Species richness and functional attributes of fish assemblages across a large-scale salinity gradient in shallow coastal areas

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Abstract. Coastal ecosystems are biologically productive and their diversity underlies various ecosystem services to humans. However, large-scale species richness (SR) and its regulating factors remain uncertain for many organism groups, owing not least to the fact that observed SR ($\mathrm{SR_{obs}}$) depends on sample size and inventory completeness (IC). We estimated changes in SR across a natural geographical gradient using statistical rarefaction and extrapolation methods, based on a large fish species incidence dataset compiled for shallow coastal areas (<30 m depth) from Swedish fish survey databases. The data covered a ca. 1,300 km north-south distance and a 12~~0~~-fold salinity gradient along sub-basins of the Baltic Sea plus Skagerrak and, depending on sub-basin, 4 to 47 years of samplings during 1975–2021. Total fish $\mathrm{SR_{obs}}$ was 144, and the observed fish species were of 74~~5~~% marine and 26~~5~~% freshwater origin. In the 10 sub-basins with sufficient data for further analysis, IC ranged from 7~~6.~~7–98~~7.7~~%, implying that ca. 2–23% of likely existing fish species had remained undetected. Sample coverage exceeded 98.5%, suggesting that undetected species represented <1.5% of incidences across the sub-basins, i.e. highly rare species. To compare sub-basins, we calculated ~~standardiz~~standardised SR ($\mathrm{SR_{std}}$) and estimated SR ($\mathrm{SR_{est}}$). Sub-basin specific $\mathrm{SR_{est}}$ varied between 35 ± 7 (SE) and 109 ± 6 fish species, being ca. three times higher in the most saline (salinity 29–~~–~~32) compared to the least saline sub-basins (salinity <3~~2.7~~). Analysis of functional attributes showed that differences~~—~~ with decreasing salinity particularly reflected a decreasing SR of benthic and demersal fish, of piscivores and invertivores, and of marine migratory species. We conclude that, if climate change continues causing an upper-layer freshening ~~lowers the salinity regime~~ of the Baltic Sea, this may influence the SR, community composition and functional characteristics of fish, which in turn may affect ecosystem processes such as benthic-pelagic coupling and connectivity between coastal and open sea areas.

1 Introduction

Biodiversity is essential for ecosystem processes, and ultimately for the humans depending on these (IPBES, 2019). Coastal ecosystems are often biologically diverse and highly productive, providing valuable ecosystem services to humans, such as food, water purification and protection against floods (Griffiths et al., 2017; Kraufvelin et al., 2018; Pan et al., 2013). However, threats to coastal biodiversity from e.g. overfishing, habitat loss, pollution, eutrophication and climate change are many and profound (Duncan et al., 2015; Griffiths et al., 2017; Pan et al., 2013)~~. At the same time, ~~, and the number of ~~actually occurring coastal ~~species ~~numbers ~~occurring in coastal habitats often remains uncertain (Appeltans et al., 2012). This makes improved understanding of their biodiversity especially important to support conservation and management measures (Pan et al., 2013; Rooney & McCann, 2012).

Taxonomic inventories, or species censuses, are required e.g. for the analysis of biodiversity patterns, delineation of species ranges, and prioritization of conservation efforts (Mora et al., 2008). Species richness (SR), i.e. the number of species in an ecosystem, is a classical indicator of biodiversity, also referred to as “alpha diversity” (Gotelli & Colwell, 2001; Hill, 1973). However, since achieving complete species inventories is often impracticable with realistic sample efforts, most censuses remain incomplete and many rare species remain unknown. Consequently, it is important to consider the effect of sample size and inventory completeness (IC) on observed SR (SR_{obs}) to avoid biased or misleading comparisons or interpretations (Chao & Chiu, 2016; Chao et al., 2020; Colwell & Coddington, 1994; Mora et al., 2008).

SR is connected to several ecosystem processes, such as productivity (Duffy et al., 2017), and the efficiency of resource use and nutrient cycling. SR may also facilitate the simultaneous provision of several ecosystem processes, i.e. an ecosystem’s multifunctionality (Byrnes et al., 2014). However, since species do not contribute equally to ecosystem functioning, the diversity of species functional attributes adds another important dimension to ecosystem understanding (Duncan et al., 2015; Reiss et al., 2009). Functional diversity can enhance long-term stability, through functional redundancy and complementarity, and can help to buffer ecosystems against disturbances (O'Gorman et al., 2011).

Salinity is a key variable influencing SR in coastal areas, as natural differences in salinity among locations function as a threshold or “ecological barrier” for the distribution of freshwater and marine species, for example in the Baltic Sea (Olenin & Leppäkoski, 1999; Vuorinen et al., 2015). At the same time, an on average intensified water cycle caused by global warming is ~~currently ~~changing the salinity regimes of marine and coastal ecosystems (Durack et al., 2012; Liblik & Lips, 2019; Meier et al., 2021). It is important to understand how salinity influences species~~’~~ distributions in aquatic ecosystems to be able to better predict how potential changes may affect ecosystem functioning.

The Baltic Sea, one of the world’s largest brackish water bodies, exhibits a pronounced, geographically stable salinity gradient that is maintained by sporadic inflows of saline water from the North Sea through the Danish Straits and by freshwater input from large rivers, especially in the north. Hence, the Baltic Sea gradient can serve as model on the influence of salinity on species distributions (Johannesson & Andre, 2006; Ojaveer et al., 2010)~~, that has been studied for various organism groups~~. SR_{obs} i~~wa~~s often higher at the more saline conditions, e.g. for macroalgae, benthic bacteria~~, benthic macroalgae~~ and benthic meio- and macrofauna (Broman et al., 2019; Klier et al., 2018; Middelboe et al., 1997; Schubert et al., -2011). In other studies, SR_{obs} was highest at highest salinity, lowest at intermediate salinity and intermediate at lowest salinity, e.g. for phytoplankton and benthic macrofauna (Bonsdorff, 2006; Olli et al., 2019; Zettler et al., 2014), or there was no clear trend between SR_{obs} and salinity, e.g. for bacterio-, pico- and mesoplankton (Herlemann et al., 2016; Hu et al., 2016).

The species composition of fish in the Baltic Sea is regulated by salinity as well (Olsson et al., 2012; Pekcan-Hekim et al., 2016), even though other factors, such as temperature or habitat complexity, might also influence large-scale patterns of fish SR in estuaries (Vasconcelos et al., 2015; Schubert et al., 2011). In the Baltic Sea, ~~with~~ fish SR_{obs} is generally~~ being~~ higher in areas of~~at~~ higher compared to lower salinities (HELCOM, 2020; Hiddink & Coleby, 2012; Lappalainen et al., 2000; MacKenzie et al., 2007; Ojaveer et al., 2010; Pecuchet et al., 2016; Thorman, 1986). Various studies have also reported changes in fish SR_{obs} or species composition over time (e.g. Ammar et al., 2021; Törnroos et al., 2019). However, despite concerns that fish SR may decline in the future due to decreasing upper layer salinity (e.g. MacKenzie et al., 2007; Pecuchet et al., 2016; Vuorinen et al., 2015), information on how the complete coastal fish assemblage varies spatially in relation to the Baltic Sea salinity gradient, including potential differences across functional groups, is lacking. Hence, there is a need to complement already existing information on the influence of salinity on various Baltic Sea organism groups with more complete information in relation to fish diversity, taxonomically and functionally. This kind of understanding for multiple trophic levels is needed to better understand and predict how changing salinity, in the Baltic Sea and in coastal areas in general (Durack et al., 2012; Liblik & Lips, 2019), may affect ecosystem structure and functioning (MacKenzie et al., 2007). For example, if different species groups are differently affected, this may also change biotic interactions such as benthic-pelagic coupling, with effects on exchanges of energy, mass or nutrients between benthic and pelagic habitats (Griffiths et al., 2017). Moreover, understanding species richness at a broader, sub-regional scale is important to support analyses of potential species richness and species compositions at more local scales within each sub-basin.

To this aim, we compiled a large dataset on fish species observations in shallow (<30 m depth) Swedish coastal~~ and offshore~~ areas, based on multiple existing sources of Swedish mapping and monitoring combined over the years 1975–~~—~~2021~~0~~. The extensive dataset covered fish species incidence information from 1,63~~84~~8 unique observations/fishing occasions, during which in total 214,670~~415~~ species incidences were recorded. Geographically, the data covered 12 hydrographically distinct sub-basins, and a ca. 12~~ten~~-fold salinity gradient from close to freshwater conditions in the inner Baltic Sea to close to fully marine conditions at the Swedish west coast. The annual mean water temperature varies ca. 2-fold across the same area. Since SR_{obs} is strongly dependent on sample size, which differed between sub-basins, we used statistical rarefaction-extrapolation methods to estimate IC and ~~standardiz~~standardised SR per sub-basin. Further, we categorized each fish species according to origin (marine vs. freshwater) as well as three functional attributes based on coastal habitat preference, vertical preference and feeding habitat, and investigated the influence of salinity (and, for comparison, temperature) on fish SR in total and within the functional attributes. We discuss the results in the context of the regulating influence of salinity on fish SR and community composition in coastal ecosystems, and potential implications for conservation and ecosystem management.

2 Methods

2.1 Study system

The Baltic Sea, an enclosed, essentially non-tidal brackish marine region with a maximum and mean depth of 460 and 54 m, respectively, and a water residence time of 25–40 years, is, among the world's largest estuaries (area: 415,000 km^2; HELCOM, 2018). Its current brackish conditions were formed by gradual narrowing of its opening to the North Sea and have been in place since ca. 3,000 years (Russell, 1985). Due to its geographically variable but locally relatively stable salinity conditions the Baltic Sea has been called a "marine-brackish-limnic continuum" (Bonsdorff, 2006). Its surface salinity changes from <3 (psu) in the inner-most areas in the north and north-east to almost fully marine (ca. 29) in the Kattegat in the southwest (Table 1). Within this gradient, the Baltic Sea can be divided into hydrographically distinct sub-basins, mostly separated by shallow sounds or sills. To strengthen the database with respect to higher salinity areas we additionally included a North Sea sub-basin adjacent to Kattegat, i.e. Skagerrak (salinity ca. 30; Table 1).

Table 1. Salinity and temperature in Swedish coastal areas, given as mean (± SE) annual values per sub-basin across the years 1993–2019. Values represent conditions by the bottom at 0–30 m depth based on data from the EU Copernicus Marine Service Information (CMEMS, 2021).

Sub-basin	Salinity	Temperature (°C)
Bothnian Bay	2.68 ± 0.01	4.53 ± 0.23
The Quark	4.26 ± 0.01	5.38 ± 0.25
Bothnian Sea	5.10 ± 0.01	5.44 ± 0.22
Åland Sea	5.80 ± 0.01	6.44 ± 0.25
N Baltic Proper	6.37 ± 0.01	6.43 ± 0.22
E Gotland Basin	6.85 ± 0.01	7.30 ± 0.24
W Gotland Basin	6.88 ± 0.01	6.48 ± 0.20
Bornholm Basin	7.60 ± 0.02	8.15 ± 0.24
Arkona Basin	10.96 ± 0.07	8.92 ± 0.26
The Sound	23.42 ± 0.14	9.72 ± 0.24
Kattegat	29.02 ± 0.05	9.32 ± 0.21
Skagerrak	32.40 ± 0.03	9.62 ± 0.22

Reflecting its salinity conditions the Baltic Sea harbors a unique fish fauna with a mixture of freshwater species (e.g. Northern pike (*Esox lucius*), perch (*Perca fluviatilis*), pikeperch (*Sander lucioperca*)), and marine species (e.g. cod (*Gadus morhua*), herring (*Clupea harengus*); (Olsson et al., 2012). Further, many marine fish populations have adapted to the brackish conditions from their Atlantic counterparts (Laikre et al., 2005), for example Baltic cod and herring populations, and one flounder species is endemic to the Baltic Sea (Momigliano et al., 2018). Hence, the Baltic Sea may also have a unique value as a refuge for evolutionary lineages, and constitute an important genetic resource for management and conservation (Johannesson & Andre, 2006).

2.2 Species richness data

The primary source of fish species data was the Swedish National database of coastal fish (KUL; www.slu.se/kul), which holds public, quality-assured data from surveys encompassing coastal fish monitoring, mapping projects and surveillance programs over the entire salinity gradient of the Baltic Sea plus Skagerrak. Coastal areas were delineated using official national definition, and data records for 1975 to 2021 were extracted (last KUL database access 2021-04-27). Data from shallow depths <~~-~~30 m were selected, corresponding to the main represented sampling methods in the database (Table S1), and ~~with some margin~~approximately to the photic depth in the concerned coastal habitat types (Kaskela et al., 2012). This selection resulted in~~.~~ 154,172 data entries, i.e. individual fish that had been caught and identified to species by specialists, with the number of years with available data differing between sub-basins (Table S2). ~~Only sampling occasions with geographical coordinates and verified sampling references were included, giving 154,172 data entries, i.e. individual fish that had been caught and to species~~ by specialists~~. The size of the coastal shallow areas ranged from 240 km^2 (Åland Sea) to 5,798 km^2 (Bothnian Bay; Table 2). Corresponding data from shallow offshore areas (< 30 m) were also compiled for comparison (5,601 data entries).~~ Further, ~~additional,~~quality-assured data were included from 1) a national coastal trawl survey (n=4,420 ~~for coastal and n=382 for offshore areas~~), 2) the ICES-coordinated International Bottom Trawl Survey (IBTS, n=1,969 ~~for coastal and n=2,099 for offshore areas~~) and 3) national projects using ~~standardiz~~standardised methodology (n=893 ~~for coastal areas~~), all carried out in the Skagerrak, Kattegat and ~~T~~the Sound,~~ were included,~~ selecting only hauls from <30 m depth within the concerned geographical delineations. Corresponding trawl data for the inner Baltic Sea area ~~(<30 m)~~ are not collected at depth <30 m in Swedish waters. Across databases, only sampling occasions with geographical coordinates and verified sampling references were included.

Hence, data collected from multiple gears was~~ere~~ combined, including gill nets, fyke nets, seines, trap nets, low impact underwater detonations and trawls, in order to maximize the chance of including different species (Table S1). The ambition to collate information from all available fish surveys implied some differences in predominating data collection methods across the studied geographical range. The main data sources were trawls and trap net surveys in the most saline sub-basins, i.e. Skagerrak, Kattegat and t~~T~~he Sound, and gill net surveys in the remaining sub-basins (Table S1). ~~Since~~While each gear has a specific selectivity and efficiency, a previous comparison of data from gill and fyke net samplings at the Swedish west coast did not reveal consistent differences in biodiversity metrics, and the statistical~~The analytical~~ approaches were~~as~~ chosen to ~~encompass~~ minimize ~~this~~ a potential ~~variability when~~bias when ~~making comparisons~~ comparing SR among sub-basins (Bergström *et al.*, 2013, Chao et al., 2020; see also search of additional data sources below, and Sects. 2.3 and 4).

Data on observed SR, SR$_{obs}$, was available for all 12 sub-basins (Table 2), representing~~.,~~ between 4~~17~~ and 47 years of data, depending on sub-basin (Table S2). However, subsequent ~~but~~ statistical analyses and comparisons were conducted only for the 10 sub-basins containing data from at least 30~~25~~ sampling/fishing occasions, corresponding to ~~and~~ several hundred fish incidences ~~. This was the case for ten coastal sub-basins~~ (i.e. Bothnian Bay, t~~T~~he Quark, Bothnian Sea, Åland Sea, N Baltic Proper, W Gotland Basin, Bornholm Basin, t~~T~~he Sound, Kattegat, and Skagerrak~~; Table 2~~)~~, and one off-shore sub-basin (Kattegat).~~ ~~.~~This dataset is hereafter referred to as "raw data", and contained in total 160,453 entries (i.e. fish individuals caught and determined to species) from 1,638 sampling/fishing occasions at 4,571 unique locations.~~ for shallow coastal areas, and 2,762 entries from 137 sampling/fishing occasions at 199 unique locations for shallow offshore areas.~~ E Gotland Basin and Arkona Basin were not statistically analysed since we considered these sub-basins too under-sampled, with only 13 and 7 samplings, respectively, from 9 and 4 different years, and less than 100 species incidences in total (Tables 2, S2).

~~Moreover~~Additionally, we searched for evidence of fish species that had remained undetected in ~~our~~ the fish surveys (i.e. incidence database), by identifying fish species records from three additional sources, using the same criteria for geographical and depth delineations as above, i.e. 1) the SLU hosted national public database for citizens' reporting of species observations (SLU Swedish Species Information Centre, https://www.artportalen.se/;~~-~~ *n*=8,926,~~ for coastal and *n*=290 for offshore areas after~~ unreasonable species observations ~~were considered~~deemed as falsely identified were~~, and~~ discarded), 2) the national archive for oceanographic data hosted by the Swedish Meteorological and Hydrological Institute (SHARKweb, https://www.smhi.se/en/services/open-data/national-archive-for-oceanographic-data; *n*=1,259~~ for coastal and *n*=135 for offshore areas~~), and 3) published inventory data f~~or Swedish shallow coastal areas in~~rom Skagerrak, Kattegat and Bornholm Basin (Pihl & Wennhage, 2002; Pihl et al., 1994; Wikström A., 2009). ~~This~~ These "additional data sources" were used as complementary information on SR$_{obs}$ but could not be used in the statistical analysis since they did not have complete sampling and species incidence information. Further, our SR results were compared with the HELCOM (2020) checklist on macro-species containing information for all of the sub-basins and depths in the Baltic Sea region.

2.3 Analysis of species richness data

The raw data was first summarized to a dataset of *unique fish species* caught per fishing/sampling occasion in presence/absence format, and then further aggregated to an incidence frequency format, giving the observed total incidence of each species over the number of fishing/sampling occasions. This dataset is referred to as "fish incidence database". Each unique combination of a fishing/sampling location per date was defined as one sampling unit, and these were summed per sub-basin to obtain the sample sizes. Subsequently, incidence-based Hill diversity numbers of three "orders", which differ in their propensity to include or exclude relatively rarer species (Hill, 1973), were calculated to quantify the species diversity of each assemblage, i.e. 1) species richness (SR), which counts all species equally irrespective their incidence frequency, 2) Shannon diversity (ShD), which considers the incidence frequency and can be interpreted as the effective number of frequent species, and 3) Simpson diversity (SiD), which can be interpreted as the effective number of highly frequent species (Chao et al., 2014; Chao et al., 2020~~; Hill, 1973~~). Calculations were performed using the R package *iNEXT* ~~and the functions *ChaoRichness*, *ChaoShannon* and *ChaoSimpson*~~ (Chao et al., 2020; Hsieh et al., 2016), and the ~~Hill number~~values are hereafter referred to as *observed* SR, ShD and SiD, respectively. It should be noted that, using these methods, Shannon and Simpson diversity are expressed in terms of richness, i.e. number of species, which differs from other known formats. Specifically, ShD is the exponential of Shannon's entropy index, and SiD is the inverse of Simpson's concentration index (Chao et al., 2014).

SR$_{obs}$ is highly dependent on "sample completeness" (Colwell & Coddington, 1994; Hill, 1973) and ~~may~~ typically underestimates the "true" SR due to undetected species, an aspect ~~that is~~ ~~(also~~ referred to as under-sampling, sampling bias or sampling problem~~;~~ (Chao et al., 2014; Chao & Jost, 2015; Menegotto & Rangel, 2018). Similar to Hill numbers, "sample completeness" can be calculated for different "orders" (Chao et al., 2020). The zero-order sample completeness is hereafter referred to as inventory completeness (IC). It is calculated as the ratio of SR$_{obs}$ to the estimated "true" SR (i.e. observed plus undetected SR, see "estimated SR" below), hence giving the proportion of detected species without considering the species incidence frequencies. We calculated IC for the data merged over time, and including both resident and migrating/visiting fish species. The first-order sample completeness, hereafter referred to as "sample coverage" (SC), is a measure where species are weighted by their detection probabilities, giving the proportion of incidences detected from the estimated "true" incidences (Chao et al., 2020).

To correct for the effect of differing sample completeness on SR$_{obs}$, and allow accurate, unbiased comparisons between sub-basins, w~~W~~e used a coverage-based rarefaction and extrapolation method implemented for incidence data in the R package *iNEXT* (Chao et al., 2014, 2020; Hsieh et al., 2016)~~s to correct for this effect (Chao & Jost, 2012)~~. A coverage-based method was chosen because more traditional sample size-based corrections can introduce a systematic bias, since the number of samples needed to fully characterize a community depends on its SR (Chao & Jost, 2012). For each sub-basin, we obtained ~~The Chao richness method, a non-parametric asymptotic richness estimator that is based on the frequency of rare species in the sample (Chao et al., 2014), was used to estimate~~ 1) the rarefied SR, ShD and SiD, which were standardised to the minimum observed SC across all included sub-basins (~~,~~ hereafter referred to as *standardised* values~~;~~, ~~(~~i.e. SR$_{std}$, ShD$_{std}$ and SiD$_{std}$), and 2) the ~~actual, asymptotic~~ fish SR extrapolated to twice the actual sample size ~~for each sub-basin (*ChaoRichness* function in the R package *iNEXT*; Hsieh et al., 2016), and the estimated parameters were interpreted as described and exemplified in (Chao et al., 2020). The respective values are~~ , (hereafter referred to as *estimated* values ~~(;~~, i.e. SR$_{est}$, ShD$_{est}$ and SiD$_{est}$~~;~~)~~). Inventory (sample) completeness (IC) was calculated based on sample coverage (Chao & Jost, 2012; Hsieh et al., 2016). To compare data across sub-basins, SR, ShD and SiD were standardized to the minimum observed IC across sub-basins (*estimateD* function in the R package *iNEXT;* Hsieh et al., 2016). The respective values are hereafter referred to as *standardized* values (i.e. SR$_{std}$, ShD$_{std}$ and SiD$_{std}$)~~ Chao et al., 2014, 2020; Hsieh et al., 2016). Similar analyses were also conducted for SR of fish with different functional attributes (see Sect. 2.4). All calculations were conducted using R version 4.0.4 (R Core Team, 2021).

2.4 Fish functional attributes

All observed fish species were assigned functional attributes based on ecological and behavioral traits, as well as into being of either marine or freshwater origin (Kullander, 2002). The affinity of each species to different parts of the coastal habitat, or habitat preference, was assigned based on (Elliott & Dewailly, 1995; Pihl & Wennhage, 2002), however with certain adaptations to suit both marine and brackish conditions (Table S3-S4~~6~~). Applied categories were: Catadromous or anadromous migrants (CA), using coastal habitats only when migrating between marine and freshwaters for spawning and feeding; Marine juvenile migrants (MJ), using coastal habitats primarily as nursery or feeding grounds; Marine visitors (MV), occurring irregularly in the coastal area, having their primary habitat in deeper waters; Marine seasonal migrants (MS), making regular seasonal visits to coastal habitats, usually as adults; and Coastal residents (CR), spending almost their complete life cycle in coastal habitats or the littoral coastal zone. The main vertical distribution of each species in the water column, considering the adult stage, was assigned based on (Elliott & Dewailly, 1995; Koli, 1990) as: Pelagic (P), living mainly in the water column; Demersal (D), mainly associated with the bottom substrate; Demersal-pelagic (DP), alternating between the water column and bottom substrate; and Benthic (B), staying close to the seabed. Main feeding habits were assigned by combining information on feeding guild (Elliott & Dewailly, 1995) with trophic levels (TL) and principal diet composition (Froese and Pauly, 2021), as: Piscivores (Pi; TL 3.6–~~—~~4.4); Invertivores~~ebrate~~ and piscivore~~fish eater~~s (IP~~F~~; TL 2.9–~~—~~3.9); Invertivore~~ebrate eater~~s (I; TL 2.8–~~—~~3.9); Planktivores (PL; TL 3.1–~~—~~3.2) and Omnivores (O; TL 2.8–~~—~~3.5).

2.5 Sea water salinity and temperature

For each sub-basin, data on ambient salinity and temperature was extracted from the “Baltic Sea Physics Reanalysis” product, as calculated by the Swedish Meteorological and Hydrological Institute (SMHI) with the coupled physical-biochemical model system NEMO-SCOBI, and available from year 1993 (CMEMS, 2021). This encompassed full coverage layers with a 4 km x 4 km grid. Monthly mean values close to the sea bed for all grid cells representing areas less than 30 m depth were first identified, and then used for calculating long-term means and standard deviations for the years 1993–~~-~~2019.

2.6 Statistical analyses

Linear regressions were used to analys~~z~~e the relationships between salinity and temperature, respectively, and observed, ~~standardiz~~standardised and estimated SR, ShD and SiD. To test for any additional explanatory effect of temperature, after accounting for the effect of salinity, we used ANOVA to compare models with salinity as the only explanatory factor with models with salinity plus temperature as explanatory factors. Furthermore, relationships were tested between the different functional attributes and salinity. To reduce skewness and approximate normality, left-skewed response variables were $\log_{10}$-

transformed prior to analysis, or, in two cases where the response variable included zero-values, Yeo-Johnson transformed (Yeo and Johnson, 2000). All analyses were conducted using R version 4.0.4 (R Core Team, 2021).

3 Results

3.1 Salinity and temperature

The annual mean salinity varied more than 12~~ten~~-fold in the shallow coastal areas across the studied sub-basins, from 2.7 in the northernmost Baltic Sea to 32.4 in the Skagerrak. Across the same geographical range, the annual mean water temperature varied from 4.5°C in the north to ca. 9–~~-~~10°C in the Sound and outwards (Table 1).

3.2 Fish species observations and distribution

SR_{obs} varied from 23 (Arkona Basin) to 101 (Kattegat) ~~in shallow coastal areas~~ (Table 2, that also contains related information on e.g. sample size and species incidences per sub-basin), and amounted to 125 across sub-basins and years. Since IC was <100% (see Sect. 3.3), this can be assumed a lower bound estimate of the true SR. Indeed, the additional data sources contained 19 more species that were not represented in the fish incidence database, resulting in a total fish SR_{obs} of 144 ~~in coastal areas~~ (Tables S3, S4). Of the species in the fish incidence database, 49% occurred only in the higher salinity Skagerrak-Kattegat region including t~~T~~he Sound, 15% occurred only in the Baltic Sea region (i.e., inside t~~T~~he Sound), and 36% occurred in both these regions. The ~~most widely ranging~~ species ranging most widely ~~in coastal areas~~ were herring (*Clupea harengus*), brown trout (*Salmo trutta*), European sprat (*Sprattus sprattus*) and eelpout (*Zoarces viviparous*), with incidences reported from all 12 sub-basins (Tables S3, S4~~2~~).

~~For shallow offshore areas, SR_{obs} varied from 11 (N Baltic Proper) to 74 (Kattegat; Table 2), and amounted to 96 across sub-basins and years. The additional data sources contained information on 14 more species, resulting in a total fish SR_{obs} of 110 (Table S3). Of the species in the fish incidence database, 48% occurred only in the higher salinity Skagerrak-Kattegat region including The Sound, 21% occurred only in the Baltic Sea region, and 31% occurred in both regions. Herring was the only species reported in all the nine sub-basins for which fish incidence data for shallow offshore areas was available (Table S4).~~

Table 2. Summary information ~~and statistics~~ for the fish incidence database and additional data sources, covering 12 sub-basins in Swedish shallow coastal areas (<30 m depth). Inventory completeness (IC), sample coverage (SC), s~~Standardiz~~Standardised (SR_{std}) and estimated (SR_{est}) values were ~~calculated~~ statistically estimated for sub-basins with sample size ~~>25~~>30 fishing/sampling occasions. Of these, SR_{std} was calculated for a~~n~~ S~~I~~C of 98.5%, which was the lowest S~~I~~C among sub-basins with sufficient data (i.e. Åland Sea ~~coastal areas~~).~~:~~ For comparison, the last two columns show SR_{obs} when also including presence information from additional data sources (not included in the statistical analyses, see Sect. 2.2), or for the whole of each Baltic Sea sub-basin according to HELCOM (2020), i.e. across countries and depths. NA: not applicable; n.d.: not determined.

	Species incidence data set									Including ~~A~~additional data sources	
	Observations					Statistical estimations ~~Statistical estimations~~					
Sub-basin	**Sample size ~~(i.e. fishing/sampling~~**	**Species incidences**[a]	**SR_{obs} (incidence data alone)**	**Singletons**	**Doubletons**	**IC (%)**[b]	**SC~~IC~~ (%)**[c]	**SR_{std} (with CI)**	**SR_{est} (± SE)**[d] ~~[b]~~	**SR_{obs} (incidence data plus additional data sources, Swedish waters)**	**SR_{obs} all countries and depths (HELCOM 2020)**~~[c]~~
Bothnian Bay	70	553	29	4	0	82.9	99.3	24_{25}^{28}	35 ± 7	34	51
The Quark	71	754	30	4	2	88.2	99.5	26_{24}^{28}	34 ± 5	35	56
Bothnian Sea	194	2 222	42	2	0	97.7	99.9	37_{36}^{38}	43 ± 2	50	74
Åland Sea	31	394	32	6	3	84.2	98.5*	32_{28}^{35}*	38 ± 6	45	71
N Baltic Proper	77	1 046	42	6	3	87.5	99.4	36_{34}^{38}	48 ± 6	56	67
E Gotland Basin	13	94	25	8	5	n.d.	n.d.	n.d.	n.d.	37	82
W Gotland Basin	411	5 123	53	6	2	85.5	99.9	39_{38}^{40}	62 ± 10	60	67
Bornholm Basin	68	837	46	5	1	79.3	99.4	42_{40}^{44}	58 ± 17	59	
Arkona Basin	7	67	23	7	7	n.d.	n.d.	n.d.	n.d.	37	110
The Sound	119	1 373	61	8	4	88.4	99.4	54_{51}^{57}	69 ± 7	70	144
Kattegat	353	6 012	101	11	8	92.7	99.8	78_{76}^{80}	109 ± 6	114	178
Skagerrak	230	3 195	69	13	3	76.7	99.6	52_{50}^{53}	90 ± 16	106	NA[e]

[a] Sum of the number of species observed across all sampling occasions. Please note that this does not correspond to "entries" in Sect. 2.2, which is individual fish caught and determined to species.

[b] Percentage of species detected from the estimated "true" (i.e. observed plus undetected) SR (Chao et al., 2020).

[c] Percentage of incidences detected from the estimated “true” (i.e. observed plus undetected) incidences (Chao et al., 2020).

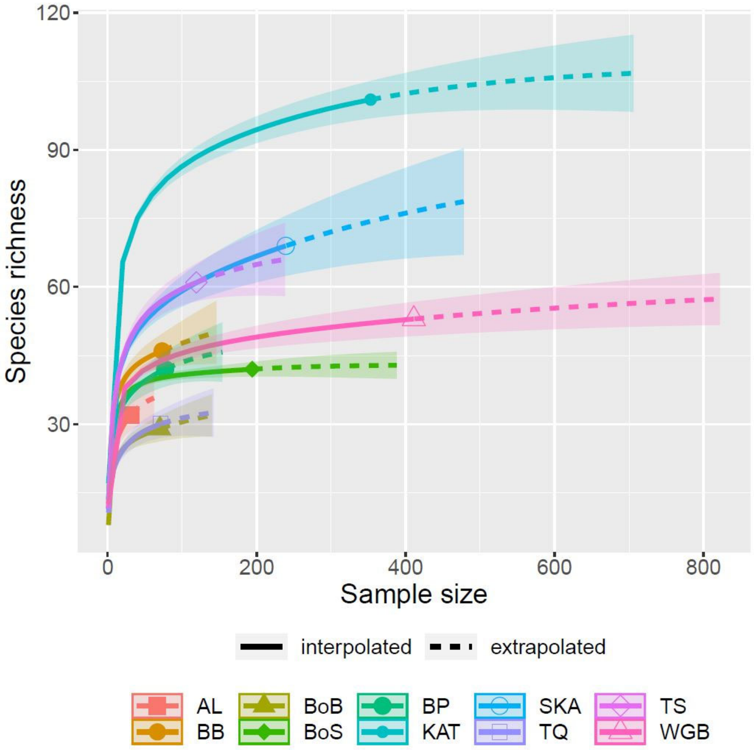
~~[b]~~[d] Considered a lower bound estimate (Chao et al., 2020).

[e] Not included in the Baltic Sea region

3.3 Inventory completeness and sample coverage

The fish species IC in Swedish shallow coastal areas varied from 76~~98~~.7~~5~~% in ~~the Åland Sea~~Skagerrak to 97~~9~~.7~~9~~% in the ~~W Gotland Basin and the~~ Bothnian Sea for the assessed sub-basins (see section 2.2), suggesting that ca. 2–23~~0.1–1.5~~% of species statistically likely to exist remained undetected (Table 2). The SC exceeded 98.5% in all sub-basins (Table 2), ~~these~~suggesting that these undetected species were highly rare, likely representing <1.5% of incidences. The species accumulation curves (SAC) show the SR_{obs} at the conducted sample sizes, and SR estimated for hypothetical smaller and larger sample sizes, including 95% confidence intervals. According to these, the steepest increase of accumulated species occurred with the first ca. 20 samplings in all sub-basins, and coastal fish SR was highest in the Kattegat, followed by the Skagerrak and t~~T~~he Sound, and lowest in the other seven sub-basins (~~i.e. confidence intervals not overlapping,~~ Fig. 1a).

The SAC’s also visualize differences in IC between sub-basins. For the three most saline sub-basins, Skagerrak, Kattegat and t~~T~~he Sound, the SACs were still clearly increasing with increasing sample size even when extrapolating to double the actual sample size. Hence, SR_{est} for these sub-basins are more uncertain and more likely biased low than for sub-basins where the curve flattened, illustrating a more complete inventory, e.g. W Gotland Basin and t~~T~~he Bothnian Sea (Fig. 1a). SR_{est}, estimated based on extrapolation of the information in the fish incidence database, were similar to SR_{obs} if complementing the incidence data with records from the additional data sources (Table 2).


120
90
60
30
Species richness
0
200
400
600
800
Sample size
interpolated
extrapolated
AL
BB
BoB
BoS
BP
KAT
SKA
TQ
TS
WGB

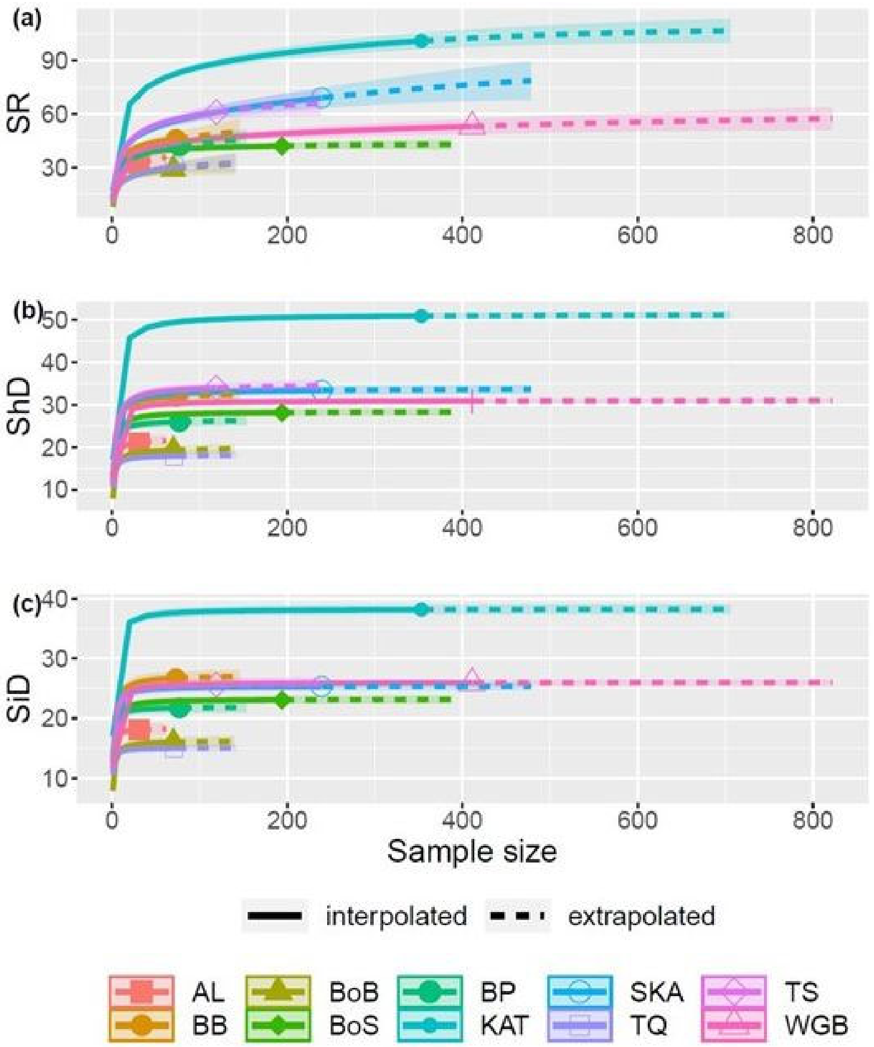


Figure 1. Sample-size-based sampling curves with 95% confidence intervals (shaded areas), showing rarefaction/interpolation (solid) and extrapolation ~~(~~up to twice the actual sample size (Chao et al., 2020; dotted) line segments for (a) species richness (SR), (b) Shannon diversity (the effective number of frequent species in the assemblage, ShD) and (c) Simpson diversity (the effective number of very frequent species in the assemblage, SiD) of fish in coastal areas of the 10 ~~analyzed~~ assessed sub-basins. The intersection points between solid and dotted lines represent the observed values. Legend acronyms are AL: Åland Sea, BB: Bornholm Basin, BoB: Bothnian Bay, BoS: Bothnian Sea, BP: N Baltic Proper, KAT: Kattegat, SKA: Skagerrak, TQ: The Quark, TS: The Sound and WGB: W Gotland Basin.

~~For shallow offshore areas, only one sub-basin had enough data to conduct statistical rarefaction and extrapolation (i.e., Kattegat, Table 2). IC amounted to 99.3%, and also here SR_{est} was similar to SR_{obs} when incidence data and species presence information from additional sources were combined (Table 2). A comparison of SR_{est} offshore areasuggests that, in Kattegat, fish SR is ca. 30% higher in coastal compared to offshore areas. A comparison based on SR_{obs} when complementing the incidence data with additional data sources suggests ca. 50% higher SR in the coastal compared to offshore shallow Kattegat waters (Table 2).~~

~~**Table 3. Shannon diversity (ShD) and Simpson diversity (SiD) for coastal and offshore areas. Calculated values are given for all sub-basins, and standardized (std) and estimated (est) values are given for the sub-basins with a sample size ≥ 25 fishings/samplingsShD gives the effective number of frequent species (the exponential of Shannon's entropy index), and SiD the effective number of highly frequent species (the inverse of Simpson's concentration index) in the assemblage (Chao et al. 2020, Chao et al. 2014). NA: not applicable; n.d.: not determined.**~~

	~~**Shannon Diversity**~~			~~**Simpson diversity**~~		
~~**Sub-basin**~~	~~**Calculated ShD**~~	~~**ShD_{std} (with upper and lower confidence limits)**~~	~~**ShD_{est} (± SE)**~~	~~**Calculated SiD**~~	~~**SiD_{std} (with upper and lower confidence limits)**~~	~~**SiD_{est} (± SE)**~~
~~Bothnian Bay~~	~~19~~		~~20 ± 1~~	~~16~~		~~16 ± 1~~
~~The Quark[a]~~	~~18~~		~~18 ± 1~~	~~15~~		~~15 ± 0.3~~
~~Bothnian Sea~~	~~28~~		~~28 ± 0.4~~	~~23~~		~~23 ± 0.4~~
~~Åland Sea[a]~~	~~21*~~	~~*~~	~~22 ± 1~~	~~18*~~	~~*~~	~~18 ± 1~~
~~N Baltic Proper~~	~~26~~		~~26 ± 1~~	~~22~~		~~22 ± 0.4~~
~~E Gotland Basin~~	~~18~~	~~n.d.~~	~~n.d.~~	~~15~~	~~n.d.~~	~~n.d.~~
~~W Gotland Basin~~	~~31~~		~~31 ± 0.2~~	~~26~~		~~26 ± 0.3~~
~~Bornholm Basin~~	~~32~~		~~33 ± 1~~	~~27~~		~~27 ± 1~~
~~Arkona Basin~~	~~18~~	~~n.d.~~	~~n.d.~~	~~15~~	~~n.d.~~	~~n.d.~~
~~The Sound[a]~~	~~34~~		~~35 ± 1~~	~~26~~		~~26 ± 1~~
~~Kattegat~~	~~51~~		~~51 ± 1~~	~~38~~		~~38 ± 0.4~~
~~Skagerrak~~	~~33~~		~~34 ± 1~~	~~25~~		~~25 ± 0.3~~

~~[a] No offshore areas occur in these sub-basins.~~

3.4 Shannon and Simpson diversity

Rarefaction and extrapolation SACs carried out for Shannon diversity (ShD) show that the effective number of frequently recorded fish species was quite well captured by the samplings in all ~~analyzed~~ statistically assessed sub-basins, illustrated by SACs with small remaining slopes at extrapolated higher sample size. As for SR_{obs}, ShD was highest in Kattegat, while the remaining nine sub-basins clustered in two separate groups. The lowest ShD~~'s~~ w~~ere~~as noted for the Åland Sea, t~~T~~he Quark and Bothnian Bay (Fig. 1b, Table S~~3~~5). The effective number of highly frequent species, i.e. Simpson diversity (SiD), was also well captured in all sub-basins, being highest in Kattegat, while SiD in the remaining sub-basins clustered in four groups (Fig. 1c, Table S~~3~~5).

3.5 ~~Standardiz~~Standardised and estimated species richness

To compare coastal fish SR, ShD and SiD across sub-basins, we estimated their ~~standardiz~~standardised values against the minimum observed S~~I~~C in any of the sub-basins. This represented a ~~standardiz~~standardisation to the ~~I~~SC of the Arkona Basin data (98.5%; Tables 2 and S3). SR_{std} was ca. three times higher in the relatively more saline Kattegat (SR_{std} = 78) compared to the least saline Bothnian Bay (SR_{std} = 24), as also confirmed by comparing the respective SR_{est} values (Table 2). The differences were smaller for ShD and SiD. For example, based on SiD_{std} and SiD_{est}, the effective number of highly frequent species was ca. two times higher in coastal areas of the Kattegat compared to the Bothnian Bay (Table S3). This implies, as also seen from the SACs (Fig. 1), that the frequent and most frequent fish species were captured quite well by the samplings for all sub-basins, and that remaining uncertainties in differences across the salinity gradient is mostly due to uncertainty in the numbers of rare and very rare fish species. The estimated SR per sub-basin (SR_{est}, statistical extrapolation of the fish incidence data) was very similar to the total observed species richness when also including species presence information from additional data sources, with a mean ratio of 1.07 ± 0.03 (calculated based on data presented in Table 2).

3.6 Relationships of SR with salinity and temperature

Species richness increased with increasing mean water salinity, which explained 37–~~-~~55% of the variance in the data based on SR_{obs}, ShD_{obs} and SiD_{obs}. Using the ~~standardiz~~standardised or estimated values, i.e. values corrected for sample size, resulted in stronger correlations, i.e. higher explained variance (40–~~-~~77%; Fig. 2a-c, Table S64). SR_{obs}, ShD_{obs} and SiD_{obs} were not correlated with mean water temperature, but, using the ~~standardiz~~standardised and estimated values, correlations with temperature were also significant (explaining 48–~~-~~77% of the variance; Fig. 2d-f, Table S64). The slope estimates of the linear regressions differed more across observed, ~~standardiz~~standardised and estimated values for SR than for ShD and SiD (~~Fig. 2,~~ Table S64). In all cases, adding temperature as explanatory variable to the regression models with salinity as explanatory variable did not improve the model (all *P*>0.14).

3.7 Fish functional attributes

Of the recorded fish species, 74% and 26% ~~of the fish species recorded in shallow coastal areas~~ were of marine and freshwater origin, respectively (based on the incidence data, i.e. SR_{obs} of 92 vs. 33 species; Table S3~~2~~). In the most saline sub-basins, i.e. Skagerrak and Kattegat, the SR_{std} of marine fish species was seven to ten times higher than that of freshwater fish species. The SR_{std} of marine vs. freshwater fish were rather similar in the central Baltic Sea, while in the northernmost and least saline sub-basins, i.e. Bothnian Sea, t~~T~~he Quark and Bothnian Bay, the SR_{std} of freshwater fish species exceeded the SR_{std} of marine fish species by two to three times. In total, the marine fish SR_{std} decreased by a factor of 8–~~-~~11 along the salinity gradient, from 39 and 57 marine species (SR$_{std}$) in Skagerrak and Kattegat to 5 in the Bothnian Bay. Freshwater fish SR$_{std}$ increased by a factor of 2–~~-~~4 along the same gradient (Fig. 3, Table S3~~2~~). These distributional patterns of freshwater vs. marine fish species were also reflected by negative univariate correlations of freshwater SR (obs, std and est) with salinity, and positive univariate correlations of marine SR with salinity (Fig. S1, Table 3~~5~~).

~~**Table 4. Statistical indicators for the correlations between fish species richness (SR), Shannon Diversity (ShD) and Simpson Diversity (SiD), and salinity or annual mean water temperature in coastal areas of the studied sub-basins. The linear regressions were carried out separately for observed (*obs*), standardized (*std*) and estimated (*est*) values in each case. n.s.=not significant.**~~

~~**Response variable**~~		~~**Salinity**~~			~~**Water temperature**~~		
		~~**Parameters (± SE)**~~	~~**Adjusted R²**~~	~~***P*-value**~~	~~**Parameters (± SE)**~~	~~**Adjusted R²**~~	~~***P*-value**~~
~~SR~~	~~*obs*~~	~~$\log_{10}(y)=1.5 (\pm0.1) + 0.014 (\pm0.004)*x$~~	~~0.55~~	~~0.004~~	~~$\log_{10}(y)=1.2 (\pm0.2) + 0.06 (\pm0.03)*x$~~	~~0.21~~	~~n.s. (0.078)~~
	~~*std*~~	~~$\log_{10}(y)=1.45 (\pm0.04) + 0.012 (\pm0.002)*x$~~	~~0.70~~	~~0.002~~	~~$\log_{10}(y)=1.1 (\pm0.1) + 0.07 (\pm0.01)*x$~~	~~0.77~~	~~0.001~~
	~~*est*~~	~~$\log_{10}(y)= 1.57 (\pm0.04) + 0.014 (\pm0.002)*x$~~	~~0.77~~	~~0.001~~	~~$\log_{10}(y)=1.2 (\pm0.1) + 0.08 (\pm0.02)*x$~~	~~0.76~~	~~0.001~~
~~ShD~~	~~*obs*~~	~~$y=19.3 (\pm3.2) + 0.7 (\pm0.2)*x$~~	~~0.48~~	~~0.007~~	~~$y=5.0 (\pm10.6) + 3.1 (\pm1.4)*x$~~	~~0.25~~	~~n.s. (0.055)~~
	~~*std*~~	~~$y= 21.0 (\pm2.9) + 0.6 (\pm0.2)*x$~~	~~0.54~~	~~0.009~~	~~$y=2.3 (\pm7.6) + 3.7 (\pm1.0)*x$~~	~~0.57~~	~~0.007~~
	~~*est*~~	~~$y=21.7 (\pm3.1) + 0.7 (\pm0.2)*x$~~	~~0.55~~	~~0.009~~	~~$y=1.4 (\pm7.9) + 4.0 (\pm1.1)*x$~~	~~0.58~~	~~0.006~~
~~SiD~~	~~*obs*~~	~~$y=17.1 (\pm2.5) + 0.4 (\pm0.2)*x$~~	~~0.37~~	~~0.022~~	~~$y=7.8 (\pm7.8) + 2.0 (\pm1.0)*x$~~	~~0.19~~	~~n.s. (0.087)~~
	~~*std*~~	~~$y=18.4 (\pm2.3) + 0.4 (\pm0.1)*x$~~	~~0.41~~	~~0.027~~	~~$y=6.0 (\pm5.9) + 2.4 (\pm0.8)*x$~~	~~0.48~~	~~0.016~~
	~~*est*~~	~~$y=18.7 (\pm2.5) + 0.4 (\pm0.2)*x$~~	~~0.40~~	~~0.031~~	~~$y=5.3 (\pm6.2) + 2.6 (\pm0.8)*x$~~	~~0.48~~	~~0.016~~

Concerning habitat preference, half of the fish species in Swedish shallow coastal areas were classified as being coastal resident species (CR; based on incidence data only, SR$_{obs}$: 63 species, Table S3~~2~~). This group dominated coastal fish assemblages in all sub-basins, with CR SR$_{std}$ of 19–~~-~~30 across sub-basins (Fig. S2~~4~~, Table S7~~2~~), and was not linearly related to salinity (Fig. 4a, Table 3~~5~~). A similar result was noted for catadromous or anadromous fish species, with SR$_{std}$ ~~between~~ of 2–~~and~~ 6 ~~in each~~across sub-basins, ~~that was~~and CA SR$_{std}$ not related to salinity (Fig. 4b, S2, Tables 3, S7~~2, 5~~). In the more saline sub-basins, fish species classified as marine visitors or as marine juvenile or seasonal migrants contributed significant numbers to the SR_{std}, while these species groups did not exist or contributed only little to the SR_{std} in the Baltic Sea region (Fig. S2~~4~~, Table S7~~2~~). Reflecting this pattern, the SR of marine migrating or visiting fish species (i.e. MJ, MS and MV) was significantly positively related to salinity in most cases, with the strongest correlations for marine juvenile visitors (MJ; Fig. 4~~S~~c-e~~2~~, Table 3~~5~~).

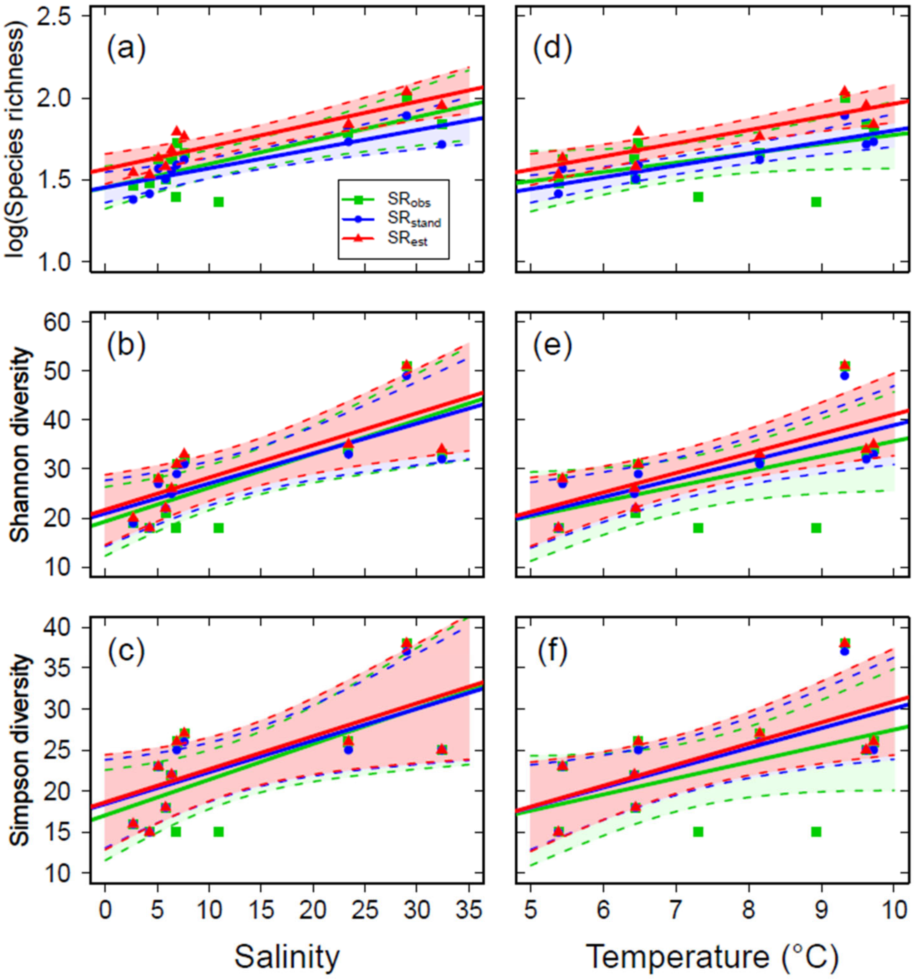


Figure 2.~~ Scatterplots of the f~~ Fish species richness estimates ~~against ~~in relation to mean salinity (left column) and mean water temperature (right column), with total species richness ($\log_{10}$-transformed; a and d), Shannon diversity (effective number of frequent species; b and e) and Simpson diversity (effective number of highly frequent species; c and f: Each plot shows the observed, ~~standardiz~~standardised and estimated values, and, when significant (*P*<0.05), the linear regression lines (solid) and 95%-confidence intervals (shaded areas surrounded by dashed lines: The different lines and shaded confidence intervals are partly overlying each other within the panels in some cases, indicating very similar regression statistics. For regression equations and statistics, see Table 3~~4~~.

Concerning vertical distribution, benthic fish species (B) were important contributors to SR_{std} in the sub-basins of higher salinity, but only few or no fish species belonged to this group in the less saline sub-basins (Fig. S3~~5~~; Table S7~~2~~). A similar, though less pronounced~~,~~ distribution pattern was also found for demersal fish species (D). Accordingly, the SR of these groups were positively related to salinity in all cases (i.e. for SR_{obs}, SR_{std} and SR_{est}, Fig. 5a,b~~S3,~~; Table 3~~5~~). The SR of demersal-pelagic (DP) fish species varied between sub-basins with a SR_{std} of 6–~~-~~16, not related to salinity (Fig. 5c, Table 3). A similar picture was found for pelagic fish species (P), where SR_{std} varied between 5–~~-~~12 across sub-basins (Fig. S3~~5~~, Table S7~~2~~) and was not related to salinity (Fig. 5d~~S3~~, Table 3~~5~~).

The two most common feeding groups~~ observed in shallow coastal areas~~, across all sub-basins, were ~~invertebrate ~~invertivore and piscivore~~fish eating~~ species (IP~~F~~) as well as invert~~ebrate feeders~~ivores (I). The third-most represented feeding group was piscivores~~ous fish species~~ (Pi), followed by ~~planktivorous ~~planktivores and ~~omnivorous ~~omnivores~~species~~ in lower and often similar SR_{std} (Fig. S4~~6~~, Table S7~~2~~). SR_{std} of Pi and IP~~F~~ increased with increasing salinity, and SR_{std} and SR_{est} of I increased with increasing salinity (Fig. S54, Table 3~~5~~).

Table 3~~5~~. ~~Statistical relationship~~Linear regressions between observed (*obs*), ~~standardiz~~standardised (*std*) and estimated (*est*) SR for fish functional attributes in Swedish shallow coastal areas and salinity. When YJ(y), the response variable was Yeo-Johnson transformed (Yeo and Johnson, 2000). n.s.=not significant.

Response variable			**Parameters (± SE)**	***n***	**R^2**	***P*-value**
Origin	Marine	*obs*	$\log_{10}(y)=1.0\ (\pm 0.1) + 0.03\ (\pm 0.01)*x$	12	0.74	<0.001
		std	$\log_{10}(y)=0.9\ (\pm 0.1) + 0.03\ (\pm 0.01)*x$	10	0.71	0.001
		est	$\log_{10}(y)=1.1\ (\pm 0.1) + 0.03\ (\pm 0.01)*x$	10	0.66	0.003
	Freshwater	*obs*	$y=22.0\ (\pm 3.0) -0.6\ (\pm 0.2)*x$	12	0.39	0.018
		std	$y=19.0\ (\pm 1.1) - 0.4\ (\pm 0.1)*x$	10	0.84	<0.001
		est	$y=25.4\ (\pm 2.5) - 0.5\ (\pm 0.2)*x$	10	0.47	0.017
Habitat preference	CR	*obs*	$y=25.3\ (\pm 4.6) + 0.1\ (\pm 0.3)*x$	12	-0.08^a	n.s. (0.661)
		std	$y=26.5\ (\pm 2.0) - 0.1\ (\pm 0.1)*x$	10	-0.04^a	n.s. (0.538)
		est	$y=32.5\ (\pm 3.0) + 0.1\ (\pm 0.2)*x$	10	-0.10^a	n.s. (0.665)
	CA	*obs*	$\log_{10}(y)=0.4\ (\pm 0.1) + 0.01\ (\pm 0.01)*x$	12	-0.10^a	n.s. (0.351)
		std	$\log_{10}(y)=0.5\ (\pm 0.1) + 0.005\ (\pm 0.004)*x$	10	-0.10^a	n.s. (0.314)
		est	$\log_{10}(y)=0.5\ (\pm 0.1) + 0.006\ (\pm 0.005)*x$	10	-0.10^a	n.s. (0.287)
	MJ	*obs*	$\log_{10}(y)=0.14\ (\pm 0.13) + 0.04\ (\pm 0.01)*x$	12	0.60	0.002
		std	$\log_{10}(y)=0.57\ (\pm 0.09) + 0.016\ (\pm 0.004)*x$	6	0.69	0.025
		est	$\log_{10}(y)=0.43\ (\pm 0.07) + 0.018\ (\pm 0.004)*x$	6	0.84	0.007
	MS	*obs*	$y=0.7\ (\pm 0.6) + 0.3\ (\pm 0.04)*x$	12	0.79	<0.001
		std	$y=2.4\ (\pm 1.0) + 0.2\ (\pm 0.1)*x$	6	0.67	0.029
		est	$y=3.0\ (\pm 1.4) + 0.2\ (\pm 0.1)*x$	6	0.55	n.s. (0.056)
	MV	*obs*	$YJ(y)=-1.0\ (\pm 0.2) + 0.09\ (\pm 0.01)*x$	12	0.81	<0.001
		std	$y=-3.4\ (\pm 7.1) + 0.7\ (\pm 0.3)*x$	4	0.65	n.s. (0.123)
		est	$y=-6.5\ (\pm 10.8) + 1.3\ (\pm 0.4)*x$	4	0.72	n.s. (0.100)
Vertical distribution	B	*obs*	$YJ(y)=-1.0\ (\pm 0.2) + 0.09\ (\pm 0.01)*x$	12	0.76	<0.001

		std	$\log_{10}(y)=0.3\ (\pm 0.1) + 0.031\ (\pm 0.004)*x$	7	0.91	0.001
		est	$\log_{10}(y)=0.4\ (\pm 0.1) + 0.039\ (\pm 0.004)*x$	7	0.95	<0.001
	D	*obs*	$\log_{10}(y)=1.0\ (\pm 0.1) + 0.02\ (\pm 0.01)*x$	12	0.44	0.011
		std	$\log_{10}(y)=0.97\ (\pm 0.04) + 0.013\ (\pm 0.013)*x$	10	0.70	0.002
		est	$\log_{10}(y)=1.1\ (\pm 0.1) + 0.014\ (\pm 0.004)*x$	10	0.54	0.010
	DP	*obs*	$y=13.1\ (\pm 2.1) - 0.1\ (\pm 0.1)*x$	12	-0.10[a]	n.s. (0.679)
		std	$y=13.9\ (\pm 1.3) - 0.1\ (\pm 0.1)*x$	10	0.16	n.s. (0.136)
		est	$y=15.5\ (\pm 1.8) - 0.03\ (\pm 0.11)*x$	10	-0.12[a]	n.s. (0.792)
	P	*obs*	$\log_{10}(y)=0.8\ (\pm 0.1) + 0.006\ (\pm 0.004)*x$	12	0.07	n.s. (0.203)
		std	$\log_{10}(y)=0.80\ (\pm 0.05) + 0.004\ (\pm 0.003)*x$	10	0.06	n.s. (0.243)
		est	$\log_{10}(y)=0.9\ (\pm 0.1) + 0.008\ (\pm 0.004)*x$	10	0.27	n.s. (0.072)
Feeding habit	Pi	*obs*	$\log_{10}(y)=0.70\ (\pm 0.06) + 0.018\ (\pm 0.004)*x$	12	0.63	0.001
		std	$\log_{10}(y)=0.69\ (\pm 0.06) + 0.014\ (\pm 0.004)*x$	10	0.64	0.004
		est	$\log_{10}(y)=0.76\ (\pm 0.06) + 0.020\ (\pm 0.004)*x$	10	0.77	0.001
	IP~~F~~	*obs*	$y=8.7\ (\pm 1.8) + 0.7\ (\pm 0.1)*x$	12	0.75	<0.001
		std	$y=9.9\ (\pm 1.1) + 0.4\ (\pm 0.1)*x$	10	0.81	<0.001
		est	$y=10.7\ (\pm 1.9) + 0.8\ (\pm 0.1)*x$	10	0.84	<0.001
	I	*obs*	$\log_{10}(y)=0.8\ (\pm 0.2) + 0.02\ (\pm 0.01)*x$	12	0.16	n.s. (0.108)
		std	$\log_{10}(y)=0.85\ (\pm 0.04) + 0.015\ (\pm 0.003)*x$	10	0.79	<0.001
		est	$\log_{10}(y)=0.93\ (\pm 0.04) + 0.018\ (\pm 0.002)*x$	10	0.86	<0.001
	PL	*obs*	$\log_{10}(y)=0.5\ (\pm 0.1) + 0.007\ (\pm 0.004)*x$	12	0.12	n.s. (0.142)
		std	$\log_{10}(y)=0.4\ (\pm 0.1) + 0.008\ (\pm 0.003)*x$	10	0.36	0.041
		est	$\log_{10}(y)=0.5\ (\pm 0.1) + 0.007\ (\pm 0.004)*x$	10	0.20	n.s. (0.108)
	O	*obs*	$y=3.6\ (\pm 0.9) - 0.1\ (\pm 0.1)*x$	12	-0.03[a]	n.s. (0.419)
		std	$y=3.2\ (\pm 0.5) + 0.1\ (\pm 0.04)*x$	8	0.23	n.s. (0.131)
		est	$y=3.5\ (\pm 0.5) + 0.1\ (\pm 0.04)*x$	8	0.33	n.s. (0.080)

[a] Adjusted R^2 can turn negative for multiple R^2 close to zero.

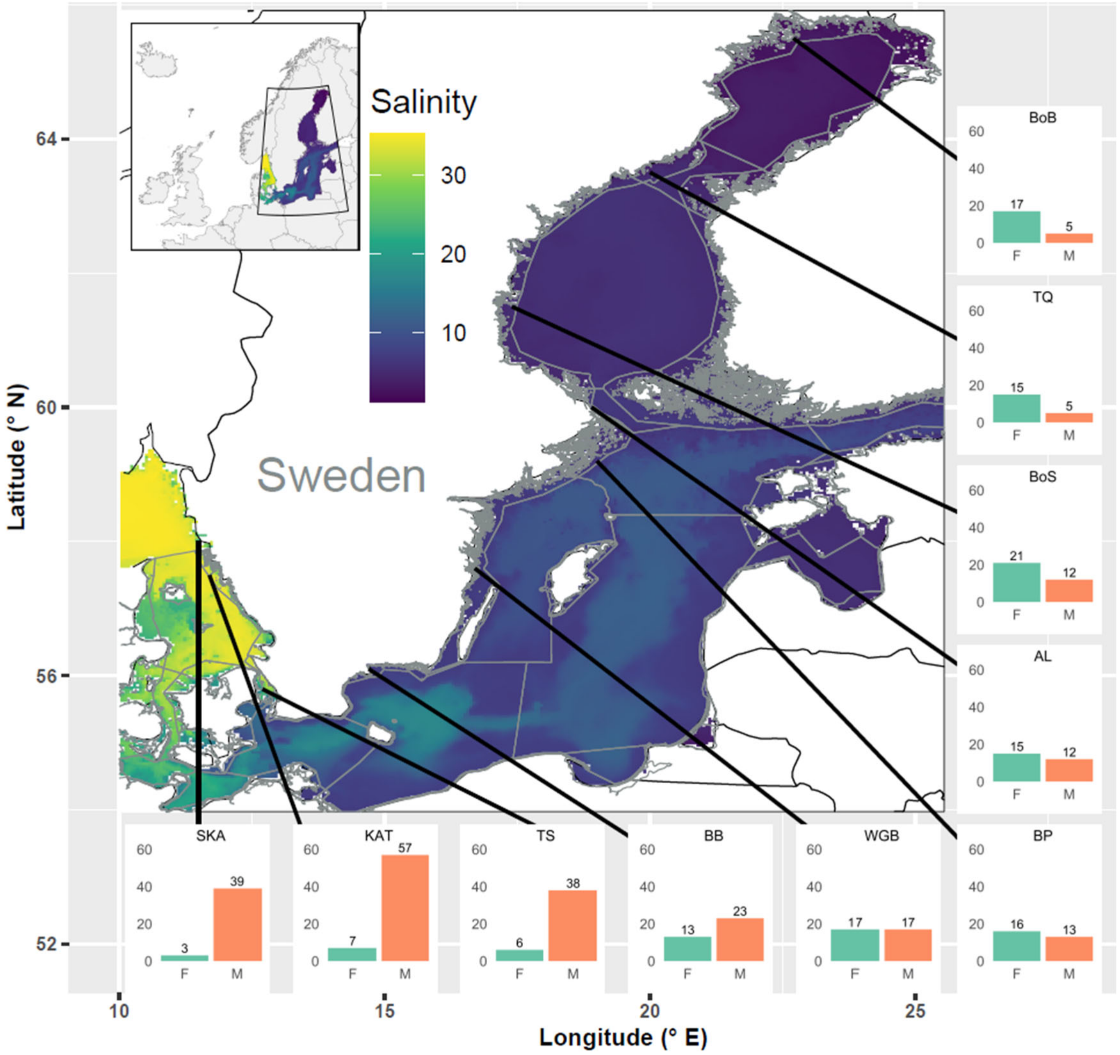


Figure 3. Map of the study area covering the Baltic Sea and the Skagerrak, color-coded by mean salinity. Grey lines delineate sub-basins, and shallow coastal areas. Bar plots show ~~standardiz~~standardised fish species richness for shallow coastal areas ~~for~~ in each of the ten ~~analyzed~~assessed sub-basins, separately for species of freshwater (F) and marine (M) origin. SR was ~~standardiz~~standardised across sub-basins to similar ~~inventory~~ sample coverage~~mpleteness~~ (Table S5~~2~~).~~:~~ Black lines indicate the positions of the sub-basins, but the exact sampling sites were spread across the shallow areas of each of the sub-basins. SKA: Skagerrak, KAT: Kattegat, TS: the Sound, BB: Bornholm Basin, WGB: Western Gotland Basin, BP: Northern Baltic Proper, AL: Åland Sea, BoS: Bothnian Sea, TQ: the Quark and BoB: Bothnian Bay.

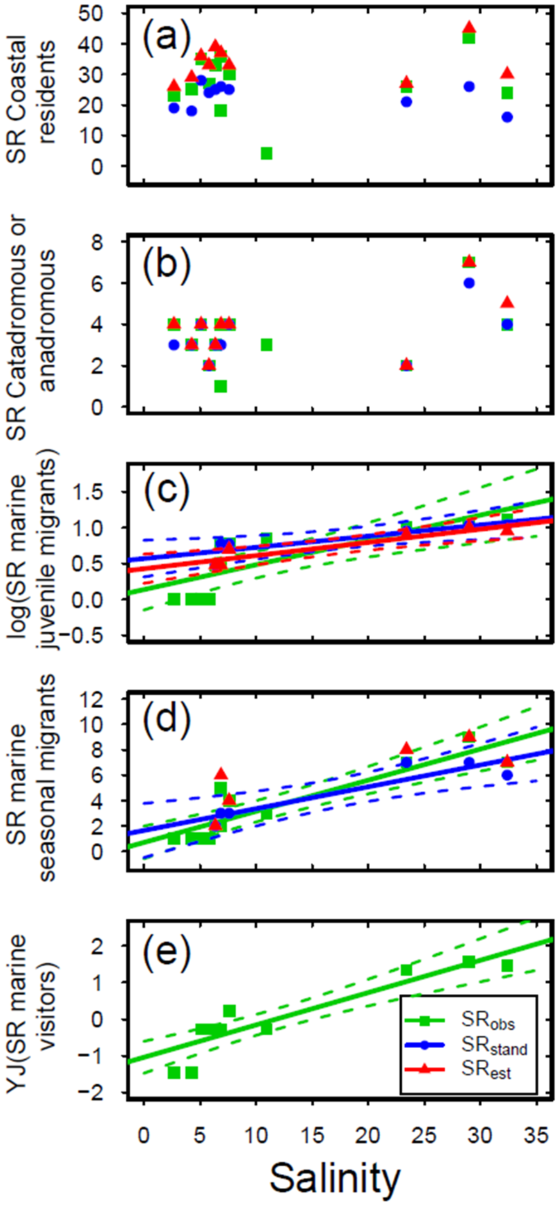
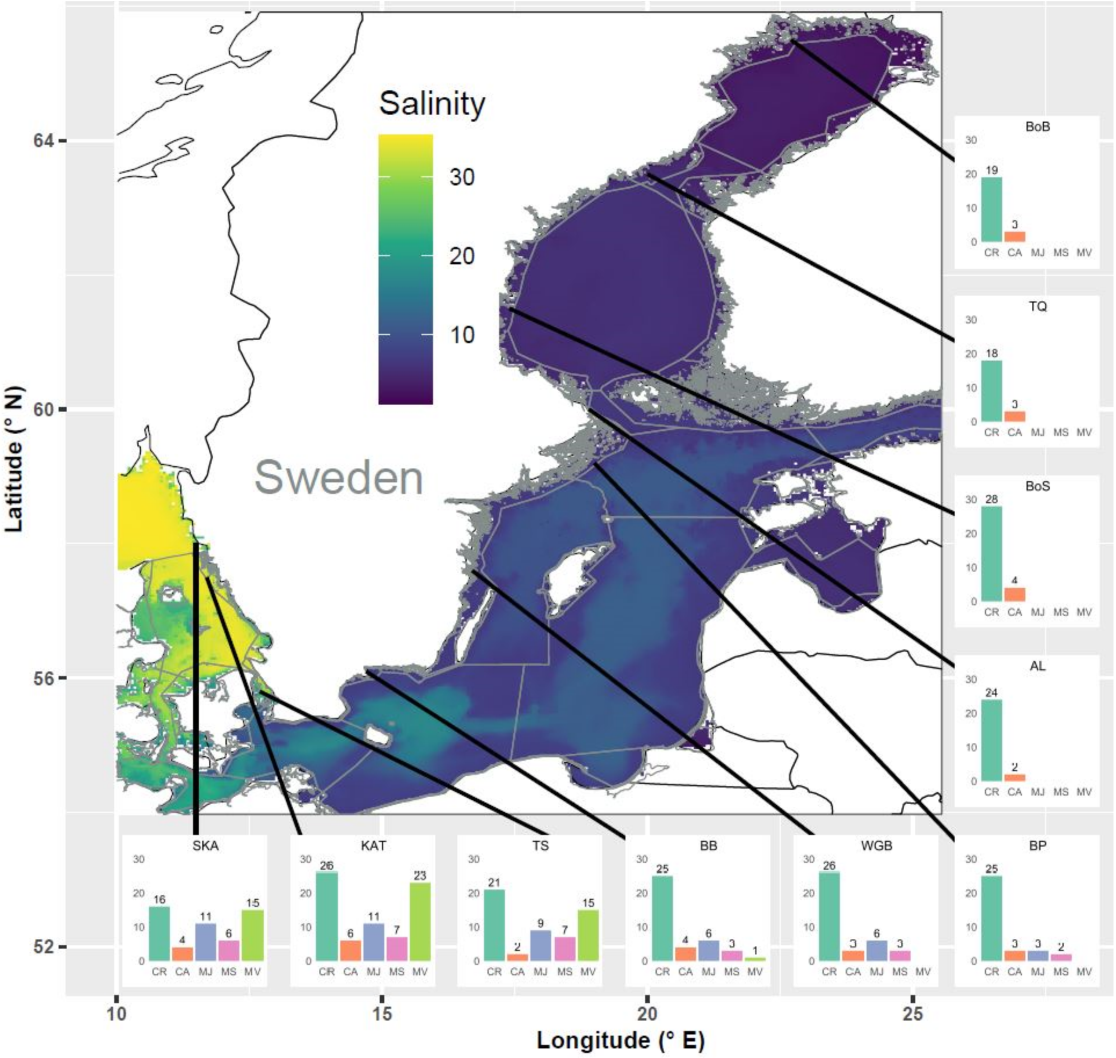


Figure 4. Fish species richness (SR) in relation to salinity in Swedish shallow coastal areas for different types of habitat preference, with (a) coastal residents, (b) catadromous or anadromous migrants, (c) marine juvenile migrants ($\log_{10}$-transformed), (d) marine seasonal migrants and (e) marine visitors (Yeo-Johnson-transformed). Each plot shows the observed, standardised and estimated SR and, when significant (*P*<0.05), the linear regression lines (solid) and 95%-confidence intervals (shaded areas surrounded by dashed lines). For regression equations and statistics see Table 3. For marine visitors (e), for clarity following transformation, only the observed SR is shown (no transformation was needed for the standardised and estimates values and there were no significant relationships, Table 3).



~~**Figure 4. Map of the study area covering the Baltic Sea and the Skagerrak, color-coded by mean salinity. Bar plots show standardized fish species richness for each of the ten analyzed sub-basins, separately by habitat preference category, as CR: coastal resident, CA: catadromous or anadromous migrants, MJ: marine juvenile migrants, MS: marine seasonal migrants and MV: marine visitors. SR was standardized across sub-basins to similar inventory completeness (Table S2: Black lines indicate the positions of the sub-basins, but the exact sampling sites were spread across the shallow areas of each of the sub-basins.**~~

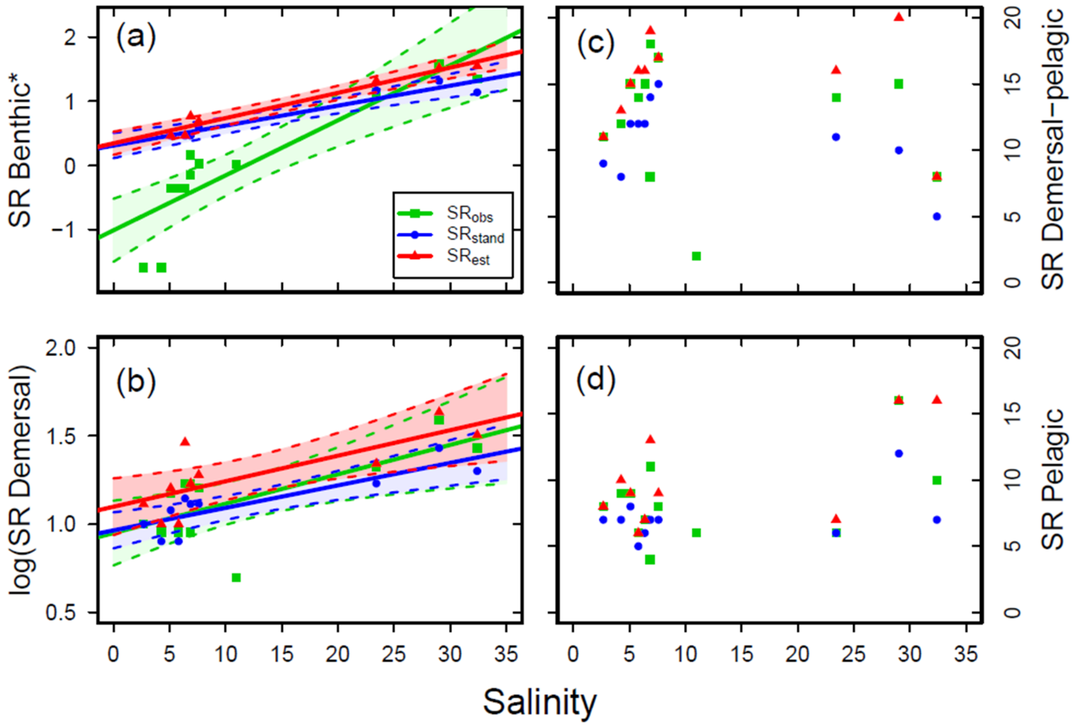
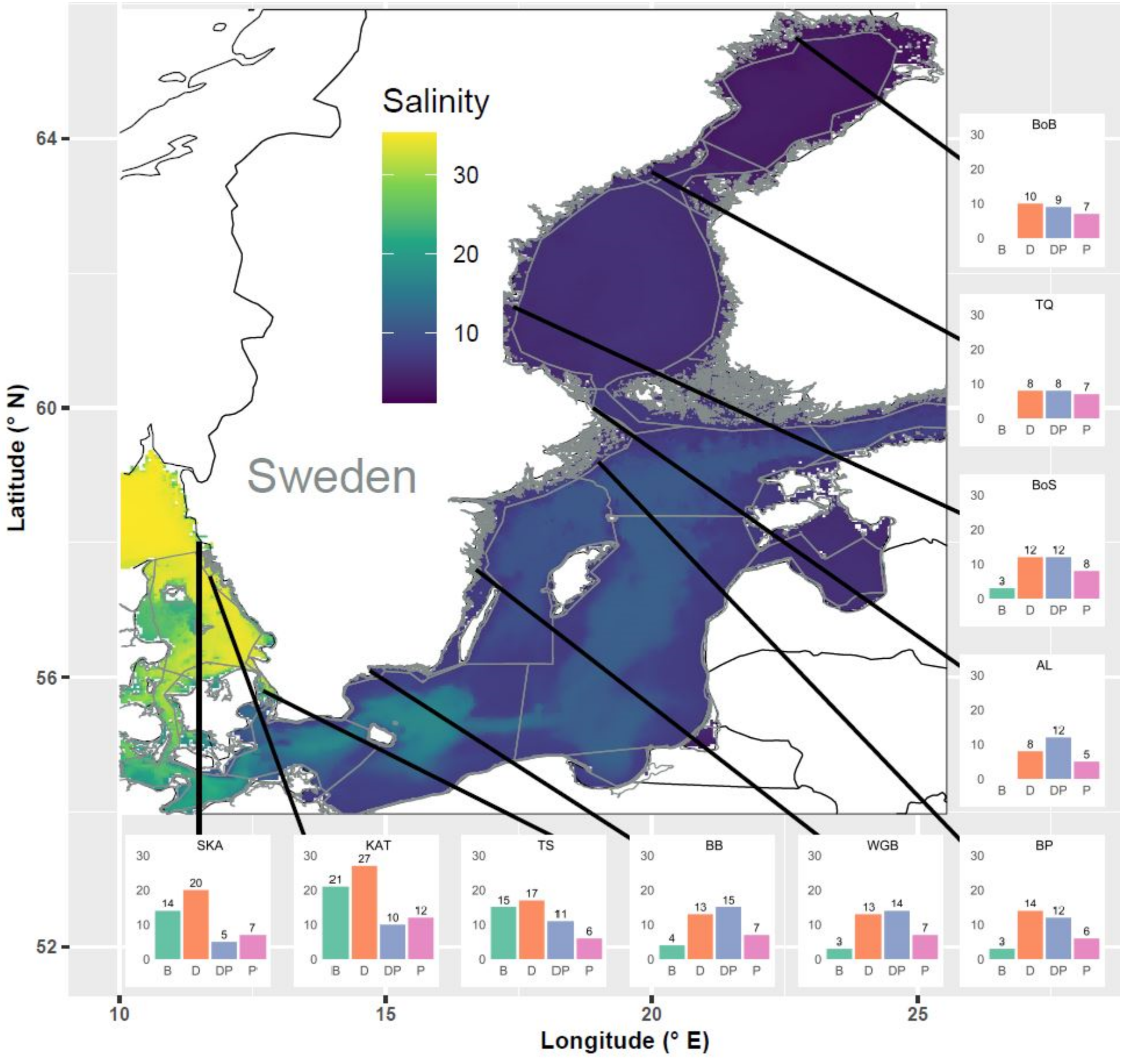
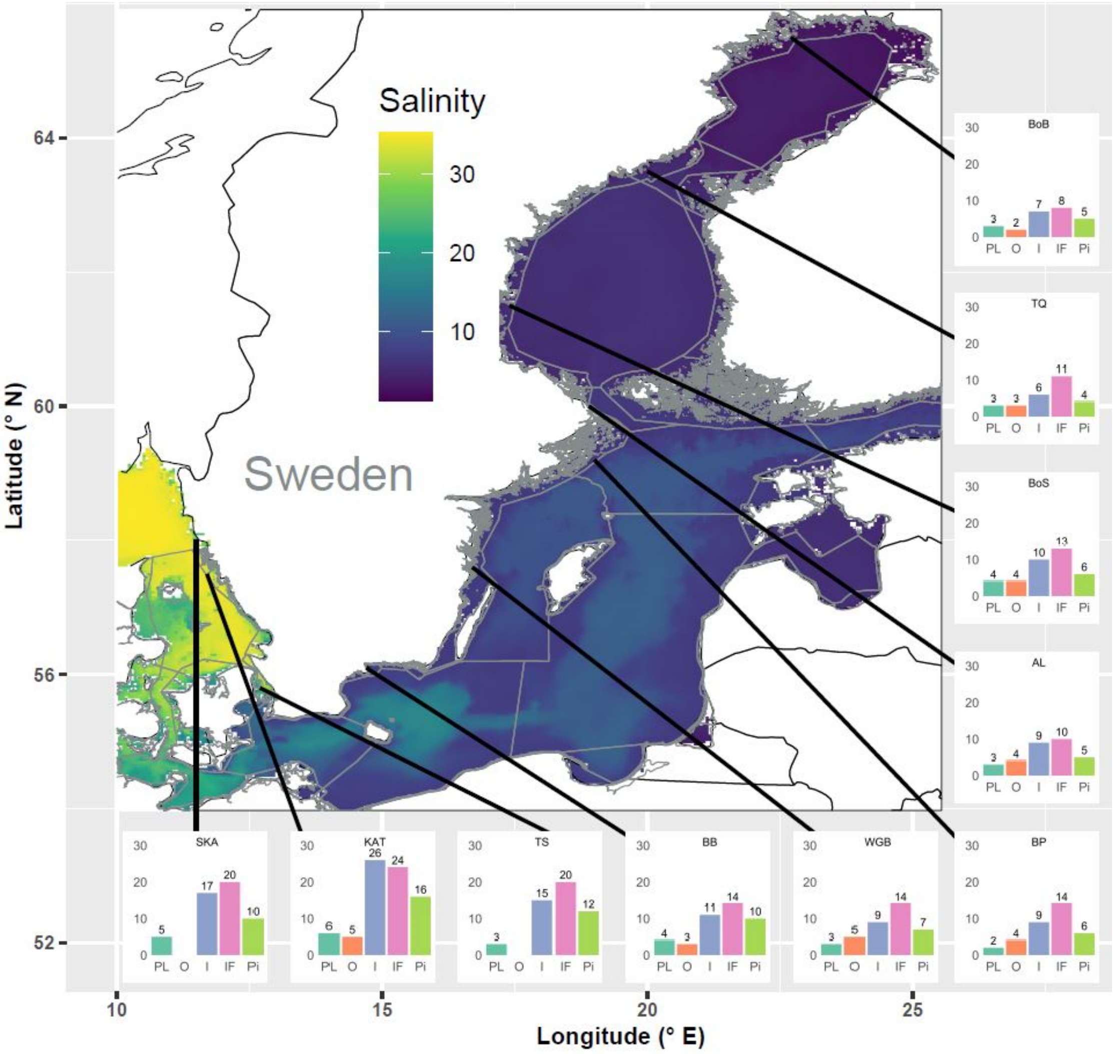


Figure 5. Fish species richness (SR) in relation to salinity in Swedish shallow coastal areas for different types of main vertical distribution, with (a) benthic (*Yeo-Johnson-transformed for SR$_{obs}$, and log$_{10}$-transformed for SR$_{std}$ and SR$_{est}$), (b) demersal (log$_{10}$-transformed), (c) demersal-pelagic and (d) pelagic fish species. Each plot shows the observed, standardised and estimated SR, and, for cases with a significant linear relationship (P<0.05), also the regression line (solid) and 95%-confidence intervals (shaded areas surrounded by dashed lines). The different lines and shaded confidence intervals are partly overlying each other within the panels in some cases, indicating very similar regression statistics. For regression equations and statistics see Table 3.



~~Figure 5. Map of the study area covering the Baltic Sea and the Skagerrak, color-coded by mean salinity. Bar plots show standardized fish species richness for each of the ten analyzed sub-basins, separately by vertical distribution category, with B: benthic, D: demersal, DP: demersal-pelagic and P: pelagic fish species. SR was standardized across sub-basins to similar inventory completeness (Table S2). Black lines indicate the positions of the sub-basins, but the exact sampling sites were spread across the shallow areas of each of the sub-basins.~~



~~Figure 6. Map of the study area covering the Baltic Sea and the Skagerrak, color-coded by mean salinity. Bar plots show standardized fish species richness for each of the ten analyzed sub-basins, separately by feeding category, with trophic level increasing from left to right, and PL: planktivores, O: omnivores, I: invertebrate eaters, IF: invertebrate and fish eaters and Pi: piscivores. SR was standardized across sub-basins to similar inventory completeness (Table S2). Black lines indicate the positions of the sub-basins, but the exact sampling sites were spread across the shallow areas of each of the sub-basins.~~

4 Discussion

Data from species censuses have been called “probably the most basic data in ecology”, as they are widely useful for example to define species ranges and biodiversity patterns, and support conservation efforts (Gaston & Blackburn, 2000). A limitation for the use of taxonomic inventory data for biodiversity purposes, however, is their completeness, i.e. the fraction of species in a given location that has been sampled (Mora et al., 2008). In this study, the coastal fish taxonomic inventory completeness (IC) ~~was found to~~ varied between ~~≥98.5~~77–98% for the ten~~10~~ assessed~~nalyzed~~ sub-basins, exceeded 80% in eight sub-basins, and averaged 86% (Table 2). This average IC in shallow Swedish coastal waters is high compared to an ~~2008~~ assessment of marine fish species census data worldwide, where global IC averaged 79%, indicating that ca. 21% of fish species still remained to be described. Marine fish IC exceeded 80% in less than 2% of marine areas worldwide, with the highest IC of 92% found for reef-associated species, and the lowest of 56% for bathydemersal species (Mora et al., 2008). Similarly, a ~~2012~~ global assessment published 2012 concluded that ca. 77% of ~~global~~ marine fish were known. ~~Consequently, the rate of new fish species descriptions continues to be high, with e.g. 1,577 new marine fish species globally described during the years 1999-2008 (Appeltans et al., 2012).~~The comparatively low IC in Skagerrak (77%, Table 2) can be related to a, in this context, rather small sample size for a relatively high number of marine migrating/visiting species (which are only more rarely present; Fig. S2, Table S7). Finally, the high similarity between SR$_{est}$ and total SR (i.e. SR$_{obs}$ plus “presence observations” from additional data sources; Table 2) suggests that the observed species lists for fish in Swedish shallow coastal areas were close to complete for the assessed sub-basins, and independently confirmed that the SR values estimated based on the fish incidence database (SR$_{est}$) were realistic.

The SR of frequent and very frequent species (i.e. Shannon and Simpson diversity, ShD and SiD) were generally well described by the sample sizes available to date in the studied sub-basins, with calculated (“observed”) ShD and SiD being similar to both ~~standardiz~~standardised and estimated values (where effects of differing sample sizes are considered; Table S5~~3~~). This indicates that the remaining uncertainty in fish SR$_{obs}$ is caused by a potential number of ~~undetected~~ rare species, corroborated by a high sample coverage (SC) across sub-basins (Table 2). This is a typical pattern, since well-known species are usually common and have large geographical ranges, whereas newly discovered species are usually (more) locally rare and geographically concentrated (Appeltans et al., 2012; Mora et al., 2008; Pimm et al., 2014).

The most recent check-list of Baltic Sea macrospecies, i.e. containing fish species reported across Baltic countries at both shallow and deeper water depths but excluding the Skagerrak, currently contains 242 fish species (HELCOM, 2020). In our analyses of Swedish shallow coastal areas the total fish SR$_{obs}$ amounted to 144 (i.e., fish incidence data plus presence only data from additional data sources), also if Skagerrak is excluded. Comparing the sample-size corrected estimates of SR in coastal areas (SR$_{est}$) with the species checklist of HELCOM (2020) suggests that ca. 50–~~-~~90% of all reported Baltic Sea fish species are found in Swedish shallow coastal areas, depending on sub-basin.

Our study reinforces that SR$_{obs}$ is strongly dependent on SC~~IC~~, as relatively rare species are more likely to be missed at lower sample size/sample coverage, and that comparisons of SR$_{obs}$ in species assemblages without accounting for this effect can lead to biased or ~~even~~ misleading conclusions (Chao & Chiu, 2016; ~~Chao & Jost, 2015; Chao et al., 2020;~~ Colwell & Coddington, 1994; ~~Colwell et al., 2012;~~ Gotelli & Colwell, 2001; Hill, 1973; ~~Hsieh et al., 2016;~~ Menegotto & Rangel, 2018; ~~Mora et al., 2008;~~ Pimm et al., 2014). When sample sizes are not uniform among sites or over time, SR$_{obs}$ need to be corrected for SC~~IC~~ before valid comparisons can be made. However, such methods have so far only rarely been used for coastal and estuarine fish assemblages (Waugh et al., 2019).

Besides the effects of sample size, SR and IC might to some extent also have been differentially influenced by differences in predominating sampling gear across sub-basins. Multi-mesh gill nets dominated in seven of the statistically ~~analyzed~~ assessed sub-basins, while trap nets and trawls dominated in the other three (Table S1). As one “sample” in each of these cases represents a different effort, due to differences in gear selectivity and sampling approach, this strictly does not allow for direct comparisons (Bergström et al., 2013; Waugh et al., 2019). For example, at the Swedish west coast, gill nets typically sample a wider range of species than fyke nets, which are more selective towards demersal and demersal-pelagic species (Bergström et al., 2013). Merging data from multiple- gear types into one analysis may have caused a certain bias in this regard. However, we argue that our approach was feasible given that the gears used in the different sub-basins are optimized for the locally prevailing conditions, i.e. aiming to sample the existing assemblages as completely as possible (Bergström et al., 2013), as additional data from relevant trawl surveys were also included, and considering the long time horizon of data collection. Further supporting our approach, biodiversity metrics that were ~~standardiz~~standardised against catch size revealed no consistent differences when comparing gill and fyke net samplings at the Swedish west coast (Bergström et al., 2013). Our assumption also appears justified given that SR$_{est}$ was similar to SR$_{obs}$ including additional data sources (i.e. incidence data plus presence observations, Table 2), giving confidence that the potentially introduced bias due to differing fishing gear and methods did not strongly influence the general patterns and results of this comparative and large-scale statistical analysis.

As anticipated based on earlier Baltic Sea studies on fish (e.g. Hiddink & Coleby, 2012; Ojaveer et al., 2010; Olsson et al., 2012) and other organism groups (e.g. Broman et al., 2019; Zettler et al., 2014), coastal fish SR~~salinity~~ was positively correlated with ~~coastal fish SR~~salinity (Fig. 2a, Table S64), with fish SR increasing ca. threefold together with the ca. 12-fold increase in salinity ~~with fish SR increasing ca. threefold across the ca. 10-fold salinity gradient~~ (Table 2). That clear predominance of marine species in the most saline sub-basins compared to freshwater species in the inner parts of the Baltic Sea is in agreement with the fact that salinity functions as threshold or “ecological barrier” for the distribution of many freshwater and marine species (Olenin & Leppäkoski, 1999; Vuorinen et al., 2015). It also corroborates patterns earlier reported for fish SR$_{obs}$ in three Baltic sub-basins (Hiddink & Coleby, 2012) and estuaries in general (Whitfield, 2015). The relatively small number of freshwater fish species incidences observed in the higher salinity sub-basins in our study (Fig. 3) likely stems from sampling close to freshwater tributaries, and reflects that many freshwater fish species can ~~with~~stand extended exposure to certain salinity levels (<ca. 9) and tolerate brief exposure to higher salinities (>ca. 15; Peterson & Meador, 1994).

While temperature did not significantly correlate with observed SR, ShD or SiD, it was positively related with the ~~standardiz~~standardised and estimated values (Fig. 2d-f, Table S64), which may indicate a temperature effect on fish biodiversity. In previous studies, temperature has shown positive correlations with SR$_{obs}$ in North Atlantic demersal and benthopelagic fish assemblages (Gislason et al., 2020), and with fish SR$_{obs}$ in the coastal Norwegian Skagerrak (Lekve et al., 2002) as well as in estuaries worldwide (Vasconcelos et al., 2015), all being examples of the often found general pattern that broader-scale SR co-varies with climatic variables such as temperature (Currie et al., 2004). However, given the clear relationship between salinity and the incidences of freshwater vs. marine fish species across the studied sub-basins (Fig. 3), we consider the studied salinity gradient to represent a case where the “physiological tolerance hypothesis” applies strongly, i.e. that SR in a particular area is limited by the number of species that can tolerate the local salinity conditions (Currie et al., 2004). In accordance, the regression models with salinity alone did not improve by adding temperature as additional explanatory variable. This conclusion is in agreement with observations from estuaries that fish SR is influenced by the broader distributions and habitat preference patterns of marine and freshwater species that can colonize these areas (Vasconcelos et al., 2015).

Besides salinity and temperature, which show a pronounced gradient over the large spatial scale of our study (Table 1) and were identified as likely main drivers here (Fig. 2), fish SR might also be influenced by other factors, such as for example human pressures. The cumulative pressure from human activities in the Baltic Sea, combining factors such as fishing, eutrophication and hazardous substances, is generally higher in the southern and south-western sub-basins. These sub-basins also show both relatively higher salinity and fish SR, compared to for example the northernmost sub-basins with lower cumulative human pressure, salinity and fish SR (Tables 1, 2; Korpinen et al., 2012; HELCOM 2018). Hence, no negative relationship between cumulative human pressure and fish SR is indicated on the large spatial and temporal scales studied here. This does, however, not contradict that variation in levels of human pressures can have effects on fish concerning other aspects, such as population sizes or growth rates (Olsson et al., 2019, Bastardie et al., 2021, Reckermann et al., 2022), or could possibly affect SR on smaller spatial scales than studied here. Evidently, since the rarefaction-extrapolation analyses that we used here are based on species incidence frequencies (Chao et al., 2020), the statistical results could potentially be influenced by human pressures that alter these frequencies, even if fish SR in itself may not be affected. However, given that the rarefied and extrapolated SR (i.e. SR_{std} and SR_{est}) are based on SC, where rare species are not influential, these statistics are rather robust against such effects (unless there would be severe changes in the incidence frequencies of common species).

Another potential explanatory factor to consider is habitat complexity, related to e.g. diversity of substrate or habitat-forming macrophytes, which can promote higher aquatic biodiversity (Soukup et al., 2021). Differences in habitat complexity may play some role in the observed large-scale patterns in fish SR given that macroalgal SR increases with increasing salinity across the Baltic Sea, with a larger share of habitat-forming and perennial species in more marine waters (Middleboe et al., 1997, Schubert et al., 2011). Hence, a greater habitat complexity with increasing salinity may enhance fish SR, further reinforcing any salinity-induced distributional pattern.

In compiling data we have assumed that salinity changes have been minor during the time period from which samples were obtained, compared to the pronounced spatial salinity gradient (observations over 17 to 47 years, depending on sub-basin, during 1975-2021; Table S2). According to monitoring data from the Baltic Sea, temporal changes in surface salinity varied between an increase of 3 [psu] in the Kattegat and a decrease of 1- [psu] in the Bothnian Sea during the past decades (1980–~~-~~2015; Ammar et al., 2021), which can be considered small compared to the spatial salinity gradient ranging from 3~~2~~ to 29. ~~Moreover, fish populations often show a lag of several years before biological changes following abiotic, environmental changes can be recorded (Daan et al., 2005).~~ Considering temporal patterns in SR and community composition, it was earlier reported that the observed fish SR increased in Kattegat, Arkona Basin and the central Baltic during 2001–~~-~~2008 (Hiddink & Coleby, 2012), and that the observed SR of demersal fish increased in the Baltic Proper and the Bothnian Sea during ca. 1971–~~-~~2013 (Törnroos et al., 2019). First-time observations of known fish species in sub-basins where they were not previously caught have been particularly related to increasing spring temperatures (+3–~~-~~6 °C during 1980–~~-~~2015; ~~(~~Ammar et al., 2021).

Such potential temporal patterns were not analys~~z~~ed in our study, where we merged the fish incidence data across years to provide as accurate as possible SR estimates at the sub-basin scale, and focused on large-scale spatial patterns.

Along with the changes in species, our study revealed changes in fish SR for different functional groups across the studied salinity gradient. As the functional groups represent differences among species groups in e.g. use of resources or level of mobility, these changes may also lead to taxonomy-driven differences in coastal ecosystem functioning across the different sub-basins (Elliott et al., 2007; Franco et al., 2008). Migrating fish species are typically of marine origin (here, marine juvenile migrants, marine seasonal migrants or marine visitors) and cannot tolerate low salinity, explaining their predominance at higher salinities (Fig. S2), and in agreement with known patterns in European estuaries in general (Elliott & Dewailly, 1995; Franco et al., 2008). This pattern, with marine open sea fish species periodically using coastal areas, may be related to enhanced prey availablity, and to hiding places and the typically more turbid waters providing protection from predators (Franco et al., 2008). Moreover, the higher SR of migratory fish at higher salinity is likely relevant for the ecological connectivity between ecosystems, i.e. by transport of local “coastal” production to the open sea and vice versa (Franco et al., 2008). It also emphasizes the important role of coastal areas as nursery grounds, migration routes and refuge areas for marine fish species (Elliott et al., 2007). This connectivity is also maintained in the less saline sub-basins, though the concerned functional groups are represented by only a few species (Fig. S2; Berkström et al., 2021).

Further, benthic and demersal fish SR decreased with decreasing salinity (Fig. 5a,b, Table 3), corroborating a previously documented decrease in demersal fish SR_{obs} from the saline Kattegat to the less saline northern Baltic Proper (Pecuchet et al., 2016), and in accordance with high benthic preference of marine fish species in European estuaries (Elliott & Dewailly, 1995; Franco et al., 2008). This pattern further corresponds with that the observed SR of benthic meio- and macrofauna, which are a dominating prey for benthic and demersal fish, also decreases with decreasing salinity in the Baltic Sea (Broman et al., 2019; Zettler et al., 2014). Taken together, these patterns suggest that benthic-pelagic coupling through fish predation likely involves a lower number of species links, or functional redundancy, towards lower salinity sub-basins. Concerning feeding habits, the general composition of feeding guilds noted in the higher~~-~~salinity sub-basins was similar to that reported on a larger European scale (Elliott & Dewailly, 1995). Also, the higher piscivorous fish SR in the more saline sub-basins (Fig. S5e) and the low omnivorous fish SR which was unrelated to salinity (Fig. S5c) was in agreement with findings from European estuaries (Franco et al., 2008). In summary, the identified differences in functional traits of fish along the salinity gradient were largely related to the respective changes in the predominating fish origin, i.e. freshwater vs. marine species. ~~Comparative analyses between coastal and offshore areas could only be conducted for the Kattegatt, indicating a lower fish SR in the shallow offshore. This could be related to a higher habitat complexity and more variable substrates in the coastal area, supporting more species (Bonsdorff, 2006).~~

5 Conclusions

Since fish SR and a number of functional attributes changed along the salinity gradient, respective changes in the coastal fish communities may be foreseen if climate change further alters salinity conditions in the Baltic Sea. While the confidence in future salinity projections remains low (HELCOM, 2021), recent ensemble simulations estimate that the two main drivers of climate-related changes in salinity in the Baltic Sea region, increasing river runoff (leading to lower salinity) and sea level rise (leading to higher salinity), approximately compensate each other, and may result in no net salinity changes (Meier et al., 2021). Mean (depth-integrated) observed Baltic Sea salinity did not change during 1982–2016, however, vertical changes were observed with freshening trends of the upper layer down to 40–50 m depth in most sub-basins, and increasing salinity below the halocline in the deep layer of some sub-basins (Liblik & Lips, 2019). Hence, if not considering potential phenotypical acclimation or genetic adaptation, an upper layer freshening would, based on the results from this and earlier studies (e.g. Hiddink & Coleby, 2012; MacKenzie et al., 2007; Pecuchet et al., 2016), likely lead to less species-rich native fish communities in shallow coastal areas, where more and more marine species are excluded. Further, successful recovery of marine overfished species may become less probable while certain freshwater fish species may be favored (MacKenzie et al., 2007; Peterson & Meador, 1994). Indeed, marine fish species were negatively affected by a period of freshened conditions in the Baltic Sea during the ca. 1970–90s (Ojaveer & Kalejs, 2005). Benthic fish species, being mostly of marine origin, may be especially vulnerable to freshening in the Baltic Sea region where their proportion in the fish assemblage is already relatively low to date. Besides salinity changes, fish SR and distribution may also be influenced by other climate-change related processes, including warming and resulting higher deep-water oxygen consumption rates, or changes in the Baltic Sea circulation (HELCOM, 2021; MacKenzie et al., 2007). Increasing water temperatures have already been linked to increased observed fish SR in the adjacent North Sea (Hiddink & Ter Hofstede, 2008), and in the Kattegat (Hiddink & Coleby, 2012). Further ecosystem-based assessments are needed to obtain realistic predictions of the net effect of such ongoing environmental changes on future fish SR/community composition and on how they may interact with human activities such as fishing patterns, and with conservation needs for biodiversity management.

Code and data availability

The data used in this study is publicly available via the SLU Database for Coastal Fish – KUL (https://www.slu.se/en/departments/aquatic-resources1/databases/database-for-coastal-fish-kul/), the SLU Swedish Species Information Centre (https://www.artportalen.se/), the SMHI SHARKweb (https://www.smhi.se/en/services/open-data/national-archive-for-oceanographic-data), the FishBase (https://fishbase.se/search.php) and the E.U. Copernicus Marine Service Information (CMEMS, 2021). The SLU Trawl Survey data (Department of Aquatic Resources) and the R code used for analysis and plotting is available from B. Koehler upon request.

Author contribution

LB, MK and BK designed the study. LB, ME and MK compiled the data. MK and LB assigned the functional characteristics to the fish species. BK analys~~z~~ed the data. BK and ME visualized the data. All co-authors discussed and validated the results. BK prepared the manuscript with contributions from all co-authors.

The authors declare that they have no conflict of interest.

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References

Ammar, Y., Niiranen, S., Otto, S. A., Möllmann, C., Finsinger, W., and Blenckner, T: The rise of novelty in marine ecosystems: The Baltic Sea case. Glob. Change Biol., 27(7), 1485-1499, https://doi.org/10.1111/gcb.15503, 2021.

Appeltans, W., Ahyong, S. T., Anderson, G., Angel, M. V., Artois, T., Bailly, N., Bamber, R., Barber, A., Bartsch, I., and Berta, A.: The magnitude of global marine species diversity. Curr. Biol., 22(23), 2189-2202, https://doi.org/10.1016/j.cub.2012.09.036, 2012.

Bastardie, F., Brown, E.J., Andonegi, E., Arthur, R., Beukhof, E., Depestele, J., Döring, R., Ritzau Eigaard, O., García-Barón, I., Llope, M., Mendes, H., Piet, G.J., and Reid, D.: Ecosystem challenges to be addressed by an ecosystem approach to fisheries management in Europe. Front. Mar. Sci., 1241, https://doi.org/10.3389/fmars.2020.629186, 2021.

Bergström, L., Karlsson, M., and Pihl, L.: Comparison of gill nets and fyke nets for the status assessment of coastal fish communities. WATERS Report, 2013:7, 2013.

Berkström, C., Wennerström, L., and Bergström, U.: Ecological connectivity of the marine protected area network in the Baltic Sea, Kattegat and Skagerrak: Current knowledge and management needs. Ambio, https://doi.org/10.1007/s13280-021-01684-x, 2021.

Bonsdorff, E.: Zoobenthic diversity-gradients in the Baltic Sea: continuous post-glacial succession in a stressed ecosystem. J. Exp. Mar. Biol. Ecol., 330(1), 383-391, https://doi.org/10.1016/j.jembe.2005.12.041, 2006.

Broman, E., Raymond, C., Sommer, C., Gunnarsson, J. S., Creer, S., and Nascimento, F. J.: Salinity drives meiofaunal community structure dynamics across the Baltic ecosystem. Mol. Ecol., 28(16), 3813-3829, https://doi.org/10.1111/mec.15179, 2019.

Byrnes, J. E., Gamfeldt, L., Isbell, F., Lefcheck, J. S., Griffin, J. N., Hector, A., Cardinale, B. J., Hooper, D. U., Dee, L. E., and Emmett Duffy, J.: Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. Methods Ecol. Evol., 5(2), 111-124, https://doi.org/10.1111/2041-210X.12143, 2014.

Chao, A., and Jost, L.: Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology, 93(12), 2533-2547, https://doi.org/10.1890/11-1952.1, 2012.

Chao, A., and Jost, L.: Estimating diversity and entropy profiles via discovery rates of new species. Methods Ecol. Evol., 6(8), 873-882, https://doi.org/10.1111/2041-210X.12349, 2015.

Chao, A., and Chiu, C. H.: Nonparametric estimation and comparison of species richness. In: eLS. John Wiley and Sons, Ltd: Chichester. https://doi.org/10.1002/9780470015902.a0026329, 2016.

Chao, A., Gotelli, N. J., Hsieh, T., Sander, E. L., Ma, K., Colwell, R. K., and Ellison, A. M.: Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol. Monogr., 84(1), 45-67, https://doi.org/10.1890/13-0133.1, 2014.

Chao, A., Kubota, Y., Zelený, D., Chiu, C. H., Li, C. F., Kusumoto, B., Yasuhara, M., Thorn, S., Wei, C. L., and Costello, M. J.: Quantifying sample completeness and comparing diversities among assemblages. Ecol. Res., 35(2), 292-314, https://doi.org/10.1111/1440-1703.12102, 2020.

CMEMS: EU Copernicus Marine Service Information, https://resources.marine.copernicus.eu/product-detail/BALTICSEA_REANALYSIS_PHY_003_011/INFORMATION, last access: 10 November 2021.

Colwell, R., and Coddington, J.: Estimating terrestrial biodiversity through extrapolation. Philos. T. R. Soc. B, 345, 101-118, https://doi.org/10.1098/rstb.1994.0091, 1994.

~~Colwell, R. K., Chao, A., Gotelli, N. J., Lin, S.-Y., Mao, C. X., Chazdon, R. L., and Longino, J. T.: Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. J. Plant Ecol., 5 (1), 3-21, https://doi.org/10.1093/jpe/rtr044, 2012.~~

Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guégan, J. F., Hawkins, B. A., Kaufman, D. M., Kerr, J. T., Oberdorff, T., and O'Brien, E.: Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecol. Lett., 7(12), 1121-1134, https://doi.org/10.1111/j.1461-0248.2004.00671.x, 2004.

Daan, N., Gislason, H., G. Pope, J., and C. Rice, J.: Changes in the North Sea fish community: evidence of indirect effects of fishing? ICES J. Mar. Sci., 62(2), 177-188, https://doi.org/10.1016/j.icesjms.2004.08.020, 2005.

Duffy, J. E., Godwin, C. M., and Cardinale, B. J.: Biodiversity effects in the wild are common and as strong as key drivers of productivity. Nature, 549(7671), 261-264, https://doi.org/10.1038/nature238862017, 2017.

Duncan, C., Thompson, J. R., and Pettorelli, N.: The quest for a mechanistic understanding of biodiversity–ecosystem services relationships. P. Roy. Soc. B-Biol. Sci., 282(1817), https://doi.org/10.1098/rspb.2015.1348, 2015.

Durack, P. J., Wijffels, S. E., and Matear, R. J.: Ocean salinities reveal strong global water cycle intensification during 1950 to 2000. Science, 336(6080), 455-458, https://doi.org/10.1126/science.1212222, 2012.

Elliott, M., and Dewailly, F.: The structure and components of European estuarine fish assemblages. Neth. J. Aquat. Ecol., 29(3), 397-417, https://doi.org/10.1007/BF02084239, 1995.

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

Franco, A., Elliott, M., Franzoi, P., and Torricelli, P.: Life strategies of fishes in European estuaries: the functional guild approach. Mar. Ecol. Prog. Ser., 354, 219-228, https://doi.org/10.3354/meps07203, 2008.

Froese, R., and Pauly, D. (Eds.): FishBase. World Wide Web electronic publication. www.fishbase.org, version 06/2021, 2021.

Gaston, K., and Blackburn, T. (Eds.): Pattern and Process in Macroecology. Blackwell Science Ltd, Oxford, England, https://doi.org/10.1002/9780470999592, 2000.

Gislason, H., Collie, J., MacKenzie, B. R., Nielsen, A., Borges, M. d. F., Bottari, T., Chaves, C., Dolgov, A. V., Dulčić, J., and Duplisea, D.: Species richness in North Atlantic fish: Process concealed by pattern. Global Ecol. Biogeogr., 29(5), 842-856, https://doi.org/10.1111/geb.13068, 2020.

Gotelli, N. J., and Colwell, R. K.: Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett., 4(4), 379-391, https://doi.org/10.1046/j.1461-0248.2001.00230.x, 2001.

Griffiths, J. R., Kadin, M., Nascimento, F. J., Tamelander, T., Törnroos, A., Bonaglia, S., Bonsdorff, E., Brüchert, V., Gårdmark, A., and Järnström, M.: The importance of benthic–pelagic coupling for marine ecosystem functioning in a changing world. Glob. Change Biol., 23(6), 2179-2196, https://doi.org/10.1111/gcb.13642, 2017.

HELCOM: State of the Baltic Sea - Second HELCOM holistic assessment 2011-2016. Baltic Sea Environment Proceedings, 155, 2018.

HELCOM: HELCOM Checklist 2.0 of Baltic Sea Macrospecies. Baltic Sea Environment Proceedings, 174, 2020.

HELCOM: Climate Change in the Baltic Sea. 2021 Fact Sheet. Baltic Sea Environment Proceedings, 180, 2021.

Herlemann, D. P., Lundin, D., Andersson, A. F., Labrenz, M., and Jürgens, K.: Phylogenetic signals of salinity and season in bacterial community composition across the salinity gradient of the Baltic Sea. Front. Microbiol., 7, Article 1883. https://doi.org/10.3389/fmicb.2016.01883, 2016.

Hiddink, J., and Ter Hofstede, R.: Climate induced increases in species richness of marine fishes. Glob. Change Biol., 14(3), 453-460, https://doi.org/10.1111/j.1365-2486.2007.01518.x, 2008.

Hiddink, J. G., and Coleby, C.: What is the effect of climate change on marine fish biodiversity in an area of low connectivity, the Baltic Sea? Global Ecol. Biogeogr., 21(6), 637-646, https://doi.org/10.1111/j.1466-8238.2011.00696.x, 2012.

Hill, M. O.: Diversity and evenness: a unifying notation and its consequences. Ecology, 54(2), 427-432, https://doi.org/10.2307/1934352, 1973.

Hsieh, T., Ma, K., and Chao, A.: iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers): Methods Ecol. Evol., 7(12), 1451-1456, https://doi.org/10.1111/2041-210X.12613, 2016.

Hu, Y. O., Karlson, B., Charvet, S., and Andersson, A. F.: Diversity of pico-to mesoplankton along the 2000 km salinity gradient of the Baltic Sea. Front. Microbiol., 7, Article 679. https://doi.org/10.3389/fmicb.2016.00679, 2016.

IPBES: Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, edited by: Brondizio, E. S., Settele, J., Díaz, S. and Ngo, H. T.~~.~~ IPBES secretariat, Bonn, Germany. 1148 pp. https://doi.org/10.5281/zenodo.3831673, 2019.

Johannesson, K., and Andre, C.: Invited review: Life on the margin: genetic isolation and diversity loss in a peripheral marine ecosystem, the Baltic Sea. Mol. Ecol., 15(8), 2013-2029, https://doi.org/10.1111/j.1365-294X.2006.02919.x, 2006.

Kaskela, A., Kotilainen, A., Al-Hamdani, Z., Leth, J., and Reker, J.: Seabed geomorphic features in a glaciated shelf of the Baltic Sea. Estuar. Coast. Shelf S., 100, 150-161, https://doi.org/10.1016/j.ecss.2012.01.008, 2012.

Klier, J., Dellwig, O., Leipe, T., Jürgens, K., and Herlemann, D. P.: Benthic bacterial community composition in the oligohaline-marine transition of surface sediments in the Baltic Sea based on rRNA analysis. Front. Microbiol., 9, 236, https://doi.org/10.3389/fmicb.2018.00236, 2018.

Koli, L.: Suomen Kalat, edited by: Porvoo, W., 1990 (in Finnish).

Kraufvelin, P., Pekcan-Hekim, Z., Bergström, U., Florin, A.-B., Lehikoinen, A., Mattila, J., Arula, T., Briekmane, L., Brown, E. J., and Celmer, Z.: Essential coastal habitats for fish in the Baltic Sea. Estuar. Coast. Shelf Sci., 204, 14-30, https://doi.org/10.1016/j.ecss.2018.02.014, 2018.

Kullander, S. O.: Förteckning över svenska fiskar, https://www.yumpu.com/es/document/read/19727234/forteckning-over-svenska-fiskar-pdf-naturhistoriska-riksmuseet, last access: 10 November 2002. In Swedish.

Laikre, L., Palm, S., and Ryman, N.: Genetic population structure of fishes: implications for coastal zone management. Ambio, 34(2), 111-119, https://doi.org/10.1579/0044-7447-34.2.111, 2005.

Lappalainen, A., Shurukhin, A., Alekseev, G., and Rinne, J.: Coastal-Fish Communities along the Northern Coast of the Gulf of Finland, Baltic Sea: Responses to Salinity and Eutrophication. Int. Rev. Hydrobiol., 85(5-6), 687-696, https://doi.org/10.1002/1522-2632(200011)85:5/6%3C687::AID-IROH687%3E3.0.CO;2-4~~<687::AID-IROH687>3.0.CO;2-4~~, 2000.

Lekve, K., Stenseth, N. C., Gjøsæter, J., and Dolédec, S.: Species richness and environmental conditions of fish along the Norwegian Skagerrak coast. ICES J. Mar. Sci., 59(4), 757-769, https://doi.org/10.1006/jmsc.2002.1247, 2002.

Liblik, T., and Lips, U.: Stratification has strengthened in the Baltic Sea–an analysis of 35 years of observational data. Front. Earth Sci., 7, 174, https://doi.org/10.3389/feart.2019.00174, 2019.

MacKenzie, B. R., Gislason, H., Möllmann, C., and Köster, F. W.: Impact of 21st century climate change on the Baltic Sea fish community and fisheries. Glob. Change Biol., 13(7), 1348-1367, https://doi.org/10.1111/j.1365-2486.2007.01369.x, 2007.

Meier, H. E. M., Kniebusch, M., Dieterich, C., Gröger, M., Zorita, E., Elmgren, R., Myrberg, K., Ahola, M., Bartosova, A., Bonsdorff, E., Börgel, F., Capell, R., Carlén, I., Carlund, T., Carstensen, J., Christensen, O. B., Dierschke, V., Frauen, C., Frederiksen, M., Gaget, E., Galatius, A., Haapala, J. J., Halkka, A., Hugelius, G., Hünicke, B., Jaagus, J., Jüssi, M., Käyhkö, J., Kirchner, N., Kjellström, E., Kulinski, K., Lehmann, A., Lindström, G., May, W., Miller, P., Mohrholz, V., Müller-Karulis, B., Pavón-Jordán, D., Quante, M., Reckermann, M., Rutgersson, A., Savchuk, O. P., Stendel, M., Tuomi, L., Viitasalo, M., Weisse, R., and Zhang, W.: Climate Change in the Baltic Sea Region: A Summary. Earth Sys. Dynam. Disc. [preprint]. https://doi.org/10.5194/esd-2021-67, in review, 2021.

Menegotto, A., and Rangel, T. F.: Mapping knowledge gaps in marine diversity reveals a latitudinal gradient of missing species richness. Nat. Commun., 9(1), 1-6, https://doi.org/10.1038/s41467-018-07217-7, 2018.

Middelboe, A. L., Sand-Jensen, K., and Brodersen, K.: Patterns of macroalgal distribution in the Kattegat-Baltic region. Phycologia, 36(3), 208-219, https://doi.org/10.2216/i0031-8884-36-3-208.1, 1997.

Momigliano, P., Denys, G. P., Jokinen, H., and Merilä, J.: *Platichthys solemdali* sp. nov. (Actinopterygii, Pleuronectiformes): a new flounder species from the Baltic Sea. Front. Mar. Sci., 5, Article 225. https://doi.org/10.3389/fmars.2018.00225, 2018.

Mora, C., Tittensor, D. P., and Myers, R. A.: The completeness of taxonomic inventories for describing the global diversity and distribution of marine fishes. P. Roy. Soc. B-Biol. Sci., 275(1631), 149-155, https://doi.org/10.1098/rspb.2007.1315, 2008.

O'Gorman, E. J., Yearsley, J. M., Crowe, T. P., Emmerson, M. C., Jacob, U., and Petchey, O. L.: Loss of functionally unique species may gradually undermine ecosystems. P. Roy. Soc. B-Biol. Sci., 278(1713), 1886-1893, https://doi.org/10.1098/rspb.2010.2036, 2011.

Olsson, J.: Past and current trends of coastal predatory fish in the Baltic Sea with a focus on perch, pike, and pikeperch. Fishes, 4(1), 7, https://doi.org/10.3390/fishes4010007, 2019.

Ojaveer, E., and Kalejs, M.: The impact of climate change on the adaptation of marine fish in the Baltic Sea. ICES J. Mar. Sci., 62(7), 1492-1500, https://doi.org/10.1016/j.icesjms.2005.08.002, 2005.

Ojaveer, H., Jaanus, A., MacKenzie, B. R., Martin, G., Olenin, S., Radziejewska, T., Telesh, I., Zettler, M. L., and Zaiko, A.: Status of biodiversity in the Baltic Sea. PloS ONE, 5(9), e12467. https://doi.org/10.1371/journal.pone.0012467, 2010.

Olenin, S., and Leppäkoski, E.: Non-native animals in the Baltic Sea: alteration of benthic habitats in coastal inlets and lagoons. Hydrobiologia, 393, 233-243, https://doi.org/10.1023/A:1003511003766, 1999.

Olli, K., Ptacnik, R., Klais, R., and Tamminen, T.: Phytoplankton species richness along coastal and estuarine salinity continua. Am. Nat., 194(2), E41-E51, https://orcid.org/0000-0003-2895-1273, 2019.

Olsson, J., Bergström, L., and Gårdmark, A.: Abiotic drivers of coastal fish community change during four decades in the Baltic Sea. ICES J. Mar. Sci., 69(6), 961-970, https://doi.org/10.1093/icesjms/fss072, 2012.

Pan, J., Marcoval, M. A., Bazzini, S. M., Vallina, M. V., and Marco, S.: Coastal marine biodiversity: Challenges and threats, in: Marine Ecology in a Changing World, edited by: Arias, A. H. and Menendez, M. C., CRC Press, Boca Raton, United States, 43-67, https://doi.org/10.1201/b16334-3, 2013.

Pecuchet, L., Törnroos, A., and Lindegren, M.: Patterns and drivers of fish community assembly in a large marine ecosystem. Mar. Ecol. Prog. Ser., 546, 239-248, https://doi.org/10.3354/meps11613, 2016.

Pekcan-Hekim, Z., Gårdmark, A., Karlson, A. M., Kauppila, P., Bergenius, M., and Bergström, L.: The role of climate and fisheries on the temporal changes in the Bothnian Bay foodweb. ICES J. Mar. Sci., 73(7), 1739-1749, https://doi.org/10.1093/icesjms/fsw032, 2016.

Peterson, M. S., and Meador, M. R.: Effects of salinity on freshwater fishes in coastal plain drainages in the southeastern US. Rev. Fish. Sci., 2(2), 95-121, https://doi.org/10.1080/10641269409388554, 1994.

Pihl, L., and Wennhage, H.: Structure and diversity of fish assemblages on rocky and soft bottom shores on the Swedish west coast. J. Fish Biol., 61, 148-166, https://doi.org/10.1111/j.1095-8649.2002.tb01768.x, 2002.

Pihl, L., Wennhage, H., and Nilsson, S.: Fish assemblage structure in relation to macrophytes and filamentous epiphytes in shallow non-tidal rocky-and soft-bottom habitats. Environ. Biol. Fish., 39(3), 271-288, https://doi.org/10.1007/BF00005129, 1994.

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M., and Sexton, J. O.: The biodiversity of species and their rates of extinction, distribution, and protection. Science, 344(6187): https://doi.org/10.1126/science.1246752, 2014.

R Core Team: R: A language and environment for statistical computing. Version 4.0.4. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/,~~.~~ 2021.

Reckermann, M., Omstedt, A., Soomere, T., Aigars, J., Akhtar, N., Bełdowska, M., Bełdowski, J., Cronin, T., Czub, M., Eero, M., Hyytiäinen, K.P., Jalkanen, J.-P., Kiessling, A., Kjellström, E., Kuliński, K., Larsén, X.G., McCrackin, M., Meier, H.E.M., Oberbeckmann, S., Parnell, K., Pons-Seres de Brauwer, C., Poska, A., Saarinen, J., Szymczycha, B., Undeman, E., Wörman, A., and Zorita, E.: Human impacts and their interactions in the Baltic Sea region. Earth Syst. Dynam., 13, 1-80, https://doi.org/10.5194/esd-13-1-2022.

Reiss, J., Bridle, J. R., Montoya, J. M., and Woodward, G.: Emerging horizons in biodiversity and ecosystem functioning research. Trends Ecol. Evol., 24(9), 505-514, https://doi.org/10.1016/j.tree.2009.03.018, 2009.

Rooney, N., and McCann, K. S.: Integrating food web diversity, structure and stability. Trends Ecol. Evol., 27(1), 40-46, 2012.

Russell, G.: Recent evolutionary changes in the algae of the Baltic Sea. Brit. Phycol. J., 20(2), 87-104, https://doi.org/10.1080/00071618500650111, 1985.

Schubert, H., Feuerpfeil, P., Marquardt, R., Telesh, I., and Skarlato, S.: Macroalgal diversity along the Baltic Sea salinity gradient challenges Remane's species-minimum concept. Mar. Pollut. Bull., 62, 1948-1956, https://doi.org/10.1016/j.marpolbul.2011.06.033, 2011.

Soukup, P.R., Näslund, J., Höjesjö, J., and Boukal, D.S.: From individuals to communities: Habitat complexity affects all levels of organization in aquatic environments. Wiley Interdiscip. Rev. Water, 9(1), e1575, https://doi.org/10.1002/wat2.1575, 2021.

Thorman, S.: Seasonal colonisation and effects of salinity and temperature on species richness and abundance of fish of some brackish and estuarine shallow waters in Sweden. Ecography, 9(2), 126-132, https://doi.org/10.1111/j.1600-0587.1986.tb01201.x, 1986.

Törnroos, A., Pecuchet, L., Olsson, J., Gårdmark, A., Blomqvist, M., Lindegren, M., and Bonsdorff, E.: Four decades of functional community change reveals gradual trends and low interlinkage across trophic groups in a large marine ecosystem. Glob. Change Biol., 25(4), 1235-1246, https://doi.org/10.1111/gcb.14552, 2019.

Vasconcelos, R. P., Henriques, S., França, S., Pasquaud, S., Cardoso, I., Laborde, M., and Cabral, H. N.: Global patterns and predictors of fish species richness in estuaries. J. Anim. Ecol., 84(5), 1331-1341, https://doi.org/10.1111/1365-2656.12372, 2015.

Vuorinen, I., Hänninen, J., Rajasilta, M., Laine, P., Eklund, J., Montesino-Pouzols, F., Corona, F., Junker, K., Meier, H. M., and Dippner, J. W.: Scenario simulations of future salinity and ecological consequences in the Baltic Sea and adjacent North Sea areas–implications for environmental monitoring. Ecol. Indic., 50, 196-205, https://doi.org/10.1016/j.ecolind.2014.10.019, 2015.

Waugh, A., Elliott, M., and Franco, A.: Debunking paradigms in estuarine fish species richness. Mar. Ecol. Prog. Ser., 613, 125-138, https://doi.org/10.3354/meps12883, 2019.

Whitfield, A.: Why are there so few freshwater fish species in most estuaries? J. Fish Biol., 86(4), 1227-1250, https://doi.org/10.1111/jfb.12641, 2015.

Wikström A., M. M.: Provfiske med nordiska kustöversiktsgarn utmed två kustområden I Hanöbukten: Pukavik/Elleholm och Skräbeåns mynning/Valjeviken. 2009. In Swedish.

Yeo, I. K., and Johnson, R. A.: A new family of power transformations to improve normality or symmetry. Biometrika, 87(4), 954-959, https://doi.org/10.1093/biomet/87.4.954, 2000.

Zettler, M. L., Karlsson, A., Kontula, T., Gruszka, P., Laine, A. O., Herkül, K., Schiele, K. S., Maximov, A., and Haldin, J.: Biodiversity gradient in the Baltic Sea: a comprehensive inventory of macrozoobenthos data. Helgoland Mar. Res., 68(1), 49-57, https://doi.org/10.1007/s10152-013-0368-x, 2014.