



Seasonal small-scale variation in distribution among depth zones in a coastal Baltic Sea fish assemblage

N. Mustamäki*, H. Jokinen†, M. Scheinin†, E. Bonsdorff, and J. Mattila

Environmental and Marine Biology and Husö Biological Station, Åbo Akademi University, Tykistökatu 6, Turku FI-20520, Finland

*Corresponding author: tel: +358 50 582 6115; e-mail: noora.mustamaki@abo.fi

†Present address: Tvärminne Zoological Station, University of Helsinki, J.A. Palménin tie 260, FI-10600 Hanko, Finland.

Mustamäki, N., Jokinen, H., Scheinin, M., Bonsdorff, E., and Mattila, J. Seasonal small-scale variation in distribution among depth zones in a coastal Baltic Sea fish assemblage. – *ICES Journal of Marine Science*, doi: 10.1093/icesjms/fsv068.

Received 14 January 2015; revised 27 March 2015; accepted 30 March 2015.

We studied seasonal and small-scale spatial variation in fish assemblage structure in the northern Baltic Proper archipelago. The study was conducted in a shallow coastal basin during three consecutive production-seasons. The structure of the fish assemblage changes significantly seasonally, from early summer (May–June) to late summer (August–September), and spatially over short distances (ca. 500 m) and small depth intervals (ca. 5 m) in an area without physical barriers. The magnitude of the seasonal variation was depth zone-specific, indicating that seasonal patterns from a given depth zone cannot be directly extrapolated to adjacent ones, let alone to a whole water body. In early summer, the adult fish displayed spawning aggregations, and their abundance was highest closest to the shoreline. In late summer, the adult fish were more evenly distributed and the assemblage was dominated by high abundances of juvenile fish. The results underline the importance of including several spatial and temporal scales into studies on fish distribution. The resulting patterns from such studies may appear idiosyncratic unless the nature and magnitude of seasonal variation and small-scale depth zone distribution are taken into account.

Keywords: archipelago, Baltic Sea, depth zone, fish community, habitat, littoral, seasonality.

Introduction

The trend towards integrated ecosystem-based management of natural resources (Ellis *et al.*, 2011; Guidetti *et al.*, 2014; Möllmann *et al.*, 2014) has increased the need to describe, explain, and predict the dynamics of fish communities in space and time (Moore *et al.*, 2010; Bergström *et al.*, 2013; Sangil *et al.*, 2013). However, spatio-temporal variation in the structure of entire fish assemblages is poorly understood at seasonal short-term and local spatial scales. Fish distribution is often described on region-wide spatial scales (Vahteri *et al.*, 2009; Bergström *et al.*, 2013; Guidetti *et al.*, 2014) and over time-scales of years or decades (Mustamäki *et al.*, 2014a; Möllmann *et al.*, 2014), but the large-scale patterns will often appear idiosyncratic without proper knowledge of the underlying small-scale variation. Without understanding how the structure of fish assemblages varies at seasonal and local scales, efforts to attribute large spatial and temporal changes in fish communities to anthropogenic causes may not be efficient.

Although there are obvious species-specific preferences among fish for certain types of habitat (Moore, 2010; Bergström *et al.*,

2013; Schultz *et al.*, 2014; Snickars *et al.*, 2014), fish are by character highly mobile and dynamic. Most types of regular fish movement events, such as larval dispersal (Hinrichsen *et al.*, 2012; Able, 2005; Cowen and Sponaugle, 2009; Sheaves *et al.*, 2014), ontogenetic habitat shifts (MacPherson 1998; Mustamäki *et al.*, 2014b), spawning migrations (Pihl *et al.*, 2002; Jung and Houde, 2003; Neuenfeldt *et al.*, 2013), and feeding migrations (Methven *et al.*, 2001; Peltonen *et al.*, 2004), take place at local scales, among adjacent habitats (Deegan, 1993; Pihl *et al.*, 2002; Able, 2005; Elliot *et al.*, 2007). These movements are difficult to tell apart from the annual variation in the abundance of young-of-the-year fish (Hinrichsen *et al.*, 2012; Axenrot and Hansson, 2004), year-class strength fluctuations in adult fish (Mustamäki *et al.*, 2014a), long-term trends in fish communities (Olsson *et al.*, 2012; Möllmann *et al.*, 2014; Mustamäki *et al.*, 2014a; Snickars *et al.*, 2015), as well as patterns of predation, competition, growth, and survival (Hixon *et al.*, 2012).

Fish populations in the temperate region display seasonal variation due to annual migrations and spawning events (Methven *et al.*, 2001; Jung and Houde, 2003; Axenrot and Hansson, 2004).

Depth is generally the most important single factor that shapes underwater habitats (Rinne *et al.*, 2011; Chappuis *et al.*, 2014) and thereby also the structure of the fish communities (Pihl and Wennhage, 2002; Malek *et al.*, 2014; Schultz *et al.*, 2014). The horizontal distribution of fish has been associated with topography, substrate type, and/or macrophyte vegetation (Anderson *et al.*, 2009; Snickars *et al.*, 2009; Vahteri *et al.*, 2009; Sangil *et al.*, 2013). In the littoral areas of the Baltic Sea, a handful of studies have addressed variation in the structure of the whole fish assemblage, either among seasons or among depth zones (Nellbring, 1985; Axenrot and Hansson, 2004; Olsson *et al.*, 2012; Snickars *et al.*, 2014). However, both types of variation have not been addressed together, and rather few such studies are published from other shallow littoral marine areas (Letourneur *et al.*, 2001; Methven *et al.*, 2001). Vahteri *et al.* (2009) have previously described the role of the archipelago zone, and Snickars *et al.* (2009) the role of the habitat isolation-exposure gradient to the structure of fish communities, whereas Bergström *et al.* (2013) have constructed large-scale fish distribution models for the archipelago habitats in the northern Baltic Proper.

This study describes variation in the seasonal depth zone distribution in the fish assemblage of a coastal basin in the archipelago of the northern Baltic Proper. We monitored the structure of the fish assemblage in relation to seasonal and spatial gradients of biotic and abiotic habitat characteristics in a semi-enclosed brackish water embayment during three consecutive ice-free production-seasons in 2008–2010. The purpose of this paper is to demonstrate the importance of understanding seasonal and local variation when interpreting larger-scale trends in fish communities. We wanted to find out (i) whether there are significant seasonal changes in species

composition of fish assemblages among the habitats studied and (ii) which environmental variables that are mainly associated with the spatial variation and/or temporal changes observed.

Material and methods

Study sites

Because of the northern latitudes, the Baltic Sea region is subjected to seasonal changes in light and temperature, which lead to annually cyclic variation in the biota (Hinrichsen *et al.*, 2012; Scheinin and Mattila, 2010; Holliland *et al.*, 2012). In the archipelago of the northern Baltic Proper, islands create an underwater environment characterized by shallow water, a variety of substrate types and highly variable exposure to wind and waves (Bekkby *et al.*, 2008). These features shape the macrophyte (Rinne *et al.*, 2011), plankton (Scheinin and Mattila, 2010; Scheinin *et al.*, 2013), and zoobenthos (Aarnio *et al.*, 2011; Törnroos *et al.*, 2013) communities creating a mosaic of littoral habitats for fish (Snickars *et al.*, 2009; Vahteri *et al.*, 2009). The majority of the fish species common in the archipelago spawn in shallow water in spring (Kääriä *et al.*, 1997; Shpilev *et al.*, 2005; Snickars *et al.*, 2009, 2010).

This study was conducted in Lumparn (60°07'N 20°07'E); a semi-isolated basin located in the southeastern Åland Islands (Finland) in the Archipelago Sea region of the northern Baltic Proper (Figure 1). The total area of the basin is ~100 km² and it is connected to the surrounding sea through narrow straits in the north and south. The seabed descends from the shorelines towards a central plane at 20 m. The basin can be divided according to water depth into three principal, structurally distinctive depth

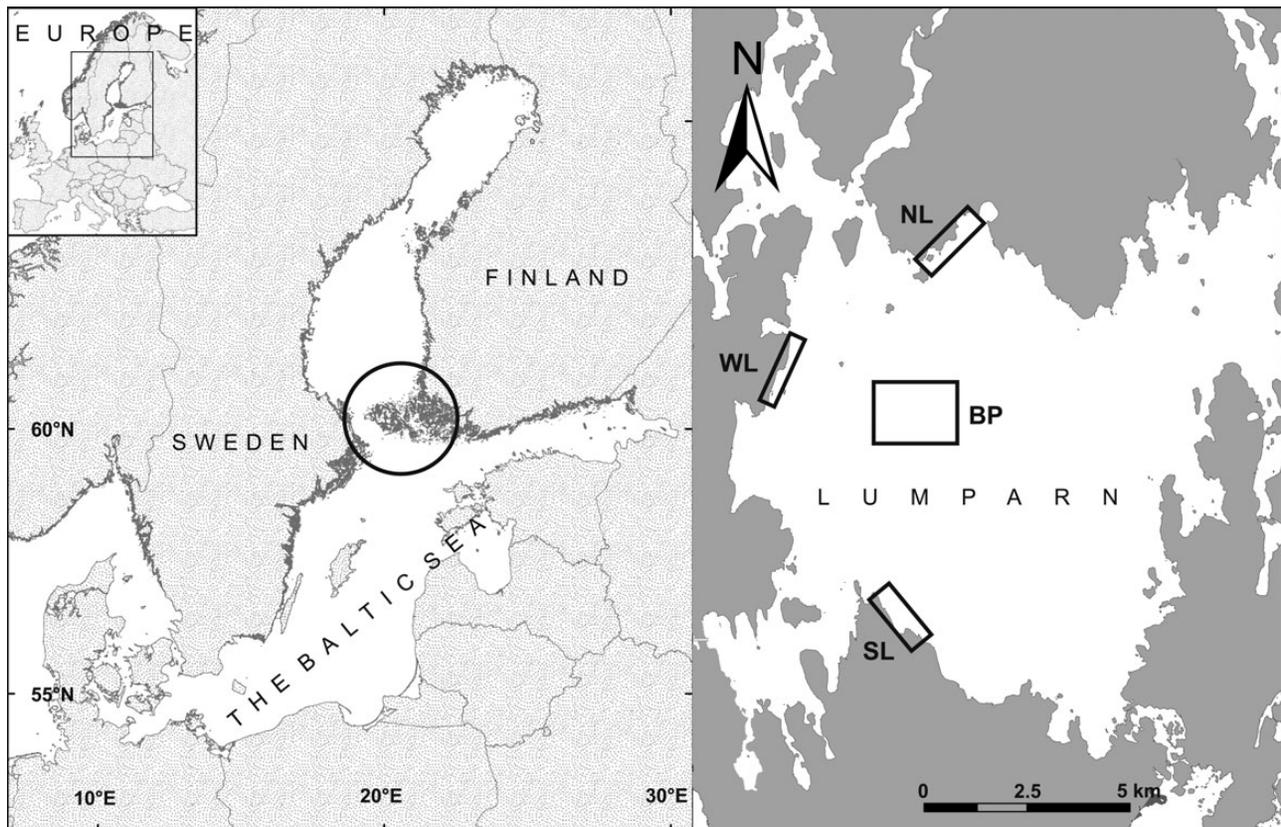


Figure 1. The studied locations in the Lumparn basin (60°07'N 20°07'E) in the Åland Islands, northern Baltic proper. Each littoral location was further divided into “shallow littoral” (0–3 m) and “deep littoral” (5–8 m) study site, resulting in seven study sites in total.

zones: the “shallow littoral”, the “deep littoral”, and the “benthopelagic (BP)”. The macrophyte communities of Lumparn form species-rich and structurally complex shallow littoral habitats regularly down to 3-m depth. In the deep littoral depth zone below, the number of resident macrophytes drops until the depth limit for all macrophyte life is reached at the depth of 8 m (Scheinin and Söderström, 2005). The BP habitat consists of the macrophyte-free bottoms and the water column above.

Three littoral locations differing in their topography and bottom substrate were chosen to cover variation in the inshore environments of the whole basin. At the northern (NL) and southern (SL) littoral locations, shores of gravel (at the NL) and sand (at the SL) slope gently towards the open basin. At the western littoral location (WL), the rocky bottom slopes steeper towards the centre of the basin. All littoral locations were sheltered [depth attenuated exposure according to Bekkby *et al.* (2008)]. Each littoral location was further divided into two study sites to represent the “shallow littoral” depth zone (0–3 m) and the “deep littoral” depth zone (5–8 m). A sampling area (1.5 × 2 km) with the total depth varying between 17 and 22 m represented the BP depth zone. On the whole, our study comprises seven different study sites: the NL shallow (NL/s), the NL deep (NL/d), the WL shallow (WL/s), the WL deep (WL/d), the SL shallow (SL/s), the SL deep (SL/d), and the BP (Figure 1).

Fish data

The fishing was conducted in May–June and August–September in 2008–2010 with Nordic multi-mesh gillnets. One Nordic gillnet is 30 m long and 1.5 m high and consists of 12 panels, each with a different mesh size (5, 6.25, 8, 10, 12.5, 15.5, 19, 24, 29, 35, 43, and 55 mm bar length; Appelberg *et al.*, 1995). The nets were soaked from 6–7 p.m. until 6–7 a.m. The number of gillnets used in each depth zone was related to the depth of the water column as described below. Gillnet is a passive gear, and the catchability varies according to fish size and species and fish mobility (Appelberg *et al.*, 1995; Olin *et al.*, 2009). Therefore, the catch obtained is not a mirror image of the fish community, but a sample of the fish assemblage catchable with the type of gillnet selected. However, subsamples obtained by fishing with the same gear, on same sampling points and at the same time each year ought to reflect patterns in the community structure.

In the shallow littoral study sites (NL/s, WL/s, and SL/s), one bottom-set-net was placed parallel with the shoreline at ca. 1.5-m depth and another perpendicular to the shoreline, starting at ca. 1.5-m depth. The mean catch of the two nets was used as a replicate. Four such replicates were taken in each shallow littoral study site during both May–June and August–September in 2009/2010, in total 96 net nights. In the deep littoral study sites (NL/d, WL/d, and SL/d), one bottom set-net was placed parallel to the shoreline at 5–6-m depth, another at a right angle to the shoreline starting at 5–6-m depth. Additionally, one surface net was placed next to the bottom set-nets so that it could freely turn with the wind. The mean catch of the three nets was used as a replicate. Four such replicates were taken during both May–June and August–September in 2009/2010, in total 144 net nights. In the BP study site, sets of five nets were used to cover the whole water column. One of the nets was set on the surface. Three midwater nets were suspended from floats to the depths of 5, 10, and 15 m, and one net was set to the bottom. The mean catch of the five nets was used as a replicate. Twelve such replicates were taken both during May–June and

during August–September in 2008 and six replicates during August–September in 2009/2010, in total 180 net nights.

Each individual fish was identified to species, measured to the nearest 1 mm in total length (L_T) and weighed to the nearest 0.1 g in total weight (W_T). The proportion of fish ripe for spawning was noted. The catch per unit effort (cpue), average number of fish per gillnet, was calculated for each species. For Baltic herring, separate cpue values were calculated for small/juvenile and large/adult fish; individuals shorter than 9 cm were classified as “small” (most of them young-of-the-year, YOY, based on the length distribution and observations during the experimental fishing). For other species, this was not considered necessary as very few juveniles were caught.

Environmental data

Several biotic and abiotic factors were measured to describe and characterize the conditions and resources available for fish in the study sites.

Water and zooplankton were sampled monthly from May to September in the middle of each study site in 2008–2010. In May and August, the sampling was performed immediately before and in June and September immediately after each fish sampling period. The total water depth in the respective sampling points was 2 m for each of the shallow littoral study sites, 5 m for each of the deep littoral study sites, and 19 m for the BP study site. Secchi depth (m) was controlled at each sampling point. Chlorophyll *a* ($\mu\text{g l}^{-1}$), temperature ($^{\circ}\text{C}$), salinity, pH, total nitrogen ($\mu\text{g l}^{-1}$), total phosphorus ($\mu\text{g l}^{-1}$), turbidity (NTU), and oxygen content (%) were measured at 1 m above the sediment surface at all study sites and at 1 m depth in the deep littoral study sites and the BP study site.

For zooplankton, the whole water column was covered by subsamples taken at even distances with sampling a Limnos ($V = 2.7 \text{ l}$) sampler, starting from the surface. Three parallel sets of subsamples were taken in each sampling point and pooled into one replicate. The total volume of the samples was 27 l for both shallow and deep littoral study sites and 54 l for the BP study site. The collected water was filtered through a 50- μm plankton mesh and preserved in unbuffered 5 vol % formaldehyde solution. The zooplankton fauna were determined to the lowest possible taxonomical level, different ontogenetic stages were identified, and the abundances (individuals, $n \text{ l}^{-1}$) of the different species/life stages were calculated. The abundances were converted to biomasses ($\mu\text{g l}^{-1}$ wet weight) as in Scheinin and Mattila (2010). The species were grouped into cladocerans, ciliates, bay barnacle nauplii/cypris (*Amphibalanus improvisus*), copepods, larvae of bivalves/gastropods/polychaetes, and rotifers. For each water variable and zooplankton group biomass, the seasonal means from each study site were used as replicates in the statistical analyses (mean of the May and June measurements to represent early summer and mean of the August and September measurements to represent late summer).

Macrophytes and the bottom substrate were studied in August 2008 and 2009. Each shallow littoral study site was studied by snorkelling along 25–100 m transects reaching from the shore to 3-m depth. The per cent coverage of each macrophyte species and different substrate types (sand, rock, stones, boulders, gravel, silt, clay) were determined visually within 1 m² squares, at 5 m intervals along the transects. Additionally, the average height of the dominant macrophytes and water depth were measured to calculate the three-dimensional coverage (% of the water column) of macrophytes as in Scheinin *et al.* (2013). In the deep littoral study sites, the

macrophytes were sampled with a Luther rake as in Munsterhjelm (2005). The macrophytes were identified to the species level and grouped into filamentous algae, drifting algae and epiphytes, bladderwrack, charophytes, pondweeds, common reed, other algae, and other vascular plants. The substrate type in the deep littoral and BP study sites was estimated from samples taken with an Ekman grab sampler (% in the sample). For each littoral study site, the means of the coverage of each macrophyte group, three-dimensional macrophyte coverages and substrate type percentages in the transect squares for each shallow littoral study site were used as replicates in the statistical analyses. For each deep littoral and BP study sites, the means of the substrate type percentages in the Ekman grab samples were used as replicates in the statistical analyses.

Zoobenthos was sampled with an Ekman grab sampler (298 cm²) in August 2009. A set of ten samples was taken within each study site. The samples were sieved through a 500- μ m sieve and preserved in 70% EtOH at 4°C until analysis. The fauna were identified to the lowest possible taxonomical level, counted (*n*), and weighted wet at 0.01 g accuracy. The abundance and biomass per m² were calculated for each species. The fauna were grouped into bivalves, snails, chironomids, isopods, polychaetes, and other fauna. In the statistical analyses, the mean biomasses of each group of taxa for each study site were used as replicates.

Statistical analyses

For the total abundance of fish (total cpue), difference among the depth zones (fixed factor) and study sites (random factor, nested in depth zone) was analysed for the ln-transformed values with nested ANOVA and Bonferroni *post hoc* test. ANOVA was run separately for early summer and late summer samples, as the data were not suitable for a parametric two-way analysis. The analyses were performed with IBM SPSS Statistics 21. Length distributions (L_T) of perch, roach, and white bream among the study sites were

compared with Kruskal–Wallis test and Dunn's *post hoc* test. The analyses were performed with GraphPad Prism 5.

Principal component analysis (PCA) with Euclidean distance was used to describe variation among the study sites in terms of the environmental conditions. The variables used as environmental factors in the multivariate analyses are listed in Table 1. The coverage percentage variables were square-rooted and all variables were normalized. Non-parametric multidimensional scaling (nMDS) was used to give a graphical presentation of the fish species abundances. The fish species cpue data were square-rooted, a Bray–Curtis dissimilarity matrix was constructed, and the matrix was subjected to the nMDS procedure. In this analysis, a stress level of less than 0.20 gives a satisfactory representation (Clarke, 1993). Permutational multivariate analysis of variance PERMANOVA (Anderson, 2001) was used to analyse differences in the fish species abundances among depth zones (fixed factor), seasons (fixed factor), and study sites (nested in depth zone). The environmental variables which best explained the variation in the fish species abundances were identified with the distance-based linear model (DistLM), a non-parametric multivariate regression analysis that performs a distance-based analysis on a linear model for a resemblance matrix (Anderson et al., 2008). A DistLM analysis with forward regression and selection based on the Aikake information criterion for finite samples AICc (Cavanaugh, 1997) was performed with the fish abundance matrix and the normalized environmental factors, and the results were illustrated with a distance-based redundancy analysis (dbRDA) plot. The analyses were performed in PRIMER 6 with the PERMANOVA + add-on program package (Clarke, 1993; Anderson, 2001; Anderson et al., 2008).

All the analyses were performed also with the fish species biomasses per unit effort and with the small Baltic herrings excluded, and separately for each depth zone and season with the appropriate environmental factors, but the results were essentially similar and therefore not reported.

Table 1. The environmental variables used in the DistLM and the Principal component ordination (PCO).

	Variable ^a	R ²	Pseudo-F
Water ^b	Depth	0.22	39.2***
	Season	0.18	30.7***
	Total phosphorus (μ g l ⁻¹)	0.01	4.5***
	Temperature (°C)	0.02	3.8**
	Turbidity (NTU)	0.01	2.6**
Zooplankton biomass (μ g l ⁻¹) ^b	Chl <i>a</i> ^d , Secchi depth, temperature ^d , total nitrogen ^d , pH, salinity		
	Cladocerans	0.03	8.6***
Macrophyte coverage (%) ^c	Rotifers ^d , bay barnacle nauplii/cypris ^d , copepods, ciliates, larvae of bivalves/gastropods/polychaetes		
	Three-dimensional total macrophyte coverage	0.13	34.3***
Substrate coverage (%) ^c	filamentous algae, bladderwrack ^d , drifting/epiphytes, common reed, charophytes, pondweeds ^d		
	Sand	0.03	8.6***
	Gravel	0.02	4.8***
Zoobenthos biomass (g m ⁻²)	Silt, clay ^d , stones ^d , boulders ^d , rock		
	Bivalves	0.01	3.8***
	Snails, chironomids ^d , isopods ^d , polychaetes, oligochaetes		

For the variables included in the DistLM (selection criterion AICc, forward regression, R² = 0.62), the R² and pseudo-F values are given. The dbRDA-axes are illustrated in Figure 5 and the PCO in Figure 2.

^aAll variables were normalized for the DistLM and PCO analyses.

^bSeasonal means = means of May–June and August–September measurements. The surface water values of temperature, phosphorus, nitrogen, salinity, pH, and oxygen from the deep littoral and BP habitat types were excluded from all analyses due to collinearity.

^cSquare-root-transformed for the DistLM and PCO analyses.

^dExcluded due to collinearity.

***p* < 0.01.

****p* < 0.001.

Results

Spatial structure and seasonal variation in the fish assemblage

In total, 26 fish species were encountered. Baltic herring (*Clupea harengus* var. *membras*) was most abundant, followed by perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), and bleak (*Alburnus alburnus*). Perch dominated the catch in terms of biomass, followed by roach and Baltic herring (Table 2, Figure 2). Perch, roach, bleak, and sticklebacks favoured the shallow waters. Ruffe (*Gymnocephalus cernua*) was most abundant in the deep littoral, whereas pikeperch favoured the deep littoral and BP areas. The populations of perch, roach, and white bream were size-distributed; the mean L_T was for all species highest in the BP depth zone and for roach and white bream lowest in the shallow littoral depth zone, whereas for perch there was no difference between the shallow and the deep littoral depth zones (Kruskall–Wallis test, $n_{\text{groups}} = 7$; perch, 75.9, $p < 0.001$; roach, 1277.0, $p < 0.001$; white bream, 69.6, $p < 0.001$; Figure 3).

In early summer, the total cpue of fish was highest in the shallow littoral depth zone and there highest at the WL/s study site, and lowest in the BP depth zone (ANOVA: zone, $F_{2,3,9} = 45.3$, $p < 0.01$; study site nested in zone, $F_{4,50} = 3.9$, $p < 0.01$). In early summer, the majority of perch, roach, ruffe, and Baltic herring and all the three-spined sticklebacks (*Gasterosteus aculeatus*) caught were ripe for spawning and the three-spined stickleback males displayed spawning colours. The ripe perch and Baltic herring were aggregated to the shallow littoral depth zone, whereas the ruffe was aggregated in the deep littoral depth zone. The three-spined stickleback was most abundant at the WL/s and NL/s study sites, whereas smelt (*Osmerus eperlanus*) and lesser

sandeel (*Ammodytes tobianus*) were most abundant at the SL/s and SL/d study sites.

In late summer, no statistically significant differences the total cpue among depth zones or study sites were observed (ANOVA, n.s.). In late summer, the fish assemblages at all study sites were dominated by the YOY Baltic herring, whereas the adult fish were more evenly distributed among study sites and depth zones than in early summer. Baltic herring was the only species in which individuals ripe for spawning were encountered in late summer. The YOY of Baltic herring were encountered in all study sites, whereas the YOY/juvenile individuals (< 10 cm L_T) of perch, roach, and white bream (*Blicca bjoerkna*) were only encountered in the shallow littoral depth zone (Figure 2).

In the MDS ordination (Figure 4), the early summer aggregation of adult fish in the shallow and deep littoral study sites and the high late summer cpue of small Baltic herring in all study sites were illustrated by a tight clustering of the early summer samples and more dispersal in the late summer samples. In the PERMANOVA results (Table 3), a significant season–study site interaction indicated that the site specific decreases and increases in species cpue valued were statistically significant.

Spatial and seasonal characteristics of the fish depth zones, resources, and physical environment

The PCA grouped samples from the same depth zone close together on the PC1-axis (which explained 40.9% of variation in the environmental data), indicating similar environmental conditions within the depth zones (Table 1, Figure 5). On the PC2-axis (which explained 16.3% of the variation in the environmental data), the

Table 2. The grand-total gillnet fishing catch in Lumparn 2008–2010, number (n), and biomass (g) per species.

Species	Scientific name	n	Biomass (g)
Baltic herring	<i>Clupea harengus</i> var. <i>membras</i>	14 943	75 189
“Large” (≥ 9 cm)		2563	52 024
“Small” (< 9 cm)		12 380	23 165
Eurasian perch	<i>Perca fluviatilis</i>	3861	243 722
Roach	<i>Rutilus rutilus</i>	2793	134 907
Bleak	<i>Alburnus alburnus</i>	1783	11 970
Three-spined stickleback	<i>Gasterosteus aculeatus aculeatus</i>	1644	3102
Ruffe	<i>Gymnocephalus cernua</i>	1172	25 852
Smelt	<i>Osmerus eperlanus</i>	534	534
White bream	<i>Blicca bjoerkna</i>	212	8252
Pikeperch	<i>Sander lucioperca</i>	188	21 833
Lesser sandeel	<i>Ammodytes tobianus</i>	109	630
Sprat	<i>Sprattus sprattus</i>	90	632
Common goby	<i>Pomatoschistus microps</i>	32	37
Ten-spined stickleback	<i>Pungitius pungitius</i>	32	42
Bream	<i>Abramis brama</i>	27	9758
Pike	<i>Esox lucius</i>	14	21 556
Greater sandeel	<i>Hyperoplus lanceolatus</i>	10	172
Brown trout	<i>Salmo trutta</i>	5	1857
Whitefish	<i>Coregonus lavaretus</i>	5	2343
Sandgoby	<i>Pomatoschistus minutus</i>	3	5
Vendace	<i>Coregonus albula</i>	3	165
Straightnosed pipefish	<i>Nerophis ophidion</i>	2	4
Common minnow	<i>Phoxinus phoxinus</i>	1	4
Common rudd	<i>Scardinius erythrophthalmus</i>	1	32
European bullhead	<i>Cottus gobio</i>	1	4
Fourhorn sculpin	<i>Myoxocephalus quadricornis</i>	1	120
Viviparous blenny	<i>Zoarces viviparus</i>	1	4
Total		27 467	562 726

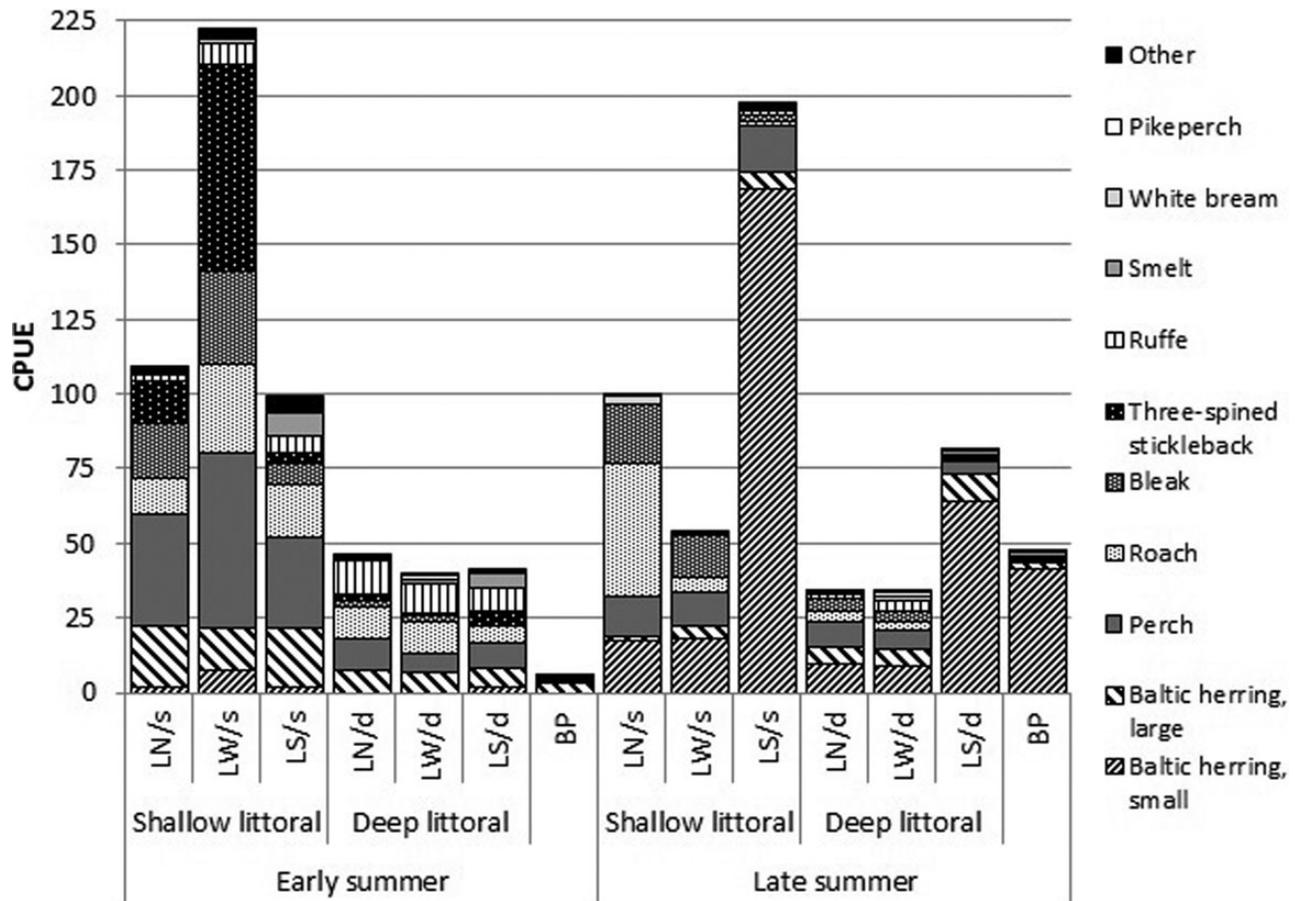


Figure 2. The fish species cpue ($n/gillnet$) in the study sites for early summer (May–June) and late summer (August–September). The column height equals to the total cpue. Other fish = species with total $n < 100$ (Table 2).

shallow littoral study sites were separated from each other, whereas the deep littoral study sites clustered together indicating larger spatial variation within the shallow littoral depth zone. Additionally, within each depth zone, the samples from May–June and August–September were separated from each other.

Temperature, Secchi depth, chlorophyll a , nutrients, salinity, and zooplankton displayed a clear seasonality, but only minor differences among the study sites. Temperature, zooplankton density, and zooplankton biomass peaked in late summer. The concentrations of total phosphorus, total nitrogen, and chlorophyll a increased from May to September, whereas the Secchi depth and salinity decreased. At 18-m depth in the BP study site, the total phosphorus peaked in late summer, which coincided with a reduction in the concentrations of dissolved oxygen. No clear temperature stratification was observed.

The substrate type, macrophytes, and zoobenthos varied mainly among the depth zones, and there was more variation within the shallow littoral depth zone than within the deep littoral depth zone. The substrate in all the shorelines consisted of cliff, boulders, gravel, silt, and sand which with increasing depth gradually changed into glacial clay. Only the WL/s study site had any rocky substrates, whereas the SL/s and SL/d were sandier compared with the other study sites. From the depth of 5–10 m onwards, the bottom substrate consisted mainly of clay, and clay was the only substrate type encountered in the BP study site. The zoobenthos was characterized by the Baltic clam *Macoma balthica* in deeper areas and

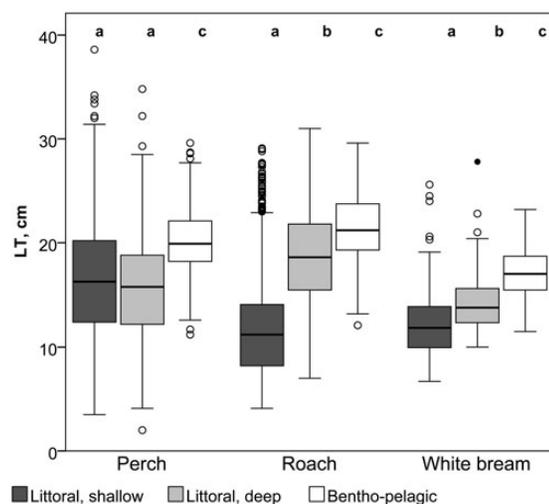


Figure 3. Length distribution (L_T , cm) of perch, roach, and white bream in the shallow littoral, deep littoral, and BP depth zones. Within species, the distributions sharing the same letter are not statistically different on $p = 0.05$ level with the Kruskal–Wallis test and the Dunn’s *post hoc* test.

especially in clay substrate, and mudsnails *Hydrobia* spp in the shallow areas. On all shorelines, common reed (*Phragmites australis*) covered the soft bottoms down to ca. 2 m depth, where

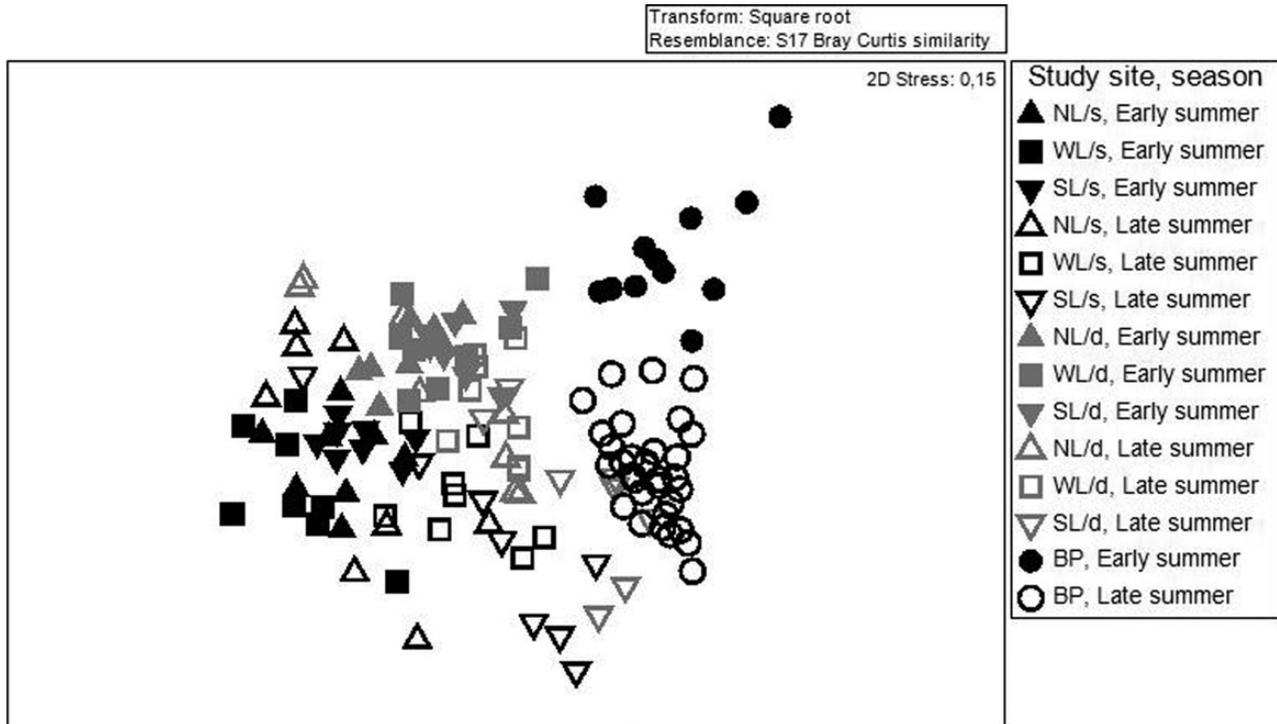


Figure 4. nMDS on the square-rooted species cpue (n /gillnet) in the study sites for early summer (May–June) and late summer (August–September).

Table 3. Results of the non-parametric permutational multivariate analysis of variance PERMANOVA.

Factor	Levels	d.f.	Pseudo-F
Habitat type (fixed)	3 (shallow littoral, deep littoral, and BP)	2126	8.6***
Season (fixed)	2 (May–June and August–September)	1126	4.2*
Study site (nested in habitat type)	7 (NL/s, NL/d, WL/s, WL/d, SL/s, SL/d, and BP)	4126	5.8***
Interaction habitat type × season		2126	2.0
Interaction study site × season		4126	3.5***

* $p < 0.05$.

*** $p < 0.001$.

pondweeds (*Potamogeton* spp. and *Stuckenia pectinata*) took over. The hard substrates were typically covered by bladderwrack (*Fucus vesiculosus*) and filamentous algae. Of the three shallowest study sites, macrophytes formed densest and highest beds and had the highest species diversity in the WL/s. In contrast, macrophytes grew sparsest, were shortest, and had lowest species diversity in the SL/s. Attached macrophytes were entirely missing from each of the deep littoral study sites as well as from the BP.

The DistLM analysis identified nine environmental variables that significantly explained the variance in the fish cpue data, although only depth zone, season, and three-dimensional macrophyte coverage contributed considerably to the R^2 which was 0.60 for the model (Table 1, Figure 6).

Discussion

This study illustrates that in a basin with no internal physical barriers, the structure (species composition and abundance) of the fish assemblage can vary significantly over a distance of a few hundred metres corresponding to 5–20 m variation in total

depth, depending on the time of the season (early summer vs. late summer). The findings support earlier ones indicating high complexity in the small-scale distribution of coastal fish (Letourneur *et al.*, 2001; Methven *et al.*, 2001; Pihl and Wennhage, 2002; Sangil *et al.*, 2013) and provide the first description of the seasonality of such patterns for a coastal Baltic Sea environment.

In early summer, the species abundances and the presence of ripe individuals indicated spawning aggregations. Perch (Snickars *et al.*, 2010) and Baltic herring (Kääriä *et al.*, 1997) use the shallow littoral depth zone for spawning, whereas the spawning of ruffe was confined to the deep littoral depth zone. The three-spined stickleback favour shallow littoral areas for spawning (Nellbring, 1985; Snickars *et al.*, 2009) and was in this study mainly encountered on the densely vegetated western and northern shorelines. Also smelt (Shpilev *et al.*, 2005) and lesser sandeel (Bonislawski *et al.*, 2014) spawn in shallow water in spring, and ripe individuals of both species were encountered on the sandy southern shore (SL/s and SL/d). In late summer, the species aggregation was weaker and the adult fish were more evenly distributed. The adult individuals of

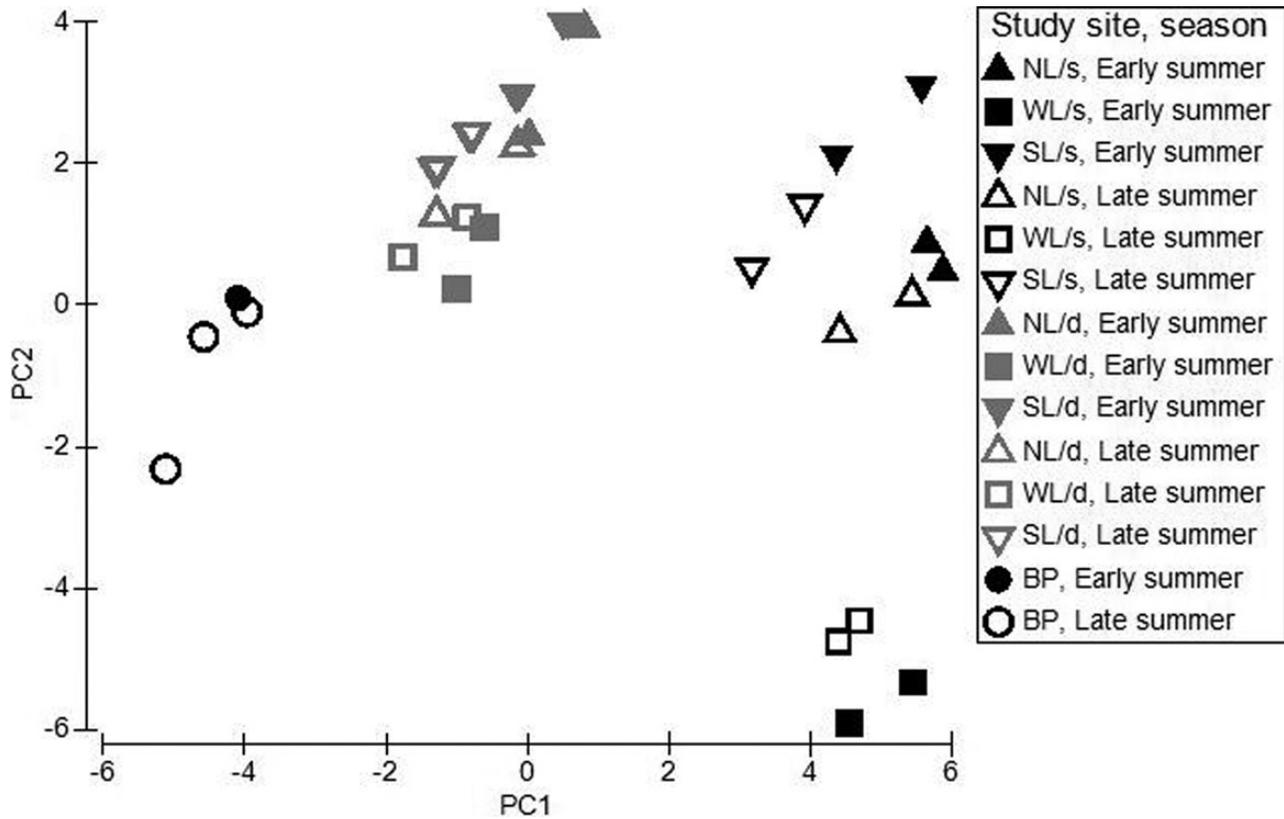


Figure 5. PCA of the normalized environmental variables for the study sites in early summer (May–June) and late summer (August–September).

many species were less abundant or nearly absent in late summer, suggesting post-spawning migration out of the main basin of Lumparn. To get a proper overall understanding of the seasonal dynamics in use of different environments/habitats by different fish species, further studies should clarify the possible connectivity of the fish assemblage in the basin with the adjacent bays and the surrounding sea areas (Deegan, 1993; Able, 2005; Sheaves et al., 2014).

In late summer, the Baltic herring YOY favoured the sandy southern shoreline (SL/s and SL/d), suggesting its importance as a nursery area (Pihl et al., 2002; Axenrot and Hansson, 2004). According to Kääriä et al. (1997), the Baltic herring in this region mainly spawns in vegetated hard bottoms located near deep areas, indicating that there are plenty of potential spawning grounds in the Lumparn basin. Single adult Baltic herrings ripe for spawning were observed also in late summer. In addition, juvenile Baltic herrings that were considered too small (<7 cm) to have been born in early summer of the previous year were occasionally caught in spring. These observations indicate that there might, in addition to the larger spring-breeding Baltic herring population (Kääriä et al., 1997), be autumn breeding individuals (McQuinn, 1997) in the study area.

The aggregation of small/juvenile individuals into the shallow littoral depth zone indicates that at least perch, roach, and white bream underwent an ontogenetic habitat shift after the juvenile stage (MacPherson, 1998). Also the increasing trend in the size of the adult individuals towards deeper areas may be due to habitat shifts; the diet of adult perch gradually changes with the size of the individual (Mustamäki et al., 2014b) and therefore they could also be expected to change foraging areas. However, the adult fish

size distribution and differences in abundance may also be a result of differences in growth, competition, predation, and survival in the different depth zones (Hixon et al., 2012).

The seasonal and spatial variation in the environmental data and the species compositions of the zooplankton (Scheinin and Mattila, 2010; Hollilund et al., 2012), macrophyte (Rinne et al., 2011), and zoobenthos (Aarnio et al., 2011; Törnroos et al., 2013) assemblages were typical for the northern Baltic Sea coastal areas. The waters of the basin seemed to be effectively mixed throughout the summer and no hypoxia was observed, although it is known to occur in the Lumparn basin occasionally. Depth zone was the most important spatial factor structuring the environmental conditions for fish, and the seasonal variation in the environmental conditions affected the whole system. Within the depth zones, the variation in the fish assemblage was further modified by the conditions defined by macrophytes, substrate, and benthic food resources.

This, to our knowledge, is the first description on depth zone-specific seasonal variation in the fish assemblage structure from the Baltic Sea. Reports by Methven et al. (2001) from Newfoundland and by Letourneur et al. (2001) from the Mediterranean indicate existence of similar regionally characteristic patterns in other coastal areas. Our results demonstrate that patterns observed in one depth zone or season cannot be directly extrapolated to larger areas and that drawing meaningful conclusions on the small-scale distribution in the fish assemblage structure requires sufficient replication of sampling in space and time. Some species may be completely missed by sampling within one season or depth zone only. Also the abundances of the encountered species may lead to misinterpretations of the commonness of the species in the area or habitat and the significance of

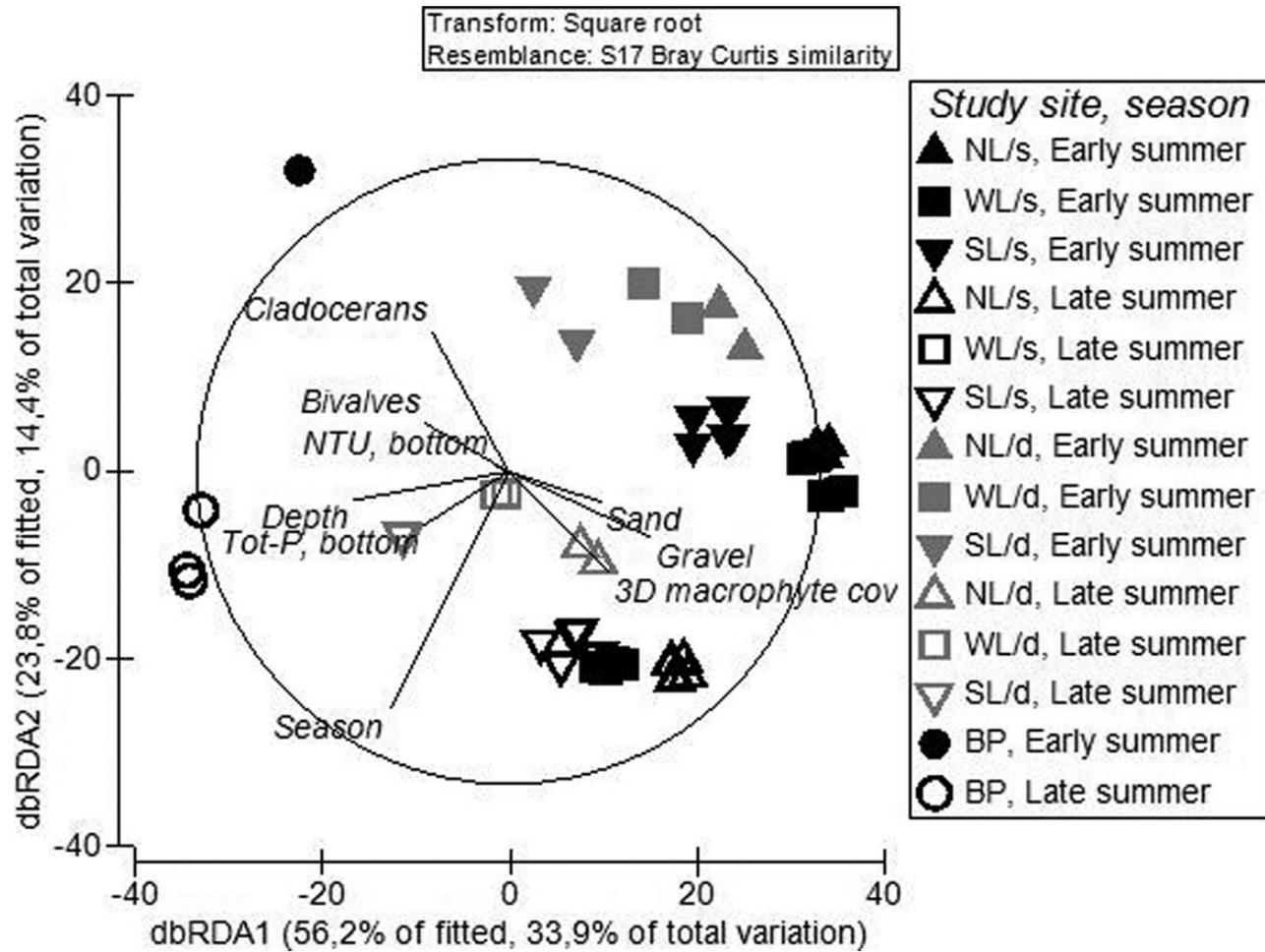


Figure 6. The dbRDA plot based on the results of the DistLM of fish species cpue. The vectors illustrate correlations between the original environmental variables and the dbRDA-axes.

the habitat for the species. Although protecting particular habitats/ areas which are known to be valuable as spawning or nursery areas certainly is of crucial importance (Snickars *et al.*, 2009, 2010), protecting them only may not yield any results in protecting a species if for instance central feeding grounds are destroyed or too heavily fished. The whole range of habitats that each species uses throughout its life cycle and seasonally should be clarified to plan effective management in the marine environment where the fish movement is not restricted by physical barriers (Able, 2005; Elliot *et al.*, 2007). Combining the effects of the multiple gradients affecting seasonally changing habitats for a better understanding of spatial distribution of fish is an important future perspective for studies on ecology and ecosystem-based management of shallow coastal areas.

Supplementary data

Supplementary material is available at the ICES online version of the manuscript.

Acknowledgements

This study was financed by the Baltic Sea 2020 Foundation, the Swedish Cultural Society in Finland, the Åbo Akademi University Endowment, and Maa- ja Vesitekniikan tuki ry. Special thanks to Tony Cederberg for help in the field analysis work, Satu Zwerver for zooplankton analysis, and everyone involved in the field studies.

References

Aarnio, K., Mattila, J., Törnroos, A., and Bonsdorff, E. 2011. Zoobenthos as an environmental quality element: the ecological significance of sampling design and functional traits. *Marine Ecology*, 32: 58–71.

Able, K. W. 2005. A re-examination of fish estuarine dependence: evidence for connectivity between estuarine and ocean habitats. *Estuarine, Coastal and Shelf Science*, 64: 5–17.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Australian Ecology*, 26: 32–46.

Anderson, M. J., Gorley, R. N., and Clarke, R. K. 2008. *Permanova+ for Primer: Guide to Software and Statistical Methods*. Primer-E Ltd, Plymouth, UK. 214 pp.

Anderson, T. J., Syms, C., Roberts, D. A., and Howard, D. F. 2009. Multi-scale fish-habitat associations and the use of habitat surrogates to predict the organization and abundance of deep-water fish assemblages. *Journal of Experimental Marine Biology and Ecology*, 379: 34–42.

Appelberg, M., Berger, H. M., Hestghagen, T., Kleiven, E., Kurkilahti, M., Raitaniemi, J., and Rask, M. 1995. Development and intercalibration of methods in Nordic freshwater fish monitoring. *Water, Air and Soil Pollution*, 85: 401–406.

Axenrot, T., and Hansson, S. 2004. Seasonal dynamics in pelagic fish abundance in a Baltic Sea coastal area. *Estuarine, Coastal and Shelf Science*, 60: 541–547.

- Bekky, T., Isachsen, P.-E., Isaeus, M., and Bakkestuen, V. 2008. GIS modeling of wave exposure at the seabed: a depth-attenuated wave exposure model. *Marine Geodesy*, 31: 117–127.
- Bergström, U., Sundblad, G., Downie, A.-L., Snickars, M., Boström, C., and Lindegarth, M. 2013. Evaluating eutrophication management scenarios in the Baltic Sea using species distribution modelling. *Journal of Applied Ecology*, 50: 680–690.
- Bonislawska, M., Tański, A., Szulc, J., Machula, S., and Formicki, K. 2014. Water salinity effects on embryogenesis of the lesser sandeel, *Ammodytes tobianus* (Linnaeus, 1758). *Central European Journal of Biology*, 9: 1068–1077.
- Cavanaugh, J. E. 1997. Unifying the derivations for the Akaike and corrected Akaike information criteria. *Statistics and Probability Letters*, 33: 201–208.
- Chappuis, E., Terradas, M., Cefali, M.-E., Mariani, S., and Ballesteros, E. 2014. Vertical zonation is the main distribution pattern of littoral assemblages on rocky shores at a regional scale. *Estuarine, Coastal and Shelf Science*, 147: 113–122.
- Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 18: 117–143.
- Cowen, R. K., and Sponaugle, S. 2009. Larval dispersal and marine population connectivity. *Annual Review of Marine Science*, 1: 443–466.
- Deegan, L. A. 1993. Nutrient and energy transport between estuaries and coastal marine ecosystems by fish migration. *Canadian Journal of Fisheries and Aquatic Sciences*, 50: 74–79.
- Elliot, M., Whitfield, A. K., Potter, I. C., Blaber, S. J. M., Cyrus, D. P., Nordlie, F. G., and Harrison, T. D. 2007. The guild approach to categorizing estuarine fish assemblages: a global review. *Fish and Fisheries*, 8: 241–268.
- Ellis, S. L., Incze, L. S., Lawton, P., Ojaveer, H., MacKenzie, B. R., Pitcher, C. R., Shirley, C. S., et al. 2011. Four regional marine biodiversity studies: approaches and contributions to ecosystem-based management. *PLoS One*, 6: e18997.
- Guidetti, P., Baiata, P., Ballesteros, E., Di Franco, A., Hereu, B., Macpherson, E., Micheli, F., et al. 2014. Large-scale assessment of Mediterranean marine protected areas effects on fish assemblages. *PLoS One*. doi:10.1371/journal.pone.0091841.
- Hinrichsen, H.-H., Kühn, W., Peck, M. A., and Voss, R. 2012. The impact of physical and biological factors on the drift and spatial distribution of larval sprat: a comparison of the Baltic and North Seas. *Progress in Oceanography*, 107: 47–60.
- Hixon, M. A., Anderson, T. W., Buch, K. L., Johnson, D. W., McLeod, J. B., and Stallings, C. D. 2012. Density dependence and population regulation in marine fish: a large-scale, long-term field manipulation. *Ecological Monographs*, 82: 467–489.
- Holliland, P. B., Ahlbeck, I., Westlund, E., and Hansson, S. 2012. Ontogenic and seasonal changes in diel vertical migration amplitude of the calanoid copepods *Eurytemora affinis* and *Acartia* spp. in a coastal area of the northern Baltic proper. *Journal of Plankton Research*, 34: 298–307.
- Jung, S., and Houde, E. D. 2003. Spatial and temporal variabilities of pelagic fish community structure and distribution in Chesapeake Bay, USA. *Estuarine, Coastal and Shelf Science*, 58: 335–351.
- Kääriä, J., Rajasilta, M., Kurkilahti, M., and Soikkeli, M. 1997. Spawning bed selection by the Baltic herring (*Clupea harengus membras*) in the Archipelago of SW Finland. *ICES Journal of Marine Science*, 54: 917–923.
- Letourneur, Y., Darnaude, A., Salen-Picard, C., and Harmelin-Vivien, M. 2001. Spatial and temporal variations of fish assemblages in a shallow Mediterranean soft-bottom area (Gulf of Fos, France). *Oceanologica Acta*, 24: 273–285.
- MacPherson, E. 1998. Ontogenetic shifts in habitat use and aggregation in juvenile sparid fishes. *Journal of Experimental Marine Biology and Ecology*, 220: 127–150.
- Malek, A. J., Collie, J. S., and Gartland, J. 2014. Fine-scale spatial patterns in the demersal fish and invertebrate community in a northwest Atlantic ecosystem. *Estuarine, Coastal and Shelf Science*, 147: 1–10.
- McQuinn, I. H. 1997. Metapopulations and the Atlantic herring. *Reviews in Fish Biology and Fisheries*, 7: 297–329.
- Methven, D. A., Haedrich, R. L., and Rose, G. A. 2001. The fish assemblage of a Newfoundland estuary: diel, monthly and annual variation. *Estuarine, Coastal and Shelf Science*, 52: 669–687.
- Moore, C. H., Harvey, E. S., and Van Niel, K. 2010. The application of predicted habitat models to investigate the spatial ecology of demersal fish assemblages. *Marine Biology*, 157: 2717–2729.
- Munsterhjelm, R. 2005. Natural succession and human-induced changes in the soft-bottom macrovegetation of shallow brackish bays on the southern coast of Finland. W & A de Nottbeck Foundation Scientific Reports, 26: 1–53.
- Mustamäki, N., Bergström, U., Ådjers, K., Sevastik, A., and Mattila, J. 2014a. Pikeperch (*Sander lucioperca* (L.)) in decline: high mortality of three populations in the northern Baltic Sea. *Ambio*, 43: 325–436.
- Möllmann, C., Lindgren, M., Blenckner, T., Bergström, L., Casini, M., Diekmann, R., Flinkman, J., et al. 2014. Implementing ecosystem-based fisheries management: from single-species to integrated ecosystem assessment and advice for Baltic Sea fish stocks. *ICES Journal of Marine Science*, 71: 1187–1197.
- Mustamäki, N., Cederberg, T., and Mattila, J. 2014b. Diet, stable isotopes and morphology of Eurasian perch (*Perca fluviatilis*) in littoral and pelagic habitats in the northern Baltic Proper. *Environmental Biology of Fishes*, 97: 675–689.
- Nellbring, S. 1985. Abundance, biomass and seasonal variation of fish on shallow soft bottoms in the Askö area, northern Baltic proper. *Sarsia*, 70: 217–225.
- Neuenfeldt, S., Righton, D., Neat, F., Wright, P. J., Svedäng, H., Michalsen, K., Subbey, S., et al. 2013. Analysing migrations of Atlantic cod *Gadus morhua* in the north-east Atlantic Ocean: then, now and the future. *Journal of Fish Biology*, 82: 741–763.
- Olin, M., Malinen, T., and Ruuhijärvi, J. 2009. Gillnet catch in estimating the density and structure of fish community—comparison of gillnet and trawl samples in a eutrophic lake. *Fisheries Research*, 96: 88–94.
- Olsson, J., Bergström, L., and Gårdmark, A. 2012. Abiotic drivers of coastal fish community change during four decades in the Baltic Sea. *ICES Journal of Marine Science*, 69: 961–970.
- Peltonen, H., Vinni, M., Lappalainen, A., and Pönni, J. 2004. Spatial feeding patterns of herring (*Clupea harengus* L.), sprat (*Sprattus sprattus* L.), and the three-spined stickleback (*Gasterosteus aculeatus* L.) in the Gulf of Finland, Baltic Sea. *ICES Journal of Marine Science*, 61: 966–971.
- Pihl, L., Cattrijsse, A., Codling, I., Mathieson, S., McLusky, D. S., and Roberts, C. 2002. Habitat use by fishes in estuaries and other brackish areas. *In Fishes in Estuaries*, pp. 10–53. Ed. by M. Elliot, and K. Hemingway. Blackwell Publishing Ltd, Oxford.
- Pihl, L., and Wennhage, H. 2002. Structure and diversity of fish assemblages on rocky and soft bottom shores on the Swedish west coast. *Journal of Fish Biology*, 61: 148–166.
- Rinne, H., Salovius-Laurén, S., and Mattila, J. 2011. The occurrence and depth penetration of macroalgae along environmental gradients in the northern Baltic Sea. *Estuarine Coastal and Shelf Science*, 94: 182–191.
- Sangil, C., Martín-García, L., Hernández, J. C., Concepción, L., Fernández, R., and Clemente, S. 2013. Impacts of fishing and environmental factors driving changes on littoral fish assemblages in a subtropical oceanic island. *Estuarine, Coastal and Shelf Science*, 128: 22–32.
- Scheinin, M., and Mattila, J. 2010. The structure and dynamics of zooplankton communities in shallow bays in the northern Baltic Sea during a single growing season. *Boreal Environment Research*, 15: 397–412.

- Scheinin, M., Sjöqvist, C., and Mattila, J. 2013. Microalgal plankton composition in shallow coastal inlets in contrasting trophic and alternative community states. *Hydrobiologia*, 701: 253–271.
- Scheinin, M., and Söderström, S. 2005. A mapping of aquatic macrophytes along two inner-outer-archipelago gradients in the North-Western and South-Eastern Åland. Research ERports from Husö Biological Station, 112. 61 pp. (In Swedish).
- Schultz, A. L., Malcolm, H. A., Bucher, D. J., and Smith, S. D. A. 2014. Depth and medium-scale spatial processes influence fish assemblage structure of unconsolidated habitats in a subtropical marine park. *PLoS One*. doi:10.1371/journal.pone.0096798.
- Sheaves, M., Baker, R., Nagelkerken, I., and Connolly, R. M. 2014. True value of estuarine and coastal nurseries for fish: incorporating complexity and dynamics. *Estuaries and Coasts*. doi:10.1007/s12237-014-9846-x.
- Snickars, M., Gullström, M., Sundblad, G., Bergström, U., Downie, A-L., Lindegarh, M., and Mattila, J. 2014. Species–environment relationships and potential for distribution modelling in coastal waters. *Journal of Sea Research*, 85: 116–125.
- Snickars, M., Sandström, A., Lappalainen, A., Mattila, J., Rosqvist, K., and Urho, L. 2009. Fish assemblages in coastal lagoons in land-uplift succession: the relative importance of local and regional environmental gradients. *Estuarine, Coastal and Shelf Science*, 81: 247–256.
- Snickars, M., Sundblad, G., Sandström, A., Ljunggren, L., Bergström, U., Johansson, G., and Mattila, J. 2010. Habitat selectivity of substrate spawning fish - modelling requirements of the Eurasian perch, *Perca fluviatilis*. *Marine Ecology Progress Series*, 398: 235–243.
- Snickars, M., Weigel, B., and Bonsdorff, E. 2015. Impact of eutrophication and climate change on fish and zoobenthos in coastal waters of the Baltic Sea. *Marine Biology*, 162: 141–151.
- Shpilev, H., Ojaveer, E., and Lankov, A. 2005. Smelt (*Osmerus eperlanus* L.) in the Baltic Sea. *Proceedings of the Estonian Academy of Sciences, Biology and Ecology*, 54: 230–241.
- Törnroos, A., Nordström, M. C., and Bonsdorff, E. 2013. Coastal habitats as surrogates for taxonomic, functional and trophic structures of benthic faunal communities. *PLoS One*, 8: e78910.
- Vahteri, P., O'Brien, K., and Vuorinen, I. 2009. Zonation and spatial distribution of littoral fish communities from the southwestern Finnish coast (Archipelago and Bothnian Sea, Northern Baltic Sea). *Estuarine, Coastal and Shelf Science*, 82: 35–40.

Handling editor: Jonathan Grabowski