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A comparison of fishing methods to sample coastal fish communities in temperate seagrass meadows

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ABSTRACT: In the face of ongoing habitat destruction and biodiversity loss, adequate sampling methods for coastal fish communities are required to conduct sound ecological research and reduce sampling impacts in vulnerable habitats like seagrass meadows. However, different active and passive fishing methods might only capture specific fragments of fish diversity, varying in their catch efficiency for certain species and traits. To aid scientists with their choice of sampling methodology, we compared 5 common fishing methods (multimesh gillnet, eelfyke, minnow trap, bottom trawl, beach seine) to test how efficiently they display taxonomic and trait diversity of seagrass fish communities and whether their catchability differs between seasons. Among passive methods, gillnets captured the highest and minnow traps the lowest fish diversity (abundance, species richness, Shannon index, trait richness, trait dispersion). Seasonal differences in fish diversity were observed when comparing beach seines and bottom trawls to gillnets. Active methods displayed increased fish diversity from summer until autumn, which is likely linked to seasonal variations in community composition among methods, i.e. active methods had a higher catchability for gobies, sticklebacks and pipefish, representing typical seagrass inhabitants. Abundances of specific species and traits (e.g. body size, vertical habitat use) differed among methods, suggesting that fishing methods complement each other in sampling fish communities. Therefore, to obtain a holistic picture of fish diversity in seagrass meadows, at least 2 fishing methods should be combined (e.g. gillnet and 1 active method), while specific methods might be sufficient to target certain species or traits dependent on the research objective.

KEY WORDS: Fishing methods · Coastal fish community · Seagrass meadows · Biodiversity · Sampling

1. INTRODUCTION

Coastal habitats are highly productive, providing essential ecosystem goods and services for humans (Rönnbäck et al. 2007, Nordlund et al. 2016, Heckwolf et al. 2021) and various functions for marine organisms. For instance, they are used for feeding, spawning, migration and as nursery grounds by different fish species (Seitz et al. 2014, Olds et al. 2018, Perry et al. 2018, Reusch et al. 2018, Lefcheck et al. 2019). However, coastal ecosystems are exposed to a multitude of environmental and anthropogenic stressors, including eutrophication, fishing and climate change, leading to the loss of habitats and declines in biodiversity (Duarte 2002, Airoldi & Beck 2007, Brustolin et al. 2019, Heckwolf et al. 2021). This has increased the need for research on the functioning of coastal habitats and their importance for fish communities, as well as for monitoring programmes documenting long-term changes in fish populations, both requiring knowledge on adequate sampling methodology to be able to implement effective management and conservation measures.

Seagrass meadows represent a prominent, particularly vulnerable, habitat in shallow coastal areas already strongly affected by anthropogenic stressors

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*Corresponding author: christina.henseler@thuenen.de and they deliver a multitude of ecological functions (Duarte 2002, Schubert et al. 2015). Besides its high contribution to primary production, seagrass stabilizes the sediment, plays an essential role in nutrient abatement and provides food and habitat for various fish and invertebrate species (Fonseca & Fisher 1986, Duarte 2002, Seitz et al. 2014, Nordlund et al. 2016). Based on their importance as nursery areas for juveniles of recreationally and commercially used fish species, seagrass meadows markedly contribute to coastal fisheries (Rönnbäck et al. 2007, Stål et al. 2008). Fish communities constitute an essential food web component in marine ecosystems, providing important links through top-down control of lower trophic levels, such as benthic invertebrates, down to the production of ephemeral algae (Eriksson et al. 2009, Östman et al. 2016), while simultaneously serving as prey for other predatory fish, mammals and birds (Holmlund & Hammer 1999).

Fish contribute not only to ecosystem functions, such as nutrient cycling, but also represent an important food resource for humans (Holmlund & Hammer 1999, Kelley et al. 2018). This significance of fish communities and coastal habitats emphasizes research on coastal fish diversity as an important scientific task commonly comprising the application of different community metrics, such as taxonomic and trait-based indices, e.g. species richness and trait expression (Törnroos et al. 2013, Henseler et al. 2019). An adequate sampling strategy for fish in shallow habitats is a prerequisite for obtaining this information. Different active and passive fishing gear are widely applied in coastal habitats for scientific and commercial purposes. All of these methods entail certain biases with respect to the sampling results, varying in their catch efficiency regarding different fish species and sizes (e.g. Rozas & Minello 1997, Portt et al. 2006, Prchalová et al. 2012). Therefore, the efficiency of methods depends on the characteristics and the handling of the gear (e.g. mesh size, towing speed) and on environmental conditions (e.g. weather, turbidity and the structural complexity of the habitat sampled) (Rozas & Minello 1997, Portt et al. 2006, Shah Esmaeili et al. 2021).

Fishing methods routinely used to sample coastal fish assemblages can be categorized as either passive or active gear and comprise, for example, gillnets, trawls and traps (e.g. Portt et al. 2006). Gillnets represent a passive fishing method relying on fish to actively move in order to be captured and are highly size-selective due to differences in mesh size. The type of twine material, time of day and turbidity (clear versus murky water conditions) additionally determine gillnet catchability (Hamley 1975, Olin et al. 2004, He 2006, Portt et al. 2006). For research purposes, the use of multimesh gillnets is a common practice to capture fish of different size classes (Olin et al. 2004), which is why they represent the standard fishing method recommended for coastal fish monitoring programmes in the Baltic Sea (HELCOM 2020). Fyke nets and minnow traps represent other passive fishing methods, the latter being rather restricted to sampling smaller fish depending on the opening size of the trap (Portt et al. 2006). Bottom trawls and beach seines are active fishing methods that are towed over the seafloor either by boat or manpower. The efficiency of bottom trawls is influenced by the method of rigging and, similar to gillnets, mesh size and material (Rozas & Minello 1997). Beach seines have been studied rather extensively regarding their scientific use to characterise fish communities, and are restricted to shallow water depths. Problems encountered during beach seining on rough seafloor are bottom snags and the rolling of the seine, which can reduce catch efficiency (Pierce et al. 1990, Portt et al. 2006, Říha et al. 2008).

In light of ongoing habitat destruction and biodiversity loss, there is a need to keep the sampling impact low by using less invasive fishing methods, i.e. passive ones with a negligible impact on the seafloor, and to avoid unwanted fish bycatch when only certain species are targeted. This requires understanding the extent to which sampling methods are biased and differ in their catch efficiency regarding fish diversity. Previous studies have compared the performance of different sampling gear, such as gillnets, beach seines and traps, in lakes, sand and reef habitats, as well as the deep sea (Wells et al. 2008, Olin et al. 2009, McIntyre et al. 2015, Baker et al. 2016, Shah Esmaeili et al. 2021). Yet, gear comparisons in seagrass meadows have mainly been restricted to the application of beach seines, visual census sampling and fyke nets, with a focus on sub-/tropical regions (Connolly 1994, Nagelkerken et al. 2001, Franco et al. 2012), showing a gear-specific efficiency regarding different fish diversity measures. In subtropical seagrass meadows, visual census provided the lowest taxon richness and fish abundance compared to fyke and seine nets (Franco et al. 2012). Regarding the functional community structure, seine nets were most efficient in catching strict benthivores, while visual census and fyke nets were better suited to capture pelagic species and fish larger than 20 cm (Franco et al. 2012). Studies from temperate seagrass meadows are limited to the comparison of enclosure drop traps and visual diving transects (Bobsien & Brendelberger 2006), while differences in gear efficiency among seasons only seem to have been investigated in freshwater systems (Krueger et al. 1998, Mehdi et al. 2021).

Trait diversity, i.e. biological characteristics of fish, has rarely been considered when comparing the catchability of different fishing methods, although fish traits, such as body size and both visual and swimming ability, play a crucial role with regard to gear selectivity (Mouchet et al. 2019, Shah Esmaeili et al. 2021). In particular, the mesh size of nets is directly linked to fish size and therefore plays an important role in influencing the size range of fish in the catches (Hamley 1975, Portt et al. 2006, Prchalová et al. 2012). Correspondingly, fishing methods vary in their catch efficiency of fish with specific trait profiles. For instance, beach seines mostly capture fish smaller than 10 cm total length and more efficiently sample school-forming species, while underwater video stations select for larger fish (>60 cm total length), as well as for solitary and demersal species (Shah Esmaeili et al. 2021). Understanding the bias of fishing methods regarding fish traits might become even more crucial in the future, as it has been suggested that traits should play a more focal role in management actions, e.g. by serving as indicators (Törnroos et al. 2016, Zaiko et al. 2017, Barnett et al. 2019). Traits, in contrast to species identities, are directly linked to the ecological functions performed by organisms, which is why they might deliver important information on changes within an ecosystem, making them valuable indicators (Bremner 2008, Gagic et al. 2015, Kelley et al. 2018). Thus, knowledge on the sampling selectivity of fishing gear with respect to specific fish traits is crucial.

To address these aspects, we compared the efficiency of 5 commonly used fishing methods (multimesh gillnet, eelfyke, minnow trap, bottom trawl, beach seine) in seagrass meadows with regard to how adequately they capture the biodiversity of fish communities in different seasons in the Baltic Sea. In addition to considering taxonomic fish diversity, we analysed the influence of fishing methods on trait diversity. Besides their importance for gear selectivity (Mouchet et al. 2019, Shah Esmaeili et al. 2021) and potential use in management, fish traits enable the transferability of our results to other regions with a different fish community composition. Study outcomes will help to identify biases of different fishing methods and aid future research studies choose appropriate sampling methods for fish in seagrass meadows depending on the study question, i.e. with respect to targeted species and sampling season. Unwanted fish bycatch and the physical impact of fishing on the habitat can be reduced if one targeted, efficient method is applied instead of using a broad array of different sampling techniques.

2. MATERIALS AND METHODS

2.1. Fish community sampling

Fish were sampled in seagrass meadows at 5 sites distributed along the coast of Schleswig-Holstein (Germany) in the western Baltic Sea (Fig. 1). The sites were chosen based on the presence of the seagrass *Zostera marina* as the dominant vegetation

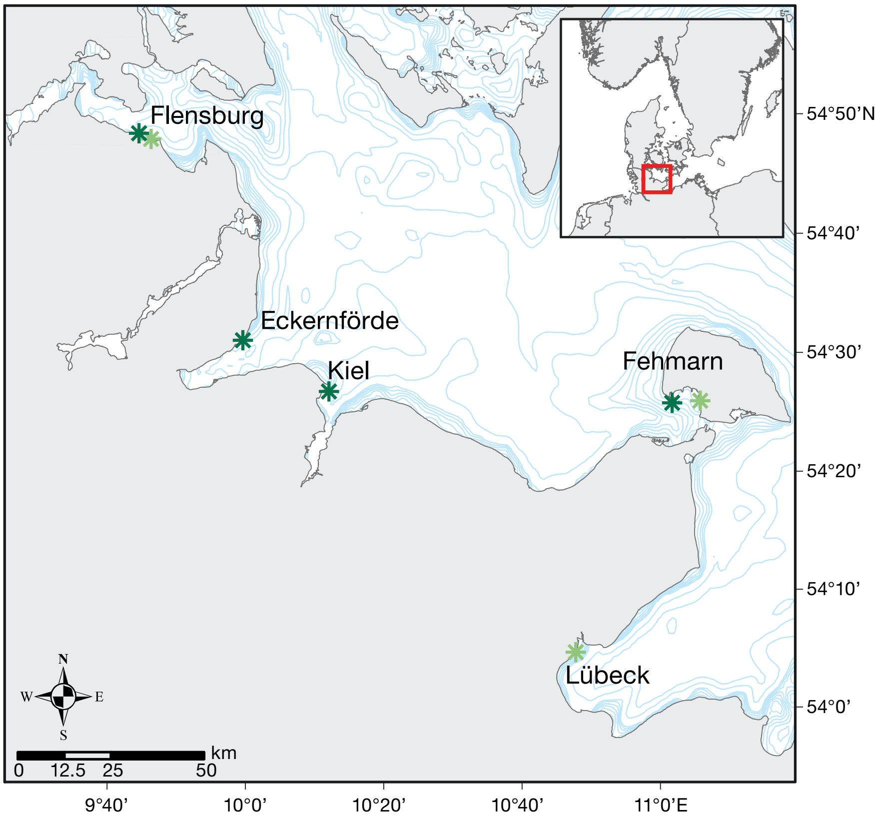

Fig. 1. Study sites along the coast of Schleswig-Holstein (Germany) in the western Baltic Sea, displaying the sampled seagrass meadows. Light green stations were sampled with the beach seine, while the other fishing methods (multimesh gillnet, eelfyke, minnow trap, bottom trawl) were deployed at the dark green stations

type (>50% coverage) representing a very common habitat type along the western German coastline (Schubert et al. 2015). Stations sampled with the beach seine (n = 3) ranged between 0.5 and 1.5 m water depth, while the other fishing methods were deployed at stations between 1.3 and 5.8 m depth (n = 4), covering the main extent of the seagrass depth range reported for the area (0.6–7.6 m depth; Schubert et al. 2015). Monthly sampling was carried out from February until October 2021. Seagrass meadows were sampled centrally with 5 different fishing methods. Passive fishing gear included coastal multimesh gillnets ('coastal surveynets', i.e. the gillnet type commonly used for sampling coastal fish communities in the Baltic Sea; HELCOM 2020), eelfykes and minnow traps (for detailed gear description, see Table S1 in the Supplement at www.int-res.com/articles/suppl/m715p091_supp.pdf), which were tied together with a rope to facilitate deployment. Three replicate lines (1 replicate = 1 gillnet, 1 eelfyke and 1 minnow trap tied together) were placed parallel to each other at each station per month. Passive gear were deployed before sunset and heaved after sunrise, thus covering both twilight periods, with a soaking time between 9 and 24 h (mean ± SD soaking time: 15 ± 3 h). Active fishing gear included a small bottom trawl (type 'YOY-trawl') and a beach seine. The bottom trawl was towed with a small boat conducting 1 haul per station and month (mean ± SD towing distance = 202 ± 36 m; towing speed = 2–3 knots), as the size of seagrass meadows did not allow a higher haul number per sampling. Three beach seine hauls were conducted at each station per month, with 2 persons pulling the seine parallel to the shore (mean towing distance: 51 ± 9 m). The beach seine was used in very shallow waters, i.e. below 1.5 m water depth, while the other fishing methods were applied in comparatively deeper areas with the purpose of using the respective fishing gear in its commonly, standardized way. The beach seine therefore serves as an additional sampling method to examine very shallow seagrass occurrence. Due to these differences in sampling depth, seine catches are not directly comparable to the other methods, but should be considered as complementary in order to cover the habitat in its entire depth range. Nevertheless, we compared the efficiency between beach seines and the other methods to provide insights about which method is best suited to display specific seagrass fish community aspects, keeping in mind that there might be depth-related differences in addition to variations caused by gear selectivity. Monthly sampling with the 5 fishing methods followed a randomized design with respect to the sequence in which they were applied at a specific site, i.e. sometimes all methods were deployed on the same day, other times on different days, dependent on weather conditions (see Section 4 for more details). When used on the same day, a maximum spatial and temporal distance was ensured between the sampling with passive and active methods. Fish were identified to species level, and total length was measured to the closest mm. When sample size exceeded approximately 150 individuals, length measurements were taken of a subsample of at least 75 individuals. Large numbers of gobies were taken to the laboratory, as identification required the use of microscopes. Live fish were released back into the sea after the identification and measurement procedure. At each sampling, water variables were recorded at the stations close to the seafloor, including water temperature, salinity, pH, oxygen concentration and Secchi depth (Table S2).

2.2. Fish traits

For the trait analysis, the categorical traits diet, habitat, schooling behaviour, caudal fin shape and body shape, and the continuous trait body size were used. These life-history and morphological traits were chosen to represent characteristics of the fish species influencing the catchability of the fishing methods (Table 1). The coding of traits and the construction of the species–trait matrix were adapted from Henseler et al. (2019) (see Text S1 for trait sources). For body size, the mean total length per species and replicate sample was used. When no length measurements were available for a certain species within a specific replicate sample (e.g. due to non-intact individuals), missing values (0.57%) were replaced with the mean length of the same species caught with the same gear at the same station in the same month, if available (0.34% length measurements still missing in the analysis).

2.3. Data and statistical analysis

For the data analysis, 1 bottom trawl haul from October at the site 'Flensburg' had to be removed due to very short fishing distance because the net became snagged on rocks. Trawling at the site 'Eckernförde' was only conducted in February, but omitted during the following months due to an uneven bottom profile, i.e. large amount of rocks. In May, only 9

Table 1. Life-history and morphological fish traits and trait categories, labels used in Table 2 and Fig. 7, and relevance of traits for catchability of fishing methods

Trait	Category	Label	Relevance
Life-history traits			
Diet	Piscivorous Benthivorous Planktivorous Generalist	pisc benth plank gen	Feeding type related to position in water column and movement
Habitat	Benthopelagic Demersal Pelagic	benp dem pel	Related to functioning of fishing methods
Schooling behaviour	Singleton Paired, sometimes small schools Always schools	singl pair scho	Related to fish movement and number of fish occurring
Morphological traits			
Body size	Continuous (i.e. mean total length per sample and species)	–	Size selectivity of fishing methods due to mesh size, size of opening etc.
Caudal fin shape	Continuous Forked Rounded Truncated	con fork roun trun	Related to movement and activity, i.e. swimming ability, potential to escape active fishing methods
Body shape	Eel-like Elongated Flat Normal	eel elon flat nor	Catchability dependent on fish body shape due to size and shape of meshes etc.

replicates of passive fishing methods could be analysed, as gear were stolen at site 'Fehmarn' during the night (for overview of sample numbers, see Table S3). Species present in fewer than 11 samples were not incorporated in the analysis (n = 14), as they were not considered to represent the typical Baltic Sea fish fauna and/or to be caught representatively with the fishing methods (for a list of fish species and corresponding traits, see Table 2). To compare the effect of fishing methods on the sampled fish community between different times of the year, fish data from the sampling months were pooled into the following 5 ‘seasons’: winter (WI; February, March), spring (SP; April, May), summer (SU; June, July), late summer (LSU; August, September) and autumn (AU; October). It should be noted that a lower number of replicate samples was analysed for autumn, as only 1 month was included in this season (Table S3).

To assess how the fish community differs among fishing methods, several taxonomic and trait-based measures were computed for each fishing method per season. Taxonomic indices comprised abundance, species richness and the Shannon index. While the Shannon index considers proportional abundances, abundance and species richness were both standardized per sampling effort. Catch data (fish abundance and species richness) were standardized to 12 h soaking time for passive gear and to 200 m or 50 m towing distance for the bottom trawl and beach seine, respectively. The purpose of this standardization was to evaluate the efficiency of fishing methods based on how they are commonly applied for the sampling of fish communities, thus, making the results directly usable for other scientists. Taxonomic composition was computed for each fishing method per season based on abundances standardized by sampling effort, and visualized in a non-metric multidimensional scaling (NMDS) plot based on Bray-Curtis dissimilarity. To test the overall between-group dissimilarity among fishing methods per season regarding taxonomic composition, a similarity percentage (SIMPER) analysis was conducted. To further investigate how fishing methods differed in displaying abundances of individual fish species, standardized abundances of the 10 most abundant fish species (across all seasons and gear types) were compared among fishing methods per season. In addition to taxonomic community measures, trait-based indices were computed using log-transformed abundances. While trait richness represents an equivalent of species richness representing the amount of trait space taken by the species of a community, trait dispersion describes the spread of the community in multidimensional trait space, thus representing trait diversity. In contrast to trait richness, trait dispersion is weighted by relative species abundances (Laliberté & Legendre 2010). To examine how the expression of trait categories differed among fishing methods, i.e. how fishing methods were biased towards catching species with specific traits, absolute trait values based on log-transformed abundances standardized to sampling effort (not weighted by the total abundance in each sample as is done for the calculation of community-weighted mean trait values) were computed for the 19 trait categories (cf. Henseler et al. 2021).

Taxonomic (total abundance, species richness, Shannon index, abundances of individual species) and trait-based variables (trait richness, trait dispersion, trait values) were statistically compared among fishing methods and seasons using (generalized) linear mixed-effects models (GLMM/LMM) with 'fishing method' and 'season' as fixed factors. The interaction of 'fishing method' and 'season' was included in the models to assess whether the efficiency among fishing methods varies with season. Study site was used as a varying-intercept random effect in the models to account for site-related differences in the fish community. For GLMMs, a gamma distribution and an identity- or log-link function were used. For LMMs, variables were square root- or log-transformed, when needed. When the residual spread differed strongly among fishing method levels, the 'varIdent' variance structure was applied in LMMs to model variance separately for the levels of the factor 'fishing method'. Model assumptions (data distribution and homoscedasticity) were examined by plotting residuals against fitted values. When assumptions could not be met, fishing methods measuring a specific species or trait value occurring in only 1 season were removed from the model. This applies to abundances of broadnosed pipefish *Syngnathus typhle* (spring, eelfyke: 0.02 ± 0.11) and the trait value 'pelagic habitat' (winter, beach seine: 0.07 ± 0.27). To assess the significance of the factors and their interaction, a Type II Wald chi-squared test was conducted for GLMMs and an *F*-test for LMMs. To test for differences among the 5 fishing methods for each season regarding the variables, post hoc tests using the Tukey method for the adjustment of p-values for multiple comparisons were applied.

All analyses were performed in the open-source software R, version 4.1.1 (R Core Team 2021), using the packages 'car' (Fox & Weisberg 2019), 'emmeans' (Lenth 2021), 'FD' (Laliberté & Legendre 2010, Laliberté et al. 2014), 'ggplot2' (Wickham 2016), 'lme4' (Bates et al. 2015), 'nlme' (Pinheiro et al. 2021) and 'vegan' (Oksanen et al. 2020).

3. RESULTS

In total, 43 fish species were caught in the seagrass meadows across all fishing methods and seasons, of which 29 were considered in the analysis (Table 2). In this section, we are focussing on the significance of the interaction term 'fishing method×season' in the models, as the study aimed to identify differences in the efficiency of fishing methods among seasons instead of merely examining seasonal fish community differences across fishing methods or vice versa.

3.1. Taxonomic indices

The efficiency of fishing methods differed significantly among seasons for all taxonomic indices (i.e. significant interaction term: fishing method×season; Fig. 2; Table S4). However, passive fishing methods showed the same pattern for abundance, species richness and the Shannon index across all seasons. While gillnets consistently displayed the highest values, the lowest values were obtained with minnow traps (Fig. 2). The Shannon index was zero for minnow traps throughout all seasons, since only 1 species was caught with this method at each sampling occasion. Bottom trawl and beach seine did not differ regarding the taxonomic indices in any season. Regarding overall fish abundance, gillnets were similar to bottom trawls from winter until summer, but higher/lower than beach seines in winter/spring and summer, respectively (Fig. 2a). In late summer and autumn, higher abundances were caught with both active methods than with gillnets. Species richness was similar in gillnets and active methods in winter and spring, while active methods displayed higher or similar values compared to gillnets from summer until autumn (Fig. 2b). The Shannon index was higher in gillnets than in the active methods in winter and spring, while values were similar in the other seasons (Fig. 2c).

3.2. Taxonomic composition

Taxonomic community composition was distinct for the fishing methods during all seasons (Figs. S1–S5). The NMDS plot shows a clear separation of active and passive fishing methods, and of gillnet and eel-

Table 2. List of species caught (n = 43), depicting whether they were considered in the analysis (‘x’ = considered; ‘–’ = not considered) and corresponding trait categories used for the species analysed. See Table 1 for complete trait category names

Species		Analysis	Diet				Habitat	Schooling behaviour			Caudal fin shape	Body shape
			pisc	benth	plank	gen		singl	pair	scho		
Agonus cataphractus	Hooknose	x	0	1	0	0	dem	1	0	0	roun	elon
Ammodytes tobianus	Small sandeel	x	0	0	1	0	dem	0	0	1	fork	elon
Anguilla anguilla	European eel	x	0	0	0	1	dem	1	0	0	con	eel
Aphia minuta	Transparent goby	x	0	0	1	0	pel	0	0	1	roun	elon
Belone belone	Garfish	–	–	–	–	–	–	–	–	–	–	–
Clupea harengus	Atlantic herring	x	0	0	1	0	benp	0	0	1	fork	nor
Ctenolabrus rupestris	Goldsinny-wrasse	x	0	1	0	0	dem	1	0	0	trun	nor
Engraulis encrasicolus	European anchovy	–	–	–	–	–	–	–	–	–	–	–
Entelurus aequoreus	Snake pipefish	–	–	–	–	–	–	–	–	–	–	–
Gadus morhua	Atlantic cod	x	0.5	0.5	0	0	benp	0	0	1	trun	nor
Gasterosteus aculeatus	Three-spined stickleback	x	0.5	0.5	0	0	benp	0	0	1	trun	nor
Gobius niger	Black goby	x	0	1	0	0	dem	1	0	0	roun	nor
Gobiusculus flavescens	Two-spotted goby	x	0	0.5	0.5	0	benp	0	0	1	roun	elon
Hyperoplus lanceolatus	Great sandeel	x	0.5	0	0.5	0	dem	0.5	0.5	0	fork	elon
Limanda limanda	Dab	x	0.5	0.5	0	0	dem	1	0	0	roun	flat
Lumpenus lampretaeformis	Snakeblenny	–	–	–	–	–	–	–	–	–	–	–
Merlangius merlangus	Whiting	x	0.5	0.5	0	0	benp	0	0	1	trun	nor
Mullus surmuletus	Surmullet	–	–	–	–	–	–	–	–	–	–	–
Myoxocephalus scorpius	Shorthorn sculpin	x	0.5	0.5	0	0	dem	0.5	0.5	0	roun	nor
Neogobius melanostomus	Round goby	x	0.5	0.5	0	0	dem	1	0	0	roun	nor
Nerophis ophidion	Straightnose pipefish	x	0	0.5	0.5	0	dem	1	0	0	con	eel
Perca fluviatilis	Perch	–	–	–	–	–	–	–	–	–	–	–
Pholis gunnellus	Rock gunnel	x	0	1	0	0	dem	1	0	0	roun	eel
Platichthys flesus	European flounder	x	0.5	0.5	0	0	dem	1	0	0	roun	flat
Pleuronectes platessa	European plaice	x	0	1	0	0	dem	1	0	0	roun	flat
Pollachius virens	Saithe	–	–	–	–	–	–	–	–	–	–	–
Pomatoschistus microps	Common goby	x	0	0.5	0.5	0	dem	1	0	0	roun	elon
Pomatoschistus minutus	Sand goby	x	0	1	0	0	dem	0	1	0	roun	elon
Pomatoschistus pictus	Painted goby	–	–	–	–	–	–	–	–	–	–	–
Pungitius pungitius	Nine-spined stickleback	x	0	1	0	0	benp	0	0	1	roun	elon
Salmo trutta	Sea trout	–	–	–	–	–	–	–	–	–	–	–
Scomber scombrus	Atlantic mackerel	x	0.5	0	0.5	0	pel	0	0	1	fork	nor
Scophthalmus maximus	Turbot	–	–	–	–	–	–	–	–	–	–	–
Solea solea	Common sole	–	–	–	–	–	–	–	–	–	–	–
Spinachia spinachia	Sea stickleback	x	0	0.5	0.5	0	benp	0.5	0.5	0	roun	elon
Sprattus sprattus	European sprat	x	0	0	1	0	pel	0	0	1	fork	nor
Symphodus melops	Corkwing wrasse	–	–	–	–	–	–	–	–	–	–	–
Syngnathus rostellatus	Nilsson's pipefish	x	0	0.5	0.5	0	dem	1	0	0	roun	eel
Syngnathus typhle	Broadnosed pipefish	x	0	0.5	0.5	0	dem	1	0	0	roun	eel
Taurulus bubalis	Longspined bullhead	x	0.5	0.5	0	0	dem	1	0	0	roun	nor
Trachinus draco	Greater weever	–	–	–	–	–	–	–	–	–	–	–
Trachurus trachurus	Atlantic horse mackerel	–	–	–	–	–	–	–	–	–	–	–
Zoarces viviparus	Eelpout	x	0	1	0	0	dem	1	0	0	con	eel

fyke samples, while minnow trap samples were unevenly distributed among other methods (Fig. 3). Community composition in the catches of the different fishing methods displayed a dissimilarity of at least 80% with few exceptions (Table S5). Bottom trawl and beach seine samples were more similar in late summer and autumn (70 and 56% dissimilarity, respectively). In autumn, gillnet and eelfyke samples were more similar than in other seasons, with 74% dissimilarity.

The 10 most abundant fish species across fishing methods and seasons were broadnosed pipefish *Syngnathus typhle*, common goby *Pomatoschistus microps*, three-spined stickleback *Gasterosteus aculeatus*, sea stickleback *Spinachia spinachia*, Atlantic cod *Gadus morhua*, European plaice *Pleuronectes platessa*, sand goby *Pomatoschistus minutus*, Nilsson's pipefish *Syngnathus rostellatus*, European flounder *Platichthys flesus* and straightnose pipefish *Nerophis ophidion*. The effect of fishing method on individual

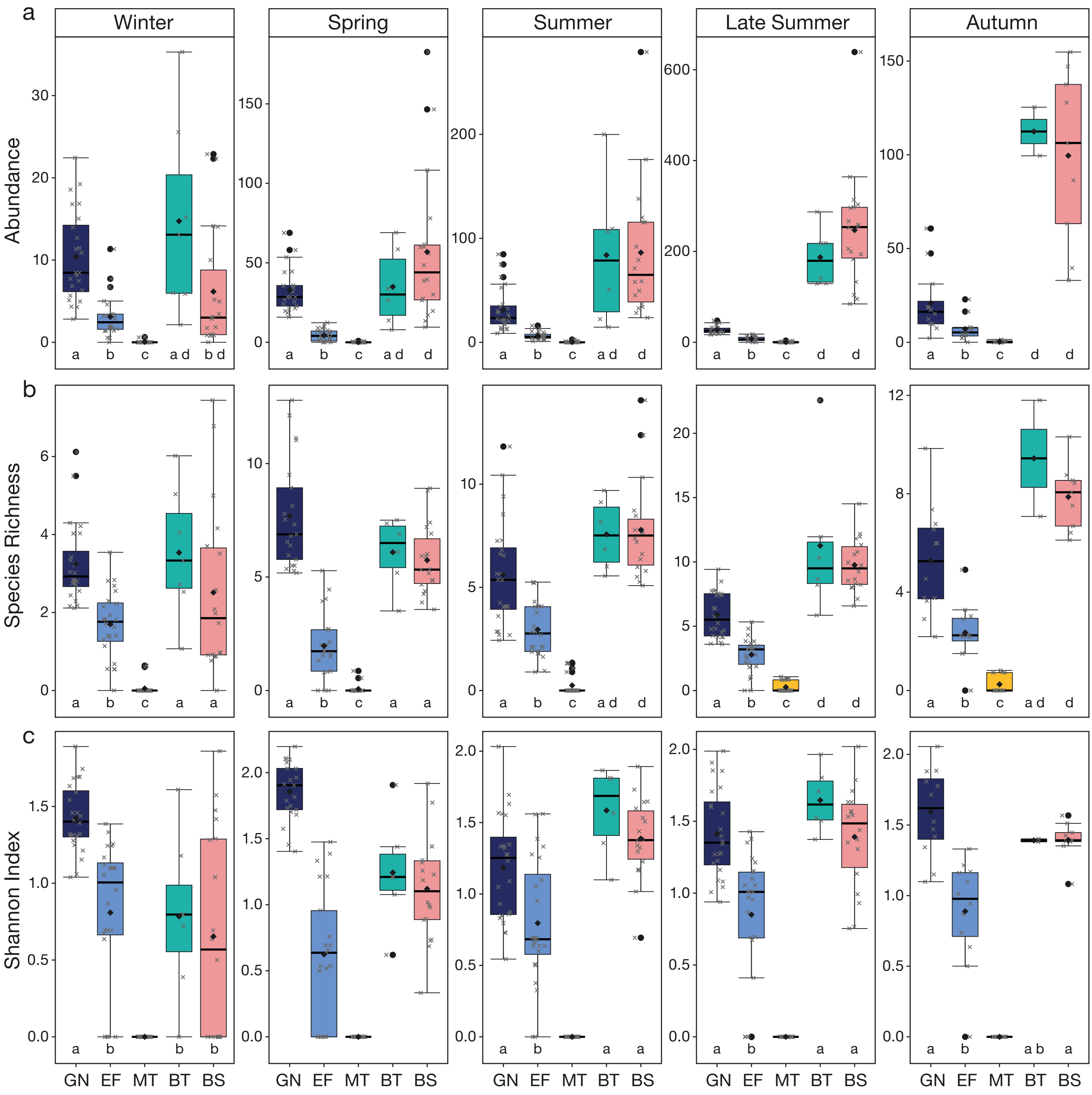

Fig. 2. Comparison of taxonomic indices among fishing methods (GN: gillnet; EF: eelfyke; MT: minnow trap; BS: beach seine; BT: bottom trawl) in the different seasons: (a) abundance, (b) species richness and (c) Shannon index. Individual sampling points are represented by 'x', while mean values are displayed as diamonds, and outliers as dots. Centre lines within the boxes depict medians, while the boundaries of the boxes define the interquartile range. Whiskers of the boxes represent the lowest/highest values that still lie within 1.5× the interquartile range from the box and thus represent minima and maxima when no outliers exist. Different letters below boxplots indicate significant differences ($p < 0.05$) between fishing methods based on post hoc results

fish abundances differed among seasons for 9 species (i.e. significant interaction term 'fishing method× season') (Figs. 4 & 5; Tables S4 & S6), but not for *S. rostellatus*, which displayed the same abundances in bottom trawl and beach seine samples in all seasons (Fig. 5c). *S. typhle*, *P. microps* and *N. ophidion* were

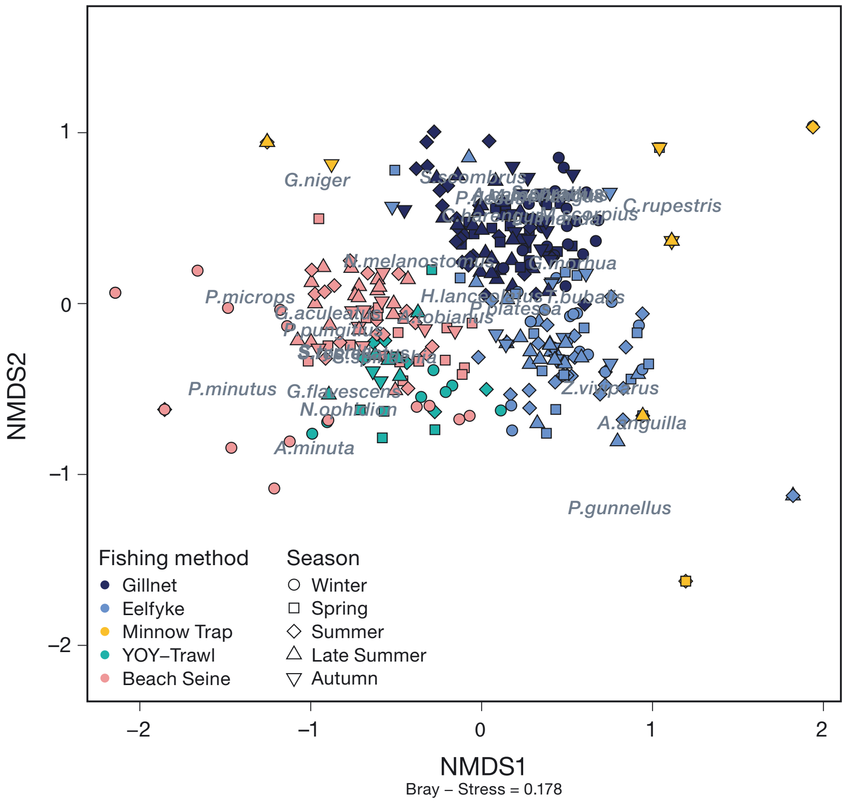

Fig. 3. Non-metric multidimensional scaling plot of taxonomic composition displaying samples obtained with 5 fishing methods in different seasons, and fish species associated with samples (full species names are given in Table 2)

likewise exclusively caught with active fishing methods (see Section 2.3 regarding *S. typhle* occurrence in eelfykes). Higher abundances of *S. typhle* were caught with the beach seine than with the bottom trawl from spring to late summer, while there was no difference in winter and autumn (Fig. 4a). *P. microps* abundances were higher in beach seine samples than in bottom trawl samples except for winter, when abundances were similar (Fig. 4b, cf. Fig. 3). Although model outputs indicated that differences between fishing methods changed with season for *N. ophidion* (p = 0.020; Table S4), post hoc results showed that abundances were consistently higher in bottom trawls compared to beach seines across seasons (Fig. 5e, cf. Fig. 3; Table S6). *P. minutus* only occurred in active methods and minnow traps (Figs. 3 & 5b), with the latter mostly showing lower abundances. In spring and late summer, *P. minutus* abundances were higher in beach seines than in bottom trawls. *G. aculeatus* was exclusively caught with active methods and gillnets (Fig. 4c). Abundances were consistently higher in beach seines than in gillnets, and higher than bottom trawls, except in late summer. Bottom trawls caught more *G. aculeatus* than gillnets in late summer (Fig. 3). *S. spinachia* abundances were mostly highest in active fishing methods (Fig. 4d), while bottom trawls captured more *S. spinachia* than beach seines in summer and late summer. Gillnets mostly caught higher abundances of *P. platessa* than other methods, while abundances in active methods were similar in most seasons (Fig. 5a). *P. flesus* abundances were highest in gillnets in all seasons, except for autumn, when there was no difference between gillnets and bottom trawls (most likely due to the low replicate number of bottom trawl samples, n = 2; Fig. 5d). *G. morhua* was caught with all fishing methods, which displayed similar abundances in winter (Fig. 4e). In the other seasons, abundances were mostly higher in gillnets. In late summer/autumn, gillnets caught similar *G. morhua* abundances as bottom trawls/beach seines, respectively.

3.3. Trait analysis

Differences of the trait indices, i.e. trait richness and dispersion, among fishing methods varied among seasons (significant interaction term ‘fishing method×season’; Fig. 6; Table S7). Trait richness could not be computed for minnow traps, since the calculation requires at least 3 functionally distinct species (Laliberté & Legendre 2010, Laliberté et al. 2014). In winter, spring and autumn, trait richness was higher in gillnets than in the other methods, except for beach seines in winter (Fig. 6). In summer and late summer, trait richness was similar in gillnets and active methods. By definition, trait dispersion takes zero values for samples with only 1 species, as was the case for minnow traps in all seasons. In winter, trait dispersion was higher in gillnets than in the other methods, while samples from gillnets and active methods did not differ with regard to trait dispersion from spring until autumn. While gillnets and active methods had higher trait dispersion than eelfykes in spring and summer, the same was valid only for gillnets in late summer. Bottom trawl and beach seine samples did not differ regarding the trait indices in any season.

Life-history (diet, habitat, schooling behaviour) and morphological (body size, caudal fin shape, body shape) trait differences among fishing methods varied

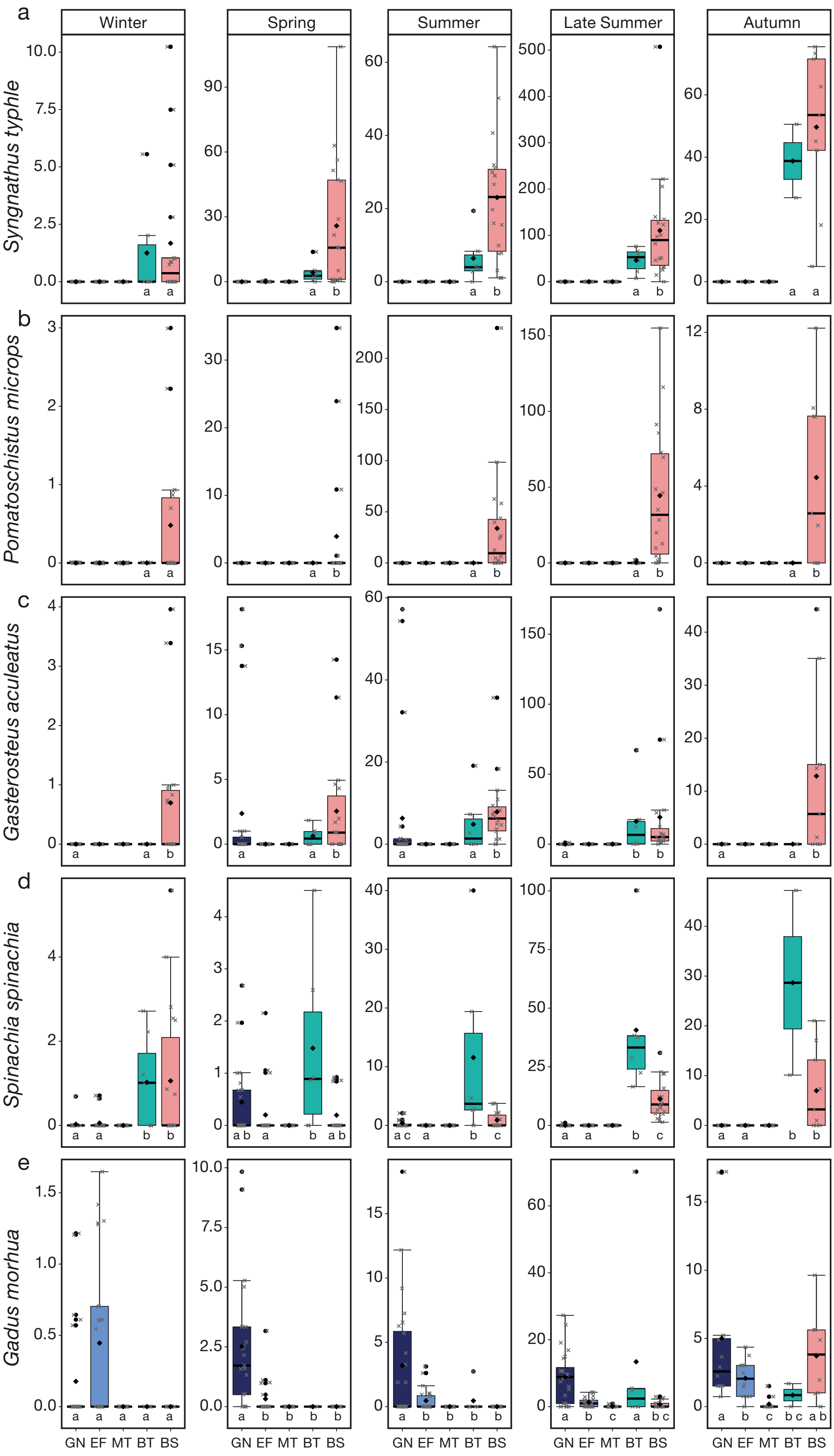

Fig. 4. Comparison of abundances of (a) *Syngnathus typhle*, (b) *Pomatoschistus microps*, (c) *Gasterosteus aculeatus*, (d) *Spinachia spinachia* and (e) *Gadus morhua* among fishing methods in the different seasons. Details as in Fig. 2. For detailed post-hoc results, cf. Table S6 in the Supplement

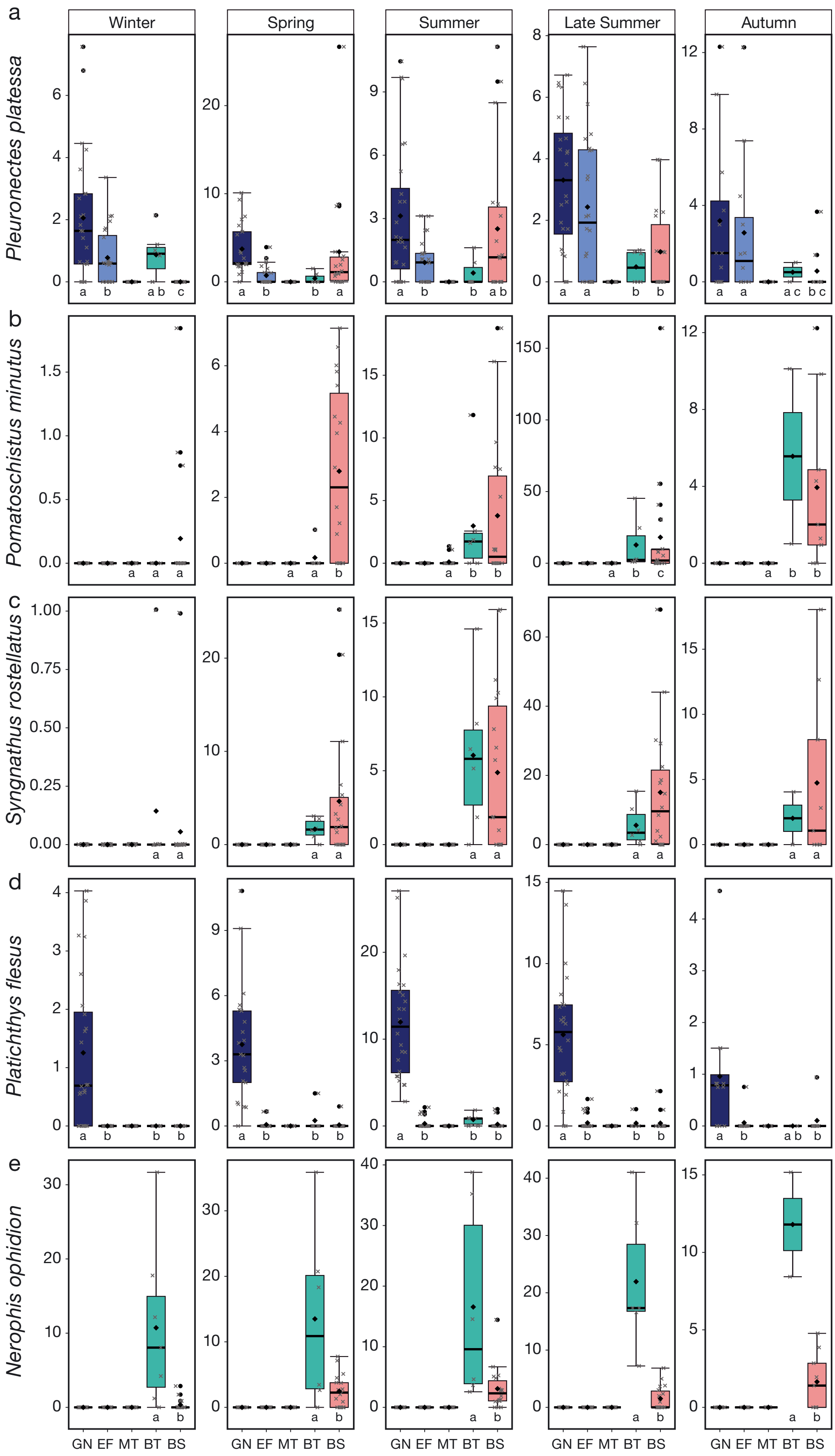

Fig. 5. Comparison of abundances of (a) *Pleuronectes platessa*, (b) *Pomatoschistus minutus*, (c) *Syngnathus rostellatus*, (d) *Platichthys flesus* and (e) *Nerophis ophidion* among fishing methods in the different seasons. Details as in Fig. 2. For detailed post-hoc results, cf. Table S6 in the Supplement

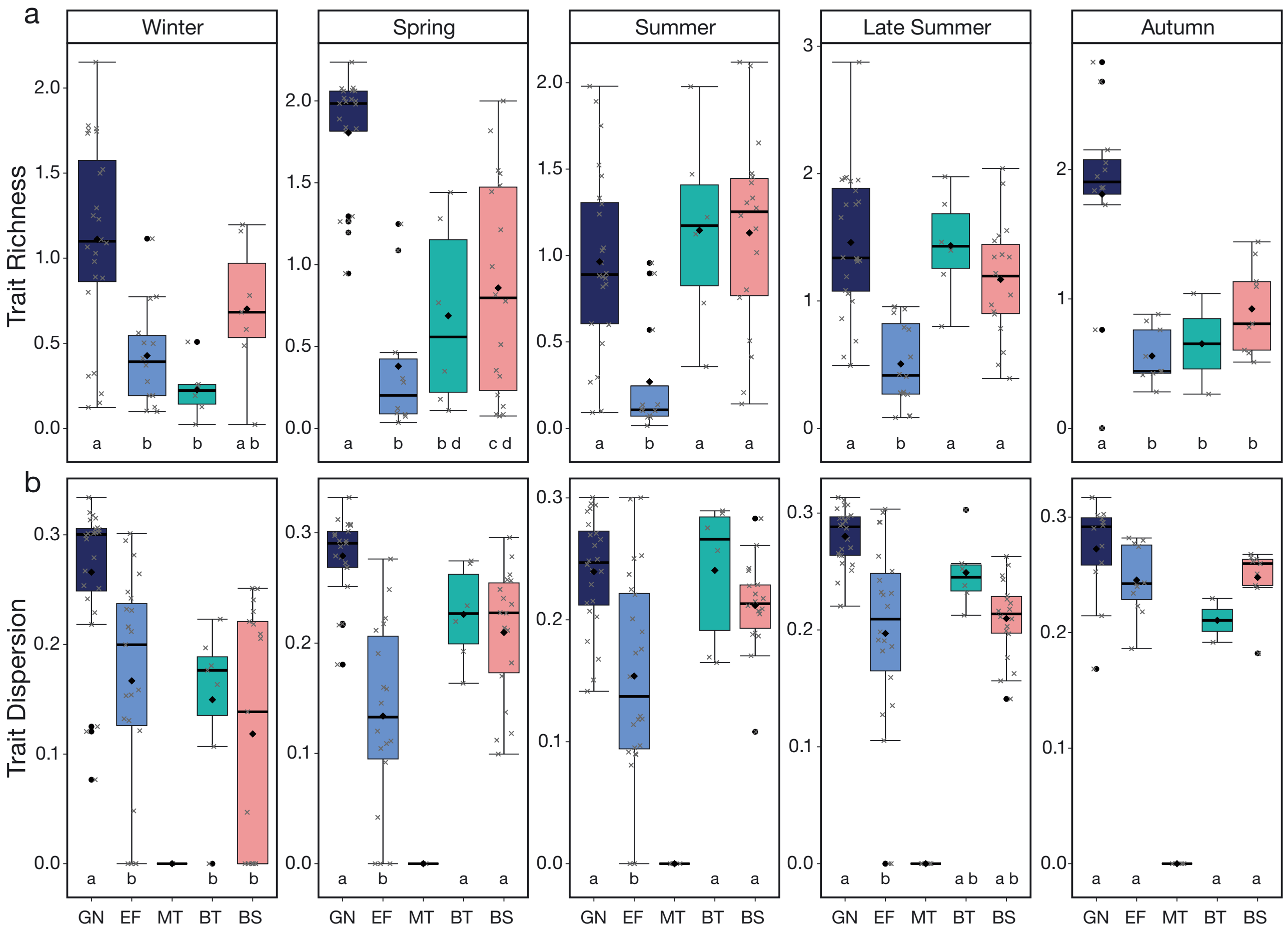

Fig. 6. Comparison of trait indices among fishing methods (GN = gillnet, EF = eelfyke, MT = minnow trap, BS = beach seine, BT = bottom trawl) in the different seasons: (a) trait richness and (b) trait dispersion. Details as in Fig. 2

among seasons for 18 out of 19 trait categories (significant interaction 'fishing method×season'; exception: 'pelagic habitat'; Fig. 7; Figs. S6–S9, Table S7). Since minnow traps predominantly displayed the lowest trait values (e.g. catching the smallest individuals in all seasons), differences between minnow traps and other methods are not described in detail in the following sections (for trait values of minnow traps, see Fig. 7; Figs. S6–S9). With regard to the diet of fish, gillnets consistently captured more piscivores than eelfykes, and also more than the active methods except in late summer and autumn (see Table S8). Gillnets caught more benthivores than eelfykes except in winter and autumn, while active methods were more efficient in catching benthivores than gillnets from summer until autumn. Eelfykes were less efficient in catching planktivorous fish than gillnets and active methods, and gillnets were less efficient than active methods from summer until autumn. Generalists were only caught with eelfykes (mean ± SD trait values: spring = 0.02 ± 0.10, summer = 0.34 ± 0.43, late summer = 0.30 ± 0.38, autumn = 0.22 ± 0.41). Gillnets mostly caught higher numbers of benthopelagic fish than eelfykes, while beach seines and bottom trawls caught more benthopelagic fish than gillnets from summer until autumn/in late summer, respectively. Gillnets captured higher numbers of demersal fish than eelfykes, and active methods caught more demersal fish than gillnets except in winter and spring. Pelagic fish were caught equally efficiently with gillnets and bottom trawls. The number of singletons was mostly higher in gillnets than eelfykes. In winter and spring, gillnets caught a higher or similar number of singletons compared to active methods, while beach seines and bottom trawls captured more singletons from summer until autumn. Fish occurring in pairs or sometimes small schools were predominantly caught more efficiently with active than passive methods from summer until autumn. Schooling fish were better represented by gillnets than eelfykes,

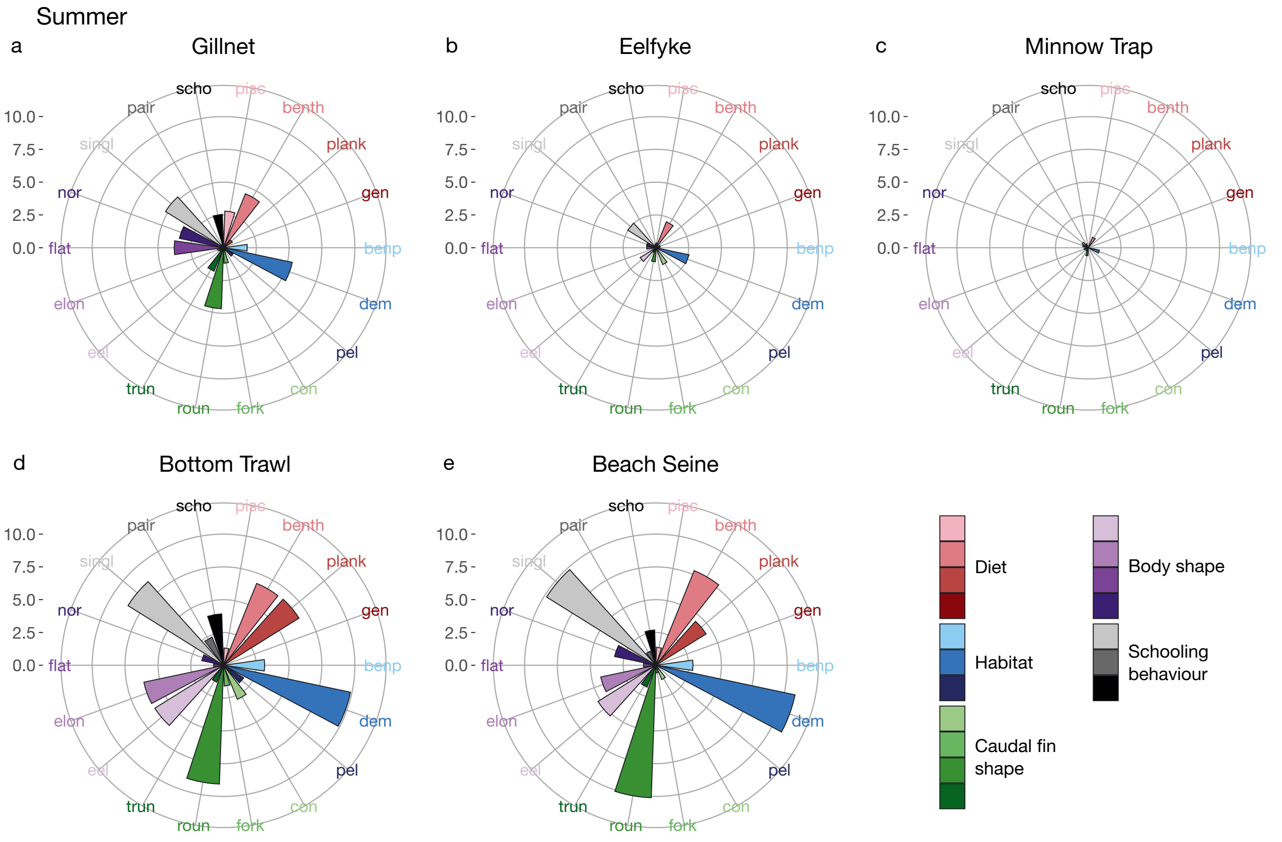

Fig. 7. Trait composition in (a) gillnets, (b) eelfykes, (c) minnow traps, (d) bottom trawls and (e) beach seines in summer (for trait composition in other seasons, see Figs. S6–S9 in the Supplement). Body size was excluded from the plots due to disproportionally large values compared to other traits. See Table 1 for complete trait category names

while active methods caught higher numbers than eelfykes in most seasons.

Regarding the size of fish, gillnets consistently caught the largest fish among passive fishing methods (Table S8). Body size was mostly smaller in eelfykes than in active methods, and larger in gillnets than beach seines/bottom trawls from winter until summer/in spring, respectively. Bottom trawls caught more fish with a continuous caudal fin than gillnets, more than eelfykes except in summer, and more than beach seines in winter and late summer. Eelfykes mostly performed better than gillnets. In most seasons, more fish with a forked caudal fin were caught with gillnets than with active methods. Gillnets caught higher numbers of fish with a rounded caudal fin than eelfykes across seasons and lower numbers than active methods from summer until autumn. Species with a truncated caudal fin were captured equally efficiently with all methods in winter. Eel-like fish were caught more efficiently with active methods than gillnets or eelfykes in most seasons, while eelfykes mostly performed better than gillnets. Fish with an elongated body shape were predominantly better represented by active methods. Gillnets captured more fish with a flat body shape than did active methods during all seasons and mostly higher numbers of flatfish than eelfykes. Fish with a normal body shape were caught more efficiently with gillnets than with eelfykes, bottom trawls (in winter, spring and autumn) and beach seines (in winter and spring).

4. DISCUSSION

To evaluate the catch efficiency of different active and passive fishing methods with respect to fish diversity in seagrass meadows, we compared several community metrics between multimesh gillnets, eelfykes, minnow traps, bottom trawls and beach seines in different seasons. The fish community sampled consisted of species typically found in seagrass meadows, not only in the Baltic Sea but also in other marine regions, including sticklebacks, gobies and pipefish (Bobsien & Brendelberger 2006, Franco et al. 2012, Perry et al. 2018, Staveley et al. 2020). However, the fishing methods displayed distinct differences regarding the diversity of these fish communities, which additionally varied among seasons. The catch efficiency of the fishing methods differed regarding taxonomic and trait diversity and composition, and also with respect to abundances of specific species and the expression of life-history and morphological traits. Correspondingly, other studies conducted in seagrass meadows found that fishing methods differ in displaying fish abundance, species richness and composition, as well as fish size and functional structure (Connolly 1994, Nagelkerken et al. 2001, Bobsien & Brendelberger 2006). However, these studies focussed on other gear types, mainly visual transects and beach seines, making a direct comparison to our results unfeasible. Thus, our study sheds new light on the catch efficiency of commonly used fishing methods with regard to how adequately they capture seagrass fish diversity, which will help scientists choose appropriate sampling gear when conducting ecological research depending on their specific study objective.

4.1. Comparison among passive methods

Among the passive fishing methods, the multimesh gillnet performed best during all seasons in representing taxonomic (abundance, species richness, Shannon index) and trait diversity (trait richness, trait dispersion), while the minnow trap displayed the lowest efficiency. The limited and non-distinct catch composition of minnow traps (Fig. 3) suggests that they do not provide reliable estimates of seagrass fish diversity or target species, which has also been demonstrated in previous studies (Lapointe et al. 2006). This low catch efficiency of minnow traps might be related to the small size of their opening restricting the catch to small fish (Portt et al. 2006), which matches the outcomes of the trait analyses showing that minnow traps consistently caught the smallest fish (Table S8). While eelfykes performed considerably better in displaying overall fish diversity than minnow traps, they also had a higher catch efficiency for fish with a particular trait profile including an eel-like body shape, a continuous caudal fin shape and a generalist diet. These traits correspond to European eel *Anguilla anguilla*, the only species with a generalist diet caught in our study and classified as 'Critically Endangered' within Europe by the IUCN (Pike et al. 2020), thus, requiring specific management and conservation measures (Feunteun 2002). Unsurprisingly, eelfykes seem to be highly efficient in catching eel (Fig. 3; Franco et al. 2012) and therefore represent a valuable gear for assessing its population dynamics in seagrass meadows, in particular since they allow fish to be generally retrieved without injuries (Krueger et al. 1998, Portt et al. 2006). In contrast, multimesh gillnets showed a high catch efficiency for Atlantic cod *Gadus morhua*, and, correspondingly, fish with a piscivorous diet, as well as for European plaice *Pleuronectes platessa* and European flounder *Platichthys flesus*, i.e. fish with a flat body shape. Cod, plaice and flounder are commercially exploited, not only in the Baltic Sea, but also in other marine waters (ICES 2022), which is why the investigation of their ecology and population dynamics is essential to provide advice for fisheries management. However, stock management often neglects the importance of coastal waters for commercial fish by primarily concentrating monitoring surveys to deeper offshore areas. Shallower, coastal waters act as significant recruitment areas for various commercially used fish species (Seitz et al. 2014, Stamp et al. 2022, Swadling et al. 2022) and can therefore have a strong influence on recruitment success and adult biomass, which has, for instance, been shown for Atlantic herring *Clupea harengus*. To understand the causes for the sharp decline in herring biomass in the western Baltic Sea since the early 2000s, the consideration of abiotic conditions in coastal habitats proved essential (Polte et al. 2021). Hence, information on the presence of commercially exploited species in coastal habitats is crucial and in support of the required ecosystem approach in fisheries management, requiring adequate sampling methods for commercially used fish species in coastal areas.

4.2. Seasonal changes in catch efficiency

Previous studies have detected seasonal differences in the catch efficiency of fishing methods. For instance, Mehdi et al. (2021) found that minnow traps caught higher fish abundances in summer than in winter compared to other fishing methods in freshwater systems. In the current study, the catch efficiency of fishing methods varied between seasons, in particular when comparing the active with the passive methods. From winter until summer, the gillnet displayed predominantly higher (Shannon index, trait richness and dispersion) or similar (abundance, species richness) taxonomic and trait diversity compared to the bottom trawl and beach seine, while the active methods performed mostly better (abundance, species richness) or equally well (Shannon index, trait richness and dispersion) from summer until autumn. Thus, the catch efficiency of active methods compared to the gillnet regarding overall fish diversity increased throughout the year, displaying the highest efficiency from summer until autumn, which is most likely linked to the distinct species composition captured with the different fishing methods (Krueger et al. 1998, Mehdi et al. 2021). Both the beach seine and the bottom trawl caught the highest abundances of pipefish (Nilsson's pipefish *Syngnathus rostellatus*, broadnosed pipefish *Syngnathus typhle*, straightnose pipefish *Nerophis ophidion*), sticklebacks (three-spined stickleback *Gasterosteus aculeatus*, sea stickleback *Spinachia spinachia*) and gobies (common goby *Pomatoschistus microps*, sand goby *Pomatoschistus minutus*; Figs. 3–5; Figs. S1–S5), and, correspondingly, were most efficient in catching fish with an eel-like and elongated body shape. These 3 fish families represent typical inhabitants of seagrass meadows (Bobsien 2006, Franco et al. 2012), seemingly reaching the highest abundances in this habitat from summer until autumn, and cannot reliably be caught with the passive fishing methods (Figs. 4 & 5; Figs. S1–S5). Coinciding with our results, the highest densities of the majority of the above-mentioned species are reported to occur during the summer and autumn months in shallow coastal areas of the Baltic Sea, while abundances either decrease drastically or the species cannot be found at all in winter (Jansson et al. 1985, Aarnio & Bonsdorff 1993, Bobsien 2006). The cause for the absence of e.g. *S. typhle* and gobies from shallow habitats during winter is assumed to be migrations into deeper areas when water temperatures decrease, followed by a return to shallower waters with rising temperatures in spring (Bobsien 2006, Tarnowska & Sapota 2007). The pronounced difference in gear selectivity between active methods and gillnets regarding certain species most likely results in a higher fish diversity captured with the active methods during summer and autumn. Active fishing methods are therefore important to assess overall fish diversity in seagrass meadows, especially considering that these typical seagrass species might play a significant role in the functioning of these coastal habitats (Holmlund & Hammer 1999, Chapin et al. 2000) due to their longer-lasting presence in these areas compared to species primarily migrating through the coastal zone. In accordance with our results, seine nets, tested in a Mediterranean lagoon, performed best in catching small resident fish species with a benthic-demersal habitat use and a benthivorous diet, such as marbled goby *P. marmoratus* (Franco et al. 2012), and have generally been identified as an effective fishing method (Lapointe et al. 2006, Baker et al. 2016).

Comparable to the typical seagrass species, the active methods showed an increased efficiency for catching cod in late summer and autumn, i.e. similar numbers of cod individuals were caught with the gillnet and the bottom trawl and beach seine in late summer and autumn, respectively (Figs. S4 & S5). Yet, the active methods caught comparably smaller, i.e. juvenile, cod compared to the gillnet (mean ± SD length of cod, LSU: bottom trawl = 92.67 ± 16.27 mm, gillnet = 147.53 ± 67.29 mm; AU: beach seine = 79.01 ± 16.49 mm, gillnet = 178.49 ± 49.56 mm).These smaller individuals seem to occupy seagrass meadows primarily later in the year (LSU, AU; cf. Fig. 4e), which coincides with McQueen et al. (2019) reporting that juvenile, young-of-the-year cod (<10 cm length) use waters shallower than 5 m from August until October in the western Baltic Sea. Thus, active fishing methods play an important role in assessing juveniles of this commercially important species, while gillnets seem to be more efficient in catching larger cod and underestimate abundances of small individuals (Olin et al. 2009, Prchalová et al. 2012), suggesting that a combination of active and passive methods is required to sample all life stages. A similar pattern was observed for the commercially used flounder. Juvenile flounder were exclusively caught with beach seines, while gillnets only captured larger individuals across all seasons (overall mean ± SD length of flounder: beach seine = 40.15 ± 21.99 mm, gillnet = 188.33 ± 75.20 mm).

4.3. Comparison of catch efficiency between active methods

While the beach seine and bottom trawl deviated rather strongly from the passive methods, they yielded similar results with regard to fish community metrics (taxonomic and trait indices, taxonomic composition; cf. clustering of beach seine and bottom trawl samples in the NMDS plot, Fig. 3), yet differing in their efficiency to capture specific species. Thus, these active methods can act as surrogates regarding overall fish diversity in seagrass meadows, although they are deployed in different water depths. The differing abundances of specific species in the beach seine and bottom trawl catches might possibly be related to differences in the depth distribution, i.e. reflecting habitat preferences of the respective species. A distinct depth occurrence could have been expected for *P. microps* and *P. minutus*, as the former commonly occurs closer to shore, while the latter also occupies greater water depths (Muus & Nielsen 2013). However, both species were caught more efficiently with the beach seine than with the bottom trawl, as was also the case for *S. typhle* and *G. aculeatus*. In contrast, higher abundances of *N. ophidion* and *S. spinachia* were captured with the bottom trawl. Thus, for the majority of typical seagrass species investigated, the beach seine proved to be the more suitable fishing method. This could be due to differences in species depth distributions and/or to the use of the beach seine in shallower water depths making it easier to control whether it is fishing properly, i.e. has permanent bottom contact, compared to the bottom trawl used in greater water depths.

4.4. Trait differences among fishing methods

Fishing methods not only differed regarding the taxonomic properties of fish communities, but also with respect to life-history and morphological traits in the catches. For some traits, the same seasonal pattern among gillnets and active methods was observed as for the taxonomic and trait indices: the efficiency of the beach seine and bottom trawl increased throughout the seasons in comparison to the gillnet for fish with a larger body size, a benthivorous or planktivorous diet, a benthopelagic or demersal habitat use, a rounded caudal fin, a normal body shape and for fish living as singletons or paired in small schools. As for the indices, this pattern is likely linked to the higher catchability of the active methods for typical seagrass species (pipefish, sticklebacks, gobies) from summer until autumn, since most of the trait categories correspond to these families (Table 2). The greater fish sizes caught with active methods in late summer and autumn are likely related to the high abundances of pipefish in seagrass meadows during this time of year (Franco et al. 2012). For instance, in late summer, the bottom trawl caught high numbers of large *N. ophidion* (>20 cm) (cf. Fig. S4). In general, gillnets seem to underestimate the proportion of smaller fish, while trawls are suggested to be more effective (Wells et al. 2008, Olin et al. 2009). This corresponds to our results in so far, as gillnets consistently captured larger fish than other passive methods throughout all seasons and caught larger cod and flounder than active methods (cf. Section 4.2), confirming that fish size represents a critical variable influencing gear selectivity (Portt et al. 2006, Říha et al. 2008, Mouchet et al. 2019).

The beach seine displayed a comparatively high catch efficiency for demersal fish, capturing higher abundances than most other fishing methods. However, fish numbers might still be underestimated, as small benthic fish can escape beach seines more easily compared to surface or midwater schooling species (Pierce et al. 1990, Bayley & Herendeen 2000, Lapointe et al. 2006). In contrast, pelagic species, including the transparent goby *Aphia minuta*, Atlantic mackerel *Scomber scombrus* and European sprat *Sprattus sprattus*, were only captured with the gillnet and bottom trawl with a similar efficiency. This conforms with other studies stressing the importance of these 2 fishing methods for sampling fish with a pelagic habitat use in seagrass (Krueger et al. 1998).

In addition to body size, other morphological characteristics of fish, i.e. caudal fin and body shape, also differed among fishing methods. Efficiency varied distinctly for fish with continuous and forked caudal fins. Caudal fin shape, or rather the aspect ratio of caudal fins (caudal fin depth divided by surface area), is directly related to the mode of propulsion, i.e. the swimming ability of fish (Webb 1984), determining, amongst other factors, how efficiently fish are caught with certain fishing gear. Fish have to move actively to be caught with gillnets, and their swimming ability has an impact on the distance they travel, which influences their probability of encountering passive gear. Good swimmers have a higher chance of escaping active fishing methods such as seines and trawls (Portt et al. 2006, Mouchet et al. 2019). In our study, the bottom trawl performed best in catching fish with a continuous caudal fin, e.g. *N. ophidion*, while the eelfyke was most efficient among passive fishing methods, most likely due to a high selectivity for *A. anguilla*. This is in accordance with Mouchet et al. (2019) suggesting that elongated species with no distinctly developed caudal fin, such as European conger *Conger conger*, might be able to escape trawls due to their mode of movement. Based on our results, they might therefore almost exclusively be catchable with passive fishing methods. Highest abundances of fish with a forked caudal fin, including small sandeel *Ammodytes tobianus*, Atlantic herring, great sandeel *Hyperoplus lanceolatus*, mackerel and sprat, were caught with gillnets. Considering that these species represent fast-swimming fish with streamlined bodies, it is likely that they are also able to evade active fishing methods. Indeed, a forked caudal fin (in addition to a streamlined body) has been identified as a trait linked to high swimming speed (Webb 1984). Correspondingly, other studies observed that Atlantic mackerel and horse mackerel *Trachurus trachurus* were able to escape trawls, which was put down to the high values of their caudal fin aspect ratio (Kopp et al. 2018, Mouchet et al. 2019). In contrast to our results indicating a dependence of catchability on fish body shape, Mouchet et al. (2019) did not find body shape differences between fish escaping and fish retained in bottom trawls. In our study, the highest abundances of eel-like and elongated fish were caught with the active methods, while flatfish were captured more efficiently with gillnets. Correspondingly, seines and bottom trawls are reported to underestimate abundances of fish with a flat body shape by passing over them (McLachlan & Brown 2006, McIntyre et al. 2015), suggesting that body shape plays a certain role in fishing gear selectivity.

4.5. Choosing an appropriate fishing method

The choice of fishing method does not only depend on gear selectivity for specific species and traits, but also on habitat conditions. Bottom trawls and beach seines require an even ground, since increased structural complexity due to rocks and dense vegetation can cause the snagging of the net, usually resulting in reduced catch efficiency. Yet, high macrophyte biomass has also been observed to increase gear efficiency, possibly due to fish feeling more sheltered and therefore less prone to escape (Pierce et al. 1990, Rozas & Minello 1997, Nagelkerken et al. 2001, Portt et al. 2006). Seagrass meadows are often mixed with other habitat types, for instance rocks, which can aggravate the use of beach seines and bottom trawls. Moreover, drifting algae can be problematic for active fishing methods by clogging the net after only a few minutes of towing (C. Henseler pers. obs.). The water depth of the habitat should also be taken into account, as certain gear is restricted to the use at specific depths, e.g. beach seines to areas shallower than one-half to two-thirds of their height vs. bottom trawls to waters deeper than 1 m (Rozas & Minello 1997, Portt et al. 2006). Beach seine samples are therefore not directly comparable to other methods used in greater water depths, but should rather be considered as a complementary method to sample the very shallow parts of coastal habitats, in which other methods cannot reliably be used. However, since habitats such as seagrass meadows occur both in very shallow (0.5 m depth), but also deeper areas, the use of different methodology in different depths is inevitable to assess habitats in their entirety. When using gillnets, the presence of decapod crabs (green crab *Carcinus maenas* in the Baltic Sea) causes severe problems, as these invertebrates become entangled in the net, making it very time-consuming to clear. Furthermore, they feed on the fish caught, rendering length measurements, and even fish identification, impossible when only fishbones remain. However, this issue is region dependent, at least in the Baltic Sea, where *C. maenas* only occurs in southwestern, more saline areas, while no equivalent species exist in more northern regions (C. Henseler pers. obs.).

Achieving standardization of fishing methods in different studies or for monitoring purposes in different countries can be challenging, as catchability does not only depend on the type of fishing method, but also on the specific design of the gear (e.g. net length) and how it is handled in the field (Rozas & Minello 1997, Říha et al. 2008, Franco et al. 2012). This should also be kept in mind with respect to our results, since they might not be directly transferable to other studies using different gear designs. As fishing methods were applied in their standardized way in our study, passive gear fished overnight and active methods fished during the day. Although this represents the common way of operating, it might introduce a certain bias into sampling results, as both gear efficiency and fish community composition vary between different times of day (Olin et al. 2004, Říha et al. 2008, Taal et al. 2017). Various fish species are more active during the night than in the daytime, generally resulting in higher fish abundances in night samples (Pihl & Wennhage 2002), which is also linked to the lower visibility making avoidance of passive gear less likely (He 2006). Nocturnal hunters, such as adult cod, plaice, flounder and eel (Muus & Nielsen 2013), were caught more efficiently with passive methods set during the night in our study. This might not solely be an effect of gear selectivity, but also of diel fish activity and fishing time.

The probability of fish survival varies among fishing methods and can influence the choice of sampling method depending on whether fish are needed alive (e.g. for aquarium use) or whether they will die during subsequent handling (e.g. stomach content analyses) anyway. Active methods usually allow fish survival, unless species are very small or sensitive to stress. Minnow traps and fyke nets also provide a high chance of fish survival, although predation of larger fish on smaller ones cannot be prevented in fyke nets. In contrast, gillnets generally injure fish rather severely, resulting in high mortality (Portt et al. 2006). Another aspect to consider is whether fish data need to be quantified for a specified area. Fish densities can be calculated with active methods, as the area fished is quite easily defined. However, passive methods only enable the calculation of catch per unit effort, while determining the actually sampled area is difficult. This makes a comparison between active and passive fishing methods difficult, which is why we decided to calculate fish abundances in their standardized way for each fishing method, making our results directly usable for other scientists.

4.6. Study restrictions

In this study, the efficiency of fishing methods was evaluated with regard to different aspects of fish diversity in seagrass meadows, representing a vulnerable, prominent habitat type in coastal areas worldwide (Duarte 2002, McKenzie et al. 2020). The analysis of trait-based diversity ensures the applicability of our results to other regions with a different fish community, as trait metrics are detached from species composition, focussing on the expression of commonly analysed fish characteristics (e.g. body size and shape) instead. However, study outcomes cannot directly be translated to other habitat types, as fishing methods are likely to have a different efficiency in habitats with differing structural complexity and site conditions (e.g. hydrodynamics), such as bare sand habitats (Rozas & Minello 1997, Nagelkerken et al. 2001, Franco et al. 2012, Shah Esmaeili et al. 2021). Moreover, we could only consider a certain number of fishing methods in our analyses. However, as beach seines and especially bottom trawls might have a negative impact on the seafloor (e.g. Olsgard et al. 2008, Johnson et al. 2015), it would be advisable to additionally assess the efficiency of non-invasive fishing methods in seagrass meadows, for instance SCUBA diving transects or underwater video systems (Bobsien & Brendelberger 2006, Wells et al. 2008, Baker et al. 2016), in relation to the catchability of active gear. Yet, the application of visual methods might be problematic in the often murky waters of the Baltic Sea, and can only be of use when fish do not need to be extracted, as is the case for, e.g. stomach content analyses. Fish community composition not only varies with season, but additionally underlies interannual variations (e.g. Bobsien 2006, Masuda 2008). To which extent differences in community composition among years influence the catchability of fishing methods needs to be addressed in future studies covering several years of sampling. Along the same lines, our results regarding the efficiency of fishing methods have to be verified for seagrass meadows in other marine regions with a different fish community composition and environmental conditions. Due to the random sequence in which fishing methods were used at each station, bottom trawl samples were sometimes taken before setting passive gear on the same day. Although interaction between different gear types was minimized as much as possible (i.e. maximum distance and time between deployments), it cannot be excluded that trawling potentially influenced the catchability of passive gear when conducted beforehand.

4.7. Conclusions

Overall, the comparison of different fishing methods in seagrass meadows indicated that each method entails a certain bias misjudging certain diversity components, species or traits (e.g. Portt et al. 2006). Minnow traps were generally inadequate for sampling coastal fish communities, most likely due to their small size, while gillnets proved to be the most efficient passive method for displaying overall diversity (abundance, species richness, Shannon index, trait richness, trait dispersion). However, when aiming to capture the entire fish community of seagrass meadows throughout the year, the use of gillnets would not be sufficient, as they are not suited to catch typical seagrass inhabitants, such as gobies, sticklebacks and pipefish. These fish with an eel-like or elongated body shape could only be captured effectively with the beach seine and bottom trawl. This likely causes the higher efficiency of these methods for taxonomic and trait diversity and specific traits from summer until autumn, as these species seem to be most abundant in seagrass at this time of year. Thus, to record the entire diversity spectrum in this habitat, a combination of gillnets and at least one, active method would be advisable, keeping in mind the more destructive nature of the active methods with regard to seafloor structure. In contrast, the use of a single fishing method might be appropriate when specific species or fish groups with a certain set of traits are targeted. Active methods would be adequate to sample typical seagrass species, while eelfykes are most suitable to catch fish with an eel-like body shape, a continuous caudal fin shape and a generalist diet, i.e. eel. Piscivorous fish (e.g. adult cod), flatfish (plaice, adult flounder) and fast-swimming fish with a forked caudal fin should be sampled with multimesh gillnets, while pelagic species can only be recorded with gillnets and bottom trawls. In contrast, the beach seine and bottom trawl seemed most efficient for sampling juvenile cod and flounder. Although the catchability among active methods regarding overall fish diversity was similar, they differed in their efficiency to catch certain species, although different fishing depths might be the underlying cause here. Fishing methods complemented each other in displaying diversity of fish communities in seagrass meadows, which is a conclusion also reached by other authors, even though referring to other fishing methods (Bobsien & Brendelberger 2006, Baker et al. 2016, Mehdi et al. 2021, Shah Esmaeili et al. 2021). The most appropriate fishing method for sampling specific aspects of fish diversity in seagrass meadows therefore depends on the objective of a study.

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LITERATURE CITED

Aarnio K, Bonsdorff E (1993) Seasonal variation in abundance and diet of the sand goby *Pomatoschistus minutus* (Pallas) in a northern Baltic archipelago. Ophelia 37: 19–30

Airoldi L, Beck MW (2007) Loss, status and trends for coastal marine habitats of Europe. Oceanogr Mar Biol Annu Rev 45:345–405

Baker DGL, Eddy TD, McIver R, Schmidt AL and others (2016) Comparative analysis of different survey methods for monitoring fish assemblages in coastal habitats. PeerJ 4:e1832

Barnett LAK, Jacobsen NS, Thorson JT, Cope JM (2019) Realizing the potential of trait-based approaches to advance fisheries science. Fish Fish 20:1034–1050

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Bayley PB, Herendeen RA (2000) The efficiency of a seine net. Trans Am Fish Soc 129:901–923

Bobsien IC (2006) The role of small fish species in eelgrass food webs of the Baltic Sea. PhD dissertation, Christian-Albrechts-Universität, Kiel

Bobsien IC, Brendelberger H (2006) Comparison of an enclosure drop trap and a visual diving census technique to estimate fish populations in eelgrass habitats. Limnol Oceanogr Methods 4:130–141

Bremner J (2008) Species' traits and ecological functioning in marine conservation and management. J Exp Mar Biol Ecol 366:37–47

Chapin FS III, Zavaleta ES, Eviner VT, Naylor RL and others (2000) Consequences of changing biodiversity. Nature 405:234–242

Colossi Brustolin M, Nagelkerken I, Ferreira CM, Goldenberg SU, Ullah H, Fonseca G (2019) Future ocean climate homogenizes communities across habitats through diversity loss and rise of generalist species. Glob Change Biol 25:3539–3548

Connolly RM (1994) Comparison of fish catches from a buoyant pop net and a beach seine net in a shallow seagrass habitat. Mar Ecol Prog Ser 109:305–309

Duarte CM (2002) The future of seagrass meadows. Environ Conserv 29:192–206

Eriksson BK, Ljunggren L, Sandström A, Johansson G and others (2009) Declines in predatory fish promote bloom-forming macroalgae. Ecol Appl 19:1975–1988

Feunteun E (2002) Management and restoration of European eel population (*Anguilla anguilla*): an impossible bargain. Ecol Eng 18:575–591

Fonseca MS, Fisher JS (1986) A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. Mar Ecol Prog Ser 29:15–22

Fox J, Weisberg S (2019) An {R} companion to applied regression, 3rd edn. Sage, Thousand Oaks, CA

Franco A, Pérez-Ruzafa A, Drouineau H, Franzoi P and others (2012) Assessment of fish assemblages in coastal lagoon habitats: effect of sampling method. Estuar Coast Shelf Sci 112:115–125

Gagic V, Bartomeus I, Jonsson T, Taylor A and others (2015) Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. Proc R Soc B 282:20142620

Hamley J (1975) Review of gillnet selectivity. J Fish Res Board Can 32:1943–1969

He P (2006) Gillnets: gear design, fishing performance and conservation challenges. Mar Technol Soc J 40:12–19

Heckwolf MJ, Peterson A, Jänes H, Horne P and others (2021) From ecosystems to socio-economic benefits: a systematic review of coastal ecosystem services in the Baltic Sea. Sci Total Environ 755:142565

HELCOM (2020) Guidelines for coastal fish monitoring. https://helcom.fi/wp-content/uploads/2020/01/HELCOM-Guidelines-for-coastal-fish-monitoring-2019.pdf

Henseler C, Nordström MC, Törnroos A, Snickars M, Pecuchet L, Lindegren M, Bonsdorff E (2019) Coastal habitats and their importance for the diversity of benthic communities: a species- and trait-based approach. Estuar Coast Shelf Sci 226:106272

Henseler C, Oesterwind D, Kotterba P, Nordström MC, Snickars M, Törnroos A, Bonsdorff E (2021) Impact of round goby on native invertebrate communities — an experimental field study. J Exp Mar Biol Ecol 541: 151571

Holmlund CM, Hammer M (1999) Ecosystem services generated by fish populations. Ecol Econ 29:253–268

ICES (2022) ICES Sci Rep 4. Baltic Fisheries Assessment Working Group (WGBFAS), ICES, Copenhagen

Jansson BO, Aneer G, Nellbring S (1985) Spatial and temporal distribution of the demersal fish fauna in a Baltic archipelago as estimated by SCUBA census. Mar Ecol Prog Ser 23:31–43

Johnson AF, Gorelli G, Jenkins SR, Hiddink JG, Hinz H (2015) Effects of bottom trawling on fish foraging and feeding. Proc R Soc B 282:20142336

Kelley JL, Grierson PF, Collin SP, Davies PM (2018) Habitat disruption and the identification and management of functional trait changes. Fish Fish 19:716–728

Kopp D, Morandeau F, Mouchet M, Vogel C, Méhault S (2018) What can be expected of a T90 extension piece to improve selectivity in bottom trawl multispecific fisheries in the Bay of Biscay? Fish Sci 84:597–604

Krueger KL, Hubert WA, Price RM (1998) Tandem-set fyke nets for sampling benthic fishes in lakes. N Am J Fish Manag 18:154–160

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305

Laliberté E, Legendre P, Shipley B (2014) FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12. https://CRAN.R-project.org/web/packages/FD/index.html

Lapointe NWR, Corkum LD, Mandrak NE (2006) A comparison of methods for sampling fish diversity in shallow offshore waters of large rivers. N Am J Fish Manag 26: 503–513

Lefcheck JS, Hughes BB, Johnson AJ, Pfirrmann BW and others (2019) Are coastal habitats important nurseries? A meta-analysis. Conserv Lett 12:e12645

Lenth RV (2021) Emmeans: estimated marginal means, aka least-squares means. R package version 1.6.3. https://CRAN.R-project.org/package=emmeans

Masuda R (2008) Seasonal and interannual variation of subtidal fish assemblages in Wakasa Bay with reference to the warming trend in the Sea of Japan. Environ Biol Fishes 82:387–399

McIntyre FD, Neat F, Collie N, Stewart M, Fernandes PG (2015) Visual surveys can reveal rather different 'pictures' of fish densities: comparison of trawl and video camera surveys in the Rockall Bank, NE Atlantic Ocean. Deep Sea Res I 95:67–74

McKenzie LJ, Nordlund LM, Jones BL, Cullen-Unsworth LC, Roelfsema C, Unsworth RKF (2020) The global distribution of seagrass meadows. Environ Res Lett 15:074041

McLachlan A, Brown AC (2006) Surf-zone fauna. In: McLachlan A, Brown AC (eds) Ecology of sandy shores. Elsevier, Burlington, MA, p 197–213

McQueen K, Hrabowski J, Krumme U (2019) Age validation of juvenile cod in the Western Baltic Sea. ICES J Mar Sci 76:430–441

Mehdi H, Lau SC, Synyshyn C, Salena MG and others (2021) A comparison of passive and active gear in fish community assessments in summer versus winter. Fish Res 242:106016

Mouchet M, Poirson M, Morandeau F, Vogel C, Méhault S, Kopp D (2019) Using a trait-based approach to understand the efficiency of a selective device in a multispecific fishery. Sci Rep 9:12489

Muus B, Nielsen J (2013) Die Meeresfische Europas in Nordsee, Ostsee und Atlantik. Franckh-Kosmos Verlags-GmbH & Co., Stuttgart

Nagelkerken I, Kleijnen S, Klop T, van den Brand RACJ, Cocheret de la Morinière E, van der Velde G (2001) Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. Mar Ecol Prog Ser 214:225–235

Nordlund LM, Koch EW, Barbier EB, Creed JC (2016) Seagrass ecosystem services and their variability across genera and geographical regions. PLOS ONE 11:e0163091

Oksanen J, Blanchet FG, Friendly M, Kindt R and others (2020) Vegan: community ecology package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan

Olds AD, Vargas-Fonseca E, Connolly RM, Gilby BL and others (2018) The ecology of fish in the surf zones of ocean beaches: a global review. Fish Fish 19:78–89

Olin M, Kurkilahti M, Peitola P, Ruuhijärvi J (2004) The effects of fish accumulation on the catchability of multimesh gillnet. Fish Res 68:135–147

Olin M, Malinen T, Ruuhijärvi J (2009) Gillnet catch in estimating the density and structure of fish community – comparison of gillnet and trawl samples in a eutrophic lake. Fish Res 96:88–94

Olsgard F, Schaanning MT, Widdicombe S, Kendall MA, Austen MC (2008) Effects of bottom trawling on ecosystem functioning. J Exp Mar Biol Ecol 366:123–133

Östman Ö, Eklöf J, Eriksson BK, Olsson J, Moksnes P, Bergström U (2016) Top-down control as important as nutrient enrichment for eutrophication effects in North Atlantic coastal ecosystems. J Appl Ecol 53:1138–1147

Perry D, Staveley TAB, Gullström M (2018) Habitat connectivity of fish in temperate shallow-water seascapes. Front Mar Sci 4:440

Pierce CL, Rasmussen JB, Leggett WC (1990) Sampling littoral fish with a seine: corrections for variable capture efficiency. Can J Fish Aquat Sci 47:1004–1010

Pihl L, Wennhage H (2002) Structure and diversity of fish assemblages on rocky and soft bottom shores on the Swedish west coast. J Fish Biol 61:148–166

Pike C, Crook V, Gollock M (2020) European eel *Anguilla anguilla*. The IUCN red list of threatened species 2020: e.T60344A152845178. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T60344A152845178.en (accessed on 21 October 2022)

Pinheiro J, Bates D, DebRoy S, Sarkar D, Team RC (2021) Nlme: linear and nonlinear mixed effects models. R package version 3.1-152. https://CRAN.R-project.org/package=nlme

Polte P, Gröhsler T, Kotterba P, von Nordheim L and others (2021) Reduced reproductive success of Western Baltic herring (*Clupea harengus*) as a response to warming winters. Front Mar Sci 8:589242

Portt CB, Coker GA, Ming DL, Randall RG (2006) A review of fish sampling methods commonly used in Canadian freshwater habitats. Can Tech Rep Fish Aquat Sci 2604

Prchalová M, Neal JW, Muñoz-Hincapié M, Jůza T, Říha M, Peterka J, Kubečka J (2012) Comparison of gill nets and fixed-frame trawls for sampling threadfin shad in tropical reservoirs. Trans Am Fish Soc 141:1151–1160

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reusch TBH, Dierking J, Andersson HC, Bonsdorff E and others (2018) The Baltic Sea as a time machine for the future coastal ocean. Sci Adv 4:eaar8195

Říha M, Kubečka J, Mrkvička T, Prchalová M and others (2008) Dependence of beach seine net efficiency on net length and diel period. Aquat Living Resour 21:411–418

Rönnbäck P, Kautsky N, Pihl L, Troell M, Söderqvist T, Wennhage H (2007) Ecosystem goods and services from Swedish coastal habitats: identification, valuation, and implications of ecosystem shifts. Ambio 36:534–544

Rozas LP, Minello TJ (1997) Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. Estuaries 20:199–213

Schubert PR, Hukriede W, Karez R, Reusch TBH (2015) Mapping and modeling eelgrass *Zostera marina* distribution in the western Baltic Sea. Mar Ecol Prog Ser 522: 79–95

Seitz RD, Wennhage H, Bergström U, Lipcius RN, Ysebaert T (2014) Ecological value of coastal habitats for commercially and ecologically important species. ICES J Mar Sci 71:648–665

Shah Esmaeili Y, Corte GN, Checon HH, Gomes TRC, Lefcheck JS, Amaral ACZ, Turra A (2021) Comprehensive assessment of shallow surf zone fish biodiversity requires a combination of sampling methods. Mar Ecol Prog Ser 667:131–144

Stål J, Paulsen S, Pihl L, Rönnbäck P, Söderqvist T, Wennhage H (2008) Coastal habitat support to fish and fisheries in Sweden: integrating ecosystem functions into fisheries management. Ocean Coast Manag 51:594–600

Stamp T, West E, Robbins T, Plenty S, Sheehan E (2022) Large-scale historic habitat loss in estuaries and its implications for commercial and recreational fin fisheries. ICES J Mar Sci 79:1981–1991

Staveley TAB, Hernvall P, Stjärnkvist N, van der Meijs F, Wikström SA, Gullström M (2020) Exploring seagrass fish assemblages in relation to the habitat patch mosaic in the brackish Baltic Sea. Mar Biodivers 50:1

Swadling DS, Knott NA, Taylor MD, Coleman MA, Davis AR, Rees MJ (2022) Seascape connectivity of temperate fishes between estuarine nursery areas and open coastal reefs. J Appl Ecol 59:1406–1416

Taal I, Saks L, Rohtla M, Jürgens K and others (2017) Diel changes in the fish assemblage in a coastal surf-zone area in the eastern Baltic Sea. Boreal Environ Res 22:83–96

Tarnowska K, Sapota M (2007) Presence of the broad-nosed pipefish (*Syngnathus typhle*) in coastal waters of the Gulf of Gdańsk. Oceanol Hydrobiol Stud 36:39–48

Törnroos A, Nordström MC, Bonsdorff E (2013) Coastal habitats as surrogates for taxonomic, functional and trophic structures of benthic faunal communities. PLOS ONE 8: e78910

Törnroos A, Bonsdorff E, MacKenzie B, Winder M and others (2016) Retrospective analysis of changes to biodiversity and ecosystem functioning. BIO-C3 Deliverable, D4.1. EU BONUS BIO-C3. https://oceanrep.geomar.de/id/eprint/35852/

Webb PW (1984) Body form, locomotion and foraging in aquatic vertebrates. Am Zool 24:107–120

Wells RJD, Boswell KM, Cowan JH, Patterson WF (2008) Size selectivity of sampling gears targeting red snapper in the northern Gulf of Mexico. Fish Res 89:294–299

Wickham H (2016) Ggplot2: elegant graphics for data analysis. Springer-Verlag, New York, NY

Zaiko A, Calkiewicz J, Eero M, von Dorrien C and others (2017) Response of biodiversity indicators to management measures (test of indicators). BIO-C3 Deliverable, D5.1. EU BONUS BIO-C3. https://oceanrep.geomar.de/id/eprint/41726/

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