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Diel changes in the fish assemblage in a coastal surf-zone area in the eastern Baltic Sea

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The composition of the fish assemblage in the surf zone in Eru Bay, Gulf of Finland, was highly variable in relation to the time of day (dawn, noon, dusk and midnight) during the ice-free season in 2008. The diel variation in the surf-zone fish assemblage composition was also associated with seasonal changes. Species that exhibited the most variation during the diel cycle were the European smelt (*Osmerus eperlanus*), gudgeon (*Gobio gobio*), bleak (*Alburnus alburnus*), three-spined stickleback (*Gasterosteus aculeatus*), ninespine stickleback (*Pungitius pungitius*), small sandeel (*Ammodytes tobianus*), and gobies (*Pomatoschistus* spp.). To our knowledge, this is the first study that describes diel variations in the fish assemblage composition of a non-tidal brackish surf-zone environment using an annual data set. The results imply that time of day effects species abundances, and this should be taken into account in future studies where the aim is to evaluate littoral fish assemblages of the Baltic Sea.

Introduction

Littoral areas are known to be important feeding and nursery grounds for several fish species (Thorman 1986a, Rajasilta *et al*. 1999, Ustups *et al*. 2007, Taal *et al*. 2014b). High temporal variability and the dominance of a small number of species, as well as the strong seasonal influence of juveniles, are characteristics of littoral fish communities (Thorman and Wiederholm 1986, Wilber *et al*. 2003, Vasconcellos *et al*. 2011, Rodrigues and Vieira 2013). The fish fauna of the littoral zone of the Baltic Sea consists of a mixture of species of both marine and freshwater origin (Sundell 1994, Rajasilta 1999). While many of these species have often little or no commercial importance, littoral fish communities play an important role in the functioning of aquatic ecosystems (e.g., Thorman and Wiederholm 1984, Ustups *et al*. 2007, Taal *et al*. 2014b, Morkūnė *et al*. 2016). To fully understand the mechanisms shaping such ecosystems, factors that affect littoral fish assemblages require elucidation

Diel and seasonal changes are typical to sandy-beach surf-zone fish community dynamics (Wiber *et al*. 2003, Vasconcellos *et al*. 2011, Rodriques and Viera 2013). In temperate regions,

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temperature has been suggested as the major factor affecting the timing of annual migrations, spawning, and survival of young-of-the-year (YOY), and it probably accounts for most of the variation in surf zone fish communities at a seasonal scale (e.g., Thorman 1986a, Hagan and Able 2003). At the diel scale, temporal changes in fish assemblages are mostly associated with tidal cycles and the circadian rhythms of fish, which are often linked with feeding and predator avoidance (e.g., Thorman and Wiederholm 1986, Castillo-Rivera *et al*. 2010, Vasconcellos *et al*. 2011). However, the Baltic Sea has no significant tidal activity (e.g., Järvekülg 1979), except near the Danish straits, so any diel variations would probably mainly be determined by the day/night cycle. To the best of our knowledge, there are no comprehensive assemblage-level studies of diel variations in the composition of the fish assemblage of the surf zone of the Baltic Sea. Only the diel variations of selected fish species inhabiting the shallow littoral zone of the brackish waters of the Gulf of Bothnia have been described in a single survey by Thorman and Wiederholm (1986).

To date, most of the Baltic Sea littoral zone ichthyological studies have been based on one or a few species, rather than the whole community (discussed in Sundell 1994, Horackiewicz and Skóra 1998). Seasonal dynamics, feeding ecologies, and the effects of physical factors on fish species richness and abundance have also been studied in the shallow waters of the Gulf of Bothnia (Thorman and Wiederholm 1983, 1984, Thorman 1986a, 1986b), Gulf of Finland (Sundell 1994), and the eastern coast of the Baltic Proper (Ustups *et al*. 2003, 2007). In the Archipelago Sea, Vahteri *et al*. (2008) described immediate environment-specific spatial distribution of fish in the littoral zone, as well as larger scale geographic zonation within the archipelago. The monitoring data on littoral fish populations from the 1990s were also compared with those from the 1970s and 1980s from the same region (Rajasilta *et al*. 1999). However, the aforementioned studies were based only on daytime samples. While previous reports on the temporal dynamics in fish assemblages in temperate areas have shown diel (e.g., Jansson *et al*. 1985, Thorman and Wiederholm 1986), seasonal (e.g., Jansson *et al*. 1985, Thorman and Wiederholm 1986, Wilber *et al*. 2003, Vetemaa *et al*. 2006), and inter-annual (e.g., Rajasilta *et al*. 1999, Wilber *et al*. 2003) variations in the densities of some species, no comprehensive assemblage-level studies have been conducted on the diel variations in fish communities in the littoral zone of the Baltic Sea. Thus, increased knowledge on the diel changes in fish communities inhabiting the shallow non-tidal littoral ecosystems of the brackish Baltic Sea is required in order to understand their functioning.

The aim of the present study was to describe diel variations in the composition of the fish assemblage in the surf zone (the shallow littoral area between the shore and the surf line) of a sandy beach located in the eastern Baltic Sea. Sampling was conducted four times in a day (dawn, noon, dusk, and midnight) once a month during the ice-free season in 2008, in order to assess whether the composition of the fish community changed with respect to the time of day. Such observations should allow one to determine whether sampling time is an important factor to be taken into consideration in studies of near-shore fish assemblages in the Baltic Sea is conducted. Such knowledge may also have implications for studying the ecosystem function of shallow, littoral habitats and fish communities.

Material and methods

Study area

The data was collected from Eru Bay (59°33´N, 25°49´E), at the southern shore of the Gulf of Finland, in the Baltic Sea (Fig. 1). Water temperature was measured over the whole study period (April–December) using a data logger located at an approximate depth of 1 m. Surface water salinity in the study area fluctuates annually between 4.5 and 6.5 PSU, which is typical for the central part of the Gulf of Finland (Martin *et al*. 2003). The area is non-tidal and upwelling events are highly probable. The study area is normally covered with ice during the winter months. The coastline of the southern part of Eru Bay was suitable for this study because of: (1) the location, as the area is sheltered from

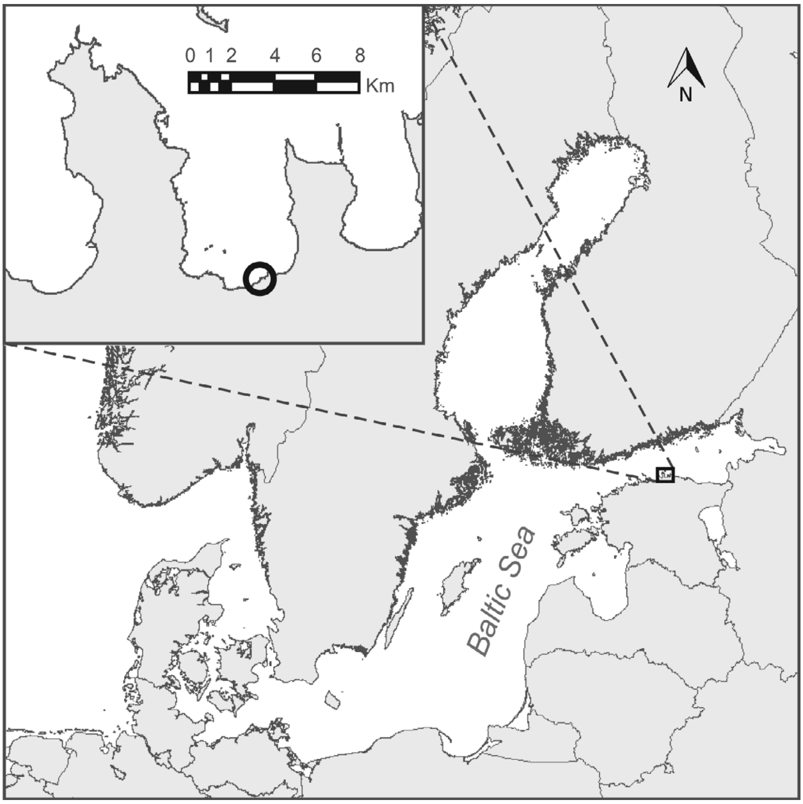

Fig. 1. Location of the study area (59°33´N 25°49´E) in Eru Bay (Gulf of Finland, Baltic Sea).

the prevailing western winds and wave action is only strongly affected by winds from northern directions; (2) the flat and gently sloping littoral zone, which is suitable for effective use of a beach seine (Lappalainen and Urho 2006); and (3) human impact in this area is very low (Martin *et al*. 2003), thus any observed phenomena are more likely to describe natural rather than anthropogenic processes.

Sampling and processing of fish samples

Fish samples were collected monthly during the ice-free period (April–December) in 2008. Surveying was always conducted under low offshore wind conditions, when wave height did not exceed 0.2 m. Sampling was carried out using a beach (hand) seine, with the following net dimensions: 1.3 m (height) × 2.2 m (length) × 1.2 m (width). The mouth of the seine was bordered on each side by wings that were 15 m long and 1.3 m wide. Mesh size of both wings was 10 mm for the first 8 m, reducing to 5 mm near the cod-end, which was cone-shaped with a mesh size of 2 mm. The seine was hauled perpendicular to the shore using 20 m ropes, then pulled on to the shore, covering a mean area of 964 m^2 per haul.

The shallow (≤ 1 m) littoral area of the sandy beach was divided into six seining stations. Those stations were always sampled as a set within a time frame of one hour, to minimize the influence of changing weather and light conditions. The sample sets were collected at dawn (starting 30 minutes before sunrise), noon (starting 30 minutes before astronomical noon), dusk (starting 30 minutes before sunset), and midnight (starting 30 minutes before astronomical midnight). Monthly sampling cycles varied from 24 to 72 hours, depending on the weather conditions. A total of 289 285 fish from 216 samples (6 samples × 4 sampling sessions per day × 9 months) were identified to the lowest possible taxonomic level and measured to the nearest 1 mm total length (TL). Total biomass of each taxa was also estimated to the nearest 0.1 g. All fish were either analysed within 12 hours post-landing or fixed on site with a 10% formalin solution for later examination.

Data analysis

The main aim of this study was to describe any diel variations in surf-zone fish-community composition. Abundance of each species in a haul was defined as the number of caught individuals per 100 m^2 of haul (indiv. per 100 m^2). Prior to PERMANOVA, SIMPER and CAP analyses (PRIMER ver. 6 and PERMANOVA+ software were used; *see* Andersson *et al*. 2008) abundance data were square-root transformed. To ascertain whether fish community composition (described as the abundance of different species per 100 m^2) was associated with the time of day, month, or their interaction, permutational multivariate analysis of variance (PERMANOVA test using PRIMER PERMANOVA+; Andersson *et al*. 2008) was used. Two-way (crossed) SIMPER analysis (Clarke and Gorley 2006) was used to describe which fish species contributed most to the differentiation among the samples with respect to the time of day and seasonality. Canonical analysis of principal coordinates (CAP using PRIMER PERMANOVA+; Andersson *et al*. 2008) was applied to illustrate how time of day was associated with surf zone fish community composition. In order to investigate, which fish species characterised the observed differences between different times of day, a vector overlay of Spearman's rank correlations of individual fish species with CAP axes were plotted. Temperature was not added as a covariate into the models due to its high collinearity with factor "month" ($r^2 = 0.74$; $p = 0.017$; regression analysis of a quadratic model). As YOY, the common goby (*Pomatoschistus microps*) and sand goby (*Pomatoschistus minutus*) were difficult to distinguish from each other, so for all statistical analyses all individuals of these species were pooled as a species group termed "gobies".

Associations between total fish (all species summed) abundance (indiv. per 100 m^2) and biomass (g per 100 m^2) with water temperature were investigated with Spearman's rank-order correlation. Monthly differences in total fish abundance and biomass were evaluated with a Kruskal-Wallis test with post-hoc multiple comparisons using STATISTICA 7.

Results

A total of 24 fish species, belonging to 14 families, were identified. The most abundant species were the three-spined stickleback (*Gasterosteus aculeatus*), ninespine stickleback (*Pungitius pungitius*), sand goby and common goby, followed by the Atlantic herring (*Clupea harengus*), European sprat (*Sprattus sprattus*), European smelt (*Osmerus eperlanus*), gudgeon (*Gobio gobio*), bleak (*Alburnus alburnus*), straightnose pipefish (*Nerophis ophidion*), small sandeel (*Ammodytes tobianus*), and European flounder (*Platichthys flesus*) (Fig. 2, Appendix 1). The anadromous brown trout (*Salmo trutta*), European whitefish (*Coregonus lavaretus*), roach (*Rutilus rutilus*), Eurasian minnow (*Phoxinus phoxinus*), vimba bream (*Vimba vimba*), Prussian carp (*Carassius gibelio*), spined loach (*Cobitis taenia*), European perch (*Perca fluviatilis*), eelpout (*Zoarces viviparous*), great sandeel (*Hyperoplus lanceolatus*), bullhead (*Cottus gobio*), and turbot (*Scopthalmus maximus*) were caught in relatively low numbers (Appendix 2).

The composition of the fish assemblage differed significantly among times of day (dawn, noon, dusk, and midnight) and months (Table 1), as illustrated by the differences in species abundances (Figs. 2 and 3; Appendices 1 and 2). A statistically significant time of day × month interaction (Table 1) and variation in fish assemblage composition indicated that diel changes also had a seasonal aspect (Fig. 2; Appendices 1 and 2). According to two-way SIMPER analysis (factors time of day and month; % contribution of each species to total dissimilarity between factor levels) the three-spined stickleback (20.5%–33.6%), ninespine stickleback (15.5%–25.8%), gobies (16.3%–19.4%), European smelt (11.4%–13.4%), small sandeel (2.9%–16.2%), gudgeon (3.9%–8.7%), and bleak (2.5%–5.7%) contributed most to assemblage differences on a diel basis, while gobies (7.7%–57.6%), the

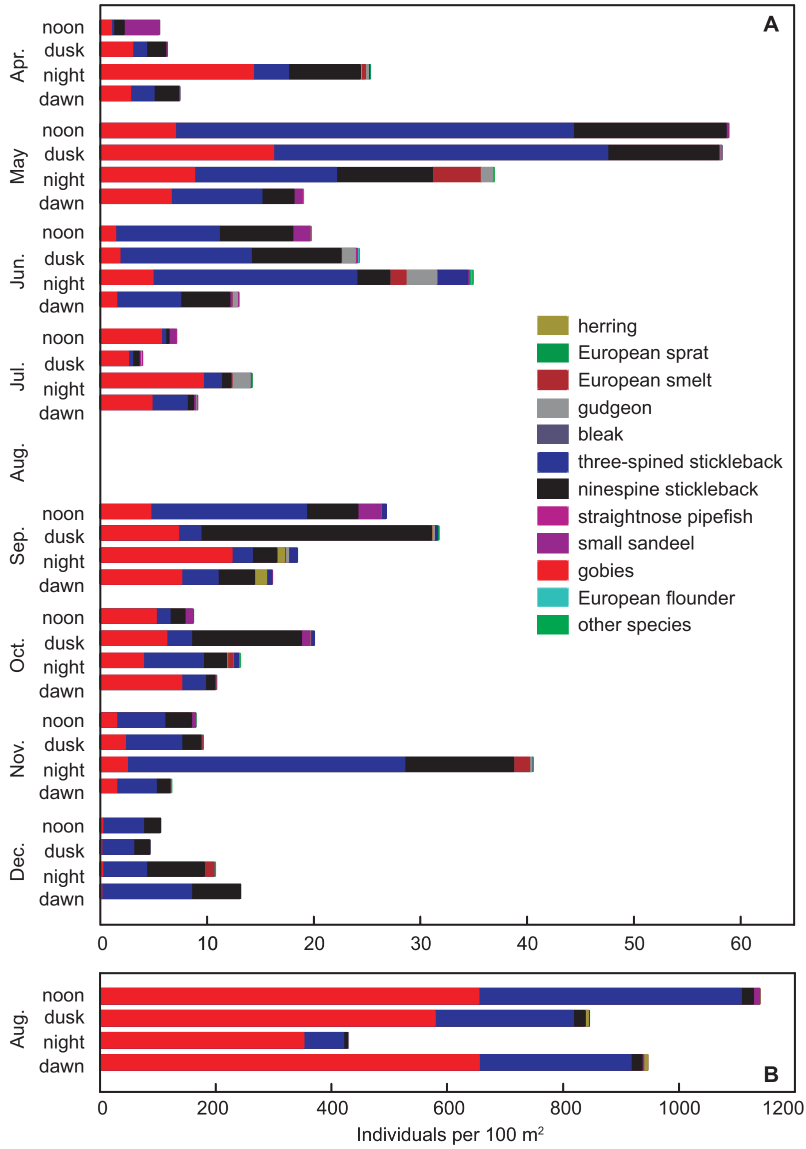

Fig. 2. Mean densities of fish at different times of day in (**A**) April–July and September–December, and (**B**) August in 2008. Note the scale difference between August and the other months. The common goby and sand goby are pooled as a species group termed "gobies".

three-spined stickleback (14.5%–42.4%), nine-spine stickleback (4.5%–28.1%), small sandeel (2.6%–14.4%), gudgeon (2.2%–14.1%), herring (2.7%–9.8%), bleak (2.7%–9.4%), and European smelt (2.4%–5.7%) contributed most to the differences on a monthly basis.

During the study, some species were captured only during certain times of day (Figs. 2 and 3; Appendices 1 and 2). The small sandeel was present in samples taken at noon, while the European smelt was most abundant in the midnight samples (Figs. 2 and 3; Appendix 1). Presence

Table 1. Permutational analysis of variance (PERMANOVA) of the effect of time of day (dawn, noon, dusk, and midnight) and month on fish assemblage composition.

	df	Pseudo-*F*	*p*
Time of day	3	27.5	0.001
Month	8	48.5	0.001
Time of day × month	24	4.7	0.001
Residual	180		
Total	215		

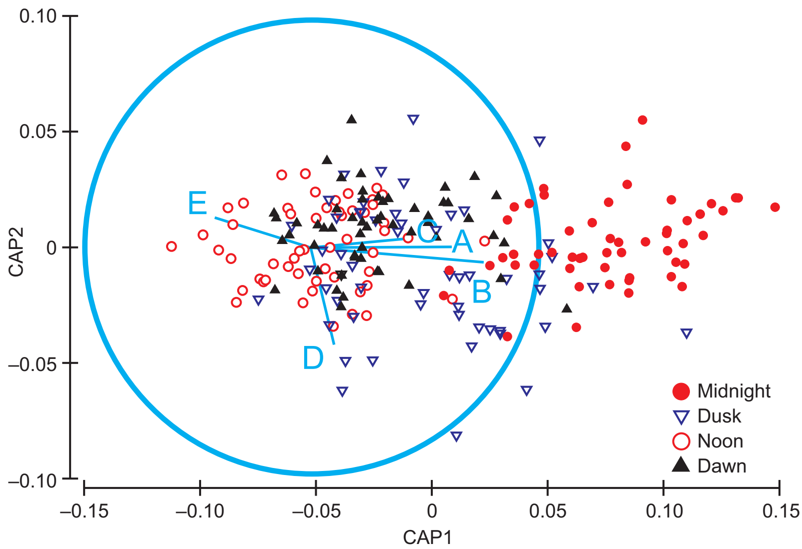

Fig. 3. Canonical analysis of principal coordinates (CAP) plot illustrating the association of abundances of the (**A**) European smelt, (**B**) gudgeon, (**C**) bleak, (**D**) ninespine stickleback, and (**E**) small sandeel with the overall fish-assemblage composition with regard to time of day.

of the gudgeon in the catch was associated with midnight and dusk sampling (Figs. 2 and 3; Appendix 1). A higher abundance of the bleak occurred in the midnight and dawn samples (Figs. 2 and 3; Appendix 1); higher abundance of the ninespine stickleback was mainly associated with dusk and noon (Figs. 2 and 3; Appendix 1). Although abundances of gobies and the three-spined stickleback varied between times of day, they were not associated with any particular time(s) of day in a straightforward manner (Fig. 2; Appendix 1).

Diel variations in the surf-zone fish assemblage were affected by season, both in terms of the presence/absence and or abundance of different fish species (Fig. 2). According to total length (TL), the bleak (22–162 mm), European smelt (78–197 mm), and gudgeon (38–143 mm) in the samples consisted of mostly sub-adult individuals (juvenile fish, i.e. older than YOY but yet to reach sexual maturity) and adults. The YOY of these species were either absent or very rare throughout the study period. In the case of gobies (sand and common goby pooled) (11–65 mm), the ninespine stickleback (12–65 mm), small sandeel (34–137 mm), and three-spined stickleback (12–74 mm), YOY specimens were also captured. YOY were present in July (gobies), August (gobies, sticklebacks, and the small sandeel), September (gobies, sticklebacks, and the small sandeel), October (gobies, sticklebacks, and the small sandeel), November (gobies and sticklebacks), and December (sticklebacks). The highest proportions of YOY were captured in August, whereas the overall proportion of YOY declined from September to December.

Higher total abundances and biomass (Fig. 4) were associated with higher temperatures (Spearman's rank-order correlation: $r_s = 0.318$, $p < 0.0001$, $n = 216$; and $r_s = 0.383$, $p < 0.0001$, $n = 216$; respectively). The total fish abundance and biomass differed significantly among sampling months (Kruskal-Wallis test: $H_{8,216} = 128.80$, $p < 0.0001$; and $H_{8,216} = 119.70$, $p < 0.0001$; respectively). Post-hoc multiple comparisons indicated that fish abundance in August was significantly higher than during other months (all $z > 4.217$, $p < 0.0009$) with the exception of May when no such difference was detected ($z = 2.224$, $p = 0.941$). Fish abundance in May was also higher than during other months (all $z > 4.070$, $p < 0.0016$) with the exception of June and September ($z = 1.976$, $p = 1.000$; and $z = 2.332$, $p = 0.708$; respectively). We found no statistically significant differences among total fish biomass in May, June and August ($z = 0.235$–1.362, all $p = 1.000$). Total fish biomass in May, June and August was higher than during other months ($z > 4.803$, $p < 0.0001$; $z > 3.676$, $p < 0.0085$; and $z > 5.039$, $p < 0.0001$; respectively). Post-hoc multiple comparisons also indicated that fish abundance in July was lower than in May,

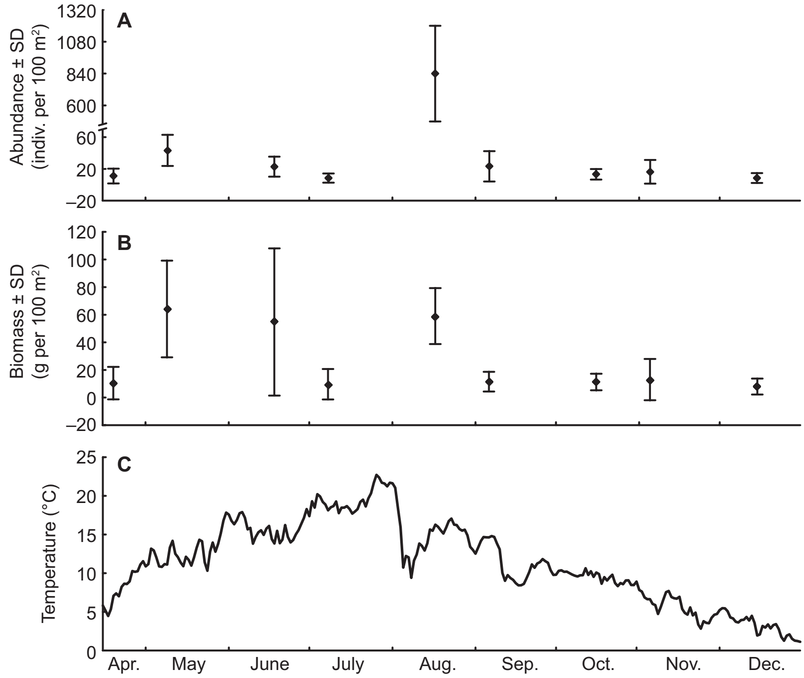

Fig. 4. (**A**) Seasonal mean abundance of all fish species (note the scale difference between August and the other months), (**B**) seasonal mean biomass of all fish species, and (**C**) daily mean water temperature (°C) in the surf zone of Eru Bay from April–December 2008 at a depth of 1 m.

June, August and September (all $z > 3.660$, $p < 0.0090$) but did not differ from that in April, October, November and December ($z > 0.635$, $p = 1.000$; $z > 1.922$, $p = 1.000$; $z > 1.678$, $p = 1.000$; and $z > 0.058$, $p = 1.000$; respectively). Total fish biomass in July was also lower than in May, June and August (all $z > 5.078$, $p < 0.0001$) but did not differ from that in April, September, October, November and December ($z > 0.057$, $p = 1.000$; $z > 1.207$, $p = 1.000$; $z > 1.401$, $p = 1.000$; $z > 0.757$, $p = 1.000$; and $z > 0.050$, $p = 1.000$; respectively).

Discussion

Our data showed high fish-assemblage-level variation according to time of day in the surf zone of the eastern Baltic Sea. To the best of our knowledge, this is the first time such diel variations in the fish assemblage of the surf zone have been described in the Baltic Sea using multivariate assemblage-level analysis, and a data set covering almost the entire year.

The three-spined stickleback, ninespine stickleback, gobies, European smelt, small sandeel, gudgeon, and bleak contributed most to assemblage differences on a diel basis. Throughout the study period, the European smelt utilized the shallow littoral zone almost exclusively during the night, whereas the gudgeon and bleak were also present there during the twilight period (dusk and dawn respectively). Midnight samples contained more species (if compared with species found in all samples) than did the dawn, noon, or dusk samples (Appendices 1 and 2). The small sandeel was most abundant at noon but extremely scarce or even entirely absent from midnight samples, whereas the always present ninespine-stickleback was more abundant during noon and dusk. Abundance of gobies and the three-spined stickleback alternated at different times of day, however no distinguishable year-round trend was found. Our data support earlier findings from different regions (Jansson *et al*. 1985, Thorman and Wiederholm 1986, Vasconcellos *et al*. 2011) indicating high complexity at the diel scale. Such diel variations in the fish assemblage of the surf zone are most probably linked with possibility of finding food, and with predator avoidance (Thorman and Wiederholm 1986, Castillo-Rivera *et al*. 2010, Vasconcellos *et al*. 2011). Additionally, it could be hypothesised that competitive interactions between different species and among size classes within a species cannot be ruled out as YOY individuals were abundant during certain months (e.g., August and September). Thus, in the case of very abundant species in our data set (the three-spined stickleback and gobies) the high YOY abundance could hamper finding overall distinguishable diel pattern in our study area as behaviour (habitat utilization, preference) of juveniles can differ from that of adults (Thorman and Wiederholm 1983, Sundell 1994, Ustups *et al*. 2007, Mustamäki *et al*. 2015). Moreover, Taal *et al*. (2014b) proposed that because of diet overlap, high abundances of YOY gobies and sticklebacks in Eru Bay may negatively affect the feeding conditions of smaller adult and sub-adult smelt. This hypothesis is not in accordance with Thorman and Wiederholm (1983, 1984, 1986) who suggested that in the Gulf of Bothnia (Baltic Sea) the competition for food is at most a subsidiary structuring mechanism shaping littoral fish assemblage due to low population density induced by unfavourable abiotic conditions (e.g., long ice season, relatively low average water temperature). Furthermore, according to Ustups *et al*. (2007), food spectra of the juveniles and adults dominating in the surf zone of the western coast of Latvia (Baltic Proper) also did not overlap significantly. However, in the case of more favourable conditions (e.g., milder climate) in a shallow estuary on the Swedish west coast, competition for food, at least temporarily, affects the interactions among fish species (Thorman 1982) probably due to lower mortality rate (Thorman and Wiederholm 1984). A change towards milder winters was observed over the past 100 years in the Baltic Sea region, thus shortening the length of the ice season (Haapala *et al*. 2015). Thus, the possible competition for food in Eru Bay cannot be ruled out completely.

A single study of diel variations in the abundance of some surf-zone fish species in the Baltic Sea was conducted by Thorman and Wiederholm (1986), who used drop-net data collected during May, August, and September. They concluded that several fish species (the sand goby, three-spined stickleback, Eurasian minnow, ninespine stickleback, (YOY) European perch, and common goby) were all more abundant in night than in daytime samples. However, one of the main results of the present study was that in the surf zone of the Baltic Sea, diel variation at fish assemblage level was influenced by the presence of sub-adults and adults of relatively larger species (e.g., the European smelt, gudgeon, bleak, and small sandeel), which seemed to have diel movement patterns, and utilised the surf zone only during certain times of day. Abundance of gobies and the three-spined stickleback varied at different time of day, but we did not find such straightforward patterns as described by Thorman and Wiederholm (1986). Differences between the results of Thorman and Wiederholm (1986) and ours may have partly resulted from methodological differences, as well as habitat-specific (e.g., bottom substrate, vegetation coverage) and regional differences in the fish fauna. For instance, while they caught fifteen fish species, only six of them occurred in sufficient numbers for analysis. In addition, in their study the total length of the drop-net caught fish varied between 10 and 70 mm while also larger fish were caught in our study. A beach seine with similar dimensions as used by us in this study also allowed for the capture of larger individuals (Wilber *et al*. 2003, Taal *et al*. 2014a, 2014b) than the drop-nets used by Thorman and Wiederholm (1986). Beach seining has become the main method for sampling young fish and small-sized littoral species in shallow marine and estuarine habitats in the Baltic Sea (Lappalainen and Urho 2006). This method is more suited for capturing as many fish species as possible from flat bottom habitats without physical obstructions, such as stones, rocks, and dense vegetation (reviewed in Lappalainen and Urho 2006). Nonetheless, larger, fast swimming species may have avoided the seine, while very small juveniles could have passed through its meshes. Therefore, the data obtained was not a mirror image of the fish community, but rather a sample of the fish assemblage catchable with the selected gear type. However, subsamples obtained by fishing with a standardized sampling method, ought to reflect patterns in the composition of communities (Mustamäki *et al*. 2015), and beach seining has been argued to be the most suitable method for long term monitoring of larger scale changes to near-shore fish communities in the Baltic Sea (Vahteri *et al*. 2009).

Results of the present study also demonstrated that variations in the surf-zone fish assemblage was affected by diel migrations between the shallow and sandy surf zone and adjacent habitats. Our results thus complement the previous findings of Mustamäki *et al*. (2015), who showed that the seasonal composition of the fish assemblage in a shallow coastal area changed significantly from early summer to late summer. In addition to supporting the findings of Mustamäki *et al*. (2015), our results demonstrate that changes in the shallow, sandy surf zone are dependent on time of day. Specifically, the absence of some fish species (e.g., European smelt, small sandeel) during particular times of the day, further stresses the effect of diel migrations on the composition of the fish assemblage in this ecosystem.

One notable phenomenon recorded during our study was that the European smelt was caught mostly, and during some months exclusively at night. This might be associated with their specific feeding behaviour as sub-adult and adult smelt prey upon juvenile fish (e.g., sticklebacks and gobies) in near-shore habitats (e.g., Taal *et al*. 2014b). This hypothesis is also supported by an observation that shoaling juvenile fish are more vulnerable to smelt predation during twilight and night (Kostrichkina 1974). Earlier studies from the Baltic Proper (Ustups *et al*. 2003, 2007) indicated that adult European smelt are abundant at depths of less than 2 m only during spring spawning migration, and leave such shallow areas by summer. Our results demonstrate that adult European smelt may regularly utilize the shallow littoral zone throughout the ice-free period. This inconsistency can be partly explained by the different study areas, but also by differences in sampling method. According to Vasconcellos *et al*. (2011), the diel activity of fish might be strongly affected by local habitat constraints, even when similar systems are compared. In Ustups *et al*. (2003, 2007), samples were only taken during daylight while this study demonstrates that smelt was mainly present in the surf zone at night. Thus, based on our results, combined with previous knowledge from different geographical areas (e.g., Thorman and Wiederholm 1986, Hagan and Able 2007, Castillo-Rivera *et al*. 2010), it can be proposed that in order to avoid biases arising from diel variations, studies of shallow littoral fish assemblages in the Baltic Sea should not rely on samples taken during only one time of day.

Diel variations in the surf-zone fish assemblage of Eru Bay were likely affected by seasonal changes in fish species abundances. Moreover, some species (e.g., the European smelt, ninespine stickleback, and three-spined stickleback) were caught during all months, whereas others (e.g., the bleak and small sandeel) were not (Fig. 2; Appendices 1 and 2). The seasonal trends found by us were in accordance with previous studies in the Baltic Sea (e.g., Thorman 1986a, 1986b, Sundell 1994). It has been suggested that temperature and salinity are the most important factors behind seasonal changes in the composition of fish species assemblages in temperate shallow waters and estuaries (e.g., Thorman 1986a, Hagan and Able 2003). In the Baltic Sea, water temperature has been shown to be the main factor regulating fish abundances and the recruitment of yearlings, whereas salinity is associated with area-specific differences in fish community compositions (Thorman 1986a, Vetemaa *et al*. 2006). Accordingly, seasonality in our data set was mostly described by variations in the number of species and density of the most numerically dominant species throughout the study season. Maximum fish density and biomass were recorded in August, mostly owing to an increase in the numbers of juvenile individuals. Fish densities and biomass were also high in May and June, probably due to this period being the spawning season and having the optimal water temperature (e.g., Breau *et al*. 2011) for most of the encountered species. Therefore, the results of the present study also showed relatively low densities of surf-zone fish in July (compared with May, June, August and September), in accordance with the mid-summer decline in fish abundance that has been observed in the Baltic Sea and the Kattegat (discussed in Thorman 1986a). The observed decline in fish abundances during the middle of the summer can be the result of several factors. First, adults of surf-zone fish species, such as the sand and common gobies, and three-spined stickleback, either die after spawning or move to deeper areas during this period (discussed in Sundell 1994, Bergström *et al*. 2015). Second, the beach seine used may not have been efficient in catching small YOY three-spined stickleback, ninespine stickleback, and sand and common goby, which were also present in the surf zone during the middle of the summer. Third, warm mid-summer conditions in the surf zone may not be optimal for some species during most of the diel period, as in deeper, cooler waters utilisation of energy from consumed food is more efficient (discussed in Thorman and Wiederholm 1986). The mid-summer decline in fish abundance in the surf zone of Eru Bay probably resulted from interactions of the aforementioned factors. Hence, our results and those of previous studies (Thorman 1986a, Sundell 1994), suggest that mid-summer sampling of surf zone fish in the Baltic Sea may lead to biased results with regard to the composition of the fish assemblage if due to the sampling method used smaller species are underrepresented.

Conclusions

The observed diel variations in the composition of the fish assemblage of the surf zone indicate that the time of day sampling is undertaken is an important factor, and should be considered when planning future research on shallow near-shore fish assemblages (at least in the Baltic Sea). The results of the present study demonstrate that the composition of a fish assemblage observed at a certain time of day cannot be directly extrapolated to another time of day, or regarded as representative of the whole astronomical day. According to our results, the midnight samples contained a more complete species list than the dawn, noon, or dusk samples. Therefore, the results indicate that midnight sampling is the most effective approach to sampling the fish assemblage. However, some species (e.g., the small sandeel) may be relatively abundant at dawn, noon, and dusk, but entirely absent from midnight samples. Therefore, at least noon and midnight data should be available in order to draw any realistic conclusions with regard to the composition of the littoral fish assemblage. However, in order to quantitatively and fully describe the fish assemblage of the surf zone of the Baltic Sea, samples covering all different times of day (dawn, noon, dusk, and midnight) should be obtained. This is important, because crucial data, such as the significance of this habitat for a certain species, could be missed if sampling is limited to a specific diel time period.

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Appendix 1. Mean densities ± SDs of the most abundant fish (indiv. per 100 m^2) at different times of day in April–December in 2008. Abbreviations: Pom tot = sand goby and common goby, G acu = three-spined stickleback, P pun = ninespine stickleback, A tob = small sandeel, C har = herring, O epe = European smelt, G gob = gudgeon, A alb = bleak, N oph = straightnose pipefish, S spr = European sprat, and "P fle = European flounder.

Month	Pom tot	G acu	P pun	A tob	C har	O epe	G gob	A alb	N oph	S spr	P fle
April											
noon	1.0 ± 0.5	0.2 ± 0.1	1.0 ± 0.7	3.3 ± 5.3	–	–	–	–	0.02 ± 0.1	–	–
dusk	3.0 ± 2.7	1.3 ± 0.9	1.8 ± 1.1	0.1 ± 0.2	–	–	–	–	0.04 ± 0.1	–	–
night	14.3 ± 2.7	3.3 ± 1.0	6.7 ± 1.1	–	0.1 ± 0.1	0.4 ± 0.4	0.3 ± 0.1	0.1 ± 0.1	–	0.04 ± 0.1	0.02 ± 0.1
dawn	2.8 ± 1.7	2.2 ± 2.0	2.3 ± 2.0	0.1 ± 0.1	–	–	–	0.02 ± 0.1	–	–	–
May											
noon	7.0 ± 1.4	37.3 ± 10.9	14.3 ± 4.7	0.2 ± 0.2	–	–	–	0.01 ± 0.04	0.02 ± 0.04	0.01 ± 0.04	0.01 ± 0.04
dusk	16.2 ± 6.3	31.3 ± 11.7	10.4 ± 4.0	0.1 ± 0.1	–	–	0.1 ± 0.1	–	0.1 ± 0.1	–	0.03 ± 0.1
night	8.8 ± 4.6	13.3 ± 2.3	9.0 ± 2.1	–	0.01 ± 0.04	4.7 ± 2.0	1.0 ± 0.3	0.02 ± 0.04	–	–	0.01 ± 0.04
dawn	6.6 ± 2.2	8.5 ± 4.5	3.0 ± 1.1	0.7 ± 0.8	–	–	–	–	0.1 ± 0.1	–	0.01 ± 0.04
June											
noon	1.4 ± 1.0	9.7 ± 9.1	6.9 ± 1.9	1.6 ± 2.9	–	–	0.1 ± 0.1	–	–	–	0.02 ± 0.1
dusk	1.8 ± 0.6	12.3 ± 6.9	8.4 ± 2.4	0.04 ± 0.1	–	–	1.3 ± 2.3	0.02 ± 0.1	0.2 ± 0.1	–	0.1 ± 0.1
night	4.9 ± 1.8	19.1 ± 10.9	3.1 ± 1.7	–	–	1.5 ± 1.5	2.9 ± 1.4	2.9 ± 1.8	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
dawn	1.5 ± 0.5	6.0 ± 2.6	4.6 ± 2.1	0.2 ± 0.2	–	–	0.5 ± 0.6	0.02 ± 0.04	0.1 ± 0.1	–	0.04 ± 0.1
July											
noon	5.7 ± 4.2	0.4 ± 0.3	0.3 ± 0.2	0.6 ± 0.9	–	–	–	–	0.1 ± 0.1	–	–
dusk	2.6 ± 1.4	0.4 ± 0.1	0.6 ± 0.4	0.1 ± 0.1	–	–	0.1 ± 0.1	–	0.1 ± 0.2	–	0.03 ± 0.1
night	9.6 ± 4.5	1.7 ± 0.4	0.9 ± 0.8	–	–	0.1 ± 0.1	1.7 ± 1.7	0.03 ± 0.1	0.1 ± 0.2	0.01 ± 0.03	–
dawn	4.8 ± 4.9	3.3 ± 2.8	0.6 ± 0.2	0.2 ± 0.1	–	–	0.1 ± 0.1	–	0.1 ± 0.1	–	–
August											
noon	653.7 ± 194.2	453.3 ± 140.3	20.7 ± 7.5	10.8 ± 9.6	0.7 ± 1.2	–	–	–	–	0.01 ± 0.03	–
dusk	577.9 ± 291.2	239.1 ± 290.2	20.1 ± 15.6	0.6 ± 1.2	5.0 ± 5.6	–	0.2 ± 0.3	1.7 ± 1.1	0.03 ± 0.1	0.1 ± 0.1	–
night	351.4 ± 88.8	68.8 ± 44.3	6.4 ± 4.3	0.1 ± 0.1	0.2 ± 0.3	0.3 ± 0.3	0.4 ± 0.2	0.5 ± 0.2	0.01 ± 0.03	–	–
dawn	654.3 ± 129.8	262.1 ± 156.2	19.0 ± 6.3	2.9 ± 3.5	7.0 ± 14.7	–	–	0.01 ± 0.03	–	–	–
September											
noon	4.7 ± 1.6	14.6 ± 27.3	4.8 ± 5.1	2.1 ± 4.5	0.03 ± 0.1	0.02 ± 0.04	0.5 ± 0.9	–	–	–	–
dusk	7.3 ± 2.8	2.1 ± 2.3	21.6 ± 17.5	–	0.03 ± 0.1	0.02 ± 0.04	0.2 ± 0.2	0.3 ± 0.3	–	0.1 ± 0.2	–
night	12.3 ± 6.0	1.9 ± 2.1	2.3 ± 1.1	–	0.7 ±0.4	0.1 ± 0.1	0.3 ± 0.1	0.8 ± 0.7	–	0.02 ± 0.04	–
dawn	7.6 ± 3.5	3.4 ± 2.1	3.4 ±1.3	0.02 ± 0.04	1.1 ± 0.4	–	0.02 ± 0.04	0.5 ± 0.7	0.02 ± 0.04	0.02 ± 0.04	0.02 ± 0.04
October											
noon	5.2 ± 1.0	1.3 ± 1.4	1.4 ± 1.2	0.7 ± 1.0	0.02 ± 0.1	–	0.04 ± 0.1	–	–	–	–
dusk	6.2 ± 1.7	2.3 ± 2.5	10.3 ± 8.5	0.8 ± 0.9	0.02 ± 0.1	0.04 ± 0.1	0.33 ± 0.5	–	0.02 ± 0.05	–	–
night	4.0 ± 1.4	5.6 ± 1.4	2.2 ± 0.4	–	0.1 ± 0.1	0.5 ± 0.3	0.02 ± 0.1	0.5 ± 0.5	–	0.04 ± 0.1	0.02 ± 0.1
dawn	7.6 ± 3.2	2.2 ± 1.2	0.9 ± 0.6	0.1 ± 0.1	–	–	–	0.02 ± 0.1	–	0.02 ± 0.1	–

November											
noon	1.5 ± 0.6	4.5 ± 2.2	2.5 ± 1.0	0.4 ± 0.9	–	–	–	–	–	–	–
dusk	2.3 ± 1.2	5.3 ± 2.9	1.8 ± 1.0	–	–	0.1 ± 0.1	–	–	0.1 ± 0.2	–	–
night	2.5 ± 0.3	26.0 ± 3.9	10.2 ± 4.0	–	–	1.5 ± 0.9	0.2 ± 0.2	–	–	0.1 ± 0.3	–
dawn	1.5 ± 0.2	3.7 ± 3.2	1.3 ± 0.8	–	–	–	–	0.02 ± 0.1	–	–	0.04 ± 0.1
December											
noon	0.2 ± 0.2	3.8 ± 2.3	1.6 ± 1.0	–	–	–	–		–	–	–
dusk	0.1 ± 0.2	3.0 ± 1.1	1.5 ± 0.7	–	–	–	0.02 ± 0.1	–	–	–	–
night	0.2 ± 0.2	4.1 ± 2.1	5.4 ± 1.5	–	–	0.9 ± 0.4	–	–	0.1 ± 0.1	–	–
dawn	0.1 ± 0.1	8.4 ± 6.4	4.6 ± 3.3	–	–	–	–	–	–	–	–

Appendix 2. Mean densities ± SDs (indiv. per 100 m^2) of less abundant fish species (combined as "other species" in Fig. 4) at different times of day in April–December in 2008 (only times of day for which data were available are listed). Abbreviations: S max = turbot, C tae = spined loach, C lav = European whitefish, H lan = great sandeel, P flu = European perch, C gib = Prussian carp, Z viv = eelpout, P pho = Eurasian minnow, C gob = bullhead, S tru = anadromous brown trout, R rut = roach, and "V vim = vimba bream.

Month	S max	C tae	C lav	H lan	P flu	C gib	Z viv	P pho	C gob	S tru	R. rut	V vim
April												
night	–	–	–	–	–	–	0.02 ± 0.1	–	–	–	–	–
May												
noon	0.01 ± 0.04	–	–	–	–	–	–	–	–	–	–	–
dusk	–	–	–	0.01 ± 0.04	–	–	–	–	–	–	–	–
night	–	0.2 ± 0.1	0.04 ± 0.1	–	0.01 ± 0.04	0.01 ± 0.04	0.03 ± 0.04	–	–	–	–	–
dawn	0.04 ± 0.1	–	–	0.1 ± 0.1	–	–	0.01 ± 0.03	–	–	–	–	–
June												
noon	0.02 ± 0.1	–	–	–	–	–	–	–	–	–	–	–
dusk	0.02 ± 0.1	–	0.02 ± 0.1	–	–	–	–	–	–	–	–	0.02 ± 0.1
night	–	0.04 ± 0.1	0.04 ± 0.1	–	0.02 ± 0.04	0.1 ± 0.1	–	0.02 ± 0.1	–	–	0.02 ± 0.1	–
July												
night	0.01 ± 0.04	0.01 ± 0.04	–	–	–	–	–	–	0.03 ± 0.04	–	–	–
August												
dusk	–	–	–	–	0.02 ± 0.04	0.01 ± 0.03	–	–	–	–	–	–
night	–	–	–	–	0.03 ± 0.04	–	–	–	–	–	–	–
September												
dusk	0.03 ± 0.1	–	–	–	–	–	–	0.02 ± 0.04	–	–	–	–
night	0.02 ± 0.04	–	–	–	–	–	–	–	–	–	–	–
dawn												
October												
noon	–	–	0.02 ± 0.1	0.04 ± 0.1	–	–	–	–	–	–	–	–
dusk	0.04 ± 0.1	–	–	–	–	–	–	–	–	–	–	–
night	0.02 ± 0.1	–	0.02 ± 0.1	–	–	–	0.02 ± 0.1	–	–	–	–	–
dawn	–	–	–	0.04 ± 0.1	–	–	–	–	–	–	–	–
November												
noon	0.02 ± 0.1	–	0.02 ± 0.1	–	–	–	–	–	–	–	–	–
night	–	–	–	–	0.03 ± 0.1	–	–	–	–	–	–	–
dawn	0.1 ± 0.1	–	–	–	–	–	–	0.03 ± 0.1	–	–	–	–
December												
night	0.02 ± 0.1	0.03 ± 0.1	–	–	–	–	–	–	–	–	–	–
dawn	–	–	–	–	–	–	–	–	–	0.02 ± 0.1	–	–