals at the post-flexion indicates a supply from the coastal spawning locations. It is one of the most abundant pelagic fish species in the southeastern North Sea with serial/batch spawning strategies. It forms large shoals with large temporal and spatial variations [46], which may explain the low supply during the study period as the adults also show inter-annual abundance fluctuations [40]. Bils et al. 2012 [63] found larvae in the stratified and saline areas in the German Bight at salinities of more than 33 which may additionally explain the low occurrence in the SRB as salinities are much lower in winter and spring. *Osmerus eperlanus* is an anadromous species [7]. The presence of individuals with lengths ranging from 5 mm to 45 mm shows its high salinity tolerance range and the significance of the nearby rivers as important spawning locations. This study showed the significance of the SRB as an acclimatization area for *A. anguilla, a* catadromous species that spawns in the southern Sargasso Sea. The leptocephalus larvae migrate to Europe [7] where they metamorphose to a post-leptocephalus stage. The unpigmented juvenile “glass-eel” then migrates to coastal waters [46] such as the SRB before transiting to freshwater habitats. The absence of YOY fish of most documented species indicates that they reach the nursery grounds as juveniles. Furthermore, the spatial and temporal variations in meteorological conditions affect the hydrodynamic circulations in the North Sea and consequently, the drift duration and mixing of fish eggs and larvae from various spawning grounds [64]. This may explain why higher numbers of larval species (42) were recorded in a similar survey in Helgoland in the open North Sea [65].

4.2 Potential effects of environmental parameters

Fish species can be divided into two thermal groups based on their spawning seasons. Those that spawn in cool months (winter-spring) and those that spawn during warm months (summer-autumn) [14]. Water temperature influences the timing of annual adult winter migrations from cool, shallow inshore waters to warmer, deeper offshore spawning grounds, triggering the start and rates of gonad development [15]. This influences the onset of YOY supply and seasonal occurrences that we observed (Fig. 6, a). Chermahini et al. 2021 [66] also observed seasonal abundance fluctuations and assemblages. The YOY fish exhibit higher physiological responses to environmental conditions in comparison to adults due to the high surface area-to-volume ratio [20]. The environmental conditions in the study area change seasonally [49], which may potentially influence the YOY survival and recruitment.

Water temperature influences larval conditions such as length at hatching, the amount of endogenous resources before the first exogenous feeding, swimming behavior, growth rates, larval duration, dispersal distance, and size at recruitment [34]. The positive correlations between *S. rostellatus* and temperature are related to its summer spawning strategy and higher survival rates of the juveniles in warm temperatures. The negative correlation between *C. harengus* and temperature is related to the spring and autumn spawning strategies when temperatures are relatively low compared to summer (Fig. 5). This indicates that the majority of *C. harengus* individuals arrive in the SRB as juveniles in early spring and summer resulting into a positive correlation with temperature as reported in Odongo et al. 2024 [40].

The low explanatory power of salinity to the community dynamics (Fig. 7) may be attributed to most fish species having wide salinity tolerance [67,68]. Salinity was within the tolerance range (26 to 32) of most species during the study. Even in the Persian Gulf, salinity ranged from 27 to 42 and had no significant effects on the larval community [66]. Nevertheless, salinity effects on egg fertilization, egg buoyancy, yolk sac resorption, swim bladder inflation, and fish larval growth have been reported [35], especially in high salinity gradient zones such as the Baltic Sea [35,69]. Similarly, in the Gulf of Alaska where different water masses and riverine runoff influence salinity, fish species distinctively showed positive and negative correlations with salinity [70]. Therefore, the low explanatory power in our study may be attributed to YOY fishes that have enough energy to withstand the salinity fluctuations [35]. However, further investigations would answer its effects on specific species at different life stages in the SRB.

Chlorophyll *a* is a key driver of zooplankton and ichthyoplankton dynamics [71] and its concentration is related to grazer-phytoplankton interactions [72]. Therefore, the strong positive correlations between chlorophyll *a* and *C. harengus* (Fig. 5) may be because the spring bloom occurs when copepod populations are still low. It may also mean a top-down control as *C. harengus* predominantly preys on copepods [73]. Chermahini et al. 2021 [65] reported a negative correlation between chlorophyll *a* and most fish species in the northern Persian Gulf. These different correlations may be because of the differences in productivity and timing in different regions. Water depth was not significantly correlated to the YOY community in this study as we targeted the horizontal distribution rather than the vertical distribution. However, water depth influence the vertical distribution of YOY fish. For instance, Maathuis et al. 2023 [55] found the highest fish densities at depths between 7 and 13 m in the Dutch Wadden Sea. Lanksbury et al. 2005 [70] also found significant effects of water depth and the sampling distance from shore to influence fish larval assemblages. The species that were positively correlated to RDA 2 (Fig. 6) were mainly the seasonal effects on their occurrences as they were also low in abundance.

4.3 Length frequency distributions

Larval trajectories such as drifting paths, distance, and duration from the spawning grounds to nursery habitats play crucial roles in their survival and recruitment [74]. The trajectory effects depend on whether the area studied is a spawning location or larvae are supplied from elsewhere. The locally hatched individuals are exposed to the local environmental conditions [75], whereas individuals supplied from other areas are exposed to multiple conditions. The timing of the most favorable feeding conditions when the prey abundance is high during the onset of exogenous feeding promotes larval survival [76]. For instance, the high zooplankton abundance after spring phytoplankton bloom favors the summer-hatched individuals as high feeding rates promote faster growth [20,34]. The differences in trajectories, environmental conditions, and larval conditions at hatching may result in fluctuating occurrences and abundances. For example, high survival rates for *S. rostellatus* (Fig. 8) compared to *C. harengus* (Fig. 9) whose eggs and larvae face numerous threats such as predation in the early stages [20].

The newly released *S. rostellatus* from the male brood pouches represents the first stage of the juvenile period [48]. The presence of males with larvae in their brood pouch and juveniles in June in the SRB shows that larval development starts in spring. Temperature triggers the onset of gonad maturation [15]. Since the study did not target adults, the gonad timing in the three sampled years could not be determined. However, the low juvenile density in June 2021 compared to 2022 and 2023 (Fig. 8) indicates the temperature effects as 2021 had severe winter and low spring temperatures (Fig. 2). There was only one cohort of *S. rostellatus* in the SRB. On the contrary, in the Ems-Dollard estuary, two generationally linked spring and summer juveniles with little temporal overlap were observed [8]. The cohorts were linked to migrations searching for nursery habitats and temperature differences between the estuarine and the coastal areas that influenced growth [77]. Since the SRB is a rich nursery ground, minimal or no juvenile emigration may exist. Besides, there is a low estuarine influence in the SRB compared to Ems-Dollard, which minimizes the effects of temperature fluctuations on the growth or use of thermal niches. Even the seemingly two cohorts in October of 2022 and 2023 (Fig. 8) are an extension of spawning periods that are not restricted to summer months only.

The presence of *C. harengus* at various early developmental stages and the different cohorts (Fig. 9) indicates that spawning takes place in the bight, in nearby waters and additionally supplied by the open North Sea spawned individuals. Besides the local spring spawners in the SRB [6] and nearby waters, *C. harengus* has two spawning populations that are genetically distinct, the North Sea autumn spawners and the Norwegian spring spawners. They spawn under different environmental conditions as the former spawns from August to December while the latter spawns between February and March [76,78]. The larval period is longer in autumn-spawned larvae than spring-spawned larvae because of the differences in growth rates [79] as cohorts experiencing warmer temperatures grow faster than cohorts in colder temperatures [22,80].

At the beginning of each sampling year, the different *C. harengus* cohorts co-existed as shown by the bimodal distribution patterns (Fig. 9). The co-existence occurs despite the differences in the early life histories of exposure to different environmental conditions [79]. In February and March, juveniles arrive from autumn spawners of the open North Sea from the previous year, and mix with the larvae from the local spring spawners (Fig. 9). In February, the peak abundance of autumn-hatched *C. harengus* occurs (Fig. 9), a similar pattern was observed in Skagerrak [76]. In spring, larvae originate from the SRB and the coastal embayment in the Wadden Sea as shown by the presence of one cohort (Fig. 9) unlike in the Norwegian Shelf where the co-existence of autumn- and spring-spawned larvae were observed in May [76]. These results also show that the

Norwegian spring-spawned larvae do not reach the Wadden Sea as larvae, as they have to drift anti-clockwise from the spawning grounds southwards to the British coast and then northwards to the nursery areas in the eastern North Sea [81]. These populations mix with those spawned in the Wadden Sea resulting in high juvenile and adult abundances at the beginning of the summer months [40]. From July onwards, larvae around 15 mm (Fig. 9) are from the spring spawned in the SRB and adjacent coastal areas.

5. Conclusions

This study investigated the seasonal and annual patterns of YOY fish in the SRB and determined which species spawn in the area and those that are supplied by the adjacent waters. We found evidence of a few species spawning in the SRB and the adjacent coastal areas while the majority of documented species arrive as juveniles. Species occurrences coincided with spawning seasons, as a result, higher seasonal variations were observed. The SRB acts as one of the acclimatization areas for diadromous species such as *A. anguilla*. Various environmental parameters were correlated to the variations in the YOY fish but the interaction of factors had a higher influence. Nevertheless, more than half of the variations were unexplained, which can be addressed by further investigations focusing on the spawning stock and the effects of more environmental parameters such as turbidity, dissolved oxygen, light intensity, predator-prey interactions, etc. on the community dynamics. The size-dependent processes such as growth, prey availability, vulnerability to predators, and mortality must be considered when determining the variability in the survival and recruitment of marine and freshwater fishes [20]. Our results showed the cohort structures of the two dominant species at different times of the year. The cohort structures can be used to infer the somatic growth, survival, and mortality at different life stages. However, partitioning the length frequency into fixed monthly length classes ignores the differences in growth rates between individuals, which may lead to a biased estimation of growth and mortality of a length class [82]. This is because of the differences in prey availability and feeding rates [25]. Therefore, further investigations on the population dynamics of a single species incorporating the size-dependent processes is recommended.

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CHAPTER 5

GENERAL DISCUSSION

5.0 General Discussion

One of the aims of studying organismal diversity and the interactions between biotic and abiotic environments is to advance knowledge and understanding of how ecosystems function (Courchamp et al. 2015) and to predict the species' vulnerability to changes in environmental conditions such as global warming (Dahlke et al. 2020). Community ecology studies aim to determine species distribution patterns over time and space, and the physical and biological drivers of the patterns (Fletcher et al. 2019). Such aims can be achieved through spatio-temporal biodiversity observations that report the taxa occurrence, abundance, biomass, species distributions, etc. (Maureaud et al. 2024). These support research on identifying community dynamics and temporal patterns, interactions, and responses to global change. These are essential in decision-making on conservation and management (Maureaud et al. 2024). In this thesis, I aimed to investigate if the fish species composition in a cold temperate tidal lagoon, the Sylt-Rømø Bight (SRB) changed compared to previous investigations and if there were common patterns and trends exhibited by various species in relation to changes in environmental conditions. I investigated the temporal patterns of the fish community structure and diversity and correlated them to changes in temperature conditions. Besides, I assessed if fish species utilize the numerous intertidal habitats of the SRB during high tide. Finally, I investigated if the SRB acts as a spawning and/or a nursery ground and for which fish species and assessed the cohort structures of the dominant young-of-the-year (YOY) fish species.

To understand the dynamics of marine ecosystems precisely, consistent measurements at small spatial scales over time provide important information on community responses to changes in local environmental conditions. **Chapter 1** of this thesis provides a general overview of climate change effects on coastal fish communities including the Wadden Sea. A description of the SRB where the current study was undertaken and the past fish related researches. Fish species composition between 2007 and 2019 changed compared to 1989 to 1995, six Lusitanian species, one boreal, and one Atlantic species were observed for the first time in the SRB (**Chapter 2)**. Four species present in the previous investigations were not found anymore. Fish species exhibited three main trend patterns and the community was partitioned into three seasonal assemblages based on species' temperature preference. Water temperature, chlorophyll *a*, and salinity were significantly correlated to the community dynamics while the North Atlantic Oscillation (NAO) winter indices had an indirect correlation.

The fish community structure changed seasonally due to species migration patterns. Higher community diversity occurred at low temperatures since a few species dominated the community at higher temperatures. Spatial distribution patterns indicated the usage of intertidal habitats for various purposes during high tides and within the tidal channels (**Chapter 3**). The young-of-the-year (YOY) fish sampling revealed that only a few species spawn in the SRB while the nearby waters supply the majority. For instance, from the fish monitoring (**Chapter 2**), 55 fish species were recorded while only 15 were present in the YOY fish survey. The cohort structures of dominant YOY fish species revealed the population-level processes such as the presence of different cohorts at different times of the year and somatic growth. In this final **Chapter**, the synthesis of results from the three chapters (**Chapters 2**, **3,** and **4**) is discussed and compared to coastal areas in other regions of the world. Inferences are drawn from other studies and model projections of what might occur in future warming scenarios. Conclusions on the effects of climate change on coastal fish communities, critical reviews of the sampling methods, the significance of the high-resolution monitoring, and the knowledge gaps that future investigations and analyses could address are presented. The major results of this thesis are discussed below.

5.1 Changes in species compositions

Marine ectotherms such as fish have temperature limits and tolerance ranges that determine their latitudinal distributions and responses to climate change. Species response to global warming may be an expansion of poleward range boundaries or a contraction of equatorward boundaries in an attempt to maintain waters with suitable temperatures (Sunday et al. 2012; Gordó-Vilaseca et al. 2023). Thus, the ecological effects of global warming are region-specific and vary widely depending on species and community characteristics and the specific regional conditions (Walther et al. 2002). For a certain region, species range shifts can result in species additions or losses. For instance, in the tropics, no warmer-adapted species will replace fish species that shift their latitudinal ranges due to high temperatures resulting in net loss (Palomares and Pauly 2019). On the other hand, range shift will increase species richness at higher latitudes but the fate of cold water adapted species remains unclear in case there will be no conducive environments further north. To assess the overall species' range shifts in a region, the guild approach that simplifies complex communities by partitioning species with similar temperature preferences, roles, or functions into tractable units (Jiming 1982; Tulp et al. 2008; Benoit et al. 2021) is appropriate. Based on temperature preferences, fish species in the North Sea region can be classified into three biogeographic guilds comprising Lusitanian (preferring warm water), boreal (preferring cold water), and Atlantic (often pelagic or deep-water widespread in the North Atlantic) (Jiming 1982; Tulp et al. 2008; ter Hofstede et al. 2010). This thesis used the guild approach to assess the changes in fish species composition in the SRB compared to previous investigations.

Changes in species composition (**Chapter 2**) were observed, as six Lusitanian, one boreal, and one Atlantic species were observed for the first time in the SRB. On the contrary, two boreal, one Lusitanian, and one circum-temperate species present in the previous investigations were not found anymore. The new species were rare in occurrence and had low abundance. However, the six Lusitanian and Atlantic species indicate that the warm water-adapted species are expanding their ranges northwards and increasing in the Wadden Sea. Previous studies showed that five Lusitanian species comprising European anchovy (*Engraulis encrasicolus*), red mullet (*Mullus surmuletus*), scaldfish (*Arnoglossus laterna*), solenette (*Buglossidium luteum*), and lesser weever (*Echiichthys vipera*) had expanded their ranges in the North Sea (Hiddink and ter Hofstede 2008). *Arnoglossus laterna* and *E. vipera* were among the species observed for the first time in the SRB while the other species were present in the previous surveys.

The correlations of temperature to fish recruitment are strong at the geographical limit of species ranges and less at the center (Myers 1998). Thus, the relatively low changes in species composition in the SRB are attributed to being at the latitudinal center of distribution ranges for northern and southern species. Generally, 25% of the North Sea fish species have shifted their ranges northwards (Gordó-Vilaseca et al. 2023). Jones et al. (2023) observed low changes in species richness between 1991 and 2019 in the central North Sea compared to the northern North Sea, the east of Shetland, and the southeast coast of the UK. There was a range expansion and population growth of Lusitanian species and an increased frequency of occurrence of Atlantic species such as Atlantic bluefin tuna (*Thunnus thynnus*) on the UK coast. Concurrently, there was a reduction in the habitat extent and quality and the abundance of many boreal species (Wright et al. 2020). For bottom-dwelling fish species, future projections show that their distribution will be constrained by the availability of habitats at suitable depths in the North Sea (Rutterford et al. 2015). This is already occurring in the Wadden Sea, which has lost its habitat suitability for various flatfish species (van der Veer et al. 2022).

Coastal areas are prone to the effects of global warming since the changes in species' distributional patterns depend on habitat types. For example, in the Bay of Biscay, eastern North Atlantic Ocean, demersal species are projected to migrate into the deeper areas while pelagic species are projected to migrate to higher latitudes leading to species losses. The species loss is projected to be balanced by the range expansion of southern species. This would lead to trophic interactions such as predation and competition with native species and may alter ecosystem functions (Le Marchand et al. 2020). On the Canadian Pacific coastline, the migration and spawning areas of Pacific hake (*Merluccius productus*) expanded northwards. Its population and that of South American pilchard (*Sardinops sagax*) increased due to warming (Okey et al. 2014). On the other hand, warming caused population declines for Pacific cod (*Gadus microcephalus*) and poor recruitment of Pacific herring (*Clupea pallasii*) (Okey et al. 2014; Weatherdon et al. 2016). These changes are projected to cause severe declines in fishery catches in the southern parts and will influence the economy of many coastal communities (Weatherdon et al. 2016). If the SRB will experience such changes in species distributional patterns due to range shifts in the future is only a matter of time should warming continue.

5.2 Trend patterns of the dominant fish species

Three major dynamic rate functions including mortality, growth, and recruitment influence fish abundance in an area (Allen and Hightower 2010). Any fluctuations in one of them would result in changes in fish abundance. For northern species, the temperate zone such as the SRB is within the distributional range, therefore, a strong response to climate change is not expected (van der Veer et al. 2015; van Walraven et al. 2017). However, temperature in the Wadden Sea changes seasonally and changes in seasonal patterns have been observed due to climate change (Rick et al. 2023). The changes in seasonal patterns, for instance, severe/cold winters versus mild/warm winters can potentially influence the recruitment of fish species. During the study period, severe winters i.e. winters with 15 to 32 days of below zero temperatures all day and cold winters i.e. winters with 15 to 22 days of maximum temperatures below 0°C (Beukema 1992), occurred in 2009/2010 and 2010/2011, respectively. During this period, three boreal species comprising herring (*Clupea harengus*), small sandeel (*Ammodytes tobianus*), and great sandeel (*Hyperoplus lanceolatus*) had the highest recruitments while the recruitment of other species was low except for Nilsson's pipefish (*Syngnathus rostellatus*). Surprisingly, even some species that utilize the area in summer e.g. whiting (*Merlangius merlangus*) and Atlantic cod (*Gadus morhua*) had low recruitments. After mild and warm winters, the recruitment patterns were reversed, as there were relatively low recruitments of *C. harengus, A. tobianus,* and *H. lanceolatus* while the recruitment of the other species increased.

The trend patterns were different even for species of the same biogeographic guilds. For example, higher recruitment of *A. tobianus* and a low recruitment of *G. morhua,* after severe/cold winters, both are boreal benthopelagic species. The differences in recruitment patterns show the variations in species' responses to changes in abiotic and biotic conditions. For instance, due to climate change, the Wadden Sea has been experiencing fewer colder days in winter and more warmer days in summer since 1990 compared to the period between 1962 and 1990 (de Amorim et al. 2023). These changes can potentially influence the growth and mortality of fish, especially at early developments stages, which in turn influences species abundances. However, this needs further investigation for different species in the SRB. For example, in the Dutch Wadden Sea, the growth and abundance of 0-group (individuals in the first year of life) sole (*Solea solea*) have increased because of longer periods with optimal growth conditions especially after warm winters (Meyer et al. 2016; van der Veer et al. 2022). On the contrary, the mortality rates of 0-group plaice

(*Pleuronectes platessa*) have increased in relation to warming (van der Veer et al. 2022). Another example is on the Portuguese coast where long-term data (1927 – 2011) show high landings for species with an affinity for subtropical/tropical waters in warm years and low landings for species with an affinity for temperate waters and vice versa in cold years (Teixeira et al. 2014). Some species such as eelpout (*Zoarces viviparous*) did not show any trend pattern in the SRB (**Chapter 2**), which may be attributed to higher mortality caused by higher temperatures beyond their tolerance range in the Wadden Sea (Pörtner and Knust 2007). In general, the trend patterns highlight the significance of water temperature on fish species recruitment. In addition, other factors such as density-dependent controls, larval mortality, and/or migration to areas with favorable environmental conditions may influence species populations in an area. Nevertheless, species-specific knowledge on physiological requirements and predator-prey relations in the Wadden Sea could provide more information.

5.3 Common patterns and changes in species phenology

Fish respond in various ways to environmental conditions (Tulp et al. 2017). At the individual level, changes in temperature influence physiology and behavior, and at the population level, it can cause changes in mechanisms that influence dispersal, recruitment, and migration (Harley et al. 2006). The common patterns described in **Chapter 2** were based on species with similar temperature affinities displaying similar seasonal occurrences and migration patterns over the study period. In shallow coastal systems such as the Wadden Sea with no deeper areas having cooler waters, an increase in temperature causes emigration of boreal species and immigration of Lusitanian species (Tulp et al. 2017; van Walraven et al. 2017). Thus, the onset of seasonal migration is triggered by temperature changes. Shifts in the phenology of fish at various life stages in the global oceans (Langan et al. 2021) provide evidence of the ecological effects of climate change (Walther et al. 2002). For example, the delayed autumn emigration for species such as whiting (*Merlangius merlangus*) is related to warmer autumn temperatures (Rick et al. 2023). We could not detect if there is an earlier emigration or earlier immigration of boreal and Lusitanian species, respectively, in the SRB during the study period because fish monitoring takes place once per month. Therefore, it might have missed the earlier changes in migration patterns as van Walraven et al. (2017) observed in the Dutch Wadden Sea using daily monitoring data.

Climate change influences ecosystem functions for various species in various ways. For instance, the Wadden Sea has lost its function for Atlantic cod (*Gadus morhua*) (Tulp et al. 2017). However, it was more abundant in autumn in the SRB during the study but with high inter-annual variations. This shows a shift in the usage of the Wadden Sea as the juveniles arrive in late summer utilizing the area in autumn. Thus, the decreasing trends in the Wadden Sea (Tulp et al. 2022) may be attributed to a mismatch with potential prey or shorter residence times than before. Langan et al. (2021) showed that there was an increased residence times (the difference in days between the first and last observation) of seven warm-adapted seasonal migrant species and a reduction for four cold-adapted species related to global warming in Narragansett Bay, USA, based on continuous weekly monitoring since 1959. Such phenological changes may be happening in the SRB but could not be detected fully because of the reasons stated above. Furthermore, climate change influences the migration patterns of resident species within the SRB habitats. For instance, the delayed local migration of common goby (*Pomatoschistus microps*) and sand goby (*Pomatoschistus minutus*) from the intertidal areas to subtidal areas is related to warmer autumns.

5.4 Changes in fish community structure and diversity

Fish communities can be described according to the number of species present, abundance distributions, and ecological interactions such as predator-prey relationships. Fish diversity is related to factors that operate at various temporal and spatial scales for instance favorable water temperature, habitat and prey availabilities, etc., (Elliott et al. 2022). Effects of climate change on one or a few key species and populations may drive community-level changes. At the community level, climate change affects species interactions and interaction strengths resulting in ecological responses such as altered distribution patterns and biodiversity, which in turn influence the ecosystem functions (Harley et al. 2006). Water temperature is the key driver of the fish community structure and diversity in the Northeast Atlantic shelf seas (from southern Spain to northern Norway) (Rutterford et al. 2023) as it influences range shifts and inter- and intra-annual abundance fluctuations. Therefore, this study investigated the effects of annual and seasonal temperature changes on the fish community structure and diversity (**Chapter 3**).

The fish community structure and diversity changed per season related to migrations that caused species reorganizations following co-occurrences and exclusions at different times of the year. Six dominant species caused dissimilarities in community structures between seasons. The contributions of each species to dissimilarities differed per season with high contributions when a particular species was in high abundance that influenced the community compositions. For instance, the recruitment of various species was related to winter temperatures (**Chapter 2**), thus, community structures after severe/cold winters significantly differed from those after warm winters.

There were no directional changes in species richness related to global warming during the study period except for the relatively higher taxa numbers during and after warm winters compared to cold winters. This is because individuals of some species over-winter in the bight and probably earlier immigration of Lusitanian species after warm winters. This shows the effects of seasonal extremes on species compositions. Hiddink and ter Hofstede (2008) also observed higher species richness after warm winters in the North Sea. The magnitude of changes in species richness is not spatially and temporally uniform (Hiddink and ter Hofstede 2008). This may explain the relatively higher species richness during the winter/spring transition phase compared to the summer/autumn phase in the SRB. The difference may be attributed to the nursery function of the SRB as individuals of boreal and Lusitanian species at early developmental stages may be using the SRB in earlier months of the year taking advantage of high productivity during and after spring phytoplankton bloom and only a few species utilize the area in autumn.

Compound diversity indices (evenness and Shannon-Wiener Index) showed a decreasing tendency with increasing temperature while the opposite was true for dominance. In every community, a few species are always present in the highest numbers (Verberk 2011; Murphy and Smith 2021), thus, in the SRB, the negative correlation between evenness and the Shannon-Wiener Index was because of the relative abundance of *C. harengus* and *A. tobianus* in winter, spring, and summer and *M. merlangus* in autumn. A similar scenario was reported in the southern Yellow Sea where species diversity in winter was negatively correlated to the relative biomass of the Japanese anchovy (*Engraulis japonicus*) (Xu and Jin 2005). The diversity was relatively stable when *E. japonicus* was removed from the analysis (Xu and Jin 2005). Since the analysis in the SRB was all year round, applying the same species exclusion in analyses could have resulted in the omission of more than one species, which could not have reflected the true nature of the seasonal community dynamics.

5.5 Potential effects of other environmental parameters

In addition to temperature, salinity is an important parameter that determines the distribution of fish as it affects metabolism by influencing osmoregulation and oxygen consumption (Gillanders et al. 2011). Salinity had low explanatory power in the fish community dynamics in this study (**Chapter 3** and **Chapter 4**). This is because of the relatively low variability (26 to 33) with highs in summer and autumn because of lower freshwater runoff and a lower ratio of precipitation to evaporation during this time (Rick et al. 2023). Most fish species especially diadromous species show wide salinity tolerance (Elliott et al. 2007; Gillanders et al. 2011) so a slight increase in salinity might not have a high impact. However, salinity affects egg fertilization and incubation, yolk sac resorption, swim bladder inflation, and larval growth (Boeuf and Payan 2001). Thus, rapid changes in salinity could lead to larval mortalities, decreased richness of diadromous species, and low diversity (Gillanders et al. 2011). Climate change effects on salinity in the SRB are correlated to sea level rise that would cause more seawater intrusion and a decrease in intertidal areas (Becherer et al. 2018). For instance, in some parts of the Ria Formosa lagoon, southern Portugal, it is projected that a sea level rise of 0.5 m would cause an increase in salinity by 0.5 - 3 (Rodrigues et al. 2021). These changes might influence fish larval growth and species distribution patterns.

Predator-prey interactions influence fish communities. This study used chlorophyll *a* as a proxy for primary production, a key driver of zooplankton and ichthyoplankton dynamics (Capuzzo et al. 2018). Chlorophyll *a* had a low explanatory power to the fish community dynamics (**Chapter 3** and **Chapter 4**) because it is at the base of the food web while most fish species in the SRB occupy the third trophic level (Baird et al. 2004; de la Vega et al. 2018). Chlorophyll *a* in the SRB shows seasonality with high concentration during the spring bloom. Long-term chlorophyll *a* pattern shows high proliferations after the severe winters of 1996/1996 and 2009/2010 and the cold winter of 2012/2013 (Rick et al. 2023). Whether the zooplankton abundance follows this pattern remains unclear. Therefore, the availability of continuous zooplankton data would provide more information. Nevertheless, climate change might influence predator-prey interactions in temperate zones in various ways. For instance, the onset of primary production is less dependent on temperature than on light (Eilertsen et al. 1995), therefore, if winters become warmer, earlier fish spawning might occur but not earlier spring phytoplankton bloom (Harley et al. 2006). This might cause shifts in species distributions and productivity since the changes at the bottom of the food web cascade through all trophic levels leading to match-mismatch events, changes in growth rates, and predator-prey interactions (Harley et al. 2006; Alvarez-Fernandez et al. 2015) with unknown impacts on food web stability.

5.6 Spatial distribution and utilization of intertidal habitats

The distribution of fish in space exhibits spatial patterns. Understanding what drives the patterns is a fundamental ecological question and a requirement for conservation and management (Planque et al. 2011). External and internal factors control spatial distribution in fish communities. The external factors are mainly environmental forcing that influence the suitability and availability of habitats while the internal factors include but are not limited to population size, age structure, diversity, and behavior. The internal factors control spatial distribution through density-dependent mechanisms, age- and/or stage-dependent habitat preference, and the differences in migration capacities (Planque et al. 2011). Tidal dynamics significantly affect the distribution of fish species on short-term scales because of the influx of numerous individuals and species into the intertidal zones during high tides and retreat with ebbing waters (Jovanovic et al. 2007; Couperus et al. 2016). Thus, this study focused on the changes in diversity indices with water depth as environmental forcing to depict spatial distribution and utilization of intertidal habitats during high tides (**Chapter 3**).

Habitat heterogeneity influences spatial distributions and is critical in maintaining diverse communities (Pratt and Smokorowski 2003). The spatial distribution of fish in the SRB followed distinct patterns that were assumed to be shaped by a combination of habitat availability and tradeoffs between prey availability, competition, and predator avoidance. The changes in diversity patterns near seagrass meadows and bivalve beds with water depths depict the usage of these habitats as nurseries during high tides. Hylkema et al. (2015) demonstrated the stepwise life cycle migrations for juvenile fish between seagrass beds to adult habitats. Freedman et al. (2016) also tracked the movements of California halibut (*Paralichthys californicus*) to show the significance of intertidal channels and different morphologies on habitat utilization. Large individuals tended to remain in channels with high water flow and sandy substratum near eelgrass (*Zostera marina*) beds because of higher prey concentrations whereas small individuals used the marshes more frequently because of temperatures that maximized growth (Freedman et al. 2016). In the SRB, there are differences in habitat structures and current velocities but water is thermally mixed except in very shallow intertidal areas in winter and summer.

The present study used the changes in diversity indices including species richness, evenness, dominance, and Shannon-Wiener Index with water depth to depict the usage of intertidal habitats. The method was ideal as a starting point to show the general pattern of species distribution and habitat usage but did not show which species or size classes use different habitats in different tidal regimes. For instance, the distribution of resident and migratory fish species differed between rocky and soft-bottom habitats on the Swedish west coast. On rocky bottoms, gastropods and amphipods were the main food sources and were associated with the substrates whereas decapods and fish as prey dominated soft bottoms (Stål et al. 2007). Also, habitat utilization by fish in the southern Gulf of Thailand showed that most species preferred specific bottom structures while some species were distributed all over the bay (Hajisamae et al. 2006). Even in the absence of rocky bottoms in the SRB, there are differences in species spatial distribution between sand flats and macrophyte systems at different times of the year (Polte and Asmus 2006a; Polte and Buschbaum 2008). In addition, mobile substratum and homogenous sandflats are less productive and offer a few refuges to juvenile or small-bodied fish that may have low diversity compared to mudflats, seagrass meadows, and bivalve beds.

Model projections show that by the end of this century, sea level rise will cause an increase in the tidal range and a transition from the current tidal-flat-dominated system to a system where large fractions will remain permanently submerged (Becherer et al. 2018). Water temperature regulates the usage of different depths and habitats (Freitas et al. 2021). This might not be the case in a tidally and thermally mixed system such as the SRB. Nevertheless, it would be interesting to see the effects of sea level rise on thermal stratification and habitat use by different fish species. For instance, in the southern Norwegian fjord, fish species used different depths at different times of the year. In summer, *G. morhua* used deeper colder waters while Pollack (*Pollachius pollachius*) and ballan wrasse (*Labrus bergylta*) occupied shallow warmer waters. The distribution patterns were reversed in winter because of the reversal of thermal patterns (Freitas et al. 2021). In the SRB, instead of thermal stratification, strong horizontal thermal differences are formed between very shallow and deeper areas in summer and winter causing the observed differences in the usage of these habitats by *P. minutus* and *P. microps* at different times of the year (**Chapter 3**).

5.7 Young-of-the-year (YOY) fish species

The spatial and temporal variability of spawning location and timing are important aspects of the fish life cycle and ecosystem management (Di Stefano et al. 2023). Most coastal fishes are characterized by a bipartite life cycle from pelagic dispersive egg and larval stages to juvenile recruitment or settlement in the nursery grounds and later to adults. These processes govern the spatial and temporal population structures (Legrand et al. 2019). Spawning and nursery grounds are of ecological significance and are considered essential habitats for their ecological role in the completion of the fish life cycles (Lelièvre et al. 2014). The choice of spawning location plays a significant role in the survival of the vulnerable egg and larval stages to juvenile stages and dispersal across different habitats while maximizing food intake and minimizing predation (Ciannelli et al. 2014). Thus, knowing when and where spawning occurs and the connectivity between spawning and the nursery grounds are of ecological significance that should form part of the focus of marine spatial planning, scientific research, and management since their protection could lead to large fisheries benefits and biological conservation (Erisman et al. 2017).

Only 15 YOY fish species were found, which was far less than the documented fish species (55 in total and 22 abundant) from the long-term fish monitoring. Only a few species were found to spawn in the SRB indicating that most species are supplied as juveniles from the surrounding waters and utilize the nursery grounds in the SRB. However, sampling only concentrated in the deep tidal channels and might have missed the larvae of species that spawn in the shallow intertidal habitats such as the *P. microps, P. minutus* (Kellnreitner et al. 2012), and three-spine sticklebacks (*Gasterosteus aculeatus*) (Polte and Asmus 2006b; Ahnelt et al. 2021). In addition, sampling the water column might have missed the settling individuals for some benthic species. For example, the O-groups of *S. solea* and flounder (*Platichthys flesus*) that were not present in the YOY samples were present in the southern German Bight and the Dutch Wadden Sea (Meyer et al. 2016; van der Veer et al. 2022). Nevertheless, the presence of larvae and recruitment/settlement may not be correlated because of the numerous physical and biological mechanisms controlling the processes (Pineda et al. 2010). High egg and larval mortality rates in marine fish species are caused by predation, limited swimming ability, and low prey density (Leggett and Deblois 1994; Arevalo et al. 2023). Besides, larval behavior plays a significant role in their survival because it affects the responses to hydrodynamics and vertical migration based on the abundance of copepod nauplii at the same time avoiding predators (a balance between visual avoidance and prey availability) (Conway et al. 1997; Pineda et al. 2010). Thus, only the individuals that survive the vulnerable larval stage reach the coastal nursery grounds. This explains why a higher larval diversity was observed in Helgoland in the North Sea (Malzahn and Boersma 2007) compared to the SRB.

Global warming may cause shifts in spring spawning phenology to earlier in the year meaning a few hours of daylight for visual hunting of larvae on prey leading to a lower prey availability during periods of high metabolic demands (Asch et al. 2019). These influence the growth, survival, and recruitment rates of YOY fish. Furthermore, species could adjust spawning times or locations and utilize different nursery grounds (Asch et al. 2019). The latter is already happening as the decreased recruitment of *P. platessa* and *L. limanda* in the Wadden Sea did not affect their recruitment in the North Sea. This indicates that other areas offer better nursery functions (van der Veer et al. 2022). On the other hand, the presence of *M. merlangus* in the YOY samples may indicate an earlier arrival of this species in the Wadden Sea.

5.8 Growth and cohort structures of the dominant YOY fish species

Body size is an ecologically important property that influences individuals' vulnerability to predators and prey-searching ability consequently determining their performance and life history (Quince et al. 2008). Most fish species can increase in size by five orders of magnitude during their life span, three of these orders occur during the planktonic stage or rather during their first year of life (Miller et al. 1988). Cohort size distributions can be used to determine the performance of individual organisms to the ecology of populations, communities, and ecosystems (Persson and De Roos 2007) as well as the effects of density dependence, spawning timing, predation, and climate change on populations (Ohlberger et al. 2013). We focused on the cohort structures and growth of two dominant YOY species, *C. harengus* and *S. rostellatus*. *Clupea harengus* cohort structures revealed two cohorts comprising individuals spawned within the SRB and surrounding areas and those hatched in the North Sea. *Syngnathus rostellatus* on the other hand had only one cohort hatched within the SRB.

The cohort structures showed high survival rates of *S. rostellatus* since the larvae are released as juveniles (Sommer et al. 2012) and higher mortality rates for *C. harengus* because of the size-related higher vulnerability to biotic and abiotic factors. Several intrinsic and extrinsic factors that influence spawning populations also affect the YOY individuals and can explain the differences in cohort size distributions (Ohlberger et al. 2013). For example, water temperature influences the energy available for growth by influencing food consumption rates, assimilation efficiency, and energy expenditure (Shelley and Johnson 2022). Climate change can cause changes in cohort structures by influencing spawning timing and location. For instance, adults migrate earlier from cool inshore habitats to warmer offshore overwintering grounds in colder years. This trigger earlier gonad maturation and spawning thus earlier peak abundances of propagules in the nursery grounds (Genner et al. 2010). Rademaker et al. (2024) observed forward temporal phenological shifts in the use of the Dutch Wadden Sea by *C. harengus* because of warming water temperatures. The observed cohort structures may give a glimpse of differences in spawning timing, and the differences in survival of larvae hatched within the SRB compared to those supplied from elsewhere.

Clupea harengus attach their demersal eggs on benthic substrates rendering reproductive success to local habitat complexity and suitability of ambient environment (Polte and Asmus 2006b; von Nordheim et al. 2018). Macrophytes provide better substrates for the attachment of *C. harengus* eggs. However, macrophyte presence during the spawning season and at an appropriate depth is critical to egg survival (Moll et al. 2018). In the Baltic Sea, mechanical forcing due to storm-induced wave action accounted for up to 29% of egg loss in a single spawning bed (Moll et al. 2018). In the SRB, seagrasses that provide additional substrates are only present in shallow areas in summer months (Polte and Asmus 2006b) and might not be very useful for spring spawners. This might explain the low occurrence and abundance of individuals hatched in spring later in the year except after mild winters when seagrass might be present at sufficient density. In contrast, *F. vesiculosus* are available during early springtime but are less effective in adhering eggs compared to seagrasses (Polte and Asmus 2006b).

The cohort structures are important in determining larval survival and recruitment. However, sampling at large temporal resolution (ones per week in this study) usually results in averaging the length-abundance data across cohorts. This produces an artificially smoothed survival curve that bears little relevance to the real mortality risks experienced by individuals (McCasker et al. 2014). For example, when monitoring a cohort of pelagic larvae, if sampling scales are not proportional to advection scales, the growth estimates may be influenced by dispersal effects. Decreasing larval density may be attributed to mortality when, in fact, larvae may be thriving elsewhere (Fontes et al. 2011). Therefore, dispersion should be discriminated from true natural mortality when measuring survival (Helbig and Pepin 1998). The YOY fish abundances for a given area may not directly reflect larval survival, especially when dispersal patterns are unknown (Fontes et al. 2011). Thus, further analyses may focus on the connectivity between spawning grounds, spawning biomass, dispersal mechanisms, and YOY fish recruitments in the SRB.

5.9 Critical review of the methods and recommendations for future research

The high-resolution monthly fish monitoring using an active sampling device taking place all year round may be the only one in the Wadden Sea. It is important in determining system-level changes such as the seasonal assemblages, trends, community structures, and diversity changes in relation to the changing environmental conditions. Besides, local studies give important information on the site specificity that improves the global understanding of coastal lagoons' responses to climate change. The sampling gear and methods were appropriate for most fish species. However, sampling was restricted to deep and shallow areas that are permanently submerged. These might be inappropriate for species such as *P. minutus* and *P. microps* that only migrate to the sampled areas due to extreme temperatures in the shallow intertidal areas in winter. Similarly, sampling was inappropriate for fivebeard rockling (*Ciliata mustela*) since it lives in intertidal habitats with sandy, muddy, or shell gravel bottoms.

Using a fyke net in surveying the intertidal habitats at Königshafen in the SRB, sand smelt (*Atherina presbyter*) was almost a hundred times abundant in the night catches compared to the day catches. Thus, this species might be using the area during the night and not represented in the day catches, which might explain its low abundance in the fish monitoring trawls. European sea bass (*Dicentrarchus labrax*) was rare four decades ago in the North Sea (Jiming 1982) and is now a resident in the western Dutch Wadden Sea (Cardoso et al. 2015). The species was not present in the fish monitoring survey in the SRB because it is difficult to catch with the sampling method as it lives close to structures like stones or groins. The sampling method may be inappropriate for *B. belone* because of very high swimming speeds and the capability to avoid nets. Similarly, the sampling method has limited catchability for sea lamprey (*Petromyzon marinus*), which is believed to be abundant in the Wadden Sea but has high escape capability. Therefore, appropriate sampling techniques targeting a specific species in both the intertidal and subtidal habitats are recommended for the true population dynamics of these species.

The correlations between water depth and various diversity indices were used to depict spatial distribution (horizontal) and the utilization of intertidal habitats. This method could not show which species or size classes used various habitats at different tidal regimes and times of the year. Thus, investigating species-specific or size-dependent distribution patterns with habitat complexity, substrate type, substrate-associated prey, water velocity, and time of the year is recommended. In addition, abundance and tidal behavior (vertical distribution) of various species could be determined by the use of techniques such as acoustic telemetry. In addition, sampling the water column in the deep tidal channels may miss settling flatfishes and YOY individuals hatched in the intertidal habitats. Thus, a combination of methods covering different depths in the intertidal and subtidal areas is recommended.

The environmental variables in this study were correlated to less than half of the variations in the fish community. This could mean the community is inherently variable and the environmental variables applied could only explain part of it. However, additional parameters such as dissolved oxygen, light intensity, turbidity, predator-prey abundance/interactions, and zooplankton abundance are recommended to gain more insights into community dynamics. For instance, Pécuchet et al. (2015) applied nine variables and explained 70% of the variations in the North Sea fish community. Besides, it is recommended to investigate species' temperature and salinity ranges per life stage, which is an important aspect of species distributions (Arevalo et al. 2023). This will provide additional information for migrating species. For instance, whether the emigration of *C. harengus* from the bight or the transition of *A. tobianus* from pelagic to benthopelagic is triggered by temperature or is size/age dependent. Further analyses could use tagging techniques to determine whether the migrating individuals return to the bight or explore other areas.

The quantity of eggs and survival of larvae partly depends on the biomass, the conditions, and the age structure of the spawners (Eriksen et al. 2011). The study did not incorporate these, thus, detailed studies on the population dynamics of a single species incorporating the size-dependent processes in combination with a multi-species approach are recommended. Further investigations on the connectivity between spawning areas, dispersal routes, and the driving forces to connectivity with the nursery grounds could provide more insights in the community dynamics. Furthermore, predator and prey biomass and distribution patterns would vary in response to global warming. Therefore, a more comprehensive approach including multispecies and ecosystem analyses, would allow more accurate predictions of the effects of global warming on the coastal fish communities.

5.10 Conclusions

The present study investigated the fish community dynamics in a cold temperate tidal lagoon, in relation to changes in environmental conditions. Seven species that have a high affinity to warm water temperature were observed for the first time in the SRB, which shows that they are increasing in the Wadden Sea. Trend patterns were correlated to winter temperatures, which demonstrates the potential effects of global warming on coastal fish communities. Besides, changes in phenology such as the late autumn emigration of some species were related to warming temperatures. Only 15 YOY fish species were sampled and just a few species showed evidence of spawning in the SRB. In comparison, there were 55 species observed in the monthly fish monitoring. This shows that the majority of the fish species in the SRB are supplied from the adjacent waters as juveniles. Individuals of some species probably arrive at earlier developmental stages, avoid outgoing currents, and persist in the intertidal habitats that were not sampled in this study. The intertidal habitats provide nursery, feeding, and refuge grounds promoting somatic growth before the individuals can be captured in the fish monitoring trawls. This shows the ecological role of the SRB in the completion of the fish life cycles. Furthermore, the study showed the utilization of the intertidal habitats by fish juveniles during high tide. Fish species with wide latitudinal distributions show different spawning patterns among sub-populations over their distributional ranges (Arevalo et al. 2023). This was evidenced in the cohort structures of *C. harengus* that revealed the supply from different spawning populations in autumn and spring compared to only one cohort of *S. rostellatus* in summer. Other parameters such as salinity and chlorophyll *a* had low explanatory power to the fish community dynamics but the interactions with water temperature had major effects. The results of this study lead to insights that are more informed for effective conservation and management of valuable coastal ecosystems.

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Mit der Abgabe meiner Dissertation (7 – 10 schriftl. Exemplare und eine elektronische Version) mit dem Thema:

Fish community dynamics in a cold temperate tidal lagoon in the Wadden Sea, in relation to changes in environmental conditions

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Anlagen

Contribution by author

I certify that the information provided and the contribution to the publications in this dissertation correspond to the truth. I refer to the following publications and manuscripts:

Chapter 2:

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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Contribution: 90%

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Chapter 3:

Community structure and diversity changes for fish in a temperate tidal lagoon, in relation to changes in water temperature and depth

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Chapter 4:

Temporal variations of the young-of-the-year fish supply in the Sylt-Rømø Bight, southeastern North Sea

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All authors except Hannah Gaber conceptualized the idea of sampling the young-of-the-year fish. I sampled weekly from March 2021 to October 2023, Hannah Gaber occasionally assisted me with sampling in 2022. I formulated the research questions, analyzed the data, and interpreted the results. I wrote the first manuscript draft and shared it with my co-authors who assisted me in improving it. I wrote the final draft, which is ready for submission.

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Erklärungen zur elektronischen Version und zur Überprüfung einer Dissertation

Hiermit betätige ich gemäß §7, Abs. 7, Punkt 4, dass die zu Prüfungszwecken beigelegte elektronische Version meiner Dissertation identisch ist mit der abgegebenen gedruckten Version.

Ich bin mit der Überprüfung meiner Dissertation gemäß §6 Abs. 2, Punkt 5 mit qualifizierter Software im Rahmen der Untersuchung von Plagiatsvorwürfen einverstanden.

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Versicherung an Eides Statt

Name, Vorname	Otieno Victor Odongo
Matrikel-Nr.	6094492
Straße	Hafenstraße 43
Ort, PLZ	25992 List-Sylt

Ich, Victor Odongo Otieno, Hafenstraße 43, 25992 List, Matr.-Nr. 6094492 (Vorname, Name, Anschrift, Matr.-Nr.)

versichere an Eides Statt durch meine Unterschrift, dass ich die vorstehende Arbeit selbständig und ohne fremde Hilfe angefertigt und alle Stellen, die ich wörtlich dem Sinne nach aus Veröffentlichungen entnommen habe, als solche kenntlich gemacht habe, mich auch keiner anderen als der angegebenen Literatur oder sonstiger Hilfsmittel bedient habe.
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List-Sylt__, 24/07/2024
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Ort, Datum Unterschrift

Curriculum Vitae

PERSONAL INFORMATION

Name: **Victor Odongo Otieno**
Alfred-Wegener-Institut, Hafenstr. 43, 25992, List/ Sylt, Germany
victor.odongo@awi.de; Victorodongo7@gmail.com
https://orcid.org/0000-0001-9760-1643
LinkedIn: Victor Odongo

EDUCATION AND TRAINING

October 2020 to present	**Doctoral student**
Doctoral thesis	Fish community dynamics in a cold temperate tidal lagoon, in the Wadden Sea, in relation to changes in environmental conditions
Institution and country	Universität Bremen, Faculty 2 Biology/ Chemistry, Germany
Completion date	Thesis handing in: 30th July 2024, Colloquium : 27th September 2024
Supervisor	Prof. Dr. Maarten Boersma

Sept. 2018 to July 2019	**Post-graduate Training in Oceanography**
Subject area	Core skills in biological, chemical, and physical oceanography. Training in instrumentation, sample collection, and analytical protocols.
Institution and country	NF-POGO Center of Excellence (Cofe) at Alfred-Wegener-Institut, Germany
Research project	Seagrass ecosystem responses to increasing water temperature attributable to global warming in the northern Wadden Sea
Supervisor	PD. Dr. Harald Asmus

2014 to 2017	**Master of Environmental Science**
Subject areas	Development and environment, statistical analysis and techniques, environmental impact assessment, climate change and global warming, ecological techniques, and ecological footprints.
Institution and country	Pwani University, Kenya
Master thesis:	Carbon sequestration in the seagrass meadows of Malindi Marine Park and Reserve, Kenya
Supervisor	Prof. Mlewa C. Mwatete

2008 to 2011	**BSc. (Honors) Environmental Science**
Subject area	Scientific principles, concepts, and methodologies to understand the interrelationships of the natural world: Key areas; natural resource management, pollution, and terrestrial and marine ecology.

Institution and country	Kenyatta University, Kenya
Bachelor thesis	Assessment of heavy metals lead (Pb) and cadmium (Cd) in edible fish species in Makupa Creek, Mombasa, Kenya
Supervisor	Prof. Mlewa C. Mwatete

WORK EXPERIENCE

October 2020 to present	**Doctoral researcher**
Employer	Alfred-Wegener-Institut: (DAAD Stipendium)
Main activities	Fish community ecology and fish larval supply into the Wadden Sea.
Sector	Research institution
Place and country	List auf Sylt, Germany

Sept. 2019 to June 2022	**TSIP Regional Manager (Africa)**
Employer	Pure Earth/Blacksmith Institute
Main activities	Review toxic polluted sites in Africa for the Toxic Sites Identification Programme (TSIP) project.
Sector	Non-governmental Organization
Place and country	Remote

Sept. 2013 to May 2018	**Part-time lecturer**
Employer	Pwani University
Main activities	Lecturing in the School of Environmental and Earth Sciences.
Sector	Institution of higher learning
Place and country	Kilifi, Kenya

May to August 2015	**Internship**
Employer	Alfred-Wegener-Institut-
Main activities	Mesocosm experiment with temperate seagrasses on ecosystem responses to elevated temperature and pH.
Sector	Research institution
Place and country	List auf Sylt, Germany

May to August 2011	**Field attachment**
Employer	Kenya Marine and Fisheries Research Institute
Main activities	Hands-on research experience on environmental pollution and marine ecology.
Sector and place	Research institution, Mombasa, Kenya

CONSULTANCIES

May to October 2018	**Mapping of seagrass and coral reef habitats**
Employer	Coast Development Authority, Kenya

Main activities	Mapping of coral reefs and seagrass habitats in Kwale County Kenya in conjunction with Herem Consultancy.
Sector	Government parastatal
Place and country	Kwale, Kenya

2013 to 2023	**Environmental Consultant**
Employer	Salim Wazaran Kenya Company Limited
Main activities	Environmental Impact Assessment and annual audits. Ensure compliance with effluent and air emission standards. Provide expertise on the facility's environmental performance and participate in energy audits.
Sector	Food processing industry
Place and country	Mtwapa, Kenya and remote

2012 to 2017	**Consultant**
Employer	Pure Earth and National Environmental Management Authority, Kenya
Main activities	Investigation of polluted sites along the Kenya coast, soil and water sampling, and analysis of heavy metal concentrations.
Sector	Non-governmental Organization and government parastatal
Place and country	Coastal Kenya

ADDITIONAL INFORMATION

2014 to June. 2018	**Teaching activities at Pwani University: Various courses for;**
Academic Programmes	Bachelor of Environmental Science Bachelor of Environmental of Environmental Planning and Management Bachelor of Environmental Studies – Community Development Diploma in Community Development

2021 to 2022	**Administration: PhD representative "DokTeam"**
Institution	Alfred-Wegener-Institut – Wattenmeerstation Sylt.
Activities	Represent doctoral students on communication, social activities, and outreach.

Publications

Odongo V, Asmus H, Ahnelt H, Boersma M, Rick J, Wiltshire KH, Horn S (2024). Seasonal variations of a coastal fish community in relation to environmental parameters - A case study of the Sylt-Rømø Bight, southeastern North Sea. Estuarine Coastal Shelf Science 300:108723. doi: 10.1016/j.ecss.2024.108723

Ericson, B., **Odongo, V**., Nganga, C., St. Fort, J., & Taylor, M. P. (2019). Assessment of the Presence of Soil Lead Contamination Near a Former Lead Smelter in Mombasa,

	Kenya. Journal of Health and Pollution, 9(21), 190307. https://doi.org/10.5696/2156-9614-9.21.190307
Manuscripts	**Odongo, V**., Asmus, H., Boersma, M., Heubel, K., Sander, L., Rubinetti, S., Sidorenko, V., Horn, S. (). Community structure and diversity changes for fish in a temperate tidal lagoon, as a response to changes in water temperature and depth.
Status	**In review:** Marine Biology
	Odongo, V., Ahnelt, H., Asmus, H., Boersma, M., Gaber, H., Horn, S. (). Temporal variations of the young-of-the-year fish supply in the Sylt-Rømø Bight, southeastern North Sea.
	Targeted journal: Fishes
Conferences	**Oral presentations**
Title	Community structure and diversity changes for fish in a temperate tidal lagoon, as a response to water temperature and depth variations
Place and date	Trilateral Swimway Conference 2024. Groningen - The Netherlands.19th April 2024
Title	Seasonality of environmental parameters drives the variations of coastal fish community – A case study of the Sylt-Rømø Bight, southeastern North Sea
Place and date	ASLO Aquatic Science meeting. Palma de Mallorca, Spain, 8th June 2023
Title	Inter- and intra-annual variations in the fish community structure related to abiotic drivers in the Sylt-Rømø Bight, southeastern North Sea.
Place and date	Small Pelagic Fish Conference. Lisbon, Portugal, 10th November 2022
Title	Carbon sequestration in the seagrass meadows of Malindi Marine Park and Reserve, Kenya
Place and date	9th WIOMSA Scientific Symposium at Wild Coast Sun, Port Edward, South Africa, 28th October 2015.
Conferences	**Poster presentations**
Title	Seasonal variations of a coastal fish community in relation to environmental parameters - A case study of the Sylt-Rømø Bight, southeastern North Sea
Place and date	Free Flow Conference. Groningen - The Netherlands, 15th/16th April 2024

Seminars/Courses

Title	**Leadership Skills**
Place and date	Alfred-Wegener-Institut (POLMAR). Bremerhaven Germany, 26th to 27th October 2023
Title	**Multivariate Analysis of Ecological Data**
Place and date	Alfred-Wegener-Institut (POLMAR). Bremerhaven, Germany, June 13th to 17th 2022

Title	**GMES&Africa** and Copernicus Marine Observation Training Course
Place and date	Maru Maru Hotel, Zanzibar, October to November 2019
Title	**InteGRADE**; a regional training workshop for young marine and lacustrine scientists “Connectivity in coastal ecosystems – our crucial life support systems.
Place and date	Mangrove Lodge, Chuini, Zanzibar, August 1 - 12, 2016
Title	**Food web analysis** from sampling to modelling.
Place and date	Alfred-Wegener-Institut- Sylt, Germany, 6th to 16th July 2015

PERSONAL SKILLS

Communication skills	Good communication skills gained through education and work experience in the academic and non-academic sectors.
Organisational / managerial skills	Interpersonal skills, ability to work as part of a team, and interact effectively with individuals from wide backgrounds.
Job-related skills	Registered Environmental Impact Assessment (EIA) and Environmental Audit (EA) expert, and socio-ecological systems analysis with excellent report writing, oral presentation, and facilitation skills.
Computer skills	Conversant with all Microsoft Office applications. Good command of data analysis software R and a basic user of GIS.