

IMRE TAAL

Causes of variation in littoral fish
communities of the Eastern Baltic Sea:
from community structure
to individual life histories



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LIST OF ORIGINAL PUBLICATIONS

The current thesis was based on the following papers, which are referred to in the text by the Roman numerals I–V:

- I. Taal I., Saks L., Kesler K., Verliin A., Jürgens K., Svirgsden R., Rohtla M., Hubel K., Albert A., Eschbaum R. & Vetemaa, M. 2017. Diel changes in the fish assemblage in a coastal surf-zone area in the eastern Baltic Sea. *Boreal Environment Research*, 22, 83–96.
- II. Taal I., Saks L., Nedolgovala S., Verliin A., Kesler M., Jürgens K., Svirgsden R., Vetemaa M., & Saat T. 2014. Diet composition of smelt *Osmerus eperlanus* (Linnaeus) in brackish near-shore ecosystem (Eru Bay, Baltic Sea). *Ecology of Freshwater Fish*, 23, 121–128.
- III. Taal I., Kesler M., Saks L., Rohtla M., Verliin A., Svirgsden R., Jürgens K., Vetemaa M. & Saat T. 2014. Evidence for an autumn downstream migration of Atlantic salmon *Salmo salar* (Linnaeus) and brown trout *Salmo trutta* (Linnaeus) parr to the Baltic Sea. *Helgoland Marine Research*, 68, 373–377.
- IV. Taal, I., Rohtla, M., Saks, L., Kesler, M., Jürgens, K., Svirgsden, R., Matetski, L., Verliin, A., Paiste, P. & Vetemaa, M. 2017. Parr dispersal between streams *via* a marine environment: a novel mechanism behind straying for anadromous brown trout? *Ecology of Freshwater Fish*. doi: 10.1111/eff.12338.
- V. Taal, I., Rohtla, M., Saks, L., Svirgsden, R., Kesler, M., Matetski, L. & Vetemaa, M. 2017. Evidence of Atlantic salmon *Salmo salar* fry movement between fresh water and a brackish environment. *Journal of Fish Biology*, 91, 695–703.

Author's contribution:

I was the lead author of all five publications. I generated the original research ideas and wrote the first drafts of the publications. I also took an active part in collecting field data and participated in data analysis.

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DEFINITIONS AND ABBREVIATIONS

ANADROMOUS: Fish that find a major part of their food in salt water, but spawn in freshwater (*e.g.* Atlantic salmon (*Salmo salar*), anadromous brown trout (*Salmo trutta*) (Jonsson & Jonsson 2011).

ABT: anadromous brown trout (sea trout).

LITTORAL (ZONE): There is no single definition of the concept of “littoral zone”, as it varies by context (*e.g.* oceans, Baltic Sea, rivers, lakes). In this dissertation, I define littoral (littoral zone) as the area ranging from the shoreline to the outer edge of the aquatic vegetation zone. In the habitats considered in this dissertation, the littoral reaches water depths of up to 10–15 metres (see also Hänninen *et al.* 2007).

NEAR-SHORE ENVIRONMENT: In this dissertation, I define near-shore as the marine environment up to 3 km from the coastline and less than 25 m deep.

PARR: Young fish (*e.g.* Atlantic salmon, anadromous brown trout) in freshwater, which are characterized by parr marks (a series of parallel vertical bars) along their flanks. Anadromous salmonids are considered parr from having consumed their yolk until smolting (Jonsson & Jonsson 2011). Post-independence of the yolk sac to the end of their first summer, young parr are also referred to as fry (*e.g.* Hendry & Cragg-Hine 2003).

SMOLTING (SMOLTIFICATION): The process involving morphological, physiological, biochemical, and behavioural changes, whereby salmonid parr pre-adapt to marine life (Jonsson & Jonsson 2011).

SSME (Stream Shifting through the Marine Environment): A previously undescribed life-history strategy of Atlantic salmon and anadromous brown trout. SSME involves salmon and ABT descending to the brackish waters of the Baltic Sea from their natal streams as parr or fry, and then migrating to non-natal streams before transforming into smolt (**IV**; **V**).

STRAY: Fish that enter a stream to spawn where they did not hatch (*e.g.* Atlantic salmon, anadromous brown trout) (Jonsson & Jonsson 2011).

SURF-ZONE: the shallow littoral area between the shoreline and the most seaward point of the breaker zone (surf line). The breaker zone is defined as the zone within which waves approaching the coastline break.

YOY (young of the year): Fish born within the past year, from transformation to juvenile until January 1st in the Northern Hemisphere and July 1st in the Southern Hemisphere (FishBase Glossary 2017).

1. INTRODUCTION

The shallow littoral is a highly productive environment characterized by the multitude of interactions within and between different trophic levels. It serves as an important reproduction, nursery, and foraging area to coastal marine biota (e.g. Thorman & Wiederholm 1986; Gibson & Robb 1996; Mustamäki *et al.* 2014; Lokko *et al.* 2016; Morkünë *et al.* 2016). Littoral fish communities are highly variable, as species composition and abundance differ over both spatial and temporal scales (e.g. Thorman & Wiederholm 1986; Sundell 1994; Rajasilta *et al.* 1999; Wilber *et al.* 2003; Vahteri *et al.* 2009; Vasconcellos *et al.* 2011; Mustamäki *et al.* 2015). Earlier studies have indicated that the factors driving the occurrence and abundance of fish in near-shore areas can be divided as: (1) climatic events that affect year-class strength; (2) reproductive and feeding movements that impose seasonal variation; and (3) short-term physico-chemical conditions (e.g. turbidity, wave height, salinity, tidal stage, temperature, photoperiod), which may influence point abundance (reviewed by e.g. Ross *et al.* 1987; Wilber *et al.* 2003).

The Baltic Sea is very shallow (mean depth of 55 m, Myrberg & Andrejev 2003) and has a highly variable coastline (reviewed in Niemelä *et al.* 2015), ranging from soft-formed depositional shores to bedrock-dominated archipelagos. There are also considerable environmental constraints on abiotic and biotic parameters (e.g. salinity, temperature, nutrient status, and food base to fish) between different sub-basins of the Baltic Sea, and from estuaries and bays to the open sea (Neumann 1977; Uusitalo *et al.* 2005). In the brackish Baltic Sea, the fauna comprises a mixture of species of marine and freshwater origin, which have adapted to the low salinities of the environment. The salinity of the Baltic Sea decreases east- and north-wards, resulting in a decrease in the number of marine species and an increase of freshwater species (Järvekül 1979; Voipio 1981; Ojaveer & Pihu 2003). The factors discussed above have a strong influence on fish community composition and abundances of different species in different areas of the Baltic Sea. Littoral habitats have often been considered important reproduction, nursery, and feeding areas for many fish species (e.g. Thorman & Wiederholm 1986; Vetemaa *et al.* 2006; Rohtla 2015). The shallow coastal zone is also inhabited by many small-sized fish species that to date have received minimal research attention (e.g. Sundell 1994; Rajasilta *et al.* 1999).

The overall economic importance (*sensu* landings biomass and revenue) of coastal fisheries in the Baltic Sea is small compared to pelagic fisheries regarding Baltic Sea herring (*Clupea harengus*), European sprat (*Sprattus sprattus*), and cod (*Gadus morhua*). However, littoral fish are important components in food chains of the whole Baltic ecosystem, transferring energy to upper trophic levels (e.g. Timola 1980; Lundström *et al.* 2007; Ustups *et al.* 2007; Mustamäki *et al.* 2014; Morkünë *et al.* 2016). Some species, such as European perch (*Perca fluviatilis*) (e.g. Saat & Eschbaum 2002), European

smelt (*Osmerus eperlanus*) (e.g. Shpilev *et al.* 2005; Popov 2006; Shvagzhdy 2009), and European flounder (*Platichthys flesus*) (e.g. Ojaveer & Dreves 2003), are also important and highly valued species to local small-scale coastal fisheries. Due to the temporally highly variable biotic and abiotic conditions in the littoral areas, fish species composition and abundance may show high seasonal and inter-annual variation (e.g. Sundell 1994; Rajasilta *et al.* 1999; Vetemaa *et al.* 2006). Moreover, it has been recently shown that the seasonal locality-specific composition of the fish assemblage in shallow coastal areas changes significantly from early to late summer (Mustamäki *et al.* 2015).

Although littoral fish communities vary significantly in both space and time, there have been relatively few ichthyological studies carried out in the littoral zone compared to the amount of research concentrated on fish in other habitats of the Baltic Sea. Mustamäki (2015) stresses that fish monitoring interests are usually centred on long-term trends and the issue of seasonal changes is often circumvented by conducting such sampling at the same time each year. For this reason, descriptions of seasonal variation in fish communities of the Baltic Sea are scarce (reviewed by Mustamäki 2015). However, inter-annual, seasonal, and spatial dynamics of near-shore fish communities have still been relatively well studied (e.g. Vetemaa *et al.* 2006; Vahteri *et al.* 2009; Mustamäki *et al.* 2015). Nonetheless, there is only one study where diel variations in abundance of selected fish species inhabiting the shallow littoral zone of the Baltic Sea have been described (Thorman & Wiederholm 1986). Community level diel movements of littoral fish species in the Baltic Sea have not been described at all.

The behaviour of fish in the littoral zone can be strongly influenced by local habitat constraints, even when comparisons are performed between similar systems (Vasconcellos *et al.* 2011). Thus, it is possible that various coastal fish may show more diverse life history patterns (e.g. Landergren 2001; Limburg *et al.* 2001; Rohtla *et al.* 2012; Rohtla *et al.* 2014; Svirgsden *et al.* 2016) owing to adaptation to the brackish conditions of the Baltic Sea, compared to conspecifics in strictly freshwater or more saline environments. It is therefore reasonable to speculate (in the context of the salinity gradient) that some coastal fish species inhabiting the Baltic Sea might even show sub-basin specific complex life history patterns. Therefore, new insight is needed into the functioning of littoral habitats as reproduction, nursery, and feeding areas, as well as local habitat spacing on short-term regular movement patterns of different fish species. Comprehensive evaluation of the ecological role of littoral habitats to mobile organisms such as fish should also include possible interactions with adjacent habitats (e.g. streams and the open sea).

Considering the gaps in our knowledge, my dissertation focuses on the dynamics of near-shore fish assemblages and alternative life-history patterns of fish species inhabiting the littoral zone in the north-eastern part of Baltic Sea. In particular, I address the topics of diel-scale variation in assemblage composition (**I**), seasonal foraging (**II**), and alternative nursery habitat use (**III, IV, V**), of anadromous fish in the littoral zone. All these factors are important in determining fish movements and elucidate a complex description of highly

dynamic Baltic Sea littoral ecosystems. The results of these studies can be applied in decision making related to the management and restoration of fish populations.

Temporal variations in surf-zone fish assemblage composition of the non-tidal Baltic Sea, with an emphasis on diel changes, were evaluated in Eru bay (I). In addition to diel behaviour, seasonal changes in fish assemblage composition are presented. To my knowledge, community level diel changes of the surf-zone fish assemblage have not been described in the Baltic Sea. Furthermore, it has been pointed out (Mustamäki 2015) that there is a trend towards community-level studies, along with recent developments in multivariate analysis methods. The need of such knowledge is furthered regarding ecosystem based management, which focuses on the system, rather than on a single species (reviewed by Mustamäki 2015). Understanding diel and seasonal variations of the littoral fish assemblage is also important to future studies where the aim is to evaluate the littoral fish assemblages of the Baltic Sea.

In this thesis, I describe the seasonal diet composition and feeding activity of the anadromous coastal fish species European smelt (*Osmerus eperlanus*) in a brackish littoral ecosystem (II). Shallow littoral areas are known as important feeding grounds to many fish species in the Baltic Sea (e.g. Thorman & Wiederholm 1986; Ustups *et al.* 2007; Mustamäki *et al.* 2014). Thus, temporal variations in fish assemblage composition in littoral areas are often related to feeding migrations (reviewed e.g. by Ross *et al.* 1987; Wilber *et al.* 2003). The knowledge of what and how much is consumed by fishes is central to understand food chains and webs, and the indirect importance of non-commercial marine biota to fisheries (Elliott *et al.* 2002). Hence, such studies may be essential to evaluate the ecological role of such species, as well as understanding the food web structure of the shallow littoral zone of the Baltic Sea. Moreover, diet composition and seasonal feeding patterns of certain species helps to understand the background mechanisms shaping diel and seasonal dynamics of the local littoral fish assemblage (I).

Unconventional types of juvenile salmonid migrations between streams and brackish littoral area of the Baltic Sea are described in the present thesis (III, IV, V). Those articles are in line with studies that document increasing complexity in the migration patterns of anadromous fish between freshwater and brackish littoral areas in the Baltic Sea (e.g. Limburg *et al.* 2001; Rohtla *et al.* 2012; Rohtla *et al.* 2014; Svirgdsen *et al.* 2016). Regular movements of migratory fish species with relatively high commercial and recreational value, such as Atlantic salmon and brown trout, have been the subject of many studies (e.g. Klemetsen *et al.* 2003; Jonsson & Jonsson 2011). However, descriptions of alternative migrations of juvenile salmonids between freshwater and brackish environments are relatively scarce (e.g. Limburg *et al.* 2001; Ibbotson *et al.* 2013; Winter *et al.* 2016). Due to a lack of information, management decisions generally do not incorporate littoral habitats as provisional or permanent nursery, and wintering areas, for Atlantic salmon and sea trout parr and fry.

Thus, the results from studies **III**, **IV**, and **V** can be applied to future decision making related to the management and restoration of fish populations.

To conclude, the aims of this thesis were:

- to assess diel variations in the composition of the fish assemblage in the surf-zone of the non-tidal Baltic Sea (**I**).
- to estimate the predatory role of European smelt in a littoral habitat by describing seasonal variation of prey composition (**II**).
- to investigate whether littoral habitats of the Baltic Sea also function as a habitat for early out-migrating Atlantic salmon and ABT fry and parr (**III**, **IV**, **V**).

2. STUDY SYSTEM

2.1. The study area

The Baltic Sea is the second largest brackish waterbody in the world. Its main basin has very limited water exchange with the North Sea *via* the narrow and shallow Danish straits, and is characterized by a significant freshwater surplus due to large river runoffs, amounting to about 2% of the volume of the sea per annum (Myrberg & Andrejev 2003; reviewed by Ojaveer & Pihu 2003). Despite the relatively small surface area, the topography of the Baltic Sea is quite complex (*e.g.* Fig. 1), resulting in specific hydrographic characteristics in different sub-basins (Myrberg & Andrejev 2003; reviewed by Ojaveer & Pihu 2003). Moreover, crucial environmental factors (*e.g.* salinity, temperature, trophic status, effect of the photoperiod) also have considerable gradients from different littoral areas (*e.g.* the open coastal zone, estuaries, and bays) to the open sea (Neumann 1977; Thorman & Wiederholm 1983; Uusitalo *et al.* 2005). Due to variability in abiotic and biotic environmental parameters, near-shore fish communities of the Baltic Sea are highly variable. For instance, the occurrence and abundance of species may differ spatially and temporally over seasonal and diel scales (*e.g.* Thorman 1986a, b; Thorman & Wiederholm 1986; Sundell 1994; Vetemaa *et al.* 2006; Mustamäki *et al.* 2015), as near-shore littoral areas are known to constitute important spawning, nursery, and feeding areas (*e.g.* Sundell 1994; Ustups *et al.* 2003; Vetemaa *et al.* 2006; Rohtla 2015).

This thesis focuses on the north-eastern Baltic Sea as the study area (Fig. 1). Specifically, the field studies were conducted in the Gulf of Finland basin (Eru Bay **(I, II, III)** and the Toolse River **(V)**), Baltic Proper basin (Ernespu Stream **(IV)**), and Gulf of Riga basin (Loode and Lemmejõgi streams **(V)**). Eru Bay was used as a model area of a brackish ecosystem to describe: (1) temporal variations in the fish assemblage composition of the surf-zone, with an emphasis on diel changes of the relative proportions of different species by photoperiod **(I)**; (2) seasonal diet composition and feeding activity of a small, but relatively abundant predator in the near-shore habitat, using European smelt as a model species **(II)**; (3) alternative life-histories of Atlantic salmon and ABT parr in a littoral habitat **(III)**. The Baltic Proper basin and Ernespu Stream were used to document whether juvenile anadromous brown trout descend to the brackish waters of the Baltic Sea from their natal streams as parr or fry, and then migrate into non-natal streams (SSME), before transforming into smolt **(IV)**. The Gulf of Finland basin, Toolse River, and Loode and Lemmejõgi streams in the Gulf of Riga basin were used as models to describe the descent of Atlantic salmon fry from their natal streams to the brackish waters of the Baltic Sea, and their use of this environment as an alternative rearing habitat, before ascending back to freshwater streams **(V)**.

Eru Bay **(I, II, III)** is located in the centre of the southern part of the Gulf of Finland (Fig. 1). The Gulf of Finland is an elongated sub-basin at the north-

eastern extremity of the Baltic Sea, with a surface area of 29,571 km² and mean water depth of approximately 37 m. Salinity of the Gulf of Finland increases from east to west, and north to south. Surface salinity varies from 5–7 psu in the West, to 0–3 psu in the East (Alenius *et al.* 1998). Ice cover is a regular winter phenomenon in the Gulf of Finland (Alenius *et al.* 1998). The average number of ice days varies from 40 at the western end of the Gulf of Finland to 130 in some coastal bays in the north-eastern part of the Gulf of Finland (Seinä & Peltola 1991). The area is characterized by a strong seasonal thermocline at depths of 10–20 m (reviewed by Alenius *et al.* 1998), as well as by occasional coastal upwelling events (Myrberg & Andrejev 2003).

Although the Loobu River discharges into Eru Bay, the influence of freshwater on salinity levels in the area is very low (Martin *et al.* 2003). Surface water salinity of Eru Bay is usually 4.5–6.5 psu, which is typical for the central part of the Gulf of Finland. In the outer part of the bay, the bottom slope is relatively steep, with a depth of 10 m reached at 400–500 m from the shoreline (Martin *et al.* 2003), whereas the inner part of Eru Bay is characterized by a relatively gentle slope (a depth of 10 m is usually reached at >1000 m distance from the shoreline).

The local fish fauna comprises both marine and freshwater species. Coastal fisheries are mostly directed at salmonids and whitefish (Saat *et al.* 2003), as there are several important salmonid rivers in Northern Estonia (Kangur *et al.* 2003a, b). The coastline of the southern part of Eru Bay was suitable as a model area to study the dynamics of littoral fish assemblages because: (1) location, the area is sheltered from prevailing western winds and is only significantly influenced by winds from northern directions; (2) the gentle slope and flat bottom are suitable to use beach seining effectively (Lappalainen & Urho 2006); (3) human impact in this area is very low (Martin *et al.* 2003).

The Ermespu Stream (**IV**) is situated on Saaremaa Island and drains into Tagalaht Bay, which is part of the Baltic Proper (Fig. 1), where surface water salinity ranges between 5–7 ‰ (Martin *et al.* 2003). The influence of freshwater in this area is very low, as Tagalaht Bay receives marginal freshwater inflow from a few small streams (Järvekülg 2001). The Ermespu Stream is an appropriate system to document the SSME of anadromous brown trout, because: (1) no suitable spawning habitat is available to brown trout (*sensu* Ottaway *et al.* 1981; Louhi *et al.* 2008; Jonsson & Jonsson 2011), as the substrate consists entirely of fine sediment (Järvekülg *et al.* 2012); (2) of a neighbouring stream (Pidula Stream) with high densities of brown trout juveniles (Kesler *et al.* 2015).

The Toolse River (**V**) discharges into Kunda Bay (Gulf of Finland), where surface water salinity is usually < 5 ‰ (Järvekülg 1979). The Loode and Lemmejõgi streams (**V**) flow into the Gulf of Riga, where surface water salinity usually ranges between 4.5–6.0 ‰ (Leppäranta & Myrberg 2009). However, the high number of inflowing streams, and the relative isolation from the open Baltic Sea, may produce considerable temporary changes to the salinity gradient. Thus, salinity in the coastal zone of the Gulf of Riga can be variable

during periods of high discharge, and occasionally fluctuate only between 0.5–2.0 psu (reviewed by Ojaveer 1997). Those streams are suitable study systems to demonstrate SSME of Atlantic salmon, because the Lemmejõgi Stream (catchment area 55.7 km²), Looe Stream (catchment area 18.5 km²), and Toolse River (catchment area 84.3 km²), are not classified as historical or potential Atlantic salmon rivers (HELCOM 2011) due to their relatively small flow volume and size (Jonsson *et al.* 1991).

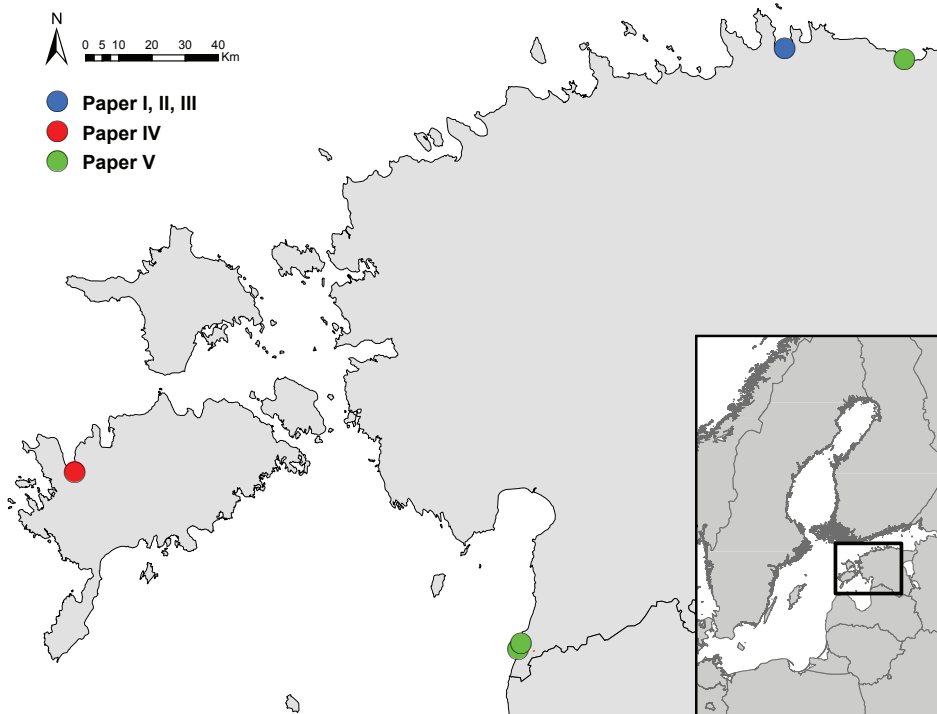


Figure 1. Study region and sampling sites of the present thesis.

2.2. Field sampling and methods

The fish samples from Eru Bay were collected with a beach (hand) seine (**I**, **II**, **III**) or gillnets (**II**, **III**). Detailed descriptions of the methods (*e.g.* beach seine dimensions, gillnet mesh sizes, weather conditions, fish sampling and processing, and otolith preparation and analysis) can be found in each specific publication (**I**, **II**, **III**).

Diel and seasonal changes in fish species composition and densities (**I**) in Eru Bay were assessed monthly during the ice-free period (April–December) in 2008. The beach seine was hauled perpendicular to the shore, covering a mean area of 964 m² per haul. The shallow (≤ 1 m) littoral area of the sandy beach was divided into six seining stations. 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). Fish were identified to the lowest possible taxonomic level and total length (TL) of each measured to the nearest 1 mm. Total biomass of each taxa was measured to the nearest 0.1 g.

Seasonal diet composition and feeding activity of adult and sub-adult European smelt in Eru Bay was studied by examining the stomach contents of 1397 individuals collected over the months of April to June and August to December 2009. Each prey item was identified to the lowest possible taxonomic level and counted (**II**).

Autumn migrant ABT and Atlantic salmon parr were collected in 2006, 2008, 2009, and 2013 from the shallow littoral zone of the Gulf of Finland. Age and migration pattern of ABT and Atlantic salmon were determined from sagittal otoliths (**III**).

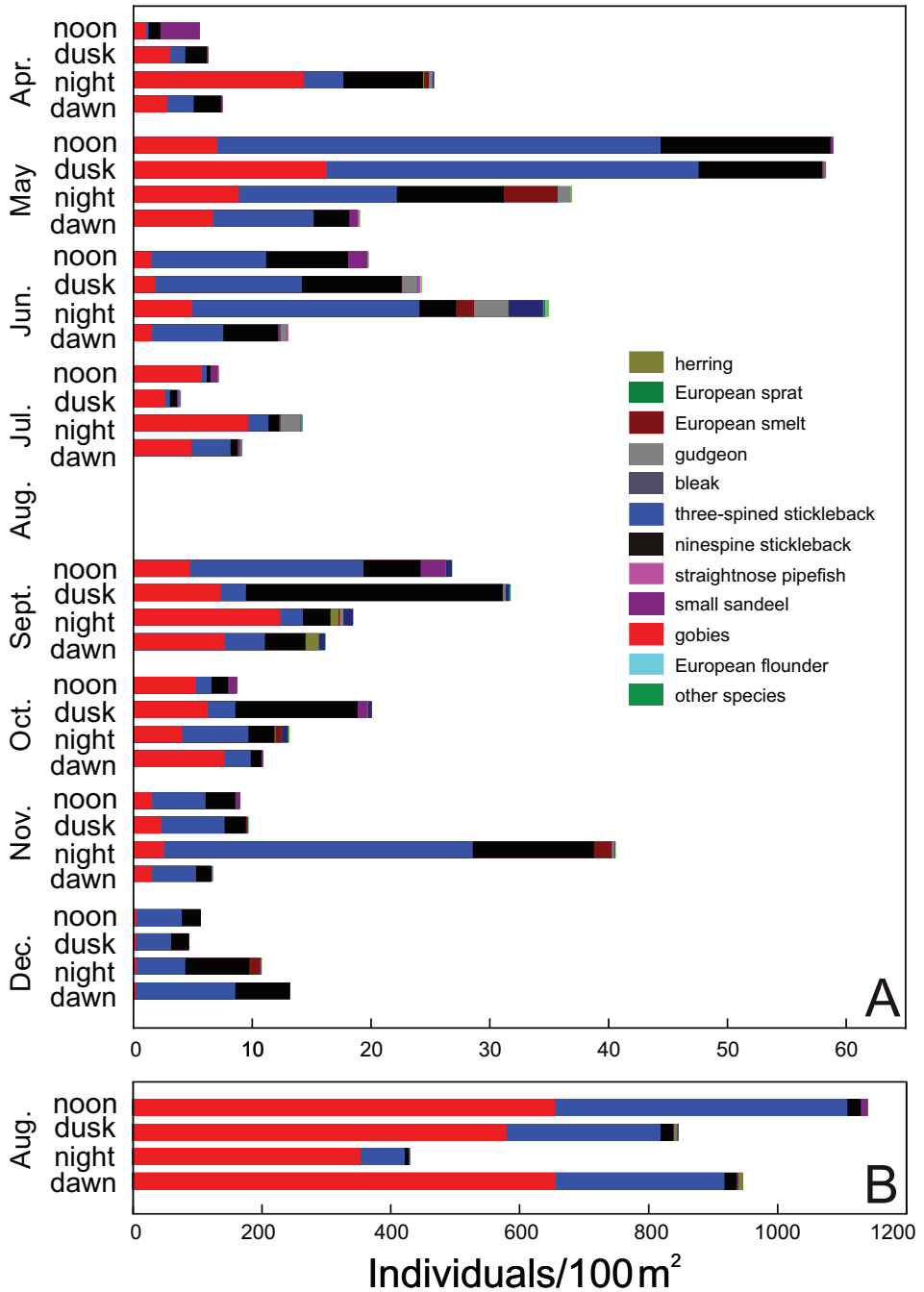
Early out-migrating ABT (**IV**) and Atlantic salmon parr (**V**) were electro-fished in the Ermespu Stream (**IV**), Lemmejõgi Stream, Loode Stream, and Toolse River (**V**). Age and use of alternative rearing habitats were determined from sagittal otoliths (**IV**, **V**). Detailed descriptions of these methods (*e.g.* fish sampling and processing, and otolith preparation and analysis) can be found in each specific publication (**IV**, **V**).

3. RESULTS AND DISCUSSION

3.1. Diel changes in the fish assemblage of a sandy surf-zone area of the Baltic Sea

The composition of the fish assemblage in the surf-zone of Eru Bay, Gulf of Finland, was highly variable (Fig. 2) in relation to the time of day (dawn, noon, dusk, and midnight) during the ice-free period of 2008. Diel variation in fish assemblage composition of the surf-zone was also linked with seasonal changes (I). To my knowledge, this is the first documentation of diel variations in the fish assemblage of the surf-zone of the Baltic Sea, using a data set covering almost the entire year (the whole ice-free season). The surf-zone fish community consisted of 24 species and was dominated by three-spined stickleback (*Gasterosteus aculeatus*), ninespine stickleback (*Pungitius pungitius*), sand goby (*Pomatoschistus minutus*), and common goby (*Pomatoschistus microps*) (I). Species that exhibited the most variation during the diel cycle were three-spined stickleback, ninespine stickleback, gobies (*Pomatoschistus* spp.), European smelt, small sandeel (*Ammodytes tobianus*), gudgeon (*Gobio gobio*), and bleak (*Alburnus alburnus*). Some species (e.g. European smelt, gudgeon, bleak, small sandeel, ninespine-stickleback) showed distinguishable diel movement patterns throughout the study period, whereas others (e.g. three-spined stickleback, gobies) did not (Fig. 2). However, in the case of three-spined stickleback and gobies, high YOY abundance during August and September could have hampered finding overall distinguishable diel patterns, as the behaviour of juveniles can differ from that of adults (e.g. Thorman & Wiederholm 1983; Ustups *et al.* 2007; Mustamäki *et al.* 2015).

One of the main results of the present thesis was that the most conspicuous diel changes at fish assemblage level were induced by the presence of sub-adults and adults of relatively large species (e.g. European smelt, gudgeon, bleak, and small sandeel), which tended to have diel movement patterns, and only utilised the surf-zone during certain times of day (Fig. 2). Furthermore, combined results (I, II) hint that European smelt might even exhibit sub-basin specific diel foraging migration, probably induced by local abiotic and biotic environmental constraints. Midnight samples contained more species compared to those collected at dawn, noon, or dusk. However, not all species showed an increase in abundance at midnight. This is not in accordance with the single previous study of diel variations of the abundance of some surf-zone fish species in the Baltic Sea by Thorman & Wiederholm (1986). These authors concluded that all the fish species studied were more abundant at night than during daytime. Differences between the results of Thorman & Wiederholm (1986) and this thesis may have partly been caused by methodological differences, as well as habitat-specific and regional differences in the fish fauna. Possible sub-basin specific diel behavioural patterns of fish species also cannot be ruled out.



This study complements the findings of Mustamäki *et al.* (2015), who showed that the seasonal composition of the fish assemblage in a similar shallow coastal area in the Baltic Sea changed significantly from early to late summer. In addition to supporting the findings of Mustamäki *et al.* (2015), the demonstrated diel migrations of fish between adjacent habitats (**I**) show that spatial changes in Baltic Sea littoral fish communities may take place over an even shorter period than described before. Specifically, the absence of some species during a particular time of day (*e.g.* European smelt, gudgeon, small sandeel), further stresses the effect of diel migrations on the composition of the fish assemblage of this ecosystem.

The results of this study also showed relatively low densities of surf-zone fish in July (compared to May, June, August, and September (Fig. 2)), which is in accordance with the mid-summer decline in fish abundance in the Baltic Sea (Sundell 1994) and the Kattegat (Thorman 1986a). The observed decline in fish abundances during July could be caused by several factors. Adult sticklebacks and gobies either die after spawning or move to deeper areas during mid-summer (*e.g.* Sundell 1994). The beach seine used may not have been efficient at catching small YOY specimens, which were present in the surf-zone. It is also possible that warmer water in the surf-zone during mid-summer may not be optimal to some species during most of the diel period, as in deeper, cooler waters, utilisation of energy from consumed food is more efficient (discussed by Thorman & Wiederholm 1986). Hence, the results of this present thesis and those of previous studies (Thorman 1986a; Sundell 1994), indicate that mid-summer sampling of surf-zone fish in the Baltic Sea may result in skewed results with regard to the composition of the fish assemblage if – due to the sampling method used – smaller species are underrepresented.

The observed diel variations in the composition of the fish assemblage of the surf-zone indicate the importance of considering the time of the day in sampling designs. 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. To fully describe the fish assemblage of the surf-zone of the Baltic Sea, samples covering several different times of day (dawn, noon, dusk, and midnight) should be obtained. For example, estimates of the significance of this habitat to particular species could be very misleading if sampling is limited to only a specific diel period.

Diel migration of fish assemblages in the various littoral habitats of the Baltic Sea is not comprehensively known, as the present results (**I**) describe only the easily accessible sandy surf-zone. The sheltered location and flat bottom habitat without physical obstructions, which is highly suitable to beach sein (reviewed by Lappalainen & Urho 2006), made our study site (**I**) an ideal model area to describe diel and seasonal changes in surf-zone fish assemblages of the Baltic Sea. Furthermore, the wide range of littoral habitats in the Baltic Basin, as well as possible sub-basin dependent diel habitat utilization (**I**, **II**) and alternative life history patterns of fish (*e.g.* Landergren & Vallin 1998;

Landergren 2001, 2004; Limburg *et al.* 2001; Rohtla *et al.* 2012, 2014; **III**, **IV**, **V**) in the Baltic Sea makes this a compelling topic for further ecological studies.

3.2. Diet composition of European smelt in a near-shore ecosystem

Prey composition and feeding activity of European smelt varied monthly and depended on the size of the individual in Eru Bay (Table 1). Gammarid amphipods (*Gammarus* spp., *Corophium volutator*) and mysids (*Mysis* spp.) were the most common prey, followed by isopods (*Idotea* spp, *Saduria entomon*), cladocerans (*Cercophagus pengoi*) decapods (*Palaemon adspersus*) and fish (*e.g.* three-spined stickleback, nine-spined stickleback, sand goby, common goby). Smelt also preyed also on molluscs, insects, insect larvae, and polychaete annelids. This study also revealed some previously unrecorded prey species of European smelt, *e.g.* bullhead (*Cottus gobio*), small sandeel, bay mussel (*Mytilus trossulus*), Baltic macoma (*Macoma baltica*), and ragworm (*Hediste diversicolor*) (see Nedolgova 2010 for details).

Whether adult smelt are a significant predator of larvae and young fish, has for a long time been the subject of discussion (reviewed by Nellbring 1989). Results of the present thesis (**II**) suggest that sub-adult and adult smelt are indeed an important predator in shallow littoral areas of the eastern Baltic Sea, as seven fish species were recorded in stomach contents. Even the smaller length classes of sub-adult and adult smelt tended to feed on fish, mostly sticklebacks and gobies.

The results of the present study suggest that European smelt inhabiting littoral areas of the Baltic Sea occupy a different ecological niche compared to smelt in offshore areas (*e.g.* Kostrichkina 1968, 1974; Shestakov 1970; Popov 1978, 2006; Urtans 1990; Ojaveer *et al.* 1997), because fish and benthic prey tend to be more important regarding the diet of coastal inhabiting smelt (**II**). Moreover, it was shown (**I**) that European smelt exhibited a distinct migration pattern to the surf-zone of Eru Bay, utilizing the habitat mostly, and during some months exclusively, at night (Fig. 2). This data conflicts with earlier studies conducted in the surf-zone of the Baltic Proper (Ustups *et al.* 2003, 2007), which indicated that adult European smelt were abundant at depths < 2m only during spawning migration in spring. This controversy can be partly explained by foraging migration induced by local environmental characteristics (**I**, **II**), and by differences in the sampling methodology (**II**). In Ustups *et al.* (2003, 2007), samples were taken in May, July, and September during daylight.

Table 1. Frequency of empty stomachs (%FES), and occurrence (%F.O., abbreviated to %O in the table) and numerical (%N) indices of prey in European smelt stomachs (L_c, size class; N, number of analysed smelt; *H. div*, *Hediste diversicolor*; *Gastr.*, *Gastropoda*; *S. ent*, *Saduria entomon*; *Gam*, *Gammaridae*; *C. vol*, *Corophium volutator*). An empty stomach was defined as the absence of any measurable organic material (Arrington *et al.* 2002). The percentages of frequency of occurrence (%F.O.) and numbers (%N) were calculated for each prey category according to the following equations (Hystlop 1980): %F.O. = 100 x Fi/n, where Fi is the number of stomachs containing a particular prey taxon; n is the total number of stomachs with any prey taxon; %N = 100 x Ni/n, where Ni is the total number of prey of a particular taxon; N is the total number of all prey identified (Paper II, Table 1).

Month	Lt	N	%FES	<i>H. div</i>	<i>Gastr.</i>	<i>Bivalvia</i>	<i>C. pengoi</i>	<i>Mysida</i>	<i>Idotea sp.</i>	<i>S. ent</i>	<i>Gam. sp.</i>	<i>C. vol</i>	<i>Insecta</i>	<i>Pisces</i>
			%O (%N)	%O (%N)	%O (%N)	%O (%N)	%O (%N)	%O (%N)	%O (%N)	%O (%N)	%O (%N)	%O (%N)	%O (%N)	%O (%N)
4	III	12	0					92 (84)	8 (1)		42 (13)			17 (2)
4	IV	13	23					100 (73)			70 (21)		10 (1)	20 (4)
5	I	75	1	7 (1)				84 (61)	1 (1)		85 (37)			1 (<1)
5	II	92	0	1 (<1)				89 (65)	5 (1)		85 (33)	1 (1)	1 (<1)	2 (<1)
5	III	42	5	3 (1)	10 (1)			65 (34)	15 (2)		63 (23)	28 (33)		3 (<1)
5	IV	91	12		6 (1)			46 (14)	20 (5)		39 (8)	44 (52)	4 (15)	10 (2)
5	V	41	20					55 (35)	39 (10)		42 (14)	24 (27)	6 (8)	18 (4)
6	I	17	6						6 (4)		100 (96)			
6	II	13	38					25 (40)			75 (60)			
6	III	21	57					11 (25)			67 (50)	11 (17)		11 (8)
6	IV	40	73					27 (17)	18 (13)		36 (25)	27 (17)		36 (29)
8	I	21	29					13 (1)	20 (2)		80 (65)	80 (27)	7 (1)	7 (1)
8	II	57	25				5 (2)	42 (5)	5 (1)	13 (3)	70 (45)	49 (33)		51 (14)
8	III	24	25				6 (<1)	33 (6)	17 (4)	2 (<1)	83 (52)	56 (19)		67 (17)
8	IV	27	11	4 (<1)				17 (2)	8 (<1)	11 (2)	75 (64)	58 (17)		58 (15)
8	V	8	13					14 (2)		21 (1)	86 (42)	86 (26)	14 (1)	86 (30)
9	I	16	56	14 (3)				57 (36)			14 (3)	14 (3)	14 (45)	29 (6)
9	II	61	36	3 (1)				49 (25)		3 (1)	49 (44)			38 (16)
9	III	52	37	3 (1)				42 (21)	18 (11)		55 (28)	3 (1)		61 (37)
9	IV	21	10	5 (1)				32 (6)	30 (12)		53 (19)			95 (57)
10	II	15	40		11 (4)			44 (22)	32 (15)	5 (1)	67 (56)			11 (4)
10	III	53	21					31 (9)	44 (15)		90 (63)		4 (1)	26 (5)
10	IV	73	22					21 (6)	55 (22)		75 (48)		2 (<1)	37 (16)
10	V	24	8					14 (3)	54 (29)		68 (26)			55 (34)
11	II	28	4					52 (48)	45 (38)		70 (39)		4 (1)	7 (1)
11	III	99	3					36 (14)	30 (10)		89 (68)		2 (<1)	9 (2)
11	IV	118	5					36 (10)	43 (16)		94 (74)		4 (<1)	14 (2)
11	V	38	3					27 (7)	37 (13)		92 (76)		3 (<1)	27 (4)
12	II	35	9					69 (59)	41 (11)		72 (36)			9 (2)
12	III	47	15	3 (1)	3 (1)			50 (43)	13 (3)		80 (39)			5 (2)
12	IV	93	14	4 (1)	1 (<1)			49 (42)	23 (15)		81 (44)		1 (<1)	21 (5)
12	V	30	0	3 (1)				43 (27)	30 (8)	3 (1)	77 (51)		3 (1)	23 (7)

Diel variation in the fish assemblages of shallow coastal areas are often related to feeding migrations (e.g. Thorman & Wiederholm 1986; Castillo-Rivera *et al.* 2010; Vasconcellos *et al.* 2011). Significant temporal variation in near-shore fish assemblages (I) could thus also be associated with the feeding behaviour of predatory fish in these habitats. Overall, based on current knowledge of European smelt diet (e.g. Popov 2006; Ustups *et al.* 2007; II), it can be speculated that European smelt may be an important predatory fish species that links shallow coastal areas to the upper trophic levels and deeper areas of the Baltic Sea. European smelt are an important part of the diet of grey seals *Halichoerus grypus* (e.g. Lundström *et al.* 2007) and various piscivorous birds, such as common guillemot (*Uria aalge*), red-throated diver (*Gavia stellata*), and great crested grebe (*Podiceps cristatus*) (e.g. Morkünè *et al.* 2016) in the Baltic basin. Moreover, Morkünè *et al.* (2016) pointed out that the fatty acid composition of anadromous smelt from the coastal zone is isotopically unique within the fish community. Morkünè *et al.* (2016) hypothesized that this phenomenon is probably caused by an interaction of anadromous migration patterns, predatory and cannibalistic feeding, starvation during the spawning period, and allocation of nutrients into the reproductive tissues during winter. According to coastal fish monitoring data (Eschbaum *et al.* 2015), the European smelt is the most common predatory fish after Eurasian perch in near-shore areas of the southern Gulf of Finland. Therefore, it seems that at least in the case of the Eastern Gulf of Finland, the impact of European smelt on the food web of the surf-zone *sensu stricto* (I, II), as well as the coastal littoral zone *sensu lato* (II), has been underestimated.

3.3. The littoral zone as a habitat of early out-migrating Atlantic salmon and anadromous brown trout juveniles in the Baltic Sea

This study presents the first records of autumn descent of Atlantic salmon and ABT to the brackish littoral habitats of the Baltic Sea Basin (Figure 3; see also Table 1 in III). The prevalence of this behaviour in these species is still unknown in the Baltic Sea. However, our relatively wide temporal range of observations (2006, 2008, 2009, and 2013) indicates that autumn descent of anadromous salmonid parr is not a random event (III). As a novel contribution to science, stream shifting through the marine environment (SSME) of early out-migrating fry and parr of ABT (Figure 4; see also Table 1 in paper IV) and Atlantic salmon (Figure 5; see also Table 1 in paper V) is presented in the current study for the first time. Moreover, residency in a saline environment has also not been previously demonstrated in the case of Atlantic salmon fry (Figure 5; see also Table 1 in paper V).

Shallow littoral habitats are important feeding areas for juvenile ABT (Klemetsen *et al.* 2003; Jonsson & Jonsson 2011), whereas Atlantic salmon

smolt usually inhabit littoral areas during a brief period at the beginning of their sea sojourn, before moving into the open sea (reviewed by Jonsson & Jonsson 2011). During smolting, salmonid parr undergo extensive physiological and morphological transformations to adapt to the saline environment (e.g. Klemetsen *et al.* 2003; Jonsson & Jonsson 2011). Juvenile salmon and ABT are traditionally considered to stay in their native stream from at least one to several years as parr, prior to their descent to the sea as smolts in spring. However, salmonids are known to have diverse life histories, which differ in the duration of freshwater and or marine rearing, age at maturation, and incidence of repeat spawning (e.g. Klemetsen *et al.* 2003; Koski 2009; Jonsson & Jonsson 2011; Roni *et al.* 2012; Bond *et al.* 2014; Shrimpton *et al.* 2014; Walsworth *et al.* 2015). It is therefore not surprising that seaward movements of Atlantic salmon and ABT have also been documented during times of the year not associated with the spring parr-smolt transformation (e.g. Cunjak *et al.* 1989; Järvi *et al.* 1996; Limburg *et al.* 2001; Winter *et al.* 2016).

Autumn descent of Atlantic salmon parr has been observed in Canada (Cunjak *et al.* 1989), Great Britain (e.g. Youngson *et al.* 1983; Riley *et al.* 2002; Pinder *et al.* 2007; Ibbotson *et al.* 2013), and Norway (Jensen *et al.* 2012). This behaviour has been recorded in the case of ABT populations in Ireland, Norway (Jonsson & Jonsson 2009), New Zealand (Holmes *et al.* 2014), Great Britain, and Denmark (Winter *et al.* 2016). However, besides autumn descent, ABT can follow other alternative migration patterns in coastal areas of the Baltic Sea. It has also been reported that fry and parr of ABT may descend to the sea soon after hatching in spring and early summer (Järvi *et al.* 1996; Limburg *et al.*, 2001; Landergren 2004), and use the littoral as an alternative nursery habitat.

The exact ecological and physiological mechanisms behind early out-migration and SSME of Atlantic salmon and ABT fry and parr (III, IV, V), are still unknown. The autumn descent of Atlantic salmon parr has been associated with high volume water flows (e.g. Youngson *et al.* 1983). Ibbotson *et al.* (2013) reviewed a number of potential mechanisms that could trigger autumn migration of Atlantic salmon. The causes behind autumn migration could include intrinsic factors such as size and position of the individual in the dominance hierarchy, and extrinsic factors associated with density and habitat, related to cover (shelter) availability, supply of food, and the presence of predators (Ibbotson *et al.* 2013). The phenomenon of early (spring-summer) out-migrating ABT fry from small Gotland streams (with high number of spawners and decreasing water levels during spring and summer) may be due to competition (e.g. for food, space) and or the result of variable hydrological conditions (e.g. decreasing water levels during dry periods in summer and early autumn), and small distance of spawning grounds from the sea (e.g. Limburg *et al.* 2001; Landergren 2004). Observed springtime out-migration of YOY Atlantic salmon in this study (V) hint that fry or young parr may also disperse downstream from their natal habitat during high volume water flows. Such an effect of high flows could be further supported by the spawning site preferences of Atlantic salmon (Jonsson *et al.* 1991).

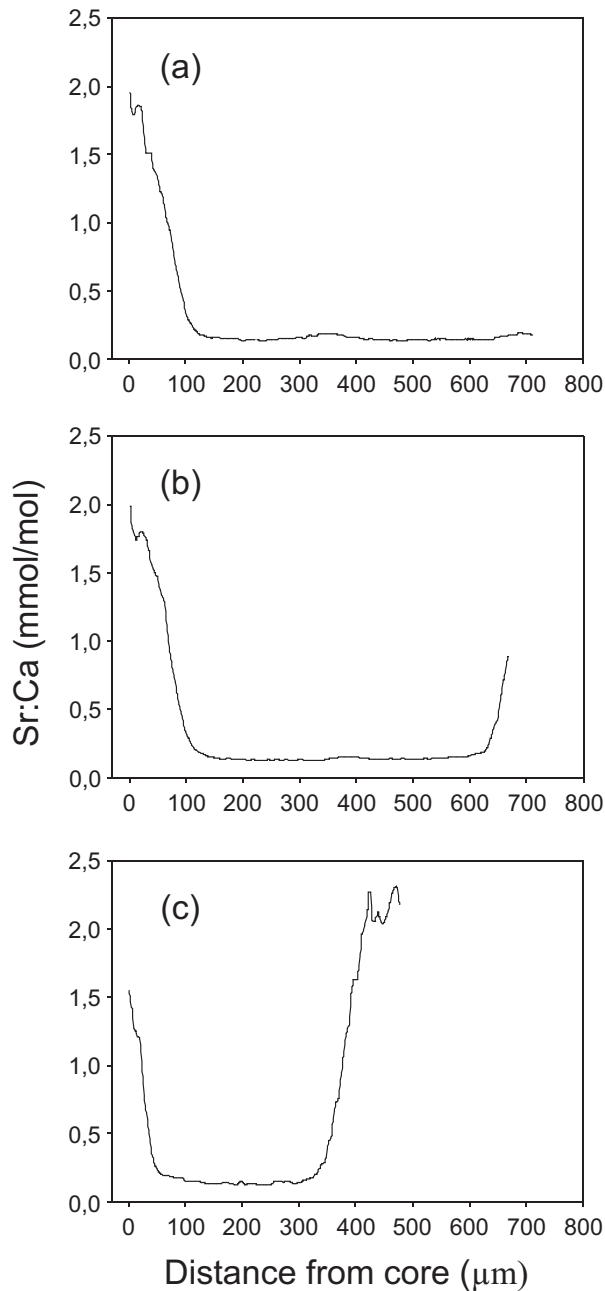


Figure 3. Examples of Sr:Ca profiles. (a) Anadromous brown trout collected from the sea on the 14th November 2009, with no seawater signal; (b) salmon collected from the sea on the 28th December 2013, with a moderate seawater signal; (c) salmon collected from the sea on the 7th December 2006, with a stabilized seawater signal. The peaks at the beginning of the Sr:Ca profiles represent the maternally derived seawater signal (Kalish 1990) (Paper III, Figure 2).

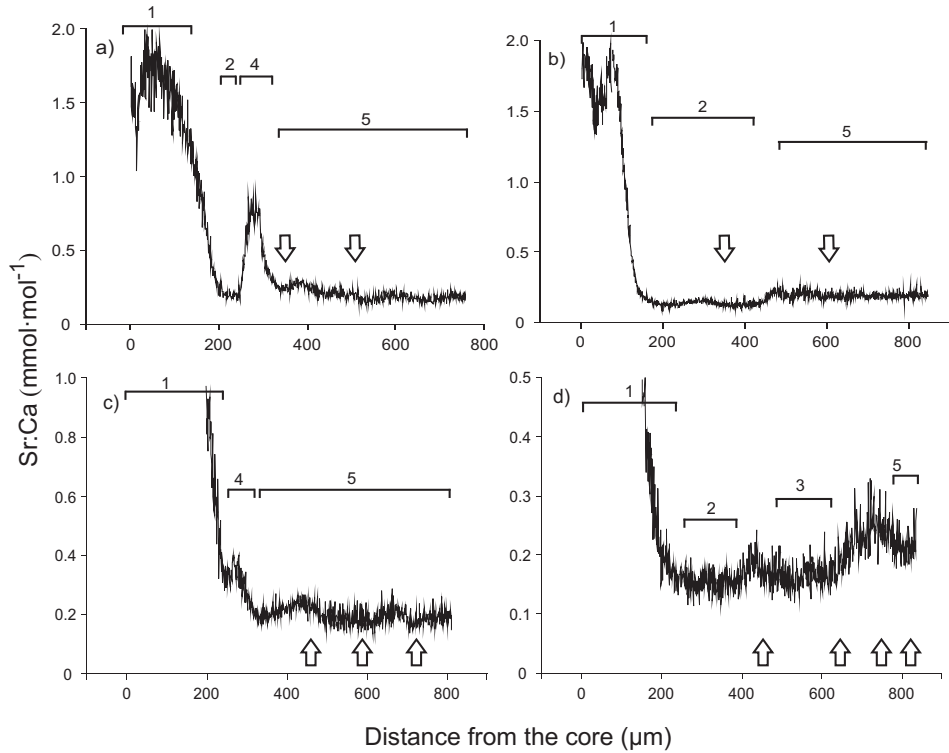


Figure 4. Representative otolith profiles (Sr:Ca) of brown trout from the Ermespu Stream: (a) parr (ID 9) with a clear Sr:Ca marine signal (note that the pre-SSME natal freshwater Sr:Ca value is not stabilized); (b) parr (ID 15) with a clear shift in Sr:Ca values; (c) parr (ID 14) that descended/drifted to the sea immediately after yolk sac reabsorption or even during it, and subsequently entered the Ermespu Stream; (d) parr (ID 1) that possibly migrated between tributaries within its natal watershed, and subsequently migrated to the Ermespu Stream *via* the marine environment, as evidenced by the increased Sr:Ca values. Numbered brackets represent distinct stages in the chemical profiles: (1) maternally influenced region (*sensu* Kalish 1990); (2) natal freshwater habitat; (3) possible migration between tributaries in the natal watershed; (4) brackish water experience; and (5) non-natal freshwater habitat (the Ermespu Stream). The Sr:Ca freshwater threshold is $< 0.5 \text{ mmol}\cdot\text{mol}^{-1}$ in the freshwaters of Estonia (Matetski 2014). Note the different scales of the Sr:Ca profiles. Arrows denote the annuli (Paper IV, Figure 2).

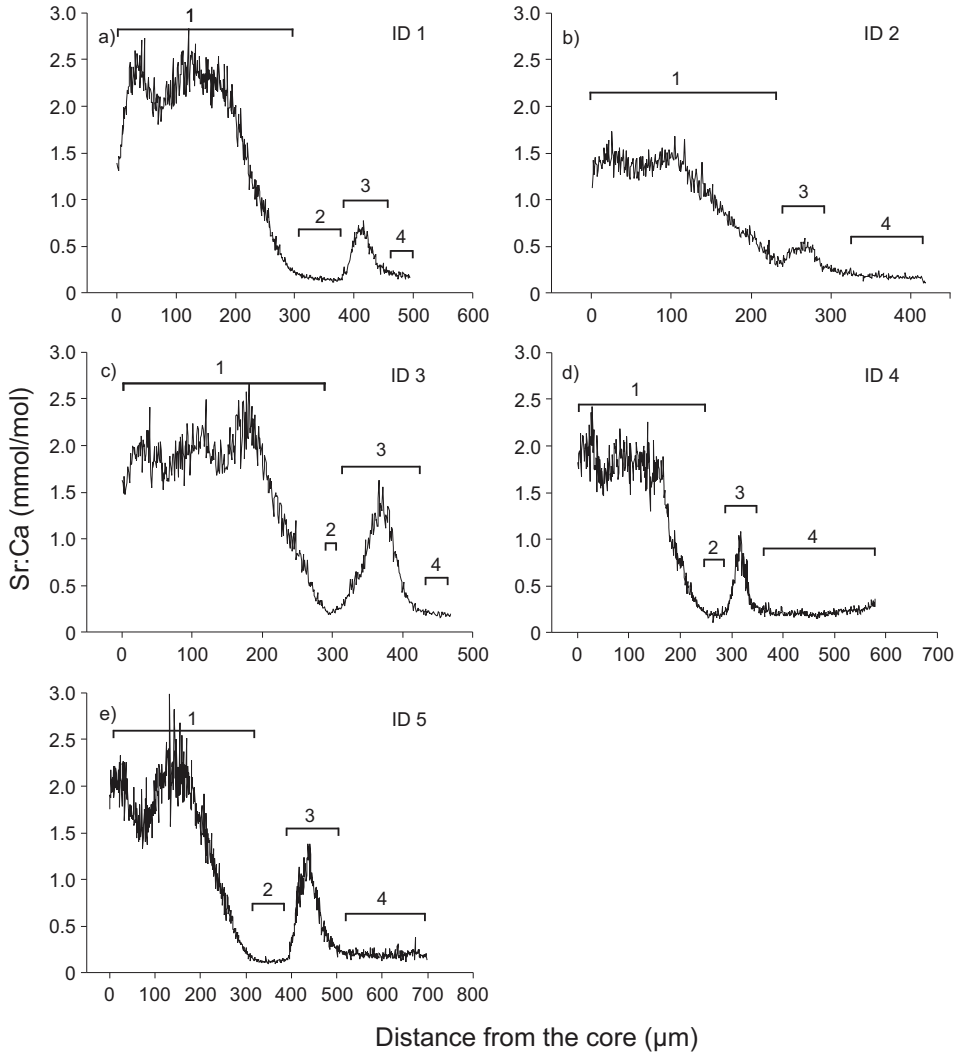


Figure 5. Otolith Sr:Ca profiles of Atlantic salmon (a, d, e) parr with distinct natal values, followed by a clear marine signal, and subsequent decrease and stabilization of values to levels different from natal ones; (b, c) parr that descended/drifted to the sea immediately after yolk sac resorption or even during it, and subsequently entered a non-natal freshwater habitat. Numbered brackets represent distinct stages in the chemical profiles: (1) maternally influenced region (*sensu* Kalish 1990); (2) natal freshwater habitat; (3) brackish water experience; and (4) non-natal freshwater habitat. The Sr:Ca freshwater threshold is $< 0.5 \text{ mmol}\cdot\text{mol}^{-1}$ in Estonian freshwaters (Matetski 2014) (Paper V, Figure 2).

According to Jonsson *et al.* (1991), Atlantic salmon prefer to spawn in relatively large rivers in terms of water volume and catchment area, compared to *e.g.* ABT. All the alternative migrations of Atlantic salmon and ABT not associated with the spring parr-smolt transformation (*e.g.* Youngson *et al.* 1983; Limburg *et al.* 2001; Jonsson & Jonsson 2009; **III**, **IV**, **V**), parallel various potamodromous movements of salmonids from inlet or outlet streams (spawning and nursery grounds) into freshwater lakes or from tributaries into the main river (Klemetsen *et al.* 2003; Jonsson & Jonsson 2011). It is also known that juveniles of anadromous Dolly Varden trout (*Salvelinus malma*) may use the marine environment to reach non-natal streams in which they overwinter (*e.g.* Armstrong 1974; Bond *et al.* 2014).

The autumn descent of Atlantic salmon (*e.g.* Cunjak *et al.* 1989; Pinder *et al.* 2007) and ABT (Jonsson & Jonsson 2009) to estuarine habitats has been previously reported for the Atlantic Ocean. However, Riley *et al.* (2008) demonstrated that autumn descending Atlantic salmon parr are physiologically not sufficiently adapted to full-strength seawater (35 ‰), and thus their expected survival is very low. Nonetheless, a low proportion of Atlantic salmon and ABT autumn migrants are reported to return as adults during the spawning run (*e.g.* Jonsson & Jonsson 2009; Riley *et al.* 2009). However, in the case of ABT it has been experimentally demonstrated (Landergrén 2001) that the low saline environment of the Baltic Sea (6–7 ‰) is not a physiological obstacle to the survival of early out-migrating parr. This may also be relevant for Atlantic salmon, as phylogeny and life history of this species is similar to brown trout (Klemetsen *et al.* 2003; Jonsson & Jonsson 2011). Hence, the results of **III**, **IV**, **V** and previous studies (Järvi *et al.* 1996; Limburg *et al.*, 2001; Landergrén 2004), suggest that the shallow littoral areas of the Baltic Sea might act as alternative nursery areas to Atlantic salmon and ABT fry and parr.

In the Baltic Sea, investigation of the origin of adult sea-caught ABT from the Gotland area revealed that some fish showed no evidence of freshwater history, thereby raising the possibility that a proportion of this population may not depend on riverine spawning at all (Limburg *et al.* 2001). However, this hypothesis is contradicted by the conclusions of Landergrén & Vallin (1998), who suggested that spawning grounds located at stream outlets could, due to the low salinity (<4 ‰), contribute to ABT recruitment. However, eggs deposited in such areas face the risk of being adversely effected by storms, thus making successful recruitment questionable (Landergrén & Vallin 1998). The conclusions of Landergrén & Vallin (1998) are also supported by the results of **IV** and **V**. In particular, I propose that Atlantic salmon (**IV**) and ABT (**V**) fry may emigrate from natal streams before environmental chemical signals are incorporated into the otolith. This hypothesis seems to be supported by an alternative explanation of the origin of brackish water born brown trout suggested by Limburg *et al.* (2001). These authors discussed whether the maternally-donated otolith Sr may obscure evidence of early residency of the egg in freshwater. In Estonia, sheltered stream outlets are mostly characterized by no suitable spawning habitat for salmonids. Stream outlets with suitable

spawning substrate (gravel), however, are exposed to the sea and ambient surface salinity probably does not stay below a 4 ‰ level throughout the incubation period. Thus, in the Estonian part of the Baltic Sea, spawning of brown trout (and Atlantic salmon) in brackish water is highly unlikely.

It is widely accepted that salmonids imprint their natal stream during smoltification, and return there to spawn as adults (“homing”) (e.g. Quinn 1993; Hansen & Jonsson 1994). Thus, ABT and Atlantic salmon parr that undergo SSME may become smolts in non-natal streams and thus fixate their homing to these new waterbodies. Furthermore, SSME (IV, V) could be a possible factor behind the adult straying behaviour documented during the spawning run of Atlantic salmon and ABT (Jonsson *et al.* 2003; Degerman *et al.* 2012). However, it is unclear whether these early out-migrating juveniles (permanently inhabiting brackish littoral areas, Limburg *et al.* 2001) return to their natal rivers as adults or become strayers. Similar, unresolved questions on early out-migrating ABT were raised by Landergren (2004). Understanding the mechanisms behind these phenomena may be important, as existing salinity values are mostly projected to drop further due to increases in rainfall over the upcoming decades (e.g. Kjellström & Ruosteenoja 2007; Meier *et al.* 2012). Thus, the issue of alternative life-histories of Atlantic salmon (III, V) and ABT (Landergren & Vallin 1998; Landergren 2001; Limburg *et al.* 2001; Landergren 2004; III, IV) in the brackish environment of the east Baltic Sea may become even more relevant in the future, especially in the context of population abundance assessment and conservation.

4. CONCLUSIONS

1. The fish assemblage inhabiting the surf-zone of the Baltic Sea can vary significantly on a diel and seasonal basis. Fine-scale assemblage level variations of littoral fish are more complex and may take place over an even shorter time frame than previously known. To accurately quantitatively describe the surf-zone fish community, samples covering different photoperiods should be obtained. This is important, because crucial aspects, such as the significance of the scrutable littoral habitat to certain species, could be missed when sampling only during a limited time-frame (**I**).
2. Even the smaller length classes of sub-adult and adult European smelt (*Osmerus eperlanus*) tend to feed on fish. Thus, smelt is an important predator in shallow littoral areas, being the second most common predatory fish in the near-shore areas of the southern Gulf of Finland. European smelt inhabiting littoral areas of the Baltic Sea occupy a different ecological niche than smelt in offshore areas (**II**). It is reasonable to speculate that at least in the case of the Eastern Gulf of Finland, the impact of European smelt is seriously underestimated in the food webs of the surf-zone *sensu stricto*, as well as in coastal littoral zone *sensu lato*.
3. Early descent, as well as stream shifting through the marine environment, of Atlantic salmon (*Salmo salar*) and anadromous brown trout (*Salmo trutta*) fry (**V**) and parr (**III**, **IV**), indicate that the shallow littoral zone of the Baltic Sea may play a significant role as a permanent or provisional nursery area to these species. Therefore, the possible life history traits of salmonids, as well as the importance of littoral areas as habitats to these species in less-saline parts of the Baltic Sea, should be taken into account with reference to stock management and the assessment of salmonid populations.
4. It is possible that Atlantic salmon and ABT parr that become smolts in non-natal streams may fixate their homing to these new waterbodies (**IV**, **V**). Thus, the phenomenon of stream shifting through the marine environment may constitute at least one possible mechanism behind the straying behaviour documented during the spawning runs of Atlantic salmon and ABT in the Baltic Sea basin.
5. It is likely that some coastal fish species inhabiting the Baltic Sea might show sub-basin specific behaviour in terms of their regular diel movements (e.g. European smelt (**I**, **II**)) and alternative life history patterns (e.g. Atlantic salmon, sea trout (**III**, **IV**, **V**)).

SUMMARY IN ESTONIAN

Läänemere idaosa litoraali kalakoosluste varieeruvus ja selle põhjused

Litoraal on veekogude (ookeanid, mered, järved jne) bentaali ökoloogiline sügavusvöönd, mis hõlmab rannikupiirkonna, kus kasvab põhjataimestik. Ookeanite ja merede (mereliste ökosüsteemide) madalaveeliseid litoraaliasid iseloomustavad muutlikud keskkonnatingimused (nt soolsus, veetemperatuur), mitmekesine elustik ja suur produktiivsus. Litoraaliasid on vee-elustikule oluliseks sigimis-, kasvu- ja toitumisalaks. Muutlike abiootiliste ja biootiliste keskkonnategurite koosmõjul varieerub litoraaliaside kalakoosluste liigiline koosseis väga suurel määral nii ajas (ööpäevane, aastaringne, aastatevaheline muutlikkus) kui ka ruumis (erinevad litoraaliaside elupaigad). Riimveelise Läänemere erinevatele piirkondadele ning ka sama piirkonna erinevatele elupaikadele – näiteks Eru lahe siseosa võrrelduna lahe suudmeala või Soome lahe avaosaga – on iseloomulik vee soolsuse, temperatuuri ja toitelisuse kiire muutumine. Läänemere kalastik koosneb nii mageveelist kui ka merelist päritolu liikidest. Merelist päritolu liikide arvukus väheneb ning mageveeliste liikide osakaal suureneb koos soolsuse vähenemisega Läänemere ida ja põhjaosas. Lisaks rannakalanduse jaoks olulistele sihtliikidele, näiteks räim (*Clupea harengus*), meritint (*Osmerus eperlanus*), ahven (*Perca fluviatilis*) ja lest (*Platichthys flesus*) on Läänemere litoraaliasid elupaigaks ka mitmete kalanduslikult ebaolulistele liikidele: rünt (*Gobio gobio*), viidikas (*Alburnus alburnus*), ogalik (*Gasterosteus aculeatus*), luukarits (*Pungitius pungitius*), väike tobias (*Ammodytes tobianus*), madunõel (*Nerophis ophidion*), pisimudilake (*Pomatoschistus microps*) jne. Need pigem väheldaste mõõtmetega kalaliigid on toiduobjektideks Läänemere rannikulähedasi alasid asustavatele loomadele (putukad, kalad, linnud, imetajad), mistõttu moodustavad olulise lüli ökosüsteemi toiduahelas.

Vaatamata litoraaliaside suurele tähtsusele mereliste ökosüsteemide funktsioneerimisel on Läänemere litoraali kalakoosluseid siiski suhteliselt vähe uuritud. Seni sel teemal avaldatud tööd on enamjaolt keskendunud aastate või aastaaegade vahelise abiootilise ja biootilise komponendi mõjule kalakooslusele või mõnele üksikule liigile. Seevastu Läänemere litoraali kalakoosluste ööpäevaringsetest muutustest on äärmiselt vähe teada. Kalakoosluste ööpäevaringset käitumist Läänemeres on minu teada analüüsitud vaid ühes avaldatud teadusartiklis ja sealgi on käsitletud vaid väheseid kalaliike. Teema päevakohasusele osutavad ka viimaste teadusuuringute tulemused, mis näitavad, et mitme Läänemere litoraali asustava kalaliigi väikesemastaabilised vee sügavusest sõltuvad elupaiga eelistused muutuvad suve jooksul oluliselt. Lähtudes eelnevast ning merelistes ökosüsteemides kirjeldatud kalakoosluste ööpäevaringse dünaamika mitmetahulisusest, võiski eeldada, et Läänemere litoraali asustava kalakoosluse valgustingimustest sõltuv ümberpaiknemine erinevate

elupaikade vahel võib olla keerukam kui seni arvatud. Valgustingimustest sõltuv kalastiku ööpäevaringne dünaamika on otseselt seotud ka liikidevaheliste vastasmõjudega nii troofiliste tasemete piires kui ka nende vahel. Mingi konkreetse liigi käitumine on seotud tema toidukonkurentide, saakobjektide ja/või kiskjate elupaigaspetsiifilise arvukuse ja käitumisega uuritavas keskkonnas. Seega võib isegi väliselt sarnastel litoraalladel kalade käitumine kohalike biotiliste ja abiotiliste tegurite koosmõjul märkimisväärselt erineda.

Kuna Läänemere alampiirkondade keskkonnatingimused on väga erinevad, on tõenäoline, et ka samade kalaliikide käitumismustrid võivad oluliselt erineda nii alampiirkondade (nt Soome laht võrrelduna Läänemere avaosaga), merealade (nt litoraallala võrrelduna avamerega) kui ka erinevate mikroelupaikade (nt erinev põhjasubstraat, põhjataimestiku katvus) vahel. Hiljutised uurimused on näidanud, et mitmetele fakultatiivselt anadroomsetele liikidele (nt meriforell (*Salmo trutta*), luts (*Lota lota*), säinas (*Leuciscus idus*), haug (*Esox lucius*) on Läänemere litoraallad oluliseks kasvualaks. Lisaks on näidatud, et kalade ränded litoraallade ja vooluveekogude vahel on palju keerukamad kui senini arvatud; seni kirjeldamata rändestrategieid on Läänemere piirkonnas täheldatud nii meriforellil, haugil, säinal, lepamaimul (*Phoxinus phoxinus*) kui ka lutsul. Piltlikumateks näideteks võib pidada osaliselt anadroomse lepamaimu populatsiooni esinemist Saaremaal ning Gotlandi saarel vaadeldavat meriforelli noorjärkude väga varajast laskumist merre (mõne kuu jooksul pärast koorumist). Kõik eelnev viitab võimalusele, et suure hulga eripalgeliste keskkonnatingimuste mõjul võivad kalad lisaks lühiajalisele (ööpäevaringsele) käitumisele omada mitmeid elupaiga- ja piirkonnaspetsiifilisi elukäigumustreid. Seega moodustavad nii Läänemere litoraallala, sinna suubuvad vooluveekogud kui ka avameri väga kompleksse ning mitmekesise ökosüsteemi.

Väitekirja eesmärk on selgitada Läänemere litoraali asustavate kalaliikide ööpäevaringseid ja aastasiseseid käitumismustreid. Kalakoosluse valgustingimustest ja aastaajast sõltuva dünaamika uurimiseks kasutati madalat litoraallala (vee sügavus ≤ 1 m) Eru lahes (**I**). Litoraali kalastiku sesoonsete toitumisökooloogiliste eripärade kirjeldamiseks (võrrelduna nt avamerealadega) kasutati mudelobjektina meritinti (**II**). Anadroomsete kalade noorjärkude alternatiivseid rändestrategieid jõgede ja Läänemere litoraallade vahel uuriti lõhe (*Salmo salar*) (**III**, **V**) ja meriforelli (**III**, **IV**) näitel.

Saadud tulemused kinnitavad, et Läänemere madalate litoraallade kalastiku liigiline koosseis muutub oluliselt nii aasta kui ka ööpäeva jooksul (**I**). Selgus, et Läänemere idaosa litoraali kalakoosluse struktuuri mõjutavad ööpäeva lõikes suurel määral suhteliselt suuremakasvuliste liikide (nt meritint, rünt, viidikas, väike tobias) täiskasvanud isendid. Mitmetel püükides võrdlemisi arvukalt esinevatel liikidel (nt meritint, rünt, viidikas, luukarits, väike tobias) kujunesid kogu püügiperioodi lõikes välja kindlad valgustingimustest (hommik, keskpäev, õhtu, kesköö) sõltuvad käitumismustrid. Näiteks meritint esines uurimisalal peamiselt öösel ning väike tobias päeval (**I**). Meritindi puhul võivad käesolevas töös saadud uurimustulemused viidata kõnealuse liigi seni kirjeldamata elupaigaspetsiifilisele toitumisele (**I**, **II**). Läänemere litoraallade

kalakooslustes domineerivate liikide, nagu ogaliku ja mudilate (väike mudilake (*Pomatoschistus minutus*) ja pisimudilake) arvukuse muutused uurimisalal sõltusid küll oluliselt valgustingimustest, kuid kogu vaadeldud perioodi (aprill kuni detsember) kattev lihtsalt selgitatav ööpäevane esinemismuster puudus (I). See tulemus on mõnevõrra vastuolus ainukese varasema Läänemere madalas litoraalis (<1,2m) elavate kalade ööpäevast dünaamikat käsitleva uuringuga, mis kirjeldas kõikide vaadeldud liikide (sh ogaliku ja pisimudilakese) arvukuse regulaarset tõusu öistes proovipüükides võrrelduna valge ajaga. Käesoleva uuringu tulemustest järeldub, et erinevatel ajahetkedel (nt päev ja öö) kogutud proovid pole omavahel üks ühele võrreldavad (I). Teiste sõnadega, mingi konkreetse litoraali piirkonna ööpäevas muutuva liigilise koosseisu täielikuks kirjeldamiseks on vajalik proovipüükide tegemine nii hommikul, keskpäeval, õhtul kui ka öösel. Lisaks viitavad käesoleva uuringu tulemused, et suve keskosa (juuli) on kaldanoodaga tehtavaks (vee sügavus ≤ 1 m) litoraali asustava kalastiku seireks ebasobiv periood, kuna siis ei ole nimetatud püügivahendiga võimalik kalakoosluse struktuuri adekvaatselt hinnata. Näiteks ogaliku, väikese mudilakese ja pisimudilakese samasuvised noorjärgud on suve keskosas kaldanoodaga tabamiseks liialt väikesed (I). Lisaks hoiduvad mitmed parema ujumisvõimega täiskasvanud kalad väga soojaveelisel perioodil tõenäoliselt kaldast kaugemale või on sigimispingutuse tagajärjel (nt ogalik, väike mudilake, pisimudilake) hukkunud.

Meritint, mitmetes Läänemere alampiirkondades suhteliselt arvukas kalaliik, on sealsetes toiduvõrgustikes oluliseks lülits. Töö tulemused näitasid, et Läänemere idaosa madalat litoraalia ala asustava meritindi toitumiskäitumine muutub aasta jooksul oluliselt ning erineb avamere elupaikades kirjeldatust (II). Samuti sõltub meritindi saakobjektide valik Eru lahes kala pikkusest (II). Kõige arvukamateks meritindi saakobjektideks Eru lahes olid erinevad kirpvähilised ja kuulmiksabad (II). Ihtüoloogilistes teadustekstides korduma kippuvale küsimusele – Kas tint on röövkala – võib uuringu tulemuste põhjal vastata jaatavalt. Nimelt esines kõikide analüüsitud pikkusrühmade saagis kalu, eelkõige ogalikke, luukaritsaid, väike mudilakesi ja pisimudilakesi. Lisaks eelpoolmainitud olid meritindi saakobjektideks Eru lahes veel kakandilised, vesikirbulised, kümnejalalised, limused, putukad ja hulkharijasussid. Mitmeid uurimuses kirjeldatud saakobjekte (nt võldas (*Cottus gobio*), väike tobias, söödav rannakarp (*Mytilus trossulus*), munajas punntigu (*Macoma baltica*), harjasliimukas (*Hediste diversicolor*) jne) pole varasemates kirjandusallikates tindi toiduobjektidena nimetatud. Käesoleva uuringu tulemused näitavad, et tindil võib litoraali-vööndis olla teistsugune ökoloogiline nišš kui avamerealadel (II). Meritinti võib Soome lahe rannikumeres pidada ahvena kõrval üheks olulisemaks röövkalaks ning on alust arvata, et liigi tähtsust litoraali-alade toiduvõrgustiku osana on seni alahinnatud.

Traditsiooniliselt on soolaseveeline litoraali lõhe ja meriforelli noorjärgudele oluliseks elupaigaks alles pärast kevadist hõbestumist (smoltifitseerumist, mille käigus kalade füsioloogia kohandub eluks merevees). Lõhilased on samas tuntud oma plastiliste elukäigustrateegiatega poolest, mis varieeruvad liigi siseselt

nii rändemustritelt (nt noorjärkude aastaajast sõltuv elupaiga valik, kuderänne jne) kui ka näiteks suguküpsuse saabumise vanuse ja suuruse poolest. Üksikutes lõhe ja meriforelli populatsioonides on täheldatud ka vastsete ja tähnikute varajast (enne smoltifitseerumist) rännet riimveelistesse elupaikadesse. Reeglina toimub lõhe ja forelli tähnikute varajane laskumine merre sügisel. Seevastu Gotlandi saare ojadest laskuvad meriforelli vastsed ja tähnikud Läänemerre juba paari kuu jooksul pärast koorumist. Kirjeldatud alternatiivsete rändemustrite põhjuseks on pakutud näiteks jõe väga väikest või väga suurt vooluhulka, suurt asustustihedust või talvitumiseks sobivate elupaikade vähesust.

Käesolevas töös näidatakse esmakordselt nii lõhe kui ka meriforelli sügisel merre laskunud tähnikute esinemist Läänemeres (**III**). Samuti näidati mõlema liigi vastsete ning tähnikute rändamist sünnijõest Läänemere litoraali ning sealt omakorda uude vooluveekogusse (**IV**, **V**). Selline läbi riimveelise litoraali toimuv mageveelise elupaiga vahetus on nii lõhe kui ka meriforelli seni kirjeldamata rändestrategia. Lõhi puhul pole kunagi varem dokumenteeritud isegi vastsete laskumist jõgedest merre.

Seega võib nii lõhe kui ka forelli noorjärkude rändestrategia magevee ning riimveelise litoraalia vahel olla seni teada olnust oluliselt keerukam. Katse- liselt on näidatud, et 6–7 % soolsusega riimvesi ei oma meriforelli tähnikute elutegevusele negatiivset mõju. Lõhe puhul on Läänemerest oluliselt soola- semas Lõuna-Ingliismaal (Inglise kanali vesikond) dokumenteeritud üksikute sügisel tähnikuna ookeanisse laskunud kalade kuderännet jõgedesse. Seega võivad Läänemere riimveelised litoraaliaalad olla seni arvatust olulisemaks kasvualaks alternatiivseid rändestrategiaid kasutavatele anadroomsetele lõhi- laste noorjärkudele. Kirjanduse andmetel jätavad lõhilased oma sünnijõe „lõhna“ meelde smoltifitseerumise käigus, et tulla täiskasvanuna samasse vee- kogusse kudema. Läbi riimvee vooluveekogu vahetavad noorkalad võivad osa- liselt olla ka anadroomsete lõhilaste populatsioonides esinevate „eksijate“ (st kalad, kes koevad oma kodujõe asemel mujal) varem kirjeldamata tekkemehha- nismiks (**IV**, **V**). Vastse või tähnikuna kodujõe vahetades vermitakse lõhi- lastele smoltifitseerumise käigus uue elupaiga „muster“ ning vastav isend on seetõttu nii-õelda „eksinud“ juba enne täiskasvanuks saamist.

Kokkuvõtteks, käesoleva väitekirja tulemused näitavad et Läänemere litoraali asustavate kalaliikide ööpäevaringne ja aastaajast sõltuv käitumine (sh toitumiskäitumine) on seni kirjeldatust oluliselt mitmetahulisem (**I**, **II**). Selgus, et litoraali ja sellega piirnevate veeökosüsteemide (nt vooluveekogud, avameri) kalastike vahelised seosed on samuti seni arvatust oluliselt keerukamad (**III**, **IV**, **V**). Ülalpool kirjeldatud tulemused aitavad täita vajakajäämisi varasematest bioloogilistest ja metodoloogilistest teadmistest, ning on seega kasutatavad nii edaspidistes teadustöodes kui kalavarude majandamisel.

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PUBLICATIONS

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Publications:

- Verliin, A., Saks, L., Svirgsden, R., Vetemaa, M., Rohtla, M., **Taal, I.** & Saat, T. 2013. Whitefish (*Coregonus lavaretus* (L.)) landings in the Baltic Sea during the past 100 years: combining official datasets and grey literature. *Advances in Limnology* 64: 133–152.
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Dissertations supervised:

- Snežana Nedolgoва, Master's Degree, 2010, (sup) Imre Taal, Toomas Saat, Feeding of smelt in Eru Bay, University of Tartu. In Estonian.
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